THE NATURE AND SIGNIFICANCE OF MICROTOPOGRAPHIC EFFECTS ON VEGETATION SUCCESSION ON SELECTED GLACIER FORELANDS, JOTUNHEIMEN AND JOSTEDALEN, NORWAY.

JACQUELINE ISABEL JEANNE FOSKETT BSc

A thesis submitted in partial fulfilment of the
requirements of the University of Greenwich
for the Degree of Doctor of Philosophy

This research programme was carried out in collaboration
with the Jotunheim Research Expedition

July 1998

To my mother, my brother Allen and Amy
and to the memory of Graham

Declaration

I certify that this work, which includes volume I and volume II, has not been accepted in substance for any degree, and is not concurrently submitted for any degree other than that of Doctor of Philosophy (Ph.D.) of the University of Greenwich. I also declare that this work is the result of my own investigations except where otherwise stated.

(Jacqueline Foskett)

(Dr. Paddy Coker)

Volume I

Ph.D. thesis: The nature and significance of microtopographic effects on vegetation succession on selected glacier forelands, Jotunheimen and Jostedalen, Norway.

Jacqueline Isabel Jeanne Foskett

ABSTRACT

This extensive study investigates the relationship between microtopography, prevailing micro-environmental factors and vegetation, with particular reference to succession, on six glacier forelands at successively higher altitudes. The study is successful in answering the three main aims of the thesis: by analysing the specific environmental parameters comprising the microtopographic gradients; by describing the distribution of individual species and plant assemblages across microtopographic gradients of similar type (i.e. moraine slopes) but different ages and altitudes; and by interrelating the vegetational and environmental variation and hence providing an explanation of the vegetation in terms of both successional stage and environmental factors. The principal research contributions are under three headings: findings; presentation techniques; and literature review.

The most important findings refer to the major influences on subalpine and alpine vegetation patterns and include the following conclusions:
a) Microtopographical effects are more complex than previously acknowledged.
b) Exposure, snow-lie and fluvial activity are confounded and the relative importance of these parameters changes with altitude so that exposure is more important on the low-alpine forelands and snow-lie is more important on the mid-alpine forelands.
c) Pioneer assemblages are distinct and are more influenced by terrain-age than altitude.
d) Most assemblages are not distinct but lichen heath, subalpine mature birch woodland and heath, and snowbed assemblages show recurrent similarities in constituent species.
e) The influence of terrain-age appears to decrease with altitude while microtopographical effects increase.
f) Altitudinal effects appear to increase with age.
g) Succession is simpler and more predictable with altitude and all types of successional pathway (i.e. divergent, convergent and parallel) are possible.

The presentation techniques are considered an improvement on previous display techniques because they allow deeper interpretation of the results at all levels of division. By using these techniques, the complex relationships between assemblages, sites and environmental parameters, at both the assemblage and population levels, are elucidated.

The literature review targets the effects of microtopography on vegetation patterns in cold climates (e.g. subalpine, alpine, arctic) and comparison with previous literature suggests that this thesis could be used to explain universal patterns.

The present study augments and improves on much of the previous work by using an objective methodology to describe vegetation patterns in a heterogeneous landscape and relate a multitude of environmental parameters to those patterns. This study has provided some interesting and original results and conclusions and the wide-ranging nature of the thesis opens up many avenues for further investigation.

ACKNOWLEDGEMENTS

I am especially grateful to my supervisors, Dr. Paddy Coker and Prof. John Matthews. Dr Coker was particularly helpful with regard to all the practical aspects of my thesis especially the funding and administrative side, as well as providing nearly all support concerning the computer software. Prof. Matthews provided necessary support in the field and I am especially indebted to him for his red "scribbles" on draft copies of the chapters.

I would like to thank my field assistants Julie Whitley, Louise Rickard and Nick Davis who provided invaluable help as well as moral support in the rain and wind. I also thank other members of the Jotunheim Research Expedition, especially Helena Crouch, Heather Pardoe, Iain Sutherland, Danny McCarroll and Rob Whittaker for their companionship, support and practical suggestions.

Many people have helped me with this thesis over the years and I thank them all. However, I would especially like to thank a number of individuals who have given up their time to advise me on what, at times, seemed an endless task. I would like to thank those who helped me with the identification of the lichens and vascular plants and they are John Matthews, Helena Crouch and Paddy Coker. I am also grateful to Dr. Dean, at the Institute of Hydrology, Wallingford, for his help and advice and to the Institute of Hydrology for their loan of a prototype Capacitance Probe. I thank Kjell Gunnar Heimark, at the Norwegian Meteorological Institute, for his help and time with regard to the provision of the latest regional weather data. I thank Martin Kent, at Plymouth University, for his advice on statistical analysis. Also Sigurður Magnússon, at the Agricultural Research Institute in Iceland, for his helpful suggestions regarding the use of detrended correspondence analysis (DCA). I am particularly indebted to Águst Ómar Ágústsson for his computer skills, and many hours of work, concerning the conversion of data written in FORTRAN to a tabulated form in MICROSOFT EXCEL. Most of the results displayed in this thesis are derived from his original tabulations of the data.

I am grateful for the financial assistance, which was provided jointly by Thames Polytechnic (now Greenwich University) and the Jotunheim Research Fund, for the expeditions. I also thank the Botanical Research Fund who provided general financial support and Thames polytechnic, who supplied most of the field equipment.

Finally, I am grateful to both my supervisors, as well as my family and friends, for their faith in my abilities and their constant encouragement and moral support.

CONTENTS

Volume I

CHAPTER ONE: Introduction and literature review

CHAPTER TWO: Methods: approach and rationale

CHAPTER THREE: The foreland environment

CHAPTER FOUR: The pattern of species assemblages on the individual forelands

CHAPTER FIVE: The relationship between sites, species and environmental parameters across the individual forelands.

CHAPTER SIX: Vegetation pattern and the relationship between sites, species and environmental parameters using the combined foreland data.

CHAPTER SEVEN: Conclusions

Table no. **List of Tables (Volume II, except where stated)** **Page**

(full titles not necessarily given; Volume I page numbers given in brackets)

Chapter One (Tables)

Chapter Two (Tables)

Chapter Three (Tables)

Chapter Four (Tables)

Chapter Five (Tables)

Chapter Six (Tables)

Chapter Seven (Tables)

Figure no.

List of Figures (Volume II, except where stated)

Page

(full titles not necessarily given; Volume I page numbers in brackets)

Chapter One (Figures)

Chapter Two (Figures)

Chapter Three (Figures)

Chapter Four (Figures)

Chapter Five (Figures)

Chapter Six (Figures)

Page

Chapter 7 (Figures)

"The continual activity of European ecologists, and to a somewhat smaller extent of American ecologists as well, in discussing the fundamental nature, structure and classification of plant associations, and their apparently chronic inability to come to any general agreement on these matters, make it evident that the last word has not yet been said on the subject."

Gleason (1926: 7)

CHAPTER ONE: Introduction and literature review

1.1 Introduction and aims

Glacier forelands (see glossary) have been long recognised for the possibility of gaining insights into primary succession (e.g. Fægri, 1933; Lüdi, 1921; and Cooper, 1923) and this work complements the information available on secondary succession (e.g. McCormick, 1968; Connell and Slatyer, 1977). Most commonly, studies of succession on glacier forelands have adopted a chronosequence methodology (e.g. Crocker and Major, 1955; Ugolini, 1968, Elven, 1978). In most of these studies the aim has been to investigate change through time whilst attempting to hold constant or control environmental factors other than time. In practice, this has resulted in the selection of sites exhibiting little or no topographic variation and therefore these studies have only yielded a relatively superficial representation of succession on glacier forelands.

Over the last 25 years, the Storbreen glacier foreland (Figs. 2.2a-b) has been used for studies of primary succession and the causal factors, both physical and biological, that affect vegetation and soil patterns. Matthews (1976) investigated vegetation patterns on the Storbreen foreland, Jotunheim, and made no assumptions about the importance of time. Spatial variation was investigated, two-dimensionally, across the foreland in order to consider aspects of plants, space and time and environment together. Matthews established that there is a large-scale chronosequence for higher plants but that the boundaries of the plant distributions along the time gradient are not as clear as some other research had previously shown (e.g. Crocker and Major, 1955). Since 1976, several studies, have developed the geoecological approach at Storbreen (Whittaker, 1985; Crouch, 1992, 1993; Matthews, 1992). Whittaker emphasised environmental factors, Crouch investigated lower plants, and Matthews attempted to review and extend the study in the light of glacier foreland studies elsewhere (see sections 1.3 and 1.4). Although previous work on the Storbreen glacier foreland recognises the importance of microtopographic effects on succession, the spatial approach has mitigated against their detailed investigation. Furthermore, the results may have been site-specific, in that no other foreland has been investigated in detail. This study, then, follows on from the previous work in the region. It is a specific investigation of the nature of the relationship between microtopography, prevailing micro-environmental factors and vegetation with particular reference to succession on six different glacier forelands at successively higher altitudes. It involves the description and analysis of both vascular plants and lichens along the microtopographical gradients (end-moraine ridges – see glossary).

The aim of the study is to examine the nature and extent of the effects of microtopography on glacier foreland vegetation in time and space. An end moraine is very suitable for this kind of study because it plainly exhibits distinct environmental gradients, the clearest of these including slope, exposure, snowlie, and small-scale temperature gradients. There are three main objectives:

1. To analyse the specific environmental parameters comprising the microtopographic gradients.
2. To describe the distribution of individual species and plant assemblages across microtopographic gradients of similar type (i.e. moraine slopes) but different ages and altitudes.
3. To interrelate the vegetational and environmental variation and hence to provide an explanation of the vegetation in terms of both successional stage and environmental factors.

In this chapter the conceptual framework used for this study is introduced. A description is made of the geography of the Jostedalsbreen and Jotunheim regions and glacier forelands (Figs. 2.1a and 2.2a). A literature review follows, comprising a discussion of previous research which is most pertinent to the subject matter of the present study. The review discusses how this study is related to, and has proceeded from, the previous studies. The review also shows how the present investigation is intended to further understanding of the vegetation patterns and mechanisms of vegetation succession on glacier forelands in the region. The chapter concludes with an outline of the thesis.

1.2 Study location and background information

Research has shown that the time-scale of advance and retreat of glaciers during the "Little Ice Age" were fairly similar between glaciers in the Jotunheim and Jostedalsbreen regions (Erikstad and Sollid, 1986). The Jotunheim and Jostedalsbreen regions have a number of glacier forelands that have been the subject of detailed research projects (Figs. 2.1a-c and 2.2a-e). The results of some of these studies will be used for comparative purposes in the concluding chapter of this thesis. The main criteria governing the choice of glacier forelands in both the Jostedalsbreen and Jotunheim region are that the forelands should have a sequence of well-formed moraines; that the moraines should be dated at least by using lichenometric methods; that the forelands should be at a range of altitudes; and lastly that the forelands should be accessible. In this section the conceptual framework of the study areas is outlined. General descriptions of the regions (i.e. the Jostedalsbreen and Jotunheimen regions) are then made concerning climate, geology and de-glaciation.

1.2.1 Conceptual framework

The mountain flora of Scandinavia has been well documented over this century (Nordhagen, 1954; Gjærevoll, 1956; Dahl, 1956). The classification of plants into groups or assemblages and further into communities is known as phytosociology. There are two schools of phytosociology which influenced the methodology of this study. The first is the Scandinavian school, which classifies plant groups on homogeneous climax (or mature) plots of differing environmental conditions (e.g. Dahl, 1956). The second is the Anglo-Saxon school, which, with its background in physiology and evolution, has approached the grouping of plant species on a successional basis (e.g. Tansley, 1920). According to Dahl (1956) these schools may have developed because of the prevailing vegetation and environmental situation. Dahl suggests that the Scandinavian school deals with relatively stable and homogeneous communities that are defined by an experienced researcher who can distinguish between two differing communities. The component plant species are identified and then the prevailing environmental conditions defined. Therefore in this situation it is the plant community that defines the site used by the researcher. The Anglo-Saxon school works on disturbed ground and the age of the ground since disturbance is of paramount importance. Plots of similar environmental conditions are used so as not to make interpretation of the results too difficult. With the Anglo-Saxon school it is the location that defines the site chosen for study (Dahl, 1956).

This study uses components of both schools insofar as the effects of environment on vegetation pattern and succession at selected sites is being investigated. A chronosequence of moraines was chosen for study across each foreland, following the "Anglo-Saxon", site-specific, methodology. The best vegetated site across a moraine was then chosen, following the "Scandinavian" methodology, and the quadrats were laid across the moraine at pre-determined positions, following the "Anglo-Saxon" methodology. The plant species and prevailing micro-environmental conditions were then recorded for each quadrat following the "Scandinavian" methodology. It is proposed that research in general, and ecological research specifically, should use a methodology most fitting to the particular investigation being carried out. To follow research within the guidelines of certain traditions can only provide a partial and simplistic account of, in this case, vegetation patterns and mechanisms of succession. This study, by using the geoecological approach (Matthews, 1976, 1992), outlined below and in section 1.1, will attempt to elucidate vegetation patterns across glacier forelands at different altitudes and hopes to further the understanding of mechanisms of vegetation succession on those forelands.

The design of the present study has followed on from research projects in the Jotunheim and Jostedalsbreen regions carried out by the Jotunheim Research Expeditions since the early 1970s. Matthews developed a geoecological approach to phytosociology (1976) which is an extension of the work developed by the Anglo-Saxon school. Matthews recognised the problem that the Anglo-Saxon school investigate the variation of vegetation pattern with terrain age, not taking into account variations in environment or topography on ground of similar ages. A spatial approach to describe vegetation pattern was therefore developed by Matthews (1976, 1978, 1979; Matthews and Whittaker, 1987) and this approach was further developed by other researchers on the Storbreen glacier foreland, (Whittaker, 1985, 1987, 1989, 1993; Crouch, 1992, 1993). This spatial approach specifically investigates the effect of landscape heterogeneity, and associated environment factors, on the vegetation pattern along a time sequence. The spatial approach selects sites objectively across the whole foreland (rather than along a chronosequence). The prevailing environmental parameters and large-scale topographical features are described and the location of the plant assemblages (and their characteristic environmental parameters) defined using a number of multivariate analysis techniques. However, a specific study of the effects of microtopography has not been undertaken heretofore. The relationship between this and previous studies will be described in greater detail in the literature review (section 1.3).

1.2.2 Regional climate

A focus of this study is to investigate the micro-environmental conditions found across a microtopographical feature. However, it is important that the prevailing larger scale climatic conditions on the foreland are described and discussed so that between-foreland differences can be assessed. For example, the influence of average wind speed and direction can influence the vegetation in terms of snow-lie and exposure. The Norwegian Meteorological Office (Det Norske Meteorologiske Institutt, Postboks 43, Blindern, 0313, Oslo) compile data for hundreds of weather stations throughout Norway every thirty years. The climatic data, described below, is taken from the most recent data records for the years (1961-1990), except where stated, and describe the averages for wind force, snow-fall, temperature and precipitation at weather stations in the vicinity of the study locations.

Snow cover is influenced by the topography of the land surface, exposure and aspect (Matthews, 1992) and patterns of snow cover across a landscape tend not to change from year to year even if the rate and amount of snow melt may vary (Dahl, 1956; Billings and Bliss, 1959). Snow cover is considered to be one of the most important influences on the micro-environment and vegetation pattern of a site (e.g. Billings and Bliss, 1959; Miller, 1982; Matthews, 1992). A site with a brief snow duration will be more exposed to winds and suffer from greater fluctuations in temperature (Miller, 1982), whereas a site with a lengthy snow duration will suffer a reduced growing season. Burrows (1990), while reviewing the general environmental trends with increased altitude within a region of similar latitude and longitude, suggests that both snow accumulation and wind force rise with altitude. Data from the Norwegian Meteorological Office support this premise. Climatic data, from the closest weather stations to the forelands (see Figs. 2.1a and 2.2a), were used to give an idea of the regional climate for each of the forelands for the present study purposes. The weather station at Bjørkehaug i Jostedal (alt: 300 m) was used to represent the climate at the two sub-alpine forelands. Bjørkehaug i Jostedal was chosen because it is located at a similar altitude and is situated between the two forelands. The data from this station can thus be used as is. Further to the east, due to continentality (Matthews, 1992), snow accumulation is less than that of the oceanic climate to the west. As can be seen in Fig. 2.2a, the weather stations at 1543 Bøverdal (701 m), and 5523 Fanaråken (2062 m) are relatively close to the glacier forelands under study, but are not at the same altitude as the forelands (see Fig. 3.1 for foreland altitudes). An estimation of the range of snow accumulation, between the low and mid-alpine forelands, can be made, although such an estimation is approximate due to the effects of relief on snow accumulation and wind force. Because of the influence of relief and locality it was decided to use the snow accumulation and wind-force (Beaufort scale) values from the two closest weather stations (in terms of space and altitude). Snow accumulation in February at Fanaråken (alt: 2062 m) was

123 cm (average 1957-1978), and at Bøverdal (alt: 701 m) was 49 cm (average 1957-1993). Estimates of the snow accumulation across the forelands therefore range between 75 cm, for the low-alpine forelands, and 95 cm, for the mid-alpine forelands. These figures are similar to the February snow accumulation found at Bjørkehaug i Jostedal (98 cm - average 1963-1993). The yearly average for wind force for Fanaråken (average 1957-1978) is 4.3 and 1.7 for Bøverdal (average 1972-1979) so an estimate of average wind forces on the low alpine forelands would be about 2.5 and for the mid-alpine forelands just over 3.1. The average wind force at Bjørkehaug is 1.8 on the Beaufort scale (average 1963-1993). In summary, the snow accumulation on the subalpine forelands is probably slightly higher than on the low- to mid-alpine forelands but the wind force on the low- to mid-alpine forelands is greater than on the sub-alpine forelands.

Between-foreland differences in moisture levels is caused by a multitude of factors including regional precipitation as well as factors influenced by topography, such as the presence of springs, fluvial activity and mires. For example, continentality, relief and rain shadow effects have a considerable influence so that the more oceanic (westerly) the location, the greater the precipitation (Matthews, 1992). Precipitation (and snow accumulation) is said to increase with altitude (Burrows, 1990), but investigation of precipitation data from the Norwegian Meteorological Office suggests that the effect of altitude on precipitation, in the region, is less predictable than previously suggested. Furthermore, precipitation does not necessarily correspond to snow accumulation data. For example, in the Jostedalsbreen region at Fjaerland (6° 46′; alt: 10 m) the annual precipitation is 1905 mm (average 1961-90) and the February snow accumulation is 62 cm (average 1957-93) and at Bjørkehaug (7° 16′; alt: 324 m) the annual precipitation is 1380 mm (average 1961-90) and the February snow accumulation is 98 cm (average 1963-93). Fjaerland (just off Fig. 2.1a) is situated at the head of a fjord running south west to north east and is further to the west than Bjørkehaug (Fig. 2.1a), which has a 28 % lower rainfall even though it is over 300 m higher (possibly because it is situated in a deep valley). The precipitation on the forelands at Austerdalsbreen and Fåbergstølsbreen may be similar to that at Bjørkehaug, with, perhaps, slightly higher rainfall further to the west at Austerdalsbreen. In the Jotunheim (Fig. 2.2a) the four nearest weather stations, to the forelands within the study, are Fanaråken (7°55′; alt: 2062 m) with an annual precipitation of 1200 mm (average 1961-1990), Vetti (7°57′; alt: 329 m) with an annual precipitation of 899 mm (average 1961-1990), Elveseter (8° 17′, alt: 710 m) with an annual precipitation of 530 mm (average 1961-1990) and Bøverdal (8°20′; alt: 710 m) with an annual precipitation of only 435 mm (average 1961-1990). These data show that locations that are lower in altitude, and further to the east (in the rain shadow of the high mountains of the Hurrungane and Jotunheim), have considerably lower rainfall. Therefore, it is suggested that Bøverbreen and Høgvaglbreen have the highest precipitation, Storbreen has a slightly lower precipitation, and Svellnosbreen, in the rain shadow of Tverrbotn-tindane, has the lowest rainfall.

Temperature is one of the most important climatic factors influencing vegetation growth and pattern. Among the factors that affect temperature at a regional scale are latitude, continentality and altitude. Based on the work of Blalock (1960), an attempt to provide an accurate statistic for the prediction of temperature at various altitudes has been provided by Green and Harding (1980), who found a gradient of -5.45 °C per 1000 m, which is considered by Matthews (1987) to be a close approximation to reality. The average yearly temperatures found at the forelands in the Jotunheim can be predicted from the equation (°C = 5.436 - 0.00545 x altitude) derived from Matthews (1987) and these are outlined in the table below. The equation, from a linear regression analysis with 95 % confidence limits, is based on climate data for the period 1931 to 1960. Matthews used data from stations above 200 m as anomalous results were found for coastal sites. The Norwegian meteorological office has recently released more recent climatic data and Table 1.2 and Fig. 1.1 show the annual temperature averages for 21 meteorological stations within 100 km of the Jotunheim. All altitudes were used, for the recent regression, since stations on fjords were inland. From the equation, $y = 164.32x + 920.58$, $r = 0.948$, $p = <0.001$, (where y = altitude and x = temperature), a 6.072 °C rise in temperature, per 1000m, can be predicted and this temperature corresponds closely to the 6.0 °C rise for every 1000m quoted by Burrows (1990) in his review of the effects of altitude on environment. Table 1.1 compares the temperature predictions from Matthews' study and those, prepared for this study, using more recent data. The predictions are similar except for the higher altitudes where the temperatures are somewhat lower (using data from low altitude, but inland, weather stations for the regression).

Table 1.1 Comparison of mean annual temperatures at the altitude of 1750 moraines on selected forelands, derived from two regressions.

FORELAND	**ALTITUDE (1750 moraine)**	**Temperature (°C)** - according to Matthews' (1987) regression (1931-1960 data)	**Temperature (°C)** - according to regression from present study (Fig. 1.1, 1961-1990 data)
Austerdalsbreen	290 m	3.85	3.84
Fåbergstølsbreen	460 m	2.9	2.80
Storbreen low	1140 m	-0.78	-1.33
Svellnosbreen	1280 m	-1.54	-2.18
Storbreen high	1310 m	-1.7	-2.37
Høgvaglbreen	1400 m	-2.2	-2.9
Bøverbreen	1500 m	-2.7	-3.52

1.2.3 Regional geology

The Jostedalsbreen and Jotunheim regions are composed of high grade metamorphic rocks which form part of the major southwest to northwest trending Caledonian fold mountain belt. The rocks of the Jostedalsbreen region are acidic granitic gneiss and the rocks of the Jotunheim are basic pyroxene gneiss. Gjærevoll (1956) emphasises the importance of the occurrence of lime in the parent rocks as influencing the plant composition of snow beds and so it is necessary to ascertain whether previous research has shown the calcium content of rocks of these two regions to be significantly different. Mellor (1985) has shown that there is little difference between the "basic" rocks of the Jotunheim, with values of calcium ranging from 0.13 to 6.40 meq $100g^{-1}$, and the "acidic" rocks of the Jostedalsbreen region which have values that range between 0.07 and 4.90 meq $100g^{-1}$. It can be concluded that any major differences in vegetation patterns, between the Jotunheim and Jostedalsbreen region, are therefore unlikely to be attributed to the geology of the region. It is anticipated that there may be some general differences in soil pH between the regions which could be influenced by the parent rocks. Mellor (1985) found differences in profile development between the Jotunheim and Jostedalsbreen region and suggested that differences in the iron content of the parent rocks could be partly responsible. However, it is likely that the most important between-foreland differences in soil characteristics and vegetation pattern can be ascribed to factors other than geology and this is confirmed by data, on regional geology, presented by Battey (1975).

1.2.4 Regional and local glaciation

The main influence on the geomorphology of the region is the glaciations that occurred during the Pleistocene, and is responsible for the major landforms, such as U-shaped valleys. More recently, at the end of the Holocene, the "Little Ice Age" caused a considerable advance of glaciers in the region, which continued until the mid-eighteenth century when the glaciers began to retreat again (Grove, 1988). This study has made use of the glacier forelands formed since the "Little Ice Age". For example, topographical features, called moraines, have been pushed up by the retreating glaciers during short episodes of advance (Bickerton and Matthews, 1993; Matthews et al., 1995) and these have been ideal for studying the effect of microtopography on vegetation pattern. Furthermore, researchers have dated the age of exposure of different parts of some of the forelands making them ideal for chronosequence studies on vegetation and soils (Matthews, 1974, 1975, 1977, 1978b, 1991, 1992; Innes, 1985; Erikstad and Sollid, 1986; Haines-Young, 1988; Nesje, 1989; Bickerton and Matthews, 1993). Given the relative importance of glaciation and its influence on the regional and local (i.e. foreland) landscape, a brief review of literature concerning the glaciation of the study locations is made in the following paragraphs.

The Quaternary is divided into two epochs: the Pleistocene, and the Holocene. The Pleistocene, which is considered to have lasted 1.8 to 2 million years, may also be referred to as the last Ice Age. The Holocene covers the period from about 10,000 years ago, when the last great ice sheet retreated, up to the present. The Pleistocene is made up of a series of cold and warm periods when ice sheets advanced and retreated over the Northern Hemisphere. It was during this time that a large part of the present Norwegian glacial landscape was formed including the main U-shaped valleys and the fjords. As the ice retreated, during the pre-Boreal period (see glossary), between about 10,000 and 9,000 BP, glacio-isostatic adjustments caused beaches, once at sea level, to rise by 10 metres near the coast and as much as 100 metres inland at the head of the Sogne fjord (Nesje and Dahl, 1990). It should be noted that glacio-isostatic adjustments have continued up to the present at a much-reduced rate.

Leirdalen, in the Jotunheim (see Fig. 2.2a), is a U-shaped valley carved out by confluent glaciers that issued in a north-easterly direction from the Smørstabb massif. Breiseterdalen was created by a glacier from the western side of the Smørstabb massif. Stordalen was carved out by a glacier moving in a south-easterly direction from the Høgvagltindane area. Visdalen was formed by a glacier issuing in a north-easterly direction from the Tverbotn massif. Four glacier forelands, which face onto each of these main valleys, have been chosen for study: Storbreen in Leirdalen; Bøverbreen at the head of Breiseterdalen; Høgvaglbreen at the head of Stordalen; and Svellnosbreen in Visdalen. Jostedalen was created by a glacier issuing from a much larger ice-cap in the Jostedalsbreen area (see Fig. 2.1a), perhaps during the late Weichselian glacial maximum (18,000 to 20,000 BP) (Nesje *et al.,* 1987). Two forelands, used in this study, lie on the south-east side of Jostedalen: Austerdalsbreen in Austerdalen; and Fåbergstølsbreen, which in recent times extended down into Jostedalen.

Some researchers regard the Holocene as a warmer phase, or interglacial period, with the possibility of a large scale re-advance in the near future. Pine and birch forests developed, below the tree-line, on newly exposed landscapes. According the Nesje (1991), based on evidence taken from lake sediments and terrestrial deposits, the ice retreated from Jostedalen in the latter half of the pre-Boreal chronozone, although glaciers re-advanced and left terminal moraines 1 km beyond the terminal moraines from the "Little Ice Age". A warmer period with summer temperatures of up to 2.7 °C warmer than today, starting 8,000 BP and ending 5,000 BP, shifted the ELA (equilibrium line altitude) above the highest point of the Jostedalsbreen area (Nesje, 1991). It is suggested that the ice-cap disappeared altogether so that between about 6,500 and 5,000 BP stands of elm (*Ulmus spp.*) grew close to the present tree line (Nesje, 1991). Significant neoglaciation is said to have occurred around 3,000 BP (Nesje 1991) and there seems to be evidence for climatic disturbances, such as torrential storms and avalanches, around 2,000 BP. The climate became significantly warmer during Medieval times, not only from scientific evidence, but also from historical evidence (Lamb, 1988). The climate started to deteriorate during the 15th century and the glaciers advanced again until the mid- 18th century "Little Ice Age" maximum (Grove, 1988). The average summer temperature during this period is said to have fallen by 0.5 °C to 1 °C (Nesje 1991).

As discussed in Matthews (1992), the "Little Ice Age" is historically documented. A large body of research has been done to estimate the "Little Ice Age" maximum and the retreat of different glaciers (e.g. Griffey and Matthews, 1978; Grove, 1985; Erikstad and Sollid, 1986; Nesje, 1989; Bickerton and Matthews, 1992, 1993). As the glaciers retreated they left a series of moraines, caused by re-advances in certain years. Bickerton and Matthews (1992,1993) have dated the moraines on a substantial number of forelands around Jostedalsbreen, and show a high degree of synchroneity in glacier retreat and re-advance and moraine formation between forelands. Their study has significant implications for the present study since it shows that the forelands (and their moraines) are comparable in terms of the prevailing climatic conditions. The advance and retreat of glaciers during the "Little Ice Age", which is summarised below, is fairly well-documented for the Jostedalsbreen region but is not so comprehensive for the Jotunheim region.

The first damage, possibly caused by glacial advance, is proposed by Grove (1988) to have started in AD 1339, as shown by a special court declaring many farms to have been deserted, and others with substantial tax reductions, in the Olden and Loen parishes north of Jostedalsbreen. Although the disaster is not specified, these concessions had to be in recompense for major physical damage, and according to Grove, may have been caused by glacier advance. These same parishes were amongst those to suffer from glacier advances and associated rock falls and avalanches that occurred in the 17th and 18th centuries. Grove suggests, however, that the evidence for a significant advance at this time is tenuous. Direct evidence for early glacial advance in the late Middle Ages should have been provided by tax claims for damage caused to farm land and buildings. However, the Black Death, widely held to have been responsible for wiping out one third of the British population between 1348-49, swept through Norway between 1349-50, and Jostedalen was deserted until some time in the 16th century after which the population levels had recovered (Grove, 1988). The earliest direct evidence of damage by ice was reported on farmland in a valley on the eastern side of Jostedalsbreen although earlier claims were made for damage, such as crop failure, as a result of a worsening climate. According to Grove (1988) the advance of the ice after 1684 was very fast and the evidence from this, and the other tax claims from that time, shows that the ice started to advance at speed between 1667 and 1692. The tax claims for crop damage and famine, starting several decades earlier, were made throughout the region at a time when it is likely that cooler climatic conditions caused the ice-caps to thicken and build up and then spill down the valleys after 1660 (Grove, 1988). Modern evidence shows that the glaciers are generally retreating in synchrony (Kasser, 1973; Muller, 1977; Bickerton and Matthews, 1993), although the size of the glacier and its continentality influences its behaviour (Grove, 1988). The advance of the steeper western glaciers of the Jostedalsbreen region may have halted a few years earlier than that of the shallow-sloping eastern glaciers (Nesje, 1991).

Early evidence for "Little Ice Age" glacier advance and retreat in the Jotunheim comes from verbal reports of glacier extent. In 1893, for example, Åmund Elveseter had said that Storbreen had crossed the river Leira 100 years previously (Matthews, 1974). However, the glacier variations have been better documented since the beginning of the century (Hoel and Werenskiold, 1962; Matthews, 1974) although the age of older parts of the forelands can only be deduced using other dating techniques, such as lichenometry.

1.3 Literature review

In this review section, an attempt is made to put the research of this thesis in the context of previous work. In addition, the review will show how the present investigation is different from the previous work in the region and it contributes to the elucidation of certain general ecological questions. Reviews, concerning both the history of successional theory and previous research on succession (carried out by members of the "Jotunheim Research Expedition") have been discussed at length in recent Ph.D. theses by Whittaker (1985) and Crouch (1992), and by Matthews (1992) in his book "*The Ecology of Recently Deglaciated Terrain*". As this thesis is a continuation of the previous work, and the aims of this study follow closely, an attempt will be made to avoid repetition of these earlier reviews. In general, the purpose of this section is to describe the previous research in the context of the effect of microtopography, and associated environmental factors, on vegetation pattern and succession. However, before a discussion of relevant research can be made it is necessary to discuss and clarify some of the terminology, especially with regard to successional theory, which will be used throughout thesis. The reasoning behind such a discussion is due to the considerable variation in the definitions that exist (e.g. Burrows, 1990).

There are four general questions, relating to successional theory, which need to be addressed:

1. What is succession?
2. What is known about the controls on succession?
3. How is successional theory relevant to this study?
4. How will this study contribute to a deeper understanding of succession?

1.3.1 Succession - a general outline

The intention of this outline is to introduce the most recent concepts of succession relating to its patterns and mechanisms. For a thorough history and discussion of successional theory refer to the following references: Whittaker, 1953; Churchill and Hanson, 1958; McCormick, 1968; Drury and Nisbet, 1974; Finegan, 1984; Whittaker, 1985; Miles, 1987; Pickett et al., 1987; Crouch, 1992; and Matthews, 1992. Succession is an important concept in ecology and Pickett et al (1987: 364) go so far as suggesting: *"the development of a broad, inclusive, mechanistic theory (of succession) is one of the principal goals of contemporary plant ecology".*

Being such an important concept it might be imagined that the most basic definition, and underlying mechanisms, of succession have been agreed upon. However, especially with regard to discussion of the mechanisms of succession, this is not the case. The problem lies mainly with the influence that the eminent ecologist Frederic Edward Clements (1874 - 1945) has had on 20th century ecology. Briefly, he proposed that succession develops as an organism develops (the organismic concept): as an orderly, unidirectional, highly predictable series of discrete communities to a single stable climax community. Individual species within each community are considered to be interacting with others within that community, like organs in a body, so that the community acts as a whole. Furthermore, each preceding community "facilitates" or "prepares the way" for each succeeding community. According to the theory, the later communities cannot colonise without the earlier communities (e.g. 1916, 1936). Those who support the Clementsian view, or variations upon it, are holistic ecologists (e.g. Margalef, 1968; Moravek, 1969; Odum, 1969) and recently this approach has developed into "systems ecology" (e.g. Odum 1971; Colinvaux, 1973; Macmahon, 1980; McIntosh, 1980) which emphasises "*complexity, interconnection, wholeness, multiple causality and unity of structure and process*" (McIntosh, 1981: 12). One of the main goals of this "systems approach" is to find the *"principals of ecosystems"* and this branch of research has been considered important enough to warrant the support of the International Biology Programme (IBP). Although alternative, and perfectly feasible, models have been in existence since Clements' time (e.g. Gleason, 1917; 1939), Clements' theory has prevailed, possibly due to the human need for order (Miles, 1987). It is hoped that the new "systems approach" will not merely be a continuation of man's need for simple answers to complex questions.

The alternative model, proposed by Gleason (1917), was that each species acts on its own and is merely "*a fortuitous juxtaposition of plant individuals*" (quoted in Matthews, 1996: 200). Gleason suggested that the Clementsian "community", with its distinct boundaries, was a human construct which does not reflect reality in nature. He suggested that individual species populations respond to the prevailing environment at any site and thus the composition of the groups of species, found at any location, is coincidental: species within the group occur at the location due to environmental conditions as opposed to reliance on the occurrence of other species within the group. This view, and research which holds with this view, is therefore reductionist. Most reductionists support some, or all, of the following concepts: 1) that succession is not necessarily unidirectional but can be retrogressive; 2) that succession does not proceed through an orderly and predictable series of stages, but rather proceeds as a gradient of populations; 3) that succession is driven by a combination of factors, for example, life-history or environmental (allogenic) mechanisms and not by a facilitative (autogenic) mechanism; and 4) that its end-point is not a stable predictable community but a mosaic of environmentally-influenced assemblages which are relatively stable but may fluctuate according to large or small-scale environmental changes influenced by local climatic or disturbance regimes (e.g. Egler, 1953; Whittaker, 1951, 1953; McCormick, 1968; Matthews, 1979d; Peet and Christensen, 1980; Tilman, 1985).

It was only in the 1950s that Gleason's view started to gain acceptance (Matthews, 1996) when, with the onset of the computer age, the analysis of large data sets (necessary for a better understanding of the mechanisms of succession) was made easier. However, Egler (1970) suggested that the computer age has problems of its own and those researchers that rely solely on computer analysis have only included easily-measured factors in their succession models and have ignored those important factors which are difficult to measure: "*... the things that count are the things that can be counted* " (quoted in Miles, 1987: 10). Factors such as topography and microtopography, many important environmental parameters (e.g. moisture, exposure, temperature, snow-lie) and the effects of herbivory and disturbance, including human disturbance, as well as plant life-history traits and other population processes tend to be left out of the equations. In general, many of the papers discussing successional sequences between the 1950s and the 1980s only described the vegetation and/or soil sequences, on "homogeneous" plots of increasing age (chronosequences) since disturbance (e.g. Crocker and Major, 1955; Persson, 1964; Walker and Chapin, 1986). Although a number of papers suggest other environmental factors are an important influence on vegetation and soil patterns, most do so only subjectively (e.g. Stork, 1963; Viereck, 1966; Scott, 1974a). A number of authors investigated the effect of microtopography (and related environmental factors) on vegetation patterns, but these studies only discussed the effects on mature vegetation patterns and not on successional sequences (e.g. Billings and Bliss, 1959; Miller, 1982). Very few have attempted to quantify and measure some of the prevailing environmental variables, including microtopography, that affect the vegetation and/or soil patterns along a time gradient (e.g. Zollitsch, 1969; Vetaas, 1986; Whittaker, 1985; Schubiger-Bossard, 1988; Crouch, 1992). No one, as far as the author knows, has specifically studied the effects of microtopography (and a wide range of associated environmental variables) on vegetation succession at a number of altitudes as has been done in the present study. A more detailed discussion of the previous work on succession (with special reference to primary succession on glacier forelands) and also work on the effects of microtopography (with a special emphasis on arctic and alpine landscapes) is made in sections 1.3.2. and 1.3.3.

In the 1970s several influential papers were published which proposed succession models designed to clarify and define succession and its mechanisms (e.g. Drury and Nisbet, 1973; Horn, 1974; Connell and Slatyer, 1977; Tilman, 1985). However, since the mid-1980s few researchers have tried to find the "*ecological grail of a single universal generalisation of succession*" (Miles, 1987: 2). Increasingly, authors have criticised both the researchers who have not attempted to consider all the possible influences on vegetation pattern, as well as the researchers who have tried to define successional theory in too restricted terms. For example Pickett (1987) proposed a coming together of ecological theories and research (i.e. holists and reductionists) to provide a more generalised, comprehensive and realistic framework for successional theory. Certainly, a more generalised approach has been called for by many workers in the field (e.g. Finegan, 1984; Fitter, 1984; Grubb, 1987; Miles, 1987; Matthews and Whittaker, 1987; Luken, 1990; Miles and Walton, 1993; Matthews, 1992, 1996).

Recently, therefore, researchers have started to use a more general approach to the definition of succession. Whittaker (1985) uses the definition that succession is a change of vegetation composition through time and that it is broadly predictable. Crouch (1992) uses a similar definition by saying that it is a term given to those changes in vegetation with respect to time which are not merely fluctuational but are directional and often predictable. Kent and Coker (1992) define succession as involving the immigration and extinction of species together with changes in their relative abundances. Matthews (1992) defines it as being a complex of processes producing gradual, directional changes in the species composition and structure of ecosystems. Burrows (1992) defines it as a directional sequence of populations of different plant species on a site. These researchers therefore define succession in a similar manner and the use of these definitions can be regarded as being fairly universal throughout the ecology literature. There is one point of dispute, However, with regard to the use of the word "directional". Some authors have shown species replacement to be "retrogressive" (e.g. Drury and Nisbet, 1973; Whittaker, 1985; Matthews and Whittaker, 1987) - i.e. pioneer or earlier colonisers (or less complex assemblages) can replace older colonisers (or more complex assemblages). Retrogression has been outlined by Moravec (1969) and Whittaker (1953) and can result from a number of factors including disturbance factors such as climate or fire (Noble et al., 1984). In their definitions of succession, Whittaker (1985) and Kent and Coker (1992) suggest that regression occurs (see section) and thus do not imply that change follows a unidirectional sequence and it is their definitions of succession that will be preferred for the purposes of this study. For the purposes of the present study, with regard to succession on glacier forelands, which are previously unvegetated and supposedly "sterile" landscapes (*sensu*: Matthews, 1992), future reference to the word succession (see glossary), in this thesis, implies **primary** succession (see glossary) and not secondary succession (see glossary).

In many dictionaries and text books the term "succession" takes on a further meaning that has been disputed for many decades. For example the *"Concise Oxford Dictionary of Ecology"* (Allaby, 1994: 374) first describes succession in a similar way to the above definitions but then goes on to describe the "classical" (holistic) concept of succession without reference to reductionist views: *"Classically, the term refers to the colonisation of a new physical environment by a series of vegetation communities until a final equilibrium state, the climax, is achieved. The presence of the colonisers, the pioneer plant species, modifies the environment so that new species can join or replace the initial colonisers. ... The characteristic sequence of developmental stages (i.e. nudation, migration, ecesis, competition, reaction, and stabilisation) is termed a sere. ... ".* There are a number of problems with this definition, originating from Clements (1916): firstly, concerning the mechanisms of succession, whereby earlier colonisers, or pioneers, "modify" the environment for later colonisers; and secondly, the use of the terms "climax", "community" and "sere". These problems are outlined below.

Facilitation (also known as reaction or autogenesis), whereby pioneers "modify" the environment for later colonisers, has long been considered as possibly not the most important driving force of succession (e.g. Gleason, 1917, 1936; Whittaker, 1951, 1953; Egler, 1954; Drury and Nisbet, 1973; Connell and Slatyer, 1977; Noble and Slatyer, 1980; Hibbs, 1983; Finegan, 1984; Pickett et al., 1987; Walker and Chapin, 1987; Chapin et al., 1994; Stöcklin and Bäumler, 1996). These authors have suggested alternative mechanisms of succession, such as life history (e.g. differences in seed dispersal or rates of growth) or allogenic mechanisms (external abiotic changes in environment with time). These alternatives are now widely accepted as at least partly explaining succession and yet the dictionary does nothing to explain that the pure form of the "classical" concept of succession was, according to Burrows (1992: 11), never generally accepted: *"Much of his* [Clements'] *terminology was never generally accepted and many of his ideas have been abandoned by most vegetation ecologists in recent times. The basic concept of sequential development of vegetation on bare surfaces (first a colonising phase, followed by immature ("seral") phases and culminating in a mature and stable ("climax") phase is firmly embedded in the literature of vegetation ecology and in the minds of many plant ecologists"*

The view that the "classical concept" is embedded in the literature is confirmed by the fact that so much literature has been produced reiterating the failings of the "classical" view of succession by emphasising mechanisms of succession other than facilitation (e.g. Gleason, 1917, 1936; Whittaker, 1951, 1953; Egler, 1954; Drury and Nisbet, 1973; Horn, 1974; Connell and Slatyer, 1977; Noble and Slatyer, 1980; Hibbs, 1983; Finegan, 1984; Pickett et al., 1987; Walker and Chapin, 1987; Chapin et al., 1994; Stöcklin and Bäumler, 1996). However, McCormick (1968: 28) suggested that those refuting the Clementsian model are, in part, to blame for its continuing to dominate the general undergraduate literature: "*... the Clementsian model still is generally accepted and is the only widely taught concept. A major pedagogic fault of the critics of the Clementsian model is their failure to offer an equally applicable alternative model.*".

It may never be possible to offer such "*an equally applicable alternative model*", rather it may be wiser to define succession, and related concepts, in more general terms. Crouch (1992), in an extensive review of the mechanisms of succession, concludes that allogenic and autogenic controls have an important influence on succession. Crouch (1992) adds that Brandani (1983) suggested a division between autogenic and allogenic factors does not exist in natural ecosystems and that the boundary between the two factors is artificial. Miles and Walton (1993: 300) came to a similar conclusion: "*except on toxic wastes, it is difficult to separate the effects of allogenic and autogenic factors, because propagules of bacteria, fungi, algae, lichens, mosses and flowering plants, as well as invertebrates appear from the outset. Their growth immediately begins to influence the physical and chemical nature of substrates, and so confounds the effects of purely allogenic factors*". Whittaker (1985) also suggests that allogenic and autogenic factors cannot be separated in primary succession.

It is apparent that many ecologists try to categorise and define the mechanisms of change in a precise manner so that they can build ecological models and systems for each type of ecosystem. In reality, such a synthetic and unnatural division of mechanisms of succession tends to subvert a true understanding of succession. The evidence suggests that the relative influence of the different (defined) mechanisms of succession are likely to vary not only between different types of succession (i.e. primary succession versus secondary succession) but also between different ecosystems (e.g. sub-alpine birch woodland versus alpine vegetation). It is also possible that the relative influence of the different mechanisms may also vary at a more local scale (e.g. between different glacier forelands in the alpine belt). For the purposes of the present study, then, only the most general definition of succession, following Whittaker (1985), namely, **succession is a change of vegetation composition through time that it is broadly predictable,** is considered appropriate. Similarly, the more wide-ranging explanation of the causes of succession, following Whittaker (1985) and Crouch (1992, 1993), namely, **mechanisms of succession comprise both allogenic and autogenic controls**, is adopted and no assumptions are made concerning the relative importance of each. The relative influence of allogenic and autogenic controls on succession will be discussed on the strength of the results derived from analysis of the field-data.

Secondly, the idea that a final equilibrium state, or "climax", is reached has long been disputed (e.g. Gleason, 1917,1939; Cooper, 1926; Tansley, 1935; Whittaker, 1951, 1953; Burrows, 1992; Matthews, 1992, 1996). Clements (1916), and adherents to holistic views (e.g. Margalef, 1968; Odum, 1969; Moravec, 1969) suggest that succession converges from a number of early or "pioneer" communities to a single "climax" community (or monoclimax). However, a growing body of evidence supports the notion that a mosaic of many "climaxes" of communities exist on the oldest terrain (a "polyclimax" *sensu*: Whittaker, 1951, 1953) with community distribution continuing to be influenced by environmental factors. This latter notion suggests that there may be a divergence of communities, from relatively few pioneer communities to a larger number of communities on the oldest terrain (Matthews, 1979; Christensen and Peet, 1984; Whittaker, 1993). Crouch (1992) suggests that there is evidence for both divergence and convergence and in this study no assumption will be made that either divergence or convergence occurs. The vegetation pattern and succession shown by the results will help to elucidate whether divergence or convergence occurs, on each of the forelands, as well as demonstrate the importance of altitudinal controls on the patterns. Crouch (1992) further implies that the concept of "climax" (a stable end-point in a succession) has become redundant as climate is ever-changing and thus a stable end-point is never reached. Both Whittaker (1985) and Burrows (1990) also suggested that the use of the term "climax" is inadvisable because it is discredited and that the use of the term "mature" is preferable. For the purposes of this study, the term "**mature**" is therefore applied to vegetation on the oldest terrain (outside the forelands) and the term "climax" is not used, except in reference to its use in other studies. The term "sere", defined as the characteristic stages of a successional sequence, has also become redundant as many authors regard the vegetation succession to be a gradual process rather than a series of distinct stages (e.g. Burrows, 1990) and thus the term will also not be used.

The term "community" is widely used in most of the literature with regard to succession. The popular "*Dictionary of Physical Geography*" (Whittow, 1984: 106) describes the term "community" as: *"an organised group of plants or animals, generally of distinctive character and related to a particular set of environmental requirements*". In general, ecological literature appears to use the term to describe associations of species growing together in a particular environment (e.g. Krebs, 1978; Kent and Coker, 1992) although the definitions from author to author differ to some extent. However, Burrows (1992) uses a more general definition that says that similar stands are often classed into abstract groups and are termed "communities" and Krebs (1978) points out that there is a wide range of meanings for the term "community": "*Plant ecologists use the term community in a very general sense, whereas the term association (a plant community of definite floristic composition) has a very specific meaning. Zoologists, on the other hand, use the word community both in the general sense and in the specific sense of the botanical association*".

The meaning of the term "community" is therefore not as clearly defined within the literature as it should be. The problem is further complicated by the term "association" which also appears to be used in a fairly indiscriminate way, throughout the literature, for plant groupings which have been found by various techniques using a variety of vegetation data (cf. Krebs, 1978; Whittow, 1978; Burrows, 1990; Kent and Coker, 1992; Matthews, 1992). However, according to Gjærevoll (1956) and Kent and Coker (1992: 250), the term "association" has a specific meaning and should be used in the sense consistent with the Zurich-Montpellier (or Braun-Blanquet) school of phytosociology: *"the basic unit of the classification system found by grouping together various sample relevés that have a number of species in common"*. According to Kent and Coker (1992: 247) a prerequisite of the Braun-Blanquet methodology is that the sample quadrats (relevés) should be both non-random (chosen subjectively) and the vegetation samples, within each relevé, should be uniform (or homogeneous): "*... the relevé or sample should be* ***uniform*** *and* ***homogeneous*** [their block letters] ... *Thus micro-environmental and micro-habitat variations should be either avoided or ignored*".

Following Whittaker (1951), the term "association" is therefore avoided in this thesis and the term "**assemblage**" is used instead. The word "association" will only be used synonymously with the word "relationship" in order to show that there is a connection between any factors being discussed. No phytosociological meaning (*sensu*: Braun-Blanquet) is therefore implied by using the word "association". Birks (1980) appears to use the terms "community", "noda" and "assemblage" interchangeably and emphasises the usefulness of delimiting abstract vegetation units (along a continuous vegetation gradient). Matthews and Whittaker (1987) also do not distinguish between the terms "assemblage" and "community" but, for the purposes of the present study, the meaning of the terms will be separated. Until analysis has shown there to be a strong relationship between members of the group, the species found together on a site are referred to as an "**assemblage**" and this term does not infer any relationship between the members. The present study will, However, use the term "**community**" once a relationship (or association), between the component species and prevailing environmental factors has been shown by analysis. Where the relationship has been shown to be weak the term "**assemblage**" is preferred. Where a distinction needs to be made of the strength of the relationships between members of any assemblage the adjectives "**loose**" (for a weak relationship) and "**tight**" (for a stronger relationship) are used - following Matthews, (1979c). The term "**gradient**" or "**gradation**" is preferred for use with the term "assemblage" as it describes a gradual change in species composition or environment. The term "**zone**" or "**zonation**", and can be used with the term "community" where the change in species composition or the environment appears to be distinct and sharply defined. The terms "gradient" and "zone" are spatial concepts that signify the type of distribution patterns shown by the plant assemblages and associated environmental parameters.

In summary, succession can therefore be considered as a change of vegetation composition through time that is broadly predictable, is caused by both autogenic and allogenic controls, and may be directional or retrogressive. The term "**assemblage**" is preferred to the term "community" initially and unless analysis shows that there is **no** strong association (with other species) or structure (in relation to environmental factors). So-called "climax" assemblages are referred to as "**mature**" assemblages in order to avoid confusing older ground assemblages with stable vegetation in a "final equilibrium state". Similarly, no assumptions will be made regarding either divergence or convergence of assemblages through time.

Using the above definitions this study will be able to examine a number of general questions relating to succession:

1. Is there a clear successional sequence of assemblages across each of the glacier forelands under study?
2. Are most of the species grouped into structured communities, with strong associations between members and with environmental factors?
3. Do the environmental parameters (and associated assemblages/communities) change gradually, and thus form gradients, or sharply, and thus occur as zones on the glacier forelands?
4. Do associations differ between the various successional stages and in relation to altitude?
5. Is there evidence that may help to explain the mechanisms of succession on the forelands?
6. Is divergence or convergence of assemblages occurring and is the succession always progressive?

1.3.2 Microtopography in relation to vegetation pattern

Since the early days of ecological research, workers investigating mature vegetation and soil patterns in arctic and alpine landscapes have recognised that the patterns can be related to microtopography-related environmental gradients. Such gradients include duration and depth of snow cover, exposure, solifluction, and moisture conditions (e.g. Shaw, 1909; Clements, 1916; Gleason, 1917; Fægri, 1937; Cooper, 1942; Whittaker, 1951, 1953; Coombe and White, 1951; Gjærevoll, 1950,1954, 1956; Hanson, 1953; Steere, 1954; Gelting, 1955; Dahl, 1956; Churchill and Hanson, 1958). However, many of these environmental parameters have not been investigated in detail or have been measured at a restricted number of sites (e.g. Dahl, 1956; Gjærevoll, 1956; Stork, 1963; Viereck, 1966; Tisdale et al., 1966; Douglas, 1972; Scott, 1974a). In addition some researchers fail to report sufficiently the number of samples taken and/or the sampling methods employed (e.g. Crocker and Major, 1955; Crocker and Dickson, 1957; Stork, 1963; Worley, 1973; examples in Kershaw and Looney, 1985; Fitter and Parsons, 1987; Chapin, 1996). The failure of researchers to quantify adequately the measurement of the prevailing environment at a site has often led to, at best, a simplification of the explanations for the vegetation patterns (and succession) at different locations and, at worst, a distortion of reality with regard to the causes of the vegetation patterns. Furthermore, lack of description of the sampling methodology for the site, as well as for each parameter, has hindered the use of results by other researchers.

The notion that microtopography has a powerful influence on prevailing environmental parameters, and hence vegetation pattern, is therefore not new. Although there are numerous studies relating vegetation patterns to small-scale environmental gradients, there are few studies which have quantitatively investigated the influence of environmental patterns on (primary) succession. Some researchers have studied the general influence of larger-scale altitudinal, macrotopographical, or landscape variations, on environmental gradients and vegetation patterns (e.g. Samson, 1930; Braun, 1936, 1956; Hanson, 1951; Wiggins, 1951; Flock, 1978; Evans, 1989; Hastings, et al., 1989; Oechel, 1989; Walker, et al., 1989; Walker et al., 1993; Lynch and Kirkpatrick, 1995; Sveinbjörnsson, 1995; Jobbágy et al., 1996). Other researchers have made specific investigations with particular reference to the vegetation patterns on certain smaller-scale microtopographical features such as across solifluction terraces or lobes (e.g. Sorensen, 1945; Hanson, 1950; Archer, 1973); tundra mounds (e.g. Hanson, 1950), polygon-patterned ground (e.g. Hopkins and Sigafoos, 1951; Schell and Alexander, 1973; Raup, 1971; Jonasson and Sköld, 1983; Jonasson, 1986); stone stripes (e.g. Taylor, 1955; Heilbronn and Walton, 1984); frost scars and peat rings (e.g. Hopkins and Sigafoos, 1951, 1954); hummocks and hollows in subarctic mires (e.g. Sjörs, 1965; Kvillner and Sonesson, 1980); mudflows (e.g. Lambert, 1972); beach ridges or raised beaches (e.g. Kershaw and Rouse, 1973; Larson and Kershaw, 1974; Chapin, 1996); *Calluna* heath hummock and hollow complexes (e.g. Watt, 1940, 1947; Barclay-Estrup, 1971); moraine ridges (e.g. Elven, 1975, 1978; Elven and Ryvarden, 1975; Parkinson and Roberts, 1985; Alexander, 1986; Vetaas, 1986; Birkeland and Birke, 1986; Parkinson and Gellately, 1991); snowbeds (e.g. Billings and Bliss, 1959; Miller, 1982; Wijk, 1986a, 1986b; Evans and Fonda, 1990; Benedict, 1990a, 1990b, 1991; Auerbach and Halfpenny, 1991; Kudo, 1991, 1992; Kudo and Ito, 1992; Komárková, 1993; Scherff, et al., 1994; Stanton, et al, 1994); sand dunes (e.g. Olson, 1958); tree "islands" (Holtmeier and Broll, 1992); tracks (e.g. Emmanuelson, 1984c); hill slopes (Kikuchi and Miura, 1993) and fumaroles (e.g. Broady et al., 1987). Some of these studies refer to the "primary succession" of assemblages of plant species on, for example, moraines across a glacier foreland, ridges in the raised beach studies or locations that have suffered severe disturbance such as mudslides (although mudslides, by their very nature, carry soil, roots and propagules so that the substrate cannot be regarded as altogether "primary"). Most of the other studies cannot be regarded as primary successional studies; rather they involve patchiness in the mature vegetation landscape related to the life-history of certain dominant plant-species and cycles of disturbance, as well as to other environmental factors including microtopography, climate, herbivory and other disturbance factors.

In many ecology texts, concerning vegetation patterns or succession, the terms "microtopography", "microsite" or "microhabitat" are not to be found in the index (e.g. Odum, 1975; Gray et al., 1987; Crawford, 1989; Luken, 1990; Kent and Coker, 1992). Others only refer to microtopography briefly (e.g. Krebs, 1978). Some texts, however, emphasise the importance of microtopography by having extensive listings for these terms (e.g. Kershaw and Looney, 1985; Harper, 1987; Matthews, 1992; Burrows, 1992; Begon et al, 1996), although, within the latter texts, the number of references given for research, specifically investigating the effects of microtopography on vegetation patterns, is limited or entirely lacking. From this it can be seen that there is a general lack of emphasis on the relative influence of microtopography on vegetation patterns.

There have been four major problems for previous researchers, working on arctic and alpine landscapes, who wish to explain the vegetation and soil mosaic in terms of microtopography (and associated environmental variables) along a time sequence:

1. Most arctic and alpine sites are isolated and weather conditions are only suitable for vegetation data collection during short field seasons, thus restricting the amount of data that can be collected.
2. It is necessary to have accurately dated substrates.
3. Until recently, there has been a lack of sufficiently powerful (and robust) multivariate analysis techniques which are capable of analysing and interrelating complex environmental and vegetation data sets.
4. Until recently, there has been a lack of consistent, proven, and simple methods of measurement for a number of the more important environmental factors associated with microtopography (possibly partly due to the inability to use non-parametric measurements in the vegetation analysis).

Generally, therefore, it has only been possible for previous researchers to concentrate on the effects of microtopography at a limited number of locations on the oldest terrain (discussed in this section) or to concentrate on vegetation, and/or soil, successions using homogenous stands of various ages (see section 1.3.3). The present study has the advantage of having a large resource of background information with regard to the study sites (e.g. Matthews, 1992); of being able to use tried and tested methods of analysis (Whittaker, 1987; Matthews and Whittaker, 1987; Crouch, 1992, 1993) which can interrelate the components of very large data sets; and of being able to use (or modify) tried and tested methods of field-data collection for use in the analyses (Whittaker, 1985; Crouch, 1992). Nevertheless, the findings of the previous work, with regard to microtopography and its effects, is very important as it shows how microtopography influences the vegetation and soil patterns in general. By using the findings of the previous research it is then possible to ascertain how microtopography (and associated parameters) may affect vegetation succession, and the prevailing soil chronosequences, at various altitudes.

The influence of microtopography on vegetation and soil patterns in arctic or alpine landscapes is exemplified by the relative winter exposure or snow-cover of any particular site (e.g. Shaw, 1909; Anderson, 1947; Churchill and Hanson, 1958; Billings and Bliss, 1959; Tisdale et al., 1966; Scott, 1974a; Knight et al., 1977; Elven, 1978; Flock, 1978; Miller, 1982; Wijk, 1986a,b; Evans et al., 1989; Evans and Fonda 1990; Walker et al., 1989; Benedict, 1990a,b, 1991; Holtmeier and Broll, 1992; Walker et al., 1993; Stanton et al., 1994; Schaefer and Messier, 1995). Snow distribution patterns have been shown to be the same from year to year and researchers have found considerable correspondence between vegetation patterns and duration of snow cover (e.g. Dahl, 1956; Billings and Bliss, 1959; Kudo, 1991; Stanton et al., 1994). For this reason, much of the previous work, relating the effects of microtopography on vegetation patterns in arctic and alpine landscapes, has specifically investigated vegetation or soil patterns in relation to snow cover duration. Benedict (1990a) made a study of lichen mortality due to late-lying snow directly above the timberline in the Colorado Front Range, USA, and found that large swathes of the alpine valley in his study are affected by late-lying snow. He proposed 5 zones of snow cover (in relation to the growth of *Rhizocarpon spp*): Zone 1 - centre of late-lying or permanent snow patches (no lichens); Zone 2 - inner snowpatch zone with a snowkill period in the 1950s which killed all *Rhizocarpon spp* so that only tiny specimens have established since 1960; Zone 3 - outer snowpatch zone with small specimens (maximum diameter <20 mm) but a low lichen cover (<1 %) dating from the last snow-kill period, probably in the "Little Ice Age"; Zone 4 - zone of late-lying general snow (90 % of valley) where largest *Rhizocarpon* can be 40-70 mm, dating from a snow-kill period occurring before the "Little Ice Age"; Zone 5 - zone of exposed and windswept areas where snowkill may have occurred in a cold period during the middle of the Holocene with largest *Rhizocarpon* > 90 mm. He suggests therefore that the lichen size zones represent past snow-kill events (of at least 5-8 years permanent snow-cover) and from his zonation it can be seen that well over 90 % of the valley floor is affected by late-lying snow thus emphasising the importance of snow effects above the tree-line at this location. As an emphasis has been placed on the importance of snow-lie on vegetation patterns in alpine regions around the world, e.g. Swedish Lapland (Gjærevoll, 1950); Rondane, Norway (Dahl, 1956); Snowy Range, Medicine Bow Mountains, Wyoming (Billings and Bliss, 1959); Frederika glacier, Alaska (Scott, 1974a); Taisetsu Mts, Hokkaido, Japan (Kudo, 1991), it is probable that the zonation demonstrated by Benedict (1990a) is a widespread phenomenon.

Snow has been shown to act as a blanket over the vegetation during the winter, not only insulating the underlying vegetation from exposure to harsh winds and fluctuating temperatures, but also by decreasing the number and severity of frost-heave cycles - this being especially important on ground with low vegetation cover (e.g. Mackinney, 1929; Anderson, 1947; Goulet, 1995). The depth and type of snow at a location apparently not only influences vegetation patterns through the relative amounts of winter exposure but affects the winter-foraging habits of rodents, which also influence vegetation patterns (Fox, 1981; Emmanuelsson, 1984; Auerbach and Halfpenny, 1991). During the growing season, the snow accumulation zone can influence such diverse factors as growing season length (e.g. Billings and Bliss, 1959; Knight, et al., 1977; Wijk, 1986a,b; Stanton et al., 1994); nutrient availability and distribution (e.g. Miller, 1982; Bowman, 1992; Stanton et al., 1994); moisture (e.g. Billings and Bliss, 1959; Flock, 1978; Walker et al., 1989); and podzol development (Alexander, 1986). The moraines in the present study are affected by gradients of differential snow-lie (e.g. Haines-Young, 1985; Matthews, 1992) with many of the footslopes of the moraines having late-lying snow-beds, particularly at high altitudes. Because of their special relevance, examples of studies concerning the vegetation patterns or soil characteristics on ground under snow-accumulation zones (associated with microtopographical position) in an arctic or alpine environment, are outlined below. Studies specifically relating to vegetation patterns/succession on moraines are discussed in the next two sections (1.3.3 and 1.3.4).

Dahl (1956) produced one of the major classifications of plant associations of alpine vegetation in Scandinavia and discussed, at length, the existence of patterns in the vegetation due to differences of environmental conditions caused by microtopography. He illustrated this point by showing the existence of a gradient of communities across a snow accumulation zone. However, he suggested that in order to study the vegetation gradient it is necessary for an experienced researcher to analyse the plant communities separately by choosing homogeneous sampling areas subjectively, according to the dominant species found on the site. Using this method he gave a detailed account of all the plant associations in the Rondane. However, using his methodology "transitionary communities" are likely to have been ignored and therefore it is impossible to ascertain their relative importance within the landscape. Only once the communities had been defined did he consider the environmental influences on the vegetation patterns. Although a number of environmental parameters were measured - soil profiles were dug and pH samples were taken - the environmental conditions of the site were described qualitatively. Dahl's research is fairly representative of the qualitative nature of environmental measurements relating to most of the earlier work (pre-1960) on vegetation patterns. Despite this, Dahl's work "*Vegetation of Rondane*" (1956) represents a major classification of plant associations in central Norway.

Churchill and Hanson (1958), described five plant assemblages commonly found in zones, on lime-poor soil, from the top of a ridge to the base of a slope:
a) *Empetrum hermaphroditum - Louiseleuria procumbens* community - snow cover is very thin or not present and the site is exposed to strong winds.
b) *Betula nana* community - snow-cover is thin and the site is less exposed to winds than "a)".
c) *Vaccinium myrtillus* community - has a complete cover of snow which melts relatively early.
d) *Deschampsia flexuosa* community - has a deep snow-cover that melts late.
e) *Salix herbacea* community - has a very deep snow-cover that melts very late or not at all in some years.
These assemblages were based on the work of several authors working on snowfield patterns in relation to environmental gradients (Leach and Polunin. 1932; Nordhagen, 1943; Gjærevoll, 1950, 1952; Hedberg et al., 1952) and their work represents the long-standing interest in the study of snow-related vegetation distribution patterns. Billings and Bliss (1959), using a quantitative methodology, investigated the effect of the melting pattern of an alpine snowbank on vegetation patterns and soil characteristics. They found a marked floristic gradient from the area released in June to the area released in mid-July. They concluded that the differences result from inconsistent tolerances of the plant species, to drought and shortness of growing season, with long snow cover cutting down productivity to nil and causing poor soil development. Flock (1978), investigating the cryptogam distribution along a snow-cover/soil-moisture gradient, also concluded that moisture, released from the snowbank, is a major influencing factor in determining cryptogam patterns. Scott (1974a) made an extensive survey of snow-melt pattern and its effect on vegetation pattern at Chitistone pass, Alaska. Using an ordination technique, he showed that depth and duration of snow is an important influence on the vegetation pattern. He concluded that the environmental factors influenced or modified by snow-cover include length of growing season, exposure to wind and supply of soil and surface water.

Miller (1982) made a detailed study of the environmental and vegetational variation across a snow accumulation area in montane tundra in central Alaska. He measured a diverse number of environmental factors, including temperature, moisture and a large number of soil nutrients. He also recorded plant biomass, above and below ground, plant nutrient content and turnover rates of evergreen leaves. Seven vegetation zones had been defined in previous years (Oberbauer and Miller, 1979; Murray and Miller, 1982). Miller suggested that the length of growing season is a constraint, but he emphasised the role of nutrients in defining the distribution of the plant species. He found that some of the plants are excluded from the snow patches, such as the deciduous-leaved shrubs, because they need a long growing season. However, others were found in different parts of the snow patch even though these species have similar growing season lengths. Miller found that there is a high nitrogen availability in the centre of the snow-patch and lower nitrogen levels above the snow-patch. He therefore concluded that the vegetation zones (or gradient) are more related to nutrient levels [possibly indirectly caused by the snow patch due to accumulation of litter in the centre of the snowpatch] than to the actual duration of snow-free periods or to moisture and pH levels. Wijk (1986a,b) also held that the effect of snow-duration is probably not as important as other environmental factors such as nutrient availability.

Evans and Fonda (1990) investigated the influence of snow on subalpine community pattern in the North Cascades in Washington state. They state that a previous study (i.e. Douglas and Bliss, 1977) had shown that, in the eastern Cascades, a gentle topography leads to an expansive vegetation pattern reflecting gradual snow-related environmental gradients and, in the western Cascades, a rugged topography leads to steep environmental gradients with abrupt changes in community type. However, Evans and Fonda also state that Douglas and Bliss did not measure the specific microclimate parameters associated with these gradients. Evans and Fonda therefore performed a systematic study measuring microclimate (snowmelt date; air and soil temperatures - as communities released from snow; soil moisture) and percentage cover vegetation across a snow-cover gradient. They concluded that the important effect that time of snow melt has on vegetation pattern is reflected in soil temperature, so that earlier sites are warmer than later. Interestingly, they did not find that snowmelt has a significant effect on the soil moisture gradient among the communities - a factor which is generally associated with snow cover (e.g. MacKinney, 1929; Tisdale et al., 1966; Billings, 1974; Whittaker, 1985; Walker et al., 1993). Walker et al., (1993), using a hierarchic geographic information system (GIS) emphasised the importance of snow distribution, as a result of topography and wind patterns, on alpine vegetation patterns at the Niwot Long-Term Ecological Research (LTER) site in the Indian Peaks of the Colorado Front Range. In their paper, they do not specify any particular aspect of the effects of snow distribution on vegetation patterns being more important. Rather, they point to a combination of effects including water availability; soil and leaf temperature; surface microclimate; and timing and duration of growing season. They also discuss the possible effects of differential nutrient distribution (as a result of snow patches) having an effect on the vegetation patterns.

Stanton et al (1994) made a comprehensive and systematic study of the vegetation, percentage bare ground, snow-melt dates, and soil organic content, water content and pH at 217 evenly spaced sites in a large (150 x 200m) alpine snowbed on an east facing slope (3650m) on Pennsylvania Mountain in Park County, Colorado. They systematically sampled soil nutrients (total N and P; K; Ca; pH) and used canonical correspondence analysis (CCA) to process the data. They found that the snow-melt occurs in a predictable pattern and thus topography leads to snowbeds which create steep microtopographical gradients that are predictable and long-lasting. Early snow-melt sites provide the most favourable conditions: vegetation growth, organic content and nutrients, are all enhanced. Litter does not accumulate in the centre of the snow-bed because of the steepness of the slope and they found, by analysis, that 30 % of the variance of the vegetation can be explained by snow-melt. They concluded that although the snow-melt gradient is clearly the most important, other environmental factors also have a significant influence on the vegetation pattern. Stanton et al (1994: 372) suggest that some of the environmental factors "*reflect the long-term effects of historically varying snow-melt regimes*" (such as organic content and rock-cover) but others are less closely associated with the snow-melt patterns, such as soil disturbance. From this, it can be seen that the influence of snow duration on the vegetation zonation/gradients found across arctic and alpine landscapes, is more complex than previously thought but is likely to be the most important environmental factor with regard to the effects of microtopography on vegetation and soil patterns in arctic and alpine landscapes. However, it is also likely that a number of other factors have a significant influence on vegetation patterns at the microtopographical scale.

Although it has been suggested that factors, other than snow lie (and associated environmental factors), may have an important influence on small-scale vegetation distributions and soil characteristics, it should be noted that the specific effects of most environmental factors are difficult to separate from one another (e.g. Whittaker, 1985) and especially from snow cover. For example, differential vegetation patterns (and soil development) across a landscape are associated with a combination of drainage, disturbance factors, slope, aspect, underlying substrate texture and these factors can be, at least partially, linked to the degree of snow-lie and exposure at a site. Geology is independent of snow cover but is unlikely to be important at the microtopographical scale. Divergent nutrient availability across the moraines has already been shown to be an important determining factor as regards vegetation and soil patterns across microtopographical features especially in relation to snow patches (e.g. Miller, 1982; Bowman, 1992) but it is likely that differential soil-nutrient status is partly caused by the pattern of snow-melt (Stanton, 1994).

Drainage and aspect tend to be inexorably linked with snow-patches: low-lying river or stream beds and water track areas and north-facing slopes are inclined to be occupied by later-lying snow. South-facing slopes (in the Northern hemisphere) tend to have a more fluctuating cover of snow at the beginning and end of the winter season, have lower and less stable sub-nivean temperatures and have a longer growing season due to earlier snowmelt (Auerback and Halfpenny, 1991). North-facing slopes generally have deeper longer snow cover with more stable sub-nival conditions and, despite lower air temperatures, ground temperatures have been shown to be higher (Auerback and Halfpenny, 1991). The higher ground-temperatures do not necessarily have a beneficial effect on the vegetation: Sturges (1989) found that the growth of pathogenic fungi is encouraged under deep and stable snow. The higher ground-temperatures under areas of deeper snow are also thought to be responsible for snow-kill, and thus distribution patterns of lichen species, because carbon depletion occurs in warm subnival conditions when the lichens can respire but cannot photosynthesise (Benedict, 1990a). Benedict (1990b) showed that lichen growth occurs throughout the year but mostly in summer, with 93 % growth explained by differences in duration of daytime snow-free thallus moisture (moisture available for photosynthesis) suggesting carbon assimilation translates into lobe elongation. Snow-kill (caused by prolonged snow cover) therefore affects lichen species differentially, with fast-growing foliose species, such as *Xanthoparmelia spp* and *Umbilicaria spp,* being most affected by snow-cover and slow-growing crustose species, such as *Rhizocarpon spp,* being least affected by long snow duration (Benedict, 1991). The divergent abilities of different species of saxicolous lichens (i.e. *Umbilicaria* and *Rhizocarpon spp*) to tolerate snow cover has been used, in the present study, to represent differential snow cover by measurement of their respective covers at each of the sites used for vegetation description (see methods chapter for more details).

Even herbivory (which can be considered a form of disturbance) by the winter-grazing of herbivores, especially rodents, is likely to be affected by the type of snow occurring at a site which in turn is influenced by local topography and aspect (Fox, 1981; Emmanuelsson, 1984a; Auerbach and Halfpenny, 1991). Emmanuelsson (1984a) investigated the intensity of grazing along ten 50m slope profiles (with a decline of elevation of 5 m) in the Abisko area and found that the intensity of winter-grazing by rodents is higher on the steeper mid-slope positions than on low and crest positions in the sub-alpine woodland [possibly exacerbating the downslope disturbance effects of solifluction], although he did not find such an effect above the tree line. Underlying substrate could be a factor that is relatively independent of snow-patch development, although Stanton (1994) suggested that a high rock-distribution, as well as soil organic content (plus various soil nutrients) is linked to snow-melt date. This suggests that substrate texture and clast-size, as well as soil development, is also, at least partially, related to snow-distribution.

There are, however, parameters that are not so dependent on the snowmelt regime but do have a marked effect on vegetation and soil patterns, in arctic and alpine landscapes. Many of these parameters are those that influence the general vegetation pattern during the summer months as well as in the autumn when the first hard frosts occur (i.e. when the influence of snow cover and early-summer snow-melt has largely disappeared). Collectively they tend to be known as disturbance variables (Stanton, 1994). These variables cause death (or damage) to plants in established vegetation (Burrows, 1990) and/or alter the underlying substrate so as to have a limiting effect on the plants/organisms established at that site. The effect of time is also an important and relatively independent factor which will be dealt with in the next section but it must be noted that most successions result from some form of disturbance (Luken, 1990).

Some of the disturbance variables, which can be considered more-or-less independent of snowmelt regimes, are recognised as being an important influence on vegetation patterns in arctic and alpine landscapes and these include: volcanic activity (e.g. Del Moral, 1993); landslides and mudslides related to factors, other than snow-melt saturated ground, such as proximity to glacier or resulting from volcanic activity (e.g. Nitychoruk and Dzierzek, 1988; Del Moral, 1993); other soil/rock creep, or nutrient movements, associated with steep slopes (e.g. Archer, 1973; Miller, 1982; Hudson, 1988; Oechel, 1989; Stanton, 1994); differential effects of summer or autumn winds, or glacier winds, across topographical features (e.g. Vetaas. 1986); fluvial activity or surface run-off (e.g. Tisdale et al 1966; Zollitsch, 1969); some aspects of grazing and other disturbance by herbivores (e.g. MacNaughton, 1983; Leader-Williams et al., 1987; Magnússon and Magnússon, 1990, 1992); trampling and other human activities (e.g. Emmanuelsson, 1984; Oechel, 1989); frost-heave on ground which is saturated due to aspect or factors other than snow-melt (e.g. Anderson, 1947; Biswell et al., 1953; Schubert, 1970; Noble and Alexander, 1977; Goulet, 1995). For example, with regard to frost-heave, Goulet (1995) suggests that serious frost-heaving mainly occurs during periods of limited snow cover and fluctuating soil and air temperatures, especially when variations are near freezing point in the autumn and spring. For frost-heave to occur a ready supply of soil moisture is needed, therefore the damper north-facing slopes tend to suffer greater amounts of heave than the south-facing slopes (Biswell et al., 1953; Noble and Alexander, 1977), so that the occurrence of frost-heave, in this case, is linked to aspect. Schubert (1970) also found intense frost-heave to be linked to open areas of bare ground during the autumn and early spring.

Other disturbance parameters, significantly related to snow-lie, have also been recognised as having an important influence on vegetation patterns in arctic and alpine landscapes and these include: avalanches (Matthews, 1998); winter exposure and wind effects on ground not covered by snow (e.g. Billings and Bliss, 1959; Viereck, 1966; Miller, 1982; Gunnlaugsdóttir, 1985; Arnalds, 1984, 1987; Benedict, 1990a; Stanton, 1994); sub-nival winter grazing (Fox, 1981; Emmanuelsson, 1984; Auerbach and Halfpenny, 1991); and frost-heave occurring on ground saturated by snowmelt or occurring on ground blown free of snow cover (e.g. Anderson, 1947; Goulet, 1995). It can therefore be seen that the relationship between vegetation patterns and disturbance variables are likely to be complex and their relationships to other environmental parameters varies depending on many different factors. Chambers et al. (1990) divided disturbance into two categories: 1) severe disturbances, such as landsliding and mining; and 2) less severe disturbances, such as burrowing and grazing by rodents. Matthews (1998) discussed the general effects of disturbance on glacier forelands and made three categories: direct glacier disturbance; glacier-conditioned disturbance; and disturbance that is independent of glacial activity. Although it may be useful to make generalisations concerning the effects of disturbance as an entity, it seems that the variable nature of disturbance factors mitigates against broad generalisations of a "disturbance variable". It is therefore the opinion of this author that disturbance variables should be dealt with individually (e.g. frost-heave effects, winter-foraging effects of rodents, fire effects, etc.) and studies describing "disturbance" as an individual parameter should be avoided.

In summary, microtopography can only be quantified by measuring a combination of environmental factors that influence vegetation patterns and soil at a microtopographical scale. This review has shown that snow-lie, exposure and nutrient-rich water supplies are likely to be the most important microtopography-linked environmental parameters which influence the vegetation (and soil) patterns on a microtopographical gradient. However, it is also possible that a number of other parameters, such as slope, disturbance factors, substrate and aspect, are, at least partially, confounded with the microtopography-related environmental factors. Due to the difficulty and complexity, of measuring the effects of microtopography, it has only recently become possible to start investigating the relationships between the various environmental parameters by using powerful and robust multivariate analysis programmes. These relationships will be further elucidated in the following two sections which discuss previous work on vegetation successions on glacier forelands and the recent research work on microtopography and succession in a regional context.

1.3.3 Glacier foreland studies in relation to succession and soil development

Vegetation successions (both primary and secondary) have been described for a wide variety of locations including volcanic substrates, dunes, floodplains and old fields in many ecology texts,(e.g. Odum, 1965; Krebs, 1978; Kershaw and Looney, 1985; Kent and Coker, 1992). However, due to the vast quantity of literature pertaining to succession, it is not within the scope of this study to describe successions other than primary successions on glacier forelands, even though it is likely that primary successions at other types of location, such as on volcanic islands (e.g. Friðriksson and Magnússon, 1992; Whittaker and Bush, 1993; Magnússon et al., 1996), may be of relevance to the present study. This section will review a cross section of successional studies which have been performed on glacier forelands **outside** the Jotunheim and Jostedalsbreen regions. Studies that have been carried out in the Jotunheim and Jostedalsbreen regions are described in the following section (1.4). The first part of the present section describes primary succession studies on glacier forelands that have not taken microtopography into consideration (i.e. the vast majority of glacier foreland studies). The second part of this section will describe those few studies that have, at least, attempted to take microtopography into account. This section has two purposes: the first is to describe the main findings of previous research work on vegetation successions and some aspects of soil development, on glacier forelands; the second is to discuss some of the failings of much of the previous work and show how studies on the effects of microtopography, on plant succession and soil chronosequences (and vegetation and soil patterns in general), can improve our understanding of vegetation succession processes, thus justifying the present study. For a more complete review of succession, and other ecological processes on glacier forelands, see Matthews (1992) or Burrows (1990).

Glacier forelands have long been used to study vegetation succession and soil chronosequences (e.g. Cooper, 1923a,b,c; Friedel, 1938; Lutz, 1930). However, the majority of glacier foreland studies have researched the vegetation succession (sometimes including a number of soil variables) or soil development on a sequence of different aged and supposedly topographically and vegetationally homogenous, plots (e.g. Crocker and Major, 1955; Crocker and Dickson, 1957; Stork, 1963; Persson, 1964; Decker, 1966; Viereck, 1966; Lawrence et al., 1967; Ugolini, 1968; Birks, 1980; Jacobson and Birks, 1980; Sommerville et al., 1982; Bormann and Sidle, 1990; Alexander and Burt, 1996; Burt and Alexander, 1996). These studies have been concerned with researching the development of different assemblage sequences across ground of different age and they have generally used so-called homogenous plots to do so. It is likely that this has been done because the field season is short and thus it is only possible to obtain a restricted number of samples in one season (e.g. Persson, 1964). These researchers assumed that they sampled from the most prevalent vegetation at each stage and so presumed that their sampling methodologies were sufficient to explain the vegetation changes. Generally these studies emphasise the importance of biotic influences on succession and only measured parameters (mainly soil characteristics) associated with vegetation development.

Cooper (1923b,c, 1931, 1939) divided the vegetation into three main stages: pioneer; willow-alder thicket; spruce forest. He emphasised that the stages were not discrete but occurred on a gradually changing gradient, but interestingly the patchiness or heterogeneity of the landscape was not emphasised. The original number of stages, which were defined by Cooper, were expanded and re-defined in more detail (Decker, 1966; Ugolini, 1968; Reiners et al., 1971) and were used as a base for later research into vegetation succession and soil development at Glacier Bay (e.g. Lawrence et al., 1967; Worley, 1973; Borman and Sidle, 1990; Chapin et al., 1994). The gradually changing, and heterogeneous, nature of the vegetation was ignored so that the presentation of the results gives an impression of relatively discrete plant/soil units within each successional stage, whether or not that was the intention (e.g. Crocker and Major, 1955; Decker, 1966; Mirskey, 1966; Ugolini, 1966; Lawrence et al., 1967; Reiners et al., 1971; Worley, 1973). Crocker and Major (1955: 432) studied soil development, in relation to surface age and Cooper's vegetation stages, at Glacier Bay using a highly subjective method of site choice: "*The main difficulty in sample site selection was to find sufficiently fine till to permit taking density samples, at the same time keeping variability of the minor relief factors and parent material to a minimum, ... between site position and vegetation units*". They emphasised the important influence of plants on the accumulation of nitrogen in soil, especially under alder and willow, but also under *Dryas drummondii* and *Shepherdia canadensis*, all of which have associated nitrogen fixers. They found especially large increases in nitrogen under alder (in relation to the young terrain) in the surface horizons, accompanied by a significant decline in pH and fine earth with similar, but less significant results associated with soils found under the other species. They found that nitrogen declines in the surface horizons under spruce and that organic carbon and the C:N ratio rises throughout the sequence. Crocker and Dickson (1957:173) found fairly similar trends, although the magnitude of some of the properties, especially carbon, is significantly different and again their sampling technique was highly subjective "*Considerable time was spent in selecting the sites most free of coarse debris from amongst those representative of specific time states*". They found the variability in the terrain "disappointing" which suggests that they had no intention to explore the effects of variability in environment on soil patterns.

During the sixties the glacier foreland studies, in general, followed a similar sampling methodology (i.e. not taking account of site heterogeneity) and the results of these studies showed fairly similar trends with regard to soil development but the vegetation development did show some significant differences. Palmer and Miller (1961) used a relatively unsystematic methodology to investigate vegetation succession in front of the Rotmoos glacier in Austria. They found the order of plant-type colonisation is angiosperm → mosses → lichens which questions the generally accepted order of primitive humus-building cryptogams preceding humus-requiring angiosperms (e.g. Clements, 1916). They found that "*some species showed a strong preference for certain stretches of moraine. No variation of physical habitat was found to account for this*" (Palmer and Miller, 1961: 83). Their last statement is remarkable since they did not actually measure any environmental parameters. Stork (1963), studying vegetation patterns in Northern Sweden found that the migration of species takes place in a series of sudden changes: one "swarm" of species replacing the former. She also found that cryptogams precede vascular plants, thus contradicting Palmer and Miller. Persson (1964) suggested that it is soil conditions (abiotically or biotically controlled) and not differential dispersal ability that causes succession to occur. His results showed moss and vascular species precede lichen species and furthermore, he discussed, and emphasised, the diversity of results between various authors with regard to the rate of colonisation shown by various species. Viereck (1966) studied vegetation succession on gravel outwash of the Muldrow Glacier river terraces, Alaska. Although this study was not specifically a glacier foreland study, the physical environment of the study area is comparable to the foreland studies. He concluded that initial invasion is by light-seeded, easily dispersed species and that mosses are not important colonisers. He found that within each of the stands, small microtopographical features, slightly higher than the surrounding ground, comprise assemblages of earlier colonisers. However, the heterogeneity of each stand was not investigated and he does not report if such features were included within the data sets.

Lawrence et al (1967) in a study at Glacier Bay, investigated the role of *Dryas drummondii* in vegetation development and concluded that *Dryas* is of major importance in speeding up succession and increasing later forest productivity. They based their assertions on previous research which had found nitrogen availability to be the main driving force of succession and described the "depauperate" nature of most pioneers which contrasted strikingly with the healthy appearance of most of the legumes. They also suggested that *Dryas drummondii* "*aids survival and stimulates growth of woody plants, such as cotton woods and willows that have no symbiotic nitrogen-fixing micro-organisms*" (Lawrence et al, 1967: 810), a statement which has been contradicted by others (e.g. Helm et al., 1996). Lawrence et al reported that *Dryas drummondii* does not grow on exposed sites or areas of high acidity or moisture and reported an investigation which showed that cottonwood grew better with *Dryas drummondii* than without - it could have been other factors, such as microenvironment, which caused the difference in growth but they do not say whether or not microenvironmental factors, for each group of cottonwoods, were recorded. On the whole many of the conclusions from this study were highly subjective and the rationale behind the research would have been much improved by considering the effect of topographical heterogeneity.

Over the last 25 years there has been a considerable variety of studies carried out on glacier forelands with regard to soil chronosequence and vegetation succession studies (see Matthews, 1992). However, many of the studies have continued to use so-called homogeneous plots for their study sites. Worley (1973), researching at Glacier Bay investigated the pioneer "black crust" phenomenon but does not describe his sampling methodology. He found that the crust develops separately towards a vegetation cover comprising clumps of *Dryas drummondii* and *Salix spp* and eventually may be overgrown by these species. The crust is complex comprising many different components, including both vascular plants and cryptogams as well as a variety of microscopic flora and fauna. He distinguished a number of different types of mat, according to component species, and suggested that the mat is tough and reduces erosion by breaking the force of rainfall. The mat holds a diversity of reproductive stages and he maintained that microtopography appears to affect the crust distribution more than time, although he did not show this quantitatively. He concluded that the mat can provide a suitable environment for germination. Scott (1974b) used a systematic sampling methodology to investigate succession on moraines of the Frederika Glacier, Alaska. He found that the sequence of vegetation is very similar to that found at Glacier Bay but reported major differences in the role of *Alnus crispa* and *Dryas drummondii* within the succession and also found the duration of each stage to be highly variable. He suggests that the role of nitrogen fixation is assumed by *Dryas octopetala* and *Sheperdia canadensis* (both associated with symbiotic bacteria) as well as a number of leguminous species.

Jacobson and Birks (1980), studying succession in front of the Klutlan Glacier, Yukon Territory, Canada, found a "strikingly" similar soil chronosequence to that at Glacier Bay but found that the foliage of species at different stages of the succession does not show signs (either actual nor visual) of nitrogen deficiency as suggested by researchers at Glacier Bay (e.g. Lawrence et al., 1967). Jacobson and Birks suggest that the pedogenic differences are possibly caused by regional differences in vegetation growth rates: the Klutlan glacier foreland is colder and thus growth rates (and also nitrogen requirements) are lower. They conclude that the similarities in the results between the two locations suggest that generalisations can be made about soil development in relation to vegetation development in subarctic ecosystems. Birks (1980) investigated the vegetation succession on ice-cored moraines on the Klutlan Glacier foreland, Yukon Territory, Canada, and described a sequence of vegetation evolving from herbs and low shrubs to taller shrubs and trees, and from acrocarpous mosses to pleurocarpous mosses to lichens. The results of his study differed from the Glacier Bay studies in that mosses are not important in the early phases on the Klutlan Glacier foreland as they are at Glacier Bay, nor is *Alnus crispa* important in the succession as it is at Glacier Bay, nor are the dominant mature tree species the same at the two locations. A striking similarity, however, is the dominance of *Dryas drummondii* on the early ground at both locations.

Sommerville et al (1982) made an interesting study to compare the succession of vegetation on lateral moraine crests across a low alpine sequence (1100m) and a mid-alpine sequence (1400m) on the Dart Glacier foreland, New Zealand. They found that the course of succession at the two altitudes was different and the rate of succession was faster at the lower altitude. They also found that the mature (climax) vegetation was different at the two sites. Colour differentiation within the soil profile and podzolisation was more obvious at the lower altitude, suggesting soil development was faster at the lower altitude. Fitter and Parsons (1987), studying nitrogen and phosphorus availability on the Athabaska Glacier foreland, Alberta, showed results that tended to disagree with Crocker and Major's (1955) research. They found that the soil changes are not rapid and that initial levels of phosphorous and nitrogen in the leaves of *Dryas drummondii* decline before increasing on the older ground (disagreeing with both Crocker and Major as well as Jacobson and Birks (1980). Furthermore, the nodules found on *D. drummondii* by Crocker and Major were not found by Fitter and Parsons; rather they found ectomychorrhizal sheaths on all plants. They suggested that *D. drummondii* may be growing in preferential sites which may partly explain why later colonisers appear to grow better where *D. drummondii* occurs. They concluded that the factors that control nutrient availability are more complex than previously thought.

Frenot et al (1995) made a study of soil development on a highly exposed glacier foreland on the Kerguelen Islands in the Subantarctic. Their study showed that soil development, for the first 200 years, appeared to be largely controlled by abiotic factors such as mechanical weathering, frost-heave and particle translocation. This study is interesting in that it shows the factors that change within the soil with very little influence from vegetation (percentage soil carbon only increased from 0.02 % to 8.20 % over 200 years): pH decreased at surface from 7.6 (surface-age 2 yrs) to 5.1 (surface-age, 200 yrs); leaching of fines occurs from 15.5 % (surface-age, 2 yrs) to 4.5 % (surface-age, 200 yrs); coarse sand increases from 51.7 % (surface-age, 2 yrs) to 68.5 % (surface-age, 200 yrs); base saturation decreased from 100.6 % (surface-age 2 yrs) to 65.3 % (surface-age, 200 yrs). They suggest that once vegetation starts to establish it stabilises the substrate and increases nutrient and water availability for later colonists. They further suggest that the slow development of vegetation (first 200 years) is due to low soil nutrients, as shown by the more rapid vegetation development in areas occupied by sea birds and elephant seals although the latter statement was made subjectively and no comment was made on the microtopography of the landscape occupied by the fauna. They emphasise the role of nutrients and vegetation in soil development, in general, and yet they made no attempt to compare areas of differing microtopography - which, in the opinion of this researcher, was a conspicuous omission.

Alexander and Burt (1996) and Burt and Alexander (1996), following on from Crocker and Dickson (1957), studied soil development on crest or shoulder positions on 6 moraines of the Mendenhall Glacier, southeast Alaska. The purpose of their study was to investigate the soil sequences previously studied by Crocker and Dickson using modern techniques. They mentioned they also wanted to investigate soil differences on ground of similar age. However, they took, at most, two samples within any age-range and so they cannot claim to have sampled sufficiently to investigate within-age-range variability. The soil development was described but no comparison was made between their study and the results of the previous work (i.e. Crocker and Dickson) nor was any mention made of the effects of microtopography on soil development. However, by comparing their results with those of the previous results it can be seen their results are similar to those of the previous work. Many authors recommend that allogenic factors and landscape heterogeneity should be taken into account and a more generalised approach to the understanding of succession should be taken (e.g. Drury and Nisbet, 1973; Finegan, 1984; Gray, 1987; Miles and Walton, 1993; Chapin, 1996). Thus a more complete picture of soil or vegetation development over time can be built up. Despite this, some recent researchers (e.g. Frenot et al, 1995; Alexander and Burt, 1996; Burt and Alexander, 1996) have used approaches that mirror those developed in the 1950s. Such methods do not adequately consider the problems of landscape heterogeneity and pseudoreplication (*sensu*: Hurlbert, 1984), where so-called homogeneous landscape types of different age are chosen for investigation.

From the above cross-section of work on glacier forelands it can be seen that a wide variety of vegetation successions have been described and it could be argued that the divergence of results is partly caused by the diversity of sampling methods, the diversity of location and also by the lack of attention paid to the heterogeneity of the various ages of ground under study. Furthermore, some of these studies, especially those carried out at Glacier Bay (e.g. Cooper, 1923a,b,c; 1931, 1939; Crocker and Major, 1955; Decker, 1966; Mirskey, 1966; Ugolini, 1966; Lawrence et al., 1967; Reiners et al., 1971; Worley, 1973) are so embedded in the literature that in many ecology texts examples of glacier foreland successions are represented as being a relatively simple progression of successional stages (e.g. Kershaw and Looney, 1985; Burrows, 1990). Burrows (1990) admits that the successional schemes at Glacier Bay are simplistic and that "*the vegetation at any locality at any time during the developmental phases is patchy*" but he did not criticise the sampling methodology. However, simplistic sampling schemes have recently been criticised (e.g. Sondheim and Standish, 1983; Hurlbert, 1984; Bormann and Sidle, 1990; Chapin et al 1994), and an increasing body of literature emphasise the complexity of glacier foreland succession (e.g. Jochimsen, 1963, 1970; Zollitsch, 1969; Elven, 1975, 1978; Whittaker, 1985, 1987, 1989; Matthews, 1976, 1978b, 1979a,b,c,d, 1992; Matthews and Whittaker, 1987; Schubiger-Bossard, 1988; Crouch, 1992, 1993; Helm and Allen, 1995).

Sondheim and Standish (1983: 502), maintain that "*Of the large number of chronosequence studies ... none have had an experimental design allowing for an assessment of the variability of properties. Rather they all appear to have concentrated on studying typical or modal individuals*". In their study at the Robson Glacier, they criticised the lack of replicates in the previous work and sought to investigate the major soil-forming processes and discover if variability in parent material reduces the validity of chronofunctions. They studied the soil chronosequence by systematically placing 10 pits along the crests of six moraines "*where the microtopography was relatively smooth*". They concluded that organic carbon, nitrogen and pH are associated with depth of soil and moraine age (and thus related to vegetation) but they found that soil mineral content (calcium carbonate, aluminium and iron) and soil texture is independent of age and soil depth and so was influenced by abiotic factors such as the variability within parent material. Bormann and Sidle (1990) and Chapin et al., (1994), in studies at Glacier Bay, also recognised some of the flaws in the sampling procedure of the previous work and also dealt with the problem of pseudoreplication (*sensu*: Hurlbert, 1984) by using ten widely-spaced sites within a vegetation zone (instead of one). Bormann and Sidle found that their results were very similar to those of previous researchers but Chapin et al., (1994) suggested that the results from Crocker and Major were probably over-estimates.

Helm and Allen (1995) investigated vegetation chronosequence near Exit Glacier, Alaska, USA using a stratified sampling design avoiding "edge effects" of vegetation type boundaries or stream beds but taking enough samples within each stand to avoid pseudoreplication. Vegetation transects and soil sampling were randomly located within each stand. They found that their succession agrees with Matthews' (1992) geoecological model suggesting that physical processes are important in the early stages of succession and biological processes become more important later. Their successional sequence differed to Cooper's (1923b.c) results at Glacier Bay in that *Populus balsamifera* is a more common coloniser than *Epilobium latifolium* and *Dryas drummondii*, possibly due to Cooper having sampled on the outwash plain and also on nearby hillslopes. The succession is also shown to be slower by Helm and Allen. The authors suggest that differences in the results of successional work in the region show that there is a need to understand local processes and species availability in order to interpret succession. (i.e. microtopographical effects should be investigated). Helm et al (1996) used the seven successional stages described by Helm and Allen (1995) to sample the mychorrhizal chronosequence from four individuals of the dominant woody species in each stage at Exit Glacier, Alaska. They found consistent trends with regard to the types of mycorrhiza found on the roots of the species under study: only ectomycorrhizae types, not arbuscular mycorrhizae, were found on the woody spp; arbuscular mycorrhizae were negligible in the chronosequence and ectomycorrhizae can develop within weeks of germination of seedling. They concluded that the fungi are associated with particular plant species and that the infections on any plant host may change with time. Diversity of mycorrhizal infection increases with time. Their study emphasises the complexity of successional processes on glacier forelands. All five of these studies, however, used samples either from vegetation zones, defined by previous workers, and/or they sampled from topographically similar sites, and thus they did not attempt to take microtopography (+ associated environmental factors) into account.

Despite the many differences, a number of important general features are shared between the various glacier foreland studies that have been outlined above:

1. Soil characteristics generally follow a similar pattern of development on ground of increasing age within a related climatic regime.

2. There is a clear succession of different plant assemblages across each of the forelands, usually progressing from a dominance of herb, low shrub and moss species through to taller shrub, lichen and tree species.
3. The vegetation change is continuous, but can develop gradually or in steps.
4. The availability of soil nutrients appears to play an important role in succession on glacier forelands.
5. The vegetation appears to be an important influence on the rate and course of soil development.
6. Climate (reflected, for example, in altitude or continentality) appears to play a significant role in determining the rate and course of succession.

It might therefore be argued that the successions and soil chronosequences described by the above studies provide, at least, an approximate representation of the successions and soil chronosequences found in nature. However, a major drawback of the approach used in these studies is that they are unable to show the variety that pathways of succession may occur across a landscape, nor are they able to consider seriously the course that these successions take in terms of divergence or convergence of assemblages (*sensu*: Matthews, 1979d). The variation in the results, from the above work, suggests that if more research took account of environmental heterogeneity, as well as sample variability, it would do much to improve our understanding of succession on glacier forelands. The few studies that have attempted this will be outlined below.

Tisdale et al., (1966) carried out a systematic study following the usual methodology (i.e. using the same slope positions) on three moraines on the Robson Glacier Foreland, British Columbia. They found a similar successional sequence to Cooper (1923b,c) and Lawrence (1967) although rapid accumulation of nitrogen was not found in the vegetation samples taken from sites of increasing age. Within the same paper, however, they also described a small study of the relative growth and vigour of *Picea engelmannii* at different positions across one of the moraines under study (73 years exposure). They found considerable differences in growth-rate of *Picea* on the three microtopographical positions with the least on the crest and the greatest on the north-facing distal slope and they suggested "*snow depth and duration, excess soil moisture, and surface runoff causing frequent disturbance to vegetation and soils in early summer may be involved*" (Tisdale et al, 1966: 520). Jochimsen (1963, 1970) working on the Rotmoosferners and Gaisbergferners glacier forelands in Austria, used maps and permanent quadrats to study vegetation successions on a variety of site-types within particular age ranges. She was able to show that the major trend is a divergence of assemblages followed by convergence. She concluded that soil texture appears to be responsible for the patchiness of pioneer assemblages but that moisture is responsible for the wide variety of successional pathways found across the forelands. Once full vegetation cover has been reached, she suggested that the effect of environmental factors, such as moisture, appears to have a less significant influence on vegetation patterns.

Zollitsch (1969) also showed the successional pathways, on the Pasterze and Ödenwinkelkees glaciers in Switzerland, were not simple except at the most environmentally stressed sites. He showed a rapid and strong divergence followed by slow convergence of assemblages. He found four pathways (of increasingly moist and sheltered sites) across nine age zones (5 to 6200 yrs). The pathways included an exposed, dry site succession comprising an exposed pioneer (*Dryas octopetala - Salix*) assemblage → lichen heath (*Loiseleuria procumbens - Cetraria*) assemblage and a sheltered, moist site succession comprising a moss-rich herbaceous assem → *Salix* assemblage → *Rhododendron* assemblage. In early stages, on wet ground, phanerogams were found to be more diverse than cryptogams. Vegetation cover increased more quickly on wetter, sheltered sites. The many successional pathways were considered to be dependent on moisture, disturbance (especially surface runoff and fluvial) and exposure. As the glacier retreats a strong directional environmental change occurs as the substrate dries, stabilises and the influence of the glacier wind decreases.

Ward (1970) made a simple, and rather subjective, study of plant colonisation across annual moraines on the foreland of the eastern lobe, Austre Okstindbreen, Norway. He randomly placed thirty 50 cm^2 quadrats across 5 moraines and so obtained a general picture of succession across the moraines. He found no evidence to suggest that cryptogams colonise first or that aspect of the moraine slopes affects colonisation. He also found that early colonisers generally grow in the shelter of large stones or boulders. Another simple, but useful, study of the microenvironmental influences on succession was carried out by Bateson (1970) on the Blåisen glacier foreland, S. Norway. Vegetation and various environmental parameters (temperature, humidity, pH, clast size, lichenometry) were sampled at 50m intervals with a 0.5 m^2 quadrat along a 1100m transect. He carried out a side-study to investigate differences in temperature across a ridge and also to discover differences in windspeeds at ground level and at 2 m above the surface. He distinguished similar zones of succession to Fægri (1933) and Stork (1963) but disputed their work in that succession proceeds as a number of steps (corresponding with the recession of the glacier) and that cryptogams are not necessarily the first colonisers. He also put forward that humus is not necessary for colonisation by vascular plants supporting Palmer and Miller's (1961) hypothesis. He found that there are significant temperature differences across a ridge and that temperature, and humidity, increase across the foreland with increasing age of substrate. Interestingly, he found that pH values do not show such a straightforward decline as previous studies have found, but, rather, there is a slight general decrease in pH with large fluctuations between sites of similar age. Bateson (1970) concluded that although the time element was clearly the most important influence on vegetation patterns across the foreland, it was also clear that topography-determined environmental factors, especially exposure to wind, snowlie and temperature, also have a marked effect. Archer (1973) investigated soil and vegetation of the lateral moraine at the Tasman Glacier, New Zealand. He was particularly interested in the relationship between vegetation pattern and the degree of disturbance on rectilinear terraces and lobate solifluction lobes on a moraine > 230 years. He found there is a distinct zonation of plants, with a general absence of vegetation on the highly disturbed tread surface (the relatively flat upper surface) and thus concluded that disturbance has a significant effect on vegetation pattern.

Elven (1975) investigated plant communities on recently deglaciated moraines at Hardangerjøkulen and Omnesbreen S Norway by placing the sampling quadrats on or between moraine ridges. The earliest vegetation was found to be open forb and grass pioneer, which was independent of position, snow cover and soil structures. However, on older ground, microtopography appeared to have a marked effect with no profile development and a marked decrease of pH was found on exposed ridges. The mid-alpine (more exposed), ridge tops were found to have cushion vegetation and a higher pH and poorer soil development. The early pioneer assemblages tended to occur around "flush" zones (where springs with a high mineral content emerge from the ground) and also early extreme *Cerastium cerastoides* snowbed assemblages. His results showed that there is a difference between successional-types found across low alpine and mid-alpine glacier forelands and the successions are influenced by both time and microtopography. He emphasised the role of snow and exposure with regard to vegetation patterns and concluded that the vegetation is not fully developed after 220 years of succession. Elven (1978) used a systematic sampling methodology to further investigate vegetation patterns on moraine crests, mid-slopes and inter-moraine flats at the glacier Hardangerjøkulen, Finse, South Norway. He used association analysis to analyse the vegetation data and found that time is the primary influence on vegetation patterns. He further suggested that microtopography also has an important effect on vegetation patterns (mainly interpreted as a snow-cover gradient) but, on pioneer sites, snow is a minor influence with age and sedimentation being more significant. He concludes that the effect of the snow-cover gradient is complex: depth and duration of snow being associated with edaphic, microclimate and hydrological factors.

Elven and Ryvarden (1975) investigated the dispersal and primary establishment of vegetation on the Hardangerjøkulen foreland at Finse, Norway. They found that as succession proceeds the effect of position becomes more noticeable. There is a constant increase of species until 50 yrs, when the more competitive dominate the others so that first invaders only occur on disturbed patches which causes an increase in the diversity of species found at a location which is dependent on microtopography. As succession proceeds further, the diversity tends to fall. The number of diaspores increase away from glacier and all species found close to the glacier are local. If species with representatives closer than 5 m, are excluded, only 13 % of diaspores are left and this suggests that the first individuals act as important centre for establishment. They noted a divergence of assemblage types, with a pioneer phase of phanerogams developing to two intermediate assemblages, dependent on snow cover: an *Empetrum hermaphroditum* lichen heath assemblage on ridge crests; a *Carex spp* - *Deschampsia alpina* wet snow-bed assemblage in sheltered hollows at the bases of ridges. *Salix herbacea* is also important but shows no preference at the earlier stage but becomes a snowbed species after 100 yrs when competition has a stronger influence. The divergence of the assemblages, according to microtopography, continues onto the oldest terrain. Another interesting finding was that smooth, heavy diaspores were found to have dispersed several hundred meters so that the morphological classification, that all pioneer plants have small light seeds, may be misleading and this is true for the longest distances travelled for seeds belonging to various species. These findings agree with Magnusson (1994b) who suggested that many of the heavy diaspores are transported relatively easily on to bare sites and that they roll along the ground surface when blown by strong winds. Rydin and Borgegård (1991) also suggest pioneer seeds are not necessarily smaller than mid-successional seeds and Grubb (1987) suggested that pioneers colonising unstable, environmentally-stressed habitats are likely to have large seeds and be long-lived.

Schubiger-Bossard (1988) produced a detailed vegetation map of the Rhone glacier foreland, Switzerland, and a large number of assemblages were defined. He found that avalanches and grazing are an important influence on the vegetation patterns on the distal part of foreland. He did not find a convergence or divergence of assemblages but found a parallel succession, for 350 yrs, determined by microenvironment (especially soil texture and moisture). Stöcklin and Bäumler, (1996) carried out a systematic investigation of seed rain, seedling establishment and clonal growth strategies on pioneer and intermediate-aged ground on the Morteratsh glacier foreland, Swiss Alps. They analysed seed-rain composition; establishment and mortality of seeds, on a chronosequence, with special regard to dispersal and growth strategies. They also investigated seedling mortality and vigour on four pioneer sites comprising different moisture conditions and age (0 to 45 years). The frequency of diaspores occurring in the different successional stages was related to dispersal method: pioneers were shown to have plenty of diaspores well-adapted to wind-dispersal. They found that pioneer seeds have a high germination success as long as there is sufficient moisture and only the pioneer seeds could tolerate the cool and moist conditions of the ground near the glacier. They suggested that the availability of safe sites (with sufficient moisture) becomes more important with increasing age of ground and drier conditions. They also found that those early colonisers that manage to grow on older ground are able to spread clonally - e.g. *Cerastium peduculatum, Epilobium fleischeri*. They concluded that clonal growth and seedling establishment are thus complementary mechanisms in primary succession on glacier forelands.

In summary, although a considerable number of studies have investigated the vegetation on moraines, surprisingly few have chosen to study the specific effects of microtopography (and associated environmental parameters) on vegetation succession and/or soil chronosequences. However, as can be seen from the small selection of studies that have begun to investigate the effects of microtopography on succession, a considerable amount of useful information has been obtained. Despite the differences in methodology and location these microtopographical studies have come to very similar conclusions:

1. Successions on glacier forelands are more complex than previously thought. There is considerable variability in the results of previous successional studies, even with regard to the colonisation and establishment of early colonisers on the young terrain (cf. Grubb, 1987).

2. The successions involve several pathways that are mainly influenced by time but are also significantly affected by environmental factors, including microtopography through snowlie, exposure and disturbance in particular.
3. The effect of microtopography appears to be least on the youngest ground with little vegetation cover, late-lying snow and a generally high soil moisture content. The effect of microtopography on vegetation pattern may be most significant on ground of intermediate age where the vegetation cover is not complete.
4. The pathways are likely to be simplest in environmentally stressed locations.
5. Both divergence and convergence and parallel succession of assemblage types are involved in the course of succession across a glacier foreland. Convergence to one mature assemblage does not appear to occur.

1.4 Regional studies, with special reference to the influence of microtopography on succession and soil development.

1.4.1 Microtopography and succession

Only one regional study (Vetaas, 1986, 1994), has specifically investigated the relative influence of microtopography on vegetation succession, and soil development, at Bødalsbreen. However, a considerable number of other studies have shown that microtopography has a distinct influence on soil chronosequences, and/or vegetation successions. Such recent studies include: development of polygons on young terrain (Ballantyne and Matthews, 1983); vegetation and environmental patterns at Storbreen (Crouch, 1992, 1993); size variation of selected saxicolous lichens on moraine slopes (Haines-Young, 1983, 1985); effect of snow cover and moisture on selected saxicolous lichens (Innes, 1985); Vegetation patterns and meso-scale environmental factors (Matthews, 1976, 1978a,b, 1979a,b,c,d,); covering all aspects of vegetation, soil and environmental processes on glacier forelands (Matthews, 1992); variability of soil on a pre-Boreal ridge crest (McCarroll and Ware, 1989); soil chronosequences on moraine ridges at four glacier forelands (Mellor, 1985, 1987); climatic influences on soil chronosequences at 18 forelands (Messer, 1988, 1989); effect of microtopography on soil and vegetation development on a subalpine foreland (Vetaas, 1986, 1994); vascular plant succession and population processes with reference to environmental patterns at Storbreen (Whittaker, 1985; 1987, 1989, 1991, 1993). Most of these studies have been reviewed in detail in Matthews (1992) and so only those aspects relevant to the present study will be covered in this section. The main intention of this review is to show how the previous work has provided the necessary background, both methodological and theoretical, for the present study.

Matthews (1974, 1975, 1976, 1977) developed a reliable lichenometric methodology to establish an areal chronology at Storbreen and his methodology has been used to establish areal chronologies for all the glacier forelands (Matthews and Bickerton, unpublished data) used in this and many of the regional studies outlined in this thesis (e.g. Whittaker, 1985; Mellor, 1985; Messer, 1988; Crouch, 1992). He developed a geoecological approach (*sensu*: Matthews, 1992) to sampling. This approach ensures an objective, general purpose description of the vegetation without presupposing factors responsible for the vegetation patterns which would take the heterogeneity of the landscape, including altitude, into consideration. He also tested many different types of statistical analysis techniques and used computer maps, as well as different sampling sizes, in order to ensure that any particular technique, or sample size, was not causing bias within the vegetation data sets (Matthews, 1976, 1978a,b; 1979a,b,c; 1987; 1992). A three-level nested sampling scheme was used on 638 permanent sites and the pattern of sites followed a systematically stratified random design. The results show that vegetation colonisation takes place as a series of waves: pioneer being replaced by snowbed at high altitude and heath at low altitude. He also found that aspect has a considerable influence on successional pathways, at the mesoscale level, with northfacing slopes comprising snowbed assemblages at lower altitudes. He suggested that the spatial discontinuity at the foreland boundary (i.e. the 1750 moraine) indicates that succession is still in progress after 250 years.

Because many species are found over a wide range of sites he recommended that few species can be used as indicators of surface age but he added that they may be used within a certain environmental range. He found that the pioneer assemblage is fairly tight (i.e. quadrats comprised similar species to each other) and that the sequence diverges to several distinct assemblages. He also found that the succession is simpler for the higher altitude sequence (mid-alpine), whereas the lower altitude sequence (low alpine) proceeds via a relatively large number of stages to a greater variety of alternative mature assemblages. The assemblages that Matthews described do not indicate a simple time sequence, but show that the foreland vegetation is the result of a complex interaction of time and landscape heterogeneity. Differences in the results, derived from the various analysis techniques, indicate that assemblage boundaries are not "natural" and there is considerable overlap between the groups causing changes between assemblages to be a gradient rather than distinct zones of assemblage types. He pointed out three major faults with the previous research on vegetation succession on glacier forelands: 1) dating techniques have usually been inaccurate and incomplete 2) landscape heterogeneity has been ignored 3) objective and quantitative methods have been little used, either in field work or analysis. The review of the previous literature by the present author (section 1.3.1-3.) confirms these thoughts entirely. Matthews (1979a: 41) concluded: "*Microtopography, though important at all levels, becomes an increasingly dominant feature of the overall pattern of types as the resolution-level is refined. The results support the general principles that: 1. the spatial structure of the vegetation landscape is jointly dependent on time and environment, and 2. the relative importance of time and environment varies at different scales. There is therefore a need for greater emphasis on the influence of space and environment on vegetation pattern and succession.*".

With regard to the use of a wide variety of statistical techniques, Matthews concludes (1979b) that his results show that most techniques applied individually give at worst a distorted view and at best a limited view of reality. This is due to each technique being concerned with different aspects of the data set. He suggests, therefore, that it is wise to use different techniques together and that difficulties can also be removed by reference to single species distribution maps in order to support inferences drawn from multivariate analysis. His suggestions have been followed through, within the present thesis, by using both a classification and an ordination technique as well as providing distribution charts of all the species (and environmental parameters) across the moraines on each of the forelands. His findings will be used to provide a point of reference with regard to the general succession of vascular plant species at two altitudes and his work, which represents one of the most complete descriptions of vascular plant succession across any glacier foreland, will be discussed and compared with results of the present study in the concluding chapter.

Whittaker (1985, 1987, 1989, 1991, 1993) followed on from the previous work by using 108 sites (4 m^2) sampled from Matthews' 638 permanent sites (16 m^2) on the Storbreen foreland. Whittaker's work is particularly important with regard to the present study because he especially concentrated on the effect of microscale environmental patterns on vegetation (vascular plants) and some of his methodology has been adopted for use within the present thesis (see chapter (2)). Many of his conclusions, especially with regard to the analysis techniques as well as the relationships found between the vegetation patterns and environmental factors, have also had an influence on the structure of the present study. He suggested that studies of primary succession require knowledge of the relationships among and between environmental parameters and that although the relationships are complex, multivariate analysis can be used to elucidate the relationships. He therefore tested a number of multivariate analysis techniques in order to ascertain which technique would give the most useful and accessible results. The techniques include non-metric multidimensional scaling (NMDS) and detrended correspondence analysis (DCA). The results of these tests have helped to decide the analytical techniques to be used within the present study.

Whittaker's (1985, 1987) results show that the environmental parameters can be grouped to form so-called factor complexes: the "*Terrain-age factor complex*" (time) and the "*Microtopographic factor complex*" (microtopography). The most important influence across the foreland is time, with the vegetation sequence on DCA ordination axis 1 following an age sequence from the oldest ground (heath) species (e.g. *Betula nana, Vaccinium uliginosum, Empetrum nigrum*) found at the positive end of axis 1 to the pioneer species (e.g. *Saxifraga cespitosa, Cerastium spp, Deschampsia alpina*) at the negative end of axis 1. On DCA axis 2, the species separated according to microtopography: the species preferring moist and sheltered sites (e.g. *Oxyria digyna, Saxifraga rivularis, Viola palustris, Sedum rosea*) at the positive end of axis 2; and those found on exposed sites (*Dryas octopetala, Lycopodium spp, Phyllodoce caerula, Silene acaulis, Trisetum spicatum*) found at the negative end of axis 2. Non-parametric correlation shows strong relationships between members of the "*Terrain-age factor complex*" and also between members of the "*Microtopographic factor complex*" (Whittaker, 1989). From the results of his population study on six pioneer species, Whittaker (1993) found that both allogenic and autogenic factors cause succession and he commented that the relative influence of these factors is difficult to separate. He suggested that the influence of autogenic factors (such as competition) on vegetation patterns and succession may be more significant in later successional phases but the role of disturbance may be more important on the young terrain. His results suggest that pioneers are short-lived species with easily dispersed seed and such species are only capable of colonising disturbed patches on the older ground. He further suggested that pioneers require high levels of nutrients and low levels of interference. He concluded: *"The successional divergence in vegetation composition identified at Storbreen (Matthews, 1979c,d) is thus of necessity underpinned by an increased sensitivity of species distribution to microsite variation, an increased range of growth forms and a diversification in patterns of resource utilisation on old ground in comparison to the pioneer zone"* (Whittaker, 1993: 134).

In a review by Matthews and Whittaker (1987) of their work at Storbreen, they showed that similarities in population patterns suggest that there are groups of species (assemblages) which have a common response to autogenic and allogenic factors and thus a "community" approach to the study of succession can be justified. However, they emphasised that glacier foreland successions are complex, with the influence of various environmental factors changing not only with altitude but also with successional stage. They added that the succession at Storbreen shows divergence and has also been shown to display regression on certain parts of the foreland so that investigations of population traits may be useful to explain the relationship between members of the various assemblages. They suggested that it is imperative that research into vegetation succession and soil chronosequences should involve the study of both allogenic and autogenic factors and they concluded that the geoecological approach has been successful in this respect.

Crouch (1992, 1993) followed the previous work by investigating both the phanerogam and cryptogam component of the vegetation at Storbreen at 190 sites (2 m^2) sampled from Matthews' 638 permanent sites (16 m^2) on the Storbreen foreland, Norway. She recorded a wide range of environmental parameters, some of which were measured using new techniques of measurement, and some of her methodology has been used within this thesis (see methods chapter).

Crouch's results were similar to those obtained by Matthews and Whittaker in that the most important influence on the pattern of vegetation is time, and microtopography is also an important influence. An association was found between the time factor and a variety of environmental parameters including soil depth of organic horizon, stoniness, frost activity and soil compaction and an association between microtopography and the snow regime was also found. Her results also show that there is a considerable divergence of assemblages from fewer assemblages on young terrain to a greater number of assemblages on older ground and that not one species has an identical distribution to that of another species. She also showed that there is a gradient of assemblages, across the foreland, with the most distinct assemblages on the pioneer and the oldest terrain and the least distinct assemblages on the intermediate ground. However, her results differ from the previous work in that she found moisture to be related to age of ground rather than to the "*Microtopographic factor complex*" (*sensu*: Whittaker, 1985). She demonstrated that cryptogams display a different set of successional pathways to phanerogams and suggested that a failing of the previous work was the neglect of cryptogams. With regard to the cryptogams, she found that they show more divergence of assemblage types on the oldest terrain and suggested that this is due to their greater sensitivity to environmental factors. For this reason she recommended separate analysis of phanerogam and cryptogam assemblages. Due to the proven sensitivity to environmental factors shown by the cryptogams the present study included data on lichen species, as well as the total cover abundance of bryophytes. However, it was decided not to separate the different plant-types in the analysis because such a separation was considered, by the present author, to be rather contrived - i.e. the species occur together on a site and so should be analysed together as it is the purpose of this study to investigate all the influences on vegetation pattern at a site. Crouch concluded that although the species show considerable individualistic behaviour, thus supporting a population approach to the study of succession, similarities in distribution between many of the species indicate that an assemblage approach is pragmatic, especially when dealing with the large data sets involved in the study of glacier foreland successions.

Vetaas (1994) made a study of primary succession of plant assemblages on Bødalsbreen glacier foreland, S Norway and his study is of particular relevance to this study as he specifically investigated the effect of microtopography on vegetation and soil patterns. His methodology is described here in relative detail so as to show the major differences between his and the present study. Five terminal moraines (no mature) were divided into three sampling sites per moraine: distal (north-facing) slope; proximal (south-facing) slope; ridge crest. Each site comprised between two and four plots which were subjectively placed to represent different physiognomic structures. The plot sizes varied according to the patchiness of vegetation: 2x2 m in open forest; 3x1 m on distal slopes; and all others 1 m^2. Cover of all species (both phanerogams and cryptogams) was estimated on a Du Rietz scale in 114 plots and he used TWINSPAN and CCA to analyse the data. He also measured a restricted number of meso-scale environmental variables including wind direction, rainfall and aspect, and micro-scale environmental parameters including temperature, soil profiles, soil organic content, humus depth, pH and soil cations. By comparing the present thesis methodology outlined in chapter (2) with that of Vetaas it can be seen that his sampling methodology, as well as the range of environmental parameters and locations that he used, differs considerably from that of the present study.

His results show that the successional sequence at Bødalsbreen can generally be described as a physiognomic (form and structure) development: cryptogams and dwarf shrubs colonise bare substrate which may then develop into a heath phase or return to bare substrate, depending on the prevailing microenvironment. He further suggested that the heath phase may be overgrown by *Betula pubescens* shrubs then *Betula pubescens* woodland. He found the most exposed sites are ridge tops and proximal slopes, and, on the youngest ground, the *Betula-Vaccinnium* assemblage was only found on the leeward distal side where snowbeds occur. He proposed that convergence of assemblages occurs on the older ground due to a decrease of micro-gradients, with time, on sub-alpine forelands where dominant trees are present and he suggests that the life-history of *Betula pubescens* is highly influential on succession. He suggested that microtopography is a much more important influence on vegetation patterns earlier in the succession and he also considers the glacier wind to be an important influence. The method of sampling differs considerably from the present thesis, especially with regard to the vegetation, as he placed quadrats according to the physiognomy of the species growing there. He reported that the majority of species grow on all moraines and occur in many plots (Vetaas, 1994) and concluded that TWINSPAN divisions were mostly based on differences in cover. However, had he used a more objective methodology, not based on differences in physiognomy, he may not have found such similarities in the richness and composition of species on the moraines belonging to each terrain-age. He also may not have found such a clear convergence of species assemblages across the foreland.

Vetaas' results, with regard to environmental parameters, are of interest but he admits they are not comprehensive, nor statistically significant, as such a small sample was taken (Vetaas - pers. comm.). He measured air temperatures, at 5 cm, at the three positions (proximal - south facing; distal - north-facing; and ridge top) across all five moraines for 10 days during the summer. He found strong temperature gradients across the moraines, due to aspect, with the warmest slopes being the south-facing proximal slopes and the oldest moraine experiencing a 6 °C difference in temperature on one particularly sunny day. Only the moraine nearest to the glacier had a proximal slope cooler than the distal slope (thus influenced by proximity to glacier). Furthermore, the differences in temperature, between distal and proximal slopes, were less significant with proximity to the glacier. Another interesting result was that he found the crests to have warmer average temperatures than the bases of the moraines which may have been due to the sinking of cool air, in calm conditions, into hollows within the landscape. With regard to development of a podzol profile, he found that the profile appears to develop slowly on the ridge crests and most rapidly on the distal slopes (north-facing), maybe due to longer snow-lie and litter accumulation in the snow patch, as well as cooler, wetter conditions. Vetaas mainly attributes the difference to the effect of a strong glacier wind, which reduces the accumulation of litter on moraine crests. This is a surprising conclusion as the glacier wind is not, apparently, significant enough to effect temperatures on any but the nearest moraine to the glacier. Despite the difference in methodology, however, Vetaas' conclusions show some similarities to the work at Storbreen especially with regard to the complexity of foreland successions as well as the relative importance of time and microtopography on succession.

Haines-Young (1983, 1985, 1988) investigated size variation of *Rhizocarpon* on proximal moraine slopes in S.Norway. Distal slopes were not used because he suggested they may be older and subject to early disturbance. He found that there appears to be a progressive downslope increase in mean maximum lichen diameter supporting the "Green zone hypothesis" which states that the maximum thallus diameters are largest at the foot of the proximal slopes of moraine ridges where snow cover remains until the late spring and provides a reliable source of moisture. The proximal slopes used by Haines-Young are above the floor of the foreland so they do not create hollows and depressions, with very late snow-lie, which would cause stress and eventual death in the case of semi-permanent snow-beds (Innes, 1985; Benedict, 1990a,b, 1991).

His work is not only relevant to the present study with regard to showing differential growth rates (and thus differential environmental conditions) across moraine ridges on forelands used in the present study, but it is also relevant with regard to showing that a green zone exists on the lower slopes of the moraines and can be used to indicate differential snow cover across the moraines. The work of Innes (1985) at Storbreen, on the effect of differential snow cover on lichen growth, further justifies the use of saxicolous lichens as indicators of snow-lie and exposure with his results confirming those of Haines-Young (see section 2.6.1).

1.4.2 Soil development

It is not possible to provide a simple description of the soils on glacier forelands in the Jotunheim and Jostedalsbreen region (and on the oldest terrain outside the forelands) because of the wide variation in the soils along the chronosequences. For this reason a review of soil development on glacier forelands, with special reference to regional development, is presented. In this thesis a number of soil characteristics will be measured in order to elucidate the relative differences in soil development on glacier forelands as a result of the meso-environmental parameters of altitude, age and microtopography. It is not within the scope of the present thesis to make a detailed investigation of soil development, but it will be shown that selected soil characteristics provide an adequate reflection of soil development in the study area. The aim of this section, then, is to introduce soil development on glacier forelands with special reference to the Jotunheim and Jostedalsbreen regions; to provide preliminary justification for the soil characteristics chosen; and, lastly, to act as a reference point so that the results from the present study can be compared with the results of previous work. A detailed description of the methodology and approach used for each of the soil parameters is provided in the methods chapter (2) (section 2.8).

Norwegian soils have been classified by Ellis (1979) but, according to Mellor (1985), most of the soils found on the forelands themselves are less than 230 years old and they have not yet developed into the mature soils described in the classification. Ugolini (1968) found that soil development at Glacier Bay, Alaska, proceeds from Regosols (first 15 years) to Podzols (15 to 100 years) to Brown Podzols (100 to 150 years) and then Podzols after 150 years. In the Jotunheim and Jostedalsbreen region soil profile development is similar, although the Regosols seem to be dominant for a longer time (Mellor, 1985). The youngest profiles at Storbreen and Austerdalsbreen are those less than 100 years old and these are defined as Orthic Regosols, which develop into Orthic Dystric Brunisols and, on the oldest moraines at Austerdalsbreen, Orthic Humo-ferric Podzols (Mellor, 1985). Messer (1988) found that Humic Regosols were the dominant soil type at high altitudes in the east of the region. Humic Regosols (Fig.1.2) have a litter (L) horizon overlying horizons of slow decomposition - the fermentation (F) and humification (H) horizons (using the modern soil terminology, *sensu*: Whittow, 1984). Unaltered parent material, mainly glacial till on the forelands, underlies the thin humus layer, which is built up in patches where vegetation occurs. This profile is fairly typical of most of the Regosols found on the forelands. Large areas of the forelands, especially on young ground and higher altitudes, consists of bare ground with little or no soil development. However, comparison of the foreland Regosol with the older soils on the oldest terrain is useful in order to infer how the soil development proceeds.

According to Mellor (1985), the soils of Storbreen are representative of a high-altitude, sparsely-vegetated and more continental climate and thus his findings at Storbreen are probably comparable to the general soil conditions found on other forelands in the Jotunheim. Austerdalsbreen, at a lower altitude below the tree-line, is well vegetated and has a temperate maritime climate where podzolisation is the dominant process (Mellor, 1985). Messer (1988) investigated a number of soil properties on 18 forelands in part of the Jotunheim, Hurrungane and Jostedalsbreen region and, in general, the results can be grouped regionally and thus altitudinally. For example, soil pH is slightly lower, and the percentage soil organic carbon, soil cation exchange capacity (meq 100^{-1}) and soil depths, are generally higher for most of the low altitude forelands in the Jostedalsbreen region.

The soils of mature sites at Storbreen have been defined as arctic-alpine Brown Soils according to the classification system of the Canada Soil Survey Committee (1978) (Ellis, 1978; Mellor, 1987; Matthews, 1992). In Fig. 1.2 it can be seen that Brown Soils consist of an organic matter accumulation zone and an organic matter decomposition zone overlying an illuvial horizon which in turn lies over unaltered till parent material (Messer, 1988). The (Eb) horizon, in Brown Soils, is dark in colour distinguishing it from the bleached appearance of the (Ea) horizon in Podzols. The colour diminishes with depth until the parent material is encountered (Messer 1988). Brown soils are defined as those possessing an (Eb) horizon high in sesquioxides and they occur in areas where precipitation is higher than evaporation, on free-draining permeable rocks. The pH of the soils is relatively basic and normally lies between pH 5 and 7 (Whittow, 1984). Mellor found that the surface horizons in the Jotunheim has a considerably higher mineral content than the almost entirely organic content of the surface horizons on the Jostedalsbreen forelands. At Austerdalsbreen, following the classification system of Ellis (1979), Mellor defined the soils as being Humo-ferric Podzols.

As can be seen in Fig. 1.2 Podzols consist of an organic matter accumulation zone and an organic matter rapid decomposition zone overlying a bleached eluviated (Ea) horizon where leaching of minerals is the dominant process. The underlying illuvial (B) horizon in Podzols accumulates soluble bases and sesquioxides and is subdivided into a (Bh) horizon, which is dominated by re-deposited humus, and the (Bs) horizon which accumulates iron sesquioxides and aluminium. Mellor (1985) found that the process of podzolisation occurs in both the Jotunheim and the Jostedalsbreen regions. However, a bleached, eluviated (Ea) horizon only occurs on sites in the Jostedalsbreen region. He concluded that the differences between the soil types are largely caused by the environmental differences between the two regions. The Jostedalsbreen region has a longer frost-free season, allowing illuviation to have a longer duration each year. Furthermore, rainfall is considerably higher in the Jostedalsbreen region, than in the Jotunheim, (e.g. 1380 mm at Bjørkehaug (alt: 324) in Jostedalen; and 899 mm at Vetti (alt: 329) in the Jotunheim) and vegetation cover is also higher so that there is a higher organic matter supply to the upper horizons and consequently a greater supply of organic-bound iron and aluminium complexes that can be eluviated to the (B) horizon. Lastly, the more basic parent rocks of the Jotunheim, combined with sparser vegetation and lower rates of eluviation, are probably responsible for the higher mineral content of the (Eb) horizons in this region.

The development of Brown Soils at Storbreen is not complete, after 230 years, as Mellor (1985) found that organic carbon on the AD 1750 moraine at Storbreen is 15 %, which is half the value for organic carbon found on the oldest terrain. Messer (1984), using extrapolation, estimated that it takes another 275 years before the organic carbon values of the 1750 moraine attains the values of the oldest terrain. Jenny (1941) suggests that between 500 and 1500 years are required for the full maturity of a podzol. For the purposes of this study, only the ground outside the 1750 moraine can be considered as the oldest terrain.

Soil development is well-documented for the Jostedalsbreen region and the Jotunheim. Generally the results of the different studies have much in common. The development follows a similar pattern in both regions, but the development is slower at the higher altitudes in the Jotunhein (Messer, 1984). The trend is that pH falls while organic content, cation capacity and soil depth increase through time (Mellor, 1985; Messer, 1988). Soil depth and organic content are dependent on microtopography (Messer, 1984; Vetaas, 1986). Whittaker (1985) also found soil depth and litter depth to increase with age but to be limited by microtopography. Crouch (1992) found that as the age of ground increases, soil organic matter increases, that soil texture becomes finer and that pH decreases. Conversely, she found that with increasing altitude, organic matter falls, soil texture is coarser and pH increases. Vetaas (1986), investigating the effects of microtopography and age on vegetation and soils at Bødalsbreen, found an increase of Calcium in the organic (O) horizon, but a decrease in calcium in the underlying moraine till ("morenejord") and an increase in magnesium for the organic horizon, with no apparent trend for the moraine till. He found that pH generally decreases, although there was a slight rise in pH for the distal slope of the oldest moraine while organic carbon, the ratio of carbon to nitrogen, and soil nitrogen, increase with age of ground.

The main findings of the research work reviewed in this section, with regard to the effect of microtopography on soil development, would suggest that although microtopography does influence soil depth and organic content (Messer, 1984; Vetaas, 1986; Whittaker, 1985) the most important influence on soil development is time (Whittaker, 1985; Crouch, 1992). The results of these studies, especially those concerned with the effects of microtopography on soil development, will be discussed at greater length and compared with the results of the present study in the concluding chapter (7).

1.4.3 Summary of regional studies

The studies using a geoecological approach (*sensu*: Matthews, 1992), within the Jotunheim and Jostedalsbreen regions, have been successful in furthering our understanding of vegetation succession and soil patterns on glacier forelands and their boundaries (comprising mature vegetation on ground considered not to have been glaciated since pre-Boreal times). These studies have the advantage of having used similar methodologies and locations. This review shows that the authors of these studies have come to the following general conclusions with regard to succession on glacier forelands:

1. Glacier foreland successions are complex and may involve several pathways from pioneer assemblages to mature assemblages.
2. Mesoscale environmental influences, such as aspect and altitude, can influence the sequence of assemblages and may also influence the relative complexity of the succession, with simpler successional sequences occurring at the more environmentally stressed locations (i.e. higher altitudes and north-facing slopes).
3. The most important influence on succession is time, but microtopography is also an important influence. The relative influence of time and microtopography on vegetation patterns, at any location, is not constant.
4. Certain environmental factors tend to be associated with time in a "*Terrain age factor complex*" such as cryoturbation, disturbance, altitude, soil and litter depth, depth of rooting. Others are associated with microtopography in a "*Microtopographic factor complex*" such as snowlie, exposure and moisture.
5. The most common successional sequence on a foreland involves the divergence of assemblages from fewer pioneer assemblages to a larger number of later assemblages.
6. In some cases, especially following some form of disturbance, it is possible for succession to regress, with earlier stages replacing later stages.
7. Complex data sets, comprising both vegetation and environmental data, should be analysed using a variety of multivariate techniques which should be supported by simple distribution charts for comparative work.
8. Although statistical significance should be used, it is important to adopt a balanced approach by considering whether or not the data are ecologically meaningful. Thus a combination of objective and subjective interpretative methods should be used for these ecological data.

These studies have been highly influential on the methodology of the present thesis providing a background without which the present work would not have been possible. The above conclusions can be used to justify much of the approach used by the present author.

1.5 Purpose of present study

A wide range of research (sections 1.3 and 1.4), with a bearing on the present study, has been reviewed. It was shown that very little work has been carried out on the actual effects of microtopography on vegetation and soil patterns even though there is a growing consensus that succession can be better understood by the study of heterogeneous landscapes using a geoecological approach. The present study complements and augments the knowledge derived from much of the previous work. Its purpose may be stated as seeking answers to the following questions:

1. Which environmental parameters are related to microtopography?
2. Does the relationship between microtopography and associated environmental parameters change with successional stage (i.e. through time)?
3. To what extent does microtopography influence the succession of assemblages across each of the forelands?
4. Is there a relationship between microtopography and the strength of the association between the species within the various assemblages?
5. Does the influence of microtopography, on vegetation, change with different stages of succession?
6. Does retrogression occur, and is it affected by microtopography?
7. Does microtopographical position affect the degree of divergence, or convergence, through time?
8. Does the influence of microtopography on succession vary with altitude?

1.6 Thesis outline

Chapter (1): Introduction and literature review

The purpose of chapter (1) has been to describe the region under study and to introduce the aims, objectives and subject matter of the present study. A comprehensive review is made of the most important previous research of relevance to the present study. The topics reviewed are: a general outline of succession; microtopography in relation to vegetation pattern; glacier foreland studies in relation to succession; and microtopography, succession and soil development in a regional context. Relevant terms, especially in relation to succession, are introduced and, where previous definitions have been ambiguous, re-defined for the purposes of the present study. The failings, as well as the conclusions, of the previous work have been described so that the methodology and rational of the present study can be justified. Lastly, the most important questions posed by the literature in relation to this thesis are listed.

Chapter (2): Methods and approach

This chapter describes the methods and approach used throughout this thesis. The sampling design is described with an introduction to each of the locations (i.e. forelands) under study. An introduction to the nomenclature is given as well as a description of the recording techniques. The methodology used, for the measurement of each of the environmental parameters, is described. Each description is accompanied by a brief background to the methodology used. The environmental parameters have been divided into four sections: macro- and meso-environmental factors; microenvironmental factors associated with climate; microenvironmental factors associated with disturbance; and microenvironmental factors associated with vegetation and soil. The analytical techniques are then outlined and justified. Lastly, a test of the between-season variability in data collection is described and discussed.

Chapter (3): The foreland environment

This is the first results chapter and its main function is to describe the environmental measurements made across the moraines on each of the forelands. It also describes the meso-scale environmental factors, such as altitude and the size of each of the forelands. Each section describes a micro-climatic variable, namely snow-lie, moisture, exposure and temperature. The results of additional environmental measurements (independent of the general data collection) made at Storbreen (temperature) and at Svellnosbreen (moisture) are also described. Most of the environmental data is presented on charts which show the distribution of the various factors across each of the moraines on every foreland.

Chapter (4): The pattern of species assemblages on the individual forelands.

This results chapter is based on the individual foreland data sets and describes the vegetation distributions, that have been found by the classification technique TWINSPAN. The TWINSPAN site (sample) groups are described and from the "final site groups" (see glossary) it is possible to construct succession diagrams. TWINSPAN species groups are then described and each of the "final species groups" (see glossary) are displayed on charts so that it is possible to see the distribution of the members of the "final species group" across each of the moraines on every foreland. The TWINSPAN "final site groups" and the TWINSPAN "final species groups" have been summarised on summary tables (Tables 4.9 and 4.10) and from this it is possible to compare the site and species separation on each of the forelands at a glance.

Chapter (5): The relationship between sites, species and environmental parameters across the individual forelands

This chapter describes the pattern of sites (and TWINSPAN "final site groups") and species (and TWINSPAN "final species groups") on individual foreland DCA axes (1) and (2) and then relates environmental parameters to the vegetation and sites. In order to relate the axes to environmental parameters it is necessary to use separate environmental data and calculate regression coefficients of environmental parameters on the ordination axes. The chapter is divided into sections representing the results for each foreland. In each section the sample, species and environmental patterns are described with reference to axes (1) and (2). Relationships are then found between the TWINSPAN "final site groups" and "final species groups" and the environmental parameter patterns and these relationships are summarised in diagrams (Figs. 5.17 to 5.32). Summary tables (Tables 5.25 and 5.26) of all the forelands has been constructed so that it is possible to compare the results for each foreland at a glance.

Chapter (6): Vegetation patterns and the relationship between sites, species and environmental parameters using the combined foreland data set.

The final results chapter shows the outcome from analysing all forelands in combination (combined data set). The multivariate techniques introduced in chapters (4) and (5) are used to analyse the combined data set. The main aim of analysing the combined data set is to provide a macro-scale representation of the relationships between the TWINSPAN "final site groups" and "final species groups" and the environmental parameter patterns. The results from both the combined TWINSPAN and DCA runs are displayed and described. Each section has a summary which provides a quick and easy reference. An evaluation of the relative merits of analysis at the mesoscale (individual foreland) and macroscale (combined foreland) is then put forward.

Chapter (7): Conclusions

The concluding chapter draws together the findings of the results chapters and uses these findings to answer the questions listed in section 1.5. The results are discussed, in the first three sections, in relation to the main aims of the thesis (section 1.1): a) the main controls on the foreland environment; b) the effects of the environment on vegetation patterns; and c) the environmental controls on vegetation succession. The methodological and technical implications of the thesis are outlined and discussed. In each section, the findings are compared with those of the previous work and the main conclusions and contribution, of the thesis, are outlined in the section summaries. In the light of the positive contributions, and limitations, future projects are proposed.

"Even where the final community seems most homogeneous and its factors uniform, quantitative study by quadrat and instrument reveal a swing of population and a variation in controlling factors ... In consequence, a floristic and physiognomic study of an association, especially in a restricted area, can furnish no trustworthy conclusions as to the prevalence of succession. The latter can be determined only by investigation which is intensive in method and extensive in scope."

Clements (1916: 3)

CHAPTER TWO: Methods: approach and rationale

2.1 Introduction

The intentions of the methodology of the present thesis is as follows:

1. Data are provided concerning the vegetation (vascular plants and lichens) and environmental sequences across selected moraines on six glacier forelands which have undergone detailed mapping and dating of the major microtopographical features (i.e. moraines) (Matthews, 1974, 1975, 1977, 1978b, 1991, 1992; Innes, 1985; Erikstad and Sollid, 1986; Haines-Young, 1988; Nesje, 1989; Bickerton and Matthews, 1993).
2. Data are provided concerning a wide range (24 environmental parameters) of the prevailing environmental factors at a range of microtopographical positions. The sampling is based on the methodologies used by previous researchers in the region (e.g. Matthews, 1976; Whittaker, 1985; Crouch, 1992; Mellor, 1985; and Messer, 1984) and some methods developed further or supplemented with new techniques.
3. The specific relationship between the vegetational succession (and prevailing soil characteristics), and microtopography (associated environmental factors) on each of the forelands will be elucidated. One of the forelands (Storbreen) has already undergone very detailed vegetation and soil studies (Matthews, 1976, 1978a,b, 1979a,b,c,d, 1992, 1997 - in press; Matthews and Whittaker, 1987; Whittaker, 1985, 1987, 1989, 1991, 1993; Mellor, 1985, 1987; Messer, 1988; Caseldine, 1989; Crouch, 1992, 1993) using the geoecological approach (*sensu*: Matthews, 1992). Two other forelands (Austerdalsbreen, Høgvaglbreen) have undergone detailed soil studies (Mellor, 1985, 1987; Messer, 1988) thus providing useful data for comparison, as well as a background, with the results from the present study.
4. Data are provided from eight successional gradients, giving an opportunity to discuss the (possible) changing effect of microtopography with time at a wide range of locations.
5. Data are provided from a range of different forelands at different altitudes giving an opportunity to discuss the (possible) changing effect of microtopography with increasingly severe climatic conditions.
6. Data are provided from a series of individual forelands that can be analysed separately, as individual data sets, or combined together, as a combined data set in order to show whether a combined data set (which requires considerably less time spent on analysis and interpretation) can provide the same depth of analysis, as well as the same conclusions, as the individual foreland data sets.

By gathering the vegetation data at sites across microtopographical features along several chronosequences and by measuring a wide range of the prevailing environmental variables at each of the sites it is hoped that the general questions pertaining to succession, at the end of section 1.3.1, can then be related to microtopography. These intensions are consistent with the main aims of the study (section 1.1) and themes derived from these intentions are discussed in the concluding chapter.

2.1.1 Methods and approach

The methodology used within the present investigation is to investigate the succession of plant assemblages found on terrain which has been exposed, from under a glacier, at sequentially greater ages. This methodology is known as "space-for-time substitution" (sensu: Pickett et al, 1987) and although it is not as accurate as the actual measurement of year to year variations in vegetation and associated environmental parameters, the description of vegetation across dated moraines is a more practical approach for the elucidation of successional patterns over longer time-scales. Pickett et al (1987) criticised previous successional work, using the "space-for-time" methodology, for only using so-called homogeneous plots. This study presents a "space-for-time" methodology which takes landscape heterogeneity into consideration by considering the effect of microtopography (a moraine ridge) on vegetation succession. Furthermore, the investigation of the effects of microtopography across forelands at several altitudes, as in the present study, elucidates landscape heterogeneity to an even greater extent than, for example, a study of moraine sequences across one foreland at a selected altitude.

The present study is a logical extension of previous work. The forelands chosen for this project have been previously studied to a greater or lesser extent. As discussed in chapter (1), the previous research has guided the choice of foreland and also the methodological approach used, particularly the extensive work that has been carried out at Storbreen (e.g. Matthews, 1976; Whittaker, 1985; Crouch, 1992). An outline of the methodologies used to date the moraines across each foreland, as well as a general description of the forelands under study, is given in sections 2.1.2 to 2.2.2.

2.1.2 Dating techniques

As outlined in chapter (1) glacier forelands are widely used for the study of primary succession (e.g. Crocker and Major, 1955; Persson, 1964; Lawrence et al, 1967; Ryvarden, 1975; Whittaker, 1985; Burrows, 1990; Matthews, 1992). Glacier forelands provide virgin ground for plants to establish and grow on. By using forelands, researchers are able to ascertain the succession of plant assemblages with distance from the glacier. If scientists can accurately age the substrate at increasing distances from the glacier they can then find the rate at which plant assemblages replace each other. They should also be able to predict assemblages associated with substrates of a given age. In order to do this glacial till, or moraines, need to be accurately dated. According to Matthews (1992) there are three categories of dating techniques: historical; biological; and "physico-chemical". These three categories are briefly outlined below and the type of evidence used to support the dating of the moraines, within the present work, is revealed in each of the sections describing the study locations and moraine sequences (i.e. section 2.2).

Historical dating uses a wide range of evidence including photographs, literature or documentary evidence, scientific mapping of glacier boundaries and physical measurement of the advance or retreat of a glacier from a fixed point. The use of historical sources is regarded to be the most accurate method, although very early records have sometimes been shown to be unreliable and confusing. If the records are accurate, historically dated substrates are the best source of "fixed points", or substrates of known age, for the estimation of unknown substrate-age using other less accurate methods such as lichenometry. Most researchers involved in the description of plant succession on glacier forelands refer to historical records in order to support their methods of dating (e.g. Cooper, 1923a,b,c; Fægri, 1933; Persson, 1964; Matthews, 1976).

The best known examples of biological dating techniques are dendrochronology, lichenometry and radiocarbon dating. Dendrochronology finds the age of the oldest tree on a substrate of unknown age. A core is taken from the tree and the age of the substrate is based on the age of the tree. The problem with this technique is that the "oldest" tree is often difficult to find - the largest is not necessarily the oldest. Additionally "ecesis", or the rate of plant establishment, is a major factor in that the time between ground exposure and tree establishment is unknown. Also, in unusual circumstances, trees are able to grow on debris located on the glacier itself and then the tree is dumped onto a newly formed moraine (Matthews, 1992). According to Matthews (1992) dendrochronology is popular in North America (e.g. Olson, 1958) but it has not been widely used in the Jotunheim for the reasons outlined above.

Lichenometry and radiocarbon dating have been widely used within the Jotunheim and Jostedalsbreen regions. Lichenometry is normally used for substrates of less than 300 years and radiocarbon dating is used for much older substrates. The technique of lichenometry was developed by Beschel (1950) to date moraines above the tree line. The method has been used, and developed further, by Matthews (1974, 1975, 1977) and all the forelands used within the present study have been dated using this technique. Lichenometry relies on at least two moraines of known age and measures the largest species of *Rhizocarpon geographicum*, a saxicolous lichen. It has been suggested that the best conditions for green lichen growth is at low-slope positions (but not where snow duration continues long into the summer) and a so-called "green zone" has been found to exist (Matthews, 1977). Further work on the measurement of *Rhizocarpon geographicum* individuals shows a progressive increase in mean maximum diameter downslope supporting the "Green zone hypothesis" which states that the maximum thallus diameters are largest at the foot of the proximal slopes of moraine ridges (Haines-Young, 1983). Only the proximal side of the moraine is used as there may be a considerable discrepancy in age between the distal and proximal slopes, with the distal slope being older (Haines-Young, 1983, 1988). In order to construct a lichenometry curve, so that the dates of unknown sites can be predicted, the largest lichens are measured along the base of the proximal moraine slopes of known age. There should be at least two moraines of known age within each series and these are then plotted onto a curve. The largest lichens from a number of sites on moraines of unknown age are then plotted and thus the substrates of unknown age can be dated. Matthews (1992) suggests that the method is accurate to within +/- 5-10 years for a substrate of less than 250 years. All the moraines in this study have been dated using this technique. Because of the short distances between the moraines, intermorainal areas can also be dated accurately (Maizels and Petch, 1985) but intermorainal sites have not been used within the present thesis.

The third category of dating are the "physico-chemical" dating techniques which include a number of non-biological techniques which measure the rate at which physical processes occur. They include weathering rates, erosional or depositional rates, tephrochronology and palaeomagnetic methods. A number of researchers, within the region discussed in the present thesis, have tested methods using rates of weathering to date substrates (Matthews and Shakesby, 1984; McCarroll, 1989) but as these methods have not been used for absolute dating their description is not relevant for present study purposes.

2.2 Sampling location

Six accessible forelands, ranging from 290 m to 1540 m, were selected on account of their well-formed and well-dated moraines at an even spread of ages. The sample sites are located on selected glacier forelands in two regions of south central Norway, namely the Jostedalsbreen and Jotunheim regions (see Figs. 2.1a and 2.2a). Austerdalsbreen (Fig. 2.1b) and Fåbergstølsbreen (Fig. 2.1c) glacier forelands were used for sampling purposes in the Jostedalsbreen region, and Storbreen (Fig. 2.2b), Svellnosbreen (Fig. 2.2c), Høgvaglbreen (Fig. 2.2d) and Bøverbreen (Fig. 2.2e) glacier forelands were used in the Jotunheim region. The purpose of section 2.2 is to introduce these locations by giving a brief description of the topography, geomorphology and general vegetation cover of each of the regions and selected forelands. Furthermore, the descriptions of each of the selected forelands will include information concerning the age and method of dating each of the moraines, used for present study purposes. In addition, a brief discussion of the relative distance between the moraines on each foreland, which is summarised in Table 2.1, will be made.

The distance between moraines may influence a number of important vegetational and environmental factors. For example, long distances between moraines could affect the rate, as well as type, of migration of plant propagules to a site (Miles and Walton, 1992). Furthermore, vegetation growing on moraines located near to the glacier snout may be influenced by the "glacier climate" (*sensu*: Matthews, 1992) to a greater extent than that growing on moraines at a greater distance from the glacier (e.g. Vetaas, 1986). The effect of distance has not been investigated specifically, within the present study, but it is still necessary to be aware of the differences in the relative size of the forelands so that distance-related anomalies in the data can be elucidated. Matthews has suggested (pers. comm.) that the distances across the forelands are unlikely to affect vegetation factors, such as migration, because the differences in relative distances across the glacier forelands are not very great. However, it is possible that the differences in foreland size between Høgvaglbreen and Austerdalsbreen may be responsible for an increased influence of the glacier climate (and related factors such as katabatic winds) across higher proportions of the foreland at Høgvaglbreen, as it is a much shorter foreland. The relative effect of proximity to the glacier is discussed, for example, in section 3.3.3.4 and in the concluding chapter (section 7.2.2), especially in relation to its influence on micro-environmental factors.

Table 2.1 Distances between moraines (m).

Note: symbols - M1 to M8 - represent moraines for each individual foreland (see Table 3.2 for ages)

INDIVIDUAL FORELAND SEQUENCES *(symbols key is given in Appendix 2)*							
AUSF	FÅSF	STLF1	STLF2	SVLF	STHF	HØHF	BØHF
600 (M1-2)	150 (M1-2)	250 (M1-2)	250 (M1-2)	125 (M1-2)	250 (M1-2)	250 (M1-2)	40 (M1-2)
660 (M2-3)	280 (M2-3)	187 (M2-3)	187 (M2-3)	150 (M2-3)	62 (M2-3)	50 (M2-3)	100 (M2-3)
300 (M3-4)	1100 (M3-4)	100 (M3-4)	100 (M3-4)	850 (M3-snout)	125 (M3-4)	100 (M3-4)	275 (M3-4)
660 (M4-5)	200 (M4-5)	225 (M4-5)	225 (M4-5)	167 (M4-5)	37.5 (M4-5)	100 (M4-5)	50 (M4-5)
250 (M5-6)	400 (M5-6)	25 (M5-6)	25 (M5-6)	67 (M5-6)	50 (M5-6)	30 (M5-6)	220 (M5-6)
850 (M6-7)	200 (M6-snout)	800 (M6-snout)	800 (M6-snout)	500 (M6-snout)	175 (M6-7)	270 (M6-snout)	200 (M6-snout)
600 (M7-snout)					275 (M7-8)		
					200 (M8-snout)		

2.2.1 Sampling sites in the Jostedalsbreen region

The study sites are located on two glacier forelands in the Jostedalsbreen region. In this section the location, geomorphology and a brief description of the vegetation, for the Jostedalsbreen region and glacier forelands under study, is introduced.

Jostedalsbreen is situated on a large plateau approximately 100 km from the coast with peaks that rise over 2000 m (Fig. 2.1a). The ice-cap is approximately 60 km long and at its widest point (from the snout of Kanndalsbreen to the snout of Tunbergdalsbreen) it is 30 km. It has a surface area of 470 km□. The large size of the ice-cap has a considerable influence on the local climate and hence vegetation (Matthews, 1992). For example, heavy rain tends to occur near the glacier, in the form of orographic showers, with clear skies and sunshine found only a few kilometers away (personal observation). A combination of low altitude, relatively mild conditions and high rainfall provides conditions on older parts of the glacier forelands (i.e. ground exposed before 1810) that support a lush vegetation within a relatively short time-scale.

The valleys surrounding Jostedalsbreen were de-glaciated during the latter half of the pre-Boreal chronozone (Nesje, 1989). Since then, there have been a number of readvances, the most recent of which was the Little Ice Age. The glaciers have been mainly in retreat since some time in the 18th century and a number of arcuate moraines have been pushed up in short periods of re-advance or stand-still (Bickerton and Matthews, 1993). The moraines are composed of a mix of differing proportions of boulders and other glacial till derived locally from the surrounding mountains. The till of the moraines therefore reflects the local geology (Whittaker, 1985). Depositional features, such as sandur, eskers and moraines, as well as erosional features, such as U-shaped and hanging valleys, rock-bars and roches moutonées, combine together to form the characteristic landscape of a region influenced by glaciation. Further erosion and disturbance of the deglaciated landscape by wind, water, freeze-thaw, avalanches and landslides sculpted the present landscape. The way in which the landscape has been eroded and then colonised by vegetation is dependent on the prevailing geology, topography and climate of the area.

Due to the warmer maritime climate of the Jostedalsbreen region, some of the glaciers have retreated considerable distances (Grove, 1988). Research (e.g. Fægri, 1933; Kasser, 1973; Müller, 1977) has shown, for example, that Nigardsbreen has retreated approximately 4 km and Austerdalsbreen has retreated approximately 3 km. In some years this retreat has been at remarkable speeds, for example at Fåbergstølsbreen the snout retreated 138m during 1966 (Nesje, 1989). Distances between moraines can therefore be very great (Table 2.1) and the cumulative distance of moraines from the snout moraines on each of the forelands is shown in Table 3.1 (this volume). Differences in distance across each of the forelands are likely to have an influence on many environmental factors, especially those directly related to proximity to the glacier, such as glacier winds. It would appear that the influence of the glacier is likely to be less important on the forelands of the Jostedalsbreen region than it is in the Jotunheim where the forelands tend to be shorter. Greater distances between moraines in the Jostedalsbreen region may also have a greater effect on the ability of certain species to colonise, especially with regard to those species with heavier seed or with seeds without some form of dispersal mechanism such as wings or edibility: some research has shown that colonising species tend to have lighter or more easily dispersed seed (e.g. Viereck, 1966; Lawrence, 1979; Birks, 1980; Chapin, 1991). However, there are others who contend that dispersal mechanisms do not necessarily reflect the ability of a species to colonise (e.g. Ryvarden, 1971; Given and Soper, 1975; Elven, 1980, Magnússon, 1994a). Although it is possible that distance may influence migration, there does appear to be disagreement upon the relative importance of distance on migration rates and, for reasons already discussed, the relative influence of distance on migration rates will be ignored for present study purposes.

The topography of the glacier forelands in the Jostedalsbreen region contrast with those of the Jotunheim (which are described in the next section). The forelands are mainly long and gently sloping, with sandur between widely spaced moraines. The glaciers, that issue from the main ice-cap, are known as outlet valley glaciers. The forelands are located in steep-sided valleys where avalanches and landslides can have an important influence on the vegetation pattern, especially along narrow sections. For example, in 1979 a large debris flow at Fåbergstølsbreen caused considerable disturbance on the younger section of the foreland (ground exposed after 1930). Disturbance factors, including the debris flow, will be taken into consideration within the discussion of the results.

2.2.1.1 Austerdalsbreen foreland

Austerdalsbreen (Fig. 2.1) is an outlet valley glacier that issues in a south-easterly direction from the southern end of Jostedalsbreen, 90 km from the Norwegian coast at Brufjorden. It is located at 61° 35' N and 7° E. The altitude of the snout is at 400 m and the foreland ranges from 290 to 380 m altitude. The foreland is approximately 3 km long and 850 m wide and has a southerly aspect. It is gently sloping up to the glacier with an altitudinal rise of 100 m over its length. The Austerdalselvi issues from the glacier. The main river channel runs through the centre of the valley and in the past has changed its course. The present study has only sampled from moraines on the western side of the river as the eastern side was inaccessible. A number of smaller streams also dissect the foreland. There is evidence of considerable fluvial and avalanche disturbance to vegetation on the flats between the moraines (Bickerton and Matthews, 1993).

There are at least 15 moraine-ridges of up to 6 m in height. The lateral moraines were not used in this study. The moraines (M2 to M6) have been dated using lichenometry (Erikstad and Solid, 1986; Matthews and Bickerton, 1993) and the ages (and symbols) of the moraines selected across this foreland (AUSF) are as follows: M1 - mature till ridge; M2 - 1785; M3 - 1853; M4 - 1871; M5 - 1908; M6 - 1935; M7 - 1960. The 1960 moraine was dated using historical records. Matthews (1991) suggests that during the "Little Ice Age", glaciers in southern Norway reached their maximum extent, since deglaciation at the end of the last Ice Age (9000 BP). The mature till ridge, which lies outside the Little Ice Age terminal moraine, is therefore considered to date back to the pre-Boreal (see glossary) and thus can be considered to be an order of magnitude older than the terminal moraine. As can be seen from Table 2.1 there was a relatively fast retreat between 1960 and 1935 and also between 1865 and 1900, suggesting that these periods may have had a warmer climatic regime and thus there could have been an accelerated rate of vegetation development within these periods. However, the investigation of such a hypothesis is outside the scope of the present study and so will only be considered with regard to apparent anomalies in the rate of development of the vegetation.

In phytosociological terms, the foreland is situated in the subalpine zone. The subalpine zone is below the uppermost tree line, which in this region occurs at 800 m, and includes a rich flora of mixed lowland and mountain species. A mixture of heath and birch woodland is the dominant vegetation occurring on older moraines while a sparse mosaic of heath and cryptogamic assemblages dominates the intermorainal sandur. Thickets of willow, alder and meadow species occur by the main and side-streams. The mature till ridge is not a moraine, rather it is a small ridge of pre-Boreal glacial debris on the surface of a large rock bar. Birch woodland comprises the dominant vegetation on the terminal moraine (M2), but the mature till-ridge is not tree-covered and comprises mainly heath vegetation. The oldest terrain is approximately 100 m higher than the 1750 moraine and is likely to have had a history of intense grazing by sheep and cattle, therefore inhibiting the growth of trees. Vetaas (1986) suggested that sheep generally avoid moraines and it is noticeable that the intermorainal vegetation is also less developed than moraine vegetation of similar age. However, it is possible that the noticeable sandy texture of the underlying substrate results from frequent flooding which would also inhibit vegetation development. A general survey of the foreland therefore shows that the development of the vegetation across the moraines has progressed without marked disturbance from the grazing and flooding that appears to affect the intermorainal areas as well as the oldest terrain.

2.2.1.2 Fåbergstølsbreen foreland

Fåbergstølsbreen (Fig. 2.1) is an outlet valley glacier that issues in an easterly direction from the north-eastern end of the ice-cap, 105 km from the Norwegian coast at Brufjorden. It is located at 61° 41' N and 7° 20' E. The snout is at an altitude of 680 m and the foreland rises 180 m from the 1750 moraine to the glacier snout. The glacier foreland is approximately 2 km long and ranges from a width of 300 m (along the narrow, steep-sided valley proximate to the glacier), widening out to 600 m, where the valley opens out into the main Jostedalen valley. The foreland has an easterly to south-easterly aspect. The Breelvane issues from the glacier and has cut through the centre of the valley. This meltwater channel has changed its course several times and has eroded broad channels through many of the moraines (Bickerton and Matthews, 1993). A number of small streams also dissect the foreland creating pockets of vegetation where boulders and moraines shelter vegetation from the glacier wind. In AD 1979, a major debris flow on the eastern slope of the valley caused considerable damage to vegetation in the proximal part of the valley (Ballantyne and Benn, 1994). The two youngest moraines sampled may well have been covered in debris from this slide.

There are at least 17 moraine ridges on the Fåbergstølsbreen foreland of up to 6 m in height. The moraines (M2 - M5) have been dated using a combination of lichenometry (Matthews and Bickerton, 1993), historical descriptions (Naumann, 1824; Durocher, 1847; Rekstad, 1900, 1901) and old photographs. The ages (and symbols) of the moraines selected across this foreland (FÅSF) are as follows: M1 - pre-Boreal moraine; M2 - 1706* (entered as 1750); M3 - 1765* (entered as 1810); M4 - 1909; M5 - 1930; M6 - 1970. The 1970 moraine has been dated approximately using old photographs. Beyond the terminal moraine is a ridge, considered to be pre-Boreal dating from 8970 ± 100 yrs (Nesje and Kvamme, 1991), which was used for determination of the mature vegetation at Fåbergstølsbreen. Unfortunately, it was only after all the analysis was complete that the author discovered that M3 may date from 1765* and not from 1810 (as entered in the data set). It should also be stated that the date of the terminal moraine could be up to 50 yrs older as lichenometry has shown the terminal moraine to date from 1706* (Bickerton and Matthews, 1993). However, Matthews suggests that the 1706 date of the terminal moraine could be overstated (Pers.comm.) because of the dampness of the site causing the lichens to grow at a greater rate than at other sites. If this is the case it could also be possible that the date of the supposed 1765 moraine is also overstated. The 1750 date for the terminal moraine (M2) will therefore be kept for present study purposes and so will that of the 1810 (M3). Neither the 1970 nor the 1930 moraines are distinct individual moraines in the traditional sense. The moraines are better described as till ridges deposited as complex fluted moraine combined with the material deposited in 1979 when a large debris flow plunged down the eastern side of the proximal slope of the valley (Ballantyne and Benn, 1994). For present study purposes, however, they will be referred to as moraines because it is difficult to ascertain the relative influence of the debris flow on the form of the 1930 and 1970 moraines prior to 1979. Intermediate-aged moraines consisted largely of boulders, the 1900 moraine used for the present study being no exception. Nearly the whole of the distal side consists of boulders, therefore the sampling at this site does not follow the normal sampling pattern (see Fig. 2.4 – this volume) so that the "mid-slope" site is located lower on the slope than normal. As can be seen in Table 3.1 the distance between the snout and pre-Boreal moraine is 2330 m so that it is unlikely that the glacier climate has a significant effect on most of the foreland.

The foreland is situated in the subalpine zone. The terrain has little sandur, except by the river, where the valley opens out. The valley itself is narrow and steep-sided and there is a prevalence of boulders and glacial till or mud, rocks and boulders from debris flows. Due to the irregular nature of the land surface, especially on the younger ground, there are a large number of sheltered and moist hollows where alder, willow, ferns and meadow species can thrive. On the older ground, the heath species give way to a birch woodland on the 1810 and 1750 moraines. The pre-Boreal moraine is dominated by dense birch woodland although the area at the base of the moraine consists of pasture land grazed by cattle.

2.2.2 Sampling sites in the Jotunheim region

The study sites are located on four glacier forelands in the Jotunheim region (Fig. 2.2a). The location, geomorphology and a brief description of the vegetation, for the Jotunheim region and glacier forelands under study, will be introduced in this section.

The Jotunheim stretches approximately 45 km from west to east and 35 km from north to south. The western side of the Jotunheim mountains is located 160 km from the Norwegian west coast. The two highest mountains in Northern Europe (Galdhøppigan 2469m and Glittertind 2452m) are located in the centre of the Jotunheim and these mountains have a significant influence on the prevailing weather conditions of the central valleys and peaks as well as on those areas located to the east of them. Ottadalen, which is located directly to the north-east of these mountains (and thus in the rain-shadow), had the lowest rainfall figures in Norway during the 1931 to 1990 period. Svellnosbreen is located on the north-eastern side of a number of peaks over 200 m in height. The three other forelands are located on the south-western and western side of the Jotunheim and so are not influenced by rain-shadow effects.

The flora of the four forelands is low- to mid-alpine. The low-alpine landscape is represented by a number of different plant assemblages. Heath species, such as *Vaccinium myrtillus*, and dwarf shrubs, such as *Salix glauca* and *Betula nana*, dominate the drier situations whereas snowbeds, bogs and moist stream-sides have their own characteristic assemblages. Species found in the mid-alpine zone are much the same although almost all of the dwarf shrub species can not survive at this altitude (Gjærevoll and Jørgensen, 1978) and the vegetation, in general, is more sparse. The vegetation of each foreland will be described in detail in the results section and briefly in the following foreland summaries.

The "Little Ice Age" forelands of the Jotunheim have been shaped by alpine valley glaciers, where several cirque glaciers have coalesced. Many of the Jotunheim glaciers have retreated to the point where they can no longer be considered as true valley glaciers but are either hanging, cirque or niche glaciers. The surviving glaciers of the Jotunheim are not in long narrow U-shaped valleys like many of those of Jostedalsbreen. Rather they are in subsidiary valleys off the main U-shaped valley which was de-glaciated about 9000 BP. They often do not have steep sides and the foreland itself tends to be steeper and shorter than on the subalpine forelands. The lack of steep sides to the forelands has a profound effect on the prevailing environmental conditions. For example, the winds can blow in many directions across the forelands and this affects snow-lie and hence vegetation patterns. High and steep sides to a valley can influence the direction and speed of winds found on a foreland (Vetaas, 1986).

The low-alpine foreland sequences are different to the mid-alpine and subalpine forelands in so much as they have a large altitudinal range. Previous studies (i.e. Matthews, 1976; Whittaker, 1985; and Crouch, 1992) have described the sequences for the low- and mid-alpine vegetation patterns in the region, but in fact they have had the same problem in so much as, at Storbreen, the upper part of the sequence (from the 1930 moraine) is at a higher altitude and so the pioneer ground is not part of an exclusive low-alpine sequence. The pioneer assemblages for the low-alpine sequences, found by the previous studies, refer to mid-alpine pioneer assemblages. This study is not different from the previous work in that it has not been possible to describe low-alpine pioneer assemblages. At Storbreen, it was therefore considered best to use a mid-alpine sequence, including the pioneer ground. Due to the considerable altitudinal gap between the 1900 and 1930 end moraines, so that the 1900 moraine is the youngest moraine in the low-alpine sequence. The 1900 moraine, at the low-alpine altitude, is considered to be of an early enough date to be able to describe the relative effects of age on vegetation and soil development. Two "replicate" low-alpine sequences were investigated, across the low-alpine sequence, in order to investigate whether the selected sequences are likely to be representative of the vegetation patterns across each foreland. At Svellnosbreen the full sequence, including the mid-alpine pioneer ground, was used because two separate sequences, at the low- and mid-alpine altitudes, was not practical. In addition, the foreland at Svellnosbreen gradually increases in altitude and does not increase sharply mid-way across the foreland as it does for the low-alpine sequence at Storbreen.

2.2.2.1 Storbreen foreland

Storbreen (Fig. 2.2) is an alpine valley glacier that issues in a north-easterly direction towards the main U-shaped valley in Leirdalen. It is located at 61° 35' N and 8° 10' E, 146 km from the Norwegian west coast at Brufjorden. The snout is at an altitude of 1400 m and the glacier is backed by four peaks, all over 2000 m, three of which are south-west of the glacier. The glacier is located on the eastern slope of the Smørstabb massif and is approximately 1300 m long and 700 m. It has a north-easterly aspect and the altitude of the foreland under study ranges between 1140 m and 1350 m. The foreland is divided by a rock bar which has been used, for the purposes of this study, to divide the foreland into a lower, or low-alpine section, and a higher, or mid-alpine section. The low-alpine section gently slopes from the 1750 moraine to the rock bar and rises 60 m (from 1140 to 1200 m) over a distance of 600 m. The mid-alpine section also gently slopes from the oldest lateral moraine down to the 1930 moraine (a drop of about 50 m in altitude) and then up to the fluted moraines (a rise of about 90 m). The total rise in altitude for the mid-alpine section, is 40 m over a distance of 500 m. The moraines of the mid-alpine section are lateral moraines and these are different to end moraines. Lateral moraines have generally been pushed up onto the valley sides by the glacier so that older moraines are often on slightly higher ground than the younger moraines. Conversely end-moraines, which have been used across the other forelands under study, are usually pushed down valley so that older moraines are usually at lower altitudes than the younger moraines. Lateral and end moraines differ in that the relative lengths of the moraine slopes differ. Although the shape is similar, with a shallow-sloping proximal moraine-side and a steep-sloping distal moraine-side, the proportions are different in so much as the shape of the lateral moraine is much more skewed with the distal slope being very short and the proximal slope being very long. It should be noted that some of the moraines are complex (the 1750; 1810; and the 1850/70), at particular points along their length, so that across certain profiles the moraines have two crests, and appear double so that the distal slope is older than the proximal slope. These complex sections of moraine are likely to have been created over a period of several years by the irregular nature of the retreat, stand-still and re-advance of different parts of the glacier snout. Differences between the moraines in size and shape, from foreland to foreland, can be seen in the profile diagrams (Figs. 4.3 to 4.10 and 6.1a-h). These diagrams have been drawn to scale and so differences in size and shape can be taken into consideration in the discussion of the results.

There are at least 10 moraine ridges on the Storbreen foreland of up to 6 m in height. The moraines have been dated using a combination of historical evidence for the 20th century (e.g. Rekstad, 1902) and lichenometry (Matthews, 1974, 1975, 1977; Erikstad and Sollid, 1986). The dates used in this study are those proposed by Matthews and most areas of the foreland are thought to be accurately dated to within ± 5 yrs. Two moraine sequences, a lower (STLF1 and STLF2) and an upper (STHF) were used in this study. The ages (and symbols) of the moraines selected for the lower sequence across this foreland are as follows: M1 - mature till-ridge; M2 - 1750; M3 - 1810; M4 - 1825; M5 - 1870; M6 - 1900. The upper sequence across this foreland are as follows: M1 - mature till-ridge; M2 - 1750; M3 - 1810; M4 - 1850/70; M5 - 1900; M6 - 1930; M7 - 1951; M8 - 1968. The mature till ridges are considered to have been exposed for the last 9000 years (Matthews, 1976). The youngest margins are not ridges but are broad and shallow fluted moraines running parallel with the path of glacier retreat (Matthews, 1976) and their shape approximates a shallow ridge. As can be seen in Table 2.1, the terminal moraine within the low alpine sequences, is considerably further from the snout than the terminal moraine within the mid-alpine sequence, and this suggests that the glacier climate may be more influential across the mid-alpine sequence.

The Storbregrove is the meltwater stream that issues from the glacier down to the River Leira. It has changed its course a number of times and has split into two channels on the early terrain, which join on the rock bar. A number of snow-patch meltwater streams create moist conditions along the southern side of the foreland. The main river channel runs centrally down the foreland, perhaps a little more towards the north side. The main channel splits below the rock bar into two main channels and a number of smaller streams. This allows for fairly widespread irrigation of the lower foreland. The moraines at Storbreen are well formed and although many of them are dissected by streams, or vestiges of streams, and consist largely of bouldery materials along their length, it is easy to find optimally vegetated profiles (see section 2.3.2) on sections of finer materials across each of the moraines. As mentioned, three sequences of transects were investigated at Storbreen, two across the low-alpine part of the foreland (STLF1 and STLF2) and one across the mid-alpine part of the foreland (STHF). The second sequence of transects across the low-alpine sequence, serves as an indicator of how representative the first series of transects are of the vegetation patterns and prevailing environment. If it is found that the vegetation patterns, and associated environmental parameters, show parallel development across these sequences, then it likely that the transects selected across the other forelands are representative of general patterns of vegetation development at those locations. Ideally, a second sequence of transects would have been advantageous across each of the forelands, but time did not permit further sequences to be investigated.

In phytosociological terms the lower section of foreland is low-alpine and the higher section is mid-alpine (Matthews, 1976). The foreland is above the birch tree-line and the sheltered, moister parts of the foreland are dominated by dwarf shrubs such as *Salix glauca, Salix lanata, Salix phylicifolia* and *Betula nana,* as well as a variety of meadow species. Heath species, such as *Empetrum nigrum, Vaccinium myrtillus* and *Phyllodoce caerula*, dominate the drier slopes and lichen heath dominates the driest or more exposed sites. Snow-patches are dominated by *Salix herbacea* as well as a number of inconspicuous species, such as *Cassiope hypnoides.*

2.2.2.2 Svellnosbreen foreland

Svellnosbreen (Fig. 2.2) is an alpine valley glacier that issues in an east south-easterly direction, 155 km from the Norwegian west coast at Brufjorden. To the north of Svellnosbreen is Galdhøpiggen, at 2469 m, the highest peak in northern Europe. Four of the six peaks in the vicinity of Svellnosbreen are over 2300 m. It is located at 61° 37' N and 8° 22' E. The snout of the glacier is at an altitude of 1600 m, although the foreland itself ranges between 1280 to 1440 m. The glacier foreland is approximately 1000 m long and 500 m wide and it has a south-easterly aspect. It is the steepest of all forelands, used in this study, with a rise of 180 m over a distance of 750 m. There are three channels, issuing from the glacier, that dissect the foreland, so that irrigation of the foreland is widespread. These channels join in the centre of the foreland. The three earliest moraines are located to the south of the channels; the three older moraines (including the oldest terrain) are located to the north of the main channel.

There are at least eight moraines on the Svellnosbreen foreland. The moraines have been dated using lichenometry (Matthews, unpubl.). Messer (1984) has also carried out investigations on the soil properties of moraines on this foreland using the dated sequences. The ages (and symbols) of the moraines selected for this foreland (SVLF) are as follows: M1 - mature gully; M2 - 1750; M3 - 1808; M4 - 1870; M5 - 1916; M6 - 1930. As can be seen in Table 3.1, the distance from glacier snout to the terminal moraine is 1000 m and thus it is likely that the glacier climate is likely to have a greater influence on the vegetation patterns across the younger moraines on the foreland than on the more distant sections of the foreland. Intermorainal differences in size and shape are greater on this foreland than on the other forelands (see profile diagrams - Figs. 4.3 to 4.10 and 6.1a-h). There is also a considerable altitudinal range across this foreland, so that the youngest moraines are found within the mid-alpine zone while the older moraines are found within the low-alpine zone. It was not possible to find a suitable till ridge on the oldest terrain, outside the foreland, so a gully was used because it possesses similar feature to a moraine – a proximal slope, a distal slope, sheltered bases and more exposed positions towards the top of each slope. The three youngest moraines are located on the western side of the glacier meltwater stream; the two older moraines and the mature gully are located on the eastern side of the stream, which means that the aspect of the distal and proximal sides is different between those two groups of moraines. This is unlike the other forelands where all the moraines are located on one side of the main glacier meltwater stream.

The young moraines are bouldery and it was difficult to find suitable sections of moraine that had well-developed vegetation on both the proximal and distal sides (see section 2.5.5). On the 1870 moraine (possibly a complex moraine dating between 1850 to 1870) a small stream ran through where the fourth quadrat should lie (see section 2.5.5). The vegetation around the stream was therefore recorded but a drier, more typical, shoulder-slope site was also sampled further along the moraine. In contrast, the older moraines consist of finer materials and are large and steep-sided. In places the sides are highly unstable, with evidence of mud-flow. The vegetation cover on the 1810 and the 1750 is relatively low: only one quadrat, of those sampled, comprised 100 % vegetation cover.

In phytosociological terms the lower, older and middle-aged portion of the foreland is low-alpine and the higher, youngest portion of the foreland is mid-alpine. The south-facing aspect of this foreland may have an effect on the component species in terms of earlier snow-melt as well as a higher risk of drought in places not well-irrigated by streams, such as ridge crests and higher slope positions. In addition, the high surrounding mountains may reduce the rainfall on this foreland. The steepness of this foreland may also have an effect on the soil and vegetation pattern. The Svellnosbreen foreland is therefore rather different from the other forelands in the study. However it is proposed that despite these differences it will be possible to elucidate the effects of altitude, age and microtopography on the vegetation patterns, and associated environmental parameters. These differences will be taken into consideration while discussing the results in the concluding chapter.

2.2.2.3 Høgvaglbreen foreland

Høgvaglbreen (Fig. 2.2) is a hanging valley glacier, the snout of which issues in a north-easterly direction, 150 km from the Norwegian west coast at Brufjorden. It is located at 61° 31' N and 8° 15' E. The glacier is backed by Midtre, at 2066 m and Høgvagltindane at 1967 m. The altitude of the snout is 1640 m and the section of the foreland under study ranges from 1400 to 1450 m. The glacier foreland is approximately 750 m long and 500 m wide and has a north-easterly aspect. It is gently sloping with an altitudinal range of 50 m over a distance of 750 m. The glacier itself is at the top of a cliff at the head of the foreland, the glacier, when it was larger, spread out into the main valley. This foreland is particularly exposed because not only does the glacier wind sweep down onto the foreland, but also winds from the east and west blow across the foreland as there are no valley sides to create shelter on the foreland.

There are at least 8 moraines on the Høgvaglbreen foreland of up to 5 m in height. The moraines have been dated using lichenometry by Erikstad and Sollid (1986) and Matthews (unpubl.). The ages (and symbols) of the moraines selected for this foreland (HØHF) are as follows: M1 - mature till-ridge; M2 - 1750; M3 - 1810; M4 - 1850; M5 - 1930; M6 - 1950. The mature till ridge is likely to date from the pre-Boreal, while the 1950 moraine can be dated from historical records. As can be seen in Table 3.1, the distance from glacier snout to the terminal moraine is the shortest of all the forelands within the survey (550 m) and thus it is possible that the glacier climate is likely to have a greater influence on the vegetation patterns across this foreland than across the other forelands.

The earliest moraine ridge is so small that it was only possible to set up five sites along the transect. The 1930 moraine has a very long and shallow distal slope, which may cause differences between low- and high-slope positions to not be very significant. The other moraines, however, within the sequence at Høgvaglbreen, are well-formed and it was easy to select well-vegetated transects across each profile (see section 2.5.5). There is no meltwater stream passing over the foreland from the glacier snout, although there is evidence of shallow pools between some of the moraines - none of these had water in them at the time of survey. Late-lying snow provides moisture for species located lower down the slope of the moraine.

In phytosociological terms, the foreland is situated in the mid-alpine zone. Lichen heath is prevalent and the larger shrubs, such as *Salix glauca,* are not as dominant as they are at lower altitudes. Vegetation on the younger ground is very scarce. Vegetation at the bases of the moraines is dominated by a bryophytic carpet with *Salix herbacea,* indicating late snow-bed communities. Parts of the foreland, especially the bases of the moraines, have very late-lying snow. In 1990, due to a cool summer, the snow covered most of the foreland during July and melted in the middle of August (Fig. 2.3). The vegetation, and associated environmental parameters, on this north-facing mid-alpine foreland are likely to be impeded not only by its exposed position, but also by late-lying snow.

2.2.2.4 Bøverbreen foreland

Bøverbreen (Fig. 2.2) is a broad glacier that issues from the Smørstabb ice-cap in a west north-westerly direction. The Sognefjell lies to the west of the glacier and the foreland is open to the wind, rain and snow that sweep across the pass. Bøverbreen is the highest and most exposed of all the sites in this study. The sparce vegetation on the west-facing side of many of the moraines in this study emphasises the importance of microtopography in harsh conditions. Bøverbreen is located 140 km from the Norwegian coast at Brufjorden, at 61° 25' N and 8° 2' E. The snout of this broad glacier is at an altitude between 1440 m and 1580 m. The section of foreland under investigation ranges in altitude from 1500 to 1540 m. The foreland is approximately 800 m broad and 800 m long and has a north-westerly aspect. The foreland can be conveniently divided into a lower and an upper section; this research has only made a study of the upper section due to time constraints. A stream runs over the foreland and it widens out into a series of small lakes along its length.

There are eight moraine ridges across the Bøverbreen foreland of up to 6 m in height. The moraines have been dated using lichenometry (Matthews et al, 1986) and the moraines of the lower sequence of moraines have been mapped (Emma Parvis, unpubl.). The ages (and symbols) of the moraines selected for this foreland (BØHF) are as follows: M1 - mature till-ridge; M2 - 1750; M3 - 1780* (entered as 1810); M4 - 1890* (entered as 1900); M5 - 1930; M6 - 1960. Unfortunately, long after the data had been analysed and described, reference to the Matthews et al (1986) paper revealed that the dates for M3 and M4 may not be correct and were in fact 1780 and 1890 respectively. Nevertheless, the differences are not considered to be so marked as to be likely to cause great changes in the data set and so the entries were not changed. They will therefore be referred to as the 1810 and 1900 moraines within the thesis. The mature till ridge is likely to date from the pre-Boreal, while the 1960 debris-covered rock bar can be dated from historical records. The distance from the snout to the terminal moraine (for the section of foreland sampled in the present study) is 845 m and so it is possible that the glacier climate will not have such a significant impact on vegetation patterns on the oldest terrain as it does on the younger terrain. The moraines on this foreland are well-formed. Semi-permanent snowbeds occur at the bases of some of the moraines and thus, in such cases, it was only possible to sample from the edge of the snowbed and not the actual base of the moraine. The youngest ridge selected for sampling at Bøverbreen was a debris-covered rock bar with two crest sites.

In phytosociological terms the foreland is mid-alpine. There is a sparse vegetation on the younger moraines and late-lying snow patches at the base of the moraines. In cool summers the snow does not disappear entirely from the bases of the moraines and there can be occasional snow showers during the summer months. The vegetation on the younger ground is sparse and the mature vegetation consists largely of lichen heath and dwarf shrubs such as *Empetrum nigrum* and *Phyllodoce caerula.* Heath species such as *Betula nana, Vaccinium myrtillus* and *Vaccinium uliginosum* were not present on any of the sites, indicating that this is a very exposed site. *Salix glauca* was not common and was not found on older ground. However, a few large specimens were found on ground exposed for about 30 years - a phenomenon which is rather difficult to explain. As at Høgvaglbreen, the influence of microtopography on the vegetation is noticeable. Exposure to westerly winds and snowlie appear, at first sight, to be particularly influential on vegetation and soil patterns at this altitude and this is discussed in greater detail in the concluding chapter (section 7.3).

2.3 Sampling design

The same data collections, using identical procedures, were performed at each of the forelands under investigation. It was considered practical to make Storbreen central to the present investigation, largely because of the extensive research work that has already been carried out at Storbreen which can be used for comparative purposes. Three sequences were therefore used for investigation at Storbreen, and subsidiary sites were located at five other forelands, so that the effects of altitude on the microtopographically and age-related vegetation patterns (and associated environmental parameters), could be investigated. The approach has thus enabled the Storbreen study to be placed in the broader perspective of an extensive range of altitudinal zones exhibited by arctic-alpine vegetation in Scandinavia.

An intensive sampling method was necessary, concentrating on the clear microtopographic gradients found across the moraines. The choice of comparable microtopographic situations on terrain of various ages was essential in order to determine, efficiently, how microtopography influences vegetation pattern with time and altitude. Comparisons of high-altitude and low-altitude sequences at Storbreen and also of other glacier forelands elsewhere in the Jotunheim and Jostedalsbreen regions, as outlined in section 2.2, were made.

2.3.1 Sampling across moraines

Once the foreland was chosen (see section 2.1.1), the moraines were surveyed and between six and eight moraines were selected, across each foreland, according to certain criteria. Each of the moraines were chosen according to their suitability of shape, size, substrate and vegetation cover: the moraines were selected if they had distinct proximal and distal slopes; had a profile that was at least 12 m in length (so that there was enough space for the placement of nine 1 x 2 m sites along its length); and the proportion of boulders was not so great that it noticeably undermined vegetation development along the profile.

Furthermore, an even spread of age across the foreland, from the youngest to the oldest moraine, was obtained as far as was practicably possible.

The choice of moraine has thus depended on an element of subjectivity and on some forelands it was not possible to find sites that closely fit the characteristics mentioned in the previous paragraph. However, on every foreland, each of the moraines have been described and their profiles drawn to scale (Figs. 4.3 to 4.10 and Figs 6.1a-h) so that potential anomalies within the data set, caused by intermoraine differences in size or shape, can be explained. It has been suggested that the investigation of the role of topography in soil (and hence) vegetation development adds another dimension of complexity to investigations concerned with vegetation succession and soil chronosequences and are therefore important and worthwhile (McCarroll and Ware, 1989). The difficulty of finding comparable sampling sites is a problem that all investigators of the role of topography come across. By selecting moraines according to certain criteria it is hoped that the approach has a greater objectivity.

2.3.2 Placing the transects

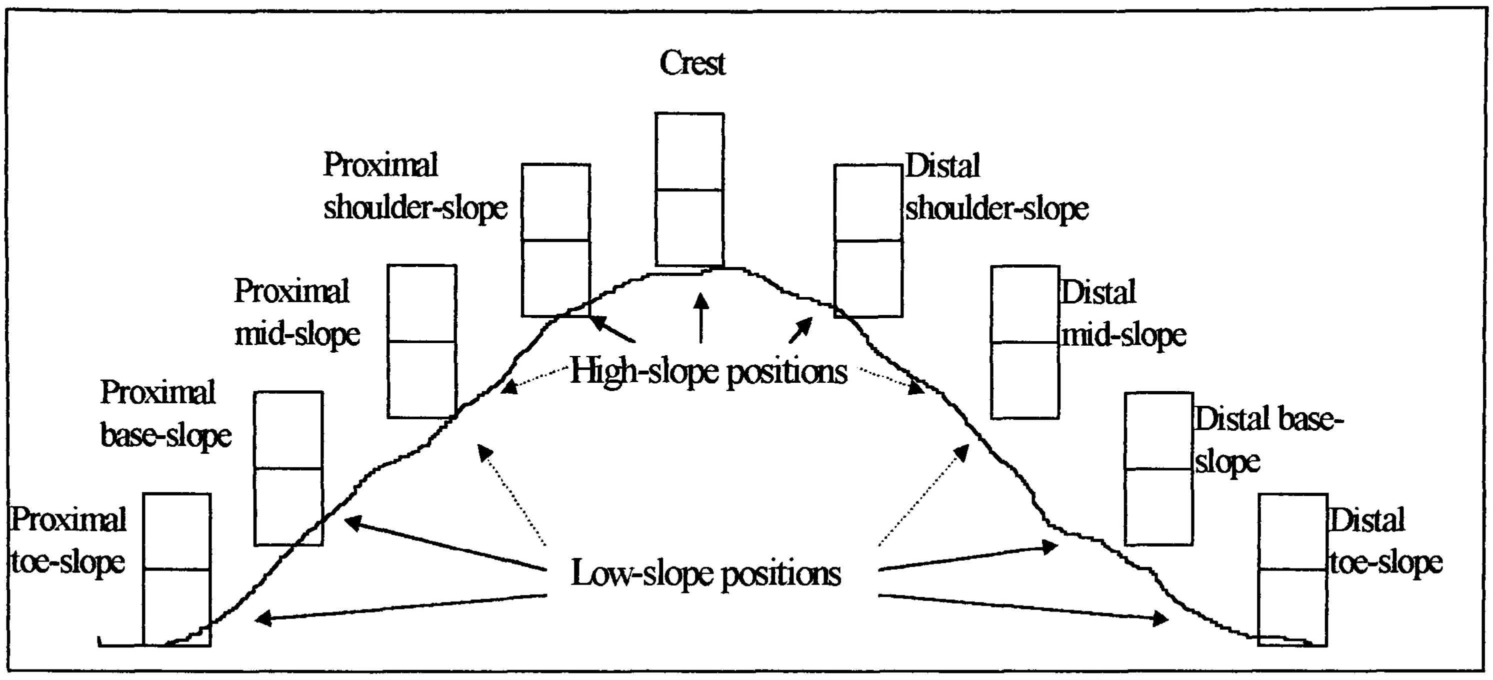
Due to the differences in both vegetation and microenvironment along each of the selected moraines it has been suggested, by previous authors, that careful site selection should be made to establish soil chronosequences (Jenny, 1980; Alexander, 1983, 1986; Birkeland, 1984) and hence vegetation pattern so that the sites can be compared impartially. The position of the transect across each moraine was therefore based on optimally vegetated profiles across each moraine, following the method of Mellor, (1985, 1987) and Messer (1988, 1989), on the principle that they represent the optimum environment for vegetation development and thus provide comparable sites for measurement. The transect was located and a long tape (30 m) laid along the transect. The beginning and end of the transect was marked using paint for ease of relocation. The profile of each moraine was recorded along the line of the transect, using a Suunto clinometer: measurements of slope were recorded at 2 m intervals, or at 1 m intervals where the slope profile was especially irregular. Each profile has been drawn to a scale of 3mm : 1 m (Figs. 4.3 to 4.10 and Figs. 6.1a-h).

2.3.3 Placing the sites and quadrats

As can be seen in Fig. 2.4, nine sites (a pair of 1 m^2 quadrats) were located across each of the moraines, with a small number of exceptions where the moraine was double (e.g. at Storbreen) or very small (1960, Høgvaglbreen). A "characteristic slope segment approach" was used to locate the sites along each transect so that sites were placed at the same relative position on each of the moraines for maximum comparability, following an approach used by numerous authors (e.g. Gittins, 1965; Elven, 1975; Sommerville et al, 1982; Vetaas, 1986; Walker et al, 1989).

Fig. 2.4 to show the characteristic slope segment approach used for site positions across moraines.

(Note: squares represent 1 m^2 quadrats)



Gjærevoll (1956: 21) recommends the use of 1 m^2 quadrats: "*a quadrat of this size is extremely convenient for scrupulously close investigation with a view to including all species, as far as that is feasible.*" Crouch (1992) made a specific study of the effect on a whole foreland species distribution using 0.25 x 0.25 m, 0.5 x 0.5 m, 1 x 1 m, 2 x 2 m, and 4 x 4 m quadrats. She found that the rare species and certain individual species, for example *Salix lanata,* had localised distributions and thus their range increased with the larger quadrat sizes. Her study suggested that the 1 x 1 m quadrat would give sufficient data with regard to the rare species or species with uneven distributions and this is also supported by Randall (1978). 2 x (1 m^2) quadrats (quadrats "a" and "b") were therefore laid side by side at each site at a maximum distance of 1 m from each other so that patches of bouldery or bare ground, between the quadrats could be avoided (following the optimally vegetated profile approach). The analysis of two quadrats, comprising a site, was considered to provide sufficient replication. As can be seen in Fig. 2.4 an average of 18 quadrats were placed across each moraine profile and site position was selected systematically using the "characteristic slope segment approach" so that each of the 9 pairs of quadrats were found at comparable positions. On both the proximal and distal slopes there were 4 sites: the "toe-slope" position, placed generally where the base of the moraine meets the floor of the foreland or where the lower portion of the moraine flattens out to a shallower slope angle; the "base-slope" position where the angle is steeper than the toe-slope site and the site is situated on the lower half of the moraine slope; the "mid-slope" position, where, as its name suggests, the site is located on the middle of the moraine-slope profile; the "shoulder-slope" position, where the angle is steeper than the crest and the site is located on the upper half of the slope. The "crest" position is located on the ridge top and generally has a shallower angle than the shoulder-slope positions. In some cases double moraines were selected for sampling so that quadrat pairs from the two crests were sampled and also quadrat-pairs from the intermorainal hollow were also sampled. As can be seen in Fig 2.4, where plant assemblages (or associated environmental parameters) are found to occur at a combination of positions, on the lower half of the moraine (which includes toe-slope, base-slope and mid-slope positions), the vegetation will be said to occur on "low-slope" positions. Conversely where plant assemblages are found to occur at a combination of positions on the upper half of the moraine (which includes crest, shoulder-slope and mid-slope positions) the vegetation will be said to occur on "high-slope" positions. The exposure index (or position index) used in this study, following a method used by Vetaas (1986), is consistent with, and relies upon, the position of the sites on each moraine (see section 2.5.6).

2.4 Taxonomy

All lichen, clubmoss, horsetail, fern and higher plant species were recorded. Higher plants are those that produce seeds and these are included with vascular plants which comprise all plants with vascular transport systems (including the spore-bearing ferns). The higher plants comprise some of the largest, and therefore most dominant, of the plant species and thus are the most important group to survey. Generally, most of the higher plant species are identified easily and so none have been excluded, although in some instances they have only been identified at the "family" taxonomic level (e.g. *Carex spp; Taraxacum spp; Hieracium, spp*). Lower plants, also referred to as cryptogams, do not produce seeds and include the lichens, mosses (bryophytes), clubmosses, liverworts, horsetails and ferns (Crouch, 1992). Bryophyte and liverwort species were excluded from the study due to the problem of time that would have been needed to identify these difficult groups of plants and therefore only the total percentage cover of bryophytes, at each quadrat, was recorded. It was considered more profitable to collect data from a greater number of moraines and forelands in order to satisfy the aims of the thesis. Crouch (1992), studying at Storbreen, showed that cryptogam assemblages display different distributions to those of the higher plants and she suggested that this was partly due to their greater environmental sensitivity. Flock (1987) suggests that bryophytes and lichens reflect the environmental conditions of their immediate surroundings and are good indicators of habitat type. Other researchers also emphasise the environmental sensitivity of cryptogams (e.g. Stork, 1963; Longton, 1988) and thus it was considered important to investigate the distribution of, at least, part of the cryptogam component.

The review in chapter (1) showed that lichen species are particularly sensitive to microtopographically-related differences in snow duration (e.g. Benedict, 1990a,b; Haines-Young, 1983) and therefore are a particularly useful group to include within the present study. Lichen dominated systems have been studied in detail by Kershaw (1977, 1978), Kershaw and Rouse (1971, 1973) and Larson and Kershaw (1974) and these studies show that the lichens are particularly useful indicators of microtopographical position. In addition, lichens are often the subject of investigations studying the effect of pollution on lichen distributions (Sochting and Johnsen, 1974, 1978; Westman, 1975; Rose and Hawkesworth, 1981), which further supports the view that lichens are particularly sensitive to environmental gradients. Lichens were also preferred to bryophytes due to the relative ease of identification of this group in the field. Crouch (1992) suggested that the cryptogam component (both bryophytes and lichens) have corresponding distribution patterns, and this suggests that lichens provide an adequate representation of the cryptogam component. The exclusion of bryophyte distribution patterns can therefore be justified, although it is admitted that the inclusion of bryophyte distribution patterns would have been of great interest and relevance, had there been time. Following Crouch (1992) only the distribution of terricolous lichen species is described. This is because saxicolous (epilithic) lichens are used for the estimation of age (*Rhizocarpon geographicum*) by previous authors (e.g. Matthews, 1974, 1975, 1977) and for the estimation of snow lie (see section 2.6.1). All clubmosses, horsetails and ferns will also be recorded.

2.4.1 Nomenclature

The mountain flora of Scandinavia has been described by many authors (e.g. Dahl, 1956; Gjærevoll, 1956). The assemblages described by these authors follow a slightly different nomenclature to that used in the present study. The nomenclature used in this thesis follows that used by Matthews (1976), Whittaker (1985), Coker, (1988) and Crouch (1992). Identification of plants in the field was achieved with help from John Matthews (higher plants) and Helena Crouch (all species). Gjærevoll (1978) was extensively used in the field for higher plant identification. The nomenclature of Lid and Gjærevoll (1985) was followed for higher plants. All higher plants were identified in the field. Nomenclature of lichen species follows Dahl and Krog (1973). Lichens and other lower plant species were identified in the field using Jahns (1980) and Moberg and Holmasen (1982), although their nomenclature was not necessarily followed. All species not identified in the field were sent to the Botany Department, at the Natural History Museum in London, to be identified by Brian Coppins. A complete list of full species names (including a few species that have not been identified), and their abbreviated forms, is given in Appendix 1. This list should be used to interpret the abbreviations for species names used in the following chapters.

2.4.2 Recording the vegetation

The vegetation recording techniques used in this study follow Crouch (1992). Data was collected concerning the percentage cover and frequency of plant species in each 1 m^2 quadrat. Crouch (1992) outlined the benefits of using percentage cover data rather than frequency data. For present study purposes, frequency, using the number of small squares in which the species occurs, does not take into account the size of each specimen and can greatly over estimate the relative importance of a small but widely dispersed species. Shoot frequency also suffers similar problems, again because the size of the plant is not taken into account, so that a tiny, but widely dispersed species will have a much greater score than a large individual specimen. In addition, the shoot frequency methodology is time consuming. Percentage cover does not suffer the problems shown by frequency data, but the main disadvantage of percentage cover data is the lack of consistency between different recorders (Matthews, 1976; Whittaker, 1985). Both Matthews (1976) and Whittaker (1985) conducted specific tests in order to look into the variations in recording between different operators and Whittaker's results show significant differences in results derived from the each of the student assistants. Both Matthews and Whittaker suggest that frequency is likely to be a more suitable method where large numbers of inexperienced assistants are being used, especially for large-scale projects involving the investigation of general vegetation patterns. However, in the case of small-scale and detailed studies, where the patterns of both higher and lower plant forms are involved, and where the recording is performed by one or two experienced investigators, it is suggested that percentage cover is likely to give a more realistic impression of the vegetation patterns (Crouch, 1992). For present study purposes, as only one recorder (the author) collected the data, percentage cover of plant species in each 1 m^2 quadrat was the preferred measure of vegetation cover, although frequency (presence or absence in 25 small squares of each 1 m^2 quadrat) was also recorded. Different vegetation layers were considered separately (Birks, 1980), so that the total vegetation cover for all the species could add up to more than 100 % cover. All species, in this case vascular plants and lichens, were recorded, including infrequent (or rare) species. The environmental factors were recorded at the same time on a separate sheet. In order to support the year to year accuracy of the data collection, for both vegetation cover and environmental parameters, a series of replicate quadrats were used for remeasurement over three field seasons and the method and results of the remeasurement test are described in section 2.10.2.

2.5 Macro- and meso-environmental factors

This section describes the macro- and meso-environmental parameters that are considered to be an important influence on the vegetation and associated micro-environmental factors. Each section includes a description of the method of recording used, and a brief justification as to the choice of methodology.

2.5.1 Altitude

Table 2.2 Altitude of moraine profiles

Moraine transect	Altitude of moraine transects on each foreland (*metres*)							
	AUSF	FÅSF	STLF1	STLF2	SVLF	STHF	HØHF	BØHF
M1	320	460	1140	1140	1310	1330	1400	1500
M2	290	470	1160	1160	1280	1350	1420	1500
M3	310	470	1170	1170	1280	1350	1420	1500
M4	320	510	1180	1180	1440	1330	1430	1540
M5	340	550	1200	1200	1440	1310	1440	1540
M6	360	630	1200	1200	1440	1310	1450	1540
M7	380					1330		
M8						1350		

(see Appendix 2 for foreland abbreviations)

The review in chapter (1) has shown that altitude is likely to be an important influence on both vegetation patterns and the prevailing microenvironment. It is likely that it is most influential in that temperatures tend to be lower, and exposure to wind greater, at increasing altitudes. It is therefore important to record the altitude of all sites within the data set. The method used to find the altitude of each moraine was to plot the position of each of the moraine profiles onto to large scale maps. The altitude of each of the moraines is displayed in Table 2.2 and was entered into the DCA ordination analysis under the abbreviation "Alt tud" (see Appendix 3). It should be possible to unravel the relative influence of altitude on vegetation patterns and associated micro-environmental parameters, by interpreting the data within the ordination results.

2.5.2 Age

As discussed in section 2.1, a "space-for-time substitution" methodology (sensu: Pickett et al, 1987), is used within the present thesis and all the moraines used for investigation have been dated using various methods (see section 2.2). Because "space-for-time substitution" is being used it was important to enter the ages of quadrats (for each moraine profile) into the data set. On the whole the dating of the moraines themselves has been relatively accurate (Matthews, 1992) but the dating of the oldest terrain, used within the present study, is not so accurate because not all the till ridges used for investigation have been dated. Nevertheless, the general opinion is that the oldest terrain is likely to be at least an order of magnitude older than the Little Ice Age terminal moraine (Matthews, 1991). It was therefore decided not to use the actual ages of the moraines and till ridges, but to use ordinal scale age categories instead, to represent the ages of each of the moraines.

Table 2.3 Age categories of moraine profiles as entered into the FORTRAN data set.

Moraine	Age category of moraine profile *(Date of moraine in brackets)*							
	AUSF	FÅSF	STLF1	STLF2	SVLF	STHF	HØHF	BØHF
M1	**11** (1750+)	**11** (1750+)	**11** (1750+)	**11** (1750+)	**11** (1750+)	**11** (1750+)	**11** (1750+)	**11** (1750+)
M2	**10** (1785)	**10** (1750*)	**10** (1750)	**10** (1750)	**10** (1750)	**10** (1750)	**10** (1750)	**10** (1750)
M3	**6** (1853)	**8** (1810*)	**8** (1810)	**8** (1810)	**8** (1808)	**8** (1810)	**8** (1810)	**8** (1810*)
M4	**5** (1871)	**4** (1909)	**7** (1825)	**7** (1825)	**6** (1870)	**5** (1850/70)	**6** (1850)	**4** (1900*)
M5	**4** (1908)	**3** (1930)	**5** (1870)	**5** (1870)	**4** (1916)	**4** (1900)	**4** (1930)	**3** (1930)
M6	**3** (1935)	**1** (1970)	**4** (1900)	**4** (1900)	**3** (1930)	**3** (1930)	**3** (1950)	**2** (1960)
M7	**2** (1960)					**2** (1951)		
M8						**1** (1968)		

(see Appendix 2 for foreland abbreviations)

Additionally, although an attempt was made to get an even spread of aged moraines across each foreland, it was not always possible. It was therefore necessary to create categories that are fine enough to display the spread of ages across each of the forelands and so eleven categories of 25 years each were formed. This gives a fairer illustration of the influence of age on the vegetation patterns. This is also a more representative method than simply numbering the moraines according to their order of occurrence across the foreland. The age categories are as follows: **1** (0-25 yrs); **2** (26-50 yrs); **3** (51-75 yrs); **4** (76-100 yrs); **5** (101-125 yrs); **6** (126-150 yrs); **7** (151-175 yrs); **8** (176-200 yrs); **9** (201-225 yrs); **10** (226-250 yrs); **11** (> 251 yrs). The age categories are deciphered by quantifying the time between the dates of the moraines to 1992 and are entered into the analysis under the abbreviation "Age Mor" (see Appendix 3). The age categories (and dates) of the selected moraines across each foreland are displayed in Table 2.3. It is hoped that the relative influence of age on vegetation patterns and associated micro-environmental parameters, can be resolved by interpretation of the data within the ordination results.

2.5.3 Size and shape of moraines

Moraine size and shape is likely to influence the pattern of vegetation and associated environmental parameters on the moraines to a certain extent. A number of simple indices were therefore tested in order to find a measurement that could represent the size and shape of the moraines, within the context of the present study, but none proved to be useful measurements. For example, a moraine height measurement does not take into account the volume of the moraine nor the shape; a volume measurement does not take into account the height or the shape; a profile length measurement does not take into account the height or shape; and a height over transect length measurement does not illustrate how big the moraine is. These simple indices were therefore not used.

The aim of the present study is to investigate the **general** effect of microtopography on vegetation patterns and associated parameters and the sampling design was such that, on the whole, moraines of similar shape and size were chosen. To investigate the effect of microtopographical shape or size, on vegetation patterns and associated environmental parameters, would require a sampling design that specifically investigates that particular question. It was therefore considered more meaningful to discuss the question of moraine shape or size in relation to the profile diagrams (Figs. 4.3 - 4.10 and Figs. 6.1a-h) which have been drawn to scale and thus are accurate representations of the moraine profiles where the transects have been laid. The profile diagrams will therefore be used as a reference point for any discussion of anomalies within the data set that appear to have resulted from moraine size or shape.

2.5.4 Aspect of moraine slope

Aspect, at the meso-scale (whole foreland) level, has been shown to have a significant influence on vegetation pattern as well as the micro-environment (Matthews, 1976; Whittaker, 1985; Crouch, 1992).

Vetaas (1986) has shown that aspect can have an effect at the microtopographical scale, across a moraine. Aspect can effect the side of the slope in terms of the amount of sunshine it receives and in turn this can influence a whole range of other factors. Aspect, however, is a problematic parameter because its influence on the foreland is difficult to separate from many other factors, including the effects of the glacier winds (always the proximal side of the moraine) and the prevailing winds (see chapter (1) for a general description of the regional climate for Jostedalsbreen and Jotunheimen and section 3.3. for a more detailed description). Nevertheless, it should be possible to decipher the relative influence of aspect, at the microtopographical level, by interpreting the data concerning the relative northerliness and easterliness of the moraine slopes within the ordination results.

Table 2.4 Aspect scales for northerliness and easterliness

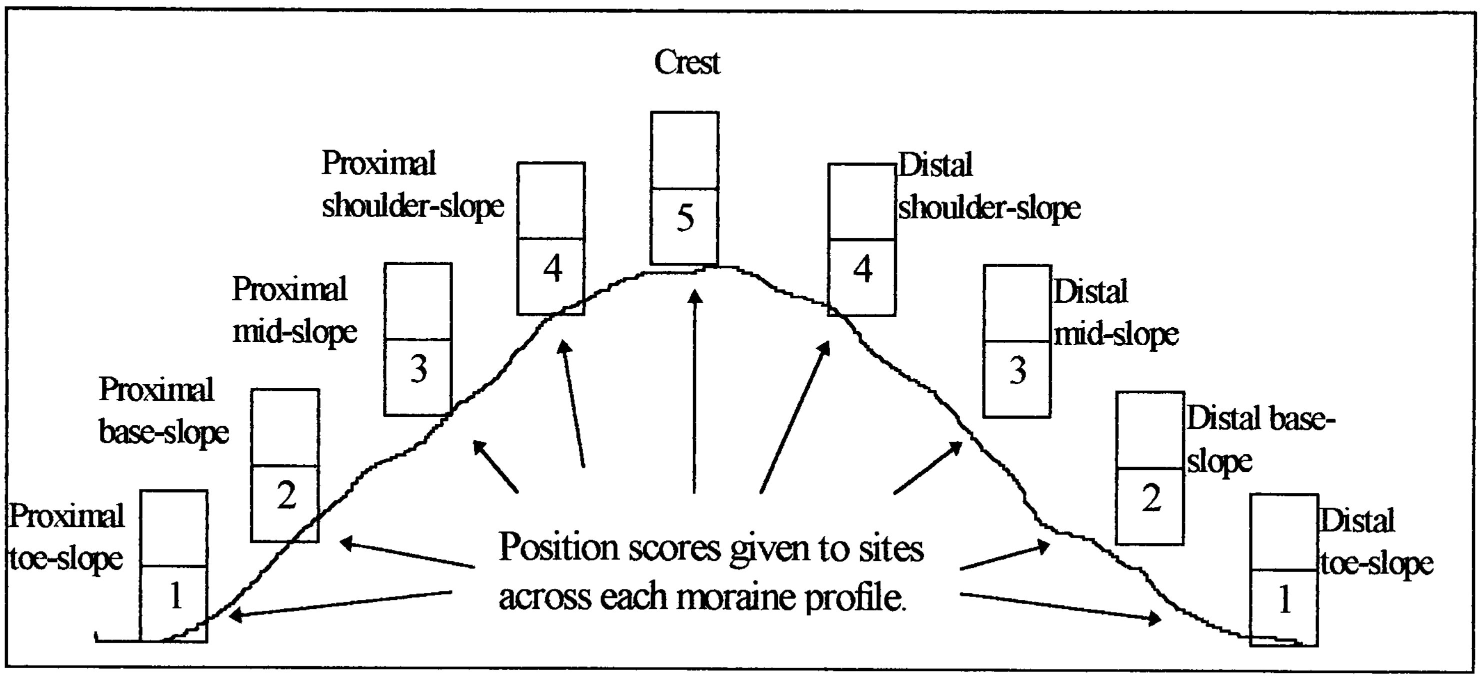
scale	northerliness (compass readings)	scale	easterliness (compass readings)
1	67.5 - 112.5°	1	337.5 - 22.5°
2	112.5 - 157.5° and 67.5 - 22.5°	2	22.5 - 67.5° and 337.5 - 292.5°
3	157.5 - 202.5° and 22.5 - 337.5°	3	67.5 - 112.5° and 292.5 - 247.5°
4	202.5 - 247.5° and 337.5 - 292.5°	4	112.5 - 157.5 and 247.5 - 202.5°
5	247.5 - 292.5°	5	157.5 - 202.5°

The measurement of aspect has been performed for both distal and proximal slopes of each of the moraine profiles used within the present study. The measurements record the direction in which the slope is facing. Two variables have been used, as entered into the FORTRAN formatted data set used for the DCA indirect ordination analysis: a) deviation from the north (on a scale of 1 to 5); and b) deviation from the east (on a scale of 1 to 5). As can be seen in Table 2.4, they have been entered into the analysis under the abbreviations "Asp ect" and "Asp eas" respectively (see Appendix 3). It should be possible to decipher the relative influence of aspect on vegetation patterns and associated micro-environmental parameters, by interpreting the data within the ordination results.

2.5.5 Exposure (position index)

Exposure is a measure of the degree to which a site is exposed to the wind. Wind is desiccating, cooling, eroding and abrasive and therefore can have a significant effect on vegetation composition and physiognomy at any site. In subalpine and alpine habitats, the influence of wind is most noticeable through its influence on snow distribution (e.g. Billings and Bliss, 1959; Knight et al, 1977; Whittaker, 1989) and these relationships are discussed in considerable detail in the review section (1.3 and 1.4). An index of exposure, based on microtopographical position, has been developed in order to provide an estimate of the exposure of each site across any moraine profile (Fig. 2.5), with the most exposed sites considered to be at crest positions and the least exposed sites at the toe-slope positions. A considerable body of research, reviewed in section 1.3.2 and 1.4.1, supports the hypothesis that exposure increases up a small ridge (e.g. Elven, 1975; Vetaas, 1986; Alexander, 1986) and this in turn endorses the use of site position to provide an estimate of relative exposure at the microtopographical scale. As can be seen in Fig. 2.5, the index is based on the relative position of quadrats on each moraine: toe-slope positions score (1); base-slope positions score (2); mid-slope positions score (3); shoulder-slope positions score (4); and crest positions score (5). The position scores of each quadrat, as entered into the FORTRAN formatted data set used for the DCA indirect ordination analysis, are displayed in Fig. 2.5 and are entered into the analysis under the abbreviation "Pos env" (see Appendix 3). It should be possible to decipher the relative influence of exposure (or microtopographical position) on vegetation patterns and associated micro-environmental parameters, by interpreting the data within the ordination results.

Fig. 2.5 The allocation of position scores to the different sites across each moraine profile.



2.6 Micro-environmental factors associated with climate

2.6.1 Snowlie

Snow-lie was measured by comparing the percentage proportion of the black saxicolous lichen *Umbilicaria* genus to the green saxicolous lichen *Rhizocarpon spp* on stones within, or near to, each quadrat. For example, if all (i.e. 100 %) of the selected saxicolous lichens in the vicinity of the quadrat are green then the percentage proportion of black to green is 0 %, whereas if 30 % of the lichens are green, then the percentage proportion of black to green is 70 %. These lichens are saxicolous and are not being recorded within the vegetation data set (only terricolous lichens are being recorded for the vegetation data set) and therefore the circular argument involving the use of plant species to relate environmental parameters to vegetation types can be avoided. The ratio of black to green lichen percentages of each quadrat, as entered into the FORTRAN formatted data set used for the DCA indirect ordination analysis, were entered into the analysis under the abbreviation "Sno lie" (see Appendix 3). It should be possible to decipher the relative influence of snow duration on vegetation patterns and associated micro-environmental parameters, by interpreting the data within the ordination results.

The present methodology was first used by Crouch (1992). Field guide taxonomists show that saxicolous lichens have clear distribution patterns (Dobson, 1979; Moberg and Holmåsen, 1982; Jahns, 1980) and the distribution of the black genus, in contrast to the green genus, is very clearly seen across the moraines on the forelands under study. The green genus occurs in less exposed hollows and in decreasing proportions up the moraine slope, whereas the black genus occurs on the ridge crests and in decreasing proportions down the moraine slope. As discussed in the review chapter (1), Benedict (1990a,b) transplanted specimens of *Rhizocarpon spp* to ridge crests, and *Umbilicaria spp* to snow banks, and found that *Rhizocarpon* is considerably more resistant to snow-kill effects. Haines-Young (1983, 1985, 1988) investigated size variations of *Rhizocarpon* on moraine slopes in S. Norway and his results support the "Green zone hypothesis" which states that the maximum thallus diameters are largest at the foot of the proximal slopes of moraine ridges where snow cover remains until the late spring and provides a reliable source of moisture. The results of Benedict's experiments, as well as the description of the green saxicolous lichen distributions by Haines-Young, show that a green zone existing on the lower slopes of the moraines can be used to indicate differential snow cover across the moraines and justifies the present method of snow-lie assessment. In addition, Crouch (1992) found that snow-lie correlates strongly with exposure, but not with site age, suggesting that there does not seem to be a difference in the rate of colonisation of the two taxa used thus further justifying its use for present study purposes.

2.6.2 Moisture

Water has an obvious and significant effect on all plant functions, including photosynthesis, and its significance, with regard to vegetation patterns, is discussed in chapter (1). Surprisingly few studies have investigated this parameter despite its obvious importance (Kershaw and Looney, 1985). Many authors describe the significance of moisture, or precipitation, in a subjective way or by quoting other authors, but have not measured the parameter quantitatively (e.g. Stork, 1963; Persson, 1964; Kershaw and Rouse, 1973; Jacobson and Birks, 1980; Wijk, 1986a,b; Walker et al, 1989). Others vaguely refer to the measurement of the parameter but nowhere do they discuss the results of that measurement (e.g. Ugolini, 1968; Crocker and Major, 1955). The reason behind the lack of useful moisture data is likely to be due to a number of reasons, largely related to methodology. Firstly, some of the techniques are cumbersome, time-consuming and inaccurate (such as moisture blocks and gravimetric analysis) and are therefore not practical for present study purposes. Another proven method was shown to be expensive and needs careful handling, and thus is inappropriate for field use, namely the neutron probe (Bell, 1976). Other methods, such as using a simple moisture meter (such as the "Rapitest" (Rapitest Ltd, London Rd, Corwen, Clywd, LL21 0DR) moisture meter) or indicator paper (such as cobalt blue) are relatively inaccurate and do not display adequate differentiation between different moisture levels, especially at the drier end of the scale.

Because of the problems associated with the collection of moisture data, this study has mainly used a simple approach developed by other researchers in the region. Whittaker (1985) used a subjective approach by estimating the relative moisture of a soil on an ordinal scale of 1 to 5. Crouch (1992) developed this into a standardised scale which she considered to be the most useful measure of relative moisture levels at different sites. She named the test the "finger test" method and her methodology is used within the present study. In addition, a quantitative approach to the measurement of moisture, using a prototype instrument called a capacitance probe, has also been performed in order to determine the accuracy of the finger test method. Both approaches are described below.

2.6.2.1 Capacitance probe

The capacitance probe is an instrument developed by the Institute of Hydrology in collaboration with Didcot Instruments. It measures moisture by determining the dielectric constant of the soil. Technical details about the instrument are available (Bell et al, 1987; Dean, 1994) and recently the instrument has been tested on ridge and furrow microtopography in order to test the sensitivity and reliability of the instrument (Robinson and Dean, 1993). The authors conclude that the instrument provides "*reliable values of water content over a wide range of moisture content*" and that "*considering the inherent errors in the gravimetric method (sample volume, weighing errors, bound water), the calibration graphs for this soil were satisfactory*" (Robinson and Dean, 1993: 83).

The instrument used, within the present study, is a prototype and was tested over two field seasons. Unfortunately it failed, without any results, in the first year due to battery failure. In the second year, after the measurement of a series of reproducibility measurements and the moisture of one foreland (Svellnosbreen) had been completed, the probe failed again but this time due to a faulty connection. Despite not having a full data set of moisture measurements taken for all forelands, the results obtained could be compared with the results of the "finger test" method and gave an indication of the reliability of the results derived from the "finger test".

To test the precision and reproducibility of the capacitance probe measurements, an experimental transect was established across the AD 1750 moraine on the Storbreen glacier foreland, the results of which are described and discussed in section 3.3.2. The transect comprised four pairs of 1 m^2 quadrats (four sites) placed at the proximal base-slope position; the crest; the distal base-slope position; and an area of impeded drainage (i.e. waterlogged) between two streams. Moisture measurements were taken after four rain free days, one in each of the 25 subdivisions of each of the quadrats (a total of 50 measurements per site). Moisture measurements were taken at the surface; at 2 cm depth; and at 5 cm depth. Later, the measurements were repeated at the same sites after prolonged rainfall. The data was used to estimate the number of measurements necessary in order to obtain representative measurements of soil moisture in any quadrat. The results of the test are described in 3.3.2.1. On the basis of the "trial run results", outlined in section 3.3.2.1, four readings (at a depth of 2.5 cm and surface) were then used in a more extensive survey of soil moisture on the Svellnosbreen glacier foreland, where each of the depth readings were taken across six moraine ridges at nine sites per moraine (see results section 3.3.2.2).

The probe records on a scale from 1 (wet) to 1.78 (air reading) and it is necessary to use a calibration chart to convert the probe readings to % water content (Fig. 3.10). Calibrations for the probe, at the three measurement depths, were performed by the Institute of Hydrology and before the measurements from the probe could be used they had to be converted, using the calibration chart provided by the Institute of Hydrology (Fig. 3.10), to a volumetric % water content. The probe was calibrated in bare soil in the Oxford area for the 5 cm depth. The calibrations for the 2.5 cm and surface depth measurements were performed in the laboratory using ex-oven dried sandstone soil with very little organic matter (in order to approximate glacial till). The laboratory calibrations were carried out using a plastic 2 litre beaker with a wet bulk density of about 1.3 - 1.4 gm/cc. Error bands arose because it was difficult to get a uniform distribution of water in the soil. The curves were drawn by eye through the points following the general shape of the 5 cm curve and it is suggested that the curve flattened off at low moisture content because the probe was running out of range and approaching the air count (Dean, pers. comm.).

2.6.2.2 Finger test method

Moisture was measured across all forelands using the "finger test" which is a standardised scale methodology developed and tested by Crouch (1992). It was used because it is convenient, relatively accurate and the results from each site are comparable. The test was carried out after a period of at least two rain-free days. As discussed in section 1.2.2, the climate and weather patterns of each of the forelands differs to some extent and thus it was not possible to maintain a sampling strategy (with regard to the weather) that was as consistent as that of Crouch (who only sampled at Storbreen). However, the moisture measurements were conducted on the same day for each of the forelands and the length of the preceding dry period was noted so that the within-foreland sampling strategy is considered to be consistent.

The "finger test" method involves a feel test of the soil dryness at three depths (5 cm; 2 cm; and surface) on a standardised scale of 1 (wet) to 5 (dry) and it was this scale that was used, for all forelands within the data set, for analysis. The number used in the analysis was all three depths combined into one reading, at each site, so that the figures for moisture are on a scale from 3 to 15. The table below shows the 1-5 scale used for each depth measurement. It should be noted that the higher the reading, the drier the ground, so that this scale could also be referred to as a "dryness" scale. The "finger test" scores of each quadrat, as entered into the FORTRAN formatted data set used for the DCA indirect ordination analysis were entered into the analysis under the abbreviation "Moi tre" (see Appendix 3). It should be possible to decipher the relative influence of moisture on vegetation patterns and associated micro-environmental parameters, by interpreting the data within the ordination results.

Table 2.5 Scale used for "Finger Test" method of moisture assessment

Scale	Description
1	Wet, push finger into substrate and pool forms
2	Wet feel, water present on finger when pulled out
3	Damp feel, can see darker stain of water
4	Substrate sticks to finger a little, no damp stain
5	Dry, no soil sticks to finger

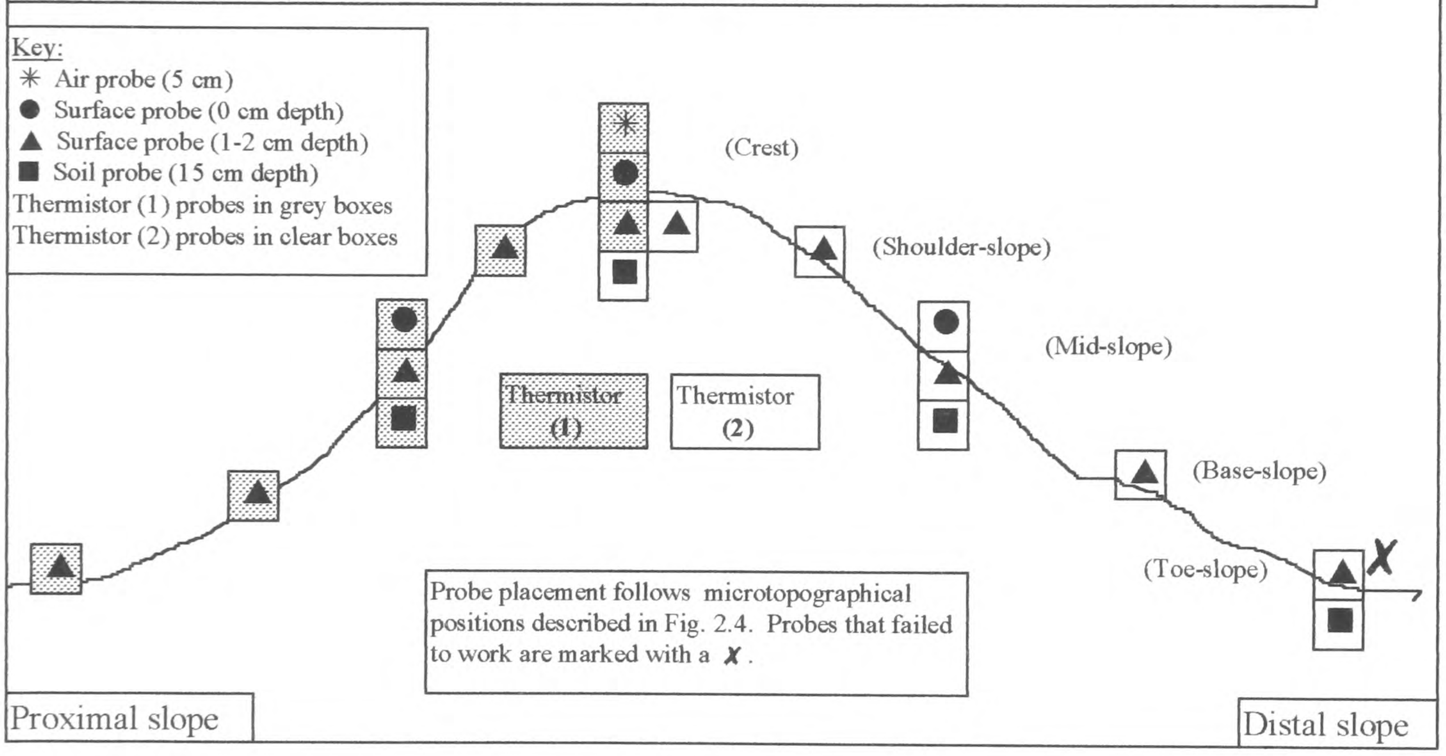
2.6.3 Temperature

Temperature is known to be a major influence on regional plant population patterns (e.g. Crawford, 1989). For example, many authors associate the effects of temperature, especially on arctic and alpine plants, with the shortness of the growing season and suggest that it is the most potent factor in determining the assemblages present (Longton, 1988; Wijk, 1986). Temperature was not measured at all sites due to the large number of sites in the study but year-long measurements, across selected moraines, was possible. Temperature measurements were made across two moraines (the 1750 and the 1900) on Storbreen foreland (alt: 1150 m) between 1989 and 1991. The measurements were made using Grant Thermistor Recorders. Grant Thermistor Recorders became obsolete in 1995 but their outdatedness has no relevance to the validity or accuracy of the collected data as long as the machines are properly serviced and regularly calibrated (Grant instruments, pers. comm., 1997). The fact that the recorders were rather old, at the time of use, should have little effect on the problem of "age-related drift", as research has found that the drift tends to be greatest in the first year or two of the instrument's life (Trolander et al, 1971). The recorders were calibrated at the beginning and end of each season and all had undergone recent servicing, either by Grants or by college technical staff. The data from probes found to be recording inaccurately at the end of each season were not used for data input, and such probes are marked with a "✗ " within the diagrams of probe placement (Figs. 2.6 to 2.8). One of the six thermistors broke down entirely and so the probe emplacement for that particular thermistor is not described.

2.6.3.1 Thermistors (1) and (2) (the 1750 moraine, 1989-90)

In the 1989 field season, two thermistor recorders were set up on the 1750 moraine at Storbreen (alt: 1150 m). These thermistors had nine probes each and temperatures used for averaging were those taken at 3 a.m. (considered to be the coolest part of the day) and 3 p.m. (considered to be the warmest part of the day). As can be seen in Fig. 2.6, the probes were placed according to the "Characteristic slope segment approach" described in section 2.3.3. It is hoped that the results derived from the thermistor recorders will reflect any differences in temperature as affected by microtopography. The main aim is to understand how microtopography affects temperature and hence vegetation patterns. For this reason, the majority of the readings (nine in all) were carried out in the top two cm at each of the nine sites, where the majority of coloniser's plant roots are found. An air temperature reading was also taken, 5 cm above the crest, in order to ascertain above ground air temperatures. Another 3 probes were placed at the surface at proximal and distal mid-slope positions, and also the crest, in order to compare temperatures of possible germinating sites. Lastly, four probes were placed at 15 cm depth at the proximal mid-slope position, the crest and the distal mid-slope and toe-slope positions in order to ascertain deeper soil temperatures. Probes were shielded from direct sunlight, either by vegetation or soil. Two probes were placed side by side at the 2 cm depth on the crest to check for consistency of temperature readings between the thermistor recorders. The measurements, two per day for each probe, were averaged (for analysis purposes) for two-weekly periods throughout the measurement period. The year-long temperature results (Figs. 3.20-23) are displayed using the temperature means (and standard deviations) for two-week periods, at different microtopographical positions.

Fig. 2.6 Thermistors (1) and (2), 1750 moraine, twice daily measurements taken between 26th August, 1989 to 19th August 1990.



2.6.3.2 Thermistors (3), (4) and (5) (the 1900 and 1750 moraines, 1990-91)

In the 1990 field season, four instruments were set up, two at the same location as in the 1989-90 measurement season, on the 1750 moraine, and two on the 1900 moraine. The positions chosen for the probes were not the same as those used in the 1989 season because two thermistors, measuring every two hours, were used and thus the rolls would run out after three months. In order to obtain a a years duration of temperature data across the entire moraine, the positions chosen for measurement in the 1990-91 period differed to those used in the 1989-90 period. However, the positions used for probes were the same for both the 1900 moraine and the 1750 moraine during the 1990-91 field season. Probes for the two-hourly thermistor were all placed at 1 cm depth at all sites, across the 1900 and 1750 moraines, except on the mid-slope positions (a total of seven sites). Probes (nine in total per moraine) from the thermistors, that were making year-long measurements, were placed on the 1900 and 1750 moraines at the following positions: at 15 cm depth on proximal and distal toe-slope positions and the crest; at 1 cm depth on the proximal and distal toe-slope, mid-slope and crest positions; and at 5 cm in the air above the crest. Probes were placed according to the same rationale used for the 1989-90 measurements. The probe placement, for the 1990-91 field season, is summarised in Fig. 2.7 (1900 moraine) and Fig. 2.8 (1750 moraine), and it should be noted that the two-hourly thermistor on the 1900 moraine failed and so the probes are not summarised in Fig. 2.7. The data used for analysis, from the two-hour thermistors, comprised averages of six measurements per day (3 am, 7 am, 11 am, 3 pm, 7 pm, 11 pm) over a series of five-day periods. The measurements for the year-long thermistors, using the same methodology as the 1989-90 season, used averages (for analysis) of two measurements per day (3 am and 3 pm) for a series of two week periods. The year-long temperature results (Figs. 3.24-27) are displayed using the temperature means (and standard deviations) for two-week periods, at different microtopographical positions. The 2-hour thermistor results are displayed using the temperature means (and standard deviations) of 5-day periods, at different microtopographical positions, for a total of four months. This was done in order to find out if by using six measurements per day (instead of two) there would be a difference in the temperature patterns shown by the results (see section 3.3.3.3-4). The means (for the six x daily measurements) used 5 days of data (instead of the two week period used for the twice daily measurements) so that the sample sizes would be similar (normally 30 readings per probe for each time period).

Fig. 2.7 Thermistor (3), 1900 moraine, twice daily measurements taken between 24th August, 1990 to 14th August 1991.

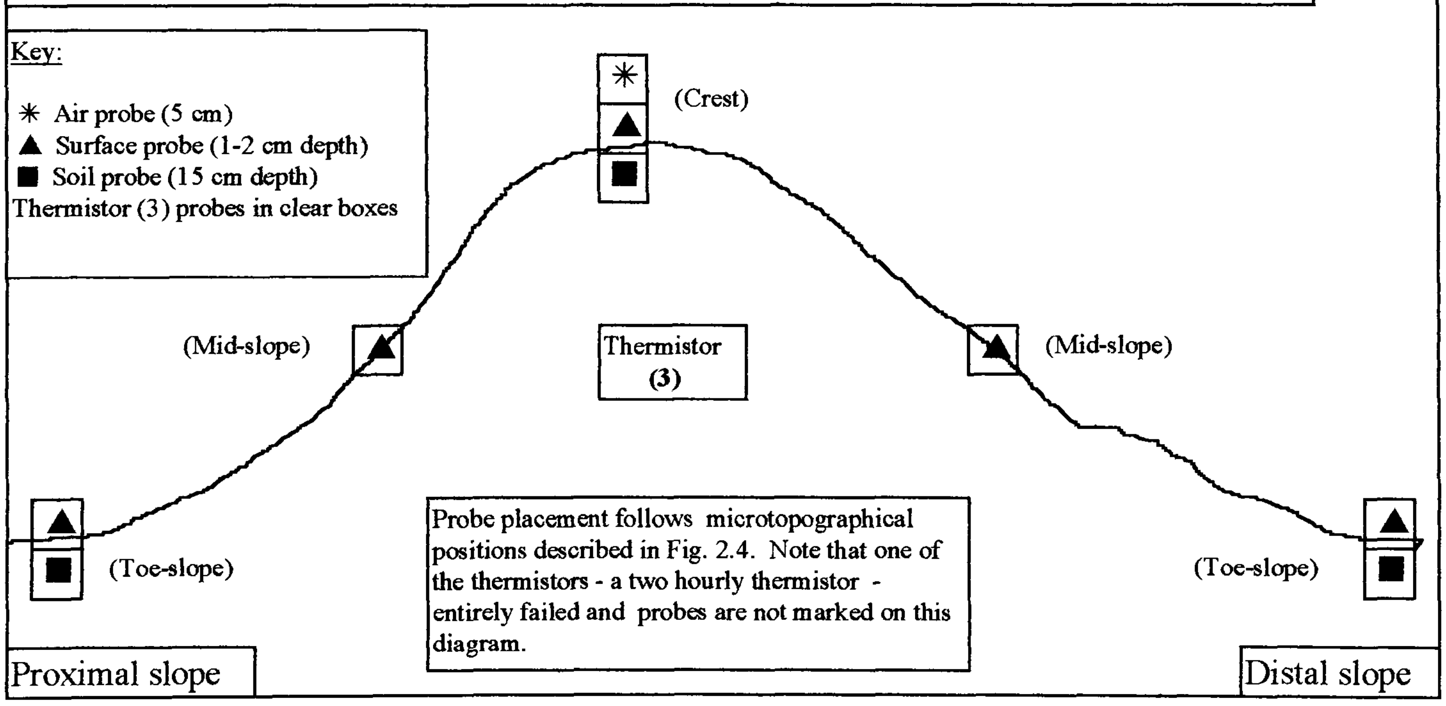
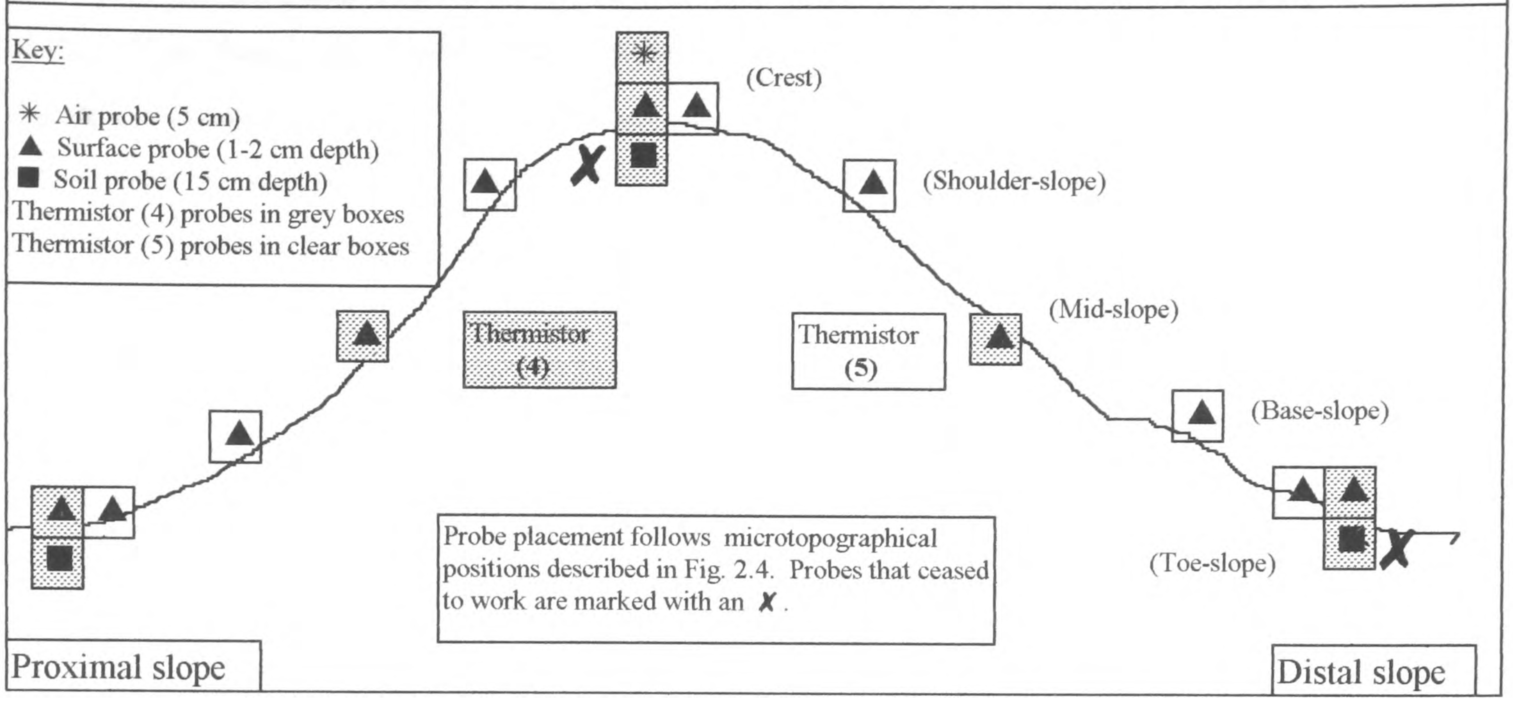


Fig. 2.8 1750 moraine: Thermistor (4), twice daily measurements taken from 24th August, 1990 to 31st May 1990; Thermistor (5), six times daily taken from 21st August 1990 to 20th December, 1990



2.7 Micro-environmental factors associated with disturbance

2.7.1 Frost evidence and frost-heave (dowel lift)

Frost-churning, or cryoturbation, has a considerable influence on the establishment and growth of plants. The heaving of plants out of the ground, causing the roots to snap or be exposed above the soil surface, are among the negative influences that frost may have on plants (e.g. Goulet, 1995). Levels of frost activity appear to be especially correlated with low vegetation cover (Anderson, 1947). Evidence of cryoturbation, was recorded according to the frequency of evidence in the 25 small squares of each 1m^2 quadrat. Features of cryoturbation that were included as evidence of frost activity include frost boils, frost sorting (into stripes or polygons), nubbins (small round or elongated lumps of earth created by needle ice) or cracks and fissures. The method of identification follows Matthews (1987, 1992), Whittaker (1985, 1987, 1989) and Crouch (1992). Actual frost-heave was recorded by placing nine dowels (match sticks), at each site, at the end of one field season and once emplaced, the matches were spray-painted. Measurement of lift, from ground level to the paint mark, was recorded the season following emplacement, and a mean was taken of the amount of lift for the nine dowels for each site. The mean lift was then used for the data set. The frost evidence scores of each moraine, as entered into the FORTRAN formatted data set used for the DCA indirect ordination analysis, were entered into the analysis under the abbreviation “Fro hve” (see Appendix 3). Actual heave of dowels (mean scores) was entered into the data under the abbreviation “Dow els”. It should be possible to decipher the relative influence of frost on vegetation patterns and associated micro-environmental parameters, by interpreting the frost evidence and dowel heave data within the ordination results.

The advantage of recording evidence of frost-heave is that it gives an indication of the history of frost activity at the site, and thus gives an idea of how vegetation development at the site may have been influenced by frost. The disadvantage is that this method does not indicate whether or not the activity is ongoing or long-since ended. The advantage of recording actual frost-heave (by using dowels) at a site is that it gives an indication of recent frost activity. However, the problem with the use of dowels is that, according to Goulet (1995) a large number of micro-environmental factors affect the heave of dowels, such as particle size, moisture, vegetation cover, winter snow-cover and chemical composition. Therefore within-site differences in soil conditions could give anomalous dowel heave results. Despite this many authors have used dowel heave to indicate recent frost-heave activity (e.g. Heidman, 1976; Whittaker, 1985; Jonasson, 1986) and so its use, in combination with the recording of evidence of frost activity, is considered worthwhile.

2.7.2 Solifluction and slope

Scale diagrams of moraine profiles were made for all moraines within the study (see profile diagrams 4.3 to 4.10 and 6.1a-h). The profiles were drawn by taking slope angles along each transect every two metres, or every metre where there were abrupt changes in slope. The position of each of the sites was drawn onto each profile diagram, according to its location along the transect. The angle of slope on the profile diagram was used to give the angle for each of the sites, and was entered into the FORTRAN formatted data set used for the DCA indirect ordination analysis under the abbreviation "Slo pe*" (see Appendix 3). Slope was expressed as degrees of deviation, from the horizontal, using a Suunto Clinometer and the readings were precise to the nearest degree.

Solifluction was measured quantitatively by noting the frequency of solifluction evidence occurring in 25 cm^2 small squares within a 1 m^2 quadrat. Evidence of solifluction, within each quadrat, was considered to be signs of slow flow of the soil mass when the soil is saturated, and included criteria such as a wrinkled surface or lobes. No distinction was made as to whether the process was solifluction or gelifluction (a kind of solifluction involving the thawing of frozen ground). For the purposes of this study the term solifluction will be used to encompass all types of downslope movement of soil saturated with water (Whittow, 1984). Disturbance from downslope movement or solifluction has been shown to be strongly correlated with slope angle (Whittaker, 1985; Crouch, 1992), and several authors have suggested that slope angle (and solifluction) are an important influence on soil development and vegetation patterns (e.g. Birks, 1980; Matthews, 1992; Parkinson and Gellately, 1991). For this reason solifluction is considered an important and useful parameter to measure. The degree of solifluction at a site was entered into the data set under the abbreviation "Sol flu".

2.7.3 Fluvial activity

Glacier forelands are usually subject to the action of glacier meltwater streams. These streams can change course from year to year and therefore it is likely that they would have an important influence on vegetation development along their courses. Whittaker (1989) suggests that small stream channels become less mobile on the older ground of a foreland, so that the influence of mobile streams becomes less as succession proceeds, but he did not measure fluvial activity as a separate disturbance variable. There are also a number of other types of water flowage across glacier forelands that may have a marked influence on vegetation patterns and obvious signs of such fluvial activity may include springs, snow-patch meltwater runoff and precipitation runoff. Crouch (1992) used a four-point scale to indicate fluvial activity on her sites (which include several types of fluvial activity) but her results show fluvial activity to be an insignificant influence, with pH and moisture only having a weak correlation with fluvial activity. Other studies, however, have found fluvial activity to be highly influential on vegetation patterns in a number of ways including destructively, by causing erosion (e.g. Oliver, Adams and Zasoski, 1985), or beneficially, by causing enhanced nutrient and moisture availability (e.g. Raven and Walters, 1956; Hastings et al, 1989). Fluvial activity is therefore likely to be an important influence across the forelands, and its measurement as a separate variable is considered to be relevant to the main aims of the study.

Fluvial activity was measured by noting the frequency of fluvial activity in 25 x 20 cm^2 small squares in each $1m^2$ quadrat. Evidence of fluvial activity, for present study purposes, includes: presence of recently used stream channels; signs of flooding; snow-patch meltwater; springs; and runoff from precipitation. Fluvial activity was entered into the FORTRAN formatted data set, used for the DCA indirect ordination analysis, under the abbreviation "Flu via" (see Appendix 3).

2.7.4 Trampling and grazing

The review in chapter (1) has shown both trampling and grazing to be important influences on vegetation patterns (e.g. Emanuelsson, 1984; Magnússon and Magnússon, 1990). In Iceland, for example, grazing pressure (including trampling) is considered to be one of the most significant factors in vegetation deterioration, as well as land surface erosion and deflation (Arnalds, 1984, 1987). Therefore, there is no doubt that grazing and trampling can be considered as important environmental parameters, especially where the pressures of these parameters are extreme. However, it is not within the scope of the present study to make a detailed investigation into the role of grazing and trampling on vegetation patterns on the foreland. Generally, the forelands within the study only suffer a very light or negligible grazing regime from domesticated herbivores. Furthermore, due to the sampling strategy adopted by the present study (i.e. choosing optimally vegetated sites), areas of heavy trampling or grazing activity are generally avoided. Grazing by wild animals is difficult to ascertain (personal observation) and thus needs detailed investigation, specifically designed for the purpose. Trampling was recorded quantitatively by recording the frequency of trampling evidence in 25 x 20 cm^2 small squares within each 1 m^2 quadrat. Grazing was recorded using the same frequency method as trampling. Evidence of trampling includes paths, broken vegetation and foot-prints; while evidence of grazing includes nibbled leaves and seed heads and/or faecal remains. Trampling and grazing were entered into the FORTRAN formatted data set, used for the DCA indirect ordination analysis, under the abbreviations "Tra mpl" and "Ani inf" respectively (see Appendix 3). For present study purposes, the superficial survey of grazing and trampling is only intended to indicate anomalies in vegetation pattern across the forelands - i.e. where sites may have suffered noticeable grazing or trampling activity. Because the sampling strategy mitigates against the use of grazed or trampled sites, any patterns shown by the trampling and grazing results should be viewed with caution.

2.8 Micro-environmental factors associated with vegetation and soil.

2.8.1 Total vegetation cover and total bryophyte cover

Vegetation can be considered as an environmental parameter in itself, as opposed to being the subject of investigation for classification purposes, where the pattern of individual species is described. The amount and type of vegetation cover can have a significant effect on nearly all the prevailing micro-environmental parameters at a site. For example, vegetation, or litter, acts as an insulator by preventing loss of heat but also acts as a barrier against cold temperatures. MacKinney (1929) found that litter reduces daily changes in minimum and maximum surface temperatures in autumn and spring from between 50 % and 85 %, and raises the mean maximum and minimum temperatures in both the autumn and spring. Moisture is also held more constant under vegetation or a litter layer. Litter and vegetation acts as a protective blanket, both reducing the effect of evaporation due to wind as well as preventing soil from excessive heating up and drying out, during the growing season. Vegetation cover also modifies soil freezing by decreasing the length of winter freezing period; decreasing the number of freeze-thaw cycles (and thus the risk of frost-heave); and decreasing the depth of freezing. Anderson (1947) found minimum air temperatures necessary for soil freezing were **-0.5 °C** for bare soil; **-1.67 °C** for light grass-covered soil; **-10 °C** for brush-covered soil; so much colder periods are needed to freeze the ground under vegetation. Litter (or any dead plant material such as hay) delays the freezing of the soil, and it also keeps the soil from freezing hard - the intergranular spaces not filling so noticeably with ice as in bare soil. Thus the water, from winter rains and thaws, penetrate the soil under the litter, instead of running off as on the more compactly frozen bare soil. It can also have inhibitive effects, for example by competing for nutrients and moisture as well as producing chemicals that act as toxins (allelopathy) that discourage other plant species. The cover of bryophytes, as opposed to other plant groups, is also useful in that bryophytes are generally more sensitive to moisture conditions than other plant groups (Crouch, 1992) and thus provide an additional indication of moisture.

Total vegetation cover was recorded by estimating the percentage cover of total vegetation (all higher and lower plant species) within each 1 m^2 quadrat. Total bryophyte cover (all bryophyte species or "black crust" *sensu*: Worley, 1973) was recorded in the same way, again by estimating the percentage cover of all bryophyte species within each 1 m^2 quadrat. Vegetation cover and bryophyte cover were entered into the FORTRAN formatted data set, used for the DCA indirect ordination analysis, under the abbreviations "Veg cov" and "Bry cov" respectively (see Appendix 3).

2.8.2 Cover of different clast sizes on bare ground

If the proportions of vegetation cover are likely to have a significant impact on micro-environmental conditions for plant species in general, it is also probable that the proportions of bare ground within a quadrat will also have a significant influence. MacKinney (1929) found that the depth of frost penetration is 40 % greater on bare ground than on ground with a litter layer. Associated with freezing of bare soil is a high surface moisture, a high evaporation rate; high surface run-off; and high rate of erosion. A bare mineral soil responds more rapidly to weather patterns than a litter and/or vegetation covered soil so that daily fluctuations in surface temperature are much lower under vegetation. After spring rains, the evaporation of excess moisture from the bare ground causes bare ground to warm up much more slowly. During the summer, winds at any time cause a lowering of the maximum surface soil temperature on bare ground because evaporation removes heat from the soil. Conversely, when there is sunshine and calm conditions, bare ground heats up excessively. From this it can be seen that the presence of bare substrates may have an important influence on plant species attempting to grow on those sites and it is likely that species which appear to prevail in areas where bare substrates are predominant are adapted to, or can tolerate, extreme environmental stress.

The type of bare ground, in terms of clast size, can also have an important impact on the micro-environment with regard to the colonisation of vegetation (Whittaker, 1985; Crouch, 1992). Clast size can influence, for example, such diverse factors as the ability of the substrate to trap seeds (Magnússon, 1994a); the ability of the substrate to hold moisture (Matthews, 1992); and the amount of disturbance that the site may suffer from frost-heave (Whittaker, 1985). It is therefore necessary not only to record the proportions of bare ground within each quadrat, but also to record the proportions of clast sizes that make up the bare ground. Substrate clast size was estimated, for each 1 m^2 quadrat, according to the method used by Crouch (1992). Fines are defined as clast-sizes < 2 mm; gravels and cobbles were included together and are defined as clasts between 2 mm and 256 mm; boulders are those clast sizes greater than 256 mm. The percentage cover of each clast group was recorded as a percentage within the analysis. The proportion of fines, gravels and boulders were entered into the FORTRAN formatted data set, used for the DCA indirect ordination analysis, under the abbreviations "Bar fin", "Bar gra" and "Bar bou" respectively (see Appendix 3). A more subjective estimate was also made of the total cover of each of the clast sizes within each quadrat (i.e. under the vegetation and not just on the bare ground) and was abbreviated "Est fin", "Est gra" and "Est bou". However, this estimate was considered as too subjective and so was not used within the final analysis.

2.8.3 General depth of humus (O) horizon, soil depth/stain (incipient Ea, Eb and B horizons) and root depth

The parameters of humus depth, soil depth and root depth were chosen for measurement for a number of reasons: a) previous researchers in the region have used these parameters as a simple representation of soil development at a site (Whittaker, 1985; Matthews and Whittaker, 1987; Crouch, 1992); b) the measurement of the parameters is simple and quantitative; and c) these parameters have shown a strong association with time (Whittaker, 1985) and it would be consistent with the main aims of the study to investigate the strength of their association with microtopography.

At each site (pair of quadrats) a small pit, no deeper than 150 mm, was dug under the dominant vegetation or substrate type and care was taken to prevent the walls of the pit from collapsing. Humus depth, soil depth and root depth were recorded, in millimetres, by observing the exposed profiles within each of the pits. Recording of humus depth comprised the measurement of all the organic horizon (O) horizons (see Fig. 1.1), as it was not possible to distinguish between them at most sites. Humus depth (i.e. depth of organic horizon) is considered an important measurement as it represents the amount of decomposed organic matter that has accumulated on the soil surface. It is well known that humus has a significant influence on soil and vegetation development at a site. For example, humus is known to increase moisture-holding capacity of soil (FitzPatrick, 1974); it affects texture by increasing the plasticity of sandy soils but reducing the stickiness of clay soils (FitzPatrick, 1974); under the cool climatic conditions within the regions under study, a humus layer hastens the leaching of underlying mineral soils through podzolisation processes (Messer, 1988); and with lowered soil water potential, soil surface temperatures become more stable and thus freeze-thaw cycles are reduced (Goulet, 1995). The measurement of this variable follows Whittaker (1985) who measured the depth of the organic horizon (litter, fermentation and humification horizons) and compares with Crouch (1992) who used a scale to represent the degree of organic horizon development. Recording of soil depth (or depth of soil stain), consists of the measurement of the incipient (Ea or Eb) and (B) horizons and thus gives an impression of soil development (Messer, 1988). The use, and method of recording, of this variable follows Whittaker (1985) as well as Messer (1988). The roots, at the side of the pit, were observed and what appeared to be a representative root length, of the turf layer, was recorded as "root depth". Whittaker (1989: 415) also noted "root depth", defining it as "*the level to which the averaged root penetrates*" and this study follows his methodology as it is considered to provide a useful indicator of the growth and development of surface vegetation. Humus depth, soil depth and root depth were entered into the FORTRAN formatted data set, used for the DCA indirect ordination analysis, under the abbreviations "Hum dep", "Sta dep" and "Roo dep" respectively (see Appendix 3).

2.8.4 pH levels

Soil reaction is a useful property to analyse as it is a reflection of the amount of bases that have been leached from the soils (Lethbridge and Lynch, 1987) as a result of rain (Viereck, 1966) and vegetation cover (Fitter and Parson, 1986). It has also been found that pH values change not only according to the presence or absence of vegetation, but also due to the particular species present (Crocker and Major, 1955; Lawrence et al, 1967; Fitter and Parsons, 1986). If noticeable differences in soil pH appear either as a result of microtopography, age or altitude (or various combinations of all three), it may be possible to relate these differences in soil pH (and other associated soil characteristics such as humus depth and soil depth) to the prevailing plant assemblages. It should be noted that the parent material in the Jotunheim is more basic than that of the Jostedalsbreen region and this fact will be taken into consideration within the discussion of the results.

One soil sample was taken for each of the 2 x 1 m^2 quadrat pairs (sites) across every moraine, and the sample was tested for pH using a portable pH meter and a consistent methodology. Soil samples were taken on the same day, from any particular foreland, as rainfall can affect the pH results (Russell, 1973). Soil samples were taken from under a patch of vegetation considered to be representative of the dominant vegetation type at sites across each moraine. The soil samples had any stones or large pieces of plant material removed and 25 ml, of each soil sample, was mixed with 50 ml of de-ionised water. The samples were stirred and left to stand for approximately ten minutes. The pH probe was placed in the soil solution and the measurement was taken once the meter readings had stabilised. Once all the samples from a moraine had been read (usually nine samples), the first sample was re-recorded in order to show that the pH meter was reading consistently. If the reading was not within one decimal place of the original reading then the soil samples were re-measured until consistent readings were given. Russell (1973) suggests that pH varies not only according to weather, but also within short distances at the same site. He suggests that rarely can one make use of highly accurate measurements of pH and that little information of value is lost if field samples are measured to the nearest 0.2 of a unit. Given the problems associated with obtaining accurate soil pH readings, it should be born in mind that this study can only provide an elementary portrayal of trends in pH in relation to altitude, age and microtopography. For the sake of accuracy, the readings will be entered into the data set to the second decimal place. pH was entered into the FORTRAN formatted data set, used for the DCA indirect ordination analysis, under the abbreviation "pH* ***" (see Appendix 3).

2.8.5 Soil texture

The texture of a soil is considered to have a significant effect on soil temperature and moisture (Lindröth, 1965) as well as disturbance of the soil by frost-heave (Ballantyne and Matthews, 1983). The texture of a soil must therefore have a significant impact on vegetation development and is therefore considered to be a useful parameter to measure. The soil samples, collected for pH analysis, were used for an assessment of soil texture at each of the 2 x 1 m^2 quadrat pairs (sites) across every moraine. Texture was recorded by using the same methodology used by Crouch (1992). The criteria and method used for the assessment of soil texture are described below.

First the soil was moistened and then the following key was used:

1. Can the soil be rolled into a ball? No SAND

Yes Other soils, see 2

2. Can the soil be rolled into a cylinder of 5 mm in diameter?

No LOAMY SAND

Yes Other soils, see 3

3. Can the soil be rolled into a thin thread?

No SANDY LOAM

Yes Other soils, see 4

4. Can the thread be formed into a horse-shoe shape without cracking?

No SILT and LOAMS

Yes CLAY LOAMS and CLAYS (see 5)

5. Can the horse-shoe be formed into a ring without cracking?

No CLAY LOAMS

Yes CLAY

Within the present study soil textures were found to comprise sands through to loams and were placed on a scale of 1 to 4: 1 (sand); 2 (loamy sand); 3 (sandy loam); and 4 (loam). Finer soils, such as clay loams and clays, were not found. Texture was entered into the FORTRAN formatted data set, used for the DCA indirect ordination analysis, under the abbreviation "Soi tex" (see Appendix 3).

2.9 Analytical techniques

There is a wide range of analytical methods available to describe and recognise patterns in vegetation, and relate these to environmental factors and gradients (Kent and Ballard, 1988). The present study has a large and cumbersome data set and in order to fulfil the aims of the study it is considered necessary to use tried and tested methods of analysis in order to avoid lengthy discussion of the analytical methodologies being used. This study has therefore used a restricted number of carefully chosen analysis methods used by other researchers at Storbreen. These methods have been chosen for several reasons: a) continuity of approach; b) the techniques have been tested by other researchers and have been found to be satisfactory methods of data analysis for the type of data set collected for the present study; c) software can be shared as advances in analytical methodology by other researchers are made; d) problems, for example that arise from the analysis of large data sets, can be shared with researchers who have had experience of the same programmes.

2.9.1 Continuity of approach

Matthews (1976, 1978, 1979a,b,c,d), Whittaker (1985, 1987, 1989), Matthews and Whittaker (1987) and Crouch (1992, 1993), used a variety of analytical approaches to investigate the relationship between vegetation patterns and associated environmental parameters. Since 1979 analytical methods have progressed considerably, and the researchers at Storbreen have changed their methodologies according to the latest advances in data testing. Matthews (1979) used a number of techniques, including DIVNF and RAGNAR, to classify the plant assemblages, at a number of different levels of complexity (using different quadrat sizes). Matthews (1979b) used the ordination technique principal components analysis (PCA) to relate plant distributions to environmental parameters and non-metric multidimensional scaling (NMDS) to make graphical representations of multidimensional inter-species similarities in a two-dimensional network (species plexus). Matthews (1978) then mapped the distributions of individual species and from this related the position to successional status and environmental tolerance.

Whittaker (1985, 1987, 1989) used NMDS to identify and analyse vegetational structures and environmental factor complexes, defined by the plexus approach. Whittaker also used detrended correspondence analysis (DECORANA), regarded as an improvement over PCA (Hill, 1979a; Hill and Gauch, 1980), to relate vegetation patterns to environmental variables. Whittaker (1989) ran an in-series application of NMDS and detrended correspondence analysis (DCA), which can superimpose environmental data onto the vegetation patterns, and compared this indirect analysis technique with canonical correspondence analysis (CCA), which directly relates the vegetation patterns to the environmental parameter patterns. Whittaker (1987) found that the multivariate analysis technique NMDS (non-metric multidimensional scaling) identified two principle structures within the environmental data which were considered to have relatively independent influences on the vegetation patterns found across the forelands: 1) a "*Terrain-age factor complex*", mainly measures of soil development and site disturbance (frost churn, disturbance, altitude, soil and litter depth, depth of rooting) 2) a "*Microtopographic factor complex*", mainly measures of exposure, moisture regime, and snow duration at the site. These complexes were then linked to DCA ordination axes (1) and (2) respectively and he considered DCA as a suitable approach because the site and species ordinations correspond precisely; as sample scores are averages of species scores and vice versa (Gauch, 1982). He dismissed the use of DCA axes (3) and (4) as they were uninterpretable and thus considered not to be ecologically meaningful. He further suggested that, with large data sets, statistical significance would be of dubious ecological value and thus the best approach is to interpret the axes only if they appear to be ecologically meaningful, this view also being supported by Matthews (1981) and Gauch (1982). He also suggested that CCA should not be used as it has linearity requirements which are too stringent to accommodate such a wide range of ecological data.

Crouch (1992) also compared DCA and CCA and found both techniques to be useful, although she preferred DCA (pers. comm.) because she found considerable variability in the vegetation patterns that could not be accounted for solely by the environmental parameters within the data set. Indirect ordination consists of the sample scores being derived from the weighted species scores and species scores being derived from weighted sample scores and is therefore not constrained by environmental variables. In order to relate the axes to environmental parameters it is necessary to use separate environmental data and calculate regression coefficients of environmental parameters on the ordination axes. The direct ordination technique (CCA) also derives species scores from sample scores (and vice versa) but the scores are linear combinations of environmental variables. In other words, by using the direct ordination method, the environmental parameters influence the scores that are obtained by the ordination. This in turn influences the position of the data points (samples and species) on the axes. In order to use the direct ordination technique it is necessary to be confident that the environmental variable measurements are reliable (Kent and Coker, 1992) and, in addition, they should be a complete representation of the prevailing environment if the purpose of the study is to investigate the relative importance of different components of the environment. If this is not the case, the relative influence of individual parameters may be exaggerated using the direct method. This in turn would cause the species and samples to be placed on the axes in a misrepresented way. On the one hand, in this study, the measurement of the % vegetation cover for each 1 m^2 quadrat uses a consistent, tried and tested method. On the other hand, the measurement of many of the environmental parameters is not consistent, with some environmental parameters being measured on an interval scale and others measured on an ordinal scale. In addition, some of the environmental techniques are relatively new and little tested and their accuracy varies considerably. Furthermore, some of the environmental data had to be converted or processed causing an increased possibility of inaccuracies within the environmental data set. Crouch (1992) found that environmental factors, other than those measured, had an important influence on vegetation pattern, especially the cryptogam component. Although she recommends using both techniques, one to support the other, her results suggest that the indirect ordination technique is better in the present context.

Coker (1988), working in the region, recommends the use of both a classification technique, to interpret vegetation patterns, in combination with an ordination technique, to relate the vegetation patterns to environmental factors, and this view is also supported by others (e.g. Kent and Coker, 1992; Crouch, 1992; Matthews, 1992). TWINSPAN is a robust and popular method of classification and is recommended by many authors (Gauch, 1982; Greig-Smith, 1983; Kershaw, 1985; Jongman et al, 1987; Kent and Coker, 1992; Crouch, 1992; Magnússon, 1994a; Vetaas, 1994; Lynch and Kirkpatrick, 1995). Recently it has come under criticism by Van Groenewoud (1992), who suggested that TWINSPAN does not perform well on complex data sets, especially after the first division. However, more recently Tausch et al., (1995: 901) were not so critical and proposed that data derived from TWINSPAN analysis is more stable than suggested by Van Groenewoud: "*Removing the infrequent species reduced the variability of the TWINSPAN analysis results to where changes did not occur in the first three division levels for any of the five data sets. Changes did occur in the fourth and higher division levels, but the number of changes decreased as the frequency of the species removed increased ...*". Despite these criticisms, ecologically meaningful data has been obtained using TWINSPAN, by researchers in the region, and so its use within the present study can be justified. Nevertheless, rare species will be down-weighted, and extra attention will be paid to the interpretation of the divisions at levels four to six, as recommended by Tauch et al.

It should be noted that there is one last justification for using DCA in preference to CCA. According to Carleton et al., (1996), in their paper concerning a new technique known as constrained indicator species analysis (COINSPAN), "*no parallel method of constrained classification has appeared to complement a CCA ordination as TWINSPAN complements a (D)CA ordination*"(Carleton et al., 1996: 126). This suggests that CCA should not be used with TWINSPAN, especially where centroids of TWINSPAN species group ordination scores are fitted onto the ordination plots, as is done in the present study. For the purposes of the present study, therefore, DCA is preferred over CCA despite the growing popularity of the latter technique (e.g. Palmer, 1993) and criticism of the former (e.g. Wartenberg et al., 1987). Following Crouch (1992), data for both the TWINSPAN and DCA programmes were entered using FORTRAN.

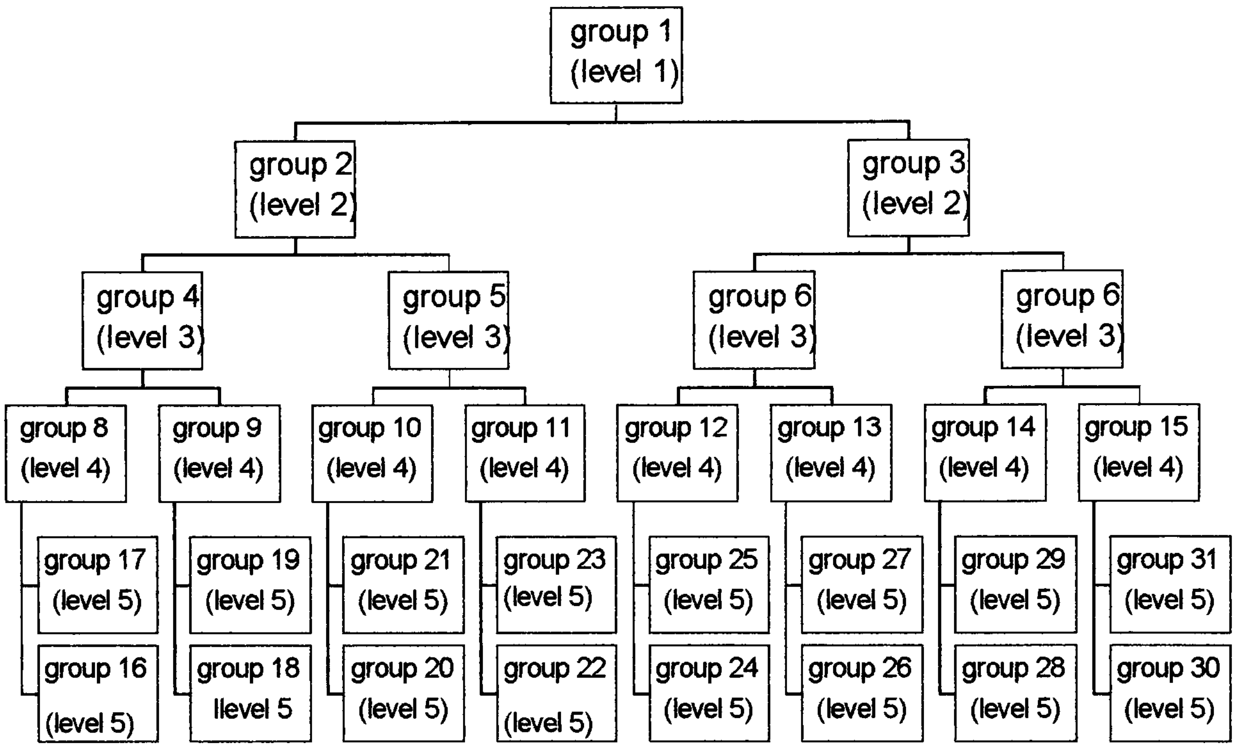
2.9.2 Classification of data using two-way indicator species analysis (TWINSPAN)

TWINSPAN is described in detail in other texts (e.g. Hill, 1979b; Gauch and Whittaker, 1981; Kent and Coker, 1992) and thus it is not considered necessary to describe the programme in detail. A description of the group levels and the options chosen for analysis, within the context of the present study, is considered necessary for an understanding of the terminology used by the present author. However, because a range of presentation techniques have been used to display the TWINSPAN results, the presentation methods will be discussed at the beginning of each of the appropriate sections in chapters (4) and (6).

TWINSPAN divides the data, in a hierarchical manner, into an increasing number of groups at up to six levels (Fig. 2.9 - only shows subdivision up to level 5). The programme starts by making the first subdivision of all the site data (level 1 or 1-group level), into two groups - (2) and (3)- (level 2 or 2-group level); then four subdivisions into groups (4), (5), (6) and (7) - (level 3 or 4-group level); then eight subdivisions into groups (8), (9), (10), (11), (12), (13), (14), (15) (level 4 or 8-group level); and then sixteen subdivisions into groups (16), (17) etc. - (level 5 or 16-group level). Further subdivisions are made at the (level 6), or 32-group level, but generally the subdivisions at this level have not been used. The sites are divided according to the species found at those sites. For each group of sites (site group) a list of preferential species, that literally prefer those sites, is made. Also a list of indicator species, which are exclusively found on those sites, is made for each group although some groups, especially at the higher levels (i.e. levels 5 and 6), do not have indicator species. The lists for both the indicator species and preferential species also give the pseudospecies (i.e. cut level) after each name as a number (1 to 9) representing each of the cut levels for the cover values. The title of the assemblage will be given according to those species in the group with the highest cover values, for example if the species with the highest cover are *Salix glauca* and *Carex spp*, then the site group is called the **Salix glauca - Carex spp** assemblage.

TWINSPAN stops dividing **site** groups when they comprise less than 5 species (default) and the manual (Hill, 1979) suggests that beyond six levels of division (default) interpretation can be difficult, even for large data sets such as the present ones. The default number (i.e. six) of divisions was chosen (not fewer) because all the data sets, both individual foreland and combined foreland (see glossary), are large. TWINSPAN then repeats the process of division with the **species** but this time according to how each individual species is related to other species in terms of distribution. Finally a sorted two-way table (final table) is produced which displays the TWINSPAN species groups and site groups (Appendix 4.1 to 4.8).

Fig. 2.9 The group and level numbering system of the TWINSPAN hierachy
(Note that this figure only displays subdivisions up to level 5, the 16-group level)



TWINSPAN is a polythetic method of analysis which is able use the cover values of each individual species. The cover values have been divided off at the following cut levels: 0 to 2 %, 2.5 to 5 %, 5.5 to 10 %, 10.5 to 20 %, 20.5 to 30 %, 30.5 to 45 %, 45.5 to 60 %, 60.5 to 80 % and 80.5 to 100 %. Each of these cut level is known as a pseudospecies and acts like a real species in the analysis. The reasons for having the maximum number of cut levels (9) was because of the high diversity and variation in cover of many of the individual species at most of the sites. For example, it was necessary that the analysis should discriminate between: a single cup lichen (<0.5 % cover), a small clump of heath species *Cassiope hypnoides* (3 % cover), a small clump of the pioneer grass species *Trisetum spicatum* (6 % cover) or a large patch of *Empetrum nigrum* (cover value 35%). The first pseudospecies (0-2 % cover value) was down-weighted in order to reduce its significance within the analysis. This was done because such low-cover species within a quadrat may represent “noise” and could complicate the interpretation of the TWINSPAN groups (Kent and Coker, 1992). Otherwise, the options used for the TWINSPAN runs, on the individual foreland data sets and the combined data set, were set to default.

2.9.3 Ordination of data using detrended correspondence analysis (DCA)

Due to the size of the data set it was only possible to present the results of one ordination technique and thus a choice had to be made between DCA, an indirect ordination technique, and CCA, a direct ordination technique. For the reasons outlined in section 2.9.1, DCA is preferred over CCA. Detrended correspondence analysis (DCA), an indirect ordination technique, is described in detail in other texts (e.g. Hill, 1979a; Hill and Gauch, 1980; Kent and Coker, 1992) and thus it is not considered necessary to describe the programme in detail. However, a description of the options chosen for analysis, within the context of the present study, is considered necessary for an understanding of the terminology within the present thesis. Because a range of presentation techniques have been used to display the DCA ordination results, the presentation methods will be discussed at the beginning of each of the appropriate sections in chapters 5 and 6.

Once the indirect ordination technique, DCA, was selected it was necessary to decide which options, within the CANOCO programme, should be chosen. If the abundance data has a very skewed distribution it is recommended that the data should be transformed by taking logarithms (ter Braak, 1986) and for this reason log transformation is used. In addition rare species are down-weighted in order to further reduce the influence of "outliers". In order that the third or fourth axes should not be related to the first axis detrending by fourth-order polynomials has been recommended (Crouch, 1992) and is performed here. Three of the environmental parameters are excluded from the ordination due to the probability of inaccuracies within those data sets: (17), estimate of boulders beneath vegetation; (18), estimate of gravels beneath vegetation; (19), estimate of fines beneath vegetation. Lastly, a number of DCA runs were made using various options in order to ascertain which options would provide the best spread of species across the plot. The option chosen under "scaling of ordination scores" was option (2) - species scores are weighted mean sample scores. This option assumes that the species' optima all lie inside the range of the sample scores, the "optima" being provided by the best vegetated transect taken across a till ridge on the oldest terrain in this study. All other options were set to default. The method of presentation of the ordination results is described in section 5.2.

2.9.4 Statistical tests

The multivariate techniques TWINSPAN and DCA are considered to be comprehensive methodologies, especially in combination with the use of distribution charts for both the vegetation (Figs. 4.19 to 4.93 and 6.13 to 6.14) and environmental (Figs. 3.1 to 3.95) data. It was, however necessary to use a small number of additional techniques, especially to elucidate the relationships between individual environmental parameters. A few techniques were used to test the reliability of the results. These additional analysis techniques are described in more detail in the relevant sections but are summarised below.

Pearson's product moment correlation coefficient (r), and its use within the present thesis, is outlined in chapter 5 (section 5.2). Correlation matrices were constructed, for each foreland, in order to elucidate the relationship between different environmental variables and the ordination axes. Pearson's correlation is a parametric technique and therefore most appropriate to normal data and thus only stringent significance levels should be used with non-normal data (Crouch, 1992). Crouch (1992) used this programme and on the basis of her findings this programme was considered to be a useful analysis technique. Following Crouch, only the intercorrelations significant at $p<0.001$ are considered important.

Calculation of the best estimate of population standard deviation was used to find the number of measurements needed to get consistent readings using the prototype capacitance probe. The calculation is outlined in chapter 2 (section 3.3.2). Spearman rank correlation was used to show whether there was a significant correspondence between the moisture measurements derived from the finger test methodology and moisture measurements derived from the prototype capacitance probe. The test methodology is outlined in this chapter (section 2.6.2) the results are described in chapter 3 (section 3.3.2).

Descriptive statistics was used for the thousands of temperature readings derived from the Grant thermistor recorders. Means of measurements from the year-long recorders, taken twice daily for two weeks, were calculated so that a chart of the temperature changes for two-weekly periods throughout the year could be constructed. The charts (Figs. 3.20, 3.22, 3.24. 3.26) show the temperature changes for probes, from one thermistor recorder, at a range of positions and depths. Another series of charts (Figs. 3.21, 3.23, 3.25, 3.27) were constructed to show the standard deviation of the two-weekly temperature means, so the degree of temperature fluctuation, at the range of depths and positions, could be elucidated. This methodology was also used for a thermistor which recorded between August and December, but this time the means and standard deviations were taken 6 x daily for 5 days at a time (Fig. 3.28, 3.29). A population correlation calculation (in Microsoft Excel, version 5.0) was used to show amount of divergence shown between measurements made by two thermistors at the same position and depth (Fig. 3.30). The population correlation calculation returns the covariance of two data sets, divided by the product of their standard deviations. Transformation was not necessary as the data was considered to be normally distributed (shown by use of draft-quality histograms).

Regression was used to show the effect of altitude on temperature (Fig. 1.1). The temperature data is the most recent available (1960 to 1990) and was obtained from the Norwegian Meteorological Office. The regression concerns temperature means, from weather stations within 100 km of the Jotunheim region, between an altitudinal range of 10 m (Fjærland) and 2062 m (Fanaråken).

Lastly, Spearman's rank correlation (a parametric statistic) and Kendall's "tau" (a non-paramtric statistic) were used to investigate the degree of correspondence between vegetation and environmental data collected at the same sites over successive years. A non-parametric statistic is generally preferred over a parametric statistic, if non-normal data are being used. However, with stringent significance levels (i.e. $p < 0.001$), parametric statistics can be considered meaningful (Crouch, 1992).

2.9.5 New methodologies and presentation techniques

All methods of data collection are summarised in a summary table (Appendix 7) and the presentation techniques are summarised in a summary table (Appendix 8). From these tables it is possible to get an overview of the contributions that this thesis has made to the development of new approaches, especially with regard to the presentation of TWINSPAN and DCA ordination data. It should be noted that the tables are simply an overview and do not fully describe the development of techniques derived from other sources. These methodological contributions are discussed in greater detail in the concluding chapter (section 7.5).

2.10 Data collection

2.10.1 Summary of field-study seasons

Four field seasons were spent in Norway from 1988 to 1991. The first season was one month and served as a preparatory excursion so that the author could become familiar with the regional plant species (lichens and higher plants). A project was chosen and started and this involved looking at the influence of "facilitation" or the reaction of pioneer species on later colonisers. This project was abandoned at the end of the field study season on the grounds that the subject matter of the project was considered to be too elaborate for one Ph.D. thesis. The present project was therefore chosen at the end of the first season.

The 1989 field season was one month and it was decided to investigate the effect of microtopography, and associated environmental parameters, on plant pattern on terrain of different age and at three altitudes (subalpine, low-alpine and mid-alpine). Transects across fifteen moraines and two till ridges were studied in detail: seven moraines (dating from AD 1968, 1951, 1930, 1900, 1850/70, 1810 and 1750) and one mature till-ridge in the mid-alpine zone at Storbreen (STHF: 1310-1350 m); five moraines (AD 1900, 1870, 1925, 1810 and 1750) and one mature till-ridge in the low-alpine zone at Storbreen (STLF1: 1140-1200 m); and three moraines (AD 1935, 1871 and 1785) at the subalpine foreland, Austerdalsbreen (AUSF: 190-380 m). It was therefore possible to become familiar with plant species occurring in all three altitudinal zones and the identification of all vascular species could be corroborated on expedition. Specimens of all recorded lichen species were sent to the Botany Department at the British Natural History Museum, to confirm the lichen identifications in the field as well as to classify unknown species. Dowels were emplaced (for direct measurement of frost-heave) in relation to each site (quadrat pair) along a transect. Two nine-probe Grant's thermistor thermometers were emplaced on the 1750 moraine at Storbreen to investigate through-year temperature variations at various microtopographic positions and depths.

The 1990 field season was two months and continued the work started in 1989. Mid-alpine data sequences were collected from five moraines and one mature till ridge at Høgvaglbreen (HØHF: 1400-1450 m) and Bøverbreen (BØHF: 1500-1540 m). A low- to mid-alpine data sequence was collected at Svellnosbreen (SVLF: 1280-1440 m), consisting of 5 moraines and a mature gully (as no mature till-ridges could be found). A second low alpine data sequence was collected at Storbreen (STLF2: 1140-1200 m). Investigations were also begun at Fåbergstølsbreen and Austerdalsbreen. Dowels were set up on each of the new sites (see section 2.7.1). Sites, used for the testing of season to season variability, were remeasured at Storbreen. In parallel with the routine measurement of environmental factors, the temperature charts were collected from the two nine-probe Grant thermistors that were set up in 1989 on the 1750 moraine. In 1990, four instruments were set up at Storbreen: two on the 1750 moraine, with probes at the same positions as in 1989; and two on the 1900 moraine (see section 2.6.3). A prototype instrument, a Capacitance Probe, was tested during the 1990 field season as an alternative measurement of soil moisture (see section 2.6.2).

In 1991, six weeks were spent in the field and the remaining data sets were completed. Measurements of dowel heave, at all emplacements, from the 1990 and 1989 field seasons, were performed. Soil samples for pH testing were collected from every quadrat pair across all the forelands in this season under comparable weather conditions: sites had been marked with paint spots so that they could be found in later years. Soil moisture measurements, using the "finger test" were made at all sites (on all forelands) for three depths. By taking the measurements for moisture within the same year, and under similar weather conditions (i.e. after a period of at least two days of dry weather), it is hoped that the between-foreland estimates would be relatively consistent. Unfortunately, the prototype Capacitance Probe again broke down early in the expedition so that a comparison with the "finger test" data could not be made for every foreland as planned (see sections 2.6.2 for methodology and 3.3.2 for results). The four thermistor chart rolls and machines from the 1900 and 1750 moraines at Storbreen were collected. Specimens of all lichen species recorded were again taken back to the UK for confirmation of their identification. The fifteen replicate "test sites" (see following section) were re-recorded for the third and final time.

2.10.2 Test of season to season variability in data collection

Replicate test quadrats were set up in order to test year to year variation in plant identification and environmental data collection. The 1750, 1810 and 1900 moraines were chosen as they provided a cross section of plant species, and associated environmental variables belonging to different stages within the successional sequence. Vegetation and environmental data sets were collected from nine replicate quadrats, first marked out and analysed on Storbreen foreland (1140-1200 m sequence) in 1989. Three quadrats were re-recorded (distal toe-slope, crest, and proximal toe-slope positions) across the three moraines. The large number of species and environmental parameters, measured within each quadrat, was considered to provide enough data for statistical analysis (Matthews, pers. Comm.): a total of 585 species samples and 153 environmental parameter readings were compared from three field seasons.

Correlation was used to investigate the degree of association between the measurements collected during each field season. Kendall's tau was preferred (Whittaker, 1985), for use with the environmental data, because the data are not normally distributed and there are unlikely to be considerable natural differences from year to year, i.e. the proportions of clast-sizes, snow-lie, position and soil parameters (etc.) are unlikely to change much over 12 months. Another non-parametric Spearman's rank correlation was also used for comparative purposes.

According to Table 2.6 and Table 2.7, the environmental data, recorded in the same quadrats over the three field seasons, are significantly correlated ($p<0.001$), using both correlation techniques. This suggests that there is little between-year variation in the recording of the environmental parameters.

Table 2.6 Kendall's correlation coefficient matrix for environmental parameter measurements taken in 1989, 1990 and 1991.

	1989	1990	1991
1989	1		
1990	0.6603	1	
1991	0.6343	0.6321	1

Table 2.7 Spearman's correlation coefficient matrix for environmental parameter measurements taken in 1989, 1990 and 1991.

	1989	1990	1991
1989	1		
1990	0.9555	1	
1991	0.9496	0.9567	1

According to Table 2.8, the vegetation data, recorded in the same quadrats over the three field seasons, are significantly correlated ($p<0.001$), using Spearman's rank correlation. Kendall's correlation does not show any correspondence between the vegetation data recorded during each of the field seasons, possibly because Kendall's tau is more stringent than Spearman's rank correlation. The natural yearly differences in the species data (caused by growth, die-back and colonisation) are likely to have caused the differences in Kendall's correlation coefficient results between the species data and environmental data. Nevertheless, the significant correlation shown by Spearman's rank correlation results suggests that the small differences in the vegetation patterns at the test sites, between the three field seasons, are unlikely to be caused by between-year differences in the recording of the vegetation.

Table 2.8 Spearman's correlation coefficient matrix for vegetation data collected at the same site in 1989, 1990 and 1991.

	1989	1990	1991
1989	1		
1990	0.8965	1	
1991	0.8423	0.8626	1

The results therefore show that there is a strong correspondence between the measurements made during 1989, 1990 and 1991, for both the environmental and vegetation data, and thus it can be concluded that the year to year variation in measurement is minimal. Differences, within the results, are unlikely to be attributable to between-year recorder variation but to some other factor.

2.11 Methodological overview and rationale

2.11.1 Selection of methods

A detailed table of the methods used within the thesis is displayed in Appendix 7. Appendix 7 shows that the majority of the methods used in this thesis follow on from the larger geoecological approach, developed by researchers, in the Jotunheim and Jostedalsbreen region (e.g. Crouch, 1992, 1993; Matthews, 1976, 1978a,b, 1979a,b,c,d, 1992); Matthews and Whittaker, 1987; Mellor, 1985, 1987; Messer, 1988, 1989; Whittaker, 1985; 1987, 1989, 1991, 1993). The main reason for not deviating from the methodologies used by previous regional authors is for reasons of continuity. The approach used in this thesis has been to improve and support previous methodologies rather than to change them. For example, dowels have been used by Whittaker (1985) but not as extensively and frequency of occurrence for frost activity, fluvial activity, solifluction, trampling and grazing are considered to be more illuminating and objective than the ordinal scales used by Whittaker (1985) and Crouch (1992). Nevertheless, a number of methodological developments have been made and these include: the investigation of succession on six forelands of different altitude; the use of transects comprising nine pairs of quadrats across at least six till ridges at every foreland; the placement of the quadrats, on comparable positions across each moraine, is also original and gives an indication of the microscale exposure of the site. In addition the prototype capacitance probe, used to quantitatively measure moisture content is used to support the ordinal scale "finger test" methodology used previously by Crouch (1992) and also extensively within the present study. The results from these methodologies are displayed in chapter (3), which describes the distribution of environmental parameters across each foreland. Chapters (5) and (6) describe the relative influence of the environmental parameters on the vegetation patterns across each foreland.

2.11.2 Reliability of approach

As can be seen in Appendix 7, most of the methodologies used within the present thesis are those used previously by other field researchers. These are therefore mainly tried and tested methodologies. They were chosen because they describe a wide range of environmental parameters and also because they are considered to be as objective and as quantitative as possible, within the confines of time and expense. Appropriate tried and tested sampling and analysis techniques have been used to collect and process the raw data (see next section). Generally, any development of the methodological approach within the present thesis has been to increase the objectivity and accuracy of the data collection (especially for analytical purposes). Only one recorder (the author) collected the data and therefore between-recorder variability does not occur. Between-season recording variability was however tested (section 2.10.2) and it was shown that it is unlikely to have an important influence on the data sets.

2.11.3 Justification of the sampling and analysis techniques

The sampling and analysis techniques used within the thesis can be justified in three ways:

a) The sampling techniques are necessary for answering the main aims of the present study, within the confines of a Ph.D. thesis (in terms of volume of data and time-scale).

b) The sampling techniques are generally based on previous work, within the region, and thus are considered tried and tested (see section 2.9.1). Messer (1988) had an important influence on the sampling strategy. Messer defines her strategy as stratified sampling, with the samples being first stratified according to age and then according to topography. Messer sampled beneath the best-developed vegetation and this study follows her methodology by sampling the line of optimal vegetation across each moraine.

c) Any new development of previous methodologies (or new methodologies *per se*) has been introduced in order to improve the scientific approach used.

The sampling techniques used within the present work are considered to be an improvement on much of the previous work. A number of recent authors have criticised earlier authors for not sampling objectively (e.g. Hurlbert, 1984; Matthews, 1992; Chapin, 1994; Helm and Allen, 1995). For example, Chapin (1994) suggests that the use of so-called homogeneous (replicate) plots of different age is not recommended because differences in the vegetation patterns may be due to parameters other than age. Such plots have been named pseudoreplicates (Hurlbert, 1984) and it is suggested that the pseudoreplication problem can be solved by the use of several plots (or stands) within any age-stage and the measurement of a diverse range of environmental parameters (Chapin, 1994). For a more detailed review of the sampling techniques see section 1.3.3.

The present study specifically investigates microtopography, so that in any one "stage" (at least 6 age-stages per foreland) nine pairs of $1m^2$ quadrats are used to investigate how microtopography affects the chronosequences of all vascular and lichen species (see sections 2.1-4). Time constraints restricted the placement of randomly placed quadrats and so a systematic sampling strategy was used (section 2.3). It has been suggested that sampling size depends on many criteria including time in the field and the variation in the vegetation (Moore and Chapman, 1986). The sampling size used in the present study (generally 18 quadrats per age-stage, with 24 environmental parameters recorded in each quadrat) is considered adequate as it compares with much of the previous work on glacier forelands – in some cases sample sizes are greater than in the present study (e.g. Elven, 1975; Birks, 1980; Sondheim and Standish, 1983), and in some cases they are smaller (e.g. Viereck, 1966; Vetaas, 1986; Alexander and Burt, 1996). In order to check that the samples are representative of general vegetation patterns across each foreland two (rather than one) x $1m^2$ quadrats at each position were recorded. In addition, at Storbreen, a second sequence of transects across each of the selected moraines was recorded. Generally, this study improves on much of the previous work by sampling the heterogeneous landscape and by measuring a large number of environmental parameters within each quadrat. Specific studies, such as that of Crouch (1992), which investigated preferred quadrat sizes, have been an important influence on the sample size used within the present study (see section 2.3.3). The results of the vegetation data collection are displayed in chapters (4) and (6), which describe the classification of the vegetation data. Chapters (5) and (6), display the ordination results, and describe the relationship between the environmental parameters and the vegetation patterns.

Following Kent and Coker (1992) it was considered best to use at least two methods of multivariate analysis to lend support to the output derived from the techniques. Kent and Coker recommend the use of TWINSPAN in conjunction with DCA and a similar approach was also used by Crouch (1992). Whittaker (e.g. 1985) used a variety of analytical methods and DCA was found to be a reliable and robust method. Crouch (1992) also used DCA as well as TWINSPAN and CCA. She found TWINSPAN to be reliable and robust and preferred DCA to CCA. DCA and TWINSPAN are therefore proven methods of analysis and, furthermore, have been shown to be compatible for complementary analysis (e.g. Kent and Coker, 1992). DCA was preferred over CCA for two main reasons: a) the vegetation data is considered more reliable than the environmental data and so it was considered better to superimpose the environmental data onto the vegetation distribution; b) DCA is compatible with TWINSPAN (Carleton et al., 1996). The analytical techniques are described in greater detail in section 2.9 and the presentation techniques used for TWINSPAN are described in section 4.1 and, for DCA, in section 5.2.

2.11.4 Justification of the presentation techniques

An extensive range of presentation techniques have been used for a number of reasons: the size of the data set is large; the data set is complex; and the main aims of the thesis require detailed interpretation of the data set. Previous methods of presentation were not considered able to elucidate the complex relationships between the species patterns, sites and environmental factor complexes for reasons that are outlined below.

The main aims (see section 1.1) require an understanding of highly complex relationships. The presentation methods were mainly developed through trial and error so that the author could visualise the complex relationships within the data set. The most important presentation methods developed for this study are for the multivariate analysis programmes TWINSPAN and DCA. The presentation methods took advantage of the spreadsheet and drawing programmes in WINDOWS – namely Microsoft Word and Excel - and these relatively recent applications are used extensively to elucidate the multivariate data.

There are a number of features of the standard TWINSPAN presentation methodologies (i.e. final tables and dendrograms) that would have made interpretation of the present data difficult, especially with regard to separation of the site data. This thesis requires a complex numbering system for the site data sets, so that the site numbers relate not only to age but also to position. In addition, the ecologically meaningful TWINSPAN "final groups" (see glossary) are taken from several levels, as recommended by Kent and Coker (1992). Final tables are not considered sufficient for easy separation of ecologically meaningful TWINSPAN "final site groups" at the different levels. Dendrograms are also not considered suitable because it is difficult to visualise the position of each of the numbered sites within each group (even though the site groups are displayed at different levels) – hence the groups are not ecologically meaningful at a glance. The profile diagrams (see section 4.1) overcome all these problems because they display the location of TWINSPAN site groups, at each level of division. Thus it is possible to separate the site groups into ecologically meaningful "final site groups", which can later be used in complementary analysis (see Kent and Coker, 1992). Using the profile diagrams it is also easier to visualise succession, according to the TWINSPAN separation, across the forelands at each level of division – a feature that dendrograms and final tables are unable to achieve. It should be noted, however, that TWINSPAN final tables and dendrograms are considered adequate for display of the TWINSPAN species data and for the separation of TWINSPAN "final species groups", and are used within the present thesis for this purpose. The dendrograms produced for the study are not described or included within the final version of the thesis due to the large amount of display material presented and also because the TWINSPAN final tables are considered to provide an adequate display of the TWINSPAN species results. However, the dendrograms are available in draft form from the author. The classification results are presented in chapters (4) and (6) and are discussed in the concluding chapter.

Previous authors generally display DCA using species plots (with environmental parameters indicated), species ranks (with environmental parameters indicated) or centroid plots (of combined TWINSPAN group scores) with the confidence interval of the groups indicated by bars (cf. Kent and Coker, 1992; and Matthews, 1992). For present study purposes plots of all species and environmental parameters are considered too cluttered (due to the high number of sites or species on each plot) for easy interpretation. A centroid plot (see section 5.2) of species or samples, with superimposed environmental factors, was chosen instead (without confidence interval bars, again due to the interpretation factor).

A simple, uncluttered centroid plot is considered useful for displaying the most important environmental influences on vegetation patterns across each foreland. It clarifies the influence of environmental factors and factor complexes (*sensu*: Whittaker, 1985) on the TWINSPAN "final groups"; and also how the TWINSPAN "final groups" are related to each other. However, these plots are not able to show, at a glance, the overlap between the groups, how distinct the groups are, and the position of individual species or samples on each axis. For this reason displays were constructed, so-called rank tables (see section 5.2, Tables 5.1-5.16 and Table 6.4), with the colour-coded TWINSPAN "final groups" superimposed onto DCA ordination axes (1) and (2) ordination (the environmental parameter sequence on each axis is also displayed). From this it is possible to understand the extent to which the DCA and TWINSPAN results correspond and, where there appears to be considerable correspondence, the most distinct assemblages can be described. It is suggested that by using these complementary rank tables, elucidation of the most distinct assemblages (see section 7.4.2 and Table 7.1) is likely to be more representative of extant vegetation patterns than if the TWINSPAN and DCA results are used separately. The ecological meaning of the sequences on each ordination axis is elucidated by displaying the eigenvalues of each axis and also by showing the distribution of TWINSPAN groups along the axis. If the two multivariate techniques show similar patterns and the eigenvalues are high (relative to each other), it is suggested that those patterns can be considered as ecologically meaningful. The ordination results are presented in chapters (5) and (6) and are discussed in chapter (7).

Lastly, considerable use of annotated summary tables (in Microsoft word) has been made for summarising the complex results. Without them it would have been more difficult to elucidate certain inter- and intra-foreland trends. The summary tables are particularly useful for swift reference and the ability to colour code the cells (for position or for level of division) also helps to elucidate patterns, derived from a highly complex data set and output, at a glance. Annotated summary tables (e.g. Tables 4.9-10 and 5.26-27, and Appendices 7 and 8) are used throughout the results chapters as well as within the concluding chapter and Appendices.

"Environmental change in space is generally along macro-, meso-, and microgradients resulting in repetitious patterns of gradients which are determined by numerous factors, such as precipitation, temperature, soil moisture and other soil characteristics, soil movement, snowbeds, wind, fire and microrelief. The vegetation is in dynamic adjustment to the environment and is manifest as a complex pattern determined by the pattern of environmental gradients."

Churchill and Hanson (1958: 180)

CHAPTER THREE: The foreland environment

3.1 The presentation of the environmental data

Due to the large amount of data produced by this study, with many environmental parameters being measured at each foreland, it was necessary to group the environmental parameters into categories in order to reduce the size of the descriptions. The original intention was to organise the environmental results chapter according to the terrain age factor complex and the microtopography factor complex described by Whittaker (1985, 1987, 1989) and supported by Crouch (1991, 1993), in order to create a continuity of approach. However, some of the 24 parameters were difficult to place into Whittaker's scheme and it was also more logical to use a system of categories that made no assumptions about the relationship between the parameters. It was therefore decided to group the parameters into macroscale and mesoscale parameters, and microscale parameters (see glossary). Matthews uses this terminology for distinguishing larger scale environmental influences from smaller scale climatic influences. Thus the term macroscale refers to regional differences between forelands (mainly altitude, latitude and continentality); the term mesoscale refers to parameters which affect whole sections of foreland (within-foreland differences of altitude, distance from glacier and age) or several sites on a moraine (size of moraine, aspect and position); microscale parameters are those which differ at the site or quadrat scale. The microscale environmental factors have been divided into three further categories according to their relative influence on the conditions and individual plants at a site. The categories chosen are: micro-climate; disturbance; and soil and vegetation.

In chapter (2) the method of measurement of the environmental parameters was discussed as well as the rationale behind the choice of environmental parameter. The implications of the results will be discussed in the concluding chapter, where a comparison will also be made with previous work on the effects of environmental factors on vegetation succession. This chapter provides a description of the prevailing environmental conditions found across each of the forelands and the moraines on those forelands. The descriptions refer to simple graphical or tabular displays of most of the parameters and each description discusses and compares the prevailing environmental factors on each of the forelands. It is important to note that this chapter mainly describes the distributions and patterns of the parameters across the moraines and foreland and, except where statistical analysis has been carried out, no assumptions will be made of the significance of the relationships between the environmental parameters. However, a preliminary discussion of the relative influence of microtopography on the environmental distribution patterns is discussed within the present chapter. The relationship between the environmental parameters, as well as the influence of these environmental factors on the vegetation pattern, will be elucidated and discussed in later chapters.

3.2 Macroscale and mesoscale environmental factors: a comparison between the forelands

Regional differences between forelands have been discussed in some detail in chapters (1) and (2). However, it is necessary to introduce the mesoscale environment in order to make **comparisons** between the forelands. The following section therefore briefly summarises the mesoscale characteristics concerning each of the forelands and the differences between the meso-environment of each foreland is briefly described. It will then be easier to elucidate any differences in pattern of the micro-environmental factors that exist across moraines on each foreland.

3.2.1 Altitude

In Fig. 3.1 it can be seen that, across the forelands under study, there is a general rise in altitude with decreasing age. The altitudinal range of each foreland, however, is relatively small: it is 40 m at Storbreen high sequence and Bøverbreen; 50 m at Høgvaglbreen; 60 m at the Storbreen low sequences (1 & 2); 90 m at Austerdalsbreen; 160 m at Svellnosbreen; and 170 m at Fåbergstølsbreen. Because increasing altitude generally follows ground of decreasing age, it is difficult to separate the effects of altitude and age. Whittaker (1985) did not consider a 50 m difference in altitude to have a considerable effect on vegetation and soil development so ignored the small differences in altitude in his study. However Matthews (1976, 1979) Whittaker (1985, 1987, 1989) and Crouch (1991, 1993) did show that altitude differences, of over 100 m, between the Storbreen low moraine sequences (1140 to 1200 m) and the Storbreen high moraine sequences (1310-1350 m), had a marked effect on the pattern of succession. Furthermore, for each rise of 100 m a lapse rate of approximately 0.5 °C can be anticipated (Green and Harding, 1980; Matthews, 1987). Precipitation is likely to increase with altitude (e.g. Burrows, 1990) and an increase in mean wind speed with increased elevation has also been found (Gloyne, 1967), accentuating the biological impact of temperature lapse rates. It is also likely that the effects of the temperature lapse rates and increasing wind speeds become exaggerated with increasing altitudes and especially above the tree line. Altitude differences of greater than 100 m will be taken into consideration in the discussion of the pattern and relative influence of the various environmental factors. Furthermore, the relative importance of altitude as an influence on both environmental and vegetation patterns will be elucidated and discussed further in chapter (6), and in the concluding chapter.

3.2.2 Distance from snout

As can be seen in Table 3.1 the distances that the glaciers have retreated since 1750 is far greater on the subalpine forelands than on the low- and mid-alpine forelands. The glaciers have been found to have a marked effect on the mesoclimate of the foreland (Matthews, 1992; Vetaas, 1986). Glacier winds persist close to the glacier but only within a relatively short distance (Oke, 1987). In a study at Skaftafellsjökull, it was found that temperatures are considerably depressed up to 200 m of the glacier and are affected up to a distance of 600 m (Lindröth, 1965). In addition Ballantyne and Matthews (1982) showed that moisture conditions are considerably higher within 50 m of the snout, although this does not affect moraines in this study as all the youngest moraines are separated by a considerably greater distance than 50 m. It can be seen in Table 3.1 that the effect of the glacier wind, in terms of temperature depression, would have an influence on only the youngest moraines at the lower altitudes but would affect almost all the moraines on the foreland at the highest altitudes.

Table 3.1 Comparison of the cumulative distance between the glacier snout and each successive moraine.

(Distance in meters) FORELAND *(see Appendix 2 for abbreviations)*

Moraine symbol	AUSF	FÅSF	STLF1	STLF2	SVLF	STHF	HØHF	BØHF
snout	0	0	0	0	0	0	0	0
M8	-	-	-	-	-	200	-	-
M7	600	-	-	-	-	475	-	-
M6	1450	200	800	800	500	650	270	200
M5	1700	600	825	825	567	700	300	420
M4	2360	800	1050	1050	734	737	400	470
M3	2660	1900	1150	1150	850	862	500	745
M2	3320	2180	1337	1337	1000	925	550	845
M1	3920	2330	1587	1587	1125	1175	800	885

(see Table 3.2 for age of moraines on each foreland)

It is anticipated therefore that the proximal slopes of the youngest moraines at all altitudes, and the proximal slopes of most of the moraines at the higher altitudes, will be affected by proximity to the glacier and this will be taken in consideration when discussing the prevailing micro-environmental and vegetation patterns on the moraines. By referring to the work at Glacier Bay it can be seen that distance also has implications for migration rate (Matthews, 1992), although it is likely that the distances between moraines, within the present study, are too small to be of significance (Matthews, pers. com.)

3.2.3 Age

The sequence of moraines across each forelands is described in section 2.2 and the method used to date the moraines, as well as the method used to enter their ages into the statistical analysis, is described in sections 2.1.2 and 2.5.2. In Table 3.2 the dates of the moraines have been listed so that they can be used for reference in later chapters. This is a useful reference table as the moraine symbol (i.e. M1, M2 ...etc.), along with the name of the foreland in question, are used to distinguish the moraines on each foreland.

The moraines were chosen for comparability in shape and size and it was not always possible to chose moraines of the same age across all forelands. In addition, as discussed in section 2.2.1.2, the dates of the 1810* and 1750* moraines at Fåbergstølsbreen, and also the 1810* and 1900* at Bøverbreen, may be slightly earlier than those entered into the data set. The specific ages of all the moraines will thus be taken into consideration in the discussion of the results. The relationship between vegetation and environmental patterns, with age, will be elucidated throughout these chapters according to the chronosequence approach adopted by this study. The present study differs from previous chronosequence work in that it is investigating the relative importance of factors other than time, notably microtopography and altitude, on vegetation and associated environmental patterns. For a detailed description of the foreland sequences refer to section 2.2.

Table 3.2 Comparison of the date of moraines and mature till-ridges on each foreland.

FORELANDS *(see Appendix 2 for abbreviations)*

Moraine symbol	**AUSF**	**FÅSF**	**STLF1**	**STLF2**	**SVLF**	**STHF**	**HØHF**	**BØHF**
M8	none	none	none	none	none	1968	none	none
M7	1960	none	none	none	none	1951	none	none
M6	1935	1970	1900	1900	1930	1930	1950	1960
M5	1908	1930	1870	1870	1916	1900	1930	1930
M4	1871	1909	1825	1825	1870	1850/70	1850	1900*
M3	1853	1810*	1810	1810	1808	1810	1810	1810*
M2	1785	1750*	1750	1750	1750	1750	1750	1750
M1	mature	mature	mature	mature	mature	mature	mature	mature

3.2.4 Size of moraines

The profile diagrams (Figs. 4.3 to 4.10 and Figs 6.1a-h), which are scaled representations of the moraines, show that there is a considerable amount of variation in size between the moraines. The profile diagrams are referred to, throughout the thesis, with regard to the size or shape of moraine. Unfortunately it was not possible to keep the size, or shape, of the moraines constant within this study. Furthermore, as discussed in section 2.5.3, although several simple size indices (such as height above slope base) were tried out, it was concluded that their inclusion within the analysis would be misleading largely because the shape and size of each moraine would not have been accurately described using the simple indices available. Nevertheless, the profile diagrams provide an accurate point of reference so that it is possible to comment on the effect of the size and shape if there appear to be certain anomalies within the data sets which appear to be associated with very small or very large moraines as well as broad, low moraines as against steeply-sided, high moraines. Refer to section 2.5.3 for further discussion of the rationale behind not using a size index within the statistical analysis.

3.2.5 Aspect of moraine slope

The measurement of aspect, and an elucidation of the aspect indices used for statistical analysis, is detailed in section 2.5.4, and the significance of aspect is discussed in both chapters (1) and (2). Within the present study aspect is considered to affect vegetation and environmental patterns both at the foreland scale (the aspect of the foreland itself) or at the moraine scale (the aspect of the moraine slope). Table 3.3 shows the aspects of all moraine slopes across each of the forelands. On the south-facing forelands the proximal side of the moraines are generally facing a northerly direction and so, with less warmth from the sun, this may exaggerate the effects of the glacier winds. If this is the case it is anticipated that the difference in vegetation and micro-environment between the distal and proximal slope might be greater on south facing forelands than on the north-facing forelands. It may be possible to support or reject this hypothesis by comparing the levels of frost heave and snowlie as well as the occurrence of snowbed assemblages on the distal and proximal slopes of the moraines on north- and south-facing forelands.

Table 3.3 Comparison of moraine-slope aspect and also general aspect on each foreland

FORELAND *(see Appendix 2 for abbreviations)*

Moraine	**AUSF**	**FÅSF**	**STLF1**	**STLF2**	**SVLF**	**STHF**	**HØHF**	**BØHF**
distal M1	180° S	270° W	46° NE	46° NE	210° SW	90° E	20° NNE	310°NW
prox' M1	10° N	30°NNE	250°WSW	250°WSW	30°NNE	320°NW	224° SW	120°ESE
distal M2	200°SSW	220° SW	128°ESE	128°ESE	196° S	110°ESE	50° NE	15° N
prox' M2	25° NNE	30°NNE	310°NW	310°NW	30°NNE	296°WNW	234° SW	200°SSW
distal M3	165°SSE	175° S	90° E	90° E	220° SW	104° E	46° NE	0° N
prox' M3	315°NW	35° N	286° W	286° W	70°ENE	300°WNW	230° SW	180° S
distal M4	160°SSE	170° S	70°ENE	70°ENE	196° S	118°ESE	50° NE	237° SW
prox' M4	355° N	315°NW	300°WNW	300°WNW	30°NNE	310°NW	236° SW	50° NE
distal M5	230° SW	120°ESE	86° E	86° E	200°SSW	100° E	20° NNE	0° N
prox' M5	54° NE	280° W	286° W	286° W	33°NNE	296°WNW	224° SW	220° SW
distal M6	220° SW	125°ESE	120°ESE	120°ESE	180° S	116°ESE	50° NE	310°NW
prox' M6	40° NE	270° W	296°WNW	296°WNW	8° N	296°WNW	224° SW	100° E
distal M7	210°SSW					140° SE		
prox' M7	30° NNE					310°NW		
distal M8						140° SE		
prox' M8						310°NW		
General aspect	*southerly*	*south-easterly*	*north-easterly*	*north-easterly*	*southerly*	*north-easterly*	*north-easterly*	*north-westerly*

3.2.6 Slope position

Section 2.3 describes how the position for the sites across each of the moraines, on every foreland, was chosen and also discusses the relationship between position and exposure. As discussed in section 2.3 the sampling design is uniform so that there is no difference between the positioning of sites from foreland to foreland. The different positions, across each moraine, represent the differences in microtopography for each site (pair of quadrats). The microscale environmental parameters in the following sections are those measured in each quadrat at each position across every moraine. The figures, mainly in the form of graphs, display the occurrence of the various environmental factors across each successive moraine on each of the forelands thus showing the relationship between each parameter and microtopography as well as with age. The significance of the relationship between all the environmental parameters, including microtopography, as well as that between the environmental parameters and vegetation pattern will be elucidated and discussed in greater detail in chapters (5) to (7).

3.3 Micro-environmental factors associated with climate

There are three climatic micro-environmental factors that were investigated: snowlie; moisture; and temperature. Snowlie and moisture were assessed for all quadrats using methods previously used by Crouch (1992). An attempt was made, within the present study, to find an alternative quantitative, but simple, method of moisture measurement. A prototype moisture measuring device, the capacitance probe, is an instrument developed by the Institute of Hydrology in collaboration with Didcot Instruments and it is briefly described in the methods chapter (2) (further information can be obtained from the Institute of Hydrology, Wallingford, Oxon). The results from the measurement of one foreland and also a test survey are displayed and briefly discussed but unfortunately the measuring device, failed after a short period of time in both the 1990 and 1991 field seasons so that it was not possible to use the results for between foreland comparison. However, the results that were obtained, while the probe was working, could be used to corroborate the "finger test" method, developed and tested by Crouch (1992), and thus lend support to the use of this rather unconventional method in the present study. Grant's thermistor thermometers were used to measure daily temperature fluctuations over a two year period on two moraines on the Storbreen foreland and the results are displayed below.

3.3.1 Snowlie

The importance of snow and wind, as an influence on vegetation patterns, has been outlined in the literature review (section 1.3) and a brief outline of snow accumulation and wind force, within the regions under study, is given in section 1.2.2. The methodology used by the author to estimate snow-lie follows Crouch (1992) and is described in section 2.6.1. Figs. 3.2 to 3.9 display the % of black to green lichens across moraines on all the forelands which represents briefer periods of snow cover (or lack of snow) where the percentage of black lichens is high. On the two subalpine forelands not all the moraines have the black lichens, which would suggest that snow-lie would appear to be more constant on these forelands than on the other forelands: at Austerdalsbreen three moraines (M1, M2 and M4) have no black lichens while three other moraines had less than 10% black lichens on their crests; at Fåbergstølsbreen two moraines (M1 and M2) have no black lichens and three have less than 10% black lichens on their crests. On all the forelands there appears to be a slight tendency for the pioneer and developing moraines to have shorter periods of snow-lie than the older moraines as shown by the greater proportions of black lichens to green on the younger moraines. As would be expected, snow duration is longer at the low-slope positions on the moraines than on the higher positions. From these diagrams it is possible to see that microtopography has a much stronger influence on snow lie than age or altitude, although age and altitude seem to have some influence on the distribution of the snow on the subalpine forelands. Even small changes in microtopography influences snow-lie as shown by the higher snow cover in the hollows between the ridges on the "double" moraines within the survey (i.e. M2 at STLF2; M3 and 4 at STHF; and M6 at BØHF). The gully, on the oldest terrain at Svellnosbreen, has been re-drawn as a moraine and the distribution of the snow is similar to the moraines in terms of position. The differences in snowlie between the base of the moraines and the crests is probably due to the wind blowing the snow into more sheltered hollows where the snow can accumulate in drifts (Miller, 1982). On the subalpine forelands, where there is a preponderance of trees and bushes on the older ground, snow appears to accumulate more on the older ground than it does on the young terrain. On the low- and mid-alpine forelands this tendency is not apparent, possibly due to the low and dense nature of the vegetation on the older ground.

It was shown in section 1.2.2, snow accumulation on these forelands is likely to be fairly similar between the subalpine and low and mid-alpine forelands. However, as can be seen from Figs. 3.2-9 there is a considerable difference in the way the snow accumulates between the subalpine and low- and mid-alpine forelands. The spread of snow across the moraines appears to be much less even on the higher altitude forelands. The difference may be caused by the windier conditions, considered to occur at the higher altitudes, causing the crests of the moraines to be cleared of snow more quickly than at the subalpine altitude. Additionally the bushy nature of the developing vegetation on the subalpine foreland would tend to trap snow in a more efficient way than the low, prostrate vegetation found on all ages of ground on the low- and mid-alpine forelands. Lastly, on most of the low- and mid-alpine forelands there is a slight tendency for snow duration to be greater at the base of the proximal slope of the moraine than on the distal side. This could be due to the cooling effect of the glacier wind preventing earlier snow-melt, although at Svellnosbreen it could also be due to the northerly aspect of the proximal moraine slopes. However, even where the proximal slopes are south facing, such as at Høgvaglbreen and Bøverbreen, snow duration appears to be slightly longer on the proximal slope and so it is possible that, at least at mid-alpine altitudes, proximity to the glacier may be more significant than microtopographic slope aspect. The results outlined in this section are preliminary observations and their statistical significance, in relation to other environmental factors and vegetation patterns, are tested in chapters (5) and (6) and discussed in the concluding chapter.

3.3.2 Moisture

Differences in moisture found across a foreland can be caused by many factors and has been shown to be especially influenced by vegetation cover and microtopography and is linked to length of snow lie on glacier forelands (e.g. Whittaker, 1985; Crouch, 1992). The prevailing moisture conditions at a site is probably the single most important parameter affecting vegetation growth (Crawford, 1989), however, as discussed in chapter (2), there is no simple, accurate and quantitative method of the measurement of moisture. It was therefore felt necessary to find an alternative new method and thus after approaches to several companies and institutions the testing of a prototype moisture probe was proposed for this study and the results from the trial runs are described here.

3.3.2.1 Trial run for capacitance probe

Calculation of the best estimate of population standard deviation was used to test the accuracy and reproducibility of the instrument. An experimental plot was set up across the 1750 moraine and the method is described in chapter (2). There are two main aims in performing this trial:

a) To test how the moisture levels differed at the 3 depths across the whole quadrat and thus, by substitution in the equation for a 95% confidence interval (CI), provide the number of measurements needed to estimate moisture content to a stated level of accuracy at each site along a transect.

b) To test how measurement under different weather conditions has an influence on the probe readings and hence provide a calibration for results derived under different weather conditions.

The number of measurements ($\mathbf{n^*}$) needed were found by using the following equation:

$$\sqrt{\mathbf{n^*-1}} = \frac{\mathbf{t.s}}{\mathbf{CI}}$$

$\mathbf{n^*}$ = the number of measurements needed,

$\mathbf{t}$ = value of t for a sample of 50 measurements at 95% CI (~ 2.0)

$\mathbf{s}$ = the sample standard deviation for 50 measurements

$\mathbf{CI}$ = Confidence Interval (0.05 capacitance units)

As can be seen in Tables 3.4 and 3.5 the moisture measurements were found to be relatively consistent across the quadrat at each depth. At a confidence interval of 95%, four measurements were found to be necessary after dry weather and five after wet weather. One very stony site (Table 3.4) with a standard deviation of 6.48 was excluded from the final calculations due to the wide difference in measurements. In general there was a larger standard deviation on the wetter ground (i.e. at the 5 cm depth at the base sites and on the "wet sites"). Because of this it was decided to use only the surface and 2.5 cm depth measurements to compare with the "finger test" measurements at the surface and 2.5 cm depth. The capacitance probe has only been used to examine the relative accuracy of the "finger test" methodology. The slightly higher standard deviations for wet sites is not considered to have compromised the results for the reason that wet ground is easily identified in the field using the "finger test" methodology. In practice, therefore, the most important function of the capacitance probe was to check on the relative accuracy of the "finger test" on substrates of intermediate to low levels of moisture.

3.3.2.2 A comparison between two methods of measuring moisture levels

In 1990 moisture determinations were made across the Svellnosbreen foreland at each of nine sites placed across a sequence of six progressively older moraines. Before measurements from the probe could be used they had to be converted, using a calibration chart provided by the Institute of Hydrology (Fig. 3.10), to a volumetric % water content. The method for constructing the calibration chart is given in chapter (2). Figs. 3.11a and 3.11b show the relationship between the moisture levels across moraines at the surface (Fig. 3.11a) and at 2.5 cm depth (Fig. 3.11b). The probe measurements represent moisture levels, whereas the finger test measurements represent dryness. On the whole, where finger test values were high, probe values were low showing that there was a considerable degree of correspondence between these two methods. The results from both methods, for the 2.5 cm depth (Fig. 3.11b) show that the crests of the moraines are the driest positions and the low-slope positions of the moraines are the wettest, while the surface measurements do not show such a strong relationship. The stream channel on a shoulder-slope position on M4 showed a high moisture value using both methods, as would be anticipated. The strong degree of correspondence between the two methods displayed by these charts (Figs. 3.11a and 3.11b) suggest that the finger test provides an approximate measure of moisture. This is corroborated by statistical analysis. Using the Spearman rank correlation coefficient, a significant negative correlation was found with **r = -0.739 (p = <0.001)** for the surface measurements, and **r = -0.764 (p = <0.001)** for the measurements at a depth of 2.5 cm, respectively. This indicates that the correspondence between the two approaches is statistically significant, although only 55-58% of the variability in moisture content, according to one method, is accounted for by variablity in the other. However, some of the variability could be related to small differences in moisture content where the samples were made - i.e. probe readings were averages of four sampling spots, within the quadrat, but the finger test readings were from one sampling spot in the quadrat. The results from this study therefore support the use of the finger test, developed and first used in the field by Crouch (1992), as a simple method for the measurement of moisture levels at these sites.

3.3.2.3 Dryness across the forelands using the "finger test"

Figs. 3.12 to 3.19 show that the driest positions are on the crests of the moraines and the wettest are on low-slope positions. There does not appear to be any distinct difference in the patterns of moisture between moraines of different age or on different forelands, despite the possible differences in precipitation described in section 1.2.2. However, between-foreland comparisons in moisture are difficult to achieve because the date of the last rainfall for each of the foreland moisture data sets varied and this may well have affected the moisture levels measured. The importance of microtopography on the moisture patterns (Figs. 3.12 - 19) nevertheless agree with Whittaker (1985) and Crouch (1992), who suggests that microtopographic variation may be an important influence on moisture, but disagree with Crouch, who found that moisture levels increase with age and thus is a time-influenced parameter. These results will be elucidated further, and discussed, in later chapters.

3.3.3 Temperature

A total of six thermistors were emplaced over a two year period mainly on the 1750, but also on the 1900 moraine. The layout of the thermistors is described in the methods chapter and all thermistors were calibrated at the beginning and end of each season to check for the drifting of temperatures. A large quantity of data was obtained from the thermistors even though one of the thermistors failed, and the results from the five thermistors are shown in Figs. 3.20 to 3.30 and Tables 3.6 to 3.12. By comparing the differences in average foreland temperatures, as predicted in Table 1.1, with the results from the five thermistors, it is possible to speculate on the range and annual pattern of temperatures found at different positions across the moraines, on the selected forelands. It is proposed that other forelands are likely to exhibit a similar pattern to that found across selected moraines on the Storbreen Low (1100m) foreland but with a lower mean temperature on the higher forelands and a higher mean on the lower forelands. In addition, annual differences in temperature will significantly affect the actual temperatures found on the forelands. For example at Fjaerland, Myklemyr and Bjørkehaug (and thus, presumably, at all forelands within this study) the average temperatures for 1990 were the warmest for the whole 1961-90 period. In 1991 the average temperatures were cooler (but still relatively mild) and the winter was cold. Thus it is not so much the actual temperatures which are of interest, but it is the microtopographically-induced patterns shown by the various thermistors in relation to position across the moraines. These patterns are summarised below.

3.3.3.1 Thermistor (1) and (2) (the 1750 moraine, 1989-90)

Thermistor (1), recording twice daily, was placed on the proximal slope on the 1750 moraine from 26th August 1989 to 19th August 1990 and thermistor (2), recording four times daily, was placed on the distal slope of the 1750 moraine from 26th August 1989 to 17th August 1990. Two measurements per day were used for analysis - the 3 am and 3 pm measurements. As can be seen in Table 3.6a-g the annual mean does not vary much between positions, except for the temperature measurements for air which is 1 °C lower. Neither does there appear to be a gradient of mean annual temperatures from high-slope to low-slope positions. The average of all the positions on the proximal slope is 2.57 °C, and it is 2.35 °C for the distal slope, which is considerably milder than the temperatures estimated for the foreland in Table 1.1. According to temperature data from the Norwegian Meteorological Office, the 1989/90 winter was the mildest of all the winters in the 1961-90 period and so these higher temperature figures are not surprising.

Figs. 3.20 and 3.22 show a similarity in temperature between high- and low-slope positions during the summer months, from July to mid-November. During the winter and spring months, however, between-position differences in temperature are clear, suggesting that microtopographic effects have a greater influence on micro-climate during the winter and spring months. For example, low-slope positions during most of the winter period fluctuate around -1 to -2 °C, whereas high-slope positions range between -5 to -7°C. It is proposed that the main cause of these effects is snow cover, with low-slope positions having a persistent covering of snow during the winter leading to relatively constant temperatures just below freezing, while high-slope positions suffer inconsistent snow cover with greater exposure to chilling winds. This is clearly shown, on both the distal and proximal slopes, by the pattern of temperatures from the beginning of May to the middle of June. The difference in the rate of ground-thaw, at various depths, is displayed as a distinct gradient, with the probes placed at the surface at high-slope positions warming up in early May, and the probes placed deeper in the soil at low-slope positions warming up in mid-June.

The standard error and range for both thermistor (1) and (2), shown in Table 3.6a-g, are considerably greater for the crest positions than for low-slope positions and there is a clear difference between the two positions suggesting that there are greater extremes of temperature on the higher positions of the slope than at the base. Figs. 3.21 and 3.23 show the pattern of the standard deviations of temperatures at various positions, on the proximal and distal slope, through the year. The temperatures are more stable during the winter months, possibly due to snow cover, although the crest and air probes show considerable instability throughout the winter on the proximal slope and the crest and shoulder positions show instability on the distal slope. At the end of April, there is a convergence of temperature stability (except for the air probe), on both the proximal and distal slopes, possibly due to snow cover and calm conditions which does not remove snow from the crest of the moraine (but is not deep enough to cover the air probe). As with the temperature values themselves, there is a marked increase in the standard deviation values between April and the middle of June. The standard deviations of each of the probes increase in stages, depending on position, with the high-slope standard deviations increasing sharply first, in April, and the low-slope standard deviations increasing in the mid-June. The greatest standard deviations occur during the summer months, but the differences in temperature between the high- and low-slope positions is not as distinct as it is during the winter. During the summer the greatest standard deviations occur for probes placed on the crest, but otherwise there does not appear to be a clear pattern of temperature standard deviations for probes placed at the other positions.

According to Fig. 3.20, the readings from thermistor (1) show that there does not appear to be a consistent pattern of temperature at depths of 0 cm, 1 cm and 2 cm. This is also true for thermistor (2), as shown in Fig. 3.22, at depths 0-2 cm. However, the probes at 15 cm depth, at low-slope positions, show a greater degree of stability in temperature than at shallower depths. Furthermore, temperatures at 15 cm tend to change more slowly. It should be noted, however, that temperatures on the crest at 15 cm depth correspond closely with those at 2 cm depth. The effects of depth is therefore observed most clearly between April and July, at low-slope positions, where the substrate around the surface probes thaws more quickly than it does around deeper probes, suggesting the ground remains frozen for longer with increasing depth. For the rest of the year, temperatures at 2 cm and 15 cm tend to be similar at each of the positions. The population correlation calculation (in Microsoft Excel, version 5.0) matrices, Tables 3.7 and 3.8, show how closely the temperatures at the various positions follow each other through the year. The lowest correlation, for both the distal and proximal slope, is between the crest and toe positions and this confirms the importance of the effect of microtopography on temperature.

In order to elucidate the reliability of the results, from thermistors (1) and (2), the thermistors were calibrated at the end of the field season and the temperatures were found not to have drifted. Furthermore, one probe from each thermistor thermometer was placed at the same depth and position. The temperatures and standard deviation from these probes are displayed in Fig. 3.30 and the chart shows the similarity between the results of these thermistors. The annual mean only differs by 0.25 °C and a correlation of 0.99 ($p < 0.001$) for the temperatures and 0.90 ($p < 0.001$), shown in Table 3.12, for the standard deviations suggests the reliability of the temperature results for the 1989/90 season. It is therefore reasonable to assume that the results from thermistors (1) and (2) are reliable and are a fair representation of temperature variation across a moraine of this size at this altitude.

3.3.3.2 Thermistor (3) (the 1900 moraine, 1990-91)

Two thermistors were placed, from 24th August 1990 to 14th August 1991 on the 1900 moraine but only one, recording 4 times a day, worked reliably. Two measurements per day were used for analysis - the 3 am and 3 pm measurements. Comparison of temperature means across the 1900 moraine with the 1750 moraine show that temperatures are lower across the 1900 moraine: the annual mean for all positions during the August to May period, from 1990 to 1991, was -2.5 °C across the 1900 moraine, while, for the same period, thermistor (4) recorded an annual mean of 0.1 °C across the 1750 moraine. The lower annual mean, found across the 1900 moraine, is possibly due to the 1900 moraine having a slightly higher altitude and being closer to the glacier and thus may suffer lower temperatures due to mesoscale variations in climate across the foreland. The annual mean for all positions was -0.39 °C, across the 1900 moraine from

1990-91, which is close to the average predicted foreland temperatures indicated in Table 1.1 for Storbreen (i.e. between -0.78 and -1.33 °C). Nevertheless, the fact that 1991 was a mild year explains why the annual mean temperature shown above could be higher than predicted in Table 1.1, for that altitude.

Although similarities in temperature pattern, according to microtopographical position, are shared between thermistor (3) and thermistors (1) and (2), there are some important differences (see Fig. 3.24). Autumn frosts causing the mean temperatures to fluctuate around 0°C occur earlier. Furthermore, summer temperatures, across the 1900 moraine, appear to converge later in the summer and the increase in temperature, which takes place in spring, begins later at the beginning of May and is extends later to the end of June or the beginning of July. The differences in annual mean temperatures for the 1750 - thermistors (1) and (2) - and 1900 moraine -thermistor (3) - could be responsible for the difference shown in the rate of thawing. Data from the Norwegian Meteorological Office shows that 1990 had milder temperatures than 1991, which could provide an additional influence to the mesoscale differences in climate outlined earlier. Unfortunately there were no late spring and summer data for the 1750 moraine during 1991, so it is not possible to make a comparison of the thawing period temperatures on both moraines taken during the same year.

An additional explanation for the differences in the rate of thawing found across the 1900 and 1750 moraines could be due to the differences in profile between the 1900 and 1750 moraine, so that much of the moraine is blown clear of snow during the winter period, thus exposing much of the proximal slope to greater extremes of temperature. During the winter period, differences between the crest and low-slope positions of the distal slope of the 1900 moraine are especially noticeable, with the toe and distal mid-slope positions remaining fairly stable and temperatures on the crest being unstable. However, the difference between the crest and low-slope positions on the proximal slope are not discernible with the proximal mid-slope and toe-slope positions showing a large degree of instability, especially from mid-February to April. The distal slope of the 1900 moraine is close to the proximal slope of the 1870 moraine and it is anticipated that a considerable amount of snow builds up on this slope. In contrast, the proximal slope does not have a clear-cut base position so that, from the toe-slope measurement site, the slope continues gently downwards towards the river. Snow may not collect, therefore, as it does at the base of the distal slope or as it does on the 1750 moraine (see also profile diagram Figs. 4.5 and 4.6).

As with thermistors (1) and (2), the slower rate of thawing occurs at low slope-positions so that the distal toe and mid-slope positions are last to thaw at the end of June or beginning of July; the proximal toe and mid-slope positions thaw in the first half of June; and the crest positions thaw out in May. The difference in the rate of thaw between probes placed at 1 cm depth and 15 cm depth is also noticeable at all positions with the substrate at 15 cm taking longer to thaw out than substrate at the surface. For example, the substrate at 15 cm depth on the crest takes a week longer to thaw than at the surface (1 cm depth). These results confirm that microtopography and snow melt is a major influence on temperature differences through the year across the moraines.

As with thermistors (1) and (2), Table 3.6a-g shows higher standard errors and ranges for crest positions than for low-slope positions, and the proximal slope positions all have greater standard errors and ranges than the distal slope. This suggests that the greatest extremes in temperature are found on the crest, then the proximal slope and that the most stable temperatures are found at distal low-slope positions. Fig. 3.25 confirms this pattern and also shows a similar pattern to that shown by thermistors (1) and (2) in so much as winter temperatures are more stable than summer temperatures. Both Figs. 3.24 and 3.25 show that in the summer the most stable and lower temperatures are found at 15 cm depth, and during the winter the most stable and higher temperatures (around -1 °C) are found at the distal low and mid-slope positions. The population correlation calculation matrix (Table 3.9) shows the lowest correlations between crest positions and the distal toe-slope and mid-slope positions. Microtopography appears to have the greatest influence on temperatures during the winter months. Since the other thermistor thermometer, on this moraine, failed it was not possible to compare the readings from the two thermistors. However the working machine was calibrated at the end of its use and it was found to be measuring temperature accurately.

3.3.3.3 Thermistor (4) and (5) (the 1750 moraine, 1990-91)

Thermistor (4), recording 4 times a day, had probes placed at mainly 1 cm depths on both sides of the 1750 moraine and the thermistor was working satisfactorily until the end of May. Two measurements per day were used - the 3 am and 3 pm measurements. Thermistor (5) had probes at 1 cm depths on both sides of the 1750 moraine and as it recorded 12 times a day it ran out of roll on the 20th December. Six measurements per day were used: 3 am, 7 am, 11 am, 3 pm, 7 pm, 11 pm. In contrast to thermistors (1-3) this data represents only cold-season measurements.

The general trends shown by the temperature results from thermistors (1-3) for the winter and autumn measurements are paralleled by thermistors (4) and (5). As shown in Table 3.6a-g, the annual means do not show differences according to position but the annual standard errors and ranges for each position show a distinct trend with the highest standard errors and ranges represented by crest positions and the lowest ranges and standard errors represented by low-slope positions on the moraines. During the autumn the temperatures of all positions are fairly similar and follow each other closely (Figs. 3.26 and 3.28) but at the beginning of November the temperatures of high-slope positions diverge from those of low-slope positions. The standard deviations, shown in Figs. 3.27 and 3.29, for the low-slope positions, become more stable and converge at the beginning of November, while the standard deviations remain fairly high and unstable for the high-slope positions (and air). The data for both thermistors do not contain summer data and so the temperature data, for the crest and low-slope positions, show a higher degree of correlation (Tables 3.10 and 3.11) than data representing the same positions from thermistors (1-3). Despite this, the crest and low-slope positions are still the least correlated, possibly due to the differential snow-lie and exposure during the early part of the winter.

Table 3.6a-g shows the differences in mean annual temperatures, standard errors and ranges for the different periods. Comparable periods of data, processed for the 1900 moraine, have been processed for the 1750 moraine, so that the August 1990 - May 1991 period on the 1900 moraine can be compared with data from the August 1990 - May 1991 period across the 1750 moraine. As would be expected, average temperatures were cooler on the 1900 moraine than the 1750 moraine. For example the average air temperature was -3.25 °C on the 1900 but -1.4 °C on the 1750. As outlined earlier, the difference in temperature is not surprising because the 1900 moraine is at an altitude of 1200m and is also closer to the glacier. A comparison of the temperatures from thermistors (4) and (5) for the same period, position and depth, did not show such a good correspondence between the data. The crest position at 1 cm for thermistor (4) showed an annual mean of 2.96°C but the annual mean for the equivalent position for thermistor (5) was only 1.20°C. The latter figure is closer to the predicted temperatures for this foreland (see Table 1.1). It is possible that the greater number of daily readings averaged over a five-day period, as recorded by thermistor (5) (see section 2.6.3.2), may provide more accurate data. However, it is also possible that the discrepancy is (partly) caused by the thermistors themselves so that one, or both, of the thermistors are malfunctioning in some way, although both thermistors were calibrated at the end of the season and were shown to be measuring accurately. Despite the differences in the annual mean temperatures, shown by thermistors (4) and (5), the general temperature patterns for the autumn period were similar and thus both methodologies of data collation are considered worthwhile.

3.3.3.4 Summary of thermistor data

These data confirm the hypothesis that microtopography has a significant impact on temperature, but perhaps it is surprising that there was no gradient in annual mean temperature between the crest and low-slope positions of the moraine. The clearest type of temperature gradient appears to be the extremes of temperature found at any position. It appears that the effect of microtopography is most significant during the winter time with temperatures being more stable and higher at the low-slope positions and the temperatures being lower and more variable at the high-slope positions. This is almost certainly as a result of uneven snow cover and different rates of snow-melt, but the standard deviation charts also show that microtopography is influential in the summer with the greatest extremes in temperature on the crests of the moraines and the least at the low-slope positions. The effect of proximity to the glacier also appears to have an effect on temperature and the results appear to show a decrease in temperature with increasing proximity to glacier (and decreasing age which is not possible to separate from the proximity parameter). Snowmelt appears to occur later on the more proximal moraines and temperatures fall to zero earlier in the autumn. Furthermore, temperature averages tend to be lower on proximal than distal positions; the standard deviations tend to be greater on proximal than distal slopes; and there appears to be earlier snowmelt on proximal than distal slopes. The differences in temperature patterns between the distal and proximal slopes could also correspond with differences in shape (and possibly size). It is almost certain that the hollow at the base of distal slope allows for greater snow accumulation and duration than the long continuous proximal slope (without a distinct "base"). Certainly the size and shape of moraines, in relation to vegetation and environmental patterns, is of great interest and relevance to an understanding of microtopographical effects, but its detailed investigation is not within the scope of the present study. Similarities in temperature patterns were found using different collation methods. The advantage of taking averages of a greater number of measurements per day over a shorter time-scale is that the mean temperatures are likely to be more accurate and details of short-term temperature fluctuations become apparent. The advantage of averaging out fewer measurements per day over a longer time-scale is that much less time is spent in data collation and it is still possible to provide meaningful data.

3.4 Micro-environmental factors associated with disturbance

Disturbance parameters are for the purposes of this study defined as those factors that cause damage or are otherwise detrimental to the plants or soil. Disturbance in turn may alter the natural succession and cause it to be slowed down, halted or even for retrogression to occur.

3.4.1 Frost evidence and frost heave (dowel heave)

The main detrimental effect that frost can have on vegetation is through frost heave. Frost heave is caused by the movement of super-cooled water to a freezing front where ice lenses are forming. Frost heaved plants can suffer increased mortality, or loss of growth, due to mechanical breakage of roots within the soil and the lifting of the roots above the surface to be exposed and desiccated by sun and wind. For this reason recording the evidence of frost activity (nubbins, crinkles, cracks and frost heaved stones), and the measurement of actual heave (using dowels), are important environmental parameters to measure. Evidence of frost activity, was recorded according to the frequency of evidence in the 25 x 20 cm^2 small squares in each 1m^2 quadrat. Figs. 3.31 - 3.38 display the frequency results of the frost evidence survey for each quadrat across moraines on the individual forelands. Actual frost lift was recorded by inserting nine dowels (match sticks) into the ground at the end of one season and measuring the amount of lift by the following season. Figs. .3.39 - 46 display the results of the average heave (mm) of the nine dowels at each site (pair of quadrats) across moraines on each individual foreland.

As can be seen in Figs. 3.31 - 3.38 the presence of frost evidence is related to altitude, age and microtopography but there does not appear to be a difference in frost activity between proximal or distal slopes. The results indicate that frost evidence increases with altitude; with decreasing age; and on higher microtopographical slope positions. On the subalpine forelands (Figs. 3.31 - 3.32), the effects of age, as well as microtopography, are apparent, with frost activity being restricted to M4-7 at Austerdalsbreen, and mainly M4-6 at Fåbergstølsbreen. Where present, there is a distinct gradient of frost evidence across the moraines, showing the importance of microtopography as an influence on frost activity. On the low-alpine forelands (Figs. 3.33 - 3.35), frost evidence is found on all moraines but, as at the lower altitudes, is more prevalent on the high-slope positions on the moraines and on younger ground. At Storbreen high (Fig. 3.36) the pattern is fairly similar to that of the low-alpine forelands, although frost activity is greater on all moraines. At the two highest mid-alpine forelands (Figs. 3.37-3.38) the frost evidence chart shows high levels of frost activity on all moraines at all microtopographical positions.

The actual frost heave results shown by mean dowel heave (Figs. 3.39 to 3.46) provide similar patterns in the results although the levels of frost activity are not as extreme, especially on the mid-alpine forelands. On the subalpine forelands (Figs. 3.39 to 3.40) frost heave is present on the three youngest moraines and is greatest on high-slope positions of the moraines, especially at the shoulder positions, on both proximal and distal slopes. At Storbreen low (Figs. 3.41-42) there is heave at high-slope positions on every moraine, especially on shoulder or crest positions. The frost heave is greater across the Storbreen low (2) foreland (a transect of generally smaller, more acute, sections of the moraines) and the age of the moraines has less of an effect than at Storbreen low (1), which has the greatest frost heave on the two youngest moraines. Svellnosbreen (Fig. 3.43) has greater rates of frost heave than the other forelands. Higher levels of frost activity generally occurs on high-slope positions on the moraines. Although the greatest degree of frost activity occurs on the youngest moraine there does not appear to be a clear pattern of frost heave, with age, on this foreland. At Storbreen high (Fig. 3.44) the pattern of frost heave is similar to, but rates are higher than at Storbreen low (1), with frost heave occurring on the high-slope positions of all moraines but especially on the youngest ground. At Høgvaglbreen (Fig. 3.45) the pattern does not correspond with the results of the other forelands in terms of age, with the **lowest** frost heave occurring on the youngest ground, a pattern difficult to explain but possibly due to atypical soil conditions (see section 2.7.1). The higher levels of frost heave generally occurs, however, at high-slope positions, confirming that microtopography has a significant influence on frost heave. Frost heave at Bøverbreen is less than was expected (Fig. 3.46) considering the frost evidence results. Heave did not occur on the two oldest moraines and occurred on higher positions on M3 and especially on M4-6. Frost heave is generally high on the mid-alpine forelands, where it occurs, but it is surprising that it is absent from a number of moraines.

In summary, the frost evidence results show that increasing altitude, decreasing age of ground and high-slope microtopographical positions lead to increased evidence of frost activity. The actual frost lift or dowel heave results show that frost heave occurs on high-slope positions on the moraines of all forelands and, on most of the subalpine and low-alpine forelands, frost heave is greatest on the youngest ground. However, the clear altitudinal gradient, shown by the frost evidence charts, is not mirrored so clearly by the frost heave results. There does, however, still appear to be greater levels of frost heave on the four higher altitude forelands than on the four lower forelands. It is possible that the higher levels of frost activity shown by the frost evidence method is because all the evidence of the frost activity comprises features created over several years, and therefore represents a comprehensive record of frost activity at that site. In contrast, the dowel method only shows recent frost activity, over the previous winter, and the heave of individual dowels can, furthermore, be reduced by gaps between the dowel and the surrounding substrate (Heidmann, 1976). Gaps between the dowel and the substrate could be caused by placement in a coarse material which has large air spaces; careless placement by the recorder; or strong winds causing the dowels to move in their holes. In other words, the dowels may not heave while the surrounding substrate heaves and subsides around the dowel. Therefore within-site differences in soil conditions could give anomalous dowel heave results. Nevertheless, the similarity of the patterns shown by these results supports the use of both methods in combination since both methods have advantages as well as disadvantages over each other. Further discussion of these results and the relationship between vegetation patterns, soil development and frost activity are discussed in further detail in chapters (5) and (6) and a discussion of the results is made in chapter (7).

3.4.2 Solifluction and slope

Solifluction, or the down-slope movement of soil, is known to have an important effect on the soil at various positions across the slope, with the soils tending to be deeper at the base of the slope and shallower at the crest (Parkinson and Gellatly, 1991). Furthermore, down-slope movement of nutrients have also been shown to have an important effect on the nutrient content of the soil at various positions across the slope (Parkinson and Gellatly, 1991; Birkeland and Burke, 1988). Additionally, where solifluction is most extreme, physical damage to the root systems of the plants, by ripping and soil damage by the development of erosion scars, occurs. Solifluction was measured by counting the frequency of small-scale lobate forms or crenulated soil patterns in 25 x 20 cm^2 small squares in a 1m□ quadrat.

By referring to Figs. 3.47-3.54, the relationship between slope position and solifluction can be seen. The pattern of solifluction is consistent from foreland to foreland and from moraine to moraine with solifluction being greatest on mid- and shoulder-slope positions and being the least on the crest and toe-slope positions. It is therefore clear that solifluction can be related to microtopography, but it is also useful to ascertain whether it appears to show any trends with age or altitude. Solifluction does not appear to be age-related. By referring to Table 3.13 (this volume), it can be seen that the relationship of slope and solifluction to each other, as well as to other factors such as altitude, are also inconsistent. For example, solifluction appears to be greatest at the highest altitudes in the study (i.e. Høgvaglbreen and Bøverbreen) although solifluction at Storbreen high is not especially great. Levels of solifluction is very low at Storbreen low (1) foreland where the average profile length (a representation of average moraine size for each foreland) is greatest, but at Svellnosbreen, which also has a high mean profile length, the solifluction activity is moderate. According to Table 3.13, there does not appear to be a noticeable relationship between the degree of solifluction and slope angle, which at first sight is a rather surprising result but the results represent means for each foreland and do not take microtopography into account. It is likely that solifluction and slope are related and this relationship will be elucidated further in ordination chapters (5) and (6). Whittaker (1985) found some correlation between slope angle and solifluction but it was not as high as expected and the present results confirm those of Whittaker in that solifluction processes are complex and are likely to be inter-related with a number of factors such as slope, particle size and vegetation cover.

Table 3.13 Mean, range and median of solifluction, slope and mean profile length for each foreland.

Foreland	Solifluction Mean (1/25)	Solifluction Range (1/25)	Solifluction Median (1/25)	Slope Mean (°)	Slope Range (°)	Slope Median (°)	Profile length (mean)
AUSF	11.05	25	10	18.48	41	20	22.43
FASF	12.64	25	15	15.16	43	21.5	23.4.
STLF1	4.65	25	1	13.6.4	33	15	28.67
STLF2	11.07	25	10	13.4.0	36	10	22.15
SVLF	12.20	25	10	17.58	50	15	28.6
STHF	8.07	25	5	13.3.	39	12	25.3
HØHF	15.00	25	22.5	13.2.4.	30	12.5	19.4
BØHF	16.39	25	25	15.31	35	15	24.2

(see Appendix 2 for foreland abbreviations)

In summary, the results indicate that the greatest rate of solifluction occurs on the sides of moraines, and thus microtopography (and topography in general) is likely to be a major influence on solifluction processes, but there does not appear to be clear relationship with time and altitude. In chapters (5) and (6) it will be possible to elucidate these relationships further, through correlation and ordination.

3.4.3 Fluvial activity

Fluvial activity can have a highly retrogressive effect on vegetation and soil development by the stream causing erosion to the soil and till surface (Whittaker, 1985). However, as long as erosion is not great, the presence of a small slow stream can provide a permanent supply of water for moisture-loving plants causing a dramatic gradient in vegetation and soil pattern within a short distance of the stream. At Austerdalsbreen research has found that age of ground increased not only along the glacier foreland, away from the glacier, but also laterally on to higher ground towards the side of the valley (Maizels and Petch, 1985) and this effect is considered to be as a result of disturbance by fluvial activity. It is possible that at Austerdalsbreen, which has a long and flat valley floor consisting of an outwash plain (comprising sandur, very coarse gravels and cobbles in places), the base sites in this study may be younger than indicated and this will be taken into consideration when discussing the classification and ordination results. Due to the absence of clear channels or other proof of fluvial activity, it has not been possible to determine whether or not fluvial activity has influenced the vegetation since the formation of the moraine unless an actual stream bed is present. On all the other forelands, the glacial deposits consist of coarse till and boulders, while old stream channels are deeper and more obvious. Fluvial activity was measured by counting the frequency of active or inactive channels or streams in 25 x 20 cm^2 small squares in a 1m□ quadrat.

As can be seen in Figs. 3.55 to 3.62 nearly all the fluvial activity takes place at the bases of the moraines. There is one exception: on M4 at Svellnosbreen there is a site recorded at position 4 (see section 2.5.5), on the proximal slope, where a stream runs down the moraine (an additional site has been recorded at the same position, but further along the moraine, where the influence of the stream is absent). Fluvial activity therefore appears to be strongly related to microtopography. The charts also show a greater level of fluvial activity on the younger ground than on the older ground, which could be caused by the shifting position of the glacier snout and thus shifting stream origin (Matthews, 1992). This would cause the channels on the youngest ground to change position more frequently than the established stream courses further down-slope. There does not appear to be any relationship between fluvial activity and altitude. It is anticipated that fluvial activity has a significant effect on the vegetation pattern and further discussion of these results and the relationship between vegetation patterns, soil development and solifluction are discussed in further detail in chapters (5) and (6) and a discussion of the results is made in chapter (7).

3.4.4 Trampling and grazing

Grazing and trampling have a highly significant effect on vegetation pattern (Emanuelsson, 1984) and thus are important parameters to measure when investigating the relative influence of environmental parameters on vegetation and soils. Trampling can be ascertained in terms of paths and foot prints and is noted where the effect on the vegetation or soil is obvious. It is not possible to record the effects of trampling where noticeable damage does not occur, but the method of recording trampling is adequate for this study as it shows the conspicuous effects of trampling and thus is able to provide an explanation for anomalous vegetation patterns. In order to investigate the total influence of trampling on a foreland a much more elaborate plan would be needed. Grazing is recorded only where plants are visibly bitten or where droppings occur; the latter being a measure of potential grazing by herbivores. Although the results are included in the ordinations, it is anticipated that the grazing results may show only an approximate picture of grazing patterns on the foreland, especially by herbivores such as Ptarmigan, Hares and Reindeer as well as cattle and sheep where they occur. These parameters are measured by recording the frequency of trampling or grazing (as described) in 25 x 20 cm^2 small squares in each $1m^2$ quadrat.

As shown by Figs. 3.63 to 3.70, the pattern of trampling shows little association with microtopographical position, age or altitude. This is not surprising as the initial choice of transects was based on inclusion of sites which had the highest cover of vegetation; thus areas of heavy trampling were generally avoided. Paths often follow the easiest routes towards the glacier and on the whole it is possible to avoid heavily trampled spots. The trampling values are therefore not necessarily representative of the amount of trampling occurring across any one foreland. For example, at Storbreen low (1), trampling appears to be non-existent, whereas at Storbreen low (2) (Figs. 3.65 and 3.66) trampling levels are rather high. The trampling results are therefore best used to indicate trampling pressure at individual sites and thus explain any anomalies in the data set. The trampling results should not be used to indicate general trampling pressures at any particular foreland.

As with trampling, the grazing results (also Figs. 3.63 to 3.70) do not show any special pattern according to microtopography, age or altitude. It is also certain that the grazing results do not represent anything like the amount of grazing occurring on some forelands. At Austerdalsbreen, for example, there are cattle and there has been a history of sheep grazing, but very little grazing was recorded. The highest amount of grazing was recorded for the Storbreen low and high foreland sequences, which has a small number of sheep grazing on that foreland; but at Bøverbreen, which also has sheep, no grazing was recorded. The likely important influence of rodents and other wild herbivores was almost entirely ignored (except for the recording of the presence of faeces). It is therefore not possible to use these results for detailed discussion of the effects of grazing on vegetation patterns. However, the results of some of the grazing studies, referred to in the review chapter (1), can be used to discuss the possible relationship between grazing and the meso-environmental variables of altitude, age and microtopography. Thus it will be possible to speculate on the likely combined effect of these factors on vegetation patterns in the concluding chapter (7).

3.5 Micro-environmental factors associated with vegetation and soil.

In chapter (3) we are looking at environmental factors and their distribution across the moraines at each foreland at various altitudes. Vegetation is thus being treated as a biotic environmental parameter as opposed to being the subject of investigation for classification purposes, where the pattern of individual species is described (see chapter (4)). Vegetation, as a whole entity, can have a significant effect on nearly all the prevailing micro-environmental parameters at a site. For example, differences in the vegetation cover at a site can have a profound influence on the micro-environment for seed establishment and growth. Among other things vegetation can provide shelter, trap snow, hold moisture, reduce frost activity, reduce fluctuations in temperature and contribute higher levels of certain nutrients. It can also have inhibitive effects, for example by competing for nutrients and moisture as well as producing chemicals that act as toxins (allelopathy) that discourage other plant species. The cover of bryophytes, as opposed to other plant groups, is also useful to measure in that bryophytes are generally more sensitive to moisture conditions than other plant groups (Crouch, 1992) and thus provide an additional indication of moisture.

Soil factors are also important environmental parameters to measurement in terms of their influence on in-coming plant species. The chances of a seed germinating may depend, for example on the available nutrients, moisture as well as the soil texture and pH. It is not the purpose of this study to describe differences in soil profile with microtopography, age and altitude: this has been done by Messer (1988), who specifically examined the effects of regional climate on soil chronosequences across moraines, and Mellor (1985), who made a more detailed study on soil chronosequences across moraines at Austerdalsbreen and Storbreen. Although the soil data collected in the present study can confirm (or refute) the findings of these earlier researchers, its main use is to describe the distribution of certain soil parameters in relation to microtopography, age and altitude and to relate vegetation to soil patterns across the moraines in the ordination chapters (5) and (6). Certain parts of the profile were measured for each site - i.e. the organic horizon (humus depth), total soil depth (depth of staining) and average turf root depth. A full description of the soil profiles is beyond the aims of the present thesis. However, written descriptions and charts showing the levels of each parameter across the foreland are considered useful. These parameters were measured by estimating the % cover or by using a ruler to measure depth, in mm.

3.5.1 Total vegetation cover and total bryophyte cover

Figs. 3.71 to 3.78 show the cover of vegetation and bryophytes across each of the forelands and a number of general patterns emerge from these charts. At Austerdalsbreen and Fåbergstølsbreen (Figs. 3.71 - 72) vegetation cover is greater on the four oldest moraines and does not appear to be influenced by microtopography. On the younger moraines, vegetation is greatest on low-slope positions of the moraine, suggesting that microtopography does have an influence on vegetation cover on the youngest ground on the subalpine forelands. Bryophyte cover differs from vegetation cover in that it shows a difference in pattern between the forelands, possibly due to the well-developed woodland dominating the older moraines at Fåbergstølsbreen. At Austerdalsbreen, bryophyte cover is least on the older ground and greater on the younger ground, whereas at Fåbergstølsbreen the opposite is true. However, both forelands show a greater cover of bryophytes on the low-slope positions across moraines than on the high-slope positions, especially at Fåbergstølsbreen. This suggests that microtopography, and thus certain associated micro-environmental factors, is a more important influence on bryophyte cover than age of substrate.

On the low-alpine forelands (Figs. 3.73 - 3.75) the patterns for vegetation cover are fairly similar to the subalpine forelands, in that vegetation cover increases with age and the influence of microtopography on younger ground becomes more noticeable. The most obvious difference between the subalpine and low-alpine forelands is that the influence of microtopography is also important on older ground on the low-alpine forelands, with lower vegetation cover occurring on crest positions than on low-slope positions. The relative influence of microtopography on vegetation cover across the Storbreen low forelands is clear, and especially so at Storbreen low (2). However, the effect of microtopography on vegetation cover is not quite as simple at Svellnosbreen, with the lowest vegetation cover found at shoulder-slope or even mid-slope positions on some moraines, rather than the crest (except on the two youngest moraines). Svellnosbreen has some very steep-sided moraines and so it is possible that disturbance, from solifluction, may be a major influence on vegetation cover on such moraines. Bryophyte cover does not show any special trends with age and the levels of cover, between forelands, are fairly similar. There is, however, a noticeable difference in bryophyte cover between Storbreen low (2), which has a greater bryophyte cover, and Storbreen low (1), which has a lower bryophyte cover. The differences in vegetation and bryophyte cover between Storbreen low (1) and (2) can be attributed to Storbreen low (1) being the best vegetated transect across the moraine (being the first "optimal transect" to be chosen) and thus all the transects at Storbreen low (2) were the second-best optimally vegetated transects. This is clearly shown by a comparison of Figs. 3.73 and 3.74, which show slightly lower total vegetation covers across moraines belonging to the second sequence of transects investigated across the Storbreen low (2) foreland. As on the subalpine forelands, microtopography appears to be an important influence on bryophyte cover, with the greatest cover of bryophytes being at low-slope positions and the lowest bryophyte covers being at high-slope positions.

On the mid-alpine forelands (Figs. 3.76 - 78), as on the other forelands, there is a general increase in vegetation cover with age. The influence of microtopography, on the oldest terrain, is most obvious at Høgvaglbreen and Bøverbreen, although at Storbreen high foreland, the proximal shoulder-slope and mid-slope positions, on the oldest terrain, have a lower vegetation cover than the rest of the mature till ridge (possibly because of the presence of a small rock outcrop and late-lying snow). The influence of microtopography on vegetation cover is marked on the two highest forelands but at Storbreen high it is not quite as distinct. Bryophyte cover does not follow any special age-related trend at Storbreen high and the trend of increasing bryophyte cover with lower microtopographical positions, found consistently on the other forelands, does not occur at Storbreen high foreland, possibly because bryophytic crust (*sensu*: Worley, 1973) is an important vegetation type on this foreland and tends to be most prevalent at exposed sites such as on young terrain or high-slope positions on the moraines. Proportions of bryophyte cover at Høgvaglbreen and Bøverbreen, however, generally complement the bryophyte cover results from the other forelands, with increased cover occurring on the low-slope positions across the moraines.

In summary, there is a general reduction of vegetation cover with increasing altitude, an increase in vegetation cover with increasing age and vegetation cover is generally greater at the low-slope positions across moraines. The influence of microtopography on vegetation patterns, in general, appears to become greater with altitude. The pattern of bryophyte cover is different from total vegetation cover as there appears to be no conspicuous trend of increasing or decreasing bryophyte cover with altitude. The bryophytic cover patterns with age are also not as noticeable, although on most forelands there appears to be a slight increase in bryophyte cover with age. However, there is a clear relationship between higher covers of bryophytes and low-slope position (except at Storbreen high), showing that microtopography is likely to have a considerably more important influence on the general distribution of bryophytes than altitude or age. Lastly, the differences in vegetation and bryophyte covers found at Storbreen low (1) and (2) confirm the opinion that the transect series at Storbreen low (2) cannot be regarded as a true replicate of the transect series at Storbreen low (1) and can only be regarded as an additional transect from the same foreland. This additional transect is nevertheless useful in helping to investigate, and hopefully confirm, the trends found by the optimal transect - i.e. Storbreen low (1) . If the environmental patterns and vegetation distributions shown by these two transects indicate similar general trends then it is fair to propose that the results from these "optimal transects" are representative of the general trends across the other forelands in this study.

3.5.2 Cover of different clast sizes

The proportion of different clast sizes, or stoniness (*sensu*: Crouch, 1992), found on bare ground at a site has been found to have a significant impact on the ability of vegetation to establish (Whittaker, 1985). Stony sites, with a high proportion of gravels and boulders and low vegetation cover, have been shown to be difficult sites for vegetation establishment (Arnaulds et al, 1987; Magnusson, 1994) and such sites decrease with greater age of ground (Crouch, 1992). The proportions of the different clast sizes across the forelands is displayed in Figs. 3.79 to 3.86.

M1 and M2 at Austerdalsbreen and M1 to M3 at Fåbergstølsbreen are fully vegetated so it is not possible to comment on the clast size on these moraines. On the younger ground Figs. 3.79 to 3.80 show that the proportion of bare ground (all clast sizes) tends to follow the profile of the moraines, with greater proportions on the crests of the moraines and lower proportions on the base-slope positions. There is also an obvious trend of increasing proportions of bare ground with decreasing age of substrate. This trend is especially distinct for bare-ground gravels and boulders at Austerdalsbreen and all clast sizes at Fåbergstølsbreen. Fines at Austerdalsbreen do not show such clear trends with base-slope sites having a high proportion of fines, however, this result may be explained by increased glacio-fluvial deposition at Austerdalsbreen.

On the low-alpine forelands (Figs. 3.81 to 3.83) only the oldest terrain has little or no bare ground and the proportion of all clast sizes is higher than it is on the subalpine forelands. The proportions of gravels and fines increase with higher microtopographical positions and decreasing age of substrate at Storbreen low (1) and Svellnosbreen, although there are peaks of higher levels of fines at certain base-slope positions which may be associated with fluvial activity. The proportions of fines and gravels at Storbreen low (2) appear to be strongly associated with microtopography, but not so much with age, which is probably due to the vegetation cover on the second series of transects across the Storbreen low foreland being lower (see previous section). Greater proportions of boulders at Storbreen low (1) and (2), and Svellnosbreen only appear to be associated with high-slope positions on the moraines.

On the mid-alpine forelands (Figs. 3.84 to 3.86) all ages of ground have patches of bare ground and the proportion of bare ground is greater than on the other forelands. At Høgvaglbreen and Bøverbreen there is a clear gradient of increased gravels with decreasing age of ground and to a lesser extent at Storbreen high. There is no clearly defined time trend for fines or boulders on these forelands. There is a fairly clear relationship between higher proportions of gravels and boulders with high-slope microtopographical position on these forelands although the proportion of fines does not appear to show any distinct relationship with microtopographical position.

In summary there is a general trend of gravels and boulders having an increased cover at progressively higher positions on moraines; on sites of decreasing substrate age; and on forelands of increasing altitude. This shows that the larger clast sizes, at least, are affected by microtopography, age and altitude. The results, for the proportion of fines, did not show such clear trends and this may be due to inorganic and organic fines being confused. A considerable amount of research interest has been shown concerning changes in the level of fines in the soil with site age (e.g. Viereck, 1966; Mellor, 1985; Gellatly, 1986; Frenot et al., 1995). It is important to distinguish between organic fines, which have been found to increase with site age (Crouch, 1992) and inorganic fines (sand and silt) which become translocated to lower positions in the soil profile and thus decrease with site age (e.g. Frenot et al, 1995). Inorganic fines are associated with, for example, higher levels of frost activity (Whittaker, 1985) and thus the investigation of the proportions of different clast sizes is a useful parameter to measure. In future it is considered advisable to distinguish clearly between the two. From the charts it is difficult to ascertain the relative importance of altitude, age and microtopography on clast size and this will be elucidated to a greater extent in the ordination chapters (5) and (6).

3.5.3 Soil texture

Soil texture has an important effect on the drainage of the soil, with coarse sandy soils, low in organic matter tending to drain more quickly than fine soils which are high in organic matter (e.g. Matthews, 1992). Crouch (1992) also found that less sandy substrates have a higher moisture content. Figs. 3.111 - 3.118 show the changes in texture across each of the forelands. The general trend on each foreland is that soil texture becomes finer on older ground with sandy loams tending to occur on the two oldest moraines and sands occurring on the younger ground and these results correspond with those of Crouch (1992). There does not appear to be any special trend with altitude. At Storbreen low (1) there appears to be some effect of microtopography with coarser soils being found on higher parts of the moraine, but in general there does not appear to be a strong association with microtopography. Soil texture therefore appears to be a time-related soil factor and not especially affected by altitude or microtopography.

3.5.4 General depth of humus (O) horizons, soil depth/stain (incipient Ea, Eb and B horizons) root depth

A number of soil properties were measured, for each 1 m^2 quadrat, to show the effect of microtopography, age and altitude on soil development and these were: a) general humus depth (depth of organic horizons); b) soil depth of the incipient Ea, Eb and B horizons (depth of soil staining by organic particles and iron); and c) the average root depth of the predominant vegetation. For practical reasons, the maximum measurement was 150 mm so all depths greater than 150 mm were recorded as 150 mm. Thorough comparisons between the humus depth, soil depth and root profiles, on the oldest terrain, cannot be made where depths are greater than 150 mm, but by referring to the previous research it is possible to speculate on the differences in profile found, on the oldest terrain, on the forelands within the present study (see review chapter (1)).

There is a distinct increase in humus depth on the subalpine forelands (Figs. 3.95 -3.96) with age. However, the relationship between humus depth and microtopography is not as distinct on the subalpine forelands as it is on forelands of higher altitude. Furthermore, the relationship between microtopography and humus depth is more complex than was anticipated. The deepest humus appears to occur on the crest of the mature pre-Boreal moraine at Fåbergstølsbreen and on the crest and toe- and base-slope positions of the mature till ridge at Austerdalsbreen. On the 1750 moraines, at both forelands, the pattern is not distinct with the deepest humus being found on the slope-sides and shallow humus depths being found at toe- and base-slope positions at Austerdalsbreen. There is a slight trend of greater humus depth at low-slope positions at Austerdalsbreen on M3 and M4 because there is no humus at high-slope positions. However, no humus has been recorded at Austerdalsbreen at the low-slope positions on the younger ground, possibly due to fluvial activity on intermorainal areas and low-slope positions of the moraines. The root depth and soil depth (Figs. 3.87 to 3.88), on the subalpine forelands, show similar trends to humus depth, with greater depths on the high-slope positions than at the low-slope positions on the two oldest moraines. In addition, M3 at Fåbergstølsbreen also shows this trend, but to a lesser extent. Soil depth and root depth tend to become more dependent on microtopography on the younger ground with both these parameters being deeper at the bases of M3-7 at Austerdalsbreen and M4-7 at Fåbergstølsbreen. It appears that age is a more important influence, than microtopography, on soil development across the subalpine forelands.

On all the other forelands (Figs. 3.97 to 3.102) humus depth decreases with age and appears to occur mostly at low-slope positions on the moraines, showing that both age and microtopography are important influences at low- to mid-alpine altitudes. At the mid-alpine altitudes there is no humus present at the bases of the youngest moraines, possibly due to fluvial activity or a lengthy snow duration causing very slow soil development. The oldest terrain at Bøverbreen (Fig. 3.102) shows a similar pattern of behaviour to the subalpine forelands in so much as humus is deepest on the higher parts of the moraine. This is possibly due to the occurrence of a very late snowbed on either side of the mature till ridge. Stain depth (Figs. 3.89 to 3.94) appears to be higher on the low- to mid-alpine forelands than on the subalpine forelands which may be due to a greater rate of leaching of organic particles and iron at the cooler and wetter, higher altitudes. The general trend across the forelands for depth of stain and turf on moraines, other than the oldest terrain, was a general increase in soil depth with age and also with progressively higher microtopographical positions on the moraines. However, on the oldest terrain, root and soil depths showed no particular trends, except the 1750 moraine at Svellnosbreen which showed a rather high soil depth on the crest of the moraine. Otherwise the root depth and soil depth results were fairly consistent for the low- and mid-alpine forelands. There does not appear to be a distinct gradient of soil development with altitude, but it will be possible to see this more clearly in chapters (5) and (6) when the correlation and ordination of the data is presented.

In summary it is possible to see noticeable trends of all three soil development parameters according to age of substrate and microtopography, although the most distinct pattern appears to be for humus depth. The trends seem least discernible on the subalpine forelands and clearer on the low- and mid-alpine forelands. In general the effects of microtopography, on the oldest terrain, is not so discernible and this may be due to the effects of greater vegetation cover across moraines but it could also be due to inadequate sampling of profiles that descended to greater depths than 150 mm. It appears that microtopography has an important influence on soil development especially on forelands above the tree-line and on younger ground. It appears, however, that time is probably the most important influence on soil development and this will be further discussed in chapter 7.

3.5.5 pH levels

Established research shows that fluctuations in pH levels across different forelands are associated, among other things, with differences in organic content of the soil as well as the amount of bases that have been leached from the soil by rain (cf. Crocker and Major, 1955), which causes older ground to be more acid, with lower pH levels. The bedrock also causes considerable between-foreland differences in the levels of pH if the rocks are more basic or acidic at a foreland (Mellor, 1985). For example, at Austerdalsbreen the till is derived from an acidic basal gneiss which is characteristic of Jostedalsbreen while at Storbreen the till is derived from a more basic pyroxene-granulite gneiss which dominates the Jotunheim. In Table 3.14 it is shown that the pH levels are lower at Austerdalsbreen and Fåbergstølsbreen than they are on the other forelands and these results compare with those of Mellor (1985) and Messer (1988). These researchers suggest that the differences in pH between the Jotunheim and Jostedalsbreen regions are likely to result from the influence of the original acidity of the till and not differences in the climatic parameters under consideration. The lowest pH is found at Austerdalsbreen and the greatest is at Svellnosbreen (Table 3.14 – this volume). The lowest range of pH values are found across the Storbreen low sequence, which does not have early young terrain, and also at Bøverbreen, whereas the greatest range of scores are found on the two subalpine forelands and Storbreen high. Therefore there do not appear to be any clear trends, relating to pH, with increasing altitude.

The pH measurements across each foreland are displayed in Figs. 3.103 to 3.110. The levels of pH show a distinct decline with increasing age of ground, with the levels of pH being lower on the subalpine forelands than they are on the forelands in the Jotunheim. On the subalpine forelands (Figs. 3.103 to 104) the trends are similar to each other although the trend line for pH is steeper at Fåbergstølsbreen, possibly due to higher levels of past disturbance from a debris flow in 1979 (Ballantyne and Benn, 1994) affecting the younger and intermediate moraines on this foreland. As with humus depth, the patterns associated with microtopography are generally clearer on the younger ground with a slight decline (and in some cases a rather sharp decline) in pH associated with base positions. The decline in pH associated with low-slope positions, however, does not form a very distinct pattern on the subalpine forelands, especially at Austerdalsbreen, where there is a decrease in pH on crest positions, possibly due to higher rates of leaching. Mellor (1985) found podzolisation to be the dominant pedogenic process at Austerdalsbreen, which is the only foreland that appears to have a proportion of moraines with greater humus and soil depths at high-slope positions (possibly due to high rates of fluvial activity at the base-slope positions on some moraines). The most important influence, therefore, on pH levels on subalpine forelands appears to be time, as the microtopographic effects appear to work against each other.

Table 3.14 Mean, maximum, minimum and range of pH values across each foreland

FORELAND	pH MEAN	pH - minimum score	pH - maximum score	pH - range of score
AUSF	4.86	4.0	6.5	2.5
FASF	5.26	4.3	6.3	2.0
STLF1	5.67	5.0	6.2	1.2
STLF2	5.41	4.7	6.4	1.7
SVLF	6.09	5.2	7.1	1.9
STHF	5.93	5.3	7.9	2.6
HOHF	5.45	4.6	6.4	1.8
BOHF	5.75	5.2	6.8	1.6

(see Appendix 2 for foreland abbreviations)

On the low- and mid-alpine forelands (Figs. 3.105 - 110) the patterns are very similar to those found on the subalpine forelands. There is a general decline in pH found on all forelands with the steepest decline being found at Høgvaglbreen and the shallowest at Bøverbreen, a trend rather difficult to explain. As at Fåbergstølsbreen, the pH levels tend to decrease with lower positions and higher organic content, but this is not the rule with lower rates on the higher positions possibly being caused by heavy leaching. It seems that the greatest influence on pH levels across individual forelands is time and these results, in general, correspond with those of Crouch (1992), although she suggested that there was a significant increase in pH with altitude. The lack of a significant increase in pH, with altitude, shown by the present study is possibly because Crouch's pH results were confounded (i.e. high altitude sites were on young ground) and thus the relative influence of altitude on pH was exaggerated.

3.6 Summary of environmental patterns in the foreland environment

1. The results from this chapter give the most detailed description yet attempted of the variation of environmental factors across microtopographical features (moraines) on a number of forelands at a range of altitudes. These distributions will be elucidated, and discussed, further in later chapters.

2. The trends shown by the micro-environmental factors associated with climate suggest that most of these parameters are strongly influenced by microtopography. Snowlie appears to be largely influenced by micro-scale differences in exposure so that high-slope positions are blown clear of snow and low-slope positions tend to accumulate snow and have a longer period of snow duration. Age and altitude appear to have a less significant effect on snowlie. Moisture is most affected by microtopography with lower moisture at high-slope positions and also, to some extent, at proximal sites. It is likely that increased moisture is related to sites that that can be considered as micro-scale "receiving sites", where water tends to drain, or to sites that have a longer duration of snow. Moisture does not appear to be influenced by terrain age, and it is not possible to obtain comparable moisture estimates from different altitudes using the "finger test". The results therefore do not show any trends in moisture with altitude. Microtopography has an important influence on temperature extremes during the winter and summer. The most constant and higher temperatures are found at low-slope positions during the winter months and the most variable temperatures on the moraine crests during the summer months. Proximity to the glacier appears to have an effect on temperatures on the distal and proximal slopes of the moraine, especially on younger ground.

3. The regional climate of a foreland (as influenced by altitude, continentality and latitude) has to be taken into consideration while investigating the differences in the effect of micro-climatic influences between forelands. For example, the amount of wind and the amount of snowfall can have a large impact on how snow is distributed, thus affecting moisture, temperature and exposure across a moraine. Mesotopographic effects should also be taken into consideration when discussing the effects of microclimate across a foreland or between forelands. For example, proximity to a glacier can affect the amount of wind and cooling and so can small differences in altitude. It appears that all the climatic factors are strongly interrelated and thus an attempt should be made to discuss all the factors in relation to each other. For example, at any one foreland, temperature across the microtopographical features is especially influenced by snow cover and exposure in the winter, and exposure to winds in the summer; snow cover is related to exposure; moisture is related to snow cover and the amount of wind the surface receives is related to snow cover. All of these factors are, however, linked by one factor on each foreland - microtopography.

4. According to the trends shown by the micro-environmental parameters associated with disturbance, the parameters show a strong relationship with microtopography, but terrain age and altitude also appear to have an important influence. Frost activity is related to both terrain age and microtopography: it is greater on younger terrain and high-slope positions. Evidence of increased frost activity also appears to show an

association with increasing altitude but the dowel heave results do not confirm this. Solifluction is influenced by microtopography, with the greatest rates of solifluction occurring on mid- to high-slope positions on the moraines. It does not appear to be affected by age or altitude. As expected, due to patterns of drainage, fluvial activity is most related to microtopography in that it is most frequent at the bases of the moraines. The influence of fluvial activity also appears to be greater on the younger ground suggesting that this parameter is also time-related. Fluvial activity does not appear to be influenced by altitude. The distribution of trampling across all forelands did not show any special pattern and thus will only be used to help explain any anomalies in the data. The grazing data almost certainly does not show the true extent of grazing across the foreland and thus is not considered to be very useful.

5. The trends shown by the micro-environmental factors associated with vegetation and soil suggest that an increase in total vegetation cover is strongly related to increasing terrain age, low-slope positions and lower altitudes. Bryophyte cover, on the other hand, appears to be more closely related to microtopography. Gravels and boulders show a clear relationship with age, altitude and microtopography: the proportion of gravels and boulders is greater on high-slope positions; on ground of decreasing age; and at higher altitudes. The proportion of fines does not show any clear trends, possibly due to inorganic and organic fines being confounded. Time appears to be the most significant influence on humus depth, soil depth and root depth (representing soil development) across each foreland, although microtopography and altitude also have some influence. Whittaker (1985) found these factors to be mainly time-related and these results confirm his findings. The most important influence on pH and soil texture is terrain age, with soil pH decreasing, and soil texture becoming finer, on older sections of the forelands, but microtopography does not appear to be an important influence on pH or soil texture. Between-foreland differences in pH are likely to be related to geology and, possibly, levels of precipitation and vegetation cover. The effect of microtopography, on soil development, becomes more discernible on younger terrain and at higher altitudes and thus microtopography appears to have at least some influence on the factors associated with vegetation and soil development. It is therefore likely that the relative influence of altitude, age and microtopography on vegetation patterns and soil development is complex and this will be taken into consideration when interpreting the ordination results in terms of vegetation succession.

"Certain few communities do stand out but their distinctness is more apparent than real, being due to increasing dominance of a new growth form, as when the low-growing pioneers give place to tall shrubs, and these in turn to trees. We may thus, for the sake of vivid presentation, divide our vegetation into three communities, or in dynamic terms, stages"

Cooper (1923: 225)

CHAPTER FOUR: The pattern of species assemblages on the individual forelands

4.1 Introduction to TWINSPAN site groups and profile diagrams

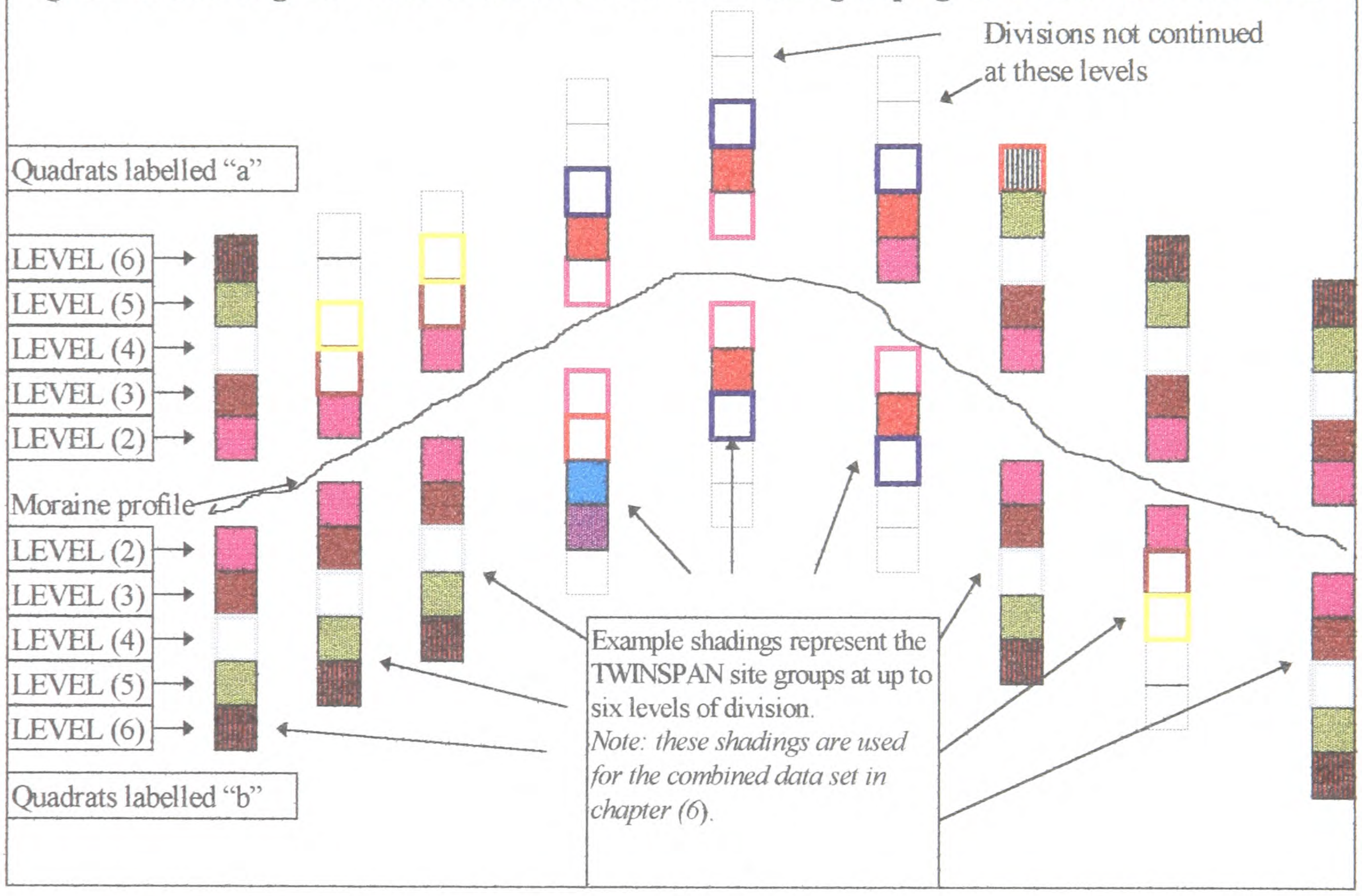
Justification for the use of TWINSPAN and the presentation methodology used has been discussed in section 2.11, while a description of the options used for the TWINSPAN runs have been described in section 2.9.2. Nevertheless, a more detailed account of the presentation methods used for the classification technique, TWINSPAN, will be given in this section. Profile diagrams (Figs. 4.2 to 4.9) have been used to elucidate how the sites have been divided at each level of subdivision for each individual foreland. The generalised profile diagram (Fig. 4.1 – this volume) and the text in this section explain the profile diagrams. A short description has been made of the TWINSPAN separation of the sites for each of the groups across every foreland. Each description includes a complete list of indicator species and a sample list of three of the preferential species (with the highest cover values). The pseudospecies (i.e. cover values) are not described specifically. The assemblages are defined according to the highest cover indicator or preferential pseudospecies. Those species already listed as indicator species are not included in the sample list of preferential species. The eigenvalue value representing the significance or strength of the relationship between sites within a group, is also given.

The individual foreland profile diagrams (Figs. 4.2 to 4.9) display how TWINSPAN has separated the groups at all levels of subdivision. The generalised profile diagram (Fig. 4.1 – this volume) explains the profile diagrams but refer to section 2.9.2 for a description of options used in the TWINSPAN runs and section 2.11.4 for a justification of the presentation techniques used for TWINSPAN. Each profile diagram represents the transects of quadrats pairs (sites) across each moraine over any one foreland. The moraine profiles are approximately to scale (given on the diagram) and the age of each moraine is given under each profile. On each diagram there are a series of coloured boxes above and below each profile which represent the approximate position of each quadrat on the moraine. The colours used for the boxes are chosen for clarity of presentation and have no significance in themselves. The colours are used to differentiate between the groups at each level of subdivision. Those boxes above the profile represent the quadrats labelled "a" and those boxes below the profile represent the replicate quadrats "b".

The boxes which are closest to the profile outline (Fig. 4.1 – this volume) represent separation at the second level (2-group level). Notice that there are only two divisions - a series of open boxes (❐) and a series of shaded boxes (■). The second layer of boxes either side of the profile represent separation at the third level of subdivision (4-group level) and there are two sets of boxes, one open and one shaded, of two different colours. Generally the larger groups are shaded and the smaller groups have open boxes (but this is not a rule).

The third layer of boxes represents the fourth level of subdivision (8-group level) and in this layer there should be four different coloured pairs of boxes. However, any group of sites which is not considered to be ecologically meaningful is not divided further so at the fourth level of subdivision there may be fewer than eight groups and at the fifth level there may be fewer than sixteen groups. At the fifth (16-group level), in the diagrams there is at most eight different coloured pairs of boxes. The fifth level is the final level of subdivision for each of the individual foreland data sets, although at Austerdalsbreen divisions are made up to the sixth level (32-group level) because the divisions are still meaningful. However, most of the combined data set site groups are separated at the sixth level of subdivision.

Fig. 4.1 Profile diagram - used to elucidate TWINSPAN site groupings at various levels of division



The eigenvalue for each of the site groups signifies the strength of relationships between sites within any group. The larger the eigenvalue the stronger or "tighter" the relationship and thus, the relative distinctness of each group can be ascertained. Each foreland is summarised in Tables 4.1 to 4.8 and a summary table for the site groups on all forelands has also been made (Table 4.9). Colour keys, displayed in Tables 4.1 – 4.8, can be used to identify site groups across each profile diagram.

The diagrams are a completely new way of presenting the TWINSPAN site data. This method is useful in elucidating the relative influence of age and microtopography, as well as slope aspect or proximity to the glacier, on the vegetation pattern. Chapter (6), in which the combined data sets is discussed, uses the profile diagrams to clarify not only the significance of age and microtopography but also the relative importance of altitude on vegetation patterns.

The profile diagrams show the separations at up to six levels of subdivision, and division at all higher levels was stopped because further division was considered not to be ecologically meaningful. The separation of groups was stopped at lower levels of subdivision than the sixth level when the group was considered to be ecologically meaningful. These ecologically meaningful groups are known as "final site groups", marked with an asterisk (*),. Site groups are not considered to be meaningful, and are therefore not separated at higher levels of subdivision, according to at least one of the following set criteria: 1) the groups contain few species; 2) at higher levels the groups are highly unbalanced with few sites in one part of the division and many in the other part; and 3) separation of the groups continues the ecological pattern of division from the previous level (e.g. separating quadrats at slightly higher slope positions from quadrats at slightly lower slope positions) showing that there is not much ecological difference between the groups. It is unnecessary to describe all the sites belonging to each of the groups from the different levels because the diagrams contain all the relevant information. Throughout this chapter symbols may be used for plant species (e.g. Sal her) and forelands (e.g. AUSF), and these are explained in Appendices 1 and 2 respectively. Moraine codes (M1 to M8) are elucidated in Table 2.3 and explained in the glossary under "moraines".

4.1.1 Austerdalsbreen (Altitude: 290-380m. Aspect: southerly)

As can be seen in Fig. 4.2, at the second (2-group) level the sites separate (eigenvalue 0.447) according to age, with M3 to M7 within site group (2) and the two oldest moraines (plus one anomalous pioneer distal low-slope quadrat) within site group (3). Site group (2), the **Betula pubescens - Calluna vulgaris** assemblage contain just two indicators: *Betula pubescens* and *Calluna vulgaris*. The preferential species include: *Solorina crocea, Cladonia portentosa* and *Stereocaulon alpinum*. Site group (3), the **Vaccinium myrtillus - Deschampsia flexuosa** assemblage contains the indicator *species Melampyrum sylvaticum, Vaccinium myrtillus, Vaccinium uliginosum, Deschampsia flexuosa* and *Deschampsia alpina.* Preferential species include *Cornus suecica, Salix glauca* and *Festuca ovina.*

At the third (4-group) level, site group (2), on younger terrain, separate into site groups (4) and (5) (eigenvalue 0.431) according to age and microtopography. Site group (3), on the oldest terrain, separate into site groups (6) and (7) (eigenvalue 0.566) also according to both age and microtopography. Site group 4, the **Stereocaulon alpinum - Carex spp** assemblage occurs on proximal and high-slope sites on the youngest moraine and is therefore an exposed pioneer assemblage. It has one indicator species, *Stereocaulon alpinum*, and the preferential species include *Carex spp, Phleum alpinum* and *Oxyria digyna.* Site group 5, the **Betula pubescens - Calluna vulgaris** assemblage occurs on the remainder of M3 to M7 and can be regarded as an early intermediate heath assemblage on intermediate and young terrain. The indicator species are *Betula pubescens* and *Calluna vulgaris* and the preferential species include *Vaccinium myrtillus, Phyllodoce caerula* and *Empetrum nigrum*. Site group (6), the **Cornus suecica - Salix glauca** assemblage is found in most of the high-slope quadrats on M1 and M2 (plus an anomalous pioneer distal low-slope quadrat) and can be described as a mature heath assemblage. This site group has no indicators and the preferential species include *Cornus suecica, Empetrum nigrum* and *Salix herbacea*. Site group (7), or the **Athyrium distentifolium - Potentilla cranzii** assemblage occurs in five low-slope quadrats on the mature till-ridge and can be considered a meadow or mature snowbed assemblage. The indicator species is *Athyrium distentifolium* and the preferential species include *Viola biflora, Juncus filiformis* and *Trientalis europaea*. The separation of site group (7*) is not described at higher levels of subdivision.

At the fourth (8-group) level separation occurs according to age, except on M7. Pioneer site group (4) separates, according to microtopography, (eigenvalue 0.566) into site groups (8) and (9). Site group (5) divides (eigenvalue 0.295) into site groups (10) and (11), separating M3 to M6 (plus one base distal quadrat, on M7) from the other base sites on M7. Site group (6) divides (eigenvalue 0.489) into site groups (12) and (13), separating the mature sites, except one proximal low-slope quadrat, from the sites on M2. Site group (8), the **Stereocaulon alpinum- Stereocaulon vesuvianum** assemblage, occurs on the three high-slope sites on M7 and is an exposed pioneer assemblage. There are no indicator species in this group and the preferential species are *Stereocaulon alpinum, S. vesuvianum* and *Cladonia chlorophaea*. Site group (9), the **Carex - Phleum alpinum** assemblage, comprises three proximal low-slope sites and one distal shoulder-slope quadrat and can be described as an exposed pioneer snowbed assemblage. This group has six indicator species which are *Carex spp, Phleum alpinum, Empetrum nigrum, Salix glauca, Stereocaulon botryosum* and *Oxyria digyna*. The preferential species include *Salix phylicifolia, Vaccinium myrtillus* and *Phyllodoce caerula*. Site group (10), the **Salix phylicifolia - Salix herbacea** assemblage, occurs in two distal low-slope quadrats and is a pioneer snowbed group. The indicator is *Salix phylicifolia* and the preferential species include *Salix herbacea, Pyrola norvegicum* and *Phleum alpinum*. Site group (11), the **Empetrum nigrum - Calluna vulgaris** assemblage, is an early intermediate heath assemblage. The indicator species of this group are *Empetrum nigrum* and *Calluna vulgaris* and the preferential species include *Vaccinium myrtillus, Betula pubescens* and *Empetrum nigrum*. Site group (12), or the **Salix glauca - Salix herbacea** assemblage, is found across the entire 1750 moraine and in one proximal low-slope quadrat on the mature till-ridge. It can be described as a late intermediate heath assemblage with a low cover (and thus influence) of *Betula pubescens* (a non-preferential species). This group has no indicators and the preferential species include *Deschampsia alpina, Phyllodoce caerula* and *Betula nana*. Site group 13, or the **Deschampsia flexuosa - Vaccinium myrtillus** assemblage, is a mature heath assemblage with a high cover of *Betula pubescens* (preferential species high cover values) and it occurs on most of the mature till-ridge (and an anomalous pioneer distal low-slope quadrat). The indicator species for this group is *Deschampsia flexuosa* and the preferential species include *Cornus suecica, Potentilla crantzii, Vaccinium uliginosum* and *Betula pubescens*. The separation of site groups (8*), (9*), (10*) and (13*) is not described at higher levels of subdivision.

At the fifth (16-group) level subdivision of the remaining moraines divide mainly according to microtopography with site group (11) separating (eigenvalue 0.240) into site group (22), comprising sixteen low-slope quadrats on younger terrain and site group (23) consisting of 57 intermediate quadrats. Site group (12), across M2, divides (eigenvalue 0.381) into site group (24), low-slope distal and proximal quadrats, and site group (25) which consists of high-slope distal quadrats. Site group (22), the **Vaccinium myrtillus - Betula pubescens** assemblage, is an early intermediate heath, which occurs in low-slope quadrats on M5 and M6, with a distal low-slope quadrat on M7, and two quadrats at low-slope positions on M4. Indicator species are *Vaccinium myrtillus, Betula pubescens, Salix phylicifolia. Deschampsia flexuosa, Deschampsia cespitosa and Salix glauca* with the preferential species including *Festuca ovina, Anthoxanthum odoratum and Vaccinium uliginosum.* Site group (23), the **Calluna vulgaris - Solorina crocea** assemblage, is an early intermediate lichen heath assemblage with the indicator species *Calluna vulgaris* and preferential species include *Solorina crocea, Cladonia portentosa* and *Cladonia bellidiflora.* Site group (24), the **Deschampsia alpina - Phyllodoce caerula** assemblage, is found on the proximal slope and in distal low-slope quadrats on M2 and is a late intermediate snowbed assemblage. *Deschampsia alpina* is the indicator and the preferential species include *Festuca ovina, Salix herbacea, Betula nana* and *Alchemilla alpina.* Site group (25), or the **Vaccinium myrtillus- Vaccinium uliginosum** assemblage, occurs in high-slope quadrats on M2 and is a late intermediate heath assemblage. There are no indicators and the preferential species include high cover values of *Vaccinium myrtillus, Vaccinium uliginosum* and *Salix glauca.* Further division of site groups (22*), (24*) and (25*) is not described beyond this level.

At the sixth (32-group) level the only subdivision which is ecologically meaningful is that of the large early intermediate lichen heath, site group (23) (eigenvalue 0.221), into groups (46*) and (47*), where the lower and older sites on M3 and M4 divide from higher and/or younger sites on M3, to M6. To make sense of site group (47*) it is also necessary to look at the non-preferential species list. Site group (46*), the **Empetrum nigrum - Betula pubescens** assemblage, occurs in low-slope quadrats on M3 and M4, and can be considered as a late intermediate late-snow lichen heath, on more sheltered and moister sites. Indicator species are *Empetrum nigrum, Betula pubescens* and *Cladonia portentosa* with preferential species *Vaccinium myrtillus, Phyllodoce caerula* and *Cladonia gracillis.* Site group (47*), or the **Solorina crocea** assemblage, is found at high-slope positions and on younger terrain and can be considered as a more exposed drier lichen heath assemblage. It has as its indicator and preferential species only *Solorina crocea.* The non-preferential species list shows that this group, like site group (46*), also contains high covers of the heath species *Calluna vulgaris, Cetraria islandica, Phyllodoce caerula* and *Empetrum nigrum* as well as the lichens *Cladonia pleurota, Cladonia coniocraea, Cladonia digitata, Cladonia chlorophaea* and *Stereocaulon alpina.* The site groups at Austerdalsbreen are summarised in Table 4.1, which also contains a more comprehensive list of preferential species for each group.

4.1.2 Fåbergstølsbreen (Altitude: 460-630m. Aspect: easterly)

As can be seen in Fig. 4.3, at the second (2-group) level the sites separate (eigenvalue 0.832) according to age, with the four older moraines (plus one crest pioneer site on M6) in site group (2) dividing from the two younger moraines in site group (3). Site group (2), the **Betula pubescens - Vaccinium myrtillus** assemblage contains no indicators and preferential species include *Betula pubescens, Vaccinium myrtillus* and *Deschampsia flexuosa.* It can be considered as a late intermediate and mature assemblage. Site group (3), the **Agrostis tenuis - Deschampsia alpina** assemblage, a pioneer assemblage, contains the indicator species *Agrostis tenuis* and its preferential species include *Deschampsia alpina, Epilobium alsinifolium* and *Phleum alpinum.*

At the third (4-group) level the older group (2) separated (eigenvalue 0.601) into site groups (4) and (5) according mainly to age while the younger site group (3) divides (eigenvalue 0.355) into site groups (6) and (7) according mainly to age and microtopography. In both site groups (4) and (5) *Betula pubescens* has high levels of cover, although the cover is greatest in group (4), and therefore it has not come up as an indicator for either group. Site group (4), the **Vaccinium myrtillus - Deschampsia flexuosa** assemblage is found only on M1 and M2. Both moraines are dominated by well-developed birch woodland and this can be considered as a mature woodland assemblage. The indicator species are *Vaccinium myrtillus, Deschampsia flexuosa* and *Luzula arcuata* and preferential species include high covers of *Betula pubescens, Vaccinium myrtillus,* and *Deschampsia flexuosa.* Site group (5), the **Calluna vulgaris - Empetrum nigrum** assemblage is an early intermediate heath assemblage with a lower cover of *Betula pubescens* and a high cover of heath and lichen species. It includes one distal site on the 1750 moraine. The indicator species for this group is *Calluna vulgaris* and the preferential species include *Empetrum nigrum, Cladonia rangiformis,* and *Vaccinium uliginosum.* Site group (6), or the **Agrostis tenuis - Phleum alpinum** assemblage occurs on most of M5 and at mainly distal low-slope positions on M6. It can be regarded as a pioneer snowbed assemblage, the indicators being *Agrostis tenuis, Deschampsia alpina* and *Phleum alpinum* and the preferential species including *Lotus corniculatus, Luzula spicata* and *Oxyria digyna.* Site group (7), the **Deschampsia flexuosa - Epilobium alsinifolium** assemblage, occurs mainly at proximal and crest positions on M6. It can be considered to be an exposed pioneer snowbed assemblage and it contains the indicator species *Deschampsia flexuosa* and preferential species include *Epilobium alsinifolium, Saxifraga stellaris* and *Cladonia arbuscula.* The separation of site group (7*) is not described at higher levels of subdivision.

At the fourth (8-group) level the divisions occur according to both age and microtopography. The mature birch woodland assemblage, site group (4), separates (eigenvalue 0.370) into site groups (8) and (9) separating M1, and distal slope of M2, from proximal and high-slope quadrats on M2. The early intermediate heath, site group (5), separates (eigenvalue 0.448) into site groups (10) and (11), separating the toe-slope site on M2, all of M3 and low-slope sites on M4 from 3 high-slope sites on M4. The pioneer snowbed assemblage, site group (6), separates (eigenvalue 0.293) into site groups (12) and (13), dividing mainly low-slope positions on M5 from other positions on M5 and M6. Site group (8), the **Vaccinium myrtillus - Gymnocarpium dryopteris** assemblage, occurs on M1 and the more sheltered distal low-slope sites on the 1750 moraine. This can be considered a birch woodland assemblage on mature or moist late intermediate sites. The indicator species are *Vaccinium myrtillus* and *Gymnocarpium dryopteris* and the preferential species include *Cornus suecica, Trientalis europaea* and *Parnassia palustris.* Site group (9), the **Phyllodoce caerula - Empetrum nigrum** assemblage, is found at the drier high-slope positions and on the proximal slope of the 1750 moraine (which has a shallow slope angle). This can therefore be considered as a birch woodland heath assemblage on dry late intermediate sites. The indicator species are *Phyllodoce caerula* and *Empetrum nigrum* and the preferential species include *Vaccinium vitis-idaea, Luzula arcuata* and *Melampyrum sylvaticum.* Site group (10), the **Betula pubescens - Calluna vulgaris** assemblage, is an early intermediate heath assemblage found on M3 and at low- and mid-slope positions on M4. The indicators are *Betula pubescens, Calluna vulgaris* and *Phyllodoce caerula* and the preferential species include *Empetrum nigrum, Cladonia rangiformis* and *Melampyrum sylvaticum.* Site group (11), the **Cladonia chlorophaea - Cladonia fimbriata** assemblage, is found at high-slope positions on M4 and is an early intermediate lichen heath assemblage. Its indicators are *Cladonia chlorophaea* and *Cladonia fimbriata* and its preferential species include *Solorina crocea, Cladonia pyxidata* and *Stereocaulon alpinum.* Site group (12), the **Lotus corniculatus - Salix phylicifolia** assemblage, is a pioneer snowbed assemblage found in five low-slope quadrats on the proximal slope of M5 and the distal slope of M2. The indicators are *Lotus corniculatus, Salix phylicifolia* and *Gnaphalium norvegicum* and the preferentials include *Phleum alpinum, Ulmus glabra* and *Sagina saginoides.* Site group (13), the **Luzula spicata-Oxyria digyna** assemblage, is found mainly in distal high-slope quadrats of M5 and M6 and it can be considered as a pioneer assemblage. It has no indicators and its preferential species include *Luzula spicata, Oxyria digyna* and *Saxifraga stellaris.* The separation of site groups (9*), (11*) and (12*) is not described at higher levels of subdivision.

At the fifth (16-group) level most of the TWINSPAN divisions are made according to microtopography. The mature birch woodland assemblage, site group (8), separates (eigenvalue 0.269) into site group (16), consisting of toe-slope quadrats on M1 and one on M2, and site group (17) consisting of other quadrats on M1 and distal low-slope quadrats on M2. The early intermediate heath assemblage, site group (10) separates (eigenvalue 0.257) into site group (20), consisting of the proximal base-slope site on M2 and low-slope sites on M4, and site group (21), consisting of all of M3 and one low- and mid-slope quadrat on M4. Lastly the pioneer assemblage, site group (13), divides (eigenvalue 0.327) into site groups (26), comprising the distal slope of M5, and site group (27) which consists of high-slope quadrats on M5 and mainly low-slope quadrats on M6. Site group (16), the **Potentilla cranzii - Melampyrum sylvaticum** assemblage, a grazed mature meadow assemblage dominated by herbs and grasses (as well as the non-preferential *Vaccinium myrtillus*). The indicator species is *Potentilla cranzii* and the preferential species include *Deschampsia flexuosa, Anthoxanthum odoratum* and *Melampyrum sylvaticum.* Site group (17), the **Betula pubescens - Gymnocarpium dryopteris** assemblage, is a mature birch woodland assemblage. The indicator species is *Betula pubescens* and the preferential species include *Gymnocarpium dryopteris, Cornus suecica,* and *Sorbus aucuparia.* Site group (20), the **Empetrum nigrum - Salix phylicifolia** assemblage, an atypical snowbed assemblage, has no indicator species and preferential species which include *Empetrum nigrum, Salix phylicifolia* and *Vaccinium uliginosum*. Site group (21), the **Vaccinium vitis-idaea - Cladonia rangiformis** assemblage, is an early intermediate lichen heath assemblage. *Vaccinium vitis-idaea* is the indicator species and preferential species include *Cladonia rangiformis, Melampyrum sylvaticum* and *Cladonia portentosa*. It should be noted that *Betula pubescens* and *Calluna vulgaris* are important non-preferentials for site groups (20) and (21). Site group (26), the **Phleum alpinum - Lotus corniculatus** assemblage, occurs on the distal slope of M5 and can be considered as a later pioneer group. The indicator species is *Phleum alpinum* and preferential species include *Lotus corniculatus, Oxyria digyna* and *Cryptogramma crispa*. Site group (27), the **Deschampsia alpina-Saxifraga stellaris** assemblage occurs at high-slope positions on M5 and mainly on the distal slope of M6 and can be considered an exposed pioneer assemblage. It has no indicators and the preferential species include *Deschampsia alpina, Saxifraga stellaris* and *Solidago virgaurea*. All division ends at the fifth level (i.e. of site groups (16*), (17*), (20*), (21*), (26*) and (27*)) since divisions at higher levels are not ecologically meaningful. The site groups at Fåbergstølsbreen are summarised in Table 4.2, which also contains a more comprehensive list of preferential species for each group.

4.1.3 Storbreen low (1) (Altitude: 1140-1200m. Aspect: north-easterly)

(note that the oldest moraine on this stretch of foreland is the 1900 moraine and therefore early young terrain is excluded)

As can be seen in Fig. 4.4, at the second (2-group) level the sites divides (eigenvalue 0.349) mainly according to age but also according to microtopography, with M1 and low sites on M2 and M3 (plus two low-slope quadrats on M4) comprising site group (2), and high-slope sites on M2, M3 and M4 and all of M5-6 being in site group (3). Site group (2), the **Betula nana - Cladonia rangiferina** assemblage, occurs on the mature till-ridge and also at low-slope positions on the older moraines across the foreland. It can be considered as a later heath assemblage. It contains the indicators *Betula nana, Cladonia rangiferina, Vaccinium myrtillus* and *Carex spp* and the preferential species include *Salix herbacea, Festuca ovina*, and *Cetraria islandica*. Site group (3), the **Solorina crocea - Cetraria nivalis** assemblage, occurs on high-slope, or at proximal positions, on M2 and M3 and occupies the majority of M4 and all of M5 and M6. It can be considered as an early intermediate lichen heath assemblage and its indicator species are *Solorina crocea, Cetraria nivalis* and *Stereocaulon alpinum* and preferential species including *Cladonia chlorophaea, Cassiope hypnoides* and *Poa alpinum*.

At the third (4-group) level site group (2) separates (eigenvalue 0.357) into site groups (4) and (5) according to age, microtopography and aspect. Site group (4) comprises mainly low-slope positions on M2 and low-slope distal M3. Site group (5) comprises M1, two proximal quadrats on M2, six low-slope quadrats on M3 and the two quadrats on M4. Site group (3) separates (eigenvalue 0.325) into site group (6) and (7). Site group (6) comprises two high-slope quadrats on M3, mostly proximal sites on M4, at low-slope positions on M5 and all of M6. Site group (7) comprises high-slope quadrats on M3 and M5 and at distal and crest positions on M4. Site group (4), the **Salix glauca - Anthoxanthum odoratum** assemblage, is a late intermediate snowbed assemblage found mainly in low-slope quadrats on M2 and M3. The indicator species are *Salix glauca* and *Anthoxanthum odoratum* and the preferential species include *Solidago virgaurea, Ranunculus acris* and *Luzula arcuata.* Site group (5), the **Betula nana - Cetraria islandica** assemblage is a heath assemblage on late intermediate and the oldest terrain. The indicator species is *Betula nana* and the preferential species include *Salix herbacea, Vaccinium myrtillus* and *Cetraria islandica.* Site group (6), or the **Salix glauca - Salix herbacea** assemblage, found at low-slope positions of the younger terrain, and all of the 1900 moraine, can be considered as an early intermediate snowbed assemblage. Indicators for this group are *Salix glauca, Salix herbacea, Stereocaulon condensatum, Stereocaulon botreosum* and *Cassiope hypnoides.* Preferential species include *Phyllodoce caerula, Trisetum spicatum* and *Poa alpinum.* Site group (7), the **Cetraria nivalis - Cetraria cucullata** assemblage, is found at high-slope positions on M5, M3 and M2 and the distal slope and crest of M4. It is an early intermediate lichen heath group and the indicators are *Cetraria nivalis* and *Cetraria cucullata.* Preferential species include *Alectoria ochroleuca, Cetraria islandica* and *Cladonia portentosa.* The separation of site group (4*) is not described at higher levels of subdivision.

At level four (8-group) level the divisions occur according to microtopography and aspect with site group (5) separating (eigenvalue 0.294) into site group (10), consisting of all sites on M1, except the crest, and site group (11) which consists of the crest position on M1 and scattered low-slope quadrats on M2, M3 and M4. Site group (6) divides (eigenvalue 0.193) into site group (12), consisting of most of the quadrats in site group (6), and site group (13) which separated off crest and two mid-slope quadrats on M6 and three proximal base-slope quadrats on M6. Site group (7) divides (eigenvalue 0.290) separating site group (14), consisting of mainly high-slope quadrats on M2, M3 and the distal slope of M4, from site group (15), consisting of high-slope quadrats on M2, M3 and M5. Site group (10), the **Festuca ovina - Salix herbacea** assemblage, is a mature late-snow heath assemblage (or atypical snowbed assemblage), and its indicator is *Festuca ovina.* The preferential species include *Vaccinium myrtillus, Cetraria islandica* and *Cladonia gracillis.* Site group (11), the **Vaccinium uliginosum - Salix lanata** assemblage, can be considered to be a late-snow early intermediate heath group with no indicators and preferential species which include *Vaccinium uliginosum, Salix lanata,* and *Salix glauca.* Site group (12), the **Empetrum nigrum - Stereocaulon alpinum** assemblage, is a late-snow early intermediate heath assemblage with indicator species which are *Empetrum nigrum, Cladonia portentosa, Phyllodoce caerula, Solorina crocea* and *Stereocaulon alpinum.* Preferential species are *Salix lanata, Cetraria islandica* and *Cladonia chlorophaea.* Site group (13), the **Salix glauca - Salix herbacea** assemblage is an exposed snowbed assemblage which has no indicators and preferentials including *Salix glauca, Salix herbacea,* and *Anthoxanthum odoratum.* Site group (14), the **Phyllodoce caerula - Cladonia portentosa** assemblage, is an early intermediate lichen heath assemblage with indicators *Phyllodoce caerula, Cladonia portentosa, Cladonia arbuscula* and *Solorina crocea.* Preferential species include *Cetraria islandica, Cladonia arbuscula* and *Stereocaulon alpinum.* Site group (15), the **Alectoria ochroleuca - Cetraria cucullata** assemblage, is an exposed lichen heath group, with the indicators species *Alectoria ochroleuca* and *Cetraria cucullata* and preferential species including *Cladonia crispata, Cornicularia divergens* and *Festuca ovina*. A description of further divisions (i.e. of site groups (10*), (11*), (12*), (13*), (14*), and (15*)) at higher levels, is not considered to be ecologically meaningful. The site groups at Storbreen low (1) are summarised in Table 4.3, which also contains a more comprehensive list of preferential species for each group.

4.1.4 Storbreen low (2) (Altitude: 1140-1200m. Aspect: north-easterly)

(note that the oldest moraine on this stretch of foreland is the 1900 moraine and therefore early young terrain is excluded)

As can be seen in Fig. 4.5, at the second (2-group) level the sites divide (eigenvalue 0.420), according to both age and microtopography, separating site group (2), consisting of M1, distal low-slope sites on M2 and M3 and a few proximal low-slope quadrats on M2, M3 and M4, from site group (3), consisting of mainly high-slope and proximal sites on M2 and M3 and all sites on the younger moraines. Site group (2), the **Cladonia portentosa - Betula nana** assemblage, is a mature and late intermediate heath assemblage and its indicators are *Cladonia portentosa, Betula nana, Vaccinium myrtillus* and *Cladonia gracillis*. Preferential species include *Cetraria islandica, Stereocaulon botryosum* and *Deschampsia flexuosa*. Site group (3), the **Solorina crocea - Cetraria nivalis** assemblage, is an early intermediate lichen heath assemblage and its indicators are *Solorina crocea* and *Cetraria nivalis*. Preferential species include *Cladonia chlorophaea, Cassiope hypnoides* and *Cladonia verticillata*.

At the third (4-group) level, site group (2) divides (eigenvalue 0.464) according to microtopography into site group (4), consisting of the distal sites on M2 and two toe-slope quadrats on M1 and M4, and site group (5), consisting of M1 and other low-slope quadrats on M2, M3 and M4. Site group (3) divides (eigenvalue 0.345) according to microtopography separating group (6), consisting of mainly low-slope quadrats on M2, M4, M5 and M6, from site group (7) which consists mainly of high-slope quadrats on M2 to M6. Site group (4), the **Salix herbacea - Ranunculus acris** assemblage, is a late intermediate snowbed assemblage and it has no indicators. Its preferential species include high covers of *Salix glauca, Solidago virgaurea* and *Carex spp*. Site group (5), the **Stereocaulon alpinum - Cladonia portentosa** assemblage, is a late-snow late intermediate heath group. Its indicators are *Stereocaulon alpinum, Cladonia portentosa, Cetraria islandica* and *Empetrum nigrum* and the preferential species are *Betula nana, Cladonia gracilis* and *Stereocaulon botryosum*. Site group (6), the **Stereocaulon alpinum - Salix herbacea** assemblage, is a late-snow early intermediate heath assemblage with the indicators *Stereocaulon alpinum, Salix herbacea, Salix glauca* and *Phyllodoce caerula*. Preferential species are *Solorina crocea, Cetraria islandica* and *Cladonia portentosa*. Site group (7), the **Cetraria nivalis - Alectoria ochroleuca** assemblage, is an exposed lichen heath assemblage and its indicators are *Cetraria nivalis* and *Alectoria ochroleuca*. Preferential species include *Cetraria ericetorum, Cornicularia aculeata* and *Cetraria cucullata*. The separation of site groups (4*) and (7*) is not described at higher levels of subdivision.

At the fourth (8-group) level divisions occur according to age, microtopography and aspect. Site group (5) separates (eigenvalue 0.322) according to age and microtopography, into site group (10), comprising mostly low-slope quadrats on M3 but also on M1, M2 and M4, and site group (11) which mainly consists of M1 sites and two sites on M3. Site group (6) separates (eigenvalue 0.210), according to microtopography, into site group (12), consisting of low-slope quadrats on M4-6 and a proximal toe-slope site on M2, and site group (13), consisting of high-slope quadrats on M4-6 and the proximal slope of M2. Site group (10), the **Salix glauca - Vaccinium uliginosum** assemblage, can be considered as a late-snow late intermediate heath assemblage and its indicators are *Salix glauca* and *Vaccinium uliginosum*. Preferential species include *Phyllodoce caerula, Salix herbacea and Bartsia alpina.* Site group (11), the **Cladonia arbuscula Cetraria ericetorum** assemblage, is a mature lichen heath assemblage and its indicators are *Cladonia arbuscula, Cetraria ericetorum* and *Stereocaulon botryosum*. Preferential species include *Empetrum nigrum, Betula nana* and *Vaccinium myrtillus*. Site group (12), the **Cassiope hypnoides - Salix herbacea** assemblage, is an early intermediate snowbed assemblage with *Cassiope hypnoides* and *Salix herbacea* as the indicators. Preferential species include a high cover value of *Phyllodoce caerula* and low covers of *Salix phylicifolia* and *Poa alpina*. Site group (13), or the **Cladonia chlorophaea - Cetraria nivalis** assemblage, is a dry early intermediate lichen heath assemblage with indicators *Cladonia chlorophaea, Cetraria nivalis* and *Solorina crocea* and preferential species which include *Cladonia cervicornis, Cetraria ericetorum* and *Cetraria cucullata*. The description of further divisions (i.e. of site groups (10*), (11*), (12*) and (13*)) at higher levels, are not considered to be ecologically meaningful. The site groups at Storbreen low (2) are summarised in Table 4.4, which also contains a more comprehensive list of preferential species for each group.

4.1.5 Svellnosbreen (Altitude: 1280-1440m. Aspect: south-easterly)

(Note that M1, on this foreland, is a gully and not a moraine (see section 2.2.2.2 for discussion). The gully has been numbered in the same manner as a moraine with site 1 being on the toe distal slope, site 5 being on the top of the slope and site 9 being on the toe proximal slope.)

As can be seen in Fig. 4.6, at the second (2-group) level the sites divide (eigenvalue 0.433), according to age and microtopography, into site group (2), a very large group consisting of all moraines on the foreland except a few sites on M6, and site group (3) consisting of proximal low-slope and crest sites on M6. Site group (2), the **Empetrum nigrum - Stereocaulon alpinum** assemblage, is a heath assemblage with the indicators *Stereocaulon alpinum* and *Empetrum nigrum*. Preferential species include *Phyllodoce caerula, Cladonia portentosa* and *Salix phylicifolia*. Site group (3), the **Deschampsia alpina - Oxyria digyna** assemblage, is an exposed pioneer snowbed assemblage with the indicator *Deschampsia alpina* and preferential species which are *Oxyria digyna, Cardaminopsis petraea* and *Cerastium cerastoides*. The separation of site group (3*) is not described at higher levels of subdivision.

At the third (4-group) level, separation occurs according to age and microtopography so that site group (2) (eigenvalue 0.427) divides into site group (4), consisting of most of M1, the distal low-slope of M2 and two distal low-slope quadrats on M6, and group (5), consisting of most of the remainder of the foreland. Site group (4), the **Salix herbacea - Cetraria islandica** assemblage, is a snowbed assemblage and its indicators are *Salix herbacea, Cetraria islandica, Festuca ovina* and *Anthoxanthum odoratum*. Preferential species include *Cladonia gracillis, Festuca ovina* and *Gnaphalium norvegicum*. Site group (5), the **Cetraria nivalis - Salix phylicifolia** assemblage, is a heath assemblage and it has no indicators. Preferential species include *Cetraria nivalis, Salix phylicifolia* and *Cladonia chlorophaea*.

At the fourth (8-group) level divisions occur according to age and microtopography. Site group (4) divides (eigenvalue 0.449) into site group (8), consisting of the two quadrats on M6, and site group (9), comprising mainly sites on M1 and low-slope distal sites on M2. Site group (5) separates (eigenvalue 0.437) into site group (10), consisting of low-slope quadrats on M2, M3, M4, all of M5 and quadrats on M6, and site group (11), consisting of high-slope quadrats on M1-4. Site group (8), the **Salix glauca - Cerastium cerastoides** assemblage, is a pioneer snowbed assemblage. It has no indicators and its preferential species include *Salix glauca, Cerastium cerastoides* and *Anthoxanthum odoratum*. Site group (9), the **Salix herbacea - Empetrum nigrum** assemblage is an atypical snowbed assemblage with indicator species *Salix herbacea*. Preferentials include *Empetrum nigrum, Festuca ovina* and *Stereocaulon alpinum*. Site group (10), the **Salix glauca - Salix phylicifolia** assemblage can be considered as an early intermediate snowbed and pioneer group with indicator species *Salix glauca* and preferential species including *Salix phylicifolia, Bartsia alpina* and *Cardaminopsis petraea*. Site group (11), the **Cetraria nivalis - Cetraria ericetorum** assemblage, is a lichen heath assemblage and has indicator species *Cetraria nivalis, Cetraria ericetorum* and *Empetrum nigrum*. Preferentials include *Alectoria ochroleuca, Cetraria cucullata* and *Solorina crocea*. The separation of site groups (8*) and (9*) is not described at higher levels of subdivision.

At the fifth (16-group) level, division of the remaining moraines occurs according to microtopography and age. Site group (10) divides (eigenvalue 0.308) separating site group (20), which generally consists of high-slope quadrats on M5 and M6, from site group (21), consisting of low-slope quadrats on M1-3 and mainly low-slope quadrats on M5. Site group (11) separates (eigenvalue 0.298) into site group (22), comprising quadrats at various positions on M2-4, and site group (23), consisting of mainly high-slope or proximal quadrats on M1, M2, M3 and M4. Site group (20), the **Salix glauca - Cardaminopsis petraea** assemblage, is an exposed pioneer assemblage and its indicator species is *Salix glauca* with preferential species which include *Cardaminopsis petraea, Cerastium cerastoides* and *Trisetum spicatum*. Site group (21), the **Empetrum nigrum - Stereocaulon alpinum** assemblage, is a late-snow early intermediate heath assemblage (or atypical snowbed) with indicators *Empetrum nigrum, Stereocaulon alpinum, Cladonia portentosa, Phyllodoce caerula* and *Cladonia chlorophaea*. Preferential species include *Saxifraga oppositifolia, Solorina crocea* and *Bartsia alpina*. Site group (22), the **Cladonia portentosa - Phyllodoce caerula** assemblage, is an early intermediate heath assemblage and indicators are *Cladonia portentosa* and

Phyllodoce caerula. Preferential species include high covers of *Stereocaulon alpinum, Betula pubescens* and *Solorina crocea.* Site group (23), the **Alectoria ochroleuca - Cetraria cucullata** assemblage, is a lichen heath assemblage with indicator species *Alectoria ochroleuca, Cetraria cucullata, Cetraria nivalis, Thamnolia vermicularis* and *Cornicularia aculeata.* Preferential species include *Cetraria ericetorum, Vaccinium vitis-idaea* and *Stereocaulon condensatum.* Divisions (i.e. of site groups (20*), (21*), (22*) and (23*)) are not described at higher levels as they were not considered to be ecologically meaningful. The site groups at Svellnosbreen are summarised in Table 4.5, which also contains a more comprehensive list of preferential species for each group.

4.1.6 Storbreen high (Altitude: 1310-1350m. Aspect: north-easterly)

As can be seen in Fig. 4.7, at the second (2-group) level the sites separate (eigenvalue 0.471) according to age and microtopography with most of the older moraines in site group (2) and low-slope or younger sites comprising site group (3). Site group (2), the **Phyllodoce caerula - Solorina crocea** assemblage, can be considered as a heath assemblage and its indicators are *Phyllodoce caerula, Solorina crocea* and *Cetraria nivalis.* Preferential species include *Alectoria ochroleuca, Cetraria islandica* and *Empetrum nigrum.* Site group (3), the **Salix glauca - Oxyria digyna** assemblage, is a pioneer and snowbed assemblage. It has no indicators and its preferential species are *Salix glauca, Oxyria digyna* and *Poa alpina.*

At the third (4-group) level the older site group (2) separates (eigenvalue 0.391) according to microtopography into site group (4), consisting mainly of high-slope quadrats on M1-6, and site group (5), consisting mainly of the low-slope quadrats. M3 and M4, are complex "double" moraines, with a hollow situated between two ridges (or "double" crests). The "double" crests are included in site group (4). The hollows are included in site group (5) (emphasising the effect of small changes in microtopography on vegetation patterns). Site group (3) separates (eigenvalue 0.489) mainly according to age, with most of the older low-slope sites, and one distal quadrat on M7, comprising site group (6) and nearly all of M7 and M8, plus one toe quadrat on M2 and the toe site on M5, comprising site group (7). Site group (4), the **Cetraria nivalis - Alectoria ochroleuca** assemblage, is an exposed lichen heath assemblage with indicators *Cetraria nivalis* and *Alectoria ochroleuca* and preferential species *Thamnolia vermicularis, Cornicularia divergens* and *Alectoria nigricans.* Site group (5), the **Salix herbacea - Stereocaulon alpinum** assemblage is a late-snow heath assemblage with its indicator being *Salix herbacea.* Preferential species include *Stereocaulon alpinum, Cassiope hypnoides* and *Salix glauca.* Site group (6), the **Salix glauca - Salix herbacea** assemblage, is an early intermediate snowbed assemblage, with *Salix glauca* as the indicator. Its preferential species include *Salix herbacea, Oxyria digyna* and *Salix lanata.* Site group (7), the **Poa alpina - Deschampsia alpina** assemblage, is a pioneer assemblage and has no indicators. Its preferential species are *Poa alpina, Deschampsia alpina* and *Arabis alpina.* The separation of site group (6*) is not described at higher levels of subdivision.

At the fourth (8-group) level site group (4) separates (eigenvalue 0.421) according to age into site group (8), consisting of high-slope sites on M1 and site group (9), consisting of high-slope quadrats on M2-6. Site group (5) separates (eigenvalue 0.297) into site group (10), consisting of sites on M5, mostly mid-slope quadrats on M4 and low-slope quadrats on M3, and site group (11), mainly consisting of the low-slope sites on M1 and M2 plus a few low-slope quadrats on M3-5. Site group (7) separates (eigenvalue 0.451), according to age and microtopography, into site groups (14), consisting mainly of sites on M7 and a few high-slope sites on M8, and site group (15) consisting of most of the lower and middle sites on M8 plus one distal toe site on M7 and M5. Site group (8), the **Betula nana - Vaccinium vitis-idaea** assemblage, is a mature lichen heath assemblage. Its indicator is *Betula nana* and its preferential species include *Vaccinium vitis-idaea, Cetraria ericetorum* and *Stereocaulon alpinum*. Site group (9), the **Phyllodoce caerula - Solorina crocea** assemblage, is an exposed early intermediate lichen heath assemblage with no indicators and preferential species which include *Phyllodoce caerula, Solorina crocea* and *Salix glauca*. Site group (10), the **Salix glauca - Cetraria nivalis** assemblage, is an early intermediate late-snow heath assemblage with indicators which are *Salix glauca, Cetraria nivalis, Phyllodoce caerula* and *Stereocaulon alpinum*. The only preferential species, which is not an indicator, is *Stereocaulon botryosum*. Site group (11), the **Salix herbacea - Cetraria islandica** assemblage, is a mature late-snow heath assemblage with indicators *Salix herbacea, Cetraria islandica* and *Cladonia gracillis*. Preferential species include *Cladonia portentosa, Cladonia uncialis* and *Juncus trifidus*. Site group (14), the **Stereocaulon alpinum - Festuca ovina** assemblage, is an exposed pioneer assemblage with indicators which are *Stereocaulon alpinum* and *Festuca ovina* and preferential species which include *Stereocaulon botryosum, Arabis alpina* and *Sagina saginoides*. Site group (15) or the **Oxyria digyna - Deschampsia alpina** assemblage, is a pioneer snowbed assemblage with the indicator *Oxyria digyna* and preferential species which are *Deschampsia alpina, Poa alpina* and *Cerastium cerastoides*. Divisions are not described at higher levels (i.e. of site groups (8*), (9*), (10*), (11*), (14*) and (15*)) as they are not considered to be ecologically meaningful. The site groups at Storbreen high are summarised in Table 4.6, which also contains a more comprehensive list of preferential species for each group.

4.1.7 Høgvaglbreen (Altitude: 1400-1450m. Aspect: north-easterly)

As can be seen in Fig. 4.8, at the second (2-group) level the sites separate (eigenvalue 0.367) according to age with the older moraines comprising site group (2) and the younger moraines, except the distal low-slope quadrats on M5, comprising site group (3). Site group (2), **the Salix herbacea - Cetraria ericetorum** assemblage, is a heath assemblage with indicators *Salix herbacea, Cetraria ericetorum, Stereocaulon alpinum* and *Cetraria nivalis*. Preferential species include *Cornicularis divergens, Cladonia gracilis* and *Thamnolia vermicularis*. Site group (3), the **Oxyria digyna - Poa alpina** assemblage, is a pioneer assemblage and its indicator is *Oxyria digyna*. The only preferential species is *Poa alpina*.

At the third (4-group) level the sites separate according to microtopography and age. Site group (3) divides (eigenvalue 0.374) into site group (4), consisting of high-slope sites on M1 and M3. and site group (5), consisting of low-slope quadrats on M1 and M3 and all of M2 and M4 plus a distal toe-slope site on M5. Site group (3) divides (eigenvalue 0.440) into site group (6), consisting of low-slope or mid-slope quadrats on M5 and toe-slope or distal quadrats on M6, and site group (7), consisting of the crest site on M5 and the crest and proximal slope of M6. Site group (4), the **Thamnolia vermicularis - Alectoria ochroleuca** assemblage, is a dry lichen heath assemblage with indicator species *Thamnolia vermicularis, Alectoria ochroleuca* and *Cetraria nivalis*. Preferential species include *Vaccinium uliginosum, Vaccinium vitis-idaea* and *Cornicularia divergens*. Site group (5), the **Cetraria ericetorum - Stereocaulon alpinum** assemblage, is a late-snow lichen heath assemblage. It has no indicators and preferential species include *Cetraria ericetorum, Stereocaulon alpinum* and *Cladonia chlorophaea*. Site group (6), the **Solorina crocea - Oxyria digyna** assemblage, is a pioneer snowbed assemblage and its indicators are *Solorina crocea, Oxyria digyna, Stereocaulon alpinum* and *Salix herbacea*. Its preferential species are *Trisetum spicatum* and *Poa alpina*. Site group (7), the **Salix glauca - Cetraria nivalis** assemblage, is an exposed pioneer assemblage. Its indicator is *Salix glauca* and its preferential species is *Cetraria nivalis*. The separation of site groups (4*), (6*) and (7*) is not described at higher levels of subdivision.

At the fourth (8-group) level, site group (5) separates (eigenvalue 0.247) according to age and also aspect into groups (10) and (11). Site group (10) consists of most the quadrats on M2 and M4, and most of the low-slope sites on M3. Site group (11) comprises all the low-slope sites on M1, plus 1 mid-slope distal quadrat on M2, one low-slope distal quadrat on M3 and three distal quadrats on M4. Site group (10), the **Cetraria nivalis - Cassiope hypnoides** assemblage, is an early intermediate late-snow lichen heath assemblage and it has no indicators. Preferential species include *Cetraria nivalis, Cassiope hypnoides* and *Cornicularia divergens*. Site group (11), the **Cladonia gracilis - Salix herbacea** assemblage, can be regarded as a mature or late intermediate snowbed assemblage. Its indicators are *Cladonia gracilis* and *Salix herbacea* and preferential species include *Cladonia squamosa, Festuca ovina* and *Sphaerophorus fragilis*. The separation of site group (11*) is not described at higher levels of subdivision.

At the fifth (16-group) level, site group (10) separates (eigenvalue 0.238) according to microtopography into site groups (20) and (21). Site group (20) consists of high-slope quadrats on moraines 2-4, while site group (21) comprises low-slope quadrats on M2-4 plus the distal toe-slope site on M5. Site group (20), the **Cornicularia aculeata - Cetraria nivalis** assemblage is an early intermediate lichen heath assemblage with indicator species *Cornicularia aculeata, Cetraria nivalis, Solorina crocea* and *Cornicularia divergens*. Preferential species include *Cladonia arbuscula, Phleum alpinum* and *Thamnolia vermicularis*. Site group (21), the **Cassiope hypnoides - Cladonia chlorophaea** assemblage, is an early intermediate snowbed assemblage and its indicator species is *Cassiope hypnoides*. Its preferential species are *Cladonia chlorophaea, Sphaerophorus fragilis* and *Cladonia gracilis*. Divisions are not described at higher levels (i.e. of site groups (20*) and (21*)) as they were not considered to be ecologically meaningful. The site groups at Høgvaglbreen are summarised in Table 4.7, which also contains a more comprehensive list of preferential species for each group.

4.1.8 Bøverbreen (Altitude: 1500-1540m. Aspect: south-westerly)

As can be seen in Fig. 4.9, at the second (4-group) level the sites separate (eigenvalue 0.508), according to age, into site group (2), consisting nearly completely of M1-4 and one proximal shoulder-slope quadrat on M5, and site group (3), consisting of M5-6 and one proximal toe-slope quadrat on M4. Site group (2), the **Cladonia chlorophaea - Salix herbacea** assemblage, can be described as a heath assemblage. Its indicators are *Cladonia chlorophaea, Salix herbacea* and *Stereocaulon condensatum* and its preferential species include *Cladonia gracillis, Cetraria nivalis* and *Cetraria ericetorum*. Site group (3), the **Oxyria digyna - Poa alpina** assemblage, is a pioneer assemblage with indicators *Oxyria digyna* and *Poa alpina*. Preferential species are *Cerastium cerastoides* and *Deschampsia alpina*.

At the third (4-group) level the sites separate according to microtopography. Site group (2) divides (eigenvalue 0.334) into site group (4), consisting of high-slope quadrats on M1, M2 and M3, and site group (5), consisting of low-slope quadrats on M1, M2 and M3, and all of M4 (except the proximal toe-slope). Site group (3) separates (eigenvalue 0.268) into site group (6), comprising mainly of high-slope quadrats on M5 and most of the proximal slope of M6, and site group (7), consisting mainly of low-slope quadrats on M5 and high-slope quadrats on M6. Site group (4), the **Alectoria ochroleuca - Cornicularia aculeata** assemblage, is a dry/exposed lichen heath assemblage, with indicators *Alectoria ochroleuca* and *Cornicularia aculeata*. Preferential species include *Cetraria nivalis, Cornicularia divergens* and *Thamnolia vermicularis*. Site group (5), the **Stereocaulon alpinum - Cladonia gracillis** assemblage, is a late-snow lichen heath assemblage and it has no indicators. Its preferential species include *Stereocaulon alpinum, Cladonia gracillis* and *Cetraria ericetorum*. Site group (6), the **Cerastium alpinum - Cerastium alpinum** assemblage, is an exposed pioneer assemblage and has one indicator *Cerastium alpinum*. The only preferential species is *Cerastium alpinum*. Site group (7), the **Oxyria digyna - Poa alpina** assemblage, is a pioneer snowbed assemblage with indicators *Oxyria digyna, Poa alpina* and *Deschampsia alpina*. Preferential species are *Cerastium cerastoides* and *Trisetum spicatum*. The separation of site groups (4*), (6*) and (7*) is not described at higher levels of subdivision.

At the fourth (8-group) level site group (5) separates (eigenvalue 0.235) according to age, microtopography and aspect, into site groups (10) and (11). Site group (10) consists of sites on M1, mainly high-slope and distal sites on M2, and mainly low-slope distal quadrats on M3. Site group (11) consists one distal mid-slope quadrat and two proximal low-slope quadrats M2, two distal low-slope quadrats and four proximal low-slope quadrats on M3 and all of M4. Site group (10), the **Cetraria islandica - Cetraria ericetorum** assemblage, is a mature or late intermediate lichen heath assemblage and it has the indicators *Cetraria islandica, Cetraria ericetorum, Cladonia arbuscula* and *Cladonia gracillis*, and preferential species which include *Cetraria nivalis, Cladonia portentosa* and *Cladonia chlorophaea*. Site group (11), the **Trisetum spicatum - Gnaphalium supinum** is a snowbed assemblage, and has no indicators and preferential species which include *Trisetum spicatum, Gnaphalium supinum* and *Poa alpina*. Divisions are not described at higher levels (i.e. of site groups (10*) and (11*)) as they are not considered to be ecologically meaningful. The site groups at Bøverbreen are summarised in Table 4.8, which also contains a more comprehensive list of preferential species for each group.

4.1.9 Summary of TWINSPAN site groups

At the second (2-group) level of subdivision, the divisions were largely made according to age on all forelands showing that age is the most significant factor affecting the vegetation patterns and thus site groups. The exception is at Svellnosbreen where the primary subdivision separates nearly all sites from the low-slope proximal quadrats on M6. The large altitudinal range on this foreland could have influenced this separation and is discussed in more detail in chapter (7). On the mid-alpine forelands, microtopography appears to have some influence on vegetation pattern on the younger terrain. Furthermore, assemblages in some of the low-slope quadrats on the oldest terrain, showed an affiliation with pioneer assemblages, suggesting that, in some cases, certain environmental factors may be common to both younger and the oldest terrain at the higher altitudes.

At the third (4-group) level of subdivision, sites occupying similar positions on the moraines were mostly grouped together showing that microtopography is a significant influence on the separation of groups at this level. At low altitudes, the influence of microtopography is significant only on the pioneer terrain as shown by the exposed pioneer assemblage (site group 4) at Austerdalsbreen and two pioneer assemblages (site groups 6 and 7*) at Fåbergstølsbreen. Sites on the remainder of the subalpine forelands divided according to age. At higher altitudes the influence of microtopography is more apparent. At Storbreen low (1 & 2) assemblages on the mature till ridge did not separate except for two proximal toe-slope quadrats on Storbreen low (2). Otherwise, on the oldest terrain, the high-slope quadrats of the moraines comprised a lichen heath assemblage and the assemblages occurring in the low-slope quadrats were either a late intermediate late-snow heath or a late intermediate snowbed. The younger parts of the foreland comprised lichen heath in the high-slope quadrats and early intermediate snowbed or late-snow early intermediate heath assemblages in the low-slope quadrats. At Storbreen low (1) the whole of M6 comprised a snowbed assemblage. At Storbreen low (1 & 2) there are no early pioneer sites so possibly the influence of microtopography, in relation to age, is exaggerated. This will be discussed in more detail in chapter (7). At Svellnosbreen both age and microtopography appear to be important as shown by the separation of a snowbed assemblage, found in the mature gully and lower distal quadrats on M2 and M6, from a heath assemblage, on the remainder of the foreland. On the mid-alpine forelands, microtopography appears to be a significant influence across all moraines. At Storbreen high the influence of microtopography is clear-cut on M1-6, with high-slope quadrats comprising lichen heath assemblages and low-slope quadrats comprising late-snow heath assemblages, early intermediate snowbed or pioneer assemblages. The pioneer vegetation on this foreland occurs on fluted moraines and the profile across these moraines has little relief. The vegetation on the youngest moraines at Storbreen high is therefore not differentiated at this level. Both Høgvaglbreen and Bøverbreen are similar to Storbreen high except that the pioneer vegetation is differentiated. The older moraines separate into exposed lichen heath in the high-slope quadrats and late-snow lichen heath in the low-slope quadrats. The pioneer vegetation separated into an exposed pioneer assemblage on the crest and proximal slopes and a pioneer snowbed assemblage in low-slope quadrats.

At the fourth (8-group) level, sites at Austerdalsbreen continue to separate according to age (i.e. M1 separating from M2 and M3-6 separating from M7). It is not until the fifth (16-group) and sixth (32-group) levels, that sites start to separate according to microtopography. The relative influence of microtopography therefore appears to be least at the lowest altitudes. At Fåbergstølsbreen the influence of microtopography becomes apparent at the fourth (8-group) level, although not on the oldest terrain. However, the site groups tend to be within a similar age range i.e. the groups are found on one or two consecutive moraines (e.g. the birch woodland on M1 and low-slope distal M2 contrasting with the birch woodland heath on high-slope proximal M2). This shows that age is an influential factor at the fourth level on this foreland and this is also true at the fifth level. Separation of site groups on the alpine forelands continues, according to microtopography, at both the fourth and fifth levels. At Svellnosbreen, the importance of microtopography becomes apparent at the fourth level on the oldest terrain, with a lichen heath assemblage in high-slope quadrats and an atypical snowbed assemblage (or early intermediate snowbed) being found in the low-slope quadrats (including the M1 gully). The early intermediate snowbed assemblage is also found on younger sites. On the young terrain another pioneer snowbed assemblage occurs on the distal slope of M6. At the fifth level of subdivision Svellnosbreen sites continue to divide according to microtopography.

From these results, it is possible to see a clear gradient of the effects of microtopography on the site groups, and hence vegetation pattern, across the forelands. The influence of microtopography appears to be greatest on the young ground at the highest altitudes, shown by sites separating according to microtopography at the second level of subdivision (at Svellnosbreen, Storbreen high, Høgvaglbreen and Bøverbreen). At the third level of subdivision the results show a gradient of the influence of microtopography, with a lack of separation of sites on the older ground, according to microtopography, on subalpine forelands (alt-290-630m), but a separation of sites, according to microtopography, on the oldest terrain on alpine forelands. At Storbreen low (1) (alt - 1140-1200m) the influence of microtopography, on the oldest moraines, is just apparent (two toe-slope quadrats), although the sites on the Storbreen low (2) replicate mature till ridge have not separated at this level. On the three mid-alpine forelands (1310-1540m) the influence of microtopography is apparent, at the third level of subdivision, on all terrain-ages. This therefore shows that microtopography has a greater influence at higher altitudes, across all terrain-ages, than at lower altitudes. At the lowest altitudes microtopography appears to have a more significant influence on the younger ground. At Svellnosbreen the trends are more difficult to interpret, perhaps due to the large altitudinal range of the foreland (1280-1440m). This is not surprising, given that altitude appears to have a significant influence on the relative effects of microtopography on vegetation pattern and thus site groups.

The individual foreland tables (Tables 4.1 to 4.8) have been summarised in Table 4.9. In this table the trends in the TWINSPAN "final site groups", marked with an asterisk (*), of each individual foreland can be compared at a glance. Each cell within the table shows: a) the descriptive name of each assemblage; b) the primary indicators; c) where each assemblage occurs; and d) the level of subdivision for the "final site group" in question. From these trends it is possible to comment on the relative influence of altitude, age and microtopography on the "final site groups", and thus the vegetation patterns and succession. The main trends shown by Table 4.9 are as follows:

1. There is a distinct series of assemblages, from pioneer to mature, on every foreland and terrain-age appears to be the most significant influence on each foreland.
2. There are a larger number of meaningful assemblages on the lower altitude forelands, and the number of sites on each of the forelands does not appear to affect this trend.
3. The assemblages at the higher altitudes tend to be more distinct (many separate at the lower levels - of subdivision - i.e. levels 3 and 4) than the assemblages at lower altitudes. For example, three out of five assemblages at Bøverbreen separate at (level 3) and at Høgvaglbreen three out of six, but at Austerdalsbreen and Fåbergstølsbreen only one out of ten assemblages separate at (level 3).
4. The distribution of the assemblages is influenced by microtopography on every foreland and on most ages of terrain. Microtopographic differences (represented by slope position on moraines) are more distinct on the pioneer than on the early intermediate terrain. The exception is at Storbreen low (1 and 2) foreland, where the youngest terrain is represented by the 1900 moraine and thus the terrain-age gradient is not quite as steep as it is on the other forelands. On most of the forelands, at all altitudes, the mature terrain also has distinct assemblages, the exception being Fåbergstølsbreen which is a birch woodland habitat where the trees cause their own understorey micro-habitat. Distinct assemblages on the oldest terrain in front of the sub-alpine forelands may well be due to factors other than microtopography, such as grazing.
5. The relative influence of microtopography on assemblage separation appears to increase with altitude.

4.2 Succession diagrams

By referring to the profile diagrams (Figs 4.2-9) it has been possible to construct simple succession diagrams for each of the forelands (Figs 4.10-17). The order of the "final site groups" in the succession diagrams is made according to where the quadrats within each of the groups most frequently occur on the foreland. These succession diagrams are unusual in that they show the "final site groups" at a number of levels, not just one. Many other studies and reviews have already shown the existence of succession on glacier forelands in the Jotunheim and Jostedals (Matthews, 1976,1992; Whittaker, 1985; Vetaas, 1986; Crouch, 1992). However, the succession diagrams from previous studies only show the groups at one level and thus the diagrams are either over-simplified at the third (4-group) level, with groups that are much too large to be meaningful, or over-complicated at the fifth (16-group) level, with many groups which were too small to be meaningful. The concept of "final site groups" was introduced in the previous section and by using the "final site groups" system (i.e. displaying ecologically meaningful groups from several levels) it is suggested that the succession diagrams give a more representative picture of the natural vegetation patterns across the forelands.

The succession diagrams show the relative influence of factors, such as age and microtopography, on vegetation succession at a number of levels of subdivision. A colour coding system has been used to show which level the "final site group" belongs to. Magenta represents groups at the second (2-group) level. Red represents groups at the third (4-group) level. Blue represents groups at the fourth (8-group) level. Green represents groups at the fifth (16-group) level. Yellow (plus stripes) represents groups at the sixth (32-group) level. Arrows in the colours of each of the levels have been used to show how the groups, divided at the higher levels, are related at the lower levels. Thus the individual foreland successions can be interpreted at a number of different levels of subdivision in one ecologically meaningful diagram.

4.2.1 Succession at Austerdalsbreen

By referring to Table 4.1 and Fig. 4.10 it can be seen that at level three (red) the successional sequence is influenced mainly by age except on the youngest ground with an exposed pioneer, **Stereocaulon alpinum-Carex spp,** assemblage (proximal and high-slope M7) being succeeded by an early intermediate heath, **Betula pubescens - Calluna vulgaris,** assemblage, (M3-6; low-slope M7) and then by a mature heath, **Cornus suecica - Salix glauca,** assemblage, (M2; high-slope M1), which may develop, on grazed low-slope quadrats, into a mature meadow, **Athyrium distentifolium - Potentilla cranzii,** assemblage (low-slope M1), which is too small to separate at higher levels of subdivision.

At level four (blue) the separation of the pioneer and mature terrain is influenced by microtopography, but the early intermediate and late intermediate terrain is divided by age. An exposed pioneer snowbed, **Carex spp - Phleum alpinum,** assemblage, on the proximal low-slope and distal shoulder-slope of M7, is succeeded by another pioneer, **Salix phylicifolia - Salix herbacea,** assemblage, on the distal low-slope of M7. Another pioneer, **Stereocaulon alpinum - Stereocaulon vesuvianum,** assemblage found on the crest of M7, is an exposed pioneer assemblage and is distinct from the other assemblages. The pioneer assemblages are succeeded by an early intermediate heath, **Empetrum nigrum - Calluna vulgaris,** assemblage, which occurs on M3-6 and is not differentiated by microtopography. This, in turn, is succeeded by a late intermediate heath **Salix glauca - Salix herbacea** assemblage, with low birch cover and not differentiated by microtopography. The latter assemblage then splits into two mature groups according to microtopography: at high-slope positions a mature heath, **Deschampsia flexuosa - Vaccinium myrtillus**, assemblage with a high birch cover; and at low-slope positions, the mature meadow **Athyrium distentifolium - Potentilla cranzii** (level 3) assemblage.

At the fifth level (green) the pioneer and mature assemblages remain as they are at lower levels of subdivision but the early intermediate terrain separates into two assemblages: a late-snow early intermediate heath, **Vaccinium myrtillus - Betula pubescens,** assemblage (low-slope M4-7); and a large lichen heath, **Calluna vulgaris - Solorina crocea,** assemblage of 57 sites, (M3-6) which does not appear to be microtopography-influenced. The (level 4) late intermediate assemblage separates, according to microtopography, into a late intermediate heath, **Vaccinium myrtillus - Vaccinium uliginosum,** assemblage (high-slope M2), and a late intermediate snowbed, **Deschampsia alpina - Phyllodoce caerula,** assemblage (proximal slope and distal low-slope M2). At the sixth level (yellow) the early intermediate lichen heath separates, according to microtopography and age, into a late intermediate late-snow lichen heath, **Empetrum nigrum - Betula pubescens** assemblage on low-slopes and the oldest terrain, and a late intermediate lichen heath **Solorina crocea** assemblage on more exposed high-slope and younger terrain.

As can be seen in the Fig. 4.10, there appears to be a separate succession of low-slope assemblages and high-slope assemblages if one considers the assemblages described by the "final site groups". Although the young terrain appears to differentiate according to microtopography, the members of assemblages of the late intermediate and early intermediate terrain are not strongly related (loose), and are separated from each other only at the highest levels of subdivision. Furthermore the two distinct groups, on the oldest terrain, may result from factors other than microtopography, such as grazing (see concluding chapter (7)). Therefore the general influence of microtopography on vegetation succession at Austerdalsbreen does not appear to be strong. There appears to be a slight convergence of assemblages, with a higher number of assemblages on younger terrain than on the oldest terrain, although the presence of two mature assemblages refutes convergence to a monoclimax (*sensu*: Clements, 1916).

4.2.2 Succession at Fåbergstølsbreen

By referring to Table 4.2 and Fig. 4.11 it can be seen that at level three (red) the successional sequence is influenced by age, except on the pioneer terrain. On the youngest terrain is an exposed snowbed, **Deschampsia flexuosa - Epilobium alsinifolium,** assemblage found on the crest and proximal quadrats on M6 and this is succeeded by a pioneer and snowbed, **Agrostis tenuis - Phleum alpinum,** assemblage which is found on low-slope M6 and at all positions on M5. This is succeeded by an early intermediate heath, **Calluna vulgaris - Empetrum nigrum**, assemblage (M3-4), which in turn is succeeded by a mature birch woodland, **Vaccinium myrtillus - Deschampsia flexuosa,** assemblage (M1-2).

At level four (blue) the succession is influenced by both age and microtopography with a snowbed assemblage (low-slope M5) separating from other pioneer assemblages on the younger terrain (M5-M6); an exposed lichen heath (crest M4) dividing from an early intermediate heath assemblage (M3-M4); and a birch heath assemblage (high-slope M2) dividing from a mature birch woodland assemblage (M1-M2). The succession proceeds, from the (level 2) exposed snowbed, **Deschampsia flexuosa - Epilobium alsinifolium,** assemblage to another pioneer, **Luzula spicata - Oxyria digyna** assemblage. The succession then follows two pathways: a low-slope sequence or a high-slope sequence. The former being a snowbed, **Lotus corniculatus - Salix phylicifolia,** assemblage; the latter being an exposed lichen heath **Cladonia chlorophaea - Cladonia fimbriata,** assemblage. Both of these assemblages then develop into an early intermediate heath, **Betula pubescens - Calluna vulgaris,** assemblage. The main pathway from this assemblage proceeds to the birch woodland heath, **Phyllodoce caerula - Empetrum nigrum** and thence to the mature birch woodland, **Vaccinium myrtillus - Gymnocarpium dryopteris,** assemblage. It should be noted that, despite its obvious importance, TWINSPAN does not recognise *Betula pubescens* as an indicator or preferential species because it is found on most of the sites on the oldest terrain and therefore only certain understorey species have been defined as indicators by TWINSPAN to separate the assemblages.

As can be seen in Fig. 4.11 at the fifth level, the remaining assemblages in the diagram split according to both microtopography and age. Succession of the "final site groups" is more complex than at Austerdalsbreen, with some "final site groups" comprising assemblages on a disordered sequence of moraines so that retrogression (*sensu*: Whittaker, 1985; Matthews and Whittaker, 1987) is likely to be occurring. Fig. 4.11 shows a high-slope succession and a low-slope succession at the highest levels of subdivision but, as at Austerdalsbreen, the influence of microtopography on succession does not appear to be very significant. However, the presence of exposed assemblages on the young terrain, and also on the individual moraines M4 and M2 at levels three and four respectively, may suggest that microtopography has a little more influence on vegetation pattern at Fåbergstølsbreen than at Austerdalsbreen. Again, there appears to be a slight convergence of assemblages, with a higher number of pioneer assemblages than mature.

4.2.3 Succession at Storbreen low (1)

It should be noted that the youngest ground on this stretch of foreland is the 1900 moraine. By referring to Table 4.3 and Fig. 4.12 it can be seen that at level three (red) the successional sequence is influenced by age and microtopography. An early intermediate snowbed, **Salix glauca - Salix herbacea,** assemblage found on M6, low-slope M5 and low-slope M4 is followed by three pathways: a lichen heath **Cetraria nivalis - Cetraria cucullata,** assemblage (high-slope M2,3,5 and distal M4); a late intermediate snowbed, **Salix glauca - Anthoxanthum odoratum,** assemblage (low-slope M2 and low-slope distal M3); and a heath, **Betula nana - Cetraria nivalis,** assemblage (M1, low-slope M2-4). There appear to be several meaningful mature assemblages and this lends support to Matthews (1979) who refuted convergence to a monoclimax.

As can be seen in Fig. 4.12 at the fourth (and final) level the divisions producing the "final site groups" are made according to both microtopography and age. An exposed snowbed, **Salix glauca - Salix herbacea** assemblage develops into two assemblages according to microtopography: an early intermediate late-snow heath, **Empetrum nigrum - Stereocaulon alpinum**, assemblage and an exposed lichen heath, **Alectoria ochroleuca - Cetraria cucullata**, assemblage. The early intermediate late-snow heath is succeeded by two pathways: the (level 2) snowbed, **Salix glauca - Anthoxanthum odoratum**, assemblage (low-slope M2 + distal low-slope M3) and a late intermediate late-snow heath, **Vaccinium uliginosum - Salix lanata**, assemblage (low-slope M2-4). The exposed lichen heath is succeeded by a lichen heath, **Phyllodoce caerula - Cladonia portentosa**, assemblage (shoulder-slope M2-3, distal M4). The early intermediate late-snow heath and lichen heath assemblages both converge on the late intermediate late-snow heath, **Festuca ovina - Salix herbacea**, assemblage (low-slope M2-4 and crest M1). Furthermore, the late intermediate snowbed assemblage and the late intermediate late-snow heath assemblage both converge on a mature late-snow heath assemblage. The general pathways of succession appear to proceed across high-slope or low-slope positions on the early intermediate terrain but there appears to be a convergence of these pathways on the mature terrain. Because the early intermediate late-snow heath assemblage found on the crest of M1 is the same as that found on low-slope quadrats of M2-4 it is conceivable that this crest assemblage could develop into the mature late-snow heath assemblage with time. The influence of microtopography on the assemblages, within the foreland boundary, is conspicuous at this altitude (low alpine) and contrasts with the apparent minor influence that microtopography has on vegetation patterns on the subalpine forelands. However, according to these results, the influence of microtopography on the later stages of succession on the oldest terrain, at first sight, does not appear to be great and this will be discussed in greater detail in later sections.

4.2.4 Succession at Storbreen low (2)

It should be noted that the youngest ground on this stretch of foreland is the 1900 moraine. By referring to Table 4.4 and Fig. 4.13 it can be seen that at level three (red) the successional sequence is influenced by age and microtopography. A late-snow early intermediate heath, **Stereocaulon alpinum - Salix herbacea**, assemblage (low-slope M2 and M4-6) proceeds to three assemblages, according to microtopography and age: a) an exposed, high-slope pathway to an exposed lichen heath, **Cetraria nivalis - Alectoria ochroleuca** assemblage (shoulder-slope and crest M2-6); b) a sheltered low-slope pathway to a late-snow late intermediate heath, **Stereocaulon alpinum - Cladonia portentosa**, assemblage (M1, low-slope M2-4); and c) a pathway leading to a sheltered late intermediate snowbed **Salix herbacea - Ranunculus acris** assemblage, (distal M2, toe-slope M1, M4). It is possible that the late intermediate snowbed could succeed the late-snow late intermediate heath assemblage. As with the Storbreen low (1) sequence, there appear to be several meaningful assemblages on the mature terrain which lends support to Matthews (1979).

As can be seen in Fig. 4.13 at the fourth level, there are two separate pathways of the "final site group" assemblages, at high-slope and low slope positions, across M2-6 and thus microtopography would appear to have an important influence on succession itself. At the high-slope positions an exposed early intermediate lichen heath, **Cladonia chlorophaea - Cetraria nivalis,** assemblage is succeeded by the (level 2) exposed lichen heath, **Cetraria nivalis- Alectoria ochroleuca**, assemblage which in turn is succeeded by a lichen heath, **Cladonia arbuscula - Cetraria ericetorum,** assemblage. At low-slope positions an early intermediate snowbed, **Cassiope hypnoides - Salix lanata**, assemblage develops either into a late-snow late intermediate heath, **Salix glauca -Vaccinium uliginosum**, assemblage or to the (level 2) late intermediate snowbed, **Salix herbacea- Ranunculus acris,** assemblage. The late-snow late intermediate heath assemblage may be succeeded either by a mature lichen heath or the late intermediate snowbed assemblage, although both pathways are weak. On the mature terrain there appears to be two main mature assemblages: a snowbed and a lichen heath. There is also a late-snow late intermediate heath assemblage on the mature terrain (toe-slope position).

4.2.5 Succession at Svellnosbreen

By referring to Table 4.5 and Fig. 4.14 it can be seen that at level 3 (red) the successional sequence is influenced by age. A small exposed pioneer assemblage from the separation at the second level is included in the successional sequence presented for (level 3). The second level pioneer, **Deschampsia alpina - Oxyria digyna** assemblage (proximal low-slope M6) is succeeded by an early intermediate heath group, **Cetraria nivalis- Salix phylicifolia,** assemblage (most of M2-5 and part of M6) which in turn is succeeded by an atypical snowbed, **Salix herbacea - Empetrum nigrum,** assemblage (most of M1, low-slope M2 and low-slope distal M6).

At the fourth level the exposed snowbed (level 2) assemblage is succeeded by a pioneer snowbed, **Salix glauca - Cerastium cerastoides,** assemblage (two low-slope distal quadrats M6) which is succeeded by an early intermediate snowbed and pioneer, **Salix glauca - Salix phylicifolia,** assemblage (low-slope M2-4, M5 and some M6). Two pathways proceed from the pioneers, according to microtopography: the high-slope pathway proceeding to a lichen heath, **Cetraria nivalis - Cetraria ericetorum,** assemblage and the low-slope pathway proceeding to an atypical snowbed, **Salix herbacea - Empetrum nigrum,** assemblage. The successional sequences displayed at this level is the least complex, but unfortunately the most meaningful assemblages do not appear until the fifth level due to the highly uneven separation of the first level of subdivision.

At the fifth level, as can be seen in Fig. 4.14, there are two successional sequences, at low-slope and at high-slope positions, across moraines on the foreland, thus showing the importance of microtopography at this level. However the succession is not simple and proceeds in a disorderly fashion so that pioneer assemblages converge on the early intermediate terrain before the assemblages diverge onto the oldest terrain. The high-slope pathway commences with an exposed pioneer, **Salix glauca - Cardaminopsis petraea,** assemblage (mainly high-slope or proximal M5-6) which is succeeded by an early intermediate heath, **Cladonia portentosa - Phyllodoce caerula,** assemblage (most positions M2-4) which is succeeded by a lichen heath, **Alectoria ochroleuca - Cetraria cucullata,** assemblage (crest M1-4). It is possible that the lichen heath assemblage succeeds the exposed pioneer assemblage directly. The low-slope position succession is also fairly complex. The exposed snowbed (level 2) is succeeded by the snowbed assemblage (level 3) which in turn is succeeded by a late-snow heath, **Empetrum nigrum - Stereocaulon alpinum,** assemblage (low-slope M1 and M3, low-slope M5) which is succeeded by the atypical snowbed assemblage (level 3). Fig. 4.14 shows that it is possible for the low-slope succession to proceed in an apparently "disorderly" fashion from a low-slope snowbed to a predominantly high-slope heath (found also on low-slope positions) to the low-slope late-snow heath assemblage. The unpredictable nature of succession on the Svellnosbreen foreland is possibly due to the large altitudinal difference between the young terrain and the oldest ground. This may therefore introduce too many elements into the analysis of the data, with the different parameters associated with age and altitude being confused. The moraines themselves are also problematic with the aspect of the proximal and distal slopes changing half way down the foreland (see map of transects on foreland). The moraines range from very large to small and some of the moraines have very steep slopes, with unusually high incidences of disturbance on the slope-sides. Lastly, there is a small stream cutting across the top of one of the moraines (M4) and the mature terrain is represented by a gully and not a till ridge. Despite these irregularities, clear patterns, which correspond with those shown on other forelands, have been elucidated and thus the results from this foreland are meaningful in the context of the study as a whole. The presence of two distinct assemblages on the oldest terrain refutes convergence to a monoclimax.

4.2.6 Succession at Storbreen high

By referring to Table 4.6 and Fig. 4.15 it can be seen that at level three (red) the successional sequence is influenced by age and microtopography. A pioneer, **Poa alpina - Deschampsia alpina,** assemblage (mainly M7-8) is succeeded by two pathways divided according to microtopography: the high-slope pathway proceeds to a lichen heath, **Cetraria nivalis - Alectoria ochroleuca,** assemblage (high-slope M1-6); and a low-slope pathway proceeds to a snowbed, **Salix glauca - Salix herbacea** assemblage (1 quadrat M7, low-slope M6, low-slope distal M2) and this, in turn, is succeeded by a late-snow heath, **Salix herbacea - Stereocaulon alpinum,** assemblage. The influence of microtopography at this higher altitude is therefore apparent at this low level of subdivision and thus shows that the influence of microtopography is important on this foreland.

At level four (blue) the groups divide according to both age and microtopography so that the successional sequence looks fairly similar to that at level 3. As can be seen in Fig. 4.15 a pioneer snowbed, **Oxyria digyna - Deschampsia alpina,** assemblage (low-slope M8) is succeeded by two pathways: a high position pathway proceeds to an exposed pioneer, **Stereocaulon alpinum - Festuca ovina,** assemblage (M7, high M8) and is succeeded by an intermediate lichen heath, the **Phyllodoce caerula - Solorina crocea** assemblage (high-slope M2-6), which in turn is succeeded by a mature lichen heath, **Betula nana - Vaccinium vitis-idaea** (high-slope M1); and a low-slope pathway proceeds to a early intermediate snowbed (level 3) and is succeeded by an early intermediate late-snow heath, **Salix glauca - Cetraria nivalis** (low-slope M3-5) and in turn this is succeeded by a mature late-snow heath, the **Salix herbacea - Cetraria islandica** assemblage. An alternative pathway from the (level 3) snowbed proceeds directly to the mature late-snow heath. The relative influence of microtopography across this foreland is emphasised by the positioning of the intermediate lichen heath across high-slope positions across five moraines, while three snowbed assemblages occupy low-slope positions on M2-7. This suggests that the successional pathways at level 4 separate according to microtopography. The successional pathways are simpler and more distinct at this altitude and the influence of microtopography appears to be important (see chapter (7), and especially section 7.4, for a discussion of the influence of environment on succession). There also appears to be a certain amount of divergence but not more than two groups on the oldest ground at this altitude. As shown by Matthews (1979) there is a considerable range of assemblages on the oldest terrain, especially if the lower altitude runs are also taken into consideration. If these are included, there are altogether five distinct assemblages on the oldest terrain at Storbreen.

4.2.7 Succession at Høgvaglbreen

By referring to Table 4.7 and Fig. 4.16 it can be seen that at level three (red) the successional sequence is influenced by age and microtopography. On the young terrain there are two assemblages, divided according to microtopography: an exposed pioneer **Salix glauca - Cetraria nivalis,** assemblage (crest M5, proximal M6) and a pioneer snowbed, **Solorina crocea - Oxyria digyna,** assemblage (low-slope M5, low-slope distal M6). These pioneer assemblages converge on a late-snow lichen heath, **Cetraria ericetorum - Stereocaulon alpinum,** assemblage which is not divided according to microtopography at this level. This assemblage is then succeeded, at the high-slope positions by a mature lichen heath, **Thamnolia vermicularis - Alectoria ochroleuca** (high-slope M1 and M3). The influence of microtopography appears to be greatest on the mature and young terrain and least on the early intermediate ground. This could be due to the relatively small size of moraines on the intermediate terrain and thus late-snow lie affecting the entire moraine (see Fig. 2.3).

At level four (blue) the succession proceeds from the two (level 2) pioneer assemblages to an early intermediate late-snow heath, **Cetraria nivalis - Cassiope hypnoides** assemblage (most of M2, M4 and low-slope M3). Two pathways proceed from the early intermediate late-snow heath, according to microtopography: the high-slope pathway proceeds to the (level 2) mature lichen heath and the low-slope pathway proceeds to a mature snowbed, **Cladonia gracillis - Salix herbacea,** assemblage. At (level 5) (green) the early intermediate late-snow heath group divides, according to microtopography, into a high-slope early intermediate lichen heath, **Cornicularia aculeata - Cetraria nivalis** assemblage (high-slope M2-4) and an early intermediate snowbed, **Cassiope hypnoides - Cladonia chlorophaea,** assemblage (low-slope M2-4 and distal toe-slope M5). As can be seen in Fig. 4.16, two simple successions can be seen across the foreland involving a high-slope successional sequence and a low-slope successional sequence at the fifth level of subdivision. Microtopography has a significant influence on the vegetation pattern on this foreland, but not as much as might be anticipated, possibly due to the small size of some of the moraines and the consistently late-snow lie found across most of the small moraine profiles (see Fig. 4.8). Vegetation patterns on the smaller moraines (M2 and M4) appear to contrast with those on the larger moraines as shown by the separation, at (level 3), of lichen heath assemblages on M1 and M3 (see Fig. 4.8). As with the lower altitude successions there is no convergence of assemblages onto the oldest terrain.

4.2.8 Succession at Bøverbreen

By referring to both Table 4.8 and also Fig. 4.17 it can be seen that at level three (red) the successional sequence is influenced by age and microtopography. The pattern of division is fairly similar to that of Høgvaglbreen with an exposed pioneer, **Cerastium alpinum,** assemblage (high-slope M5, proximal M6) and a pioneer snowbed, **Oxyria digyna - Poa alpina,** assemblage (low-slope M5, distal and crest M6) converging on a late-snow lichen heath, **Stereocaulon alpinum - Cladonia gracillis,** assemblage (low-slope M1-3 and M4). This group is succeeded by a high-slope exposed lichen heath, **Alectoria ochroleuca - Cornicularia aculeata** assemblage (crest, shoulder-slope M1-3).

At the fourth level (blue) the late-snow lichen heath divides into an early intermediate snowbed, **Trisetum spicatum - Gnaphalium supinum,** assemblage (low-slope proximal M2-3 and all M4) and a mature/late intermediate late-snow lichen heath, **Cetraria islandica - Cetraria ericetorum,** assemblage (low-slope or shoulder-slope M1-3). As can be seen in Fig. 4.17 the two pioneer assemblages converge to the early intermediate snowbed assemblage and then diverge, according to microtopography, to the (level 2) exposed lichen heath, at high-slope positions, and the mature/late intermediate late-snow lichen heath, at low-slope positions. It appears that microtopography is a significant influence on vegetation pattern on this foreland but especially so on the oldest and the youngest terrain. As with Høgvaglbreen, size of moraine could be a significant influence on the vegetation pattern. It is notable that M4 (comprising a snowbed assemblage in the low-slope proximal quadrats on M2-3) is a small and low moraine and so the anticipated high-slope and low-slope pathways are not distinct unless M4 is included with the low-slope snowbed sequence. It is then possible to follow a high-slope pathway between the pioneer high-slope assemblage and the mature/late intermediate high-slope assemblage (also see Fig. 4.18). As at Høgvalbreen, there is no convergence of assemblages onto the oldest terrain.

4.2.9 Summary of successional trends

In section 4.2 (Figs. 4.10 to 4.17) it was shown that there is a clear succession of assemblages, from pioneer to mature, on all forelands and the main influence on successional pathways described for each of the individual foreland data sets is age of ground. The succession is more complex at lower altitudes and it is necessary to divide the assemblages at higher TWINSPAN levels of subdivision (i.e. levels 5 and 6) in order to obtain groups which reflect the influence of microtopography on their distribution. Conversely the succession is simpler at higher altitudes and, most of the assemblages reflect the influence of microtopography at lower TWINSPAN levels of subdivision (i.e. levels 3 and 4).

These results show that the influence of microtopography on succession increases with altitude and this is revealed by the increasing number of assemblages that are associated with particular microtopographic positions at lower TWINSPAN levels of subdivision (i.e. levels 3 and 4). At Austerdalsbreen (Fig. 4.10) only the pioneer and mature terrain are separated from other assemblages at levels (3) and (4), according to position, and this suggests that microtopography may be more influential on pioneer and mature terrain (contrasting with much of the previous work reviewed in chapter (1)). At level (4) the successional pathway proceeds from three pioneer assemblages, with an exposed assemblage found on the crest of M7 and two snowbed assemblages found on the low-slope positions of M7, to an early intermediate heath assemblage on M3 to M6 and then to a late intermediate assemblage on M2. On M1 there are two assemblages, a level (4) birch heath and a distinct level (3) herb-rich meadow. At Austerdalsbreen there is a slight convergence of assemblages from the young terrain to the intermediate ground and then a slight divergence on the oldest terrain. It is clear that the dominant influence at Austerdalsbreen is time. At Fåbergstølsbreen (Fig. 4.11) only assemblages belonging to individual moraines are separated at level (3) and (4), according to microtopographic position, and the successional pathways are complex, possibly due to the debris flow that appears to have caused a break in the successional sequence on the site of the 1930 moraine, so that the vegetation on the 1930 moraine comprises pioneer assemblages. There are three pioneer assemblages, one distinct level (3) exposed pioneer and two level (4) pioneers and these proceed to an exposed lichen heath on M4 and an intermediate heath assemblage on low-slope positions on M4 and the whole of M3. This develops to a late intermediate heath on M2 and to birch woodland on M1. Interestingly, in contrast to the mature snowbed assemblage at Austerdalsbreen, the meadow assemblage at Fåbergstølsbreen separates at level (5) and thus is not distinct. This is possibly because the birch woodland, on the oldest terrain at Fåbergstølsbreen, is the dominant vegetation-type and the meadow vegetation is influenced (e.g. through shading, shelter and litter) by the full grown birch trees. In contrast, at Austerdalsbreen, birch trees are not important on the oldest terrain, probably due to previous grazing regimes. The mature vegetation appears to have differentiated to a greater extent according to microtopography, at Austerdalsbreen, and this supports the suggestion that trees, or tall shrub species, are likely to modify the underlying environment to a greater extent than low-growing meadow species (Sukachev & Dylis, 1964). At Fåbergstølsbreen the assemblages appear to converge from several pioneer assemblages to fewer mature assemblages. The separation of the M2 assemblages from M1 assemblages, on both subalpine forelands, suggests that succession is not complete after 250 years. It would also appear that both convergence and divergence of assemblage types is possible. The difference between the mature assemblages on the subalpine forelands supports the notion that birch woodland tends to cause a convergence in vegetation type but divergence can occur where disturbance, for example from grazing, reduces birch woodland cover.

At Storbreen all the final TWINSPAN site groups are separated at level (3) or (4) according to microtopography. The successional pathways for the low-alpine sequences are similar but slightly different, possibly due to the majority of the moraines within the Storbreen low (1) sequence being larger than those of the Storbreen low (2) sequence (see Table 3.15 and Figs. 4.4 and 4.5) so that the profiles are not as sharply defined and thus have a different snow duration - exposure regime (Figs. 3.4 and 3.5) and frost disturbance regime (Figs. 3.34-35 and 3.42-43). The high-slope succession (Storbreen low (l) sequence) proceeds from an exposed snowbed assemblage on the 1900 moraine to lichen heath assemblages on the intermediate ground to a late snow heath on the oldest terrain, whereas the high-slope positions, across the Storbreen low (2) sequence, proceeds through various lichen heath assemblages from the 1900 moraine to the oldest terrain. Late-snow heath appears to dominate the high-slope positions of the mature till-ridge of the Storbreen low (1) sequence, showing that the smoother profile of a large microtopographic feature may encourage a more even and persistent winter cover of snow whereas the smaller, more sharply defined mature till ridge crest of the Storbreen low (2) sequence is dominated by lichen heath, which is more tolerant of environmentally stressed conditions, suggesting that snow duration is not as persistent across the entire moraine profile. The low-slope position sequence, for both Storbreen low (1) and (2), proceeds from snowbed assemblages on the younger terrain through to late-snow heath or snowbed assemblages on the older ground. Low-slope positions, on the oldest terrain of the low-alpine sequence at Storbreen comprise snowbed assemblages.

The low-alpine sequences at Storbreen display parallel successional pathways from the early intermediate ground to the oldest terrain with a possible divergence of assemblages on the oldest terrain caused by microtopography - the mature assemblages belonging to each sequence are different and it is proposed that this may be due to the differences in size and shape of the mature till ridges causing the differential build up of winter snow. However, the number of moraines described for the two sequences at Storbreen was not considered enough to specifically consider the overall effects of size and shape of moraine on assemblage patterns (see section 7.7). Elven (1978), studying at Hardangerjøkulen in southern Norway, describes a slightly chionophilous (preferring some snow cover) *Empetrum* zone across low-alpine ridge tops, which fits in well with the "late-snow heaths" and "widespread heaths" shown in the present study and, in complete agreement with the present work, he outlines a strongly chionophobous (wind tolerant, snow intolerant) lichen heath dominated by, for example, *Cetraria nivalis, Cetraria cucullata* and *Alectoria ochroleuca*. He also describes snowbed assemblages consisting of many of the same chionophilous species that distinguish the snowbed assemblages in the present study (e.g. *Gnaphalium supinum* and *Veronica alpina*). His work supports the present work by suggesting that the difference in the type of assemblages found within the two sequences at Storbreen are likely to be due to differences in snow cover.

At Svellnosbreen a disturbed snowbed assemblage separated at the second level of subdivision, distorting the results so that all the other assemblages separated at the 4th and 5th level of subdivision (Fig. 4.14). This means that the assemblages, along the successional sequence, only separate according to microtopography at the 4th and 5th levels of subdivision. The high-slope sequence proceeds from an exposed pioneer assemblage found on high-slope positions of M5 and M6 to a heath assemblage on intermediate ground which then proceeds either to a late snow heath assemblage, on low-slope positions, or to lichen heath on high-slope positions. The successional pathway across the low-slope positions at Svellnosbreen appear to be especially influenced by fluvial disturbance so that the snowbed on M6 is associated with the snowbed on M1. The pathway appears to proceed from the exposed pioneer snowbed on M6 to a less disturbed snowbed on M6 to a late snow heath on the intermediate ground to an atypical snowbed on the oldest terrain. The sequence at Svellnosbreen is not as clear-cut as at Storbreen and there is some evidence for a certain amount of retrogression on this foreland (see section 7.4.3). There appears to be a convergence of assemblage types from the young terrain to the intermediate ground and then a divergence of assemblage types. The pattern of assemblages, on the oldest terrain, appear to be strongly influenced by microtopography - an effect possibly exaggerated by the use of a gully rather than a till ridge on the oldest terrain.

At Storbreen high all the assemblages separate according to microtopography at either level (3) or (4) suggesting that microtopography is an important influence on all the assemblages along the sequence. The successional pathway across high-slope positions is straightforward with an exposed pioneer assemblage on M8 proceeding to an intermediate lichen heath on M2 to M6 to a mature lichen heath on the mature till ridge. The low-slope successional pathway at Storbreen high is more complicated with evidence for a certain amount of retrogression (see section 7.4.3): a pioneer snowbed assemblage on M8 proceeds to a snowbed assemblage found on M6 and M7, but also on M2, and this proceeds to a late snow heath found only on intermediate ground or to an intermediate and mature late snow heath (see Fig. 4.15). There appears to be slight convergence of assemblage types from the pioneer and intermediate terrain to the mature terrain, but the pattern of assemblages on M1 is clearly influenced by microtopography.

At Høgvaglbreen, the mature and pioneer assemblages separate according to microtopography and they are very distinct with three out of four assemblages separating at level (3). However the assemblages on the intermediate ground do not separate until the 5th level and this may be due to the moraines being rather small and low with late snow-lie across the profiles, thus causing a greater similarity between assemblages found on low-slope positions and on the crests (see Fig. 4.16 and Fig. 4.8). The high-slope successional pathway proceeds from an exposed pioneer assemblage on M6 and M5 to an intermediate heath (at level 4) on M2 to M4 to a lichen heath at high-slope positions on M1 and M3 (showing a slight tendency towards retrogression). The low-slope successional pathway proceeds from a snowbed assemblage on M6 and M5 to the intermediate heath assemblage (at level 4) to a snowbed assemblage found mainly on M1, but also on M3 and M4 (also showing a slight tendency towards retrogression). The pathways at Høgvaglbreen show an initial convergence from the young terrain to the intermediate ground but then divergence to the oldest terrain. The assemblage patterns at Høgvaglbreen are most strongly influenced by microtopography on the pioneer and oldest terrain (contrasting with previous glacier foreland succession research). At Bøverbreen the successional pathways are simple and all the assemblages are mainly separated at level (3) or (4) according to microtopography. The exception being M4 which is a low and small moraine with an entire profile dominated by a snowbed assemblage and thus having a more persistent snow cover across the entire profile. This is likely to be the main reason why snow duration could be a more important environmental parameter than position (see also Fig. 5.16, 5.24, and sections 7.2-3). Interestingly the assemblages show a convergence of assemblage types from the young terrain to the intermediate ground and then a divergence of assemblage types to the late intermediate and the oldest terrain. As at Høgvaglbreen, the convergence on the intermediate ground is likely to have been caused by the intermediate-aged moraines being small and low. The pattern of assemblages on the oldest terrain is clearly influenced by microtopography.

These results are useful in that they have attempted to describe and elucidate, for the first time, the relative influence of altitude, age and microtopography on vegetation succession. Refer to chapter (7), and especially section 7.4, for a discussion of these results in relation to the influence of meso- and micro-environmental parameters on succession. The main trends are as follows:

1. Vegetation patterns appear to be influenced primarily by altitude, age and microtopography (and their accompanying environmental factors) in that order.
2. There is a clear succession of plant assemblages, from pioneer to mature, on all forelands and the main influence on succession on each of the forelands is terrain-age.
3. The succession is relatively complex at lower altitudes and it is necessary to separate the assemblages at levels (5) and (6), of the TWINSPAN divisions, in order to obtain ecologically meaningful groups.
4. The succession is simpler at higher altitudes, with fewer assemblages, and, generally, the assemblages are separated at levels (3) and (4) in order to obtain ecologically meaningful groups.
5. In general, the successions support the premise that the assemblages, during the course of succession, do not converge towards a monoclimax (*sensu*: Clements, 1916). However, there appear to be several ecologically meaningful assemblages at both the pioneer and mature stages which differs from those who propose divergence, from one pioneer assemblage to several mature types (e.g. Matthews, 1979).
6. Generally, at most altitudes, the assemblages are most distinct (least variable, with the highest eigenvalues) on the youngest terrain and the mature terrain, and least distinct on the early intermediate ground. This may be due to the differences in adaptations of "pioneer" species, to high environmental stress, and adaptations of "mature" species, to competition, so that these two vegetation-types tend not to

occur together. The intermediate terrain, logically, would comprise both types of species as one supersedes the other.

7. The influence of microtopography on succession appears to increase with altitude as can be seen by the greater number of assemblages, that are separated according to microtopography, on the alpine forelands.
8. By looking at the preferential species and primary indicators of each of the assemblages there appears to be an overlap of species between the assemblages. Thus the assemblages can be said not to occur in restricted communities rather they appear to occur as a gradient of continually changing patterns of species populations.

4.3 Introduction to individual foreland TWINSPAN species groups and charts

The TWINSPAN "final species groups" provide useful additional information to the TWINSPAN site data because the distribution of all the species within the data set is elucidated. The species data also shows the direct relationship between each species in terms of assemblage formation and also whether the assemblages appear to be "loose" (so that there is not a significant relationship between species) or "tight" (so that there appears to be a significant relationship between the species). Furthermore the effects of altitude, age and microtopography on the individual species and assemblages also can be clarified. The aims of presenting the species data are as follows and are the same for the combined data set (see section 6.5):

1. To examine and display the way in which the species are grouped together into assemblages.
2. To describe the relationship between individual species within each of the assemblages - i.e. whether the assemblages are loose (species distantly related) or tight (species closely related).
3. To describe the distribution of these assemblages on each foreland.
4. To compare the assemblages and their preferred location between forelands
5. To provide species groups for further analysis.

The descriptions refer to the TWINSPAN final tables (Appendix 4.1 to 4.8) and to the TWINSPAN "final species group" charts (Figs. 4.18 to 4.92) which show the distribution and % cover of each of the species within each of the species groups (final assemblages) across each of the forelands. The separate species, within each TWINSPAN "final species group", are not differentiated on these black and white distribution charts (i.e. Figs. 4.18 to 4.92). Large final assemblages, comprising more than 12 species, are split between at least two charts as "Microsoft Excel" can not combine more than 12 species within one chart. The "final species groups" have been separated according to the clearest and most ecologically meaningful groups on each TWINSPAN final table (Kent and Coker, 1992). Included with the list of species for each "final species group" is the TWINSPAN species group number; the level of subdivision; the eigenvalue (see glossary); and a brief description of the position of the species across the moraines and foreland.

Any affiliation between the assemblages from the site groups (see section 4.1 and Table 4.9) and the assemblages from the species group (section 4.3), is identified (at the most appropriate level) according to where they are situated on the moraines and foreland. The reason for doing this is to be able to relate the "final site groups" to the environmental parameters found to be associated with the "final species groups" through the DCA analysis in chapter (5). The position colour code, for the TWINSPAN "final species groups" is also given, in writing and if there is more than one group found at a particular position-type then an open (☐) box as well as a closed (■) box is used in the appropriate colour (see over page).

The position colour code for the TWINSPAN "final species groups" assemblages is as follows:

🟦 **Dark blue** - Low-slope positions mainly on older ground (mature snowbed or late-snow heath)

🟦 **Light blue** - Low-slope positions mainly on early intermediate ground (early intermediate snowbed or late-snow heath)

▨ **Blue-white** - Low-slope positions (snowbeds in general)

🟩 **Dark green** - Any positions mainly on older ground (mature heath or woodland)

▨ **Mustard** - Any positions mainly on early intermediate ground (early intermediate heath)

▨ **Purple** - Any position on early intermediate and young terrain (exposed or early intermediate heath)

🟥 **Pink** - Mainly younger ground (pioneer)

🟫 **Red** - High-slope positions of any age (dry lichen heath)

🟨 **Brown** - High-slope positions and/or exposed positions on young terrain (dry heath or pioneer)

⬜ **Yellow** - Widespread, any positions (non-selective species)

Yellow-white - Widespread, any positions (non-selective species)

4.3.1 Austerdalsbreen (Altitude: 290-380m. Aspect: southerly)

According to the TWINSPAN final table (Appendix 4.1), the TWINSPAN "final site group" summary table (Table 4.9), and the "final species group" charts (Figs. 4.19 to 4.27), the division of the assemblages is fairly clear in terms of terrain age. The mature and pioneer assemblages are distinct and have tight distributions on the older and younger moraines respectively. The assemblages found on the early intermediate terrain tend not to be distinct at either limit of their range and species within those assemblages tend to overlap onto mature and young terrain. There are more mature assemblages than pioneer assemblages and their limits tend to be influenced more by terrain-age than by microtopography. The only assemblages that appear to be related to microtopography are a number of low-slope snowbed assemblages.

<u>Species group (8): pioneer assemblage (eigenvalue 0.181)</u>

58 Car spp; 81 Ste bot; 83 Phl Alp; 84 Sax ste; 85 Sax ste; 86 Ste ves; 44 Ste alp.

This assemblage (Fig. 4.18) is a tight pioneer group (sites 117 to 109). *Stereocaulon alpinum* is the most widespread species, but does not occur on later ground or mature sites. There is a affiliation between this group and the (level 4) exposed pioneer **Stereocaulon alpinum - Stereocaulon vesuvianum** assemblage. (position colour code - pink)

Species group (9): early intermediate heath assemblage (eigenvalue 0.175)

5 Bet pub; 27 Cla gra; 45 Cla por; 46 Cla chl; 42 Sal phy; 80 Ath dis; 82 Oxy dig.

This assemblage (Fig. 4.19) forms a tight group on M3-6 and has a loose distribution on M2 and M7, but not significantly on the mature till ridge. This group corresponds with the (level 3) early intermediate heath **Betula pubescens - Calluna vulgaris** assemblage (position colour code - purple)

Species group (68): early intermediate heath assemblage (eigenvalue 0. 043)

51 Eup hel; 55 Vac vit; 57 Arc alp; 59 Cet eri; 60 Ste con; 61 Lou pro; 62 Cla car; 64 Cla ver; 65 Sol cro; 66 Cla ran; 67 Cla arb; 68 Cla def; 69 Cla pyx; 70 Cla ama; 71 Cla bel; Cla sul; 73 Cla ple; 74 Cla cri; 75 Pel pol.

This assemblage (Fig. 4.20) occurs at low-slope positions on M3 and M4 with a loose distribution on proximal high-slope sites on M3 to M6. There is an affiliation between this group and the (level 6) exposed lichen heath **Solorina crocea** assemblage. (position colour code - light blue)

Species group (69): early intermediate late-snow heath (eigenvalue 0.043)

3 Cal vul; 52 Lis cor; 53 Lyc ann; 54 Jun tri; 76 Des ces; 77 Aln glu; 78 Sal lan; 79 Lot cor; 87 Ver alp; 88 Pyr nor.

This loose assemblage (Fig. 4.21) occurs at low-slope sites on M4 to M7. *Calluna vulgaris* is the most widespread member. There is an affiliation between this group and the (level 5) early intermediate late-snow heath **Vaccinium myrtillus - Betula pubescens** assemblage. (position colour code - light blue open box)

Species group (35): early intermediate heath (eigenvalue 0.061)

48 Cla dig; 56 Pin vul; 63 Cla cer.

This is a loose assemblage (Fig. 4.22) across M4 to M7. There is an affiliation between this group and the (level 5) early intermediate late-snow heath **Vaccinium myrtillus Betula pubescens** assemblage. (position colour code - mustard)

Species group (5): widespread heath (eigenvalue 0.292)

25 Cet isl; 26 Cla squ; 1 Emp nig; 2 Phy cae; 47 Cla con.

This assemblage (Fig. 4.23) has a tight occurrence of species on M2 to M6, and a loose occurrence on pioneer and mature terrain. It has an affiliation with the (level 3) early intermediate heath **Betula pubescens - Calluna vulgaris**, assemblage. (position colour code - yellow)

Species group (6): widespread snowbed (eigenvalue 0.260)

30 Cla fim; 34 Sal her; 35 Pyr min

This assemblage (Fig. 4.24), occurs at low-slope positions on all terrain-ages except the mature till-ridge. This group has an affiliation with several "final site group" snowbed assemblages. (position colour code - blue-white)

Species group (14): late intermediate snowbed (eigenvalue 0.230)

4 Sal gla; 31 Alc alp; 39 Fes ovi; 6 Vac uli; 7 Vac myr; 14 Ant odo; 15 Des fle

This assemblage (Fig. 4.25) has a tight distribution on M1-2, and it also occurs on M3 to M6, especially at low-slope positions. It has an affiliation with several early intermediate and late intermediate snowbed assemblages. (position colour code - dark blue)

Species group (30): late intermediate heath (eigenvalue 0.149)

23 Sor auc; 18 Des alp; 36 Leo aut; 37 Sib pro; 38 Sol vir; 40 Bet nan; 41 Ran spp; 43 Mel pra; 49 Cla unc; 50 Lyc sel; 10 Ath dis; 11 Jun fil; 12 Vio bif; 16 Tri eur.

This assemblage (Fig. 4.26) occurs on M2 and loosely on M1. This group is affiliated to the (level 4) late intermediate heath, **Salix glauca - Salix herbacea,** assemblage. (position colour code - dark green)

Species group (31): mature heath (eigenvalue 0.149)

9 Mel syl; 19 Luz arc; 13 Pot cra; 17 Rum ace; 8 Cor sue; 21 Lyc cla; 22 Nar str; 24 Cla hyd; 28 Sor cup; 29 Cla lon; 32 Oxa ace; 33 Gna nor.

This tight assemblage (Fig. 4.27) occurs mainly on the mature till-ridge, although *Melampyrum sylvaticum* and *Luzula arcuata* occur on M2. This group is affiliated with the (level 3) mature meadow, **Athyrium distentifolium - Potentilla crantzii,** assemblage. (position colour code - dark green open box)

4.3.2 Fåbergstølsbreen (Altitude: 460-630m. Aspect: easterly)

According to the TWINSPAN final table (Appendix 4.2), the TWINSPAN "final site group" summary table (Table 4.9), and the "final species group" charts (Figs. 4.28 to 4.38), the separation of the plant assemblages across this foreland is greatly influenced by age. None of the assemblages have a widespread range, across all the moraines, which corresponds with the "final site group" results for this foreland. However, some of the assemblages occur across four out of six moraines: two assemblages occur on intermediate and young terrain; two assemblages occur on intermediate and mature terrain; and one assemblage occurs on young and mature terrain. The latter is difficult to place in the position colour-coding system but it has been nominated as yellow (yellow is used for assemblages that show a widespread distribution across forelands). There are a greater number of pioneer assemblages than mature assemblages, but the occurrence of two distinct mature assemblages lends support to the refutation of convergence to a monoclimax. The influence of microtopography on this foreland is limited to the occurrence of a few snowbed assemblages found at low-slope positions. According to the eigenvalues, the assemblage with the strongest affiliation between members is the pioneer snowbed assemblage, but otherwise the "final species group" assemblages are not very distinct.

Species group (8): early intermediate heath (eigenvalue 0.194)

48 Cla arb; 62 Ste alp.

This assemblage (Fig. 4.28) occurs on M3 to M6. These two species have been separated from group (36) because of their frequent occurrence on both younger and early intermediate terrain. This assemblage has an affiliation with several "final site groups" on the early intermediate and young terrain. (position colour code - purple)

Species group (36): early intermediate lichen heath (eigenvalue 0.076)

47 Cla ran; 49 Cla por; 6 Cal vul; 41 Cla cri; 42 Cal squ; 46 Cla gra; 51 Cla bel; 54 Cla crc; 55 Cla ama; 56 Cla dig; 57 Cla fur; 59 Cla ste; 60 Bro cup; 64 Cet cuc.

This assemblage (Fig. 4.29) occurs largely on M3 and M4 and to a lesser extent on younger terrain (M5 to M6). The assemblage is absent from the three crest sites on M4 suggesting that this assemblage is more susceptible to exposed or drier conditions. This group has an affiliation with the (level 4) early intermediate heath, **Betula pubescens - Calluna vulgaris,** assemblage. (position colour code - mustard)

Species group (37): early intermediate lichen heath (eigenvalue 0.076)

38 Cla fim; 40 Cla chl; 58 Cla ple; 63 Ste pas; 44 Cla coc; 45 Cla con; 50 Cla sbf; 52 Cla car; 65 Cla pyx; 66 Ste bot; 67 Bla cup; 68 Sol cro; 69 Cla ver.

This assemblage (Fig. 4.30) occurs almost exclusively on M3 and M4. It has a tight distribution on three high-slope sites on M4, suggesting a drier more exposure-resistant lichen heath. This group has an affiliation with the (level 4) exposed lichen heath **Cladonia chlorophaea - Cladonia fimbriata** assemblage. (position colour code = mustard open box)

Species group (19): widespread heath (eigenvalue 0.161)

2 Vac uli; 3 Vac vit; 4 Emp nig; 5 Phy cae; 7 Bet pub; 18 Mel syl.

This assemblage (Fig. 4.31) has a tight occurrence on M2 to M4 although not on the three high-slope sites on M4, (except *Empetrum nigrum*). It does, however, occur on the M2 crest. Most of this assemblage thins out on M1, although *Betula pubescens* and *Melampyrum sylvaticum* are abundant. *Betula pubescens* also occurs on some early intermediate sites. This group has an affiliation with the (level 3) early intermediate heath, **Calluna vulgaris - Empetrum nigrum,** assemblage. (position colour code - yellow-white)

Species group (20): mature heath (eigenvalue 0.108)

1 Vac myr; 11 Luz arc; 9 Sor cup; 37 Cer spp; 43 Str cup

This assemblage (Fig. 4.32) has a tight occurrence on M1, and is loose on the M2 crest and on M3 and M4. *Sorbus aucuparia* occurs exclusively on M1 and M2. This group has an affiliation with the (level 3) mature woodland, **Vaccinium myrtillus - Deschampsia flexuosa,** assemblage. (position colour code - dark green)

Species group (21): mature woodland (eigenvalue 0.108)

22 Tri eur; 25 Ger syl; 34 Pri spp; 35 Rub ida; 8 Jun com; 14 Ant odo; 16 Cor sue; 17 Pot cra; 19 Par pal; 23 Pol viv; 32 Vio bif; 20 Gym dry.

This mature assemblage (Fig. 4.33) occurs exclusively on M1 and the three low-slope and distal sites on M2. This group has an affiliation with the (level 4) mature birch woodland, **Vaccinium myrtillus - Gymnocarpium dryopteris,** assemblage. (position colour code - dark blue)

Species group (11): heath (eigenvalue 0.224)

12 Des fle; 15 Nar str; 24 Sol vir; 39 Pel pol.

This assemblage (Fig. 4.34) occurs mainly on M1 and M2 , but also on the youngest terrain, with a few rare occurrences on M3 and M4. This group does not have any particular affiliation with any of the assemblages from the "final site groups". (position colour code - yellow)

Species group (12): heath (eigenvalue 0.228)

31 Ort sec

This species (Fig. 4.35) contrasts with the distribution of species group (11) in that it occurs mainly on the youngest moraines, although it also occurs on M1. This species shows some affiliation with pioneer "final site group" assemblages. (Position colour code - yellow open box)

Species group (26): pioneer snowbed (eigenvalue 0.063)

36 Lot cor; 82 Uln gla; 77 Hie spp; 72 Gna nor; 75 Lot cor; 78 Phl alp; 80 Sag sag.

This assemblage (Fig. 4.36) is tightly distributed on the six low-slope sites (distal and proximal) on M5. The assemblage loosely occurs on the remainder of the youngest ground. This group has an affiliation with the (level 4) pioneer snowbed, **Lotus corniculatus - Salix phylicifolia,** assemblage. (position colour code - pink open box)

Species group (27): pioneer (eigenvalue 0.063)

70 Cet isl; 76 Cry cri; 84 Cer alp; 86 Fes ovi; 87 Epi ang; 13 Des alp; 26 Ath dis; 33 Car spp; 73 Gna sup; 74 Oxy dig; 71 Cer cer; 79 Agr ten; 81 Luz spi; 83 Epi als; 29 Alc alp; 85 Sax ste; 88 Rus spp; 89 sib pro

According to Fig. 4.37, *Cerastium cerastoides, Agrostis tenuis, Luzula spicata* and *Epilobium alsinifolium* form a tight group occurring on most of the youngest sites. *Alchemilla alpina* and *Saxifraga stellaris* occur on exposed sites and the rush species and *Sibbaldia procumbens* occur on the youngest terrain. Otherwise, the rest of the members of this assemblage occur loosely on M5 and M6. This group has an affiliation with the (level 2) pioneer, **Agrostis tenuis - Deschampsia alpina,** assemblage. (position colour code - pink)

Species group (7): pioneer snowbed (eigenvalue 0.377)

10 Sal phy; 53 Sal gla; 61 Sal her.

This assemblage occurs at low-slope positions on M4-6. The group has an affiliation with the (level 4) pioneer snowbed, **Lotus corniculatus - Salix phylicifolia,** assemblage. (position colour code - blue-white)

4.3.3 Storbreen low (1) (Altitude: 1140-1200m. Aspect: north-easterly)

According to the TWINSPAN final table (Appendix 4.3), the TWINSPAN "final site group" summary table (Table 4.9), and the "final species group" charts (Fig. 4.39 to 4.48), the separation of the plant assemblages across this foreland is not as strongly age-related as it is on the subalpine forelands. This is possibly because the youngest moraine dates from 1900 and so the vegetation on M5 and M6 has had between 30 and 60 years longer to develop than the vegetation on the youngest moraines on other forelands. However, the reason for the reduced influence of age could also be that the relative importance of factors other than age, such as microtopography, are more influential on vegetation patterns at higher altitudes. The influence of microtopography on the separation of the assemblages is more noticeable on this foreland, than it is at lower altitudes, so that assemblages at exposed sites (e.g. the lichen heath assemblages) separate from other assemblages according to slope position. Nevertheless, the separation of the mature assemblages, from the early intermediate assemblages, shows that the influence of age and microtopography have a combined influence on the assemblage divisions across the Storbreen low (1) sequence. The patterns displayed by the "final species groups" correspond with those shown by the "final site groups".

Species group (8): mature heath (eigenvalue 0.324)

55 Sph glo; 84 Sil aca; 5 Lou pro; 6 Vac vit; 29 Jun tri; 31 Lyc sel; 35 Ste pas; 47 Cet ste; 9 Jun com; 16 Vio bif; 21 Tri eur; 24 Des fle; 30 Lyc alp; 40 Cla ama; 43 Cla squ; 57 Cla alp; 83 Cla ca; 90 Coe vir; 3 Vac myr; 14 Hie alp; 7 Cal vul; 17 Gna sup; 20 Sib pro; 28 Car spp.

This assemblage (Fig. 4.39) is quite tightly distributed on M1. It also has a loose distribution on low-slope sites on early intermediate and young terrain. This group has an affiliation with the (level 3) heath **Betula nana - Cetraria nivalis** assemblage. Note that species (83) and (90) are present on the main TWINSPAN classification list but are absent from the group listed in the TWINSPAN final table (Appendix 4.3). (position colour code - dark green)

Species group (9): late intermediate snowbed (eigenvalue 0.324)

19 Ant alp; 12 Sed ros; 13 Leo aut; 18 Gna nor; 22 Sol vir; 23 Rum ace; 88 Tof pus; 15 Pol viv; 61 Jun com; 63 Eup fri; 70 Ran acr; 71 Pot cra; 72 Cam rot; 74 Alc alp; 76 Agr ten; 87 Pet fri; 91 Luz arc; 89 Ped lap; 25 Ant odo; 62 Pyr min; 66 Tar off; 73 Bar alp; 4 Vac uli.

This assemblage (Fig. 4.40 a,b) is quite tightly distributed in low-slope quadrats of M2 and M3 and is loosely distributed in other low-slope quadrats. This group has an affiliation with the (level 3) late intermediate snowbed, **Salix glauca - Anthoxanthum odoratum,** assemblage. Note that species (89) is missing from the TWINSPAN final table (Appendix 4.3) but not from the main TWINSPAN list. (position colour code - dark blue)

Species group (10): mature late-snow heath (eigenvalue 0.310)

27 Fes ovi; 11 Bet nan; 38 Cla ran; 42 Cla gra; 53 Tha ver.

This assemblage (Fig. 4.41) is tightly distributed on M1 and at some low-slope positions (especially proximal slope) on M2-4 and it has a loose distribution on other low-slope sites. This group has an affiliation with the (level 4) mature late-snow heath, **Festuca ovina - Salix herbacea,** assemblage. (position colour code - dark blue open box)

Species group (11): early intermediate heath (eigenvalue 0.310)

37 Cla por; 50 Cet isl; 81 Pel pol; 39 Cla arb; 48 Cet del; 86 Sal phy.

This assemblage (Fig. 4.42) is distributed across the entire foreland except on proximal low-slope sites on M5-6 and crest sites on M6. This group has an affiliation with the (level 4) early intermediate lichen heath, **Phyllodoce caerula - Cladonia portentosa,** assemblage. (position colour code - light blue)

Species group (12): widespread snowbed (eigenvalue 0.321)

45 Cla sul; 49 Cet eri; 56 Nep arc; 10 Sal her; 26 Des cae; 64 Ver alp; 65 Pin vul.

This assemblage (Fig. 4.43) occurs on low-slope sites. *Salix herbacea* is abundant at all sites across M1. This group has an affiliation with the (level 3) heath, **Betula nana - Cetraria nivalis,** assemblage. (position colour code - blue-white)

Species group (13): widespread heath (eigenvalue 0.321)

78 Cla unc; 85 Sal lan; 1 Emp nig; 2 Phy cae; 44 Cla con.

Most of the members of this assemblage (Fig. 4.44) are abundant across the foreland but *Cladonia uncialis* and *Salix lanata* are more plentiful in low-slope quadrats. This group has an affiliation with several of the snowbed assemblages from the "final site groups". (position colour code - yellow)

Species group (28): late-snow early intermediate heath (eigenvalue 0.299)

32 Ste alp; 36 Cla chl; 8 Cas hyp; 33 Ste bot; 60 Sal gla; 82 Pso hyp.

This assemblage (Fig. 4.45) is abundant across the whole foreland but is especially tightly distributed on M6 and low-slope quadrats on M5 and the proximal or high-slope quadrats on M2-5. This group has an affiliation with the (level 4) late-snow early intermediate heath, **Empetrum nigrum - Stereocaulon alpinum,** assemblage. (position colour code - purple)

Species group (29): early intermediate snowbed (eigenvalue 0.299)

75 Luz spi; 67 Lis cor; 68 Cla ver; 94 Tri spi; 96 Sph fra; 97 Pan pez; 99 Bet pub; 69 Sph mel; 77 Poa alp; 100 Car pet; 103 Cer cer; 104 Car bel; 106 Cla sym.

This assemblage (Fig. 4.46) occurs on M6, and is loosely distributed on low-slope sites on M5 and the proximal slope of M4. This group has an affiliation with the (level 3) early intermediate snowbed, **Salix glauca - Salix herbacea,** assemblage. Note (106) is missing from the TWINSPAN final table but not from the TWINSPAN classification list. (position colour code - purple open box)

Species group (30): Exposed early intermediate snowbed (eigenvalue 0.253)

52 Sol cro; 101 Oxy dig; 105 Cla cen..

This assemblage (Fig. 4.47) is found on younger and/or exposed terrain and only *Solorina crocea* is abundant. This group has an affiliation with the (level 4) exposed early intermediate snowbed, **Salix glauca - Salix herbacea,** assemblage. (position colour code - brown)

Species group (31): exposed lichen heath (eigenvalue 0.253)

46 Cet niv; 51 Cet cuc; 58 Arc alp; 59 Arc uva; 80 Ale cha; 92 Cor div; 93 Ale och; 98 Ale nig; 34 Ste con; 41 Cla cri; 54 Cor acu; 79 Cla cer; 102 cer alp; 95 Cla pyx.

This assemblage (Fig. 4.48) is distributed on the high-slope sites on M2-5. It has a looser distribution on mid-slope sites on M2-4 and also the crest site on M1. *Cetraria nivalis* also occurs on other young sites. This group has an affiliation with the (level 4) exposed lichen heath, **Alectoria ochroleuca - Cetraria cucullata,** assemblage. Note (102) and (95) are missing from the TWINSPAN final table but are included on the TWINSPAN classification list. (position colour code - red)

4.3.4 Storbreen low (2) (Altitude: 1140-1200m. Aspect: north-easterly)

According to the TWINSPAN final table (Appendix 4.4), the TWINSPAN "final site group" summary table (Table 4.9), and the "final species group" charts (Fig. 4.49 to 4.58), the influence of microtopography and age on vegetation pattern is noticeable. These results correspond closely with those of the Storbreen low (1) sequence of transects. There are several mature assemblages, suggesting that the hypothesis that assemblages converge to a monoclimax on the oldest terrain should be rejected. In addition, many of the assemblages, apparently associated with microtopographical position, are distinct. The influence of microtopography on the division of the assemblages is therefore noticeable, with several assemblages occurring at similar positions across a wide age-range of moraines. Despite the similarities between the two sequences across the Storbreen low foreland, there are also differences between the two sequences. This could be due to a complex combination of factors including differences in moraine-size, as well as other topographical factors such as proximity to rivers and position on the foreland. These differences will be discussed in more detail in the concluding chapter (7).

Species group (30): late intermediate snowbed (eigenvalue 0.205)

113 Cer cer; 100 Cla bel; 84 Ran pyg; 76 Sau alp; 75 Gym dry; 74 Mel rub; 73 Sib pro; 70 Gna nor; 39 Luz tri; 26 Ran acr; 23 Sol vir; 20 Tar spp; 29 Sed ros; 27 Vio bif; 22 Pol viv; 19 Tri eur; 15 Car spp.

This assemblage (Fig. 4.49) is tightly distributed on the distal slope of M2 and low-slope quadrats on M1. It is loosely distributed in distal or low-slope quadrats on M3-4 and at other positions on M1-2. This group has an affiliation with the (level 3) late intermediate snowbed, **Salix herbacea - Ranunculus acris,** assemblage. (position colour code - dark blue)

Species group (31): late-snow late intermediate heath (eigenvalue 0.205)

108 Lis cor; 38 Nar str; 32 Pyr min; 28 Ver alp; 24 Ped lap; 21 Leo aut; 105 Sil aca; 104 Squ cup; 40 Des alp; 33 Eup fri; 25 Ped spp; 18 Jun spp; 30 Bar alp.

This is a loose assemblage (Fig. 4.50) on proximal or low-slope quadrats on M2-3. This group has an affiliation with the (level 4) late-snow late intermediate heath, **Salix glauca - Vaccinium uliginosum,** assemblage. (position colour code -dark blue open box)

Species group (14): mature lichen heath (eigenvalue 0.283)

60 Cla squ; 48 cla gra; 46 Cla unc; 45 Cla ran; 44 Cla arb; 42 Ste bot; 107 Tof pus; 43 Cla por; 49 Cla cri; 10 Vac uli; 58 Cla alp; 36 Hie alp; 35 Lyc alp; 17 Des fle; 9 Vac myr; 3 Bet nan; 64 Cla sul; 62 Far red; 59 War gra; 52 Cla con; 50 Cla ama; 47 Cla ste; 31 Vac vit; 14 Jun tri; 8 Cal vul.

This assemblage (Fig. 4.51 a,b) has a tight occurrence on the mature till-ridge and is fairly tight in low-slope quadrats on M3. It has a loose distribution on all other moraines. This group has an affiliation with the (level 4) mature lichen heath, **Cladonia arbuscula - Cetraria ericetorum,** assemblage. (position colour code - dark green)

Species group (6): early intermediate snowbed (eigenvalue 0.373)

37 Phl alp; 34 Gna sup; 13 Ant odo; 71 Rum ace; 12 Fes ovi; 65 Cla fur; 55 Cet isl; 4 Jun com; 106 Pin vul; 16 Luz spi.

This assemblage (Fig. 4.52) occurs loosely on all moraines, but is most prevalent on the proximal slope of M2 and low-slope sites on M3-6. It is not found at all on crest sites and is infrequent on M1. This group has an affiliation with the (level 4) early intermediate snowbed, **Cassiope hypnoides - Salix herbacea,** assemblage. (position colour code - light blue)

Species group (10): exposed early intermediate lichen heath (eigenvalue 0.430)

109 Ste spp; 81 Oxy dig; 6 Phy cae; 77 Cer alp; 66 Tri spi; 56 Cet eri; 51 Cla fim.

This assemblage (Fig. 4.53) is fairly tight at high-slope sites (but not crest positions) on M2, and M4-6. This assemblage occurs loosely on most other sites, but infrequently on mature sites and exposed crest sites. This group has an affiliation with the (level 4) exposed early intermediate lichen heath assemblage **Cladonia chlorophaea - Cetraria nivalis**. (position colour code - purple)

Species group (11): widespread heath (eigenvalue 0.430)

57 Pel pol; 5 Emp nig; 1 Sal gla.

This assemblage (Fig. 4.54) occurs on all moraines, but *Peltigera polydactyla* does not occur on young or exposed terrain and has a low cover on other moraines. This group has an affiliation with several "final site group" assemblages. (position colour code - yellow)

Species group (18): early intermediate lichen heath (eigenvalue 0.210)

86 Ste con; 63 Cla chl; 61 Cla dig; 41 Ste alp.

This assemblage (Fig. 4.55) is tight on M4-6 and especially on high-slope quadrats. It has a loose distribution on M1 and low-slope quadrats. This group has an affiliation with the (level 4) exposed early intermediate lichen heath, **Cladonia chlorophaea - Cetraria nivalis,** assemblage. (position colour code - brown open box)

Species group (19): early intermediate snowbed (eigenvalue 0.210)

82 Ant alp; 69 Sal phy; 112 Car bel; 111 Lyc sol; 7 Cas hyp; 95 Pan pez; 89 Sph fra; 67 Poa alp; 2 Sal her.

This assemblage (Fig. 4.56) occurs mainly at low-slope positions on M2 (proximal slope), and M4-6. It is a loose assemblage on M2 and also at low-slope positions on M3. This assemblage is infrequent at crest positions or mature terrain. This group has an affiliation with the (level 4) early intermediate snowbed, **Cassiope hypnoides - Salix herbacea,** assemblage. (position colour code - blue-white)

Species group (16): exposed lichen heath (eigenvalue 0.218)

78 Car pet; 79 Sal lan; 54 Cet cuc; 53 Cet niv; 110 Sph glo; 101 Tha ver; 93 Cor acu; 92 Cor div; 91 Ale nig; 90 Ale och; 83 Lou pro; 11 Arc alp.

This assemblage (Fig. 4.57) has a tight distribution at crest positions on M2-6. It also occurs on other high-slope quadrats on the younger moraines. Some members of this assemblage occur very loosely on low-slope sites on the younger moraines and also on the mature till-ridge, notably *Cetraria cucullata* and *Cetraria nivalis*. This group has an affiliation with the (level 3) exposed lichen heath, **Cetraria nivalis - Alectoria ochroleuca,** assemblage. (position colour code - red)

Species group (17): exposed early intermediate heath (eigenvalue 0.218)

94 Pso hyp; 116 Dry oct; 103 Cla ple; 102 Cla car; 96 Cla fri; 88 Cet del; 80 Arc uva; 99 Cla ver; 98 Cla cer; 115 Gre Cla; 114 Sag sag; 97 Cla pyx; 85 Sol cro.

This is a fairly loose assemblage (Fig. 5.58), occurring mainly on high-slope quadrats on younger terrain. It is not prevalent on M2-3, or at crest positions, and does not occur on M1. This group has an affiliation with the (level 4) exposed early intermediate lichen heath, **Cladonia chlorophaea - Cetraria nivalis,** assemblage. (position colour code - brown)

4.3.5 Svellnosbreen (Altitude: 1280-1440m. Aspect: south-easterly)

According to the TWINSPAN final table (Appendix 4.5), the TWINSPAN "final site group" summary table (Table 4.9), and the "final species group" charts (Fig. 4.59 to 4.69), the division of the assemblages across this foreland is not distinct at the lower levels of subdivision (i.e. levels 3 and 4). Many of the assemblages are loose and have a fairly widespread distribution across the foreland, possibly due to the large altitudinal range on this foreland or due to greater levels of disturbance on the older ground caused by solifluction and fluvial activity (see chapter (3)). Microtopography appears to be an important influence even at lower levels of subdivision. There are several mature assemblages but they are not distinct, the tightest assemblages are the snowbed assemblages and the pioneer assemblages which refutes the hypothesis (Margalef, 1968) that assemblages are more distinct with age. These results are discussed at greater length in chapter (7).

Species group (7): exposed pioneer snowbed (eigenvalue 0.318)

100 Cer cer; 92 Des alp.

This assemblage (Fig. 4.59) occurs on M6 and crest quadrats on M5. This group has an affiliation with the (level 2) exposed pioneer snowbed, **Deschampsia alpina - Oxyria digyna** assemblage. (position colour code - pink)

Group (13): widespread snowbed (eigenvalue 0.182)

27 Tar spp; 16 Sal her.

Salix herbacea is found on low-slope quadrats on all moraines except M6. *Taraxacum spp* occurs in low-slope quadrats in the mature terrain gully. This assemblage (Fig. 4.60) has an affiliation with the (level 4) atypical snowbed, **Salix herbacea - Empetrum nigrum,** assemblage. (position colour code - blue-white)

Species group (25): mature snowbed (eigenvalue 0.093)

39 Rum ari; 38 Pol viv; 37 Gna sup; 36 Gna nor; 32 Sib pro; 31 Pyr nor; 30 Ger syl; 29 Alc glo; 28 Leo spp; 26 Ran niv; 15 Sed ros; 14 Ver alp; 61 Cla cen; 41 Cet isl; 34 Vac myr; 33 Sol vir; 18 Hie spp; 17 Lyc alp; 13 Cal vul; 107 Sax ste; 24 Car spp; 23 Ant odo; 22 Fes ovi.

This assemblage (Fig. 4.61 a,b) occurs in low-slope quadrats on M1 and the distal slope of M2. It also has a loose distribution on M6 and a very loose distribution on low-slope quadrats on all other moraines. This group has an affiliation with the (level 4) atypical snowbed, **Salix herbacea - Empetrum nigrum,** assemblage. (position colour code - dark blue)

Species group (24): mature late-snow heath (eigenvalue 0.093)

47 Pel pol; 45 Cla gra; 12 Ane ver; 4 Jun com; 3 Ant dio; 1 Vac vit; 49 Cla ama; 44 Sol cro; 60 Cla dig; 35 Bar alp.

This assemblage (Fig. 4.62) is concentrated in low-slope quadrats on M1 and on the distal slope of M2. It has a loose distribution on all other moraines except M6. This group has an affiliation with the (level 4) atypical snowbed, **Salix herbacea - Empetrum nigrum,** assemblage. (position colour code - dark green)

Species group (11): early intermediate heath (eigenvalue 0.157)

46 Ste alp; 103 Cla bel; 48 Cla cer; 21 Cas hyp; 11 Ant alp; 42 Cla por; 40 Cet del; 19 Emp nig; 2 Vac uli; 51 Cla chl.

This assemblage (Fig. 4.63) occurs mainly on M1-5, at all positions, and has a loose distribution on M6. This group has an affiliation with the (level 5) early intermediate heath, **Cladonia portentosa - Phyllodoce caerula,** assemblage. (position colour code - yellow)

Species group (42): early intermediate heath (eigenvalue 0.054)

84 Cla con; 82 Cla coc; 78 Cla ran; 58 Cla fim.

This is a loose assemblage (Fig. 4.64), most prevalent at shoulder and mid-slope positions on M2-4. It has a loose distribution on low-slope quadrats on M3-4 and all positions on M5. This group has an affiliation with the (level 5) early intermediate heath, **Cladonia portentosa - Phyllodoce caerula,** assemblage. (position colour code - brown)

Species group (43): lichen heath (eigenvalue 0.054)

55 Cet eri; 43 Cla arb; 5 Bet nan; 85 Sph glo; 83 Ste con; 79 Bet pub; 77 Ale nig; 64 Cam rot; 57 Cor aca; 56 Cor div; 54 Tha ver; 53 Cet cuc; 52 Cet niv; 50 Ale och; 9 Nar str; 8 Arc uva; 7 Arc alp; 6 Cam rot.

This assemblage (Fig. 4.65) is tight on the crest and proximal shoulder sites on M1-4. It is loosely distributed on low-slope sites on M3-5 and the proximal slope of M2. It is very loosely distributed at other sites. This group has an affiliation with the (level 5) lichen heath, **Alectoria ochroleuca - Cetraria cucullata,** assemblage. (position colour code - red)

Species group (83): early intermediate snowbed (eigenvalue 0.070)

98 Tri spi; 95 Cer alp; 74 Cla pyx; 20 Phy cae.

This assemblage (Fig. 4.66) has a loose distribution at low-slope positions on M3-4, the proximal slope of M2 and also most positions on M5-6 (but not crest and proximal low-slopes). It has a very loose distribution at crest positions on M1 and M3-4. This group has an affiliation with the (level 4) early intermediate snowbed and pioneer, **Salix glauca - Salix phylicifolia,** assemblage. (position colour code - light blue open box)

Species group (84): late-snow early intermediate heath (eigenvalue 0.070)

108 Ara alp; 106 Lou pro; 105 Sal ret; 102 Cla car; 101 Pan pez; 99 Pyr min; 97 Car bel; 96 Dra alp; 94 Cla unc; 93 Luz arc; 91 Lyc sel; 90 Vis alp; 89 Sal lan; 88 Sax cer; 87 Sax opp; 86 Cla ple; 81 Cla def; 80 Eup fri; 76 Pso hyp; 75 Cla ver; 73 Ste bot; 72 Nep arc; 71 Cla fur; 70 Sal myr; 69 Tof pus; 68 Sil aca; 67 Luz spi; 66 Pin vul; 59 Cla cri; 10 Jun tri.

This assemblage (Fig. 4.67 a,b) has a loose distribution at low-slope positions on M3-5 and the proximal slope of M2. This group has an affiliation with the (level 5) late-snow early intermediate heath, **Empetrum nigrum - Stereocaulon alpinum,** assemblage. (position colour code = light blue)

Species group (40): early intermediate snowbed (eigenvalue 0.085)

63 Sal phy

This species (Fig. 4.68) is concentrated at low-slope positions on M3-4 and the proximal slope of M2. It also occurs on M5 and most of M6 (except the crest and proximal base-slope positions). It is infrequent at crest positions on M1 and M3-4. This group has an affiliation with the (level 4) early intermediate snowbed and pioneer, **Salix glauca - Salix phylicifolia,** assemblage. (position colour code - mustard)

Species group (4): pioneer snowbed (eigenvalue 0.253)

104 Car pet; 65 Poa alp; 62 Sal gla; 25 Oxy dig.

This assemblage (Fig. 4.69) is concentrated at low-slope positions on M3-4 and the proximal slope of M2. It also occurs on M5 and most of M6 (except the crest and proximal base-slope positions). It has a very loose distribution at all other sites. This group has an affiliation with the (level 4) pioneer snowbed, **Salix glauca - Cerastium cerastoides,** assemblage. (position colour code - purple)

4.3.6 Storbreen high (Altitude: 1310-1350m. Aspect: north-easterly)

According to the TWINSPAN final table (Appendix 4.6), the TWINSPAN "final site group" summary table (Table 4.9), and the "final species group" charts (Fig. 4.70 to 4.77), the division of the plant assemblages across this foreland is distinct in terms of both age and microtopography. Most of the assemblages show clear distribution patterns, but, as at Svellnosbreen, the tightest assemblages are on the young terrain. Interestingly, all of the assemblages have members which occur on the oldest terrain which shows that species at this altitude do not belong to exclusive seres, or stages of succession, (*sensu*: Odum 1969). These results will be discussed at greater length in chapter (7).

Species group (16): widespread heath (eigenvalue 0.205)

42 Sol cro.

This species (Fig. 4.70) is densely distributed on M1-5. It has a loose distribution at high-slope positions on M6-8. This group has an affiliation with the (level 2) heath, **Phyllodoce caerula - Solorina crocea,** assemblage. (position colour code - yellow)

Species group (17): lichen heath (eigenvalue 0.205)

37 Ale nig; 38 Ale och; 40 Cor div; 41 Tha ver; 65 Phy sch; 68 Cor acu; 76 Sph fra; 4 Bet nan; 29 Cla ran; 22 Cet niv; 23 Cet cuc; 6 Vac vit; 20 Ste con; 21 Ste pas; 26 Cet eri; 35 Cla ste.

This assemblage (Fig. 4.71) is almost exclusively found at high-slope positions on M1-6. This group has an affiliation with the (level 3) lichen heath, **Cetraria nivalis - Alectoria ochroleuca,** assemblage. (position colour code - red)

Species group (18): late-snow late intermediate heath (eigenvalue 0.129)

2 Phy cae; 27 Cla chl; 46 Cas hyp; 60 Car bel; 13 Jun tri; 28 Cla por; 30 Cla arb; 33 Cla gra; 36 Cla cri; 58 Cla cer; 24 Cet isl.

This assemblage (Fig. 4.72) is abundant at low-slope positions on M1-5. It also occurs at other slope positions on M1-5. This group has an affiliation with the (level 4) mature late-snow heath, **Salix herbacea - Cetraria islandica,** assemblage. (position colour code - dark blue)

Species group (38): late-snow early intermediate heath (eigenvalue 0.126)

7 Gna sup; 14 Luz arc; 8 Hie spp; 9 Lyc spp; 17 Nar str; 31 Pso hyp; 32 Cla squ; 34 Cla unc; 39 Cla con; 43 Nep arc; 56 Sib pro; 71 Ran alp; 73 Lec qua; 75 Och fri.

This assemblage (Fig. 4.73) has a fairly tight distribution at low-slope positions on M1-5. This group has an affiliation with the (level 4) mature late-snow heath **Salix herbacea - Cetraria islandica** assemblage. (position colour code - light blue)

Species group (39): late-snow early intermediate heath (eigenvalue 0.126)

25 Cet del; 54 Pyr min; 57 Dry exp; 59 Ver alp; 62 Pyr spp; 66 Cla ver; 67 Cla ple; 72 Car pet; 77 Sal ret; 79 Sph mel; 80 Cla sul; 84 Ale spp; 86 Ath dis; 18 Ant alp.

This is a very loose assemblage (Fig. 4.74) occurring at low-slope positions on M1-4 (including the "hollow" site, between the two crest sites, on M4). Members of this assemblage occur at most positions on M5 and high-slope positions on M6. This group has an affiliation with the (level 3) late-snow heath, **Salix herbacea - Stereocaulon alpinum,** assemblage. (position colour code - light blue open box)

Species group (5): widespread heath (eigenvalue 0.352)

3 Sal her; 5 Vac myr; 19 Ste alp; 70 Sal phy; 1 Emp nig; 15 Car spp; 69 Vac uli.

This assemblage (Fig. 4.75) has a tight distribution on M1-6 and is found loosely across most positions on M7-8. This group has an affiliation with several "final site group" assemblages. (position colour code - yellow)

Species group (6): early intermediate snowbed (eigenvalue 0.380)

11 Ant odo; 12 Luz spi; 51 Tar spp; 45 Sal lan; 55 Cer alp; 85 Pan pez; 44 Sal gla; 50 Pol viv; 74 Pel pol; 82 Des fle; 81 Sax ste; 83 Gym dry; 87 Woo alp.

This snowbed assemblage (Fig. 4.76) has a fairly loose distribution at low-slope sites on M1-7. It is prevalent on the distal slope of M2 and the low-slopes of M6-7. This group has an affiliation with several assemblages but especially the (level 3) early intermediate snowbed, **Salix glauca - Salix herbacea,** assemblage. (position colour code - blue-white)

Species group (7): pioneer (eigenvalue 0.380)

52 Oxy dig; 53 Cer cer; 61 Arc alp; 16 Phl alp; 47 Des alp; 48 Tri spi; 49 Sag sag; 63 Poa alp; 88 Sax ces; 10 Fes ovi; 78 Ara alp; 64 Ste bot.

This assemblage (Fig. 4.77) has a tight distribution on M6-8 and a loose distribution at low-slope positions on M1-5. It is infrequent at high-slope positions on older ground. This group has an affiliation with the (level 3) pioneer, **Poa alpina- Deschampsia alpina,** assemblage. (position colour code - pink)

4.4.7 Høgvaglbreen (Altitude: 1400-1450m. Aspect: north-easterly)

According to the TWINSPAN final table (Appendix 4.7), the TWINSPAN "final site group" summary table (Table 4.9), and the "final species group" charts (Fig. 4.78 to 4.84), the division of most of the assemblages across this foreland is influenced by both age and microtopography. Most of the assemblages have separated according to microtopography. However, the two most distinct assemblages (with high eigenvalues), a widespread heath and a pioneer assemblage, appear not to have separated according to microtopography. Most of the assemblages are quite distinct but the least distinct are found on the oldest terrain, refuting the notion that pioneer assemblages tend not to be distinct. Furthermore there are a greater number of mature assemblages than pioneer, lending additional support to the hypothesis that succession does not end in a monoclimax. A more detailed discussion of these results is made in chapter (7).

Species group (8): lichen heath (eigenvalue 0.275)

19 Cet niv; 20 Cet cuc; 8 Vac vit; 9 Vac uli; 34 Ale och; 35 Ale nig; 38 Tha ver; 43 Cla ran; 10 Jun tri; 32 Cor acu; 33 Cor div; 42 Sph glo.

This assemblage (Fig. 4.78) is abundant at high-slope positions on M1-5. It occurs loosely at low-slope positions on M5. This group has an affiliation with the (level 3) dry lichen heath, **Thamnolia**

vermicularis - Alectoria ochroleuca, assemblage and also the (level 5) early intermediate lichen heath, **Cornicularia aculeata - Cetraria nivalis,** assemblage. (position colour code - red)

Species group (36): mature heath (eigenvalue 0.142)

2 Fes ovi; 21 Cla gra; 29 Cla arb; 30 Cla por; 31 Cla unc.

This assemblage (Fig. 4.79) has a tight distribution at nearly all positions on M1. It also occurs in low-slope quadrats on the distal slope of M2-4. It has a fairly tight distribution at high-slope positions on M2-4. This group has an affiliation with the (level 2) heath, **Salix herbacea - Cetraria ericetorum,** assemblage. (position colour code - dark green)

Species group (37): late-snow heath (eigenvalue 0.142)

1 Sal her; 7 Sil aca; 11 Car spp; 17 Cet eri; 25 Cla chl.

Salix herbacea, Cetraria ericetorum and *Cladonia chlorophaea* are abundant across low-slope positions on M1-4 and loosely distributed at low-slope positions on M5. The other species are loosely distributed across M1-5. This group (Fig. 4.80) has an affiliation with the (level 3) late-snow lichen heath, **Cetraria ericetorum - Stereocaulon alpinum,** assemblage. (position colour code - blue-white)

Species group (38): early intermediate snowbed (eigenvalue 0.098)

4 Cas hyp; 5 Luz spi; 27 Cla fim; 45 Phy cae; 49 Ran gla; 28 Cla cer; 41 Cla ver; 46 Pol viv; 47 Phl alp; 51 Emp nig; 52 Luz arc; 53 Ant alp; 54 Nar spp.

This assemblage (Fig. 4.81) has a loose distribution across M1-4, but it is more abundant on M2, low-slope quadrats on M3 and most of M4. This group has an affiliation with the (level 5) early intermediate snowbed, **Cassiope hypnoides - Cladonia chlorophaea,** assemblage. (position colour code - light blue)

Species group (39): mature snowbed (eigenvalue 0.098)

3 Lyc sel; 6 Gna sup; 12 Hie spp; 14 Ste spp; 22 Cla squ; 23 Cla car; 24 Cla cri; 26 Cla pyx; 36 Sph fra; 37 Cla dig; 39 Cla ama; 40 Cla bel; 44 Cla coc; 18 Cet isl.

This assemblage (Fig. 4.82) has a loose distribution on M1-4. It is most abundant on the base-slope site on M1 and quadrats at distal positions on M2-4. This group has an affiliation with the (level 4) mature snowbed, **Cladonia gracilis - Salix herbacea,** assemblage. (position colour code - dark blue)

Species group (5): widespread heath (eigenvalue 0.438)

13 Ste alp; 15 Ste bot; 16 Sol cro.

Stereocaulon alpinum and *Solorina crocea* are distributed widely and abundantly across the whole foreland. This group (Fig. 4.83) has an affiliation with several "final site group" assemblages. (position colour code - yellow)

Species group (3): pioneer (eigenvalue 0.503)

48 Ste con; 50 Poa alp; 55 Tri spi; 56 Oxy dig; 57 Sal gla.

This tight pioneer assemblage (Fig. 4.84) occurs on M5-6. This group has an affiliation with the (level 2) pioneer, **Oxyria digyna - Poa alpina,** assemblage. (position colour code - pink)

4.4.8 Bøverbreen (Altitude: 1500-1540m. Aspect: south-westerly)

According to the TWINSPAN final table (Appendix 4.8), the TWINSPAN "final site group" summary table (Table 4.9), and the "final species group" charts (Fig. 8.85 to 4.92), the division of the plant assemblages across this foreland is influenced by both age and microtopography. Members of the mature assemblages, are generally not abundant on the younger terrain but the pioneer species spread onto, or continue to grow on, the oldest ground. On all ages of moraine, the effects of microtopography appears to be important (corresponding with other mid-alpine forelands) shown by the occurrence of certain assemblages at the high-slope positions (e.g. the exposed lichen heath assemblage), and other assemblages at low-slope positions (e.g. the snowbed assemblage). The most distinct assemblages are a pioneer, a widespread heath, and a widespread snowbed assemblage; the least distinct assemblage is the mature late-snow lichen heath. These results correspond strongly with those from Høgvaglbreen and are discussed in greater detail in chapter (7).

Species group (16): exposed lichen heath (eigenvalue 0.178)

37 Sph glo; 38 Ale och; 40 Cor acu; 41 Cor div; 39 Ale nig; 60 Arc alp; 1 Emp nig; 9 Hie spp; 21 Cet eri; 58 Jun tri; 22 Cet cuc.

This is a tight assemblage (Fig. 4.85) located on crest sites on M1-4. This group has an affiliation with the (level 3) exposed lichen heath, **Alectoria ochroleuca - Cornicularia aculeata** assemblage. (position colour code - red)

Species group (17): mature late-snow lichen heath (eigenvalue 0.178)

32 Cla ama; 42 Tha ver; 4 Car spp; 44 unc cup; 54 Cla cri.

This loose assemblage (Fig. 4.86) occurs on M1 and M2. This group has an affiliation with the (level 4) mature late-snow lichen heath, **Cetraria islandica - Cetraria ericetorum,** assemblage. (position colour code - dark blue)

Species group (36): early intermediate snowbed (eigenvalue 0.159)

18 Ste bot; 49 Gna sup; 53 Cla cer; 3 Phy cae; 11 Lyc sel; 36 Cla fur; 48 Cas hyp; 55 Cla dig; 57 Pso hyp.

This loose assemblage (Fig. 4.87) mainly occurs on M4, and low-slope or proximal quadrats on M2 and M3. It also occurs, to a lesser extent, on M1 and at other positions on M2. This group has an affiliation with the (level 4) snowbed, **Trisetum spicatum - Gnaphalium supinum,** assemblage. (position colour code - light blue)

Species group (37): heath (eigenvalue 0.159)

6 Luz spi; 16 Ste con; 23 Sph fra; 24 Cla chl; 26 Cla fim; 30 Cla ran; 43 Pel pol.

This assemblage (Fig. 4.88) is fairly tightly distributed across M1-4. This group has an affiliation with the (level 2) heath, **Cladonia chlorophaea - Salix herbacea,** assemblage (position colour code - mustard)

Species group (19): mature late-snow lichen heath (eigenvalue 0.105)

20 Cet eri; 19 Cet isl; 25 Cla pyx; 27 Cla squ; 33 Cla gra; 35 Cla ver; 62 Cet del; 10 Vac vit; 12 Ran gla; 13 Nep arc; 17 Ste spp; 28 Cla por; 31 Cla unc; 34 Cla car; 45 Cla ste; 46 Cla bel; 47 Pan pez; 51 Sag sag; 56 War red; 29 Cla arb.

This assemblage (Fig. 4.89) has a tight distribution across M1 and the crest and distal slope of M2. It also occurs on M3. This group has an affiliation with the (level 4) mature late-snow lichen heath, **Cetraria islandica - Cetraria ericetorum,** assemblage. (position colour code - dark green)

Species group (5): widespread heath (eigenvalue 0.274)

2 Sal her; 5 Fes ovi; 8 Ant alp.

This assemblage (Fig. 4.90) is most abundant on M1-4, but the species within this assemblage occur across the entire foreland, with *Salix herbacea* being most abundant. This group has an affiliation with the (level 2) heath, **Cladonia chlorophaea - Salix herbacea** assemblage. (position colour code - yellow)

Species group (6): snowbed (eigenvalue 0.510)

15 Ste alp; 50 Tri spi; 63 Sal gla.

This assemblage (Fig. 4.91) occurs at low-slope positions across the entire foreland and all positions on young ground. *Stereocaulon alpinum* is particularly abundant. This group has an affiliation with the (level 4) snowbed, **Trisetum spicatum - Gnaphalium supinum,** assemblage. (position colour code - blue-white)

Species group (7): pioneer (eigenvalue 0.510)

14 Sol cro; 7 Poa alp; 52 Oxy dig; 61 Des alp; 64 Cer cer; 59 Cer alp.

This assemblage (Fig. 4.92) forms a tight group, at all sites, on the young moraines. It is also found at low-slope positions on M1-3. This group has an affiliation with the (level 2) pioneer, **Oxyria digyna - Poa alpina,** assemblage. (position colour code - pink)

4.3.9 Trends demonstrated by the "final species groups"

TWINSPAN classification of the species is achieved by placing the species in groups according to their fidelity, or the degree of faithfulness of that species to the group (Kent and Coker, 1992). The summary table (Table 4.10) displays the TWINSPAN assemblages formed by the "final species groups", on all forelands, for easy comparison. The information given about each assemblage, within each cell on the table, consists of: a) the "final species group" number; b) the name of the assemblage; c) the eigenvalue;

and d) the position of the assemblage across the foreland and on the moraines. The cells are colour-coded to show the position of each assemblage. From this table it is possible to see the following trends:

1. Most of the assemblages belong to restricted terrain-age ranges, demonstrating that age is probably the most important influence, on vegetation patterns, across each of the forelands.
2. All forelands at all altitudes have mature assemblages which show similar (fairly low) eigenvalues demonstrating that the fidelity of the species to those groups is not very high. The highest eigenvalues, for the mature assemblages, are on Storbreen low (1 and 2) forelands, possibly because there is a lack of early pioneer assemblages (on the other forelands the pioneer assemblages tend to be the most distinct). The lowest eigenvalues, for the oldest terrain, were found on Svellnosbreen foreland which has a large altitudinal range and high disturbance across the entire foreland (with fluvial activity and solifluction being important on the older ground). High levels of disturbance may encourage so-called pioneer species to be abundant on the older ground, thus reducing the distinctness of mature assemblages.
3. All forelands have more than one "ecologically meaningful" mature assemblage, and in some cases several, showing that the "monoclimax" hypothesis (Clements, 1916) can not be supported. The mature assemblage eigenvalues are generally not very high (except for the Storbreen low foreland sequences) suggesting that these mature assemblages are not very distinct, and this questions the notion that groups become more distinct as succession proceeds (e.g. Margalef, 1968). This also suggests that there is a general continuum of assemblages on the oldest terrain, as opposed to distinct communities.
4. There are a larger number of assemblages at the sub- and low-alpine altitudes than at the mid-alpine altitudes. Furthermore, the assemblages themselves are, in general, less distinct (with lower eigenvalues) on the subalpine forelands than on the alpine forelands. Thus, the pattern of assemblages, as influenced by age and microtopography, is simpler and more conspicuous at higher altitudes.
5. At all altitudes the most distinct assemblages tend to be pioneer assemblages thus disputing the suggestion that pioneer assemblages are indistinct assemblages determined by chance (cf. Margalef, 1968).
6. Two other distinct assemblages are: a) the "widespread" heath, which usually comprises a small group of abundant and widely distributed species across the forelands; and b) the snowbed assemblages, which are also mainly widespread. It is possible that these assemblages are distinct due to the special adaptations of the member species to their particular niche.
7. On subalpine forelands, the single most important influence on the separation of the "final species group" assemblages appears to be terrain-age. This is demonstrated by the majority of assemblages occurring at most positions across moraines of a particular age. The only assemblages that appear to be influenced by microtopography are snowbed assemblages which, nevertheless, occur within a narrow age-range.
8. The influence of microtopography is demonstrated where assemblages are distributed at a particular position across several moraines (e.g. low-slope positions across M1-3). The influence of microtopography, on assemblage separation, is greater with altitude. On the sub-alpine forelands there are only a few snowbed assemblages, but on the alpine forelands the assemblages commonly form zones

at particular positions across many or, in some cases, all the moraines. This is especially apparent with the lichen heath "final species groups" which generally occupy the high-slope positions, of most of the moraines, across the alpine forelands.

9. The early intermediate assemblages are not distinct. However, the influence of microtopography becomes more important at higher altitudes, so that some early intermediate assemblages are more prevalent at low-slope positions and others are more prevalent at high-slope positions.

4.4 Summary of trends demonstrated by TWINSPAN analysis of individual foreland data

By referring to the summary tables (Tables 4.9 and 4.10), as well as the summaries (sections 4.1.9, 4.2.9 and 4.2.9) it can be seen that the general trends found by the "final site groups" correspond with those of the "final species groups". A brief discussion of these findings has been made in each of the summaries and a more detailed discussion is made in the concluding chapter (7). The main trends, demonstrated by the results of chapter (4), are as follows:

1. The most important influence on vegetation pattern, across all of the forelands, is terrain-age. However, the relative importance of terrain-age appears to change with altitude: it is the most important influence on vegetation pattern on the sub-alpine forelands, but on the alpine forelands other influences, such as microtopography, are also important.

2. The influence of microtopography on vegetation pattern increases with altitude. Its influence appears important on all moraines on the alpine forelands, but only on the youngest terrain on the sub-alpine forelands.

3. There are more ecologically meaningful assemblages found on the sub-alpine forelands than at higher altitudes so that the vegetation succession is more complex.

4. The assemblages are less distinct on the subalpine forelands than on the alpine forelands, which suggests that there is a greater overlap between members of the subalpine assemblages.

5. The most distinct assemblages are the pioneer and snowbed assemblages at the sub-alpine altitude and the pioneer, snowbed and lichen heath assemblages at the low to mid-alpine altitudes. This suggests that those species adapted to particular extremes of environment (i.e. disturbed terrain, high winds or long snow duration) comprise a group of specialist species. This suggestion is supported by the increasing distinctness of assemblages, and influence of microtopography, with altitude: at higher altitudes small microtopographical differences are likely to influence the build up of winter snow and thus influence a whole range of associated environmental factors (see chapter (7) for detailed discussion).

6. The least distinct assemblages tend to be the early intermediate assemblages, where pioneers are being superseded by later colonisers.

7. There is more than one mature assemblage on all forelands refuting the "monoclimax" hypothesis.

8. There is considerable correspondence shown between most "final site group" assemblages and the "final species group" assemblages. Both sets of data lend support to the hypothesis that there are differences in vegetation distributions across all the forelands which are related to age and microtopography. However, most of the species can not be described as having strong allegiances to particular groups (possible exceptions being the pioneer, snowbed and lichen heath assemblages). This suggests that the differences in plant distributions across the foreland can be described in terms of vegetation gradients and not in terms of vegetation zones.

"Effective displays are desired for final results, obviously. They are equally important, however, for preliminary scanning because often many ordinations and many variables are scanned in the early stages of successive refinement, and poor results and lack of pattern need to be identified rapidly without wasting time".

Gauch (1982: 168)

CHAPTER FIVE: The relationship between sites, species and environmental parameters across the individual forelands.

5.1 Introduction and aims

In chapters (3) and (4) the patterns of vegetation and environmental factors across the forelands are described by the use of the classification technique TWINSPAN, various graphical and tabular displays and simple statistical tests. In this chapter the relationship between the environment and the vegetation patterns described by TWINSPAN will be elucidated further by the use of ordination. The use of both a classification technique and an ordination technique on the same data set has been recommended by many authors (Kent and Coker, 1992; Matthews, 1992; Crouch, 1992). This is because the vegetation and sample patterns found using the classification method can be compared, and hopefully supported, by the patterns displayed using ordination. In addition, the ordination technique can relate the vegetation and sample patterns to the environmental data. In brief, it is the purpose of this chapter to confirm the findings of chapters (3) and (4) as well as to relate the vegetation patterns to the environmental parameters in an objective manner. This is done using the indirect ordination technique DCA in the CANOCO programme as described in chapter (2).

The aims of the present chapter are as follows:

1. To describe the pattern of the samples (quadrats and sites) on individual foreland DCA axes (1) and (2) and to discuss the degree of correspondence between the sample patterns shown by the DCA output and the TWINSPAN site groups displayed in the profile diagrams of chapter (4).
2. To describe the pattern of species on individual foreland DCA axes (1) and (2) and to discuss the degree of correspondence between the species patterns shown by the DCA output and the TWINSPAN species patterns presented in chapter (4).
3. To describe the pattern of the environmental parameters on the individual foreland DCA axes (1) and (2) and to elucidate these patterns with reference to the environmental patterns across forelands displayed in Chapter (3).
4. To elucidate the relationship between the TWINSPAN "final site groups" (group numbers marked with an asterisk *) and the environmental parameters using the DCA ordination centroid plots and correlation matrices.
5. To elucidate the relationship between the TWINSPAN "final species groups" and the environmental parameters using the DCA ordination centroid plots and correlation matrices.
6. To summarise the relationship between the TWINSPAN "final site groups", the TWINSPAN "final species groups" and the environmental parameters, across all forelands, using the DCA ordination rank lists, centroid plots and correlation matrices.

5.2 Choice of DCA ordination data presentation and chapter layout

Data has been collected from eight individual forelands in order investigate the relationship between microtopography (and prevailing environmental variables) and vegetation pattern with age and altitude. Because of the huge amount of data and plots that can be derived from using the CANOCO programme, a number of choices had to be made in order to display the findings of the ordination in the clearest possible way. A description of multivariate techniques as well as the rationale behind the use of the DCA analysis technique, for indirect ordination purposes, has been given in section 2.9.3.

Plots are made for all species, sites (samples) and environmental parameters on axes (1), (2), and (3), but, with the exception of the environmental data, most of these plots are difficult to interpret, especially towards the centre of the diagram. The data points, in both the species and sample plots, are especially dense over the centre of the plot and it is not possible to label individual species or samples. It is therefore deemed necessary to place the individuals into groups and make use of the TWINSPAN "final site groups" (sample scores) and TWINSPAN "final species groups" (species scores) for the centroid plots on the ordination axes, as recommended in Kent and Coker (1992). The environmental variables, using the environmental biplot scores (see Appendix 5.1-5.16) are plotted onto both the sample score and species score centroid plots. To make centroids it is necessary to take an average of the ordination scores of members of the TWINSPAN "final site groups" and TWINSPAN "final species groups" on each axis for all forelands and then plot the average score of each group along with the scores for the environmental variables (see Appendix 5.1 to 5.16). By using these plots (Fig. 5.1 to 5.16) it is possible to ascertain the position of the TWINSPAN "final site groups" and "final species groups" in relation to different environmental parameters and suggest the relative influence of environmental parameters on the pattern of vegetation on each foreland. From these plots it is also possible to investigate whether different parameters appear to be acting together to influence the vegetation patterns - so-called environmental factor complexes (Whittaker 1985, 1989; Matthews and Whittaker, 1987). As can be seen in Fig. 5.1 to 5.16, the spread of environmental variables across the plots displays three major characteristics: a) some of the variables (shown by the longest arrows) have a more important influence on the vegetation pattern than others; b) some of the variables appear to be clustered together, and thus are associated parameters, while others appear to be fairly independent of one another; and c) the spread of environmental variables and TWINSPAN groups differs from foreland to foreland. A fairly even spread of variables across most of the plots shows a low correspondence between the variables and any particular axis suggesting that the influence of the variables on one another is complex, whereas a clustered distribution of variables, especially along one of the axes, shows associations between the variables (and/or axes) suggesting that the relationship between the vegetation pattern and the environment is a simpler one. The relative importance of different environmental parameters on the pattern of vegetation on each foreland will be elucidated further in later sections and is summarised in section 5.11.

In order to display the rank of individual samples and species along the ordination axes the list of scores is displayed on both axes (1) and (2) (Tables 5.1 to 5.8 and Tables 5.9 to 5.16). The TWINSPAN "final site groups" and "final species groups" have been superimposed onto the rank lists by using the colours that have been accorded them in chapter (4). The "final site groups" (Tables 5.1 to 5.8) have been given the same colours as displayed in the profile diagrams (Figs. 4.2 to 4.9) and summary table (Table 4.9). The colours for the "final site groups" are representative of the TWINSPAN groups on the profile diagrams and are used only to identify the group. The "final species groups" in the species rank tables (Tables 5.9 to 5.16) are accorded the colours displayed in Table 4.10 (the TWINSPAN "final species group" summary table) and also Table 6.3, which compares the TWINSPAN individual foreland "final species groups" with the TWINSPAN combined foreland "final species groups". The colours for the species groups not only identify the groups but also give a generalised indication of the location of the group across the foreland. Only the scores from axes (1) and (2) are used, because the eigenvalues of axis (3) and (4), in general, are low, difficult to interpret and ecologically meaningless. For the same reasons, Whittaker (1985) and Crouch (1992) dismissed axis (3) and (4) as being of little ecological importance. The ranks of species, sample (site) and environmental variable scores are displayed so as to elucidate the order of each individual on each axis. The average scores shown by the centroid plots do not show the fine details and, where the scores within a particular TWINSPAN group are very divergent, the groups tend to cluster around the centre of the diagram. The rank tables, on the other hand, show the relationship between individuals of each parameter group (i.e. groups involving samples, species and environmental parameters) along axes (1) and (2). Thus it is possible to see which members of each parameter group are least related. It is also possible to investigate the relationship between the parameter groups by comparing the species, samples (sites) and environmental parameters at particular segments along any one axis. Lastly, the TWINSPAN groups have been superimposed onto the axes in order to compare the results derived from classification and ordination methods, as well as to discuss the relative influence of environmental parameters on individual members of the TWINSPAN groups.

Within CANOCO there is an option which calculates the correlation coefficients between unconstrained ordination axes and environmental variables that are supplied as a separate file. Correlation matrices of Pearson's product moment correlation coefficients between the different environmental variables have been constructed for each foreland (Tables 5.17 to 5.24). Following Crouch (1992) only the intercorrelations significant at $p<0.001$ are considered important. The critical values for " r " range from 0.307 for 110 samples to 0.264 for 150 samples and will be given for each foreland. This is based on the principal of using a stringent significance level to ensure that any data characteristics that do not satisfy the parametric assumptions of the statistic (e.g. normality) do not have an undue influence on the results. The use of this stringent significance level also takes account of the fact that a large sample size can yield significant but ecologically meaningless correlations. The correlation matrices have been constructed for each foreland in order to elucidate further the relationship between environmental variables and the ordination axes. The correlation matrix can also show how environmental parameters are correlated with each other and, most importantly, the matrix can display which parameters are most correlated with the meso-scale environmental parameters of age and microtopographical position. They therefore give an indication of how the parameters work together as complexes to influence the environment of sites of any particular age or position. The highest intercorrelations for age and position with the other environmental variables are described for each foreland. These intercorrelations are summarised in section 5.11 in order to elucidate the relative influence of the meso-scale environmental variables on vegetation and environmental patterns across the foreland. In addition, the matrix displays the relative importance of these meso-scale environmental parameters, in relation to each other, allowing conjecture upon which of the other environmental parameters may be the most important influences on vegetation pattern across the foreland.

The layout of chapter (5) has been designed with ease of reference in mind. Each major section deals with the DCA ordination results for the individual forelands. The first part of each section describes the relationship between the samples and the environmental parameters using the rank of TWINSPAN "final site groups", as well as individual sites, on DCA ordination axes (1) and (2). The second part of each section describes the relationship between the species and the environmental parameters using the rank of TWINSPAN "final species groups", as well as individual species, on DCA ordination axes (1) and (2). In the section that follows, there is a description of the species and sample plots in relation to the environmental biplot scores and the significance of the major environmental parameters is discussed using the most important correlation coefficients between the unconstrained ordination axes and environmental variables. The last part of each of these sections consists of a summary which discusses the main findings of that section. Within these summaries a comment will be made on the apparent tightness of the TWINSPAN final groups (in terms of the distribution of sites or species on the ordination axes) in order to discuss the relative distinctness of the groups. By doing this it will be possible to assess whether distinct groups or "communities" have been recognised. At the end of the chapter is a general summary which describes the major trends shown by comparison of the results between forelands.

5.3 Austerdalsbreen

5.3.1 Site (sample) patterns on DCA axes (1) and (2) at Austerdalsbreen

By referring to Table 5.1, and the profile diagram (Fig. 4.2), for the location of specific sites where the pattern is not clear, the following site patterns emerge on DCA ordination axes (1) and (2). Axis (1) has an eigenvalue of 0.443 showing that there is good species and sample separation along the axis and that this axis is ecologically meaningful. The environmental variables explain 93.4% of the variation along this axis. Axis (2) has an eigenvalue of 0.299 which is high enough to suggest relatively good separation along the axis. The environmental variables explain 74.8% of the variation along this axis. The TWINSPAN "final site groups" correspond with the patterns of sites along axis (1) but do not correspond as well on axis (2), except towards the positive end of the axis.

At the positive end of axis (1) are mature low-slope sites belonging to the TWINSPAN mature meadow (site group 7*), the **Athyrium distentifolium - Potentilla crantzii** assemblage followed by members of the mature heath (site group 13*), the **Deschampsia flexuosa - Vaccinium myrtillus** assemblage. The corresponding environmental variables at the positive end of axis (1) are root depth, humus depth, age, stain depth, soil texture and fluvial disturbance. On the whole these parameters suggest mature sites with well-developed soils. The sites that follow the above groups are mainly from M2 with members of the late intermediate snowbed (site group 24*), the **Deschampsia alpina - Phyllodoce caerula** assemblage followed by the late intermediate heath (site group 25*), the **Vaccinium myrtillus - Vaccinium uliginosum** assemblage. Interspersed within site groups (24*) and (25*) are members of the early intermediate moist heath (site group 22*), the **Vaccinium myrtillus - Betula pubescens** assemblage and the pioneer snowbed (site group 10*), the **Salix phylicifolia - Salix herbacea** assemblage. Further down the axis, site group (22*) becomes interspersed with the late intermediate lichen heath (site group 46*), the **Empetrum nigrum - Betula pubescens** assemblage and the late intermediate lichen heath (site group 47*), the **Solorina crocea** assemblage until these two large groups become dominant on the negative half of axis (1). Interspersed between site groups (46*) and (47*) are members of the exposed pioneer snowbed (site group 9*), the **Carex spp - Phleum alpinum** assemblage. At the negative end of the axis is the exposed pioneer (site group 8*), the **Stereocaulon alpinum - Stereocaulon vesuvianum** assemblage. The corresponding environmental variables at the negative end of axis (1) are high bryophyte cover, high frost activity, high proportions of bare ground and low snow cover.

At the positive end of axis (2) is the exposed pioneer (8*) and the exposed pioneer snowbed (9*) and the pioneer snowbed (10*). The corresponding environmental variables at the positive end of axis (2) are altitude, bare gravels, pH and fluvial activity. These pioneer groups are followed by the moist early intermediate heath (22*), interspersed with the mature meadow (7*) as well as the odd member of the large heath groups (46*) and (47*). Most of the sites at the positive end of the axis are low-slope sites. After group (22*), the negative half of axis (2) is dominated by groups (46*) and (47*) and these are interspersed by the remaining mature heath (13*), late intermediate heath (25*) and late intermediate snowbed (24*). The corresponding environmental variables at the negative end of axis (2) are age, stain depth, vegetation cover and high-slope positions.

These results are summarised in Fig. 5.17 and on axis (1) there appears to be a strong age-related sequence from the oldest terrain at the positive end of axis (1) to the young terrain at the negative end of axis (1). Superimposed onto each section of the axis is a position-related sequence from low-slope, sheltered positions to more exposed high-slope positions. This shows that age is the most influential factor on axis (1) but microtopography-related factors, such as snow-lie and frost evidence, are also important. The ages of sites on axis (2) appear to be more disordered than they are on axis (1) although the age trend is still apparent on this axis. Position is more prominent on axis (2) than on axis (1) with a trend of low-slope (and younger sites) at the positive end of axis (2) proceeding to high-slope (and older sites) at the negative end. Disturbance appears to be an important influence on both axes, with frost activity is important on axis (1) and fluvial activity on axis (2).

5.3.2 Species patterns on DCA axes (1) and (2) at Austerdalsbreen

By referring to Table 5.9 and Table 4.10 it is possible to relate the sequence of species on DCA axes (1) and (2) to the TWINSPAN "final species groups" described in chapter (4) and thus elucidate the influence of particular environmental variables on the species pattern across Austerdalsbreen foreland. The eigenvalues for sample and species separation as well as the influence of the measured environmental variables on each axis are described in section 5.3.1. The TWINSPAN species assemblages correspond well with the sequence of species along axis (1) although the middle portion has a slightly disordered sequence. However, they do not correspond well on axis (2) except towards the positive end and negative end of the axis.

At the positive end of axis (1) is the mature heath (species group 31) interspersed with members of the late intermediate heath (species group 30). Following these is (species group 30) interspersed with members of the late intermediate snowbed (species group 14) and, further down, with members of the early intermediate late-snow heath (species group 69). These groups correspond with root depth, humus depth, age, stain and soil texture. Following these groups is a relatively disordered sequence of species starting with members of the widespread snowbed (species group 6), interspersed with members of (species group 69) and the early intermediate heath group (9). Following this is the widespread heath (species group 5) interspersed with members of species groups (9), (69) and the early intermediate heath (species group 68). Following these groups are members of (species group 9) and the pioneer (species group 16) which in turn is replaced by the early intermediate heath (species group 68). Members of (species group 16) are found at the negative end of axis (1). The negative end of the axis corresponds with bryophyte cover, frost-heave, bare ground, low snow and dowel heave.

At the positive end of axis (2) is the pioneer (species group 16) interspersed with members of the early intermediate late snow heath (species group 69). The positive end of the axis corresponds with altitude, bare gravels, pH, fluvial activity and bryophyte cover. This is followed by a disordered sequence of mainly low-slope species groups dominated by (species group 69). Further towards the negative end, the late intermediate heath (species group 30), the widespread heath (species group 5) and the mature heath (species group 31) become more prevalent and form another disordered sequence. The negative end of axis (2) is dominated by the early intermediate heath (species group 68), and corresponds with age, stain depth, vegetation cover, high-slope position and soil texture. These results complement the site results described in the previous section and are summarised in Fig. 5.25.

5.3.3 TWINSPAN group centroids of sample and species scores at Austerdalsbreen

Fig. 5.1 shows the DCA centroids of TWINSPAN "final site group" sample scores and reveals the position of the site groups on both axes in relation to the environmental parameter biplot scores. Fig. 5.9, showing the DCA centroids of TWINSPAN "final species group" species scores, reveals the position of the species groups on both axes in relation to the environmental parameter biplot scores. In addition, Table 5.17, the weighted correlation matrix, can be used to elucidate further the relative influence of environmental parameters on the TWINSPAN "final site groups" and "final species groups". These plots and the correlation matrix are used to outline and corroborate the main findings of the previous two sections at Austerdalsbreen. The critical value for " *r* " on this foreland is 0.289.

Towards the positive end of axis (1) are an important cluster of environmental parameters suggesting mature vegetation and soils. These parameters are highly correlated with axis (1) and they are age *(r = +0.*764), root depth *(r = +0.*882), humus depth *(r = +0.*746), stain depth *(r = +0.*602), vegetation cover *(r = +0.*517), soil texture *(r = +0.*525) and fluvial activity *(r = +0.*472). The correlation matrix shows that these parameters, except fluvial activity, are highly correlated with each other. Towards the negative end of axis (1) are some environmental parameters, mainly associated with poorly developed soils. Some of these parameters are important and have a high negative correlation with axis (1) such as bryophyte cover (*r* = -0.584), frost activity (*r* = -0.472), bare boulders (*r* = -0.37), bare gravels (*r* = -0.32), bare fines (*r* = -0.303), while others are significant but slightly less important, such as low snow cover (*r* = -0.273) and altitude (*r* = -0.257). The most important parameters towards the positive end of axis (2) are altitude *(r = +0.*575), pH *(r = +0.*37) and bare gravels *(r = +0.*326) and towards the negative end of axis (2), age (*r* = -0.335), stain depth (*r* = -0.28), vegetation cover (*r* = -0.236) and position (*r* = -0.207).

Those parameters which are significantly and positively correlated with age, and thus associated with the oldest terrain, are root depth *(r = +0.*831) humus depth *(r = +0.*748), stain depth *(r = +0.*606), soil texture *(r = +0.*684) and vegetation cover *(r = +0.*627). Those parameters negatively correlated with age are altitude (*r* = -0.7530), bryophyte cover (*r* = -0.686), bare ground gravels (*r* = -0.47), frost-heave (*r* = -0.467), bare ground boulders (*r* = -0.446), dowel heave (*r* = -0.467). The parameters most correlated with high-slope position are frost-heave *(r = +0.*52), low snow cover *(r = +0.*425), trampling *(r = +0.*309) and bare ground fines *(r = +0.*255) and the parameter most negatively correlated with high-slope positions is vegetation cover (*r* = -0.213). It is surprising that dryness (low moisture) is not more correlated with high-slope position *(r = +0.*118) but it is correlated to some extent with frost-heave *(r = +0.*277) and bare fines *(r = +0.*286) which are both positively correlated with high-slope position. Refer to Fig. 5.3 for intercorrelations between parameters other than those mentioned.

Fig. 5.1, summarises the distribution of DCA centroid scores of TWINSPAN "final site group" assemblages on a plot. The mature meadow (site group 7*) and the mature heath (site group 13*) show correspondence with the positive end of axis (1) (with parameters associated with older ground, deeper more developed soils, and higher vegetation cover). Around the centre of the axis is a cluster of groups comprising mainly late intermediate or snowbed site groups of intermediate soil development. The pioneer site groups (8*), (9*) and (10*) are found at the positive end of axis (2) which is associated mostly with altitude.

According to Fig. 5.9, which displays the DCA centroid scores of TWINSPAN "final species groups", the mature heath (species group 31), the late intermediate heath (species group 30) and the late intermediate snowbed (species group 14) show some correspondence with the positive end of axis (1) where the soils and vegetation are most developed. Clustered around the centre of the plot are the widespread snowbed (species group 6), the widespread heath (species group 5), the early intermediate heath (species group 68) and the early intermediate heath (species group 35) and are representative of groups of intermediate vegetation and soil development. The early intermediate heath (species group 9) and the early intermediate late-snow heath (species group 69) show some correspondence with the negative end of axis (2) representing higher altitude and poorly developed soils and vegetation. The pioneer (species group 8) corresponds strongly with the positive end of axis (2).

From the spread of environmental parameters, TWINSPAN "final site groups" and "final species groups", on Figs. 5.1 and 5.9, it emerges that axis (1) is influenced mostly by age and soil development and axis (2) is influenced more by altitude and age and position. As seen in chapter (3) (section 3.8.3) soils are generally less developed at the low-slope positions on the moraines than on the crests of the moraines, possibly due to fluvial activity across low-slope positions on this foreland, so this explains the positive correlation between age and high-slope positions. Although age and altitude are quite independent variables they are generally linked so that there has been "confounding" of the results (*sensu*: Whittaker 1989): pioneer groups are found with the high altitude variables, towards the positive end of axis (2), and the late intermediate groups are found towards the positive end of axis (1). Whittaker (1985) suggested that small altitude differences across the foreland are unlikely to have a significant influence on vegetation patterns and so, for present study purposes, are ignored. The DCA centroid scores of TWINSPAN "final site groups" and "final species groups" correspond well with the pattern of environmental parameters on axis (1) and (2), suggesting that the trends found on both axis (1) and (2) are ecologically meaningful. These results complement and further elucidate the findings in section 5.3.1.

5.3.4 Summary of DCA ordination results at Austerdalsbreen.

The rank tables (Tables 5.1 and 5.9), displaying the distribution of the TWINSPAN "final site groups" and "final species groups" on the DCA ordination axes, provide clear and easily interpreted representations of the results on axis (1) but not on axis (2). The TWINSPAN "final species groups" correspond well with the sequence of species along axis (1) although the middle portion has a slightly disordered sequence. However, they do not correspond well on axis (2) except towards the positive and negative ends of the axis.

The TWINSPAN "final site groups" correspond well with the patterns of sites along axis (1) but do not correspond well on axis (2) except towards the positive end of the axis. The plots and correlation matrices provide further elucidation and confirmation of the results derived from the rank tables, especially concerning axis (2). The main findings from sections 5.3.1. to 5.3.3., derived from the DCA ordination results for Austerdalsbreen are summarised below. The DCA centroid scores of TWINSPAN "final site groups" and "final species groups" correspond well with the pattern of environmental parameters on axis (1) and (2), suggesting that the trends found on both axis (1) and (2) are ecologically meaningful.

There appears to be a strong age-related sequence from mature and late intermediate assemblages at the positive end of axis (1) to pioneer assemblages at the negative end of axis (1). Correlation shows root depth and age to be the most important influences on axis (1). Those parameters correlated with the oldest terrain are root depth, humus depth, stain depth, soil texture, and vegetation cover. Those parameters correlated with younger ground are altitude, bryophyte cover, bare ground gravels, frost-heave, bare ground boulders, and dowel heave. The "*terrain-age*" factor complex (Whittaker, 1985,1987, 1989) of age, altitude, soil characteristics and frost activity, has thus been found to be the main influence on species and site separation on axis (1). Superimposed weakly onto axis (1) is a microtopography-related sequence, from low-slope, sheltered snowbed assemblages to more exposed, low snow cover heath assemblages.

The separation of species and sites on axis (1) and (2) has been confounded by the combined influence of age and altitude, and thus, due to the relatively small altitudinal differences on the individual foreland, the influence of altitude on vegetation patterns is overlooked. The relative importance of altitude on foreland vegetation patterns, however, is considered in chapter (6) which describes the results from analysis of the combined foreland data set. Refer to sections 7.2.1 and 7.3.1 for a discussion of the relative influence of altitude on vegetation patterns and associated environmental parameters. Position appears to be more prominent on axis (2) than on axis (1) with a trend of low-slope and younger assemblages at the positive end of axis (2) proceeding to high-slope and older assemblages at the negative end. High-slope positions tend to be associated with better developed soils, possibly due to fluvial disturbance at low-slope positions. The "*Microtopographic (exposure-moisture-snowmelt) factor complex*" (*sensu*: Whittaker, 1985,1987,1989) has not been found to be an important influence on this foreland although the components of the complex (i.e. low snow cover, dryness and high-slope positions) cluster fairly closely together on the ordination plot showing there is some association between these variables. According to Table 5.17, the parameters correlated with high-slope positions are frost-heave *(r = +0.52)*, low snow duration *(r = +0.42)*, trampling *(r = +0.39)* and bare ground fines *(r = +0.25)*. The parameter least correlated with high-slope positions is vegetation cover *(r = -0.21)*.

On axis (1) the most distinct site groups are the mature herb-rich (site group 7*), the pioneer snowbed (site group 10*), the late intermediate lichen heath (site group 47*) and the exposed pioneer (site group 8*) and none on axis (2). The most distinct species groups on axis (1) are the mature heath (species group 31) and the early intermediate heath (species group 68) and none on axis (2). This suggests that most of the other members of the TWINSPAN site and species groups overlap to a certain extent with one another on the ordination sequence. Generally, therefore, the evidence supports the notion that there is a gradient of assemblages, some tighter than others, across the foreland as opposed to distinct and exclusive communities at Austerdalsbreen (see chapter 7 for detailed discussion).

5.4 Fåbergstølsbreen

5.4.1 Site (sample) patterns on DCA axes (1) and (2) at Fåbergstølsbreen

By referring to Table 5.2 and the profile diagram (Fig. 4.3), for the location of specific sites where the pattern is not clear, the following site patterns emerge on DCA ordination axes (1) and (2). Axis (1) has an eigenvalue of 0.81 showing that there is extremely good species and sample separation along the axis and that this axis is ecologically meaningful. The environmental variables explain 96.8% of the variation along this axis. Axis (2) has an eigenvalue of 0.501 which suggests a good separation along the axis. The environmental variables explain 79.1% of the variation along this axis. The TWINSPAN "final site groups" correspond well with the patterns of sites on the positive half of axis (1) and quite well on the negative half of axis (1). On axis (2) the TWINSPAN groups correspond well with sites at either end of the axis but the pattern is not clear in the middle section.

At the positive end of axis (1) is the exposed pioneer (site group 27*), the **Deschampsia alpina - Saxifraga stellaris** assemblage and the later pioneer (site group 26*), the **Phleum alpinum - Lotus corniculatus** assemblage interspersed with the pioneer snowbed (site group 12*), the **Lotus corniculatus - Salix phylicifolia** assemblage. These groups are followed by the exposed pioneer snowbed (site group 7*), the **Deschampsia flexuosa - Epilobium alsinifolium** assemblage. These groups correspond with fluvial activity, bare ground, dowel heave, frost-heave and pH. Further along the axis, are sites from the lichen heath (site group 11*), the **Cladonia chlorophaea - Cladonia fimbriata** assemblage interspersed with the atypical snowbed (site group 20*), the **Empetrum nigrum - Salix phylicifolia** assemblage mainly found on M4. Following this are a mixture of sites which include the grazed mature meadow (site group 16*), the **Potentilla crantzii - Melampyrum sylvaticum** assemblage; the mature birch woodland (site group 17*), the **Betula pubescens - Gymnocarpium dryopteris** assemblage; the lichen heath (site group 21*), the **Vaccinium vitis-ideae - Cladonia rangiferina** assemblage; and birch woodland heath (site group 9*), the **Phyllodoce caerula - Empetrum nigrum** assemblage. The dominant groups at the negative end of axis (1) are site groups (21*), (17*) and (9*). The corresponding environmental variables at the negative end of axis (1) are soil stain, root depth, age, humus depth and vegetation cover.

At the positive end of axis (2) is (site group 21*), and this is followed by (site group 11*) which are both lichen heath assemblages. These groups correspond with dry positions, low snow cover, higher proportions of boulders and gravels and fluvial activity, suggesting that these are disturbed or exposed sites at this end of the axis. The central portion of axis (2) comprises a disordered sequence of assemblages. The negative end of the axis consists primarily of (site group 6*) and (site group 17*) which represent mature sites. The corresponding environmental parameters are humus depth, root depth, age, easterly aspect and animal influence.

These results are summarised in Fig. 5.18 and from this it is possible to see that axis (1) is largely influenced by age in terms of bare ground and disturbed sites, with pioneer assemblages, at the positive end of the axis and well developed soils and high vegetation cover, with mature assemblages, at the negative end. Position does not seem to be of particular importance on axis (1). Axis (2) is possibly an exposure axis but does not conform to the anticipated patterns. The separation of sites suggests that dry and snow-free areas are the important influences on the second axis. It appears that exposure, in terms of dryness and low snow cover, is more related to particular moraines than it is to microtopography. The driest and most snow-free sites, found on moraines (3) and (4), occur at the positive end of the axis. Sites of intermediate moisture and snow cover, consisting of a disordered sequence of pioneer and late intermediate sites, occur at the centre of the axis. The moistest sites, with highest snow cover on the oldest terrain, occur at the negative end of the axis. This may also explain the heath assemblage (species group 11) at Fåbergstølsbreen which showed more correspondence between pioneer and late intermediate sites than with early intermediate sites.

5.4.2 Species patterns on DCA axes (1) and (2) at Fåbergstølsbreen

By referring to Table 5.10 and Table 4.10 it is possible to relate the sequence of species on DCA axes (1) and (2) to the TWINSPAN "final species groups" described in chapter (4) and thus elucidate the influence of particular environmental variables on the species pattern across Fåbergstølsbreen foreland. The TWINSPAN species assemblages correspond well with the sequence of species along axis (1) although the end portion has a slightly disordered sequence of the older ground TWINSPAN assemblages. The sequence on axis (2) corresponds well with the TWINSPAN "final species groups".

At the positive end of axis (1) is the pioneer (species group 27) interspersed with the pioneer snowbed (species group 26). This is followed by the pioneer snowbed (species group 7) and the heath (species groups 11 and 12) associated with mature and young terrain, and these groups are interspersed with the early intermediate heath (species group 8). The positive portion of axis (1) corresponds with fluvial activity, bare gravels, bare boulders, dowels and frost-heave. Further along the axis is the early intermediate heath (species group 37) and this in turn is followed by a disordered sequence of mainly mature assemblages consisting of the early intermediate heath (species group 36) interspersed with the widespread heath (species group 19), the mature woodland (species group 21) and the mature heath (species group 20). The negative end of axis (1) corresponds with stain depth, root depth, age, humus depth, vegetation cover and bryophyte cover.

At the positive end of axis (2) is the early intermediate heath (species group 36). This is followed by the early intermediate heath (species group 37) which is interspersed with the early intermediate heath (species group 8) and the widespread heath (species group 19). The positive portion of axis (2) corresponds with dryness, low snow duration, bare boulders and gravels, and fluvial activity. Towards the negative end of the axis are the pioneers (species groups 26 and 27) interspersed with (species group 19) and the pioneer snowbed (species group 7). Following the pioneer groups is the mature heath (species group 20), the heaths (species groups 11 and 12) and, at the negative end of the axis, the mature woodland (species group 21). The negative end of the axis corresponds with humus depth, root depth, age, easterly aspect and animal influence. These results complement the site results described in the previous section and are summarised in Fig. 5.26.

5.4.3 TWINSPAN group centroids of sample and species scores at Fåbergstølsbreen

Fig. 5.2 shows the DCA centroids of TWINSPAN "final site group" sample scores and reveals the location of the "final site groups" on both axes in relation to the environmental parameter biplot scores. Fig. 5.10, showing the DCA centroids of TWINSPAN "final species group" scores, reveals the position of the "final species groups" on both axes in relation to the environmental parameter biplot scores. In addition, Table 5.18, the weighted correlation matrix, can be used to elucidate further the relative influence of environmental parameters on the site and species groups. These plots and the correlation matrix are used to outline and corroborate the main findings of the previous two sections at Fåbergstølsbreen. The critical value for " r " on this foreland is 0.307.

Towards the positive end of axis (1) are an important cluster of environmental parameters mainly associated with poorly developed soils which are highly correlated with axis (1) and they are fluvial activity ($r = +0.721$), bare gravels ($r = +0.682$), and bare boulders ($r = +0.561$). Towards the negative end of axis (1) is stain depth ($r = -0.879$) and vegetation cover ($r = -0.453$). Half way between the negative ends of axis (1) and (2) are a tightly clustered group of environmental parameters associated with developed soils which is highly negatively correlated with axis (1), namely humus depth ($r = -0.616$), age ($r = -0.648$) and root depth ($r = -0.657$). This cluster of parameters is also negatively correlated with axis (2) with humus depth ($r = -0.358$), age ($r = -0.346$) and root depth ($r = -0.352$) suggesting that age is important on both axis (1) and (2). Easterly aspect ($r = -0.316$) and animal influence ($r = -0.284$) are also negatively correlated with axis (2) and appear to be relatively important influences on this axis. At the positive end of axis (2) is dryness ($r = +0.323$) and low snow cover ($r = +0.247$). High-slope position is also correlated with the positive end of the axis but the correlation is low ($r = +0.08$). In the previous section it is suggested that exposure and snow cover are associated more with age than with high-slope position and the sequence of the parameters lends support to this view. Axis (1) appears to be especially related to age, vegetation cover and fluvial disturbance, whereas axis (2) is more related to snow cover, moisture and age.

Those parameters which are most positively correlated with age, and thus associated with mature terrain, are root depth (r = +0.789), humus depth (r = +0.781), stain depth (r = +0.725), vegetation cover (r = +0.661) and bryophyte cover (r = +0.585). Those parameters negatively correlated with age, and thus associated with younger ground, are bare ground gravels (r = -0.671), bare ground boulders (r = -0.614), fluvial activity (r = -0.502), frost-heave (r = -0.366), dowel heave (r = -0.277). The parameters most correlated with high-slope position are dryness (r = +0.318), solifluction (r = +0.312) and slope (r = +0.295) and the parameters most negatively correlated with high-slope position are bryophyte cover (r = -0.492) and fluvial activity (r = -0.346). However, position has a low correlation with both axis (1) (r = -0.136) and axis (2) (r = +0.08) which adds support to the contention that microtopography does not appear to be a significant influence on this foreland.

According to Fig. 5.2 there is a noticeable division between the DCA centroid scores of TWINSPAN "final site group" pioneer, or exposed assemblages, and the assemblages found on older or more sheltered sites. The exposed pioneer (site group 27*), the lichen heath (site group 26*), the pioneer snowbed (site group 12*) and the exposed pioneer snowbed (site group 7*) show correspondence with the positive end of axis (1) and thus the parameters associated with young terrain, poorly developed soils and low vegetation cover. The rest of the groups occur towards the negative end of axis (1), and thus show correspondence with parameters associated with developed soils and higher vegetation cover. Towards the positive end of axis (2) is the lichen heath (site group 21*) and the lichen heath (site group 11*) corresponding with drier snow-free sites. Towards the centre of the axis is the atypical snowbed (site group 20*) and at the centre is the birch woodland heath (site group 9*). Towards the negative end of axis (2) is the mature birch woodland (site group 17*) and a little further down is the grazed mature meadow (site group 16*) and these groups correspond with moist sites with higher snow cover. The separation of the groups by soil development and vegetation cover on axis (1) and by moisture and snow cover on axis (2) is clearly presented in the DCA centroid plot.

According to Fig. 5.10 there is also a noticeable division between the DCA centroid scores of TWINSPAN "final species group" pioneer assemblages, and the more developed assemblages. Towards the positive end of axis (1) is the pioneer (species group 27) and the pioneer snowbed (species group 26) and a little towards the centre is another pioneer snowbed (species group 7). Close to the centre of the axis is the early intermediate heath (species group 8) and then the rest of the assemblages are located slightly towards the negative end of axis (1) showing that these assemblages have well developed soils and a high cover of vegetation. Towards the positive end of axis (2), which corresponds with the drier snow-free sites, is the early intermediate heath (species group 36) followed by the early intermediate lichen heath (species group 37) and the early intermediate heath (species group 8). Towards the centre is the widespread heath (species group 19). Furthest towards the negative end, corresponding with the moister sites with a higher snow cover, is the mature woodland (species group 21), the heath (species group 11) and towards the centre, the mature heath (species group 20).

From the spread of environmental parameters, TWINSPAN "final site groups" and "final species groups", on Figs. 5.2 and 5.3, it emerges that the sequence of sites and species on axis (1) is influenced mostly by vegetation cover, soil development and age and axis (2) is influenced more by moisture, snow cover and age. It appears that microtopography is not an important influence on this foreland and the so-called "*Microtopographic (exposure-moisture-snowmelt) factor complex*" (*sensu*: Whittaker, 1985) is related more to age than it is to microtopography at Fåbergstølsbreen. This is a most interesting result and will be discussed at greater length in the concluding chapter. As at Austerdalsbreen, some of the mature terrain environmental parameters, including age, are found clustered between axis (1) and (2), suggesting that the influence of age cannot be separated from other environmental parameters and thus the results are to some extent obscure. Despite these problems, however, it is still possible to make useful and ecologically meaningful interpretations from the environmental data as has been shown by these results. The DCA centroid scores of TWINSPAN "final site groups" and "final species groups" correspond well with the pattern of environmental parameters on axis (1) and (2) suggesting that the trends found on both axis (1) and (2) are ecologically meaningful.

5.4.4 Summary of DCA ordination results at Fåbergstølsbreen

Both axis (1) and (2) have high eigenvalues and there is very good separation of sites and species on these axes suggesting that the results from the ordination on both axis (1) and (2) are ecologically meaningful. The rank tables (Tables 5.2 and 5.10), displaying the distribution of the TWINSPAN "final site groups" and "final species groups" on the DCA ordination axes, provide clear and easily interpreted representations of the results on axis (1) and most of axis (2). The TWINSPAN "final species groups" correspond well with the sequence of species along axis (1) and axis (2), although the end portion of axis (1) has a slightly disordered sequence of the older ground species groups. The TWINSPAN "final site groups" correspond especially well with the patterns of sites on the positive half of axis (1), and quite well on the negative half of axis (1). On axis (2) the TWINSPAN site groups correspond well with sites at either end of the axis but the pattern is not clear in the middle section. The plots and correlation matrices have provided further elucidation and confirmation of the results derived from the rank tables, especially concerning axis (2). The main findings from sections 5.4.1. to 5.4.3., derived from the DCA ordination results for Fåbergstølsbreen, are summarised below. The DCA centroid scores of TWINSPAN "final site groups" and "final species groups" correspond well with the pattern of environmental parameters on axis (1) and (2) suggesting that the trends found on both axis (1) and (2) are ecologically meaningful.

There appears to be a strong age-related sequence from bare ground and disturbed sites (with pioneer assemblages) at the positive end of axis (1), to sites associated with developed soils and a high vegetation cover (with mature or late intermediate assemblages) at the negative end of axis (1). Correlation shows age, and associated factors related to soil and vegetation development, to be highly negatively correlated with axis (1), while fluvial activity and bare ground gravels and boulders are highly positively correlated with axis (1). Position does not seem to be of particular importance on axis (1). As at Austerdalsbreen, some of the environmental parameters associated with mature terrain, including age, are found clustered between axis (1) and (2), suggesting that the influence of age cannot be separated from other environmental parameters. Most of the environmental variables are significantly correlated with age and thus the influence of factors other than age, on the sequence on axis (2), could be obscured. Despite these problems, however, it is still possible to make useful and ecologically meaningful interpretations from the environmental data.

Despite the obvious influence of age on axis (2), the main influence appears to be dryness and low snow cover, which are both positively correlated with axis (2). The sequence on axis (2) progresses from dry sites with a low snow cover, associated with lichen heath species groups, at the positive end through a combination of late intermediate and pioneer species groups, of intermediate moisture, to moist sites with a long snow cover associated with woodland and meadow species groups. Correlation shows that humus depth, age and root depth are negatively correlated with axis (2) suggesting that age is an important influence on this axis. The sequence on axis (2) may explain the TWINSPAN "final species groups", at Fåbergstølsbreen, which showed greater correspondence between pioneer and late intermediate ground assemblages (sites of higher or intermediate moisture) than with the early intermediate assemblages (the driest sites on the foreland). On this foreland, it appears that the degree of exposure, in terms of dryness and low snow cover, is more related to particular moraines than it is to microtopography. Microtopography is therefore not an important influence on this foreland and the so-called "*Microtopographic (exposure-moisture-snowmelt) factor complex*" (*sensu*: Whittaker, 1985) is related more to age than it is to position at Fåbergstølsbreen. This will be discussed at greater length in the concluding chapter (see sections 7.2.3, 7.3.3 and 7.4).

On axis (1) the most distinct site groups are the exposed pioneer snowbed (site group 7*) and the lichen heath (site group 11*) and on axis (2), the mature birch woodland (site group 17*) and the lichen heath (site group 21*). The most distinct "final species assemblages" on axis (1) are the pioneer (species group 27), the pioneer snowbed (species group 7) and the heath (species group 11) and on axis (2), the heath (species group 11), the mature woodland (species group 21), the early intermediate heath (species group 36), the early intermediate lichen heath (species group 37) and the pioneer (species group 27). This suggests that most of the other members of the TWINSPAN site and species groups overlap with one another on the ordination sequence. Generally, therefore, the evidence supports the notion that there is a gradient of assemblages, some tighter than others, as opposed to distinct and exclusive communities at Fåbergstølsbreen

5.5 Storbreen low (1)

5.5.1 Site (sample) patterns on DCA axes (1) and (2) at Storbreen low (1).

By referring to Table 5.3 and the profile diagram (Fig. 4.4), for the location of specific sites where the pattern is not clear, the following site patterns emerge on DCA ordination axes (1) and (2). Axis (1) has an eigenvalue of 0.351 showing that there is quite good species and sample separation along the axis and this axis is ecologically meaningful. The environmental variables explain 94.4% of the variation along this axis. Axis (2) has an eigenvalue of 0.229 which is high enough to suggest fair separation along the axis. The lower eigenvalues for axis (1) and (2) on this foreland, in comparison to most of the other forelands, is explained by the lack of early pioneer sites on this foreland and thus the separation of sites is thus not as clear. The environmental variables explain 85.2% of the variation along this axis. There is a relatively clear correspondence between the TWINSPAN "final site groups" and the pattern of sites on axes (1) and (2), especially towards either end of the axes.

At the positive end of axis (1) is the exposed lichen heath (site group 15*), the **Alectoria ochroleuca Cetraria cucullata,** assemblage and the early intermediate lichen heath (site group 14*), the **Phyllodoce caerula - Cladonia portentosa,** assemblage. This is followed by members of (site group 12*), the late-snow early intermediate heath, the **Empetrum nigrum - Stereocaulon alpinum,** assemblage interspersed with, the lichen heath groups and the exposed early intermediate snowbed (site group 13*), the **Salix glauca - Salix herbacea** assemblage. Dryness, high-slope position, bare gravels, trampling and lack of snow correspond with the positive end of the axis. Following the more exposed groups is the late-snow early intermediate heath (site group 11*), the **Vaccinium uliginosum - Salix lanata,** assemblage and after this the late intermediate snowbed (site group 4*), the **Salix glauca - Anthoxanthum odoratum,** assemblage and lastly the mature late-snow heath or atypical snowbed (site group 10*), the **Festuca ovina - Salix herbacea,** assemblage. Stain depth, humus depth, age, solifluction, vegetation cover and soil texture correspond with the negative end of the axis.

At the positive end of axis (2) is the late intermediate snowbed (site group 4*) interspersed with the exposed early intermediate snowbed (site group 13*). This is followed by the late snow early intermediate heath (site group 12*). These are low-slope position groups and they correspond with root depth, bare boulders and gravels, northerly aspect, slope and bare ground fines. The middle section of the axis has a disordered sequence of sites that is difficult to interpret, mainly consisting of the late intermediate snowbed (site group 4*) and the two lichen heaths (site groups 14* and 15*). The negative end of the axis is dominated by the early intermediate lichen heath (site group 14*), the mature late snow heath (site group

10*) and the late snow early intermediate heath (site group 11*). The negative end of axis (2) corresponds with solifluction, soil texture, frost activity, age and vegetation cover.

These results are summarised in Fig. 5.19 and can be seen that axis (I) appears to be influenced by exposure, high-slope position and age, with the more exposed, high-slope positions and/or younger sites being prevalent at the positive end of axis (1) and the mature low-slope sites being prevalent at the negative end of the axis. With the appearance of a considerable number of older sites at the positive end of this axis, it would seem that exposure and position are almost as important as age. Axis (2) is also influenced by both age and exposure. The positive end of axis (2) mainly comprises low-slope positions, including low-slope positions on older ground, and the sequence graduates through a mixture of exposed sites to the oldest terrain, and/or high-slope positions, at the negative end. Axis (2) is especially difficult to interpret and the low eigenvalue suggests that the results from this axis are not very ecologically meaningful. The site separation on ordination axis (1) corresponds with the TWINSPAN "final site groups" but is not identical.

5.5.2 Species patterns on DCA axes (1) and (2) at Storbreen low (1).

By referring to Table 5.11 and Table 4.10, it is possible to relate the sequence of species on DCA axes (1) and (2) to the TWINSPAN "final species groups" described in chapter (4) and thus elucidate the influence of particular environmental variables on the species patterns across Storbreen low (1) foreland. The TWINSPAN "final species groups" correspond quite well with the sequence of species along axis (1) although the end portion has a slightly disordered sequence of the older ground TWINSPAN "final species groups". The sequence on axis (2) does not correspond well with the TWINSPAN species groups, except towards the positive end.

At the positive end of axis (1) is the exposed lichen heath (species group 31) followed by the exposed early intermediate snowbed (species group 30). This is replaced by the early intermediate snowbed (species group 29) interspersed with the late-snow early intermediate heath (species group 28) and the widespread heath (species group 13). These groups correspond with dry and high-slope positions, bare gravels, trampling, low snow cover and higher pH. In the middle of the axis is the early intermediate heath (species group 11) and the widespread snowbed (species group 12). The negative portion of the axis consists of older ground assemblages starting with the mature late-snow heath (species group 10) and followed by a disordered sequence of the late intermediate snowbed (species group 9) and the mature heath (species group 8), the latter being more prevalent at the far negative end of the axis.

At the positive end of axis (2) is the late intermediate snowbed (species group 9) interspersed mainly with the early intermediate snowbed (species group 29) and, further down the axis, by the widespread snowbed (species group 12). These groups correspond with root depth, bare ground, northerly aspect, and slope. The negative two thirds of the axis consists of a highly disordered sequence of species belonging to all of the species groups. These results are summarised in Fig. 5.27 and they complement the TWINSPAN "final site group" results of the previous section.

5.5.3 TWINSPAN group centroids of sample and species scores at Storbreen low (1).

Fig. 5.3 shows the DCA centroids of TWINSPAN "final site group" sample scores and reveals the position of the "final site groups" on both axes in relation to the environmental parameter biplot scores. Fig. 5.11, the DCA centroids of TWINSPAN "final species group" scores, reveals the location of the "final species groups" on both axes in relation to the environmental parameter biplot scores. In addition, Table 5.19, the weighted correlation matrix, can be used to elucidate further the relative influence of environmental parameters on the site and species groups. These plots, and the correlation matrix, are used to support and outline the main findings of the previous two sections at Storbreen low (1). The critical value for " r " on this foreland is 0.307.

The most important environmental variables on Fig. 5.11 are widely distributed between the axes and their relative influence, on the TWINSPAN "final groups", are to some extent obscured. The most important variables towards the positive end of axis (1) are dryness ($r = +0.696$), position ($r = +0.523$), bare ground gravels ($r = +0.436$), trampling ($r = +0.403$), snow-lie ($r = +0.388$) and pH ($r = +0.373$). Position and snow-lie are found half way between axes (1) and (2), showing that these are important variables on both axes. The most important variables towards the negative end of axis (1) are stain depth (r = -0.808), humus depth (r = -0.755), age (r = -0.667) and vegetation cover (r = -0.399). Age, solifluction and vegetation cover are found half way between the negative ends of axis (1) and (2), showing that these are important variables on both axes. It would appear that axis (1) is influenced by soil development, age and microtopography. Towards the positive end of axis (2) is root depth ($r = +0.436$), bare ground boulders ($r = +0.446$), bare ground gravels ($r = +0.321$) and to a lesser extent fluvial activity ($r = +0.158$) and towards the negative end of the axis is solifluction (r = -0.513), frost-heave (r = -0.438), soil texture (r = -0.456), vegetation cover (r = -0.348), position (r = -0.335) and snow-lie (r = -0.313). It would appear that although axis (1) and (2) are related, axis (2) is influenced more by disturbance factors and microtopography. The most disturbed bare ground sites occur at low-slope positions on the younger terrain, possibly due to a combination of fluvial activity and long snow duration. However, the high-slope sites are also effected by frost activity, solifluction and exposure, due to low snow cover, so there appears to be disturbance at both ends of axis (2). Vegetation cover and soil development appears to be greater at high-slope positions, although not on the crests (which are associated with bare ground).

Those parameters which are most positively correlated with age, and thus associated with mature terrain, are humus depth ($r = +0.762$), stain depth ($r = +0.791$), solifluction ($r = +0.643$) and vegetation cover ($r = +0.391$). Those parameters negatively correlated with age are bare ground gravels (r = -0.612), bare ground boulders (r = -0.479), pH (r = -0.36) and slope (r = -0.343). Age is probably less important on this sequence of moraines because the early young terrain is missing from the data set. The parameters most correlated with high-slope position are dryness (r = +0.803), snow-lie (r = +0.77), frost-heave (r = +0.697) and dowels (r = +0.318). The parameters most negatively correlated with high-slope position are fluvial activity (r = -0.477) and root depth (r = -0.398). The high correlations that position has on both axis (1) (r = +0.523) and axis (2) (r = -0.335) suggests that microtopography is a highly significant influence on this foreland.

According to Fig. 5.3 there is a wide distribution of TWINSPAN "final site groups" across the plot showing that the groups are fairly distinct and thus the relative influence of the most important environmental variables, on each of the groups, can be seen. The exposed lichen heath (site group 15*) and, to a lesser extent, the early intermediate lichen heath (site group 14*) shows correspondence with the positive end of axis (1) and parameters associated with dry, poorly developed soils at high-slope positions. Towards the centre of the axis are the early intermediate site groups (12*), (13*) and (11*) of intermediate soil development and moisture conditions. A little towards the negative end of axis (1) are the late intermediate snowbed (site group 4*) and the mature late-snow heath (site group 10*) showing correspondence with parameters associated with developed soils, higher moisture and vegetation cover, and age. Towards the positive end of axis (2) is the late intermediate snowbed (site group 4*) and the exposed early intermediate snowbed (site group 13*) corresponding with low-slope sites with a long snow duration and, to some extent, higher fluvial activity. Towards the centre of the axis is the late-snow early intermediate heath (site group 12*). At the centre, to the right of the axis, is the exposed lichen heath (site group 15*) and towards the negative end of axis (2) is the early intermediate lichen heath (site group 14*) corresponding with drier, more exposed, sites of intermediate vegetation cover. A little towards the negative end of axis (2), is the late-snow early intermediate heath (site group 11*) corresponding with high-slope positions, more developed soils and intermediate moisture and further to the negative end of axis (1), the mature late snow heath (site group 10*) corresponding with solifluction, more developed soils and high moisture. It is apparent that axis (1) is most related to moisture, soil development and age, whereas axis (2) is more related to exposure and disturbance.

According to Fig. 5.11 there is greater similarity between the TWINSPAN "final species groups", than there is between the "final site groups", as many of the groups are clustered around the centre of the plot. This would suggest that the species groups are more similar to each other than on the previous forelands and this can be explained by the lack of early pioneer assemblages on this foreland. Slightly towards the positive end of axis (1) is the exposed lichen heath (species group 31) and the exposed early intermediate snowbed (species group 30). At the centre of axis (1) the early intermediate heath (species group 11), the widespread snowbed (species group 12), the widespread heath (species group 13), the late-snow early intermediate heath (species group 28) and the early intermediate snowbed (species group 29). The mature late-snow heath (species group 10), the late intermediate snowbed (species group 9) and, furthest, the mature heath (species group 8) occurs slightly towards the negative end of the axis showing that these assemblages have well developed soils and a high cover of vegetation. Towards the positive end of axis (2), which corresponds with the low-slope sites with a long snow duration, is the late intermediate snowbed (species group 9) followed by the early intermediate snowbed (species group 29) and the exposed early intermediate snowbed (species group 30). At the centre is a disordered sequence of species groups (31), (28), (13), (12), (11), and (8). Slightly towards the negative end of axis (2), corresponding with age and solifluction, is the mature heath (species group 8) and the mature late-snow heath (species group 10). The location of species groups on axis (2) suggests an exposure and disturbance axis but the sequence is not distinct.

From the spread of environmental parameters, TWINSPAN "final site groups" and "final species groups", on Figs. 5.3 and 5.11, it emerges that the sequence of sites and species on axis (1) is influenced mostly by moisture, soil development and age, while axis (2) is influenced more by exposure and disturbance variables. It appears that microtopography is an important influence on this foreland and the so-called *"Microtopographic (exposure-moisture-snowmelt) factor complex"* (*sensu*: Whittaker, 1985) is apparent at Storbreen low (1). Some of the factors associated with mature terrain are found clustered, between axis (1) and (2), with microtopography-related variables, suggesting that the relative influence of the variables is difficult to separate and thus the relationships are obscured. Despite these problems, however, it is still possible to make useful and ecologically meaningful interpretations from the environmental data. The relative influence of microtopography, in comparison to age, has possibly been exaggerated, due to the lack of early pioneer sites across this foreland sequence. The DCA centroid scores of TWINSPAN "final site groups" and "final species groups" correspond well with the pattern of environmental parameters on axis (1) but are less distinct on axis (2) suggesting that the trends found on axis (2) are not very meaningful.

5.5.4 Summary of DCA ordination results at Storbreen low (1).

Axis (1) has an eigenvalue (0.351) suggesting relatively good separation of sites although the low eigenvalue (0.229) of axis (2) suggests poor separation of sites and species and thus a difficult axis to interpret. The rank tables (Tables 5.3 and 5.11), displaying the distribution of the TWINSPAN "final site groups" and "final species groups" on the DCA ordination axes, provide clear and easily interpreted representations of the results on axis (1) but the rank on axis (2) is considered almost ecologically meaningless. The TWINSPAN "final species groups" correspond quite well with the sequence of species along axis (1) although the end portion has a slightly disordered sequence of the older ground TWINSPAN "final species groups". The sequence on axis (2) does not correspond well with the TWINSPAN species assemblages except towards the positive end. There is a relatively clear correspondence between the TWINSPAN "final site groups" and the pattern of sites on axes (1) and (2), especially towards either end of the axes. The plots and correlation matrices have provided further elucidation and confirmation of the results derived from the rank tables on axis (1), and have contributed to interpretation of axis (2). The main findings from sections 5.5.1. to 5.5.3., derived from the DCA ordination results for Storbreen low (1) are summarised below.

There appears to be a strong moisture and soil development-related sequence on axis (1) from drier, exposed high-slope sites (characterised by lichen heath assemblages) at the positive end of axis (1) to mature, low-slope and moist sites, characterised by mature heath or late-snow heath assemblages, at the negative end of the axis. With the appearance of a considerable number of older sites, at the positive end of this axis, it would seem that exposure and position are almost as significant as age. Correlation shows stain depth, humus depth, dryness, age and position to be the most important variables on axis (1). It therefore appears that microtopography is an important influence on this foreland and the so-called *"Microtopographic (exposure-moisture-snowmelt) factor complex"* (*sensu*: Whittaker, 1985) is apparent at Storbreen low (1). Microtopography is related to both dryness, on axis (1), and disturbance variables (i.e. frost and fluvial activity) on axis (2), and thus clear differences, between axis (1) and (2), have been obscured. Despite these problems, however, it is still possible to make useful and ecologically meaningful interpretations from the environmental data. The importance of microtopography as an influence on vegetation pattern, in comparison to age, has probably been exaggerated due to the lack of early pioneer sites on this foreland sequence.

The sequence on axis (2) progresses from mainly low-slope positions, with relatively low vegetation cover and disturbed by fluvial activity characterised by snowbed species groups, graduating through a mix of sites, with intermediate vegetation cover and frost activity, to the oldest or high-slope positions with higher vegetation cover and high disturbance by solifluction, characterised by late intermediate mature heath species groups. These mature species groups occur towards the negative end of axis (1), so are not likely to be highly disturbed by frost activity. Correlation shows that solifluction, frost-heave, soil texture, root depth, bare ground boulders and gravels are the most important influences on this axis but the low eigenvalue suggests that the results from this axis are not highly significant.

On axis (1) the most distinct species groups on axis (1) are the exposed lichen heath (species group 31) and the early intermediate heath (species group 11) and none on axis (2). The most distinct site-groups on axis (1) are the mature late-snow heath (site group 10*) and the exposed lichen heath (site group 15*) and none on axis (2). This suggests that most of the other members of the TWINSPAN site and species groups overlap with one another on the ordination sequence. Generally, therefore, the evidence supports the notion that there is a gradient of species groups, some tighter than others, across the foreland as opposed to distinct and exclusive communities at Storbreen low (1).

5.6 Storbreen low (2)

5.6.1 Site (sample) patterns on DCA axes (1) and (2) at Storbreen low (2)

By referring to Table 5.4 and the profile diagram (Fig. 4.5), for the location of specific sites where the pattern is not clear, the following site patterns emerge on DCA ordination axes (1) and (2). Axis (1) has an eigenvalue of 0.425 showing that there is good species and sample separation along the axis and this axis is ecologically meaningful. The environmental variables explain 95.4% of the variation along this axis. Axis (2) has an eigenvalue of 0.277 which is high enough to suggest relatively good separation along the axis. The slightly lower eigenvalues for axis (1) and (2) on this foreland, in comparison to most of the other forelands is explained by the lack of early pioneer sites and thus the separation of sites is not as clear. The environmental variables explain 79.1% of the variation along this axis. There is a relatively clear correspondence between the TWINSPAN groups and the pattern of sites on axes (1) and (2), especially towards either end of the axes.

At the positive end of axis (1) is the exposed lichen heath (site group 7*), the **Cetraria nivalis - Alectoria ochroleuca,** assemblage and this is followed by the exposed early intermediate lichen heath (site group 13*), the **Cladonia chlorophaea - Cetraria nivalis,** assemblage which is increasingly dominated by the early intermediate snowbed (site group 12*), the **Cassiope hypnoides - Salix herbacea,** assemblage slightly further down the axis. The corresponding environmental parameters, at the positive end of the axis, are bare gravels, frost-heave, altitude, dryness and lack of snow. Site group (12*) is tightly distributed towards the centre of the axis and further down becomes interspersed with both site group (13*) and a few members of the mature lichen heath (site group 11*), **Cladonia arbuscula - Cetraria ericetorum**, assemblage. Towards the negative end of axis (1) is a striking change to a combination of the late-snow late intermediate heath (site group 10*), **Salix glauca - Vaccinium uliginosum** assemblage; the late intermediate snowbed (site group 4*), the **Salix herbacea - Ranunculus acris** assemblage; and site group (11*). The negative end of the axis corresponds with the environmental variables root depth, vegetation cover, humus depth, soil texture, stain depth and age.

At the positive end of axis (2) is the late intermediate snowbed (site group 4*) followed by a mix of mainly late-snow late intermediate heath (site group 10*) and exposed lichen heath (site group 7*) interspersed with the early intermediate snowbed (site group 12*) and the exposed early intermediate lichen heath (site group 13*). The corresponding environmental variables are bare boulders, fluvial activity, altitude, bare gravels and bryophyte. Most of the central portion of the axis is dominated by the early intermediate snowbed (site group 12*) and the exposed early intermediate heath (site group 13*) interspersed with the exposed lichen heath (site group 7*). The negative end of the axis is dominated by the mature lichen heath (site group 11*). The corresponding environmental parameters at the negative end of axis (2) are vegetation cover, solifluction, position and stain depth.

These results are summarised in Fig. 5.20 and from this it is possible to see that axis (1) appears to be influenced mainly by age, but also by microtopography. At the positive end of axis (1), exposed younger sites are prevalent and these give way to relatively young low-slope positions which in turn give way to older low-slope positions and from there to mature heath. Axis (2) appears to be influenced mostly by position, but also age, with mainly snowbed site groups, and the corresponding environmental variables of fluvial activity, low-slope position and higher bryophyte cover at the positive end, contrasting with mainly heath groups, and the corresponding variables of high vegetation cover, solifluction, high-slope positions and stain depth, at the negative end of axis (2). The site separation on ordination axis (1) is relatively close to that found by the TWINSPAN "final site groups" but not identical.

5.6.2 Species patterns on DCA axes (1) and (2) at Storbreen low (2)

By referring to Table 5.12 and Table 4.10 it is possible to relate the sequence of species on DCA axes (1) and (2) to the TWINSPAN "final species groups" described in chapter (4) and thus elucidate the influence of particular environmental variables on the species patterns across Storbreen low (2) foreland. The TWINSPAN "final species groups" correspond quite well with the sequence of species along axis (1) although the end portion has a slightly disordered sequence of the older ground TWINSPAN "final species groups". The sequence on axis (2) corresponds quite well with the TWINSPAN "final species groups".

At the positive end of axis (1) is the exposed lichen heath (species group 16) followed by the exposed early intermediate heath (species group 17) interspersed with the early intermediate lichen heath (species group 18). These groups are in turn replaced by the early intermediate snowbed (species group 19) interspersed with the exposed early intermediate lichen heath (species group 10). These groups correspond with bare gravels, frost-heave, altitude, dryness and low snow cover. On the negative half of the axis is the early intermediate snowbed (species group 6), interspersed with the widespread heath (species group 11). This is followed by a fairly disordered sequence of mature assemblages consisting, firstly, of the mature lichen heath (species group 14) interspersed with the late snow late intermediate heath (species group 31) and then, towards the negative end, the late intermediate snowbed (species group 30) interspersed with (species group 31). The negative end of the axis corresponds with root depth, vegetation cover, humus depth, soil texture, stain depth and age.

At the positive end of axis (2) is the late intermediate snowbed (species group 30) which is replaced by the late-snow late intermediate heath (species group 31) interspersed by a number of species but mainly those belonging to the early intermediate snowbed (species group 6), the early intermediate snowbed (species group 19) and the exposed early intermediate lichen heath (species group 10). These groups correspond with bare boulders, fluvial activity, altitude, bare gravels, and bryophyte cover. In the middle portion of the axis there is a disordered sequence of exposed assemblages consisting mainly of the exposed lichen heath (species group 16), the exposed early intermediate lichen heath (species group 17) and the early intermediate lichen heath (species group 18) interspersed with the early intermediate heath (species group 11). At the negative end of the axis is the mature lichen heath (species group 14). The negative end of the axis corresponds with vegetation cover, solifluction, position, stain depth, low snow cover and easterly aspect. These results are summarised in Fig. 5.28 and correspond with those of the TWINSPAN "final site groups" described in the previous section.

5.6.3 TWINSPAN group centroids of sample and species scores at Storbreen low (2).

Fig. 5.4 shows the DCA centroids of TWINSPAN "final site group" sample scores and reveals their location on both axes in relation to the environmental parameter biplot scores. Fig. 5.12, showing the DCA centroids of TWINSPAN "final species group" scores, reveals the location of the species groups on both axes in relation to the environmental parameter biplot scores. In addition, Table 5.20, the weighted correlation matrix, can be used to elucidate further the relative influence of environmental parameters on the site and species groups. These plots, and the correlation matrix, are used to support and outline the main findings of the previous two sections at Storbreen low (2). The critical value for " *r* " on this foreland is 0.307.

The most important environmental variables on Fig. 5.4 and 5.12 are quite widely distributed between the axes, suggesting that variables associated with microtopography and age are difficult to separate. The most important variables, towards the positive end of axis (1), are bare ground gravels (*r* = +*0.*794), frost activity (*r* = +*0.*767), altitude (*r* = +*0.*738), dryness (*r* = +*0.*594), low snow cover (*r* = +*0.*524) and position (*r* = +*0.*523). Position, dryness and snowlie are found half way between axes (1) and (2) showing that these are important variables on axes (1) and (2). The most important variables towards the negative end of axis (1) are root depth (*r* = -0.788), humus depth (*r* = -0.746), vegetation cover (*r* = -0.746), soil texture (*r* = -0.716), stain depth (*r* = -0.715) and age (*r* = -0.713). The spread of these soil development and age variables suggests that they are much more important on axis (1) than on (2), although vegetation cover is the most negatively correlated parameter with axis (2). Axis (1) is therefore mostly related to age but it is also influenced considerably by microtopography, as shown by the occurrence of the high-slope, drier sites towards the positive end of axis (1). The correlations with axis (2) are not very strong: the most correlated parameters towards the positive end of axis (2) being bare ground boulders (*r* = +*0.*341) and fluvial activity (*r* = +*0.*268); and towards the negative end of the axis are vegetation cover (*r* = -0.286), solifluction (*r* = -0.237), and position (*r* = -0.23). As at Storbreen low (1), axis (1) and (2) are related, but axis (2) is influenced more by disturbance factors and microtopography. It would appear that sites disturbed by fluvial activity, with a high proportion of bare ground boulders and long snow-lie, occur at low-slope positions while the high-slope sites are effected by solifluction and exposure due to low snow cover. As at Storbreen low (1) and Austerdalsbreen, the vegetation cover appears to be greater at high-slope positions on the moraines, but probably not the crests, which are associated with bare ground.

Those parameters which are most positively correlated with age, and thus associated with the oldest terrain, are root depth ($r = +0.733$), soil texture ($r = +0.706$), humus depth ($r = +0.682$), stain depth ($r = +0.57$), and vegetation cover ($r = +0.555$). The parameter most negatively correlated with age is altitude ($r = +0.962$) and this should be the same as the Storbreen low foreland (1) which records a correlation of only ($r = +0.218$). Investigation of the original data set showed that two altitude data points (out of one hundred and ten altitude data points) are missing from the Storbreen low (1) data set possibly being the cause of the difference. This further reinforces the view that an indirect ordination technique, with superimposed environmental parameters, should be used, especially on very large data sets where mistakes are easily overlooked. Apart from altitude, those parameters negatively correlated with age are bare ground gravels ($r = -0.633$), frost-heave ($r = -0.483$) and dryness ($r = -0.427$). Age is more important on this sequence of moraines than it is on the Storbreen (1) sequence, possibly due to the difference in shape and size of the moraines used for the two sequences thus causing microtopography to be more significant on the Storbreen low (1) sequence. This will be discussed at greater length in the concluding chapter. The parameters most correlated with high-slope position are snow-lie ($r = +0.808$), frost-heave ($r = +0.577$), dryness ($r = +0.552$), dowels ($r = +0.454$) and bare fines ($r = +0.422$). The parameters most negatively correlated with high-slope position are bryophyte cover ($r = -0.546$), fluvial activity ($r = -0.391$), vegetation cover ($r = -0.367$) and stain depth ($r = -0.356$). The relatively high correlations that position has, on both axis (1) ($r = +0.468$) and axis (2) ($r = -0.23$), suggests that microtopography appears to be a significant influence on this sequence of moraines. There is a fair correspondence in the results from the two sequences at Storbreen low, but the differences suggest that there are within-foreland differences. This indicates that the present study gives a useful general understanding of the influence of microtopography on vegetation patterns and the prevailing environment, across the forelands, but that more research is needed in order to provide a comprehensive understanding of microtopographical effects.

According to Fig. 5.4 there is a broad distribution of TWINSPAN "final site groups" across the plot showing that the groups are fairly distinct from one another and a considerable correspondence emerges between the location of site groups belonging to the Storbreen low (1) and (2) on their respective axes. The exposed lichen heath (site group 7*) and, to a lesser extent, the exposed early intermediate lichen heath (site group 13*) and show correspondence with the positive end of axis (1) (associated with dry, younger and poorly developed soils at high-slope positions). Towards the centre of the axis are the early intermediate snowbed assemblages (intermediate soil development and moisture conditions). A little towards the negative end of axis (1) are the rest of the assemblages spanning a wide range on axis (2) and they are the late intermediate snowbed (site group 4*) and towards the centre the late-snow late intermediate heath (site group 10*) and the early intermediate snowbed (site group 12*), corresponding with low-slope positions, long snow-lie and high fluvial disturbance. Towards the positive end of axis (2) is the late intermediate snowbed (site group 4*) and this is followed, towards the centre, by site groups (10*) and (12*). At the centre are the early intermediate lichen heath site groups (13*) and (7*), corresponding with intermediate snow cover fluvial disturbance. Towards the negative end of axis (2) is the mature lichen heath (site group 11*) with low snow cover, solifluction and high vegetation cover. It is apparent from the plot that axis (1) is most related to soil development, age (and microtopography to a lesser extent), whereas axis (2) is more related to exposure and disturbance variables.

According to Fig. 5.12. there is a wide distribution of TWINSPAN "final species groups" across the plot showing that the groups are fairly distinct from one another and thus the relative influence of the various most important environmental variables on each of the groups can be seen. Towards the positive end of axis (1) is the exposed lichen heath (species group 16) and towards the centre the exposed early intermediate lichen heath (species group 17) and the early intermediate lichen heath (species group 18) corresponding with frost-heaved and high-slope positions with younger poorly developed soils. Near the centre of axis (1) is the early intermediate snowbed (species group 19) and the exposed early intermediate lichen heath (species group 10) and the widespread heath (species group 11). These assemblages correspond with intermediate soil development and frost disturbance. Towards the negative end is, the early intermediate snowbed (species group 6) followed by assemblages spanning a wide range along axis (2) which are the late intermediate snowbed (species group 30), the late-snow late intermediate heath (species group 31) and the mature lichen heath (species group 14). These assemblages correspond with developed soils and low frost disturbance. Towards the positive end of axis (2), which corresponds with the low-slope sites with a long snow duration, is the late intermediate snowbed (species group 30) and towards the centre the early intermediate snowbed (species group 6) and the late-snow late intermediate heath (species group 10) corresponding with long snow cover and fluvial disturbance. Towards the centre are species groups (19), (11), (10), (17) and (18) corresponding with intermediate snow cover and fluvial disturbance. Towards the positive end of axis (2) is, the early intermediate lichen heath (species group 18) and then the mature lichen heath (species group 14) corresponding with low snow cover, fluvial disturbance, high solifluction and vegetation cover. The sequence of assemblages on axis (2) reflects the importance of exposure and disturbance and thus microtopography.

The distribution of environmental parameters, TWINSPAN "final site groups" and "final species groups", on Figs. 5.4 and 5.12, suggests that the sequences on axis (1) are influenced mostly by soil development, age and to a lesser extent microtopography. On axis (2) the sequence is influenced by exposure and disturbance variables. It appears that microtopography is an important influence on this foreland and the so-called *"Microtopographic (exposure-moisture-snowmelt) factor complex"* (*sensu*: Whittaker, 1985) is apparent at Storbreen low (2). Variables related to age and microtopography are found distributed between axis (1) and (2), suggesting that the influence of these parameters cannot be separated. Despite these problems, however, it is still possible to make useful and ecologically meaningful interpretations from the environmental data. As with the Storbreen low (1) sequence the importance of microtopography, in comparison to age, has probably been exaggerated due to the lack of early pioneer sites across this foreland sequence. The DCA centroid scores of TWINSPAN "final site groups" and "final species groups" correspond well with the pattern of environmental parameters on axis (1) and (2) suggesting that the trends found on both axis (1) and (2) are ecologically meaningful.

5.6.4 Summary of DCA ordination results at Storbreen low (2).

Both Axis (1) and (2) have eigenvalues high enough to suggest relatively good separation of sites. The rank tables (Tables 5.4 and 5.12), displaying the distribution of the TWINSPAN "final site groups" and "final species groups" on the DCA ordination axes, provide clear and easily interpreted representations of the results on axis (1) and (2). The TWINSPAN "final species groups" correspond quite well with the sequence of species along axis (1) although the end portion has a slightly disordered sequence of the mature TWINSPAN assemblages. The sequence on axis (2) corresponds quite well with the TWINSPAN "final species groups". There is a relatively clear correspondence between the TWINSPAN "final site groups" and the pattern of sites on axes (1) and (2) especially towards the positive end and the negative end of the axes. The plots and correlation matrices, have provided further elucidation and confirmation of the results derived from the rank tables on axis (1) and especially on axis (2). The main findings from sections 5.6.1 to 5.6.3, derived from the DCA ordination results for Storbreen low (2), are summarised below. The DCA centroid scores of TWINSPAN "final site groups" and "final species groups" correspond well with the pattern of environmental parameters on axis (1) and (2) suggesting that the trends found on both axis (1) and (2) are ecologically meaningful.

The separation of species and sites along axis (1) appears to be influenced mainly by soil development and thus age (but also by microtopography). At the positive end of axis (1), exposed younger sites, represented by exposed lichen heath assemblages, are prevalent and these give way to snowbed assemblages (young low-slope positions), which in turn give way to mature lichen heath assemblages older (best developed soils). Axis (1) is therefore mostly related to age but it is also influenced considerably by microtopography as shown by the occurrence of the high-slope, drier sites of various ages towards the positive end of axis (1). Correlation shows bare ground gravels, root depth, frost activity, humus depth, vegetation cover, altitude, soil texture, stain depth and age to be the most important variables on axis (1), but dryness, low snow cover and position also have high correlation values (r = >0.5). It therefore appears that microtopography is an important influence on this foreland and the so-called *"Microtopographic (exposure-moisture-snowmelt) factor complex"* (*sensu*: Whittaker, 1985) is apparent at Storbreen low (1). Age and microtopography-related variables, are found spread between axis (1) and (2), so that the influence of many of these parameters is difficult to separate. Despite these problems, however, it is still possible to make useful and ecologically meaningful interpretations from the environmental data as has been shown by these results. As with the Storbreen low (1) sequence the importance of microtopography, as an influence on vegetation pattern, in comparison to age, has probably been exaggerated due to the lack of early pioneer sites on this foreland sequence.

The sequence on axis (2) progresses from mainly snowbed assemblages at low-slope positions (with low vegetation cover and high fluvial disturbance) through a disordered sequence of sites, with intermediate vegetation cover and fluvial activity, to the lichen heath assemblages at high-slope positions on the mature terrain (with higher vegetation cover, high solifluction and low snow duration). Correlation shows that bare ground boulders, vegetation cover, fluvial activity, solifluction, and position are the most important influences on this axis although the correlations are generally not very significant. As at Storbreen low (1), axis (1) and (2) are related, but axis (2) is more influenced by disturbance factors and microtopography. Sites disturbed by fluvial activity, with a high proportion of bare ground boulders and long snow-lie, occur at low-slope positions, while the high-slope sites are effected by solifluction and exposure due to low snow duration.

On axis (1) the most distinct site-groups are exposed lichen heath (site group 7*) and the mature lichen heath (site group 11*) and on axis (2), the mature lichen heath (site group 11*) and the late intermediate snowbed (site group 4*). The most distinct "final species group" on axis (1) is the exposed lichen heath (species group 16) and on axis (2), the mature lichen heath (species group 14) and the late intermediate snowbed (species group 30). This suggests that most of the other members of the TWINSPAN site and species groups overlap to a certain extent with one another on the ordination sequence. Generally, therefore, the evidence supports the notion that there is a gradient of assemblages as opposed to distinct communities at Storbreen low (2).

5.7 Svellnosbreen

5.7.1 Site (sample) patterns on DCA axes (1) and (2) at Svellnosbreen.

By referring to Table 5.5, and the profile diagram Fig 4.6, for the location of specific sites where the pattern is not clear, the following site patterns emerge on DCA ordination axes (1) and (2). Axis (1) has an eigenvalue of 0.442 showing that there is good species separation along the axis and this axis is ecologically meaningful. The environmental variables explain 88.9% of the variation along this axis. Axis (2) has an eigenvalue of 0.357 which is high enough to suggest relatively good separation along the axis. The environmental variables explain 91.6% of the variation along this axis. The correspondence between TWINSPAN groups and axis (1) is relatively clear at either end but not so clear on the middle section of the axis. There is a relatively clear correspondence between TWINSPAN groups and axis (2).

At the positive end of axis (1) is a pioneer exposed snowbed (site group 3*), the **Deschampsia alpina - Oxyria digyna,** assemblage. This is followed by the two members of the pioneer snowbed (site group 8*), the **Salix glauca - Cerastium cerastoides,** assemblage and the exposed pioneer (site group 20*), the **Salix glauca - Cardaminopsis petraea,** assemblage. The corresponding environmental variables at the positive end of axis (1) is fluvial activity and a number of parameters normally associated with low-slope and older positions, namely humus depth and stain depth. The pioneer sites are followed by a mix of the late-snow early intermediate heath (site group 21*), the **Empetrum nigrum - Stereocaulon alpinum,** assemblage and the mature atypical snowbed (site group 9*), the **Salix herbacea - Empetrum nigrum,** assemblage on the central portion of the axis. This is followed by the early intermediate heath (site group 22*), the **Cladonia portentosa - Phyllodoce caerula,** assemblage and then the lichen heath (site group 23*), the **Alectoria ochroleuca - Cetraria cucullata,** assemblage which forms a tightly distributed group at the negative end of axis (1). The corresponding environmental variables at the negative end of axis (1) are low snow duration, high-slope position, frost, dryness and age.

At the positive end of axis (2) is the mature atypical snowbed (site group 9*) interspersed with mature members of the lichen heath (site group 23*). Three members of the pioneer exposed snowbed, (site group 3*), are also found within this section and the rest are found within the central portion of the axis, along with the two members of the pioneer snowbed (site group 8*). The corresponding environmental variables for the positive end of axis (2) are humus depth, age, stain depth, root depth and vegetation cover. Following this are members of the lichen heath (site group 23*) and the early intermediate heath (site group 22*) interspersed with older sites belonging to the late-snow early intermediate heath (site group 21*). Members of site group (21*) are densely distributed on this section of the axis and then further down are interspersed by sites belonging to the exposed pioneer (site group 20*) at the negative end of axis (2). The negative portion of axis (2) corresponds with pH, bare gravels and boulders, northerly aspect, frost and altitude.

These results are summarised in Fig. 5.21 and axis (1) appears to be influenced mainly by position, with low-slope positions, especially effected by fluvial activity, being found at the positive end of axis (1) and high-slope positions, with low snow cover, frost and dry conditions, being found at the negative end of the axis. This would explain why the environmental parameters that normally correspond with late intermediate ground are found alongside parameters normally associated with young terrain. Axis (2) is quite clearly an age-related axis with, generally, the oldest sites at the positive end of the axis and the youngest, pioneer, sites towards the negative end. The site separation on ordination axis (1) is relatively close to that found by the TWINSPAN groups except towards the middle of the axis.

5.7.2 Species patterns on DCA axes (1) and (2) at Svellnosbreen.

By referring to Table 5.13 and Table 4.10 it is possible to relate the sequence of species on DCA axes (1) and (2) to the TWINSPAN "final species groups" described in chapter (4) and thus elucidate the influence of particular environmental variables on the species patterns across Svellnosbreen foreland. The TWINSPAN species assemblages correspond well with the sequence of species along axis (1), at either end of the axis, but the species sequence is rather disordered in the central portion of the axis. The sequence on axis (2) corresponds well with the TWINSPAN species assemblages.

The positive three quarters of axis (1) is made up of a fairly disordered sequence of members of the TWINSPAN "final species groups" but a general trend can be found within the sequence. At the positive end of axis (1) is the exposed pioneer (species group 7) and the pioneer snowbed (species group 4) interspersed with members of the widespread snowbed (species group 13) and the early intermediate snowbed (species group 83). Corresponding with the positive end of the axis are fluvial activity, humus depth, stain depth, bryophyte cover, and trampling. Following this is the mature snowbed (species group 25) which is interspersed with members of the late-snow early intermediate heath (species group 84) and the early intermediate snowbed (species group 40). Further down, species group (84) becomes more dominant and is interspersed first with species group (25) and then with the mature late snow heath (species group 24), the early intermediate heath (species group 11) and even further down the early intermediate heath (species group 42). At the negative end of the axis is a tight group of the lichen heath (species group 43). Corresponding with the negative end of the axis are low snow, high-slope position, frost-heave, dryness and age.

The pattern of TWINSPAN groups is much clearer on axis (2). At the positive end is mainly the mature snowbed (species group 25) interspersed with the widespread snowbed (species group 13) and this is replaced by the mature late-snow heath (species group 24). The environmental parameters corresponding with the positive portion of the axis are humus depth, age, stain depth, root depth, and vegetation cover. Following this is the lichen heath (species group 43), interspersed with the early intermediate heath (species group 11). The negative third of the axis is dominated by the large late-snow early intermediate heath (species group 84) interspersed with a disordered sequence of smaller groups consisting of the early intermediate heath (species group 42), early intermediate snowbed (species group 83), the early intermediate snowbed (species group 40) and the two pioneer (species groups 4 and 7). The environmental parameters corresponding with the negative end of the axis are pH, bare gravels and boulders, northerly aspect, frost-heave and altitude. These results are summarised in Fig. 5.29 and they complement the site results described in the previous section.

5.7.3 TWINSPAN group centroids of sample and species scores at Svellnosbreen .

Fig. 5.5 shows the DCA centroids of TWINSPAN "final site group" sample scores and reveals the location of the site groups on both axes in relation to the environmental parameter biplot scores. Fig. 5.13, showing the DCA centroids of TWINSPAN "final species group" scores, reveals the location of the species groups on both axes in relation to the environmental parameter biplot scores. In addition, Table 5.21, the weighted correlation matrix, can be used to elucidate further the relative influence of environmental parameters on the site and species groups. These plots and the correlation matrix are used to elucidate and outline the main findings of the previous two sections at Svellnosbreen. The critical value for " *r* " on this foreland is 0.307.

The most important environmental variables on Fig. 5.5 and 5.13 are quite widely distributed between the axes so that the influence of the variables, related to age and microtopography, is difficult to separate. The greatest influence on the plot is an outlier (or very different) group which appears to have distorted the distribution of all other parameters on this plot. This outlier is the pioneer exposed snowbed (site group 3*), associated with young ground and fluvial activity, possibly causing the most important influence on the sequence of species and sites at Svellnosbreen to be microtopography. The ordination results at this foreland are different to those of the other forelands, possibly due to this outlier group. Axis (1) and (2) have similar eigenvalues, (0.442 and 0.357 respectively) suggesting that the separation along both axes is significant. The environmental variables explain a higher percentage (91.6%) of the species separation on axis (2) than the environmental variables on axis (1) (88.9%) which is unusual. Furthermore, correspondence between the TWINSPAN "final site groups" is greater on axis (2) than it is on axis (1). This leads to the possibility that axis (2) is a more ecologically meaningful axis than axis (1) and that the distorting effect of the outlier has somehow caused the influence of age to be more significant on axis (2). Previous (preliminary) research (e.g. Whittaker, 1985; Crouch, 1992), as well as the results from other forelands within the present study, suggests that age is likely to have a greater influence on the general pattern of species and sites on glacier forelands (i.e. on succession) than microtopography. This suggests that the ordination results from the Svellnosbreen data set, showing that the influence of microtopography is superior or at least equal to age, needs careful interpretation.

The only important variable towards the positive end of axis (1) is fluvial activity (r = +0.286). The most important variables towards the negative end of axis (1) are low snow cover (r = -0.654), position (r = -0.599), frost-heave (r = -0.578), dryness (r = -0.439) and age (r = -0.326). This is a south-facing foreland and it is drier and sunnier than the other alpine forelands which could explain the correspondence between lower snow cover and drier conditions with the age variable (i.e. on the older ground, proximity to the glacier has less influence and snow melts faster). Axis (1) is most correlated with microtopography, and to a certain extent age, with the moist, low-slope, younger sites with longer snow cover and fluvial disturbance occurring towards the positive end of the axis and the drier, high-slope, older sites occurring towards the negative end of axis (1). Axis (2) is influenced by age with the most important parameters at the positive end of axis (1) being humus depth (r = +0.669), age (r = -0.667), stain depth (r = +0.648) root depth (r = +0.635), vegetation cover (r = +0.521), solifluction (r = +0.434) and soil texture (r = +0.383) and these parameters reflect older ground with developed soils and high vegetation cover. The most important variables correlated with the negative end of axis (2) are pH (r = -0.584), bare gravels (r = -0.436), bare boulders (r = -0.335) and frost-heave (r = -0.245) and these parameters reflect young terrain with low vegetation cover and poorly developed soils.

Those parameters which are most positively correlated with age, and thus associated with the oldest terrain, are root depth (r = +0.565), solifluction (r = +0.564), vegetation cover (r = +0.531), stain depth (r = +0.521), humus depth (r = +0.471) and soil texture (r = +0.437). The parameter most negatively correlated with age is bare gravels (*r* = -0.5), pH (*r* = -0.371), bare boulders (*r* = -0.314). Age is highly correlated with both axis (1) (*r* = -0.326) and axis (2) *(r* = +*0*.667) suggesting that it is important on both axes. The parameters most positively correlated with high-slope position are snow-lie *(r* = +*0*.765), frost-heave *(r* = +*0*.664), dryness *(r* = +*0*.545), bare fines *(r* = +*0*.436) and dowel heave *(r* = +*0*.433). The parameters most negatively correlated with high-slope position are humus depth (*r* = -0.437), root depth (*r* = -0.409) and stain depth (*r* = -0.386). Position is only important on axis (1) (*r* = -0.578) and not on axis (2) (*r* = -0.083).

According to Fig. 5.5, there is a wide dispersal of DCA centroid scores of TWINSPAN "final site groups" across the plot showing that the groups are fairly distinct from one another. Furthest along axis (1), towards the positive end, is the exposed pioneer snowbed (site group 3*) and this group is largely associated with fluvial activity, long snow-lie, low-slope position and moist conditions. Another pioneer snowbed (site group 8*) is also relatively far along this axis, towards the positive end, and this is followed by the exposed pioneer (site group 20*). Towards the centre is the late-snow early intermediate heath (site group 21*) and the atypical mature snowbed (site group 9*). Slightly towards the negative end of axis (1) is the early intermediate heath (site group 22*) and, further on, the lichen heath (site group 23*) reflecting the high-slope, driest and most snow-free sites on the foreland. Towards the positive end of axis (2) is the atypical mature snowbed (site group 9*) and at the centre (not including site group (3*) which does not fit the pattern) the early intermediate heath and lichen heath. Towards the negative end of axis (2) is the pioneer snowbed (site group 8*), the late snow early intermediate heath (site group 21*) and the exposed pioneer (site group 20*). The sequence of site groups on axis (1) is influenced strongly by microtopography and to a lesser extent age, while on axis (2) the main influence is age.

According to Fig. 5.13. there is a wide dispersal of the DCA centroid scores of TWINSPAN "final species groups" across the plot showing that the groups are fairly distinct from one another and thus the relative influence of the various most important environmental variables on each of the groups can be seen. At the positive end of axis (1) is the exposed pioneer snowbed (species group 7) corresponding with low-slope positions, long snow-lie, moisture and fluvial activity. Half way along the positive end of the axis is the pioneer snowbed (species group 4) and this is followed by the widespread snowbed (species group 13) and the mature snowbed (species group 25). Towards the centre are a cluster of assemblages comprising the early intermediate snowbed (species group 40), the early intermediate snowbed (species group 83), and the late-snow early intermediate heath (species group 84). At the centre is the early intermediate heath (species group 11). Slightly towards the negative end of axis (1) is the mature late-snow heath (species group 24) and the early intermediate heath (species group 42) and furthest towards the negative end is the lichen heath (species group 43) reflecting the driest, high-slope and most snow-free sites. Towards the positive end of axis (2) is the mature snowbed (species group 25), reflecting the oldest and most developed soils and vegetation. This is followed by the widespread snowbed (species group 13) and the mature late snow heath (species group 24). At the centre (excluding species group 7) is the lichen heath (species group

43) and the early intermediate heath (species group 11). Slightly towards the negative end of axis (2) is the early intermediate heath (species group 42) followed by the late-snow early intermediate heath (species group 84), the early intermediate snowbed (species group 83), the pioneer snowbed (species group 4) and a little further, the early intermediate snowbed (species group 40) which reflect the younger, less vegetated end of the axis. The sequence of species groups on axis (1) is influenced strongly by microtopography, and to a lesser extent age, while on axis (2) the main influence is age.

From the spread of environmental parameters, TWINSPAN "final site groups" and "final species groups" on Figs. 5.5 and 5.13 it is possible to see that the sequence of sites and species on axis (1) is influenced by microtopography, and to a lesser extent age, while axis (2) is influenced more by soil development, age, exposure and disturbance variables. The sequence suggests that microtopography is the most important influence on this foreland and the so-called *"Microtopographic (exposure-moisture-snowmelt) factor complex"* (*sensu*: Whittaker, 1985) is apparent at Svellnosbreen, as it is on the sequences for the Storbreen low foreland sequences. Some of the age-related variables are widely distributed between axis (1) and (2), suggesting that the relative influence of these parameters on the TWINSPAN "final groups" are obscured to some extent. In addition, the exposed pioneer (site group 3*), or species group (7), seems to have had a powerful influence on the distribution of all the other site and species groups. The notion that this group is quite different from the other groups is corroborated by the TWINSPAN division which showed this small group separating at the second level of subdivision. This group has behaved like an outlier (a quadrat or in this case a group of quadrats that are very different to the others in the data set) and has possibly distorted the results. Although the removal of outliers is often recommended (Kent and Coker, 1992), it was decided not to remove this group because the remaining groups could still be interpreted and the data set provides an interesting and unbiased comparison with the other forelands. The DCA centroid scores of TWINSPAN "final site groups" and "final species groups" correspond well with the pattern of environmental parameters on axis (1) and (2) (apart from the outlier) suggesting that the trends found on both axis (1) and (2) are ecologically meaningful.

5.7.4 Summary of DCA ordination results at Svellnosbreen

Both axis (1) and (2) have eigenvalues high enough to suggest relatively good separation of sites and species. The rank tables (Tables 5.5 and 5.13), displaying the distribution of the TWINSPAN "final site groups" and "final species groups" on the DCA ordination axes, provide representations of the results on axis (1) and (2). The TWINSPAN "final species groups" correspond well with the sequence of species along axis (1) at either end of the axis but the species sequence is rather disordered in the central portion of the axis. The sequence on axis (2) corresponds well with the TWINSPAN "final species groups". The correspondence between TWINSPAN "final site groups" and axis (1) is relatively clear at either end but not so clear on the middle section of the axis. There is a relatively clear correspondence between TWINSPAN "final site groups" and axis (2). The interpretation of the results has been complicated by an important pioneer outlier group that appears to have distorted the ordination results to some extent. The plots and correlation matrices, have provided further elucidation and confirmation of the results derived from the rank tables on both axis (1) and axis (2). The DCA centroid scores of TWINSPAN "final site groups" and "final species groups" correspond well with the pattern of environmental parameters on axis (1) and (2) (apart from the outlier) suggesting that the trends found on both axis (1) and (2) are ecologically meaningful. The main findings from sections 5.7.1. to 5.7.3., derived from the DCA ordination results for Svellnosbreen, are summarised below.

The separation of species and sites along axis (1) appears to be influenced mainly by microtopography (and to a lesser extent age) with low-slope positions, especially affected by fluvial activity and the corresponding pioneer or snowbed assemblages, being found at the positive end of axis (1) and high-slope positions with low snow cover, frost and dry conditions, with corresponding lichen heath assemblages, being found at the negative end of the axis. This would explain the environmental parameters normally corresponding with late intermediate ground being found alongside parameters normally associated with young terrain. Axis (1) is most correlated with low snow duration, position, frost-heave, dryness and, to a lesser extent, age and fluvial activity. The sequence suggests that microtopography is the most important influence on this foreland and the so-called *"Microtopographic (exposure-moisture-snowmelt) factor complex"* (*sensu*: Whittaker, 1985) is apparent at Svellnosbreen. However, the exposed pioneer (site group 3* or species group 7) seems to have had a powerful influence on the distribution of all the other site and species groups. This group has behaved like an outlier and has possibly distorted the results but it was decided not to remove this group as the remaining groups could still be interpreted and the complete data set provided an interesting comparison with the other forelands. From the results it is possible to see sequences related to both microtopography and age but, due to the distorting effect of the outlier, it is not possible to ascertain whether age or microtopography is more important. Nevertheless, results from previous research, as well as evidence from other forelands in the present study, would suggest that age is probably the greater influence.

In general, the sequence on axis (2) progresses from mature snowbed assemblages, with developed soils and a high vegetation cover, at the positive end of axis (2), to early intermediate and pioneer assemblages, with poorly developed soils, a high pH and low vegetation cover, at the negative end. Axis (2) is influenced by age and is most correlated with humus depth, age, stain depth, root depth, pH, vegetation cover, and bare ground gravels and boulders. Due to the outlier group on axis (1) the importance of age on this foreland probably appears to be less than it is.

On axis (1) the most distinct site-groups on axis (1) are pioneer exposed snowbed (site group 3*), the exposed pioneer (site group 20*) and the early intermediate heath (site group 22*) and on axis (2), the mature snowbed (site group 9*). The TWINSPAN "final species group" separation on ordination axis (1) is quite close to that found by the TWINSPAN "final site groups" but rather disordered in the central portion of the axis. The most distinct species groups on axis (1) are the lichen heath (species group 43), the pioneer snowbed (species group 4) and the exposed pioneer snowbed (species group 7) and on axis (2), the mature snowbed (species group 25). Generally the evidence further supports the notion that there is a gradient of assemblages, as opposed to distinct communities, at Svellnosbreen and this will be further discussed in the summary 5.11 and the concluding chapter.

5.8 Storbreen high

5.8.1 Site (sample) patterns on DCA axes (1) and (2) at Storbreen high.

By referring to Table 5.6 and Table 4.6 as well as the profile diagram (Fig. 4.7), for the location of specific sites where the pattern is not clear, the following site patterns emerge on DCA ordination axes (1) and (2). Axis (1) has an eigenvalue of 0.483 showing that there is good species and sample separation along the axis and that this axis is ecologically meaningful. The environmental variables explain 89% of the variation along this axis. Axis (2) has an eigenvalue of 0.223 which is high enough to suggest fair separation along the axis. The environmental variables explain 80.1% of the variation along this axis. There is a good correspondence between the TWINSPAN "final site groups" and the pattern of sites on axis (1), but there is only a poor correspondence on axis (2) except towards the positive end.

At the positive end of axis (1) is the pioneer snowbed (site group 15*), the **Oxyria digyna - Deschampsia alpina,** assemblage and this is followed by the exposed pioneer (site group 14*), the **Stereocaulon alpinum - Festuca ovina,** assemblage which in turn is replaced by the early intermediate snowbed (site group 6*), **Salix glauca - Cetraria nivalis,** assemblage. These three groups correspond with the environmental parameters, fluvial activity, pH, trampling, bare fines and easterly aspect. There is a distinct division between the snowbed and pioneer site groups and the following groups which comprise the early intermediate late-snow heath (site group 10*), **Salix glauca - Cetraria nivalis,** assemblage, interspersed with the mature late-snow heath (site group 11*), the **Salix herbacea - Cetraria islandica,** assemblage. In turn there is another clear change to the mature lichen heath (site group 8*), the **Betula nana - Vaccinium vitis-idaea,** assemblage and the early intermediate lichen heath (site group 9*), the **Phyllodoce caerula - Solorina crocea,** assemblage at the negative end of axis (1). The site at the negative end of axis (1) correspond with age, position, lack of snow, soil texture and dryness.

At the positive end of axis (2) are some members of the early intermediate snowbed (site group 6*) followed by a mix of members of the early intermediate late-snow heath (site group 10*), interspersed with members of the early intermediate lichen heath (site group 9*). Odd members of the pioneer (site groups 14* and 15*) also occur in a disordered sequence along this positive portion of the axis. Corresponding environmental variables at the positive end of the axis are bare boulders and gravels, slope, frost-heave, dryness and bryophyte cover. Site groups (9*) and (10*) give way to the mature late-snow heath (site group 11*) and the pioneers (site groups 14* and 15*). At the negative end of the axis is the mature lichen heath (site group 8*). The corresponding environmental variables at the negative end of axis (2) are stain depth, vegetation cover, humus depth, root depth, age, soil texture and altitude.

These results are summarised in Fig. 5.22 and from this it is possible to see that on axis (1) there appears to be a strong age-related sequence from young terrain at the positive end of axis (1) to the oldest terrain at the negative end of axis (1). Superimposed onto each section of the axis is a position-related sequence from low-slope, sheltered low-slope positions to more exposed high-slope positions. This shows that age is the most influential factor on axis (1) but microtopography-related factors, such as fluvial activity at the positive end of axis (1) and position, snow-lie and dryness at the negative end are also important. Axis (2) has a very disordered sequence of sites and is very difficult to interpret. In general the order of TWINSPAN "final site groups" suggests that vegetation cover and frost disturbance are the most important influences on this axis. The order of environmental parameters suggests that the sequence along the axis is influenced by exposure as well as age, with the positive end of the axis comprising frost-disturbed sites with low vegetation cover, and the negative end comprising sites that are less disturbed and have the most developed vegetation and soils (i.e. older sites). The pioneers (site groups 14* and 15*), are located towards the negative end, and this suggests that these sites have relatively low frost disturbance and better developed soils and vegetation and this is not logical. It is therefore suggested that axis (2) may not be ecologically meaningful. The site separation on ordination axis (1) is close to that found by the TWINSPAN "final site groups", although the sequence is not identical.

5.8.2 Species patterns on DCA axes (1) and (2) at Storbreen high.

By referring to Table 5.14 and Table 4.10 it is possible to relate the sequence of species on DCA axes (1) and (2) to the TWINSPAN "final species groups" described in chapter (4) and thus elucidate the influence of particular environmental variables on the species pattern across Storbreen high foreland. The TWINSPAN "final species groups" correspond well with the sequence of species along axis (1). There is some correspondence on axis (2), especially towards the positive end of the axis, but on the whole the group of the TWINSPAN "final species groups" is not distinct.

At the positive end of axis (1) is the pioneer (species group 7) which is replaced by the early intermediate snowbed (species group 6). The environmental parameters that correspond with these assemblages are fluvial activity, pH, trampling bare fines and easterly aspect. Following this is the late snow early intermediate heath (species group 39) interspersed with (species group 6) and the widespread heath (species group 5). At the centre of the axis is the late snow early intermediate heath (species group 38) and the late snow late intermediate heath (species group 18) followed by a few members of (species group 39). At the negative end of the axis is a tight group of the lichen heath (species group 17). Corresponding with the negative end of axis (1) is age, high-slope position, low snow, soil texture, dryness and frost-heave.

The sequence of TWINSPAN "final species group" assemblages on axis (2) is disordered but a vague trend can be ascertained and it is as follows. At the positive end of axis (2) are mainly members of the early intermediate snowbed (species group 6) and these are followed by members of the late-snow early intermediate heath (species group 39). The positive end of the axis corresponds with bare boulders and gravels, slope, frost-heave and dryness. Following this is a sequence of members of the lichen heath (species group 17), the pioneer (species group 7) and the widespread heath (species group 5). On the negative portion of the axis the late-snow late intermediate heath (species group 18) and, towards the negative end, the late-snow early intermediate heath (species group 38) are most prevalent. The negative portion of the axis corresponds with stain depth, vegetation cover, humus depth, root depth and age. These results complement those found by the site groups, described in the previous section, and are summarised in Fig. 5.30.

5.8.3 TWINSPAN group centroids of sample and species scores at Storbreen high .

Fig. 5.6 shows the DCA centroids of TWINSPAN "final site group" sample scores and reveals the location of the site groups on both axes in relation to the environmental parameter biplot scores. Fig. 5.14, showing the DCA centroids of TWINSPAN "final species group" scores, reveals the location of the species groups on both axes in relation to the environmental parameter biplot scores. In addition, Table 5.22, the weighted correlation matrix, can be used to elucidate further the relative influence of environmental parameters on the site and species groups. These plots and the correlation matrix are used to support and outline the main findings of the previous two sections at Storbreen high. The critical value for " *r* " on this foreland is 0.264.

The only important environmental variables, on Fig. 5.6 and 5.14, which occur between axis (1) and (2) are age and soil texture, suggesting that age is important on both axes. Otherwise the most of the important variables tend to be more related to either axis (1) or axis (2). The most important variables, towards the positive end of axis (1), are fluvial activity ($r = +0.48$) and pH ($r = +0.304$). The most important variables at the negative end of axis (1) are age (r = -552), position (r = -0.496), low snow cover (r = -0.486), soil texture (r = -0.463) and dryness (r = -0.456). Axis (1) is most correlated with age, fluvial disturbance and microtopography, with the moist, low-slope, younger sites (with longer snow duration and fluvial disturbance) towards the positive end of the axis (1), and the drier, high-slope, older sites towards the negative end. Axis (2) is influenced by age so that variables, associated with the youngest sites, are most correlated with the positive end of axis (2), these being bare boulders ($r = +0.355$)), bare gravels ($r = +0.325$), and frost-heave ($r = +0.209$). Towards the negative end of axis (2), the most important parameters (associated with mature vegetation and soils) are stain depth (r = -0.603), vegetation cover (r = -0.453), humus depth (r = -0.445), root depth (r = -0.437) and age (r = -0.408).

Those parameters which are most positively correlated with age, and thus associated with the oldest terrain, are stain depth ($r = +0.787$), soil texture ($r = +0.75$), altitude ($r = +0.522$), humus depth ($r = +0.485$), root depth ($r = +0.41$) and vegetation cover ($r = +0.32$). The parameter most negatively correlated with age is bare gravels ($r = -0.386$), bare fines ($r = -0.364$) and .pH ($r = -0.288$). Age is highly correlated with axis (1) ($r = -0.552$) and axis (2) ($r = +0.408$). The parameters most correlated with high-slope position are snow-lie ($r = +0.836$), dryness ($r = +0.672$), frost-heave ($r = +0.659$), dowels ($r = +0.433$), and bare gravels ($r = +0.323$). The parameters most negatively correlated with high-slope position are humus depth ($r = -0.272$) and root depth ($r = -0.253$). Position is only important on axis (1) ($r = -0.496$), and not on axis (2) ($r = -0.098$).

According to Fig. 5.6, there is a wide distribution of TWINSPAN "final site groups" assemblages across the plot showing that the groups are fairly distinct from one another and the relative influence of the most important environmental variables, on each of the assemblages, can be seen. Furthest along axis (1), towards the positive end, is the pioneer snowbed (site group 15*) and this group is largely associated with young ground, fluvial activity, long snow-lie, low-slope position and moist conditions. A little towards the centre is the exposed pioneer (site group 14*) and the early intermediate snowbed (site group 6*). Slightly towards the negative end of axis (1) is the early intermediate late-snow heath (site group 10*) and the mature late-snow heath (site group 11*) reflecting intermediate conditions of moisture and snow cover. Towards the negative end of the axis is the early intermediate lichen heath (site group 9*) and the mature lichen heath (site group 8*), comprising the high-slope, driest and most snow-free sites on the foreland. Towards the positive end of axis (2) is the early intermediate snowbed (site group 6*), and towards the centre the early intermediate lichen heath (site group 9*) and early intermediate late-snow heath (site group 10*). These assemblages reflect less developed soils on axis (2). At the centre of the axis the sequence is disordered. Towards the negative end of axis (2), is the mature late-snow heath (site group 11*) and the mature lichen heath (site group 8*) reflecting well-developed soils and low proportions of bare ground. The sequence of site groups on axis (1) is influenced strongly by age and also microtopography. Axis (2) is mainly influenced by age and soil development, but the order of some groups on the axis suggests that the relationship is not strong and thus axis (2) is not a very meaningful axis.

According to Fig. 5.14, there is a fairly wide dispersal of TWINSPAN "final species group" assemblages across the plot showing that the groups are fairly distinct from one another and thus the relative influence of the most important environmental variables, on each of the assemblages, can be seen. At the positive end of axis (1) is the pioneer (species group 7) followed by the early intermediate snowbed (species group 6) corresponding with young terrain, low-slope positions, long snow-lie, moisture and fluvial activity. At the centre are the late-snow early intermediate heath (species group 39) and the widespread heath (species group 5). Slightly towards the negative end of axis (1) is the late-snow early intermediate heath (species group 39), the late-snow late intermediate heath (species group 18) and the widespread heath (species group 16) and furthest towards the negative end is the lichen heath (species group 17) reflecting the driest, high-slope and most snow-free sites. Towards the positive end of axis (2) is the early intermediate snowbed (species group 6), reflecting sites with high proportions of bare ground and poorly developed soils. This is followed by the widespread heath (species group 16) and the late-snow early intermediate heath (species group 39). Slightly towards the negative end of axis (2) (excluding species group 7) is the widespread heath (species group 5), the late-snow late intermediate heath (species group 18) and the lichen heath (species group 17). Furthest towards the negative end of axis (2) is the late-snow early intermediate heath (species group 38) reflecting the most developed soils and highest vegetation cover. The sequence of species groups on axis (1) is influenced strongly by age and also microtopography. Axis (2) is mainly influenced by age and soil development but the order of some species groups on the axis further supports the notion that the relationship is not a strong one and thus axis (2) is not a very meaningful axis.

From the spread of environmental parameters, TWINSPAN "final site groups" and "final species groups", on Figs. 5.6 and 5.14, it emerges that the sequence of site and species groups on axis (1) is influenced by age and microtopography, while axis (2) is influenced by soil development and vegetation cover. The sequences suggest that microtopography is an important influence on this foreland and the so-called *"Microtopographic (exposure-moisture-snowmelt) factor complex"* (*sensu*: Whittaker, 1985) is apparent at Storbreen high as it is on the sequences for the low-alpine forelands. The only important parameter found distributed between axis (1) and (2) is age and soil texture, suggesting that the influence of age is difficult to separate from other important environmental parameters and thus the pattern on each axis is obscured. The DCA centroid scores of TWINSPAN "final site groups" and "final species groups" correspond well with the pattern of environmental parameters on axis (1), but some of the pioneer groups, most related to axis (1), did not relate well to the environmental trend on axis (2), suggesting that axis (2) may not be a very meaningful axis.

5.8.4 Summary of DCA ordination results at Storbreen high

Both axis (1) and (2) have eigenvalues high enough to suggest relatively good separation of sites and species. The rank tables (Tables 5.6 and 5.14), displaying the distribution of the TWINSPAN "final site groups" and "final species groups" on the DCA ordination axes, provide a clear representation of the results on axis (1) but interpretation of the sequence on axis (2) is difficult. The TWINSPAN "final species group" assemblages correspond well with the sequence of species along axis (1). There is some correspondence on axis (2), especially towards the positive end of the axis, but the sequence of TWINSPAN "final species group" assemblages is not distinct. There is a good correspondence between the TWINSPAN "final site groups", and the pattern of sites on axis (1), but there is only a poor correspondence on axis (2), except towards the positive end. The plots and correlation matrices, provide further elucidation and confirmation of the results derived from the rank tables on axis (1) but on axis (2) the pattern is not as meaningful. The DCA centroid scores of TWINSPAN "final site groups" and "final species groups" correspond well with the pattern of environmental parameters on axis (1), but not well on axis (2), suggesting that the trends found axis (2) are not very meaningful. The main findings from sections 5.8.1. to 5.8.3., derived from the DCA ordination results for Storbreen high are summarised below.

The separation of species and sites along axis (1) appears to be influenced mainly by age and microtopography and the so-called *"Microtopographic (exposure-moisture-snowmelt) factor complex"* (*sensu*: Whittaker, 1985) is apparent at Storbreen high, as it is on the sequences for the low-alpine forelands. The sequence on axis (1), from the positive end, progresses from younger snowbed assemblages, located on moist, low-slope, younger sites with longer snow duration and fluvial disturbance, to mature lichen heath, towards the negative end of the axis, located on the drier, high-slope, older sites. The variables most highly correlated with axis (1) are age, position, low snow cover, fluvial activity, soil texture, dryness and pH. The only important parameter found spread between axis (1) and (2) is age and soil texture, suggesting that age is important on both axis (1) and (2).

In general, the sequence on axis (2) progresses from snowbed assemblages, on low-slope, younger sites with low vegetation cover, to older heath assemblages with developed soils and higher vegetation cover. However the pattern of environmental parameters does not correspond well with the pattern of TWINSPAN "final site groups or "final species groups" and thus it is suggested that axis (2) is not very meaningful. It is possible that the dual effects of age on both axes has confounded the results on axis (2) and this will be discussed further in the concluding chapter.

The site and species separation on ordination axis (1) is close to that found by the TWINSPAN "final groups", although the sequences are not identical. The most distinct site-groups on axis (1) are the pioneer snowbed (site group 15*), the early intermediate lichen heath (site group 9*) and the exposed pioneer (site group 14*) and the early intermediate snowbed (site group 6*) and none on axis (2). The most distinct species group on axis (1) is the lichen heath (species group 17) and on axis (2), the pioneer (species group 7). Generally the evidence further supports the notion that there is a gradient of assemblages, as opposed to distinct communities, at Storbreen high and this will be further discussed in the summary 5.11. and the concluding chapter.

5.9 Høgvaglbreen

5.9.1 Site (sample) patterns on DCA axes (1) and (2) at Høgvaglbreen.

By referring to Table 5.7 and the profile diagram (Fig. 4.8), for the location of specific sites where the pattern is not clear, the following site patterns emerge on DCA ordination axes (1) and (2). Axis (1) has an eigenvalue of 0.378 showing that there is quite good species and sample separation along the axis and this axis is ecologically meaningful. The environmental variables explain 90.6% of the variation along this axis. Axis (2) has an eigenvalue of 0.22 which is high enough to suggest fair separation along the axis.

The environmental variables explain 91.1% of the variation along axis (2). The lower eigenvalues for axis (1) and (2), in comparison to most of the other forelands, is possibly explained by the shortness of foreland and thus relative close proximity of most of the moraines to the glacier. There is a good correspondence between the TWINSPAN groups and the pattern of sites on axis (1) and there is some correspondence on axis (2) especially towards the positive end.

At the positive end of axis (1) is the pioneer snowbed (site group 6*), **Solorina crocea - Oxyria digyna,** assemblages followed by the exposed pioneer (site group 7*), **Salix glauca - Cetraria nivalis,** assemblage. These sites correspond with the environmental variables of altitude, fluvial activity, pH, bare gravels and boulders. Following the pioneer groups is the large early intermediate snowbed (site group 21*), the **Cassiope hypnoides - Cladonia chlorophaea,** assemblage and further down this becomes interspersed with the mature or late intermediate snowbed (site group 11*), the **Cladonia gracilis - Salix herbacea,** assemblage which in turn is replaced by the early intermediate lichen heath (site group 20*), the **Cornicularia aculeata - Cetraria nivalis,** assemblage. At the negative end of axis (1) is the dry lichen heath (site group 4*), the **Thamnolia vermicularis - Alectoria ochroleuca,** assemblage. The negative end of axis (1) corresponds with age, lack of snow, vegetation cover, position and soil texture.

At the positive end of axis (2) are members of the mature/late intermediate snowbed (site group 11*) and the dry lichen heath (site group 4*). This corresponds with the environmental parameters associated with the oldest terrain, namely stain depth, humus depth, root depth, vegetation cover, age and soil texture. These groups are followed by the early intermediate snowbed (site group 21*) interspersed with the pioneer snowbed (site group 6*). These groups give way to a fairly disordered sequence of sites belonging to the pioneer (site group 7*), the early intermediate lichen heath (site group 20*), and the dry lichen heath (site group 4*) at the negative end of axis (2). The negative end of axis (2) corresponds with pH, altitude, bare gravels, position lack of snow, dowel heave and dryness.

These results are summarised in Fig. 5.23 and the sequence is relatively similar to that found on the Storbreen high foreland although the sequence on axis (2) is clearer. On axis (1) there is a strong age-related sequence from young terrain at the positive end of axis (1) to the oldest terrain at the negative end. Superimposed onto each section of the axis is a position-related sequence from sheltered low-slope positions to more exposed high-slope positions. This shows that age is the most influential factor on axis (1) but microtopography-related factors, such as fluvial activity and snow duration, are also important. The sequence of sites, on axis (2), is relatively disordered towards the negative end but it is still possible to see a sequence from snowbed to lichen heath which is mainly related to microtopography. The order of environmental parameters also suggests an axis influenced by exposure and position, with the positive end of the axis consisting of sites that are more sheltered, and a more developed vegetation and soils, and the negative end, comprising exposed and bare-ground sites. The site separation on ordination axis (1) matches that of the TWINSPAN "final site groups" although the sequence is not identical.

5.9.2 Species patterns on DCA axes (1) and (2) at Høgvaglbreen

By referring to Table 5.15 and Table 4.10, the sequence of species on DCA axes (1) and (2) can be related to the TWINSPAN "final species groups" described in chapter (4), and thus the influence of particular environmental variables on the species pattern across Høgvaglbreen foreland can be elucidated. The TWINSPAN "final species groups" correspond quite well with the sequence of species along axis (1). On axis (2) the sequence of members of the TWINSPAN "final species groups" is disordered but, nevertheless, a clear trend can be seen.

At the positive end of axis (1) is the pioneer (species group 3) followed by the widespread heath (species group 5). Following these assemblages is the early intermediate snowbed (species group 38). The environmental parameters which correspond with this part of the axis are altitude, fluvial activity, pH, bare gravels and boulders. Species group (38) is replaced by the mature snowbed (species group 39) interspersed with the late-snow heath (species group 37). The negative portion of the axis consists of more members of species group (38) and the mature heath (species group 36). At the negative end of the axis is a tight group of the lichen heath (species group 8). The negative end of the axis corresponds with age, low snow duration, vegetation cover, high position and soil texture.

The order of TWINSPAN "final species groups" on axis (2) is disordered but a general trend of assemblages can be seen. The positive end of the axis comprises the mature snowbed (species group 39) with the mature heath (species group 36) interspersed with mainly phanerogam members of the lichen heath (species group 8). This part of the axis corresponds with stain depth, humus depth, root depth, vegetation cover and age. The central portion of the axis comprises most of the late-snow heath (species group 37), the widespread heath (species group 5) and the pioneer (species group 3). The early intermediate snowbed (species group 38) dominates the negative portion of the axis interspersed with most of the members of the lichen heath (species group 8). The environmental parameters corresponding with the negative end of the axis are pH, altitude, bare gravels, position, low snow cover and dowel heave. These results are summarised in Fig. 5.31 and the sequence complements the results of the TWINSPAN "final site groups", from the previous section.

5.9.3 TWINSPAN group centroids of sample and species scores at Høgvaglbreen.

Fig. 5.7 shows the DCA centroids of TWINSPAN "final site groups" scores and reveals the location of the site groups on both axes in relation to the environmental parameter biplot scores. Fig. 5.15, displays the DCA centroids of TWINSPAN "final species group" scores, and reveals the location of the species groups on both axes in relation to the environmental parameter biplot scores. In addition, Table 5.23, the weighted correlation matrix, can be used to elucidate further the relative influence of environmental parameters on the TWINSPAN "final groups". These plots, and the correlation matrix are used to support and outline the main findings of the previous two sections at Høgvaglbreen. The critical value for " *r* " on this foreland is 0.321.

The most important environmental variables on Fig. 5.7 and 5.15 are quite widely dispersed between the axes so that the influence of variables associated with age and microtopography are difficult to separate. The important variables positively correlated with axis (1) are altitude (*r* = +*0*.617), fluvial activity (*r* = +*0*.454), pH (*r* = +*0*.406), bare gravels (*r* = +*0*.388) and bare boulders (*r* = +*0*.334). The variables negatively correlated with axis (1) are age (*r* = -0.586), low snow cover (*r* = -0.583), vegetation cover (*r* = -0.518), position (*r* = -0.455) and soil texture (*r* = -0.407). Axis (1) is most correlated with age, altitude and to a large extent microtopography: the higher altitude, moist, low-slope, younger sites with longer snow cover and fluvial disturbance occur towards the positive end of the axis and the drier, high-slope, older sites occurring towards the negative end of axis (1). This axis compares strongly to axis (1) at Storbreen high. Axis (2) is very similar to axis (1) in that it is influenced by altitude and age, especially with regard to soil development and position. On axis (2), high-slope positions and low snow cover are related to younger ground and higher altitude sites, whereas low-slope positions are related to more developed soils and higher vegetation cover. The most important variables, correlated with the positive end of axis (2), are stain depth (*r* = +*0*.685), humus depth (*r* = +*0*.606), root depth (*r* = +*0*.588), vegetation cover (*r* = +*0*.527), and age (*r* = +*0*.48). The most important variables, correlated with the negative end of axis (2), are pH (*r* = -0.688), altitude (*r* = -0.553), bare gravels (*r* = -0.532), position (*r* = -0.414), low snow (*r* = -0.371), dowel heave (*r* = -0.35) and dryness (*r* = -0.338)

Those parameters which are most positively correlated with age, and thus associated with the oldest terrain, are stain depth (*r* = +*0*.572), soil texture (*r* = +0.564), vegetation cover (*r* = +*0*.527), root depth (*r* = +*0*.501), and humus depth (*r* = +*0*.443). The parameters most negatively correlated with age are altitude (*r* = -0.916), pH (*r* = -0.771) and bare ground gravels (*r* = -0.476). Age is highly correlated with both axis (1) (*r* = -0.586) and axis (2) (*r* = +*0*.48). The parameters most correlated with high-slope position are snow-lie (*r* = +*0*.797), dowels (*r* = +*0*.416) and dryness (*r* = +*0*.408). The parameters most negatively correlated with high-slope position are humus depth (*r* = -0.352) and root depth (*r* = -0.265). Position is important on both axis (1) (*r* = -0.455) and axis (2) (*r* = -0.414).

According to Fig. 5.7. there is a very poor dispersal of DCA centroids of TWINSPAN "final site groups" across the plot with the centroids clustered around the centre of the plot. It is only possible to interpret the location of the "final site groups", in relation to the environmental variables, by referring to the table of plot co-ordinates (Appendix 5.7). The reason for this appears to be the difference in scale for the species plot and the environmental plot. Despite this, it is possible to elucidate the relationship between the site groups and the environmental variables. Slightly towards the positive end of axis (1) is the pioneer snowbed (site group 6*) and this group is largely associated with young ground, fluvial activity, long snow-lie, low-slope position and moist conditions. Near the axis centre, is the exposed pioneer (site group 7*), the early intermediate snowbed (site group 21*) and the mature late intermediate snowbed (site group 11*). Slightly towards the negative end of axis (1), is the early intermediate lichen heath (site group 10*) and the dry lichen heath (site group 4*) comprising high-slope, dry and snow-free sites. The pattern of "final site groups", on axis (1), is very similar to that found on axis (1) across the Storbreen high foreland sequence. Towards the positive end of axis (2) is the mature late intermediate snowbed (site group 11*), and very slightly towards the negative end of the axis is the pioneer snowbed (site group 6*), followed by the dry lichen heath (site group 4*), the early intermediate snowbed (site group 21*), the exposed pioneer (site group 7*) and lastly the early intermediate lichen heath (site group 20*). The order of groups on axis (2) suggests that microtopography is an important influence on this axis and complements the spread of environmental parameters on the plot.

According to Fig. 5.15, there is a very poor spread of DCA centroids of TWINSPAN "final species groups" across the plot with the species groups clustered around the centre of the plot. It is only possible to discuss the location of the groups in relation to one another by referring to the table of plot co-ordinates (Appendix 5.15). As with the "final site groups", the reason for this appears to be the difference in scale for the species plot and the environmental plot, but it is still possible to elucidate the relationship between the species groups and the environmental variables. Slightly towards the positive end of axis (1) is the pioneer (species group 3), which is associated with young terrain with fluvial activity, long snow-lie, low-slope and moister conditions. Towards the centre is the widespread heath (species group 5), followed by the early intermediate snowbed and mature snowbed (species groups 38 and 39). Slightly towards the negative end is the late-snow heath (species group 37), the mature heath (species group 36) and lastly the lichen heath (species group 8) corresponding with high-slope, drier older sites. On axis (2), slightly towards the positive end, is the mature heath (species group 36) and mature snowbed (species group 39) and this is followed by the late-snow heath (species group 37) and the lichen heath (species group 8). At the centre is the pioneer (species group 3) and towards the negative end is the widespread heath (species group 5) and this is followed by the early intermediate snowbed (species group 38). There is an indistinct trend, from better developed mature assemblages with higher vegetation cover, to poorer developed assemblages with lower vegetation cover. The microtopographical trend from low-slope to high-slope positions is indiscernible across the axis (2) sequence.

From the spread of environmental parameters, TWINSPAN "final site groups" and "final species groups", on Figs. 5.7 and 5.15, it emerges that the sequence of sites and species on axis (1) is influenced by age (and altitude) and microtopography. Axis (2) is also influenced by these variables especially regarding the sequence of "final site groups". On both axis (1) and (2), the sequences suggest that microtopography is an important influence on this foreland and the so-called *"Microtopographic (exposure-moisture-snowmelt) factor complex"* (*sensu*: Whittaker, 1985) is apparent at Høgvaglbreen, as it is on the sequences for Storbreen high and the low-alpine sequences. Many of the important parameters are widely distributed between axis (1) and (2) suggesting that the relative influence of the most important environmental parameters is difficult to separate and thus the pattern on each axis is obscured. The DCA centroid scores of TWINSPAN "final site groups" and "final species groups" correspond well with the pattern of environmental parameters on axis (1), and relatively well on axis (2), suggesting that axis (1) is meaningful and axis (2) is quite meaningful.

5.9.4 Summary of DCA ordination results at Høgvaglbreen

Axis (1) has an eigenvalue high enough to suggest relatively good separation of sites and species, although the eigenvalue on axis (2) suggests only fair separation. The rank tables (Tables 5.7 and 5.15), displaying the distribution of the TWINSPAN "final site groups" and "final species groups" on the DCA ordination axes, provide a clear representation of the results on axis (1) and the sequence on axis (2) is disordered but, nevertheless, identifiable. The TWINSPAN "final species groups" correspond quite well with the sequence of species along axis (1) and a trend is discernible on axis (2). There is a good correspondence between the TWINSPAN "final site groups" and the pattern of sites on axis (1) and there is some correspondence on axis (2). The plots and correlation matrices, provide further elucidation and confirmation of the results derived from the rank tables on axis (1) and axis (2). The DCA centroids of TWINSPAN "final site groups" and "final species groups" correspond well with the pattern of environmental parameters on axis (1) and to some extent on axis (2). The main findings from sections 5.9.1. to 5.9.3., derived from the DCA ordination results for Høgvaglbreen are summarised below.

The separation of species and sites along axis (1) appears to be influenced mainly by age (and altitude) and microtopography and the so-called *"Microtopographic (exposure-moisture-snowmelt) factor complex"* (*sensu*: Whittaker, 1985) is apparent at Høgvaglbreen. The sequence on axis (1), at the positive end, progresses from younger pioneer and snowbed assemblages located on moist, low-slope, younger sites (with longer snow cover and fluvial disturbance), to mature lichen heath assemblages located on the drier, high-slope, older sites, towards the negative end of the axis. This sequence bears a great resemblance to the sequence on axis (1) at Storbreen high. The most highly correlated variables with axis (1) are altitude, age, low snow cover, vegetation cover, position, fluvial activity, pH and soil texture. Many of the important parameters are dispersed between axis (1) and (2) suggesting that the influence of many of the variables cannot be separated, and thus differences in the relative influence of individual variables on the separation of species and sites on each axis is obscured.

The sequence of environmental variables on axis (2) suggests that this axis is related largely to soil and vegetation development as well as position. The sequence on axis (1), at the positive end, progresses from older or low-slope assemblages located on moist sites (with longer snow cover and high vegetation cover) to pioneer and heath assemblages, with lower vegetation cover and soil development, towards the negative end of the axis. The pattern of environmental parameters corresponds quite well with the pattern of TWINSPAN "final groups". It is possible that the dual effects of age and altitude has confounded the results on axis (2) so that the sequence is similar to that on axis (1) and this will be discussed further in the concluding chapter.

The site and species separation on ordination axis (1) corresponds with the TWINSPAN "final groups", although the sequence is not identical. The most distinct site-groups, on axis (1), are the dry lichen heath (site group 4*) and the pioneer snowbed (site group 6*) and on axis (2), the mature/late intermediate snowbed (site group 11*). The most distinct "final species groups" on axis (1) are the lichen heath (species group 8), the pioneer (species group 3), the mature heath (species group 36) and the widespread heath (species group 16) and none on axis (2). Generally the evidence further supports the notion that there is a gradient of assemblages as opposed to distinct communities at Høgvaglbreen although, at this high altitude, they appear to be more distinct than they are at lower altitudes and this will be further discussed in the summary 5.11 and the concluding chapter

5.10 Bøverbreen

5.10.1 Site (sample) patterns on DCA axes (1) and (2) at Bøverbreen.

By referring to Table 5.8 and the profile diagram (Fig. 4.9), for the location of specific sites where the pattern is not clear, the following site patterns emerge on DCA ordination axes (1) and (2) in relation to the TWINSPAN "final site groups" as well as the corresponding environmental biplot scores. Axis (1) has an eigenvalue of 0.501 showing that there is good species and sample separation along the axis and axis (1) is ecologically meaningful. The environmental variables explain 93.1% of the variation along this axis. Axis (2) has an eigenvalue of 0.26, which is high enough to suggest fair separation along the axis. The environmental variables explain 82.5% of the variation along this axis. There is a good correspondence between the TWINSPAN "final site groups" and the pattern of sites on axis (1) and there is some correspondence at either end of axis (2) but there is poor correspondence on the middle section of axis (2). At the positive end of axis (1) is the pioneer snowbed (site group 7*), the **Oxyria digyna - Poa alpina,** assemblage and this is followed by the exposed pioneer (site group 6*), **Cerastium alpinum - Cerastium alpinum,** assemblage. These pioneer groups correspond with bare gravels, fluvial activity, bare fines, dowels, solifluction and position. Following the pioneers is the snowbed (site group 11*), the **Trisetum spicatum - Gnaphalium supinum,** assemblage which in turn is followed by the mature or late intermediate lichen heath (site group 10*), the **Cetraria islandica - Cetraria ericetorum,** assemblage. At the negative end of axis (1) is a disordered sequence of site group (10*) and the exposed lichen heath (site group 4*), the **Alectoria ochroleuca - Cornicularia aculeata,** assemblage.

At the positive end of axis (2) is the exposed lichen heath (site group 4*) and this is followed by a disordered sequence of groups dominated by the snowbed (site group 11*) but interspersed with pioneer (site groups 6* and 7*). These groups correspond with the environmental parameters of low snow duration, bare gravels, bare fines, dowels, slope and high-slope positions. Further down the axis the pioneer groups dominate, especially the exposed pioneer (site group 6*). At the negative end of axis (2) is the mature/late intermediate lichen heath (site group 10*). This corresponds with stain depth, bryophyte cover, vegetation cover, humus depth, root depth and age.

These results are summarised in Fig. 5.24 and the sequence is relatively similar to that found on the Storbreen high and Høgvaglbreen forelands. From the sequence it is possible to see that on axis (1) there appears to be a strong age-related sequence from young terrain at the positive end of axis (1) to the oldest terrain at the negative end. Superimposed onto each section of the axis is a position-related sequence from sheltered low-slope positions to more exposed high-slope positions. This shows that age is the most influential factor on axis (1) but microtopography-related factors, such as fluvial activity and snow-lie are also important. On axis (2) the order of TWINSPAN "final site groups" suggests that position and exposure is probably the most significant influence on this axis. The order of environmental parameters also suggests an axis influenced by exposure and position, with the positive end comprising exposed and bare-ground sites and the negative end of the axis consisting of sites that are more sheltered and that have a more developed vegetation and soils. The site separation on ordination axis (1) is close to that found by the TWINSPAN "final site groups" although the sequence is not identical.

5.10.2 Species patterns on DCA axes (1) and (2) at Bøverbreen

By referring to Table 5.16 and Table 4.10, it is possible to relate the sequence of species on DCA axes (1) and (2) to the TWINSPAN "final species groups" described in chapter (4) and thus elucidate the influence of particular environmental variables on the species patterns across Bøverbreen foreland. There is some correspondence between TWINSPAN "final species groups" and the sequence of species along axis (1), although the negative part of the axis consists of a rather disordered sequence of mature assemblages. There is a relatively good correspondence on axis (2), especially towards the positive end and negative end of the axis.

At the positive end of axis (1) is the pioneer (species group 7) followed by the snowbed (species group 6) which in turn is followed by the widespread heath (species group 5) and the early intermediate snowbed (species group 36). These groups correspond with bare gravels, fluvial activity, bare fines, dowel heave and solifluction. They are followed by the heath (species group 37) and, in turn, by the mature late-snow lichen heath (species group 19), interspersed with the exposed lichen heath (species group 16), and, towards the negative end, the mature late-snow lichen heath (species group 17). The negative end of axis (1) corresponds with age, root depth, stain depth, humus depth, low snow cover and vegetation cover.

At the positive end of axis (2) is the exposed lichen heath (species group 16) and this is followed by a disordered sequence of TWINSPAN assemblages consisting mainly of the widespread heath (species group

5), the snowbed (species group 6) and the pioneer (species group 7) and then the heath (species group 37) and the early intermediate snowbed (species group 36). The positive half of the axis corresponds with low snow cover, bare ground, dryness and dowel heave. The negative end of the axis is dominated by the mature late-snow lichen heath (species group 19), interspersed with the mature late-snow lichen heath (species group 17), and corresponds with stain depth, bryophyte cover, vegetation cover, humus depth, root depth and age. These results are summarised in Fig. 5.32 and the TWINSPAN "final species group" sequences complements those of the TWINSPAN site groups described in the previous section.

5.10.3 TWINSPAN group centroids of sample and species scores at Bøverbreen

Fig. 5.8 shows the DCA centroids of TWINSPAN "final site group" scores and reveals the location of the "final site groups" on both axes in relation to the environmental parameter biplot scores. Fig. 5.16, showing the DCA centroids of TWINSPAN "final species group" scores, reveals the location of the "final species groups" on both axes in relation to the environmental parameter biplot scores. In addition, Table 5.24, the weighted correlation matrix, can be used to elucidate further the relative influence of environmental parameters on the TWINSPAN "final groups". These plots and the correlation matrix are used to support and outline the main findings of the previous two sections at Bøverbreen. The critical value for " r " on this foreland is 0.307.

The most important environmental variables, on Fig. 5.8 and 5.16, are quite widely spread between the axes and the relationships appear to be obscured by the effect of the most important environmental parameters on other variables associated with older, more developed soils. The most important variables positively correlated with axis (1), are bare gravels ($r = +0.428$) fluvial activity ($r = +0.394$) and bare fines ($r = +0.328$). The most important variables negatively correlated with axis (1) are age ($r = -0.609$), root depth ($r = -0.552$), stain depth ($r = -0.547$), humus depth ($r = -0.439$) and low snow cover ($r = -0.261$). Axis (1) is most correlated with age and soil development, but also to microtopography, with the younger sites (and longer snow duration and fluvial disturbance) at the positive end of the axis and the high-slope and older sites at the negative end of axis (1). This axis corresponds with axis (1) at Høgvaglbreen and Storbreen high. The variables, positively correlated with axis (2), are low snow duration ($r = +0.591$), bare gravels ($r = +0.396$), dryness ($r = +0.336$) and bare boulders ($r = +0.316$). The variables which are negatively correlated with axis (2) are stain depth ($r = -0.561$), bryophyte cover ($r = -0.447$), vegetation cover ($r = -0.43$), humus depth ($r = -0.4$) and root depth ($r = -0.373$). Axis (2) is related to microtopography and soil development and vegetation cover (age-related variables).

Those parameters which are positively correlated with age, and thus associated with the oldest terrain, are stain depth ($r = +0.65$), root depth ($r = +0.603$), and humus depth ($r = +0.549$). The parameters that are negatively correlated with age are bare gravels ($r = -0.568$), dowels ($r = -0.369$) and bare fines ($r = -0.343$). Age is significantly correlated with axis (1) ($r = -0.586$), but not with axis (2) ($r = -0.187$)), suggesting that it is more important on axis (1). However the soil development variables are highly correlated with axis (2), which suggests that age is important on this axis. There are no parameters which are significantly correlated with high-slope position, but there are a number that are correlated with snow-lie which has been shown to be related to microtopographical position and moisture. Snowlie (low duration) is found to be correlated with dryness ($r = +0.382$), dowel heave ($r = +0.354$), and slope ($r = +0.279$) and is found to be negatively correlated with bryophyte cover ($r = -0.571$) and fluvial activity ($r = -0.263$).

According to Fig. 5.8 there is a good spread of DCA centroids of TWINSPAN "final site groups" across the plot, suggesting that the site groups are distinct from one another and the relative influence of the environmental variables on each of the groups can be understood. Slightly towards the positive end is the pioneer snowbed (site group 7*) and this group is largely associated with young ground, fluvial activity, long snow-lie, low-slope position and moist conditions. Towards the centre is the exposed pioneer (site group 6*) and near the centre is the snowbed (site group 11*). Towards the negative end, are the exposed lichen heath (site group 4*) and the mature/late intermediate lichen heath (site group 10*) and these two groups reflect high-slope, older positions. At the positive end of axis (2) is the exposed lichen heath (site group 4*), reflecting the high-slope and driest snow-free sites with lower vegetation cover. At the centre is the snowbed (site group 11*), corresponding with long snow duration, and the pioneer groups, which are related to the snow cover trend on axis (2), but are more related to the soil development sequence on axis (1). Towards the negative end of axis (2) is the mature lichen heath (site group 10*), which corresponds with high vegetation cover and long snow-lie.

According to Fig. 5.16 there is a good spread of DCA centroids of TWINSPAN "final species groups" across the plot suggesting that the groups are distinct from one another and the relative influence of the environmental variables on each of the groups can be elucidated. Slightly towards the positive end of axis (1) is the pioneer (species group 7) which is associated with young terrain with fluvial activity, long snow-lie, low-slope and moister conditions. Towards the centre is the snowbed (species group 6) and at the centre is the widespread heath (species group 5). Slightly towards the negative end is the early intermediate snowbed (species group 36). Further towards the negative end are a band of assemblages spanning a range of co-ordinates along axis (2) and they are the heath (species group 37), the exposed lichen heath (species group 16), the mature late-snow heath (species group 19) and another late-snow heath (species group 17) corresponding with high-slope and older sites. Towards the positive end of axis (2) is the exposed lichen heath (species group 16) and this corresponds with high-slope, drier and snow-free sites. Assemblages at the centre include the widespread heath (species group 5) and the early intermediate snowbed (species group 36) and slightly towards the negative end is the mature late-snow lichen heath (species group 17) and the heath (species group 37) and this is followed by the mature late-snow lichen heath (species group 19). These assemblages correspond with older more developed soils and vegetation with longer snow-lie and higher moisture.

From the spread of environmental parameters, TWINSPAN "final site groups" and "final species groups", on Figs. 5.8 and 5.16, it emerges that the sequence of sites and species on axis (1) is influenced by mainly by age and, to a lesser extent, microtopography. Axis (2) is influenced by microtopography (snowlie and dryness parameters). The sequence on axis (2) suggests that microtopography is an important influence on this foreland and the so-called *"Microtopographic (exposure-moisture-snowmelt) factor complex"* (*sensu*: Whittaker, 1985) is apparent at Bøverbreen and the other low and mid-alpine forelands. Many of the important parameters, especially the age-related variables of soil and vegetation development, are spread between axis (1) and (2) so that the relative influence of environmental variables, on the separation of species and sites on each axis, is obscured. The DCA centroid scores of TWINSPAN "final site groups" and "final species groups" corresponded well with the pattern of environmental parameters on axis (1) and quite well on axis (2) suggesting that both of these axes are ecologically meaningful.

5.10.4 Summary of DCA ordination results at Bøverbreen

Axis (1) has a high eigenvalue that suggests good separation of sites and species although the eigenvalue on axis (2) suggests only fair separation. The rank tables (Tables 5.8 and 5.16), displaying the distribution of the TWINSPAN "final site groups" and "final species groups" on the DCA ordination axes, provide a clear representation of the results on axis (1) and the sequence on axis (2) is interpretable on axis (2). There is some correspondence between TWINSPAN "final species groups", and the sequence of species along axis (1), although the negative part of the axis comprises a rather disordered sequence of mature assemblages. There is a relatively good correspondence on axis (2), especially towards either end of the axis. There is a good correspondence between the TWINSPAN "final site groups" and the pattern of sites on axis (1) and there is some correspondence at either end of axis (2) but there is poor correspondence on the middle section of axis (2). The plots and correlation matrices, have provided further elucidation and confirmation of the results derived from the rank tables on axis (1) and axis (2). The DCA centroid scores of TWINSPAN "final site groups" and "final species groups" correspond well with the pattern of environmental parameters on both axis (1) and (2). The main findings from sections 5.10.1. to 5.10.3, derived from the DCA ordination results for Bøverbreen, are summarised below.

The separation of species and sites along axis (1) appears to be influenced mainly by age, but also microtopography and the so-called *"Microtopographic (exposure-moisture-snowmelt) factor complex"* (*sensu*: Whittaker, 1985) is apparent at Bøverbreen, as well as across the other alpine forelands. The sequence on axis (1) at the positive end progresses from younger pioneer and snowbed assemblages, located on moist, low-slope, (with longer snow cover and fluvial disturbance), to mature lichen heath assemblages located on the drier, high-slope, older sites towards the negative end of the axis. This sequence bears a great resemblance to the sequences on axis (1) across both the Høgvaglbreen and Storbreen high foreland sequences. The most highly correlated variables, with axis (1), are age, root depth, stain depth, humus depth, bare gravels, fluvial activity, bare fines and low snow cover. Many of the important age-related parameters are found to be spread between axis (1) and (2), so that the influence of the environmental parameters on the separation of species and sites on each axis is obscured.

The sequence of environmental variables on axis (2) suggests that this axis is related to snow-lie and dryness and also soil and vegetation development. The sequence on axis (2) at the positive end progresses from the lichen heath assemblage on dry and snow-free sites, with a low vegetation cover, to the mature lichen heath located on sites which are moister and have a longer snow cover. The most highly correlated variables with axis (2) are low snow duration, stain depth, bryophyte cover, vegetation cover, humus depth, bare gravels, root depth, dryness and bare boulders. Position is shown to be correlated with snow cover and dryness but there does not appear to be a highly significant relationship. This is a surprising result and is discussed further in the summary (section 5.11) and the concluding chapter (section 7.5.1).

The site and species separation on ordination axis (1) is quite close to that found by the TWINSPAN "final groups" although the sequence is not identical. The most distinct species groups on axis (1) are the pioneer (species group 7), the snowbed (species group 6), the widespread heath (species group 5) and the early intermediate snowbed (species group 36) and on axis (2), the mature late-snow lichen heath (species group 19) and the early intermediate snowbed (species group 16). The most distinct site-groups on axis (1) are the exposed pioneer (site group 6*), the pioneer snowbed (site group 7*) and the snowbed (site group 11*) and on axis (2), the exposed lichen heath (site group 4*) and the mature/late intermediate lichen heath (site group 10*). Generally the evidence further supports the notion that there is a gradient of assemblages, as opposed to distinct communities although, at this high altitude, they may be more distinct than they are at lower altitudes, but this is further discussed in the summary (section 5.11) and the concluding chapter (section 7.4.2).

5.11 Summary of individual foreland DCA ordination results

This chapter has elucidated the relationship between the vegetation patterns and environment across moraines on a number of forelands at different altitudes. The different methods of presentation of the DCA ordination sequences have produced results which are complementary. Each method has been found necessary for a comprehensive evaluation of these rather complex results. The rank tables (Tables 5.1 - 5.16), with colours and accompanying sequence diagrams (Figs 5.17 – 5.32) representing the TWINSPAN site groups and species groups on each foreland, display a clear and easily interpreted representation of the ordination results. The centroid plots (Figs. 5.1 – 5.16) and correlation matrices (Tables 5.17 – 5.24) provide further information and confirm the results derived from the rank tables, especially concerning axis (2) (which is often much more difficult to interpret). The results are summarised in Tables 5.25 to 5.28. By referring to these tables, as well as earlier sections in chapter (5), the main conclusions are listed and described as follows:

1. The relative influence of age. Age has been found to be the main influence on species and site separation on axis (1) on all forelands, with the possible exception of Svellnosbreen. At Svellnosbreen an outlier group may have affected the results so that microtopography appears to be a more important influence on the separation of species and sites along axis (1). However, on axis (2) age is the only important meso-scale variable and the similarity in eigenvalue, between both axis (1) and (2), suggests that age is an important influence at Svellnosbreen. Correlation (Table 5.28) confirms the importance of age on each of the forelands. In general, according to Table 5.27, the parameters most correlated with age, and thus associated with mature or late intermediate assemblages, are root depth, humus depth, stain depth and vegetation cover and there does not appear to be any noticeable difference between forelands. The parameter with the strongest negative correlation with age, and thus associated with young terrain, is bare ground (mainly bare gravels and boulders) and, on half of the forelands, altitude, pH and frost activity are also significantly negatively correlated with age. It has therefore been shown that the "*terrain-age*" factor complex (Whittaker, 1985,1987, 1989) of age, altitude, soil characteristics and frost activity is an important influence on vegetation pattern on all of the forelands. However it can also be seen that the relationship between the soil characteristics and age appears to be stronger than the relationship between age and frost or altitude. These results are discussed in greater detail in chapter 7.

Table 5.28 Weighted correlation results (*r*), for age and position (including most associated parameters in *italics*), on DCA ordination axes (1) and (2).

FACTOR	**AXIS**	**AUSF**	**FÅSF**	**STLF1**	**STLF2**	**SVLF**	**STHF**	**HØHF**	**BØHF**
Age	*Axis (1)*	0.764	-0.648	-0.667	-0.713	-0.326	-0.552	-0.586	-0.809
Age	*Axis (2)*	-0.335	-0.346	-0.38	-0.1	0.667	-0.408	0.48	-0.187
Stain depth	*Axis (1)*	*0.602*	*-0.879*	*-0.808*	*-0.715*	*0.194*	*-0.213*	*-0.269*	*-0.261*
Stain depth	*Axis (2)*	*-0.28*	*-0.11*	*-0.156*	*-0.227*	*0.648*	*-0.603*	*0.685*	*0.561*
Position	*Axis (1)*	-0.114	-0.136	0.523	0.468	-0.599	-0.496	-0.455	0.097
Position	*Axis (2)*	-0.207	0.08	-0.335	-0.23	-0.083	0.098	-0.414	0.082
Snow-lie	*Axis (1)*	*-0.273*	*-0.71*	*0.388*	*0.524*	*-0.654*	*-0.486*	*-0.583*	*-0.201*
Snow-lie	*Axis (2)*	*-0.127*	*0.247*	*-0.313*	*-0.204*	*-0.599*	*0.078*	*-0.371*	*0.591*

2. The relative influence of microtopography/position. Slope-position has a significant influence on vegetation pattern on most forelands. However, it appears not to be very important on the sub-alpine forelands. In addition, its importance at Bøverbreen mid-alpine foreland is not as significant, within the correlation matrix, as that of the snow lie and moisture variables, possibly due to the influence of a low and small moraine (M4) on the results. It appears the small moraine has a long snow duration across its entire profile thus reducing the apparent influence of position within the data set. On all the other alpine forelands, position is strongly related to dryness and snow-lie. It is therefore considered acceptable to use snow-lie as a substitute for position in order to evaluate the relative importance of microtopography at Bøverbreen. According to Table 5.27, high-slope positions tend to be correlated with low snow cover,

dryness, frost-heave and dowel heave and to a certain extent bare fines. Low-slope positions tend to be associated with fluvial activity higher vegetation and bryophyte cover and developed soils. Microtopography has thus been shown to be an important influence on vegetation pattern and the prevailing environment on most of the forelands and the so-called *"Microtopographic (exposure-moisture-snowmelt) factor complex"*, (*sensu*: Whittaker, 1985), is apparent on most forelands.

3. The relationship between age and microtopography. As can be seen in Tables 5.27 to 5.28, both age (or other components of the "*Terrain-age factor complex*") and position (or other components of the "*Microtopographic factor complex*") are often highly correlated with both axes (1) and (2). This is especially apparent at Høgvaglbreen where position and terrain-age are negatively correlated with axis (1), but position has a negative correlation and age has a positive correlation with axis (2). The cause of this, at Høgvaglbreen, appears to be that, on Axis (1), terrain-age is related to high-slope positions and, on axis (2), terrain-age is related to low-slope positions. The "switching" relationship, between age and microtopography, on axis (1) and (2) is also visible across most of the other forelands. Table 5.26 shows that on most forelands, low-slope assemblages are associated with older ground on one axis, and high-slope assemblages are associated with older ground on the other axis. This explains why microtopography and age are often important on both axes and further confirms that these meso-scale variables are the most significant influences on vegetation pattern and the prevailing micro-environment across each foreland. By referring to Table 5.26 there appears to be a trend between forelands of different altitude. On the subalpine forelands, and the Storbreen low sequences, low-slope positions tend to be related to older ground and high-slope positions tend to be related to younger ground on axis (1) and vice versa on axis (2). At Svellnosbreen, and on the mid-alpine forelands, high-slope positions tend to be related to the older ground on axis (1) and low-slope positions tend to be related to the younger ground and vice versa on axis (2). This suggests that at the lower altitudes, low-slope positions tend to be more strongly associated with higher vegetation and soil development, while high-slope positions are associated with bare ground and disturbance. However, at the higher altitudes the opposite is true, with low-slope positions being associated with poor vegetation cover and disturbance, while high-slope positions are associated with better vegetation and soil development. These results are completely new and original and suggest that the influence of microtopography on vegetation patterns is more complex than suggested previously (e.g. Whittaker, 1985). Furthermore they show not only that the relative influence of microtopography changes with altitude, but also that the way in which microtopography influences vegetation and soil development changes with altitude. These results are elucidated further in chapter (6) and are discussed in greater detail in the concluding chapter (7).

4. The confounding of age and altitude. On some forelands, the gradient of age across the foreland exactly parallels the gradient of altitude so that the relative importance of altitude, on the ordination axes, is exaggerated. This confounding of the results is especially noticeable on axis (1) at Storbreen low (2) and Høgvaglbreen and on axis (2) at Austerdalsbreen and Høgvaglbreen. It is surprising that age and altitude

are not confounded at Storbreen low (1) as the altitude and age data are confounded at Storbreen low (2). It is possible that the difference may have been caused by a small mistake in the data input. It is questionable whether altitude should have been retained in the individual foreland data but because the ranges vary from foreland to foreland it was decided that altitude should be kept.. However, on forelands where there is a significant altitudinal range, namely at Fåbergstølsbreen and Svellnosbreen, altitude does not appear to be a significant factor almost certainly because of the confounding effect of age. This suggests that the altitude results, for the individual foreland data sets, should be interpreted with great care and in future studies should be omitted.

5. Assemblage distinctness (in relation to zones or gradients). The most distinct assemblages are considered to be those TWINSPAN groups whose members remain close together on the ordination axes and are widely separated on the "centroid" plots (Figs. 5.1 to 5.16). Tables 5.25 and 5.26 show that the most distinct assemblages are those which are found at either end of the axis and this makes it fairly simple to associate certain environmental parameters with certain types of assemblages. There does not appear to be any special trends towards distinctness with altitude. On most forelands the mature assemblages, and the lichen heath, pioneer and snowbed assemblages, appear to be the most distinct. In contrast, the indistinct assemblages tend to belong to intermediate terrain-ages or a mixture of slope-positions. Mature assemblages are associated with age, developed soils, and often solifluction, whereas lichen heath assemblages are generally associated with low snow duration, dryness, bare gravels and dowel heave (although mature lichen heath assemblages are correlated with age, vegetation cover and low frost-heave). Pioneer assemblages are associated with bare ground, pH, fluvial activity, frost activity, and on some forelands, bryophytes. Snowbed assemblages differ according to terrain-age: pioneer snowbed assemblages are associated with similar environmental parameters to the pioneer assemblages; and late intermediate snowbed assemblages are more associated with developed soils (but not necessarily high vegetation cover). It appears that the most distinct assemblages tend to be those occupying the oldest terrain and/or the extremes of microtopographical position, namely the high-slope position lichen heaths or the low-slope position snowbeds. This may suggest that there is a certain amount of zoning of assemblages across microtopographical features, especially at the extremes (i.e. at low-slope positions, where the snow duration, moisture and shelter is greatest; or on moraine crests, where snow duration, moisture and shelter is least). The occurrence of distinct mature assemblages, on most of the forelands, and the suggestion that microtopography is an important influence on the pattern of these assemblages, lends support to the notion that there is a certain amount of microtopography-related zoning which causes a divergence of assemblages rather than a convergence (Matthews, 1979). However, there is always some overlap of constituent sites and species, between even the most distinct TWINSPAN "final groups", which suggests that so-called distinct environmental "zones" should be referred to as "steep environmental gradients". Despite the presence of distinct TWINSPAN "final groups", most of the TWINSPAN "final groups" are not distinct and the rank tables (Tables 5.1. to 5.16) show that there is considerable overlap of constituent sites and

species between the TWINSPAN “final groups”. This suggests that a higher proportion of each foreland is affected by “gentle environmental gradients” and not “steep environmental gradients”.

6. Assemblage or community? The site separation on ordination axis (1) is generally close to that found by the TWINSPAN “final groups” but, nevertheless, is not identical. Furthermore, some of the TWINSPAN “final groups” are more tightly clustered, on the ordination axis, than other groups. This suggests that some of the TWINSPAN “final groups” are relatively distinct whereas some of the TWINSPAN “final groups” have component sites and species which overlap. The two sequences at Storbreen low (1 and 2) show that although there is considerable similarity between the general patterns derived from these sequences, there are differences that suggest that the traditional phytosociological approach of providing specific lists of species belonging to defined communities cannot be considered as realistic. These results suggest that classification or ordination cannot be used rigidly to define the specific members of “communities”. A preferable approach is to consider that the “final site groups” and “final species groups” are approximate, without definite edges, and that they respond to gradients of environmental patterns across the foreland. This supports the use of the word “assemblage”, which describes a group of species occurring on a similar type of site as opposed to the word “community” which suggests a more definite and integrated group of species that inter-relate with each other in one way or another. This also justifies the approach used in this study to use the TWINSPAN classification method to provide ecologically meaningful “final species groups” and “final site groups” and, additionally, to place these “final groups” onto ordination axes in order to describe the general trends or patterns of vegetation in relation to the prevailing environment. For this reason, individual species and sites have generally not been referred to in this chapter except for those dominant species which provide names for the “final groups”.

"Facilitation, tolerance, inhibition and allogenesis are interdependent mechanisms in succession and may affect the same individual successively or simultaneously during its life cycle. The relative importance of the various mechanisms is likely to vary widely between environments, but attempts to classify succession on the basis of a single underlying mechanism only obscure understanding and inhibit progress".

Finegan (1984:114)

CHAPTER SIX: Vegetation patterns and the relationship between sites, species and environmental parameters, using the combined foreland data.

6.1 Introduction and aims

Five months and two weeks of field work resulted in the collection of vegetation and environmental data from a total of 926 quadrats (463 sites) across eight individual foreland sequences. 210 phanerogam and lichen species were identified and 27 environmental parameters were recorded for each quadrat. Chapters (3), (4), and (5) have described the pattern of vegetation and environmental parameters, as well as the relationship between them, across each of the individual forelands. The intention of this chapter is to describe the results obtained from the multivariate techniques presented in chapters (4) and (5) which were used to analyse the entire combined data set. The options chosen for both techniques are the same as those used for the individual foreland data sets to permit maximum comparability. This allows the relative importance of altitude, age and microtopography to be investigated. By combining these data, a general picture of the most important or meaningful TWINSPAN "final site groups" and "final species groups", at the regional level, are revealed. It is also possible to confirm, or deny, the existence of environmental factor complexes at the larger regional (between-foreland) scale. At the individual foreland level, the "*Terrain-age factor complex*" and the "*Microtopographic (exposure-moisture-snowmelt) factor complex*" (*sensu*: Whittaker, 1985) were identified. At the individual foreland level the relative importance of altitude cannot be separated from age because the age and altitude data are generally confounded. By analysing the combined data set it should be possible to separate those environmental parameters most associated with altitude and those most associated with age and hence define an "*Altitude factor complex*".

A description of the relative importance of each of the environmental parameters and their overall influence is made in order to elucidate the environmental parameters that provide the most useful information. This may be beneficial for future studies, especially where time is limited in the field and thus only the most proven environmental parameters can be chosen for measurement. By analysing the combined data set it may be possible to describe where the vegetation, and associated environmental parameters, appears to exist as distinct assemblages (or communities), or where it forms indistinct assemblages along environmental gradients.

The main aims of this chapter may be summarised as follows:

1. To minimise within-foreland (mesoscale) detail, and provide between-foreland (macroscale) elucidation of the TWINSPAN "final site groups" and TWINSPAN "final species groups" and, hence, successional pathways.
2. To identify the environmental factor complexes for altitude, age and microtopography at the meso- and macro-scales.

3. To examine the relative importance of each of the environmental parameters and their overall influence.
4. To assess the extent to which the TWINSPAN "final site groups" and "final species groups" represent distinct assemblages (communities), forming zones in the landscape, or indistinct assemblages along gentle environmental gradients.
5. To evaluate the relative merits of analysis at the within-foreland, and between-foreland, levels.

6.2 Data presentation and chapter layout

The multivariate techniques, TWINSPAN and DCA, are described fully in chapter (2) and the layout of chapter (6) is based upon the layout of chapters (4) and (5). Firstly the profile diagram for the TWINSPAN combined data set is described and the separation of the TWINSPAN "final site groups" are elucidated at each level (Fig. 6.1a-i). Following this, generalised macro-scale successional pathways are interpreted and outlined (Fig. 6.2). The TWINSPAN "final species groups" are then outlined and their distributions discussed (Figs. 6.4 to 6.15). In order to elucidate further the most distinct TWINSPAN "final species groups", and thus assess whether some species exist as distinct communities, a comparison is made between the individual foreland "final species groups" and the combined foreland "final species groups" (Table 6.3). TWINSPAN analysis, in the form of the profile diagram (Fig. 6.1a-i) is also used to assess the relative influence of age, altitude and microtopography on these assemblages at a mesoscale.

The last part of the chapter describes the DCA centroid scores of the combined TWINSPAN "final species groups" and the environmental biplot scores. As in chapter (5), the relative distinctness of the TWINSPAN "final species groups" on ordination axes (1) and (2) is discussed using the colour rank table (Table 6.4). The relative influence of the environmental parameters is described in terms of their location on the rank sequence as well as their Pearson's product-moment correlation coefficient (r) score in the correlation matrix (Table 6.5). Scatter plots of centroids of the DCA-ordination scores for members of the TWINSPAN "final species groups" are also displayed, and from these plots (Figs. 6.16 to 6.17) the TWINSPAN species patterns, in relation to the environmental patterns across the range of forelands, can be described. A discussion of the rank of sites on ordination axes (1) and (2), as well as the DCA centroids of TWINSPAN "final site groups" is considered not to be necessary because the individual foreland results show that the species and site results tend to contain the same information (see chapter 5). Most sections are concluded with a brief summary and there is a final chapter summary.

6.3 TWINSPAN site groups

The method of presentation of the results from the combined data set follows the individual foreland data set presentation (see chapter 4). The only difference between the profile diagrams for the individual forelands in chapter (4) (Figs. 4.3 - 4.10) and the profile diagram in this chapter (Fig. 6.1a to h) is that the former consist of eight independent diagrams for eight separate TWINSPAN analyses, whereas the profile diagram, in this chapter, represents one spread over eight pages. There is also a hierarchy diagram (Fig. 6.1i) which displays the colours representing the site groups at the various levels of subdivision. A colour-coded key (see Fig. 6.1a-i), for identification of the TWINSPAN site groups, is provided at the end of the diagrams and the colour code used in the profile diagrams, for each TWINSPAN site group, is given in brackets after the naming of each group in the description. In addition a star (*) is used to signify that the group will not be divided at a higher level of subdivision and this is referred to as a "final site group".

The diagrams are a new way of presenting TWINSPAN data and this method is especially useful in showing the relative significance of the meso-scale environmental variables altitude, age and microtopography on vegetation patterns across the forelands. In this chapter, as in earlier chapters, the term "site group" will be used to signify a group that has resulted from the TWINSPAN division of the sites. This is in order to distinguish the site groups from the "species groups" (see section 6.5. and also the glossary). The method of presentation used in earlier chapters is used to present the results in this chapter. However, only the indicator species (and not the preferential species) are listed in order to simplify the diagrams. The site groups are therefore named according to the indicator species listed by TWINSPAN. Where no indicator species are listed, only the site group number (and associated eigenvalue) will be presented.

6.3.1 Site groups at the second level of subdivision

According to Fig 6.1(a to i), at the second (2-group) level the sites separate (eigenvalue 0.523) according to altitude but also, to a lesser extent, to age and microtopography. Site group (2), the **Stereocaulon alpinum - Salix herbacea** assemblage (magenta closed), occurs on: all the alpine forelands; on young terrain (M5 and M6) and at high-slope positions on M4 at Fåbergstølsbreen; and on the pioneer moraine (M7), at high-slope positions on M3 and 4, and on low-slope or at proximal positions on M2 at Austerdalsbreen. This site group has the two indicators as listed above. Site group (3), the **Vaccinium myrtillus - Betula pubescens** assemblage (magenta open), occurs on most of the mature and early intermediate ground on the subalpine forelands at Austerdalsbreen and Fåbergstølsbreen and, strangely, in a crest quadrat on M5 and six quadrats on the proximal low-slope of M6 at Fåbergstølsbreen. Site group (2) comprises alpine assemblages and site group (3) comprises subalpine assemblages.

At the second level of subdivision, the most significant influence on the differences in vegetation between site group (2), the alpine assemblages, and site group (3), the subalpine assemblages, is altitude. The inclusion of pioneer, and some exposed or snowbed sites, from the subalpine forelands within the site group (2), suggests that some species from these sites form a distinct group irrespective of altitude, suggesting that some subalpine assemblages have more species in common with alpine assemblages than they do with other subalpine assemblages. From this, it is suggested that there is a greater diversity of assemblage-types on the subalpine forelands than there is on the alpine forelands.

6.3.2 Site groups at the third level of subdivision

According to Fig 6.1(a to i), the third (4-group) level the subdivision of site group (2) (eigenvalue 0.525) is influenced by a factor other than altitude, age and microtopography, namely disturbance. Site group (4), the **Cerastium cerastoides - Deschampsia alpina** assemblage (dark red open), occurs on M4 and M5 at Fåbergstølsbreen, and in a few pioneer quadrats on all the other forelands (not including the Storbreen low sequences). There are three indicator species, the above species and also *Oxyria digyna*. Site group (5), the **Cladonia chlorophaea - Stereocaulon alpinum** assemblage (dark red closed), occurs on nearly all the alpine forelands and also most of the pioneer moraine at Austerdalsbreen. There are three indicators, the other being *Solorina crocea*. Site group (4) can be described as a disturbed pioneer assemblage and site group (5) can be described as representing alpine assemblages in general.

Site group (3) separates (eigenvalue 0.400) into site groups (6) and (7) according mainly to age. Site group (6), the **Calluna vulgaris - Phyllodoce caerula** assemblage (scarlet closed), occurs on: most of M2 to M6 at Austerdalsbreen; and the crest and proximal slope of M2, all of M3 and low-slope positions on M4 at Fåbergstølsbreen. There are four indicators, the others being *Empetrum nigrum* and *Cladonia chlorophaea*. Site group (7), the **Deschampsia flexuosa - Vaccinium myrtillus** assemblage (scarlet open), occurs on: M1 and in two distal quadrats on M2 at Austerdalsbreen; and M1 and the distal slope of M2 and, strangely, in a crest quadrat, on M5, and six quadrats on the proximal low-slope of M6 at Fåbergstølsbreen. Site group (6) can be described as a subalpine early intermediate heath assemblage and site group (7) can be described as a subalpine mature birch woodland assemblage.

At the third level of subdivision, the most significant influence on the differences in vegetation between the site group (4), the disturbed pioneer assemblage, and site group (5), the alpine assemblages, is possibly disturbance. The young terrain at Fåbergstølsbreen suffered severe disturbance by way of a debris flow in 1979 (Ballantyne and Benn, 1994) as well as by high levels of fluvial activity on the young terrain. Furthermore, most of the other pioneer sites, within this group, at Austerdalsbreen, Svellnosbreen, Storbreen high, Høgvaglbreen and Bøverbreen, have also been shown (see chapters 3 and 5) to sustain intense fluvial activity. The inclusion of younger and/or disturbed sites, from the subalpine forelands, within the alpine group, suggests that species from these sites form a distinct exposed or pioneer group, irrespective of altitude. The most significant influence on the differences in species composition between site groups (6) and (7), where the subalpine heath assemblage is separated from the subalpine woodland assemblage, is certainly age. The separation of groups at level three is not significantly influenced by altitude. At subalpine altitudes the groups separate according to age and not so much according to between-foreland differences. Age has the greatest influence on the separation of assemblages on the subalpine forelands, at this level. The separation of the disturbed pioneer assemblage, from the alpine group, has prevented division of the rest of the alpine group according to the meso-environmental parameters of age, altitude and microtopography. However, this does not suggest that assemblages are necessarily more distinct on the subalpine forelands than at the alpine altitude. In order to ascertain the relative distinctness of the site groups it is necessary to refer to the respective eigenvalues for each of the "final site groups", marked with an asterisk (*), at subsequent levels of subdivision.

6.3.3 Site groups at the fourth level of subdivision

According to Fig 6.1(a to i), the fourth (8-group) level site group (4) separates (eigenvalue 0.554) into site groups (8) and (9), according to foreland. All the Fåbergstølsbreen sites are separated from all the other pioneer sites. The difference may be caused by the contrast in the type of disturbance, with the debris flow being the major type of disturbance at Fåbergstølsbreen, and fluvial activity being the major type on the other forelands. Site group (8), the **Agrostis tenuis** assemblage (yellow open), occurs on the pioneer sites at Fåbergstølsbreen. *Agrostis tenuis* is the only indicator species in site group (8). Site group (9) (yellow closed) occurs on the other disturbed .pioneer sites on all the forelands except the Storbreen low sequences. There are no indicator species representing site group (9). Site group (8) may be described as a debris-flow disturbed pioneer assemblage, whereas site group (99 may be described as a fluvially-disturbed pioneer assemblage. Site groups (8*) and (9*) are considered to be ecologically meaningful, at this level, and so are not separated further.

Site group (5) separates (eigenvalue 0.325) into site groups (10) and (11), according to altitude, microtopography and, to a lesser extent, age. Site group (10), the **Solorina crocea - Cetraria nivalis** assemblage (dark grey closed), occurs on: all Høgvaglbreen and Bøverbreen sites; most of the mature till ridge at Storbreen high; and at high-slope positions on most early intermediate moraines at the alpine altitude. There are three indicator species, the other being *Cetraria ericetorum*. Site group (11), the **Salix glauca - Anthoxanthum odoratum** assemblage (dark grey open) occurs on: all mature till-ridges; most low-slope sites across the low-alpine forelands; low-slope sites on M2 and M6 and mid-slope M3 and crest M4 at Austerdalsbreen; and the distal mid-slope M1 and most low-slope sites at Storbreen high (except M8). There are four indicator species, the others being *Empetrum nigrum* and *Phyllodoce caerula*. Site group (10) is a mid-alpine and exposed lichen heath assemblage and site group (11) is a low-alpine late-snow heath assemblage.

Site group (6) separates (eigenvalue 0.264) into site groups (12) and (13) according to altitude, age and microtopography. Site group (12) (dark blue closed) occurs on most sites at Austerdalsbreen (except distal sites on M3) and low-slope sites on M4 at Fåbergstølsbreen. This site group has no indicators. Site group (13), the **Melampyrum sylvaticum - Vaccinium vitis-idaea** assemblage (Dark blue open), occurs on: low-slope distal sites on M3, at Austerdalsbreen; and crest and proximal sites on M2, all of M3 and in one toe-slope quadrat on M4, at Fåbergstølsbreen. There are seven indicators, the others being *Empetrum nigrum, Betula pubescens, Cladonia arbuscula, Cladonia rangiferina* and *Luzula arcuata*. Site group (12) is a subalpine early intermediate heath assemblage and site group (13) is a subalpine late intermediate heath assemblage, mostly separated due to age and, possibly, due to the different vegetation patterns occurring on the two forelands which could be related to slight differences in altitude, aspect or topography. Site group (13*) is considered to be ecologically meaningful and so is not separated at higher levels of subdivision.

Site group (7) divides (eigenvalue 0.666) into site group (14) and (15) according to age. Site group (14), the **Vaccinium myrtillus** assemblage (cyan closed), occurs on: the M1 at Austerdalsbreen; and M1 and the distal slope on M2 at Fåbergstølsbreen. There is only one indicator. Site group (15) (cyan open) occurs in a crest quadrat on M5 and six quadrats on the proximal low-slope of M6 at Fåbergstølsbreen and it has no indicators. Site group (14) is a subalpine mature woodland heath assemblage and site group (15) is a subalpine pioneer assemblage. Site group (15*) is ecologically meaningful, at this level of subdivision, and is not separated further.

At the fourth level of subdivision it can be seen that the most significant influence on the differences in vegetation between the site groups (8*) and (9*), with pioneer sites at Fåbergstølsbreen separating from other pioneer sites, is possibly a difference in the type of disturbance. The most significant influence on the differences in species composition between the site groups (10), the alpine lichen heath, and (11), the low-alpine late-snow heath, is altitude and microtopography and this complements the results presented in chapters (4) and (5), which show that microtopography is a significant influence. It has been suggested, however, that the relative influence of microtopography on the low-alpine forelands may be exaggerated by the lack of early pioneers across the Storbreen low sequences and the effect of an outlier pioneer group, and use of a mature gully, at Svellnosbreen. The most significant influence on the division of site groups (12) and (13*), separating mainly early intermediate heath at Austerdalsbreen from mainly late intermediate heath at Fåbergstølsbreen, is due to age, as well as to between-foreland differences in altitude, aspect or topography. The most significant influence on the separation of site groups (14) and (15*) is age, with subalpine mature woodland separating from a subalpine pioneer assemblage. In general the divisions are influenced by altitude and microtopography on the alpine forelands and, on the subalpine forelands, by age or between-foreland differences such as those of altitude, aspect or topography.

6.3.4 Site groups at the fifth level of subdivision

According to Fig 6.1(a to i), at the fifth (16-group) level site group (10) separates (eigenvalue 0.345) into site groups (20) and (21) according to altitude and microtopography. Site group (20), the **Salix herbacea** assemblage (closed black), generally occurs at low-slope positions on the mid-alpine forelands but only very rarely on young terrain. There are also a few quadrats from low- and subalpine forelands, most notably the crest and shoulder-slope sites on M7, Austerdalsbreen. This group only has one indicator. Site group (21), the **Cetraria nivalis - Alectoria ochroleuca** assemblage (black open), mainly occurs on exposed high-slope positions on alpine forelands. There are three indicators, the other being *Empetrum nigrum*. Site group (20) is a mid-alpine snowbed assemblage and site group (21) is an exposed lichen heath assemblage.

Site group (11) separates (eigenvalue 0.313) into site group (22) and site group (23), according mainly to age. Site group (22), the **Salix glauca** assemblage (mustard open), occurs at low-slope positions on early intermediate or pioneer terrain on the low-alpine forelands and Storbreen high. There is only one indicator. Site group (23), the **Cladonia portentosa - Cladonia gracillis** assemblage (mustard closed), occurs mainly on: low-slope positions on M1 to M3 or distal positions on the early intermediate terrain of the low-alpine forelands; and a few sites on the Storbreen high foreland. There are six indicators, the others being *Empetrum nigrum, Vaccinium myrtillus, Betula nana* and *Cetraria nivalis.* Site group (22) is a low-alpine pioneer or early intermediate snowbed, and site group (23) is a low-alpine mature or late intermediate late-snow heath assemblage.

Site group (12) separates (eigenvalue 0.271) into site groups (24) and (25) according mainly to age and microtopography. Site group (24), the **Vaccinium myrtillus - Festuca ovina** assemblage (dark green open), occurs generally on older and low-slope positions, mainly on Austerdalsbreen but also on Fåbergstølsbreen. This group has 3 indicators, the other being *Salix phylicifolia.* Site group (25), the **Calluna vulgaris - Cetraria islandica** assemblage (dark green closed), occurs mainly on younger terrain and higher slope positions, than site group (24). There are three indicators, the other being *Cladonia chlorophaea.* Site group (24) is a subalpine late intermediate late-snow heath assemblage and site group (25) is a subalpine early intermediate heath assemblage. Site groups (24*) and (25*) are ecologically meaningful and are not separated further at higher levels of subdivision.

Site group (14) separates (eigenvalue 0.464) into site groups (28) and (29) according to microtopography. Site group (28) (purple closed) occurs on most of M1, and some distal sites on M2, on the subalpine forelands. This group has no indicators. Site group (29), the **Athyrium distentifolium** assemblage (purple open), occurs on the two toe-slope sites, and in one proximal mid-slope quadrat, on M1, at Austerdalsbreen. Site group (28) is a subalpine mature woodland assemblage and site group (29) is a subalpine mature snowbed assemblage. Site groups (28*) and (29*) are considered to be ecologically meaningful and are not separated further.

At the fifth level of subdivision the most significant influence on the differences in vegetation between the site groups (20) and (21), where the mid-alpine snowbed assemblage separates from the alpine exposed lichen heath, is altitude and microtopography. The most significant influence on the differences in species composition between the site groups (22), the low-alpine pioneer snowbed assemblage and (23), the low-alpine late intermediate snowbed, is age. The most significant influence on the division of site groups (24*) and (25*) is age, in terms of the subalpine late intermediate late-snow heath being separated from the subalpine early intermediate heath. The most significant influence on the separation of site group (28*), the subalpine mature woodland, and (29*), the subalpine mature snowbed, is microtopography. In general the divisions are influenced by altitude, age and microtopography on the alpine forelands, and by age and microtopography on the subalpine forelands. The influence of altitude is less apparent at this level.

6.3.5 Site groups at the sixth level of subdivision

According to Fig 6.1(a to i), at the sixth (32-group) level, site group (20) separates (eigenvalue 0.346) into site groups (40) and (41), mainly according to age and microtopography. Site group (40), the **Oxyria digyna** assemblage (light grey border, black and white stripes) occurs on pioneer positions, mainly on mid-alpine forelands but also on exposed pioneer sites at Austerdalsbreen. There is only one indicator species. Site group (41), the **Cladonia chlorophaea - Salix herbacea** assemblage (black and light grey stripes) occurs on all the other low-slope positions at Høgvaglbreen and Bøverbreen and a few other isolated quadrats on other forelands. This group has four indicator species, the others being *Cetraria ericetorum* and *Cladonia gracillis*. Site group (40) is mainly a mid-alpine pioneer assemblage, and site group (41) is a mid-alpine snowbed assemblage. Neither site group (40*) nor (41*) will be separated further.

Site group (21) separate (eigenvalue 0.321) into site group (42) and site group (43) according to altitude and age. Site group (42), the **Cornicularia divergens - Cornicularia aculeata** assemblage (yellow border, black and white stripes) occurs on mature or late intermediate high-slope positions at the mid-alpine altitude. This group has four indicator species, the others being *Thamnolia vermicularis* and *Alectoria ochroleuca*. Site group (43), the **Empetrum nigrum** assemblage (black and yellow stripes) occurs on: high-slope positions on the early intermediate and late intermediate terrain on the low-alpine forelands; on the early intermediate terrain at Storbreen high foreland; and in three crest quadrats at Høgvaglbreen. This group has one indicator. Site group (42) is a mid-alpine mature lichen heath assemblage and site group (43) is a low-alpine exposed heath assemblage. Neither site group (42*) nor (43*) will be separated further

Site group (2) separates (eigenvalue 0.303) into site group (44) and site group (45) according to age. Site group (44), the **Stereocaulon alpinum - Phyllodoce caerula** assemblage (cyan and black stripes), occurs mainly on: low-slope positions on early intermediate, or young terrain, at the low-alpine altitude; and at low-slope positions on M7 at Austerdalsbreen. This group has three indicators, the other being *Empetrum nigrum*. Site group (45), the **Salix glauca - Solidago virgaurea** assemblage (cyan border, black and white stripes) occurs mainly at low-slope positions on late intermediate terrain on the low-alpine forelands. This group has four indicator species, the others being *Rumex acetosa* and *Anthoxanthum odoratum*. Site group (44) is a low-alpine early intermediate late-snow heath and site group 45 is a low-alpine late-snow heath. Neither site group (44*) nor (45*) will be separated further

Site group (23) separates (eigenvalue 0.268) into site group (46) and site group (47) according to age and microtopography. Site group (46), the **Stereocaulon alpinum - Salix glauca** assemblage (red and black stripes) occurs on the low-alpine forelands, at low-slope and shoulder-slope positions on terrain of intermediate age, and at the high-slope positions on the oldest terrain. This group has three indicator species, the other being *Empetrum nigrum*. Site group (47), the **Salix herbacea - Festuca ovina** assemblage (red border, black and white stripes), occurs only at low-slope positions on the mature or late intermediate terrain on the low-alpine forelands. This group has four indicator species, the others being *Anthoxanthum odoratum* and *Gnaphalium supinum*. Neither site group (46*) nor (47*) will be separated further

At the sixth level of subdivision it can be seen that the most significant influences on the differences in vegetation between the site groups (40*) and (41*) are age and microtopography, where a mid-alpine pioneer (and AUSF exposed pioneer) assemblage is separated from a mid-alpine snowbed assemblage. The most significant influence on the differences in species composition between the site groups (42*), the mid-alpine lichen heath assemblage, and (43*), the low-alpine exposed heath assemblage, is altitude and age. The most significant influence on the division of site groups (44*), the subalpine and low-alpine pioneer snowbed assemblage, and (45*), the low-alpine late intermediate late-snow heath assemblage, is age. The most significant influences on the separation of site groups (46*) and (47*) are age and microtopography, where a low-alpine widespread heath assemblage separates from a low-alpine mature snowbed assemblage. In general age is the main influence at this level so that sites belonging to different forelands tend to separate from others because of age. The influence of microtopography and altitude, at level (6), is not as striking as it is at the lower levels of subdivision.

6.3.6 Summary of TWINSPAN site groups for the combined data set

Table 6.1 summarises the findings of section 6.3, and from this the following points, concerning the separation of the site groups, are made:

1. The suitability of this presentation method: This method of data presentation is generally able to provide ecologically meaningful, and interpretable site groups, at each of the levels of subdivision despite the large size of the data set. Initial examination of these data suggests that many of the inferences drawn from the individual foreland data are confirmed by the analysis of the combined data set. This suggests that analysis of a large combined data set may be sufficient for analysis and interpretation, especially where researchers are short of time. The differences between the results derived from the individual foreland data sets and the combined data sets are discussed in the concluding chapter (section 7.5.1).
2. The most important influence on site separation: The greatest influence on the separation of sites at the second level of subdivision is altitude separating vegetation above the tree line (alpine vegetation) from that below (subalpine vegetation).
3. The diversity of assemblages at different altitudes: Some pioneer, snowbed and exposed assemblages at the subalpine altitude have an affinity with alpine assemblages which suggests that these assemblages are more sensitive to age and microtopography than to altitude. The fact that alpine assemblages occur at the subalpine altitude suggests that there is a greater diversity in assemblage type on the subalpine forelands and this will be discussed further in the following section.

4. The most important influences on subalpine site separation: The subalpine assemblages separate according to age at the third level of subdivision, which suggests that this is the most important meso-environmental influence on the general vegetation pattern on subalpine forelands of similar altitude. At the fourth level of subdivision the influence on the separation is highly complex, but can be summarised in terms of age and between-foreland differences in types of disturbance, as well as smaller scale differences in altitude and topography. At the fifth level of subdivision the main influences on site group separation are age and microtopography. High eigenvalues of the groups at all levels of subdivision suggest that these site groups are distinct. By referring to the profile diagrams (Figs. 6.1a-i) it appears that age is the most important influence on general vegetation patterns on subalpine forelands but microtopography has some influence on vegetation pattern, especially with regard to the extremes of topographical position such as crest or toe-slope positions and also with regard to pioneer or disturbed ground.
5. The most important influence on alpine site separation: The alpine disturbed pioneer site group, at the third level, separates from the rest of the alpine assemblages. This suggests that disturbance is a major influence on vegetation pattern on alpine forelands. All the members of the disturbed group are pioneers so the influence, on this separation, could also be regarded as age-related. At the fourth level of subdivision, the disturbed pioneer site group separates, according to foreland, and thus the type of disturbance (debris flow versus fluvial) appears to be influential on the separation. The (level 4) large alpine site group separates, according to altitude and microtopography, so that the alpine lichen heath assemblage divides from the low-alpine late-snow heath. At the fifth level the alpine lichen heath assemblage divides according to altitude and microtopography whereas the low-alpine snowbed assemblage divides according to age. At the sixth level most of the divisions are according to age or microtopography. It would appear, therefore, that microtopography is a more important influence on the vegetation pattern on the alpine forelands than it is on the subalpine forelands. The eigenvalues of the site groups, at level 6, are generally as high as those of the subalpine forelands, at level 5, suggesting that these assemblages are distinct even at the highest level of subdivision.
6. The relative influence of disturbance: The relative importance of the meso-environmental factors, at each level of subdivision, does not follow a simple pattern and is complex. The influence of all three meso-environmental factors (i.e. altitude, age and microtopography) is apparent at each of the levels of subdivision. Disturbance can also be considered to be a significant influence on the separation of some of the TWINSPAN site groups. In this study, severe disturbance is age-related, with the most disturbed sites appearing on the young terrain of the foreland. It is, however, suggested that severe disturbance, such as debris flows or intense fluvial activity, can occur on terrain of any altitude, age or microtopographical position, and thus could be regarded as a separate meso-environmental factor. This will be discussed further in later sections.

6.4 Successional pathways based on TWINSPAN "final site groups".

By referring to Table 6.1. it is possible to construct generalised succession sequences for the combined foreland data set (Fig. 6.2.) using the TWINSPAN "final site groups" marked with an asterisk (*). The "final site groups" tend to belong to either the subalpine (Austerdalsbreen and Fåbergstølsbreen), or the low-alpine (Storbreen low (1) and (2), and Svellnosbreen), or the mid-alpine (Storbreen high, Høgvaglbreen, Bøverbreen) altitudinal zones. Thus the construction of the successional pathways is relatively straight forward. However, it should be noted that Storbreen high has characteristics of all the alpine forelands: the low-alpine exposed heath tends to dominate the high-slope positions; and a combination of low-alpine late-snow heath and mid-alpine snowbed dominate the low-slope positions on the early intermediate ground. On mature terrain, the mid-alpine lichen heath dominates the high-slope positions and the mid-alpine snowbed dominates the low-slope positions. At Storbreen high the early intermediate ground is therefore generally low-alpine in character, whereas the oldest terrain is mid-alpine in character. This further demonstrates that the term "assemblage" should be used in preference to the term "community". The following paragraphs will describe the generalised successional pathways at each altitudinal level.

The successional pathway across the subalpine forelands appears to be more complex than it is across the alpine forelands insofar as there appear to be greater differences, in assemblage type, between the subalpine forelands. At Austerdalsbreen, the succession starts with young terrain comprising the mid-alpine pioneer assemblage (site group 40*) at high-slope positions and the sub- to low-alpine pioneer and early intermediate snowbed assemblage (site group 44*) and the disturbed pioneer assemblage (site group 9*) at low-slope positions. These assemblages are succeeded by the subalpine early intermediate heath (site group 25*) which in turn is succeeded by the subalpine late intermediate late-snow heath (site group 24*) with low-alpine exposed early intermediate heath on the most exposed positions. These assemblages are replaced by the subalpine mature woodland (site group 28*) on most positions and the subalpine mature snowbed on the toe-slope positions. At Austerdalsbreen there is a divergence of mature assemblages.

At Fåbergstølsbreen two pioneer assemblages dominate the two youngest moraines and they are the subalpine pioneer assemblage (site group 15*) and the disturbed pioneer assemblage (site group 8*). These assemblages are succeeded by the subalpine early intermediate heath assemblage (site group 25*) at the low-slope positions and the low-alpine exposed early intermediate heath assemblage (site group 43*) at the high-slope positions. These, in turn, are succeeded by the subalpine late intermediate heath assemblage (site group 13*) and, lastly, by the subalpine mature woodland (site group 28*). Divergence at Fåbergstølsbreen is not indicated by this successional pathway. Although some of the assemblages are shared between these two forelands, most notably the mature woodland assemblage, most of the assemblages are different and this is most noticeable on the young terrain, possibly as a result of the 1979 debris flow at Fåbergstølsbreen (Ballantyne and Benn, 1994).

On the subalpine forelands a number of different meso-environmental influences seem important. Age and disturbance and between-foreland differences are the most important factors. Microtopography also appears to be an influence although there is no clear trend of influence across all moraines. Rather, the effect of microtopography is noticeable on particular moraines (M2-4 and M7 at Austerdalsbreen; and M4 and M6 at Fåbergstølsbreen). These results complement those of the individual forelands, across Fåbergstølsbreen, (see chapters 4 and 5) where it is suggested that snowlie and moisture, found to be part of a "*Microtopographic factor complex*" (*sensu*: Whittaker, 1989), is related more to age than to microtopography.

The successional sequences across the low-alpine forelands are more consistent. At Svellnosbreen, on the youngest young terrain, the succession starts with a disturbed pioneer assemblage (site group 9*) and the sub- to low-alpine pioneer and early intermediate snowbed (site group 44*). The latter assemblage provides the starting point for the succession sequence on the Storbreen low forelands. At the high-slope positions site group (44*) is replaced by the low-alpine exposed early intermediate heath (site group 43*) and then, on the mature terrain, the low-alpine widespread heath (site group 46*). At the low-slope positions it is replaced by the low-alpine late intermediate late-snow heath (site group 45*) and then by the low-alpine mature snowbed (site group 47*) on the oldest terrain. There appears to be consistency between the low-alpine forelands even though Svellnosbreen is in the rain shadow of Tverrbotn-tindane and has a greater altitudinal range. These results show that the low-alpine assemblages are less diverse in type and tend to be more predictable in their distribution patterns than the subalpine assemblages. These results also suggest that age and microtopography are important influences even though it has been shown in earlier chapters that the influence of microtopography may have been exaggerated on the low-alpine forelands. Furthermore, the successional sequence, displayed in Fig 6.2, supports the contention that there is a divergence of assemblages from fewer pioneers to a greater number of mature assemblages (Matthews, 1979).

On the mid-alpine forelands at Høgvaglbreen and Bøverbreen, the successional pathway is even simpler than it is across the low-alpine foreland sequences. The succession starts with the disturbed pioneer assemblage (site group 9*), at toe-slope positions, and the mid-alpine pioneer assemblage (site group 40*) at most other positions on M5 and M6 across each foreland. These assemblages are succeeded by the mid-alpine lichen heath assemblage (site group 42*), at high-slope positions, and the mid-alpine snowbed assemblage at low-slope positions (site group 41*). It is clear that age and microtopography are very important at these high altitudes and there is a great similarity between the pattern of assemblages found on the different forelands. The successional pathway is very simple and the assemblages, which separate at the fifth level of subdivision, are not diverse. Nevertheless the eigenvalues are fairly high (> 0.268), so the assemblages can be considered as being relatively distinct. As discussed in the previous section, Storbreen high foreland appears transitional between the low-alpine and mid-alpine assemblages. The successional sequence at Storbreen high follows from: the disturbed pioneer assemblage (site group 9*) on M7 and at

M8 low-slope positions; and low-alpine pioneer and early intermediate snowbed (site group 44*) on M7 and at M8 high-slope positions. These assemblages proceed to a combination of: the low-alpine pioneer and early intermediate snowbed (site group 44*); mid-alpine snowbed (site group 40*) at low-slope positions; and low-alpine exposed early intermediate heath (site group 43*) at high-slope positions on the early intermediate and late intermediate terrain. These assemblages are succeeded by mid-alpine snowbed assemblages at the low-slope positions, and mid-alpine lichen heath at the high-slope positions on the mature terrain. The pathway at Storbreen high is too complex to record on the general combined foreland succession diagram but it suggests that there is a gradient of change with altitude from the low-alpine to the mid-alpine assemblages. Age and microtopography are important influences on the vegetation pattern at Storbreen high.

The main trends shown by the successional pathways (Fig. 6.2) are as follows:

1. The pioneer stage of the successional pathway is generally complex and tends to vary from foreland to foreland according to degree and type of disturbance
2. The pioneer assemblages appear to be less influenced by altitude and more influenced by age of ground and type of disturbance.
3. There is a considerable difference between the assemblage types, and successional pathways, on subalpine forelands and on alpine forelands.
4. There appears to be a gradient of change in the type of assemblages, and successional pathways, between the alpine altitudes as displayed by the transitionary assemblages on Storbreen high foreland.
5. Successional pathways appear to be more complex and less predictable at the subalpine altitudes and, conversely, are simpler and more predictable at successively higher altitudes.
6. There is a greater variety of assemblage types at subalpine altitudes, where some "alpine" assemblages are found on the younger terrain.
7. The most distinct assemblages (shown by the highest eigenvalues) are: a) the disturbed pioneer assemblages; and b) the subalpine mature woodland and snowbed assemblages. Otherwise most of the assemblages have similar eigenvalues, suggesting that distinctness is associated with the extremes of terrain-age and environmental gradients.
8. The majority of the most distinct "final site groups" are on subalpine forelands suggesting that altitude has an influence on assemblage distinctness. This appears to contradict the conclusion, in chapter (4), that the subalpine forelands do not have distinct assemblages as their eigenvalues are rather low. However, by combining the forelands within the same data set, it has been possible to compare the relative distinctness of assemblages taken from a range of altitudes. This is an interesting result and justifies the analysis and interpretation of a large combined data set. These findings will be discussed further in the concluding chapter (7).

6.5 TWINSPAN "final species groups"

The TWINSPAN "final species group" charts (Figs. 6.3. to 6.14.), for the combined data set, display the patterns of TWINSPAN "final species groups" displayed in the TWINSPAN final table (Appendix 6.1) which, due to its size, has been included with this thesis in a separate pocket. As with the individual foreland data sets, TWINSPAN "final species groups" are separated from the other TWINSPAN "species groups" according to being the clearest, and most ecologically meaningful, on the TWINSPAN final table. Large "final species groups" are split between at least two charts and are labelled with lowercase letters (a,b,c,d ... etc.). These "final species group" distribution charts are in colour with the more abundant species, within each of the "final species groups", represented by a colour (given in a key). A list of all the species, within each of the "final species group", is described (see Appendix 1 for list of abbreviations). Included with the list of species is the group number; the level of subdivision; the eigenvalue; and a brief description of the location of the members of the "final species group" across the moraines and forelands. The degree of correspondence between the site groups (section 6.3) and the "final species groups" (this section) will be made at the most appropriate level, according to where they are situated on the moraines and foreland. This is done in order to ascertain the degree of correspondence between the TWINSPAN site and species data. The same position colour code, used for the individual foreland data sets, is used for the combined data set in order to distinguish the different "final species groups" on the colour rank tables in the ordination section. However, because the positions often vary between altitudinal zones, generalisations about the relative positions of most of these groups, from foreland to foreland, can only be regarded as an approximation. The position colour code is given in writing, after each of the "final species group" descriptions, and where two groups occur in similar types of position, they are represented by a closed box " ■ " and an open box " □ " of the relevant colour. The position colour code for the combined data set is as follows:

The position colour code for the TWINSPAN "final species groups" assemblages is as follows:

Dark blue - Low-slope positions mainly on older ground (mature snowbed or late-snow heath)

Light blue - Low-slope positions mainly on early intermediate ground (early intermediate snowbed or late-snow heath)

Blue-white - Low-slope positions (snowbeds in general)

Dark green - Any positions mainly on older ground (mature heath or woodland)

Mustard - Any positions mainly on early intermediate ground (early intermediate heath)

Pink - Mainly younger ground (pioneer)

Red - High-slope positions of any age (dry lichen heath)

Brown - High-slope positions and/or exposed positions on young terrain (dry heath or pioneer)

Yellow - Widespread, any positions (non-selective species)

The descriptions of the TWINSPAN "final species groups" charts, from the combined data set, follows the same format used for TWINSPAN "final species group" charts, from the individual foreland data sets. Refer to Appendix 1 for a list of the abbreviations and full names of each species.

6.5.1 Species group 32: alpine exposed lichen heath species assemblage (eigenvalue 0.080).

This species group contains the following species:

59 Cet eri; 60 Ste con; 86 Ste ves; 108 Cet cuc; 128 Cet niv; 131 Tha ver; 132 Cor acu; 133 Sph glo; 136 Arc alp; 137 Arc uva; 145 Ale cha; 152 Cor div; 153 Ale och; 156 Sph fra; 158 Ale nig; 165 Phs spp; 178 Ste spp; 181 Dry oct; 182 Cla fri; 184 Ane ver; 189 Cor aca; 200 Phy sch; 204 Ale spp; 207 Ran gla; 208 Nar spp; 209 Unn cup; 210 War red. (n = 27).

According to Appendix 6.1 and Figs. 6.3a-c, this species group has a tight distribution, at high-slope positions on the oldest terrain, at the mid-alpine altitude. It is tight at high-slope positions on young terrain or intermediate-aged terrain at the low-alpine altitude. It is quite tight at low-slope positions on the mid-alpine forelands. It is loose on: pioneer sites at Austerdalsbreen; the low-slope positions on the distal slope of M2; on the three Storbreen sequences; and the low-slope positions on younger ground at the low-alpine altitude. It is very loose on the oldest terrain, and low-slope sites, at Austerdalsbreen and the low-alpine forelands. It is occasional at low-slope positions of young terrain. It very rarely occurs on the oldest terrain. In summary, it has a tight distribution, mainly at high-slope positions on older ground, at the mid-alpine altitude, and on younger ground at the low-alpine altitude. This species group corresponds with the level (4) alpine lichen heath (site group 10), the **Solorina crocea - Cetraria nivalis** assemblage. (Colour position code = Red)

6.5.2 Species group 33: alpine snowbed assemblage (eigenvalue 0.080)

This species group contains the following species:

34 Sal her; 44 Ste alp; 49 Cla unc; 64 Cla ver; 113 Hie spp; 122 Cas hyp; 142 Cam rot; 154 Tri spi; 164 Sph mel. (n = 9)

According to the final table (Appendix 6.1) and Fig. 6.4, this species group has a tight distribution at low-slope positions on the mid-alpine forelands, with *Salix herbacea* and *Stereocaulon alpinum* being particularly abundant over most positions, although noticeably less on the subalpine forelands. Otherwise this assemblage is widespread over most of the alpine forelands. It is, however, not common on young sites at Fåbergstølsbreen and Austerdalsbreen. Its members are very rare on M1 (and distal M2), on the subalpine forelands, as well as M2 and M3 at Fåbergstølsbreen. In summary, this group is tightest at low-slope positions, on mid-alpine forelands, although it is widespread on most alpine forelands. This species group corresponds mostly with the level (3) alpine (site group 5), the **Cladonia chlorophaea - Stereocaulon alpinum** assemblage. (Colour position code = Blue-white)

6.5.3 Species group 34: low-alpine late intermediate late-snow heath assemblage (eigenvalue 0.186)

This species group contains the following species:

36 Leo aut; 40 Bet nan; 41 Ran spp; 57 Arc alp; 58 Car spp; 81 Ste bot; 85 Sax aiz; 87 Ver alp; 88 Pyr nor; 92 Pol viv; 94 Alc glo; 123 Sed ros; 124 Hie alp; 125 Ant alp; 126 Des cae; 127 Lyc alp; 129 Cet ste; 130 Cet del; 134 Nep arc; 135 Cla alp; 138 Eup fri; 139 Tar off; 140 Hie alp; 141 Ran acr; 143 Bar alp; 146 Pso hyp; 147 Sil aca; 148 Pet fri; 149 Tof pus; 150 Ped lap; 151 Coe vir; 155 Cla pyx; 157 Pan pez; 160 Des cae; 161 Cla cen; 162 Cla sym; 163 Car bel; 166 Jun spp; 168 Ped spp; 169 Luz tri; 170 War gra; 171 Far red; 172 Mel rub; 173 Sau alp; 174 Ran pyg; 175 Pel pol; 176 Squ cup; 177 Tof pus; 179 Lyc sol; 180 Gre cla; 183 Ant dio; 185 Ran niv; 186 Leo spp; 187 Rum ari; 188 Cet del; 190 Sal myr; 191 Sax opp; 192 Sax cer; 193 Vis alp; 194 Dra alp; 195 Sal ret; 197 Lyc spp; 198 Dry exp; 199 Pyr spp; 201 Ran alp; 202 Lec qua; 203 Och fri; 205 Woo alp. (n = 68)

According to the final table (Appendix 6.1) and Fig. 6.5a-f, this species group has a loose distribution on, mainly, the oldest terrain and at low-slope positions at Storbreen low (1 and 2) and Svellnosbreen. It has a very loose distribution at low-slope positions on the middle-aged and younger ground on the low-alpine forelands. This group is occasional at Høgvaglbreen, Bøverbreen and Storbreen high, on the oldest terrain, and high-slope positions on most moraines at the alpine altitude. This group is very rare on subalpine forelands and rare on a number of pioneer quadrats on many of the forelands (members of the disturbed pioneer assemblage). In summary, this assemblage occurs mainly on the oldest low-slope positions on low-alpine forelands. This species group corresponds mainly with the level (4) low-alpine late-snow heath (site group 11), the **Salix glauca - Anthoxanthum odoratum** assemblage. (Colour position code = Light blue closed)

6.5.4 Species group 35: pioneer and snowbed assemblage (eigenvalue 0.186)

This species group contains the following species:

82 Oxy dig; 83 Phl alp; 111 Gna sup; 112 Cry cri; 115 Sag sag; 116 Luz spi; 117 Uln gla; 119 Epi ang; 120 Rus spp; 121 Cer alp; 144 Poa alp; 159 Car pet; 167 Tar spp; 196 Ara alp; 206 Sax ces.

(n =15)

According to the final table (Appendix 6.1). and Fig. 6.6a-b, this species group has a quite tight distribution on young sites at Austerdalsbreen, Fåbergstølsbreen, Svellnosbreen, Storbreen high, Høgvaglbreen and Bøverbreen but the majority of the quadrats are alpine. This assemblage is loose on other low-slope positions on young terrain on the mid-alpine forelands, as well as Austerdalsbreen. It is found loosely at low-slope positions on younger sites at Storbreen low (1 and 2) and other young or middle-aged sites at Svellnosbreen and Storbreen high. It is very loose on the low-slope sites of older ground, and at most mid-alpine positions, as well as at high-slope positions on the low-alpine forelands. It is almost absent (except where stated) from the subalpine forelands. In summary, this is mainly a pioneer and snowbed assemblage found at all altitudes. This species group corresponds mainly with the level (5) low-alpine pioneer snowbed (site group 22), the **Salix glauca - Salix glauca** assemblage and also the level (6) mid-alpine pioneer (site group 40*), the **Oxyria digyna- Oxyria digyna** assemblage. (Colour position code = Pink)

6.5.5 Species group 18: low-alpine late-snow heath assemblage (eigenvalue 0.136)

This species group contains the following species:

4 Sal gla; 35 Pyr min; 37 Sib pro; 39 Fes ovi; 54 Jun tri; 78 Sal lan; 105 Cla ste; 18 Des alp; 33 Gna nor; 110 Cer cer. (n = 10)

According to the final table (Appendix 6.1) and Fig. 6.7, this species group has a tight distribution mostly at low-slope positions on older ground at the low-alpine altitude. It is quite tight at high-slope positions on older ground (low-alpine) and all pioneer positions (low-alpine). It is also quite tight at low-slope positions on young moraines at Austerdalsbreen, Storbreen and Svellnosbreen. It is loose on other sites, however, it is very rare on Fåbergstølsbreen crest and proximal M2 and M3, as well as the oldest and intermediate subalpine terrain. In summary, this assemblage is mainly low-alpine and found especially at low-slope positions on older ground. This species group corresponds mainly with the level (4) low-alpine late-snow heath (site group 11), the **Salix-glauca - Anthoxanthum odoratum** assemblage. (Colour position code = Light blue open)

6.5.6 Species group 19: lichen heath assemblage (eigenvalue 0.136).

This species group contains the following species:

25 Cet isl; 46 Cla chl; 50 Lyc sel; 63 Cla cer; 65 Sol cro; 67 Cla arb; 69 Cla pix; 107 Ste pas; 27 Cla gra. (n = 9)

According to the final table (Appendix 6.1) and Fig. 6.8, this species group has a very tight distribution at the low-slope positions on the mid-alpine forelands. It is also very tight on the high-slope and proximal positions on the low-alpine forelands as well as on some high-slope positions on the mid-alpine forelands. It has a tight distribution on the older low-slope positions on the low-alpine forelands. It is quite tight on many other low-slope positions on low-alpine forelands as well as pioneer proximal and high-slope positions at Austerdalsbreen and low-slopes positions on M4 at Fåbergstølsbreen. This assemblage is also quite tight at the low-slope positions of M3 at Austerdalsbreen and all M3 at Fåbergstølsbreen. It is quite rare on low-slope pioneer positions on the mid-alpine forelands and also on the disturbed pioneer sites. It is also not common on most of M1 and M2 at the subalpine altitude. It is also very loose on a number of low-slope sites on M6 at Svellnosbreen and low-slope sites on M3-5 at Austerdalsbreen. In summary, this assemblage is found mainly on low-slope sites, especially on older ground but also on younger ground, on the alpine forelands but also, to some extent, on the subalpine forelands. It is tightest at the low-slope positions on mid-alpine forelands and high-slope positions on the low-alpine forelands. This assemblage corresponds strongly with the level (4) alpine lichen heath (site group 10), the **Solorina crocea - Cetraria nivalis** assemblage. (Colour position code = Brown)

6.5.7 Species group 5: low- and subalpine late intermediate snowbed assemblage (eigenvalue 0.208).

This species group contains the following species:

56 Pin vul; 38 Sol vir; 114 Agr ten; 14 Ant odo; 17 Rum ace; 90 Jun com; 45 Cla por; 70 Cla ama; 74 Cla cri; 75 Pel pol; 30 Cla fim; 62 Cla car; 100 Cla coc. (n = 13)

According to the final table (Appendix 6.1). and Fig. 6.9a-b, this species group has a tight distribution on the oldest terrain and at low-slope positions on low-alpine forelands. It is quite tight on most middle-aged sites at Austerdalsbreen and on proximal M2, all M3 and at low-slope positions on M4 at Fåbergstølsbreen. It is loose on the subalpine M1 and M2 sites and also on some pioneer sites. It is very loose at the low-slope positions on pioneer moraines at Storbreen and Svellnosbreen. It is almost absent from high-slope young positions on the mid-alpine forelands. In summary, this assemblage is mainly found on mature and low-slope sites on the low-alpine forelands and also intermediate terrain on the subalpine forelands. This assemblage corresponds with the level (4) low-alpine late-snow heath (site group 11), the **Salix glauca - Anthoxanthum odoratum** assemblage and also the level (3) subalpine heath (site group 6), the **Calluna vulgaris - Phyllodoce caerula** assemblage. (Colour position code = Dark blue closed)

6.5.8 Species group 6: low and subalpine late-snow heath assemblage (eigenvalue 0.551).

This species group contains the following species:

1 Emp nig; 2 Phy cae; 52 Lis cor; 66 Cla ran; 104 Cla fur; 61 Lou pro; 72 Cla sul. (n = 7)

According to final table (Appendix 6.1) and Fig. 6.10, this species group has a tight distribution on the oldest terrain, and low-slope positions, on low-alpine forelands. It is quite tight on middle-aged ground on subalpine forelands. It is loose at low-slope positions on middle-aged to young ground at subalpine altitudes. It is very loose on high-slope sites on mid-alpine forelands. It is also very loose on most low-slope positions on the mid-alpine forelands, as well as older terrain on subalpine forelands. It is very rare on disturbed pioneer or mid-alpine pioneer sites. In summary, this assemblage mainly occurs at low-slope positions on the oldest terrain on the low-alpine forelands. However, it is fairly widespread on other positions at other altitudes. This assemblage corresponds with the level (4) low-alpine late-snow heath (site group 11), the **Salix glauca - Anthoxanthum odoratum** assemblage. (Colour position code = Dark blue open)

6.5.9 Species group 14: subalpine early intermediate lichen heath assemblage (eigenvalue 0.320).

This species group contains the following species:

26 Cla squ; 48 Cla dig; 79 Lot cor; 101 Cla con. (n = 4)

According to the final table (Appendix 6.1) and Fig. 6.11, this species group has a loose distribution on middle-aged ground on subalpine forelands and on older terrain on the mid-alpine forelands. It is very loose on the Storbreen low-alpine forelands but rare at Svellnosbreen and Storbreen high.. It is also rare on young sites at Fåbergstølsbreen and very rare on most other sites. This assemblage corresponds with the level (4) subalpine early intermediate and late intermediate heath assemblages (site groups 12 and 13*), and the level (6) mid-alpine snowbed (site group 41*), the **Cladonia chlorophaea - Salix herbacea** assemblage. (Colour position code = Mustard)

6.5.10 Species group 30: sub- to low-alpine late-snow heath assemblage (eigenvalue 0.209).

This species group contains the following species:

12 Vio bif; 42 Sal phy; 47 Cla con; 80 Ath dis; 84 Sax ste; 118 Epi als; 6 Vac uli; 55 Vac vit; 93 Ger syl. (n = 9)

According to the final table (Appendix 6.1) and Fig. 6.12, this species group has a quite loose distribution on the middle-aged ground on the subalpine forelands. It is loose on the subalpine oldest terrain and distal M2 sites, and widespread across Svellnosbreen foreland. It is very loose on the oldest low-slope positions on the Storbreen low-alpine sequences, and on the oldest terrain at Høgvaglbreen and it is also very loose on odd pioneer sites. It is occasional at high-slope positions on the low-alpine forelands. It is absent from the two highest mid-alpine forelands, except on the oldest terrain. In summary, this assemblage is found on mature and low-slope sites on the subalpine forelands and is fairly widespread across older and middle-aged ground at the low-alpine altitude. This assemblage corresponds best with the level (4) low-alpine late-snow heath (site group 11), the **Salix glauca - Anthoxanthum odoratum** assemblage and also a number of subalpine assemblages including the subalpine late intermediate late-snow heath (site group 24*) and the subalpine mature snowbed (site group 28*). (Colour position code = Yellow)

6.5.11 Species group 62: subalpine mature/late intermediate woodland heath assemblage (eigenvalue 0.191).

This species group contains the following species:

7 Vac myr; 8 cor sue; 9 Mel syl; 10 Ath dis; 11 Jun fil; 13 Pot cra; 15 Des fle; 16 Tri eur; 19 Luz arc; 20 Gym dry; 21 Lyc cla; 22 Nar str; 23 Sor auc; 24 Cla hyd; 28 Sor cup; 29 Cla lon; 31 Alc alp; 32 Oxa ace; 91 Par pal; 95 Ort sec; 96 Pri spp; 97 Rub ida. (n = 22)

According to the final table (Appendix 6.1) and Fig. 6.13a-b, this species group has a very tight distribution on M1 and distal M2 on the subalpine forelands. It is quite tight on proximal M2, and all M3, at Fåbergstølsbreen. It is very loose on the high-slope sites on M2 Austerdalsbreen and a few low-slope M3, M5 and M6 (Austerdalsbreen) and M4 (Fåbergstølsbreen). It is also loose on mostly low-slope positions on older ground on the low-alpine forelands. It is rare on the disturbed pioneer sites, as well as high-slope positions on all the forelands, and other young sites on the low- and subalpine forelands. It is almost absent from the mid-alpine altitude. In summary, this assemblage is most prevalent on the oldest and late intermediate terrain at the subalpine altitude, but is also prevalent on other older subalpine sites and the oldest and late intermediate terrain on the low-alpine forelands. This assemblage corresponds mainly with the level (4) subalpine mature woodland (site group 14), the **Vaccinium myrtillus** assemblage. (Colour position code = Dark green)

6.5.12 Species group 63: subalpine woodland heath assemblage (eigenvalue 0.191).

This species group contains the following species:

3 Cal vul; 5 Bet pub; 43 mel pra; 51 Eup hel; 53 Lyc ann; 68 Cla def; 71 Cla bel; 73 Cla ple; 76 Des ces; 77 Cla arb; 89 Aln glu; 98 Cer spp; 99 Str cup; 102 Cla sbf; 103 Cla crc; 106 Bro cup; 109 Bla cup. (n = 17)

According to the final table (Appendix 6.1) and Fig. 6.14a-b, it can be seen that *Calluna vulgaris* and *Betula pubescens* have a very tight distribution while the other species have a loose distribution on the middle-aged ground on the subalpine forelands (as well as M5 at Austerdalsbreen). *Betula pubescens* is tight on the oldest terrain at Fåbergstølsbreen and distal M2, but the other species in this assemblage are not. Otherwise this assemblage is rare on mature and late intermediate low-slope sites on the low-alpine forelands and is absent from all other sites. In summary, this assemblage is distributed on the middle-aged ground at Austerdalsbreen, and the oldest and late intermediate terrain at Fåbergstølsbreen. This assemblage corresponds best with the level (2) subalpine assemblage (site group 3), the **Vaccinium myrtillus - Betula pubescens** assemblage. (Colour position code = Dark green open)

6.5.13 Summary of TWINSPAN "final species groups".

Table 6.3 displays the TWINSPAN separation of the "final species groups" contained in the combined foreland data set. Table 6.3 lists the "final species group" name; the number of species within each assemblage; the general location of each of the "final species groups"; and the name of the site group (s) to which it corresponds most closely. Fig. 6.15 elucidates the general location of the "final species groups", across the forelands, belonging to each altitudinal zone. From this it is possible to summarise and discuss the distribution of the assemblages and also to see whether or not TWINSPAN separation, of the combined species data set, can provide ecologically meaningful groups for discussion as well as further analysis and interpretation. From Table 6.2 and Fig. 6.15, it is possible to make the following generalisations, but these findings will be discussed in detail in the concluding chapter (7):

1. Most of the assemblages are found in two, of the three, altitudinal zones (i.e. subalpine, low-alpine or mid-alpine zones), used within the present study. This suggests that the altitudinal zones are not distinct and that it is difficult to make a clear separation between the successional sequences belonging to each of the altitudinal zones. However, it is apparent that altitude is an important general influence on assemblage patterns.
2. Only two assemblages (species groups 35 and 19) are found in all three of the altitudinal zone, further supporting the contention that altitude is an important influence of group separation. Species group (19)

is prevalent on low and mid-slope positions, on the mid-alpine forelands, and high-slope positions at lower altitudes, suggesting that altitude has an influence on this assemblage. Only one assemblage (species group 35), the pioneer and snowbed assemblage, is found on similar types of location (i.e. young and low positions) in all three of the altitudinal zones. This could suggest that the influence of age, on assemblage patterns, is greatest on the young ground and the influence of microtopography is greatest at disturbed low-slope positions.

3. Many of the assemblages, as well as species group (19), differ in their distribution patterns (in relation to age and microtopography) between the altitudinal zones. For example, species group (33), the alpine snowbed assemblage, has a tight distribution at low-slope positions on mid-alpine forelands, but is loose at most positions across all alpine forelands. This suggests that it is not possible to generalise about the position of assemblages without reference to altitude.
4. Most of the assemblages are tightly distributed on certain terrain-ages or microtopographic positions, but are also found, to some extent, on other sites. This suggests that age and microtopography are important influences on vegetation patterns, but that the assemblages overlap.
5. Assemblages, on the alpine forelands, are differentiated by microtopography, as well as age, whereas on the subalpine forelands the main influence on the separation of assemblages is age and microtopography is less important.
6. Divergence of assemblages through succession, from the pioneer to mature stages, is especially apparent in the low-alpine zone. This supports Matthews (1979) who suggests that there is a divergence of assemblages on older ground.
7. The greatest number of assemblages are found in the low-alpine zone and this greater diversity is caused by the low-alpine foreland assemblages comprising subalpine and mid-alpine assemblages, in addition to characteristic low-alpine assemblages. This contradicts the individual data sets, which show that the greatest diversity occurs across the subalpine forelands (see chapter 7).
8. Species are not strictly “faithful” to specific microtopographic positions, terrain-ages or altitudes and that plant distributions can only be described generally or approximately. It appears, therefore, that the terms “assemblage” and “environmental gradient” have more ecological meaning than the stricter terms of “community” and “environmental zone”.
9. These results show that the TWINSPAN analysis of the combined species data set has provided useful complementary material for interpretation, discussion and further analysis.

6.6 Comparison between individual foreland TWINSPAN species groups and combined foreland TWINSPAN species groups.

The summary Table 6.3 displays the “final species groups” for both combined and individual forelands. The species are originally listed according to the “final species groups” made by the combined foreland TWINSPAN analysis. The colour codes for the position of the individual foreland TWINSPAN assemblages (and their constituent species) are the same as those used for Table 4.10, Tables 5.9.-5.16. and

Table 6.2. Table 6.3 shows the extent to which species tend to occur together in similar assemblages and/or on similar types of location (in relation to terrain-age and microtopographic position) from foreland to foreland. If similar assemblages exist there are few gaps, and large blocks of uniformly coloured cells, across the series of columns. If the assemblages have very different constituent species there are a considerable number of gaps across the columns and the cells comprise different colours. A key for the position colour code is given with Table 6.3

This colour-coded summary table also provides a clear visual display of the points listed in Table 6.2. For example, it is possible to see that species group (32) is largely an alpine assemblage. There are four main aims:

1. To relate the "final species groups" to particular forelands and thus altitudinal zones.
2. To show whether the same species tend to occur together in similar assemblages on each of the forelands and thus suggest whether the presence of one species is likely to reflect the presence of other members of an assemblage.
3. To show whether the same species tend to occur on similar locations (in relation to terrain-age and microtopographical position) on each of the forelands, and to suggest whether the representative species can be used to indicate a particular type of location.
4. To list the most representative species of the combined TWINSPAN "final species groups".

The following paragraphs briefly describe how the constituent members of the combined foreland "final species groups" compare with the "final species groups" on the individual forelands.

Species group (32) is a lichen heath assemblage and it is clear that most of the members of this group belong to widespread assemblages found at high-slope positions on the alpine forelands. The block of red colour shows that this is a distinct group and that most of the species, within this group, show a strong fidelity not only to each other but also to the high-slope positions on each of the forelands. The most representative species within this group are *Cetraria ericetorum, Stereocaulon condensatum, Cetraria cucullata, Cetraria nivalis, Thamnolia vermicularis, Cornicularia aculeata, Sphaerophorus globosus, Arctostaphylos alpina, Arctostaphylos uva-ursi, Cornicularia divergens, Alectoria ochroleuca, Sphaerophorus fragilis and Alectoria nigricans.* The distinctness of this assemblage suggests that it could be described as a community and whether it is associated with particular environmental parameters, in a distinct environmental zone, is discussed in the following ordination section. It is considered possible to use each of these species to indicate high-slope exposed positions as well as to indicate the likelihood of the presence of other members of the assemblage.

Species group (33) is a small and tight snowbed assemblage and most of the members of this group belong either to pioneer, widespread or low-slope assemblages. Members of this group show some fidelity towards each other from foreland to foreland. Members generally are widespread except on the subalpine forelands where they tend to be found on young terrain. The most representative species of this group are *Salix herbacea, Stereocaulon alpinum, Cladonia uncialis, Cladonia verticillata, Hieracium spp, Cassiope hypnoides and Trisetum spicatum.* This is not a distinct assemblage and thus should not be described as a community.

Species group (34) is a large loose late-snow heath assemblage and is generally found on low-slope positions on low-alpine forelands. Members of this group show a fair amount of fidelity towards each other from foreland to foreland and they also show a strong tendency towards occurring on low-slope positions. Assemblages tend to belong to mature low-slope positions, middle-aged low-slope positions or widespread low-slope (snowbed) positions. The most representative species are *Leontodon autumnalis, Carex spp, Stereocaulon botreosum, Veronica alpina, Polygonum viviparum, Antennaria alpina, Nephroma arcticum, Psoroma hypnorum, Silene acaulis, Pannaria pezizoides and Cardamine bellidifolia.* This is a fairly distinct assemblage and but not enough to be described as a community.

Species group (35) is a fairly tight pioneer and snowbed assemblage found at all the altitudinal zones but especially on the low-alpine forelands. Members of the group show fidelity towards each other from foreland to foreland and they also show a strong tendency towards occurring on pioneer or low-slope (snowbed) positions. The most representative species are *Oxyria digyna, Phleum alpinum, Gnaphalium supinum, Sagina saginoides, Luzula spicata, Cerastium alpinum, Poa alpina and Cardaminopsis petraea.* This is a fairly distinct assemblage and thus could possibly be regarded as a community and whether it is associated with an environmental zone will be discussed in the following ordination section. It is considered possible to use each of these species to indicate low-slope (snowbed) positions or young terrain as well as to indicate the likelihood of the presence of other members of the assemblage.

Species group (18) is a late-snow heath assemblage and it is especially tight at low-slope positions on the low-alpine forelands but is also widespread on pioneer and low-slope positions on the subalpine forelands, and to a lesser extent at Høgvaglbreen and Bøverbreen, the mid-alpine forelands. Storbreen high foreland sequence appears to have more species in common with the low-alpine foreland sequences. Members of the group show some fidelity towards each other from foreland to foreland but the location of the members of the group shows considerable differences between forelands. The most representative species of this assemblage are *Salix glauca, Pyrola minor, Sibbaldia procumbens, Festuca ovina, Juncus trifidus, Salix lanata, Cerastium cerastoides, Deschampsia alpina* and *Gnaphalium norvegicum*. This is not a distinct assemblage and thus cannot be regarded as a community.

Species group (19) is a widespread lichen heath assemblage but is especially tight on: the oldest terrain on the mid-alpine forelands; high-slope positions or widespread on the low-alpine forelands; and intermediate or young terrain on the subalpine forelands. The species show considerable fidelity, especially at the higher altitudes, but occurs in very different locations (in relation to terrain-age and microtopography) between forelands. All the members of this assemblage are representative and they are *Cetraria islandica, Cladonia gracilis, Cladonia chlorophaea, Lycopodium selago, Cladonia cervicornis, Solorina crocea, Cladonia arbuscula, Cladonia pyxidata* and *Stereocaulon paschale*. There is considerable fidelity of species, within this assemblage, but the distribution is not uniform enough to suggest that this assemblage should be described as a community.

Species group (5) is a late intermediate snowbed assemblage and is fairly tight on mature or low-slope positions on the sub-and low-alpine forelands. It also occurs on low-slope or mature sites on the mid-alpine forelands. The species show some fidelity from foreland to foreland and, on the whole, the species are distributed on similar types of location (in relation to terrain-age and microtopography). The most representative species of this assemblage are *Anthoxanthum odoratum, Rumex acetosa, Cladonia fimbriata, Solidago virgaurea, Cladonia portentosa, Pinguicula vulgaris, Cladonia cariosa, Cladonia amaurocraea, Cladonia crispata, Peltigera polydactyla* and *Juniperus communis*. This assemblage is fairly distinct but the distribution is not uniform enough to suggest that this assemblage should be defined as a community.

Species group (6) is a late-snow heath assemblage and is mostly found on the subalpine and low-alpine forelands, but is also found on the mid-alpine forelands. Many of the species belong to widespread assemblages but there is not much fidelity between the species of this assemblage from foreland to foreland. There is also little similarity between the locations (in relation to terrain-age and microtopography) where the species are found. The most representative species of this assemblage are *Empetrum nigrum, Phyllodoce caerula, Loiseleuria procumbens, Cladonia rangiferina, Cladonia sulphurina* and *Cladonia furcata*. This assemblage is not distinct enough to be regarded as a community.

Species group (14) is a small lichen heath assemblage which is tightest on the oldest terrain on subalpine forelands, and fairly tight on low-alpine forelands, but is widespread on other sites and also occurs on low-slope positions on the mid-alpine forelands. The species, within this assemblage, show a certain amount of fidelity and the distribution of the species is fairly consistent at lower altitudes. All the species are representative and they are *Cladonia squamosa, Cladonia digitata, Lotus corniculatus* and *Cladonia coniocraea*. This assemblage is not distinct enough to be regarded as a community.

Species group (30) is a late-snow heath assemblage and is most prevalent on the subalpine forelands, but its members are also present on the low-alpine forelands. This assemblage shows little fidelity between species, on each of the forelands, and also the species show a variety of distribution patterns. The most representative species are *Vaccinium uliginosum, Viola biflora, Salix phylicifolia, Vaccinium vitis-idaea* and *Saxifraga stellaris*. This assemblage is not distinct enough to be regarded as a community.

Species group (62) is a subalpine mature/late intermediate woodland heath assemblage and is tightest on the oldest terrain on the subalpine forelands. Some of the members of this assemblage are found on low-slope positions on the oldest terrain, on the low-alpine forelands, and a few members on low-slope positions on the mid-alpine forelands. The species show considerable fidelity and generally occur on similar locations from foreland to foreland. The most representative species are *Vaccinium myrtillus, Potentilla cranzii, Deschampsia flexuosa, Trientalis europaea, Luzula arcuata, Gymnocarpium dryopteris, Nardus stricta* and *Alchemilla alpina*. This assemblage is fairly distinct and should be regarded as a community. Whether it is associated with particular environmental parameters, comprising a distinct environmental zone, will be discussed in the following ordination section. It is considered possible to use some of these species to indicate low-slope positions and/or the oldest terrain on subalpine (or low-alpine) forelands, as well as to indicate the likelihood of the presence of other members of the assemblage.

Species group (63) is a subalpine woodland heath assemblage and is tightest on the subalpine forelands. Some of its members are also found at Svellnosbreen and a few on the other forelands. Its members show considerable fidelity on the subalpine forelands but the distribution appears to be different between the forelands. The most representative species are *Calluna vulgaris, Betula pubescens, Cladonia bellidiflora* and *Cladonia pleurota*. This assemblage does not appear to be distinct enough to be defined as a community.

The main trends shown by Table 6.3 are as follows:

1. Most of the combined foreland species groups are not distinct enough to be regarded as communities and tend to comprise species which do not have strong fidelities with other species or with particular locations (in relation to terrain-age and microtopography). This suggests that the vegetation across most of the forelands can only be described in general terms and that there is an overlap, or gradient of assemblages, as opposed to distinct divisions between the different assemblages (i.e. communities) into "zones".
2. The most distinct assemblages are: species group (32), the lichen heath assemblage; species group (35), the pioneer and snowbed assemblage; and species group (62), the subalpine mature/late intermediate woodland heath assemblage. These assemblages should be regarded as communities, as there appears to be considerable fidelity between the species belonging to these assemblages from foreland to foreland. Furthermore the species tend to occur on similar types of location (in relation to terrain-age and microtopography) from foreland to foreland. Only species which are members of these assemblages could conceivably be used to indicate the location-type, or the possible presence of other members of the same assemblage. Nevertheless, it is likely that, even with these distinct assemblages, errors would probably be made, and thus the use of species as indicators of location-type, or assemblage-type, should be carried out with great caution.
3. It appears that altitude, age and microtopography play an important role in influencing the separation of the assemblages. The most distinct assemblages appear to be those occurring at: a) the extremes of

microtopographical position (i.e. exposed lichen heath occurring at the crest positions and snowbed, or fluvially disturbed, assemblages occurring at low-slope positions); and b) the extremes of terrain-age (i.e. pioneer assemblages occurring on the youngest ground and mature woodland heath occurring on the oldest ground). Assemblage distinctness therefore does not appear to be altitude-related.

4. Generally the assemblages do not strictly belong to one altitudinal zone and tend to overlap, so that, on the whole, most of the assemblages tend to occur in two altitudinal zones, even though only one zone may be favoured.
5. These results confirm the results from chapters 3 to 5 that assemblages tend not to occur as distinct entities and there seems to be an overlap, or gradient, between the assemblages in relation to altitude, age and microtopography. It is, nevertheless, possible to see clear changes in the assemblages with altitude, age and microtopography and thus it is considered ecologically meaningful to attempt to describe the effects of these meso-environmental factors on the different assemblages. In the next section a more specific discussion of the effect of environmental parameters on these assemblages is made.

6.7 DCA-ordination analysis

The combined data set is analysed using the DCA option in the CANOCO ordination programme. All the options chosen follow those used for the individual foreland data sets and the rational behind the use of these options is described in chapters (2) and (5). The presentation and layout of this section also follows that of chapter (5) to maximise comparability. In chapter (5) both the species and site patterns on axes (1) and (2), and their relationship to environmental parameters, are displayed and discussed by using the colour rank lists of the sites, species and environmental parameters on each of the ordination axes (Tables 5.1-16). In this section only the rank of species (Table 6.4) is displayed and discussed. This is, firstly, because the sample and species results in chapter (5) give similar results so it is unnecessary to display and discuss the sample ranks. Secondly, the sample list is very long and cumbersome (926 samples on each axis) so it is questionable whether the rank list for both axis (1) and (2) would provide a useful and easily interpretable table. The colours displayed in Table 6.5, represent the combined data set TWINSPAN "final species groups" and give an approximate indication of the general location of the groups across the forelands. By using these rank tables it is possible to show how the individual species are related to each other across all altitudinal zones on each axis. The relative influence of environmental parameters on the rank of species is also be discussed. The difference between the TWINSPAN separation of species (represented by the different colours) and the DCA-ordination (represented by the rank list) is also discussed.

In chapter (5) DCA centroid scores of the TWINSPAN "final site groups" and "final species groups" are displayed on ordination plots, along with biplots of environmental parameters scores, in order to elucidate the relationship between "final groups" and the environmental parameters on each individual foreland. As with the rank tables, the results from the centroid plots show a considerable similarity between centroid plots of the TWINSPAN "final site groups" and centroids of the TWINSPAN "final species groups", so it is considered reasonable to plot the centroid scores of the "final species groups", along with the environmental biplot scores (Figs. 6.17 to 6.18) for discussion. In addition, a correlation matrix of Pearson's product moment correlation coefficient (Table 6.5) has been used to elucidate further the relationship between the different environmental variables and the ordination axes. In chapter (5), only the most important variables, which are significant at $p<0.001$, are described. In this chapter, all the environmental parameters are discussed even though only those environmental parameters significant at $p<0.001$ are considered significant or important (the critical value for "r" is 0.216 for 200 samples). The use of such a stringent significance level is justified on the grounds of the parametric nature of the technique (Crouch, 1992). The main aims of this section are those outlined in chapter 5 (section 5.1), except the site analyses are excluded.

6.7.1 Species patterns on DCA axes (1) & (2)

By referring to Table 6.4 and Table 6.2 it is possible to relate the sequence of species on DCA axes (1) and (2) to the TWINSPAN "final species groups", described in the previous sections, and thus elucidate the influence of particular environmental variables on the species pattern across the combined foreland data set. Axis (1) has an eigenvalue of 0.539 showing that there is good species separation along the axis and that this axis is ecologically meaningful. The environmental variables explain 89.7% of the variation along this axis so it can be considered reasonable to use these parameters to explain the patterns shown by axis (1). Axis (2) has an eigenvalue of 0.409 which is also high enough to be considered an ecologically meaningful separation along the axis. The environmental variables, however, only explain 68.7% of the variation along this axis which suggests that 31.3% of the variation along axis (2) is explained by parameters other than those measured. Interpretation of the relationship between the environmental data and the vegetation pattern on axis (2) is therefore less certain. This low figure further supports the use of DCA over CCA in that the environmental variable data do not represent the total environment and thus should not be used to influence the pattern of species on the axes.

At the positive end of axis (1) is the subalpine mature/late intermediate woodland heath assemblage, species group (62), which is followed by the subalpine woodland heath assemblage, species group (63), interspersed with members of the sub- to low-alpine late-snow heath assemblage species group (30). The positive end of axis (1) corresponds with environmental variables which are vegetation cover, root depth, humus depth, stain depth, bryophyte cover and age. Following these assemblages is a mixed sequence of assemblages interspersed within the large low-alpine late intermediate late-snow heath assemblage, species group (34). There is some order shown by the interspersing assemblages. Firstly, within the sequence, is the low- and subalpine late intermediate snowbed assemblage, species group (5); the low- and subalpine late-snow heath assemblage, species group (6); and species group (30). These assemblages are replaced by the low-alpine late-snow heath assemblage, species group (18). This is then replaced by the lichen heath assemblage, species group (19); the pioneer and snowbed assemblage, species group (35); the alpine snowbed assemblage, species group (33). At the negative end of axis (1) is most of the exposed lichen heath assemblage, species group (32), interspersed with the alpine snowbed assemblage, species group (33), and species group (35). The negative end of axis (1) corresponds with environmental variables which are altitude, bare gravels, frost heave, lack of snow, bare ground boulders and pH.

At the positive end of axis (2) is the pioneer and snowbed assemblage, species group (35) interspersed with a mixture of seven other assemblages. The positive end of axis (2) corresponds with environmental parameters which are fluvial activity, pH, bare ground boulders, easterly aspect, bare ground fines, animal influence and bare ground gravels. The middle section of axis (2) is very disordered and the sequence is dominated by the large low-alpine late intermediate late-snow heath assemblage, species group (34) interspersed, firstly by the subalpine mature/late intermediate woodland heath assemblage, species group (62) and other assemblages including species group (18), species group (33) and species group (30). Further down the axis, species group (34) becomes interspersed with a higher proportion of members of the low- and subalpine late intermediate snowbed assemblage, species group (5), and other assemblages consisting of species group (6), species group (19) and species group (14). At the negative end of axis (2) is the alpine exposed lichen heath assemblage, species group (32), interspersed with the subalpine woodland heath assemblage, species group (63). The negative end of axis (2) corresponds with environmental parameters which are age, low snow-lie, stain depth, dryness, high-slope positions, vegetation cover and frost heave.

The TWINSPAN "final species groups" correspond quite well with the separation of species along axis (1), especially at either end of the axis. On axis (2), the sequence is more disordered except at the positive and negative ends. The most distinct assemblages on axis (1) are the subalpine mature/late intermediate woodland heath assemblage, species group (62) and the alpine exposed lichen heath assemblage, species group (32). On axis (2), the only distinct assemblage is species group (32), although the pioneer and snowbed assemblage, species group (35), is quite distinct. Generally, therefore, the evidence supports the notion that there is a gradient of assemblages, as opposed to distinct communities, across the forelands of the combined data set. The most distinct assemblage on the subalpine forelands has therefore separated according to age, whereas, on the alpine forelands, it has separated according to microtopography. According to these results, therefore, microtopography has a greater influence on the determination of the most distinct assemblages across the alpine forelands than it does on the subalpine forelands. Age appears to be the most important influence on the determination of the most distinct assemblages on the subalpine forelands.

These results are summarised in Fig. 6.16, and on axis (1) there is a strong altitude-related sequence, from subalpine assemblages, at the positive end of axis (1), to alpine assemblages at the negative end of axis (1). Superimposed onto axis (1) is an age-related sequence, from the mature assemblages, at the positive end of the axis, to pioneer assemblages, at the negative end of the axis. There also appears to be a microtopography-related sequence, with low-slope assemblages at the positive end, and high-slope assemblages, at the negative end of the axis. This shows that altitude is the most important meso-environmental influence on vegetation pattern across all the forelands, but age and microtopography are superimposed onto this sequence showing that the effects of these variables cannot be altogether separated from each other as independent parameters. This also shows that the lower altitude, older ground and low-slope assemblages, associated with higher vegetation cover and more developed soils, have more species in common with each other than higher altitude, younger ground and high-slope assemblages, associated with bare ground, frost activity, low snow cover and higher pH. On axis (2), the main influences on the separation of species appears to be fluvial disturbance and microtopography with, mainly, pioneer, snowbed and late-snow heath assemblages, associated with young ground, long snow duration, fluvial activity, high pH, and bare ground, at the positive end of the axis, and heath (or lichen heath) assemblages, associated with age, lack of snow, dryness and high-slope positions, at the negative end of the axis. Altitude does not appear to be an important influence on the sequence of species on axis (2). The sequence on axis (2) would suggest that disturbance is related to low-slope positions and is independent of altitude and, in contrast to axis (1), low-slope positions are associated with younger ground on axis (2). Microtopography is thus an important and complex meso-environmental parameter insofar as it is influential on both axis (1) and (2), so that its influence is difficult to separate age and altitude. In addition, its relationship with age appears to differ according to site disturbance. These results further support the earlier suggestion that disturbance should be considered as a meso-environmental influence, along with altitude, age and microtopography, comprising a number of associated micro-environmental parameters that form a "*factor complex*" (*sensu*: Whittaker 1989) and this proposal will be expanded in the next section and in the concluding chapter.

6.7.2 Environmental parameter patterns and their significance

Fig. 6.17 reveals the location of the environmental parameter biplot scores in relation to the DCA centroids of the TWINSPAN "final species groups". The location of these parameters, in relation to each other, is described and from this it is possible to discuss the relationship between these parameters. In addition, Table 6.5, the weighted correlation matrix, is used to outline and corroborate the main findings in this and the previous section.

The first notable feature of Fig. 6.17 is that the spread of environmental parameters across the plot appears to have been affected by the fluvial activity parameter at the positive end of axis (2). Most of the other parameters occur towards the centre or negative end of axis (2) causing the plot to appear "bottom heavy". This suggests that fluvial activity is a highly influential parameter on other environmental variables, although its location on axis (2) suggests that its influence is not as significant as those parameters associated with axis (1). Another feature of the plot is that there is a wide dispersal of parameters across the negative section of the plot, suggesting that many of the parameters are influential on axis (1) and the negative end of axis (2) and this is especially indicated by the positioning of the stain (or soil) depth, age and lack of snow parameters half way between the axes on the plot.

According to Fig. 6.17 and Table 6.4, towards the positive end of axis (1) is a cluster of environmental parameters associated with developed soil and vegetation. Table 6.5 shows that these parameters are significantly and positively correlated with axis (1) and they are: vegetation cover (*r* = *+0.467*), root depth (*r* = *+0.437*), humus depth (*r* = *+0.37*), stain depth (*r* = *+0.336*) and bryophytic cover (*r* = *+0.279*). Towards the centre of axis (1) are less significant parameters, including animal influence, soil texture, northerly aspect, slope, and easterly aspect. The insignificant parameters on axis (1), at the centre but towards the negative end of axis (1), are fluvial activity, solifluction, dryness (low moisture), trampling, position, bare fines, dowels and pH. Towards the negative end of axis (1) are those parameters which are significantly and negatively correlated with axis (1) and they are: altitude (*r* = *-0.79*), bare ground gravels (*r* = *-0.57*), frost heave (*r* = *-0.53*), snow-lie (*r* = *-0.41*) and bare ground boulders (*r* = *-0.22*). On axis (2), the only parameter significantly correlated with the positive end of the axis is fluvial activity (*r* = *+0.44*), while those parameters which are insignificant but positively correlated with axis (2) are pH, bare ground boulders, easterly aspect, bare ground fines, animal influence and bare ground gravels. Those parameters most significantly and negatively correlated with axis (2) are age (*r* = *-0.4*) and lack of snow (*r* = *-0.34*) and the rest of the environmental parameters are insignificantly correlated with axis (2).

These results show which of the micro-environmental parameters are most closely related to each of the meso-environmental parameters. High altitude is most positively correlated with frost heave (*r* = *+0.444*), bare ground gravels (*r* = *+0.359*), lack of snow (*r* = *+0.351*) and pH (*r* = *+0.222*), and most negatively correlated with vegetation cover (*r* = *-0.356*) and bryophyte cover (*r* = *-0.29*). Age, in terms of older ground, is most positively correlated with stain depth (*r* = *+0.627*), root depth (*r* = *+0.521*), humus depth (*r* = *+0.52*) and vegetation cover (*r* = *+0.351*) and most negatively correlated with bare ground gravels (*r* = *-0.46*). Microtopography, in terms of high-slope position, is most positively correlated with low snow cover (*r* = *+0.424*), frost heave (*r* = *+0.321*) and dryness (*r* = *+0.223*), and most negatively correlated with fluvial activity (*r* = *-0.22*). Within the combined data set the overall influence of fluvial activity has been to reduce the importance of microtopography as an influence on soil development and vegetation cover. Fluvial disturbance is negatively correlated with slope (r = -0.23) and position (r = -0.22) and is not significantly and positively correlated with any other micro-environmental parameters. This suggests that fluvial activity does not form a "factor complex" in the same way as the other meso-environmental factors. However, the relative influence of this parameter, on the vegetation pattern, sets it apart from the other micro-environmental parameters. Snow-lie is the most important parameter within the microtopographic factor complex and this confirms the findings in the previous chapter. These results are summarised in Table 6.6.

It is quite apparent from these results that the most significant environmental influences on the vegetation pattern on axis (1) are altitude and, to a lesser extent, age and microtopography whereas on axis (2) the most significant influence is disturbance, age and microtopography. There is some complication in the results due to the effects of disturbance by fluvial activity on some low-slope positions causing high-slope positions to have better developed vegetation and soils. These influences reflect the relative importance of meso-environmental parameters on, and between, each of the forelands used in this study.

6.7.3 DCA centroids of TWINSPAN "final species groups" and environmental parameter biplot scores

Fig. 6.17 shows the DCA centroids of TWINSPAN "final species group" scores for the combined data set, and displays the location of the species groups, on both axes, in relation to the environmental parameter biplot scores. As can be seen in Fig. 6.17, the centroids are close together in the centre of the plot so as to make interpretation difficult. Fig. 6.18 displays the DCA centroids of the TWINSPAN "final species group" scores, without the environmental parameters, and from this the pattern of the centroids, on each axis, can be described and discussed. The pattern of centroids of the "final species groups", on Fig. 6.18, can then be compared to the pattern of environmental parameters on Fig. 6.17. Thus the relationship between the assemblage patterns and environmental patterns can be elucidated.

As can be seen in Fig. 6.18. the subalpine mature/late intermediate woodland heath assemblage, species group (62) shows most correspondence with the positive end of axis (1) and is known to be an assemblage belonging to the lowest altitude, the oldest ground and the most developed soils and vegetation, and lower microtopographical positions. This corresponds entirely with the environmental parameters which are low altitude, vegetation cover, root depth, humus depth, stain depth, bryophytic cover, age and long snow duration. Next, further towards the centre, is the subalpine woodland heath assemblage, species group (63) and the sub- to low-alpine late-snow heath assemblage, species group (30). Towards the centre are the low- and subalpine late-snow heath assemblage, species group (6), the low- and subalpine late intermediate snowbed assemblage, species group (5), the subalpine early intermediate lichen heath assemblage, species group (14), and at the centre the low-alpine late intermediate late-snow heath assemblage, species group (34). Also at the centre, but towards the negative end of the axis is the low-alpine late-snow heath assemblage, species group (18). These assemblages, found within the central portion of the axis, are known to correspond with intermediate altitudes, ages and microtopographical positions, and this agrees closely with the environmental parameters suggested by the DCA-ordination. Towards the negative end of axis (1) is the lichen heath assemblage, species group (19), the pioneer and snowbed assemblage, species group (35), the alpine snowbed assemblage, species group (33), and, furthest towards the negative end, the alpine exposed lichen assemblage, species group (32). These assemblages are known to correspond with higher altitudes, younger ground and high-slope position and again this corresponds with the environmental parameters associated with the negative end of the axis, which are altitude, bare ground gravels, frost heave, lack of snow, bare ground boulders and high pH.

At the positive end of axis (2) is the pioneer and snowbed assemblage, species group (35), known to be a young ground or late snow-lie assemblage, which corresponds perfectly with the environmental parameters: fluvial activity, young ground, long snow-lie, high pH and low-slope positions. Next, on the plot, is the subalpine and low-alpine late-snow heath assemblage, species group (30), the low-alpine late-snow heath assemblage, species group (18), and the subalpine early intermediate lichen heath assemblage, species group (14). These assemblages are generally late snow-lie assemblages and, in chapter (3) (section 3.3.1), it was shown that snow-lie has a relatively uniform and consistent duration across moraines over the winter period, on the subalpine forelands, which may explain the overlap of a lichen heath assemblage with late-snow heath assemblages. Towards the centre of the axis is the low- and subalpine late intermediate snowbed assemblage, species group (5), the subalpine mature/late intermediate woodland heath assemblage, species group (62), the low-alpine late intermediate late-snow heath assemblage, species group (34) and the alpine snowbed assemblage, species group (33). These assemblages are also late-snow assemblages, but by referring to section 3.73, it can be seen that the sites, where these assemblages occur, have relatively low fluvial disturbance. At the centre, but towards the negative end of axis (2), is the low- and subalpine late-snow heath assemblage, species group (6), the subalpine early intermediate woodland heath assemblage, species group (63), the lichen heath assemblage, species group (19) and, furthest towards the negative end, is the alpine exposed lichen heath assemblage, species group (32). These assemblages correspond with older ground sites, at high-slope positions, with the least fluvial disturbance and the lowest snow duration.

In section 6.5, the location, of each of the "final species groups", is described in detail and the most important mesoenvironmental influences (i.e. altitude, age and microtopography) on each of the TWINSPAN "final species groups" is suggested, in accordance with the distribution patterns. There is excellent correspondence (with regard to the major mesoenvironmental influences on "final species group" patterns) between the suggestions put forward in section 6.5, and the relationships (found by calculating regression coefficients of environmental parameters on the ordination axes) between the "final species group" and environmental parameters described in the present section. It is therefore proposed that the factor complexes suggested in Table 6.6 are a good representation of the most important micro-environmental parameters associated with each meso-environmental factor.

6.7.4 Summary of DCA-ordination results

The rank table (Table 6.4), provides a clear and easily interpreted representation of the ordination results on axis (1) and, to a lesser extent, on axis (2). The TWINSPAN "final species groups" correspond well with the sequence of species along axis (1) although the middle portion has a somewhat disordered sequence. There is better correspondence towards either end of axis (2). The plots and correlation matrix have provided further elucidation and confirmation of the results derived from the rank tables, which is especially useful in relation to axis (2). The DCA centroids of TWINSPAN "final species groups" correspond well with the pattern of environmental parameters on axis (1) and (2), suggesting that the trends found on both axis (1) and (2) are ecologically meaningful. The following major trends can be seen from the DCA-ordination of the combined data set and these trends have been listed under sub-headings for ease of reference. These trends will be discussed in greater detail in the concluding chapter (7).

1. The "Altitude factor complex". Altitude is the most important influence on the vegetation pattern across the series of forelands which make up the combined data set. Those parameters that appear to be most associated with changes of altitude, which are summarised in Table 6.6, include frost activity, vegetation cover or bare ground gravels, snow duration and soil pH. Frost activity, snow duration and vegetation (in terms of shelter) also, indirectly, indicates the temperature and exposure of the location, with increased exposure and decreased temperatures at the higher altitudes. Whittaker (1985) combined the effects of altitude and age together within the same "factor complex" as his data set did not have a wide altitudinal range. However the results from this study indicate that the effects of altitude and age can be separated from each other in a meaningful way since a component of the "*Altitude factor complex*" in this study is snow duration. Snow duration is not included in Whittaker's "*Terrain-age factor complex*" and, furthermore, the altitude factor complex does not include the soil development parameters so prominent in the aforementioned "*Terrain-age factor complex*".
2. The "Age factor complex". Age appears to be the second most important influence on vegetation pattern at the mesoscale. Those parameters that seem to be most associated with changes of age include depth of stain (or soil depth), root depth, humus depth, vegetation cover and cover of bare-ground gravels. The effects of age appear to be confounded with altitude, with the more developed vegetation being found at the lower altitudes. However the increased frost activity on younger ground indicated by the "*Terrain-age factor complex*" of age, altitude, soil characteristics and frost activity described by Whittaker (1985) has not been found to be significant in this study. The "*Age factor complex*" has been so named to distinguish it from the "*Terrain-age factor complex*" described by Whittaker. These results clearly indicate that it is ecologically meaningful to separate the component micro-environmental parameters for age and altitude.
3. The "Microtopographic factor complex". Microtopography is an important influence on vegetation pattern but its effect is complex and varies according to the amount of fluvial disturbance, and extremes in the duration of snow-lie, at low-slope positions. On axis (1), where microtopographical position is also related to age, the most developed vegetation and soils is found at low-slope positions (along with longer snow duration, higher moisture and lower frost activity) and the least developed on the crests of the moraines. On axis (2), where microtopographical position is related to disturbance and long snow duration, the most developed vegetation is found on the crests of moraines and the least developed at low-slope positions, and thus the association with age on axis (2) is exactly opposite to what it is on axis (1). The environmental parameters most associated with high-slope positions are low snow duration, frost

activity, dryness and low fluvial activity. The results on axis (1) correspond well with the "*Microtopographic factor complex*" of exposure, moisture and snowmelt described by Whittaker (1985), so that high-slope positions are associated with bare ground and lower vegetation cover. Although the parameters associated with microtopography are the same on axis (2), their relationship with bare ground and vegetation cover is the reverse, so that low vegetation cover and bare ground are associated with low-slope positions. These results confirm the necessity for describing a large number of environmental parameters for any given site and it also suggests that the effect of microtopography on vegetation pattern is more complex than that proposed by Whittaker (1985). Despite these problems the most important micro-environmental parameters associated with microtopography (i.e. snow duration, moisture, fluvial activity and frost activity) remain the same even though their influence on the vegetation pattern can differ.

4. Fluvial disturbance. The results have shown this parameter to be a highly significant influence on vegetation pattern. Not surprisingly, it is most associated with slope (flat ground) and low-slope positions (i.e. microtopography) but it is not associated with any other micro-environmental parameters. Because it is closely associated with microtopography it cannot be regarded as a factor complex in the same way as altitude, age and microtopography and thus should only be considered as a highly important individual micro-environmental parameter, associated with microtopography.
5. Environmental gradients or zones? Although there are distinct changes in environment, associated with altitude, age and microtopography, the relationship between the meso-environmental parameters, and their associated micro-environmental parameters, has been shown to be complex. This complexity prevents the definition of distinct environmental zones at the macroscale, the mesocale and the microscale and thus supports the general existence of environmental gradients between forelands of different altitude, terrain of differing age, and sites at different microtopographical positions. However, sites which are affected by high levels of fluvial activity, at all altitudes, or by low snow duration, dryness and high-slope position, on alpine forelands, are possibly distinct enough to be regarded as representing environmental zones. In addition, the complete vegetation cover and well-developed soils, on the oldest terrain on subalpine forelands, also appear to provide a distinct environment that could be considered as a zone. It is, therefore, possible to tentatively suggest that a number of environmental zones occur on certain parts of the forelands. It is, however, more ecologically meaningful to use the term environmental gradient and to recognise that there are gentler gradients, where the changes are more gradual, and sharper gradients where differences in the vegetation and prevailing environment are more noticeable between forelands or sites.
6. Assemblage or community? On axis (1), the most distinct TWINSPAN "final species group" is the subalpine mature/late intermediate woodland heath assemblage, species group (62) and the alpine exposed lichen heath assemblage, species group (32) and; on axis (2), only species group (32) is considered to be distinct although the pioneer and snowbed assemblage, species group (35), has some claim to be recognised as distinct. This suggests that the most distinct assemblages are influenced by microtopography, on the alpine forelands, and age, on the subalpine forelands.

6.8 Chapter summary

Analysis of the combined foreland data set using TWINSPAN and DCA-ordination has provided interpretable and ecologically meaningful results. The combined data results not only give support and further insight into the results of chapter (3) to (5) but have also brought to light several new findings, which analysis of the individual forelands cannot provide. For a thorough and comprehensive elucidation of data, the results from chapters (3) to (6) show that analysis of both individual foreland, and combined foreland data sets, is necessary. However, analysis of the combined data set has been found to provide most of the major points found by analysis of the individual forelands and so a researcher, who is short of time, should feel confident that a combined data set will elucidate most of the important trends. The main trends, described in each of the section summaries (i.e. 6.3.6, 6.5.13, and 6.7.2), are drawn together in the following chapter summary:

1. Altitude and the "*Altitude (bare ground gravels - frost - vegetation cover - snow duration - pH) factor complex*". Altitude has the greatest influence on the separation of the TWINSPAN site groups, with the greatest difference in assemblage-types occurring between the subalpine range and the alpine range. This study has shown that it is possible to separate the most important micro-environmental parameters, associated with altitude, and form the "*Altitude factor complex*" comprising bare ground gravels, frost activity, vegetation cover, snow duration and pH. There appears to be an altitudinal gradient, which could be the cause of an overlap of assemblages between different altitudinal zones. Altitude also affects the positioning of assemblages, in terms of age of ground or microtopographical position, across forelands in different altitudinal zones. Altitude also appears to affect succession, with simpler and more predictable successions occurring at higher altitudes. The influence of the other meso-environmental parameters (i.e. age and microtopography), on vegetation pattern, can change according to altitude in as much as an assemblage associated with a particular terrain-age and microtopographical position, within one altitudinal zone, may be associated with ground of a different age or microtopographical position at another altitude. Altitude does not appear to have a significant effect on the distinctness of assemblages. Altitude does not appear to have a strong influence on pioneer or snowbed assemblages, so that the composition of pioneer and snowbed assemblages are similar between altitudinal zones.

2. Time and the "*Age (soil depth, root depth, humus depth, vegetation cover and cover of bare-ground gravels) factor complex*". Age appears to be the second most important influence on the separation of TWINSPAN site groups. Age and disturbance are the most important influences on the subalpine forelands, and a combination of age, microtopography and disturbance on the alpine forelands. The influence of age is complex and is confounded with other meso-environmental parameters, especially altitude. It is, nevertheless, possible to separate the most important micro-environmental parameters, associated with age, and form the "*Age factor complex*", comprising depth of stain (or soil depth), root depth, humus depth, vegetation cover and cover of bare-ground gravels. The influence of age, on the

distinctness of assemblages, tends to be greatest on the youngest terrain or on the oldest terrain. There also appears to be a greater diversity of TWINSPAN "final species groups" on the oldest ground on alpine forelands, especially in the low-alpine zone, an outcome which appears to be influenced greatly by microtopography. This in turn supports the view that there is a divergence of assemblages on the oldest ground (cf. Matthews, 1979). In general, most of the assemblages, occurring on terrain of intermediate age (the early intermediate assemblages) are not distinct and this shows that on the whole there is a gentle age-related gradient of assemblages across the foreland, which suggests that succession progresses in a gradual manner rather than in a series of steps.

3. Microtopography and the "*Microtopographic (snow-lie, moisture, frost activity and fluvial disturbance) factor complex*". Microtopography is an important influence on vegetation pattern but its influence is complex insofar as its influence is confounded with age and disturbance. Low-slope positions tend to be associated with older ground, accompanied by more developed soils under late-snow heath or woodland, and the high-slope exposed positions tend to be associated with younger ground comprising less developed soils and vegetation. However, in relation to disturbance, the low-slope positions are associated with younger sites with high proportions of bare gravels and a high soil pH, and the high-slope positions are associated with older ground with better developed soils under dry heathland. Despite these associations with age and disturbance the micro-environmental parameters forming the "*Microtopographical factor complex*" remain the same, and they are snow duration, moisture (or dryness), frost activity and fluvial disturbance.

4. The greatest influence of microtopography appears to be at the extremes of microtopographical positions on the alpine forelands, and least on the older ground on the subalpine forelands. On the alpine forelands, where woodland is absent, the highest microtopographical positions have a short snow duration and low moisture and only assemblages that are tolerant of exposure, such as the lichen heath assemblages, can flourish. At the low-slope microtopographical positions, where snow duration is longest, or fluvial activity is greatest, only members of snowbed or pioneer assemblages are found. The most distinct assemblages, on the alpine forelands, are the exposed lichen heath species group (32), and the snowbed and pioneer assemblage, species group (35). This shows that microtopographical position has a considerable influence on the separation of the most distinct assemblages on the alpine forelands and supports the notion that the influence of microtopography is greater at successively higher altitudes. The separation of assemblages on the subalpine forelands is mainly related to age, with the different assemblages tending to belong to specific age ranges. The influence of microtopography, however, is evident on the young terrain of the subalpine forelands. On the alpine forelands, microtopography has a greater influence on the separation of the assemblages with most of the assemblages belonging to a particular microtopographical position. The majority of the members of assemblages, however, tend to overlap with other assemblages and, given the relative importance of microtopography on the alpine forelands, this suggests that there is an effective microtopography-related gradient of environmental

parameters prevailing across microtopographical features such as moraines and hollows. In addition, the diversity of assemblages tends to increase with age on the alpine forelands, which supports the notion that there is a microtopography-related divergence of assemblages on alpine forelands (Matthews, 1979).

5. Disturbance. Disturbance by fluvial activity, and a debris flow at Fåbergstølsbreen, is responsible for the distinct TWINSPAN site groups (8*) and (9*) and influenced the results of the DCA-ordination on axis (2) for the combined data set. It is apparent that members of the assemblages most associated with severely disturbed ground have considerable fidelity to such sites and that these assemblages are distinct. Furthermore, disturbance is not related to altitude but is related to age with greater disturbance occurring on the youngest ground. Although disturbance appears to exert a considerable influence on the vegetation pattern, especially on young terrain, it is not associated with many other micro-environmental parameters, except position and slope, and thus it can only be considered as an important micro-environmental parameter, associated largely with microtopography.

6. Environmental gradient or zone?. The relationship between different meso-environmental parameters is complex and this suggests that environmental gradients related to all three meso-environmental parameters (i.e. altitude, age and microtopography) can be discerned across the forelands. The term "environmental gradient" is preferred to the term "environmental zone" because the changes in assemblages and environment have generally been found to be gradual rather than distinct. To distinguish between the types of gradient the terms "gentle gradient" (referring to gradual change between locations) and sharp gradient (referring to relatively distinct differences between locations) are used.

7. Community or assemblage? The most distinct assemblages, on DCA ordination axis (1) are the subalpine mature/late intermediate assemblage, species group (62), and the alpine exposed lichen heath assemblage, species group (32) and, on axis (2) the most distinct assemblage is the pioneer and snowbed assemblage, species group (32). This suggests that the most distinct assemblages are influenced by microtopography, on the alpine forelands, and age, on the subalpine forelands. It is also suggested that most of the species from the other TWINSPAN "final species groups" overlap with each other to a greater or lesser extent and thus are not considered as distinct communities. Nevertheless, an ecologically meaningful change, of species belonging to different "final species groups", occurs along the rank sequences (Table 6.4) thus lending further support to the notion that there is a gradient of assemblages, as opposed to distinct communities.

8. Successional pathways. Successional pathways are proposed using the results from the TWINSPAN "final site groups". The relative influence of the meso-environmental parameters on succession, not including the pioneer stage, varies with altitude. The most important influence on subalpine forelands is age, and, on the alpine forelands, age and microtopography are important. The effects of

microtopography and disturbance override the influence of altitude at the pioneer stage. Successions in the subalpine zone are more complex, with a large number of meaningful assemblages and apparent successional regressions complicating the pathways. Little significant agreement is found between the successional pathways of assemblages on the two subalpine forelands suggesting that prediction of succession on subalpine forelands is more difficult. Despite the large number of assemblages across the low-alpine sequences, there is greater agreement between the pathways found on each of the forelands and so the successional pathways are simpler. The simplest successions are found on the mid-alpine forelands, with the least number of assemblages and the greatest between-foreland agreement in the successional pathways. These results suggest that the assemblage sequences on the alpine forelands are more predictable than those of the subalpine forelands. These points are discussed at greater length in the concluding chapter.

"The geoecological approach that has been developed aims to provide a more comprehensive, integrated and interdisciplinary treatment of the ecology of recently deglaciated terrain than has been attempted before. The areas in front of retreating glaciers are particularly appropriate for such a holistic approach because of the almost unique opportunity to define an accurate timescale"

Matthews (1992: 7)

CHAPTER SEVEN: Conclusions

7.1 Introduction

This chapter draws together results described in chapters (3) to (6), assesses them in relation to the aims of the study, and discusses the broader implications of the findings of the thesis. It is useful to repeat the aims of the study here:

1. To analyse the specific environmental parameters comprising the microtopographic gradients.
2. To describe the distribution of individual species and plant assemblages across microtopographic gradients of similar type (i.e. moraine slopes) but different ages and altitudes.
3. To interrelate the vegetational and environmental variation and hence to provide an explanation of the vegetation in terms of both successional stage and environmental factors.

The first three of the following sections respectively evaluate these aims. In addition, section 7.5, covers the major methodological implications of the thesis including the relative advantages and disadvantages of using individual foreland data sets compared to those of a large combined foreland data set; and section 7.6 points out some of the limitations of the thesis and makes suggestions for further investigation.

7.2 Controls on micro-environmental parameters

The main aims of the thesis relate to investigating the effects of microtopography on vegetation and micro-environmental patterns. However, it is also necessary to investigate further the relative effect of altitude and time, which are important mesoscale influences on vegetation patterns (e.g. Sommerville et al, 1982; Fitter and Parsons, 1987; Matthews, 1992) and are likely to have an important influence on the relative effect of microtopography.

7.2.1 Effects of altitude on micro-environmental parameters

The results from chapters (3) and (6) show that there is a decrease in total vegetation cover with increasing altitude, while evidence for frost activity and the proportions of bare ground, boulders and gravels increase (Figs. 3. 31 to 3.38 and 3.71 to 3.86). The proportion of total bryophyte cover does not display any trends with altitude and thus the ratio of total bryophyte to total vegetation cover increases with altitude. Although there are some anomalies, there is a general decrease in soil, humus and root depth with altitude and the rate of soil development is slower across forelands at the higher altitudes (Figs. 3.87 to 3.18). These figures show that the differences between soil development and total vegetation cover at different positions across the moraines (i.e. the effect of microtopography) is more visible at higher altitudes.

Although the effect of microtopography at different altitudes has not been investigated specifically, on a larger scale (e.g. spur crests and watersheds). Ellis (1980) suggests that the degree of exposure of sites (and prevailing vegetation) is a major influence on the differentiation of Brown Soils from Podzols: Brown Soils tend to develop on exposed sites (spur crests and watersheds) and Podzols tend to develop on intermediate snow sites. The present results appear to correspond with those of Ellis, although the scale is smaller and thus the differences in soil type are not so great. Furthermore, the division of the combined data set TWINSPAN site and species groups show that higher altitude groups are more closely associated with particular microtopographical positions (Fig. 6.2 and Tables 6.1-2). The evidence therefore suggests that the influence of microtopography on soil development and vegetation cover increases with altitude (Fig. 7.1), and this may be due to small-scale differential snow-lie patterns, as outlined in the following paragraph.

Using data from the Norwegian Meteorological Office it was shown, in section 1.2.2, that the alpine forelands suffer significantly higher wind speeds and lower temperatures than the subalpine forelands but they do not have a significantly different annual snow accumulation. Grace and Unsworth (1988) also found increased wind and decreased temperature with altitude, and Pearsall (1950) suggests that temperature is the most important influence on altitudinal zonation. Within the present, combined, data set (Table 7.1), the results show that snow-lie and altitude are highly significant influences on the vegetation patterns and, contrary to previous research (e.g. Burrows, 1990), low snow and high altitude are associated (Fig. 6.17). However the low snow-lie associated with altitude may not be related to actual lower snow accumulation, rather the low snow-lie (and higher altitude) may be associated with exposed ground blown clear of snow (and thus having low snow cover). It would appear, therefore, that the apparent increased effect of low snow-distribution patterns at higher altitude may be related to two main factors: a) higher winds, redistributing the snow so that the majority of sites (mid- to high-slope positions) have fluctuating snow cover and sheltered hollows accumulate snow patches; and b) lower temperatures causing longer snow duration in hollows (and thus causing a greater differential between high-slope positions and low-slope positions). This suggests that although snowfall is generally considered to increase with altitude (Burrows, 1990), higher snowfall, *per se,* is not necessarily the main influence on micro-environmental (and vegetation) patterns. Previous research suggests that snow duration (which includes growing season length and shelter from scouring winds) is the main snow-induced influence on vegetation patterns (e.g. Scott, 1974a; Knight et al, 1977; Coker, 1994). Regional meteorological data suggests that the accumulation of snow is highest on the subalpine (due to proximity to coast) and mid-alpine forelands (due to altitude, despite being continental) and lowest on the low-alpine forelands (due to continentality) which shows that there is no snow-accumulation gradient related to altitude for the glacier forelands within the present study. Although the results from the present study suggest that snow-lie decreases with altitude, the decrease in snow-lie is unlikely to result from actual lower levels of snow accumulation but from snow being blown clear of a larger proportion of the sites into accumulation areas, such as hollows and moraine bases. This emphasises the need for careful interpretation of the ordination results.

As shown in the combined data set correlation matrix (Table 6.5) those parameters that appear to be most associated with higher altitudes are: a) increased frost activity; b) lower vegetation cover; c) increased proportions of bare ground gravels; d) lower snow duration; and e) higher soil pH. Messer (1988) found that soil development patterns do not necessarily fit into easily interpreted patterns, and the results from the present study support this in that the patterns shown are complicated by the inter-relationship between different factors. It is notable, for example, that snow has been shown to decrease (see previous paragraph) with altitude when the general opinion is that snow increases with altitude (e.g. Burrows, 1990). Nevertheless, the increase in frost activity and gravels and the decrease in vegetation cover corresponds with other research findings (e.g. Burrows, 1990). Given the significant decreases in temperature and increases in exposure with altitude, exposure and temperature should also be included within the complex to form an *"Altitude - exposure - temperature - frost - vegetation cover - bare ground gravels - snow cover - pH - factor complex"* (or *"Altitude factor complex"*). Total vegetation cover also has a significant influence on prevailing environment and constituent species. Khil'mi (1962) argued that the ability of vegetation to modify the environment is proportional to vegetation biomass and the rate of metabolic activity of the component species. It is reasonable to suggest, therefore, that the canopy species comprising the woodland on the subalpine forelands, have a marked influence on the prevailing environment of species found under the canopy (cf. Sukachev and Dylis, 1964; Vetaas, 1994; Jobbágy, et al., 1996). As vegetation cover and stature decrease with altitude it should follow that the influence of the vegetation decreases so that other factors, namely snow-lie, frost activity, bare ground and pH, may become more important and this notion is supported by referring to the proposed *"Altitude factor complex"* (see Fig. 7.1). It is interesting that pH is significant within the complex and this is likely to be due to two main factors: first, the two subalpine forelands have a more acidic substrate; and second, soils develop faster on the lower altitude forelands.

The parameters that do not appear to be related to altitude are generally those factors which are related to disturbance, namely solifluction, fluvial activity, trampling and grazing (Table 6.5). However, research shows that solifluction is related to frost activity (e.g. Brink et al, 1967), which the present study shows to increase with altitude. It is therefore possible that the present method of solifluction assessment can only provide information as to the occurrence of solifluction, but not the degree of solifluction activity. Because the degree of fluvial activity across any foreland is dependent on many factors (such as precipitation, rain-shadow effects, breadth of valley and slope angle) it is likely that fluvial activity is relatively independent of altitude (as shown by the present study). However, if all other influencing factors are kept constant, fluvial activity would be expected to increase with increasing altitude due to increases in altitude-related precipitation.

Also showing no relationship with altitude is the proportion of fines, which can be divided into two components: a) the inorganic component, resulting from increased disturbance and sediment deposition; and b) the organic component, which makes up an important part of soils. As these two components are confounded, the measurement of fines have resulted in relatively meaningless data (Fig. 6.17). Moisture is not significantly related to altitude and this is possibly due to two factors: first, the precipitation in the mountainous valleys depends on rain-shadow effects as much as altitude; and second, the method of measurement (i.e. the finger test method) was only useful as a rough comparative method between different sites on each moraine. Grace and Unsworth (1988) and Burrows (1990) reported a general increase in precipitation with altitude but this suggestion is likely to be an unreliable generalisation, especially within the region. It would appear that precipitation at a particular glacier foreland is not necessarily reliant on altitude and is likely to be related to additional meso-environmental factors such as aspect and rain-shadow effect.

The effect of altitude on micro-environmental parameters, as shown by the results presented in this thesis, has been elucidated and is summarised as follows (see also Fig. 7.1):

1. The effect of microtopography is greater at higher altitudes.
2. Vegetation cover, soil, humus and root depth decrease with altitude. Frost, bare ground boulders and gravels increase with altitude. Climatic data (yearly averages taken for the 1960 to 1990 period) show wind speed to increase, temperature to decrease and snow accumulation to remain similar, with altitude. The ratio of bryophyte cover to total vegetation cover, increases with altitude.
3. Vegetation patterns are related to snow cover, but snow cover is related to wind and temperature. The distribution of snow is a more critical influence on vegetation pattern than accumulation. The decrease in snow cover, with altitude, may be due to snow re-distribution, and not due to lower snow accumulation at higher altitudes.
4. An *"Altitude - exposure - temperature - frost - Vegetation cover - bare ground gravels - snow cover - pH - factor complex"* is proposed, which may be shortened to *"Altitude factor complex"* for convenience. However, pH may not necessarily be part of this complex - especially where high altitude rocks are acidic.
5. Those factors not related to altitude are solifluction, fluvial activity, trampling, grazing, bare ground fines, and moisture, although the methodology used for fines and moisture may have been partly responsible.

7.2.2 Effects of time on micro-environmental parameters

As shown by the results, displayed in chapters (3), (5) and (6), terrain-age clearly influences the development of soil across each of the forelands. Both the individual foreland and combined data sets show that the most significant gradient is the increase in soil depth (recorded as soil staining), root depth (recorded as average depth of turf roots), humus depth and vegetation cover (Table 7.2). These results parallel those of previous workers who have studied soil chronosequences across glacier forelands (e.g. Crocker and Major, 1955; Stork, 1963; Viereck, 1966; Ugolini, 1968; Jacobson and Birks, 1980; Mellor, 1985, 1987; Messer, 1988, 1989). The relationship between soil development and time is stronger than that between soil development and vegetation cover which suggests that there are factors, other than vegetation, which influence the development of the soil (e.g. Frenot et al., 1995), although it is difficult to separate the influence of allogenic processes from autogenic influences (Miles and Walton, 1993; Whittaker, 1993). The main direct and indirect influence on the development of soil, however, is likely to be vegetation and this is corroborated by vegetation cover being significantly correlated with age and soil development on most of the forelands (cf. Khil'mi, 1962). The leaching process, an important component of soil development and soil depth on glacier forelands, relies upon three factors: first, on the time needed to leach the minerals; second, on the presence of organic acids which hasten the leaching process; and third, on the amount of precipitation. Soil depth is likely to be a more objective measure of soil development than humus or rooting depth because it has a less patchy distribution than the latter two factors and so is less reliant on the choice of site for sampling, and this is born out by soil depth generally having a stronger correlation with time than the other soil factors (see Table 5.27 and Table 6.5).

Another soil parameter that is influenced by the time gradient is soil texture, with sandy substrates predominating on young terrain and loamy substrates predominating on the oldest terrain, corresponding with Crouch (1992). The combined foreland data set shows that pH decreases with time, although the gradient is neither smooth nor strong (Table 6.5). This is not surprising as pH tends to decrease in soils with a higher organic content (e.g. Burt and Alexander, 1996) and thus is likely to fluctuate according to the organic content of the soil and this is further supported by Fitter and Parsons (1986) who found that pH decreases with age only in vegetated areas. The present sampling strategy is such that there is likely to be a variation in the organic content of soils of similar age. The individual foreland correlation results (Tables 5.17 to 5.24) show considerable differences in the correlation between pH and time with very low correlations being shown for the two subalpine forelands, the Storbreen low (2) and the Bøverbreen forelands and stronger correlations being found between time and pH on the other forelands. The low *pH - time* correlations may be due to a stronger relationship between pH and altitude (partly caused by the confounding of age and altitude, within the individual foreland data sets, but also by differences in substrate) and this is corroborated by a relatively strong correlation between pH and altitude at Fåbergstølsbreen, Storbreen low (2), and Bøverbreen.

Because vegetation cover increases with age the influence of bare ground (and associated factors) is likely to be more significant on the younger ground. For example, Anderson (1947) found that bare ground is associated with increased freezing and surface moisture, increased evaporation and high surface runoff and erosion and these findings are confirmed by Chambers et al., (1990). Figs. 3.79 to 3.86 show that the proportion of bare ground gravels is greater on the younger ground and correlation of the combined data set (Table 6.5) confirms that gravels are significantly correlated with younger ground (r = -0.46) and frost heave (r = 0.48). Whittaker (1985) found frost activity to have a strong correlation with younger ground. However, results from the present study show that the relationship between frost activity and position (r = 0.321) and altitude (r = 0.44) to be significantly correlated while only an insignificant correlation (r = -0.11) occurs between frost and time. Other variables, namely fluvial activity and late-lying snow, are also associated with bare and unstable younger substrates although the relationship between these parameters and time is complex (see section 7.2.3). Another disturbance factor, namely debris flowage at Fåbergstølsbreen (Ballantyne and Benn, 1994), was not specifically measured as an environmental parameter and could, theoretically, influence ground of any age. It is likely, however, that the occurrence of debris flows is greater near the glacier snout where the substrate is poorly consolidated, is saturated with moisture, and there is little vegetation to stabilise it. This notion is supported by Whittaker (1985) who found disturbance to be correlated with younger ground at Storbreen.

According to the results (Table 5.27, Table 6.5 and Fig. 6.17) those parameters most related to time are: soil depth (or depth of stain); root depth; humus depth; vegetation cover; and the proportion of bare-ground gravels. These factors are strongly correlated to each other and it is therefore possible to recognise an *"Age - soil - depth - root depth - humus depth - vegetation cover - bare-ground gravels - factor complex"*. These results correspond well with Whittaker (1985) but only to some extent with Crouch (1992) who found an increase in organic content and a decrease in stones but then found an increase in moisture and the proportion of fines as well as a decrease in pH with age. Crouch argued that a high soil-moisture content is related to vegetation cover, and this has long been accepted (e.g. MacKinney, 1929; Anderson, 1947; Viereck, 1966), but previous work has also shown that high soil-moisture is linked to topography and snow patterns (e.g. Billings, 1974; Flock, 1978; Kvillner and Sonesson, 1980; Birkeland and Burke, 1988; Stanton et al, 1994) and even young ground proximate to the glaciers (Zollitsch, 1969; Matthews, 1992). The complexity of the relationship between moisture and other influencing factors is emphasised by Larson and Kershaw (1974) who found that peat depth and moisture are associated on lichen heath within raised beach systems, but greater variation in moisture is found with microtopography (thus supporting the present results). Holtmeier and Broll (1994) researched the influence of tree islands and microtopography on pedoecological conditions in the forest-alpine tundra ecotone on Niwot Ridge in the Colorado Front Range, USA. They conclude that soil moisture is complex and depends on precipitation patterns as well as microtopography and snow-lie. Under dry conditions moisture is greater under trees but under humid conditions was greater outside due to interception. A strong moisture gradient with time is therefore not necessarily to be expected and the combined data set results (Table 6.5), as well as a previous work, confirm this notion.

A significant finding of the present study is that the *relative influence of age* on the environmental patterns across the forelands could be controlled by altitude. For example, the individual foreland correlation results, summarised in Table 5.27, show that at Austerdalsbreen and Fåbergstølsbreen age is the only significant meso-environmental factor on axis (1) and is also significant on axis (2) but, on all the other forelands, a combination of age and other meso-environmental factors influence the sequences on both axes (1) and (2). This suggests that the effect of age is most important on the lower altitude forelands, where microtopography is least important, and is less significant with increasing altitude, as microtopography becomes a more important influence. These findings, as far as the author is aware, are original as the effect of microtopography on succession at different altitudes has not been investigated. However, these effects are not surprising as the vegetation cover is lower (both horizontally and vertically) at higher altitudes and thus its influence as an environmental buffer is therefore reduced (cf. Khil'mi, 1962) so that succession is slower and plants adapted to environmental stress (particularly long snow duration or high exposure) persist for longer (cf. Grace and Unsworth, 1988). Additionally, the relationship between the soil factors and time also appear to be influenced by altitude: root or humus depth are the most highly correlated, with age, on subalpine and low-alpine forelands; while soil depth is the most highly correlated, with age, on the mid-alpine forelands. This could be due to the patchier distribution of vegetation at the higher altitudes thus causing the root and humus depths to be more erratic at higher altitudes. Soil depth on the other hand, is possibly a more general phenomenon on ground of a certain age, resulting from a combination of abiotic and biotic influences.

According to Tables 5.17 to 5.24 and Table 6.5, parameters that appear unrelated to time are those which are either strongly related to microtopography or those that appear to have a random distribution across the forelands. The combined data set results (Table 6.5) show that the parameters with a low correlation with age are snow-lie (r = 0.052), position (r = -0.01), dowel-heave (r = -0.02), slope (r = 0.005), aspect (r = 0.09), trampling (r = -0.04), animal influence (r = 0.06), bare boulders (r = -0.07) and bare fines (r = -0.02). Previous research found decreases with age in bulk density of fines (Crocker and Dickson, 1957; Persson, 1964; Viereck, 1966; Ugolini, 1968; Jacobson and Birks, 1980). The differences between these results, and those of the present study, may be due to the method of measurement which was not accurate enough to distinguish small differences between sites and only involved the surface expression of fines. Inorganic and organic fines were, moreover, confounded during the estimation process.

These results are further supported by the correlation results from the individual foreland data sets (Tables 5.17 to 5.24), which show that position has a low correlation with age on all forelands and snow-lie has a low correlation with age on all forelands but Fåbergstølsbreen. The individual foreland results also show that slope or solifluction are usually not correlated with either age or dowel-heave, and the relative correlation of these three factors with age does not appear to be related to altitude. Although some research has found that solifluction decreases with terrain-age (Rose, 1990), the lack of a strong association between solifluction and age corresponds with other research in the region (Whittaker, 1989; Matthews et al, in press). This result may due to the method of sampling used within the thesis (i.e. a variety of slope angles are used for each terrain-age which would cause apparent differences in solifluction, between older and younger ground, to be obscured). The lack of association between dowel-heave and age is not surprising as the relationship between frost heave and age was not strong within the present study. This latter finding contrasts with Whittaker (1989) but again may be due to the method of sampling. Matthews et al (in press) found that frost churning continues on ridge tops on older ground (corresponding with the results of the present study) which would cause apparent differences in frost activity, between older and younger ground, to be obscured. As expected, the relationship between age and trampling, grazing and aspect is also not significant, although there is considerable variation between forelands.

The effect of time on micro-environmental parameters, as shown by the results of the present thesis, is summarised as follows:

1. An *"Age - soil depth - root depth - humus depth - vegetation cover - bare ground gravels - factor complex"* was found to occur, which may be shortened to *"Age factor complex"* for convenience.
2. Soil depth, humus, root depth and vegetation cover increase with time. Soil depth may be a more objective measure of soil development than root or humus depth. Frost was found to decrease with time but was found to be more related to microtopography. pH decreased slightly with age but the relationship is not consistent.
3. The confounding of age and altitude was identified within the individual data set results.
4. The significance of age, as an influence on the distribution of species along DCA ordination axes (1) and (2), appears to be greatest on the subalpine forelands and least on the mid-alpine forelands, according to the individual foreland results.
5. Factors that have a low correlation with age are snow-lie, position, dowel-heave, slope, aspect, trampling, animal influence, bare ground boulders and bare ground fines.

7.2.3 The relationship between microtopography and micro-environmental parameters

In general, the individual foreland results support the hypothesis that microtopography has an important influence on vegetation pattern although it is not a highly significant influence on the subalpine forelands (see Table 5.27). On most of the alpine forelands high-slope positions tend to be correlated with low snow cover, dryness, frost heave and dowel-heave and to a certain extent bare fines. Low-slope positions tend to be associated with fluvial activity, higher vegetation and bryophyte cover, and more developed soils. The so-called *"Microtopographic (exposure-moisture-snowmelt) factor complex"* (*sensu*: Whittaker, 1985), is apparent on most forelands. The combined foreland results (Table 6.5) suggest that exposure, snow duration, frost activity, moisture and fluvial activity are related to microtopography and, for the purposes of this study, these parameters are included in a *"Microtopography - exposure - snow duration - frost activity - moisture - fluvial activity - factor complex"*. However, the DCA ordination results also show that the relationship between age and microtopography, and altitude on the ordination axes shows a considerably more complex relationship between elements of the *"Microtopographic factor complex"* than that suggested by Whittaker (1985).

Previous research, reviewed in chapter (1) (section 1.3.2) shows that microtopography has a significant effect on the pattern of micro-environmental factors and this in turn influences the microscale pattern of vegetation and soils (e.g. Billings and Bliss, 1959; Elven, 1978; Vetaas, 1986; Komárková, 1993; Walker et al, 1993; Stanton, et al, 1994). In the literature the parameters, most closely related to microtopography and thought to have the greatest influence on vegetation patterns and soils, are snow-lie, exposure (which includes temperature) and the nutrient status of the water supply (e.g. Miller, 1982; Stanton et al, 1994). However, other parameters, including disturbance factors (e.g. fluvial activity, solifluction, frost activity and animal activity), substrate texture, clast size, and aspect, also have an important influence and can be related to microtopography (see section 1.3.2). By referring to Table 5.27 and Table 6.5, the results from the individual foreland and combined data sets, within the present study, generally support those of the previous work by showing that the factors most related to high-slope positions are short snow duration, low moisture levels, higher proportions of gravels and boulders, and greater disturbance from frost activity (cf. Nordhagen, 1943; Vetaas, 1986; Matthews et al, in press). Solifluction, as expected, is greater on the slope sides and fluvial activity is greatest at the bases of the moraines (see Figs. 3.47 to 3.62).

The temperature results, described in section 3.6.3, confirm previous work which suggests that microtopography has a significant effect on temperature (e.g. Billings, 1974; Vetaas, 1986; Grace and Unsworth, 1988). Interestingly, the data show that there is no simple gradient in annual mean temperature between high-slope and low-slope positions on the moraines, although lower temperature means occur on high slope positions during winter. The main effect of microtopography on temperature variations appears to be on the range of temperature fluctuations and extremes during the winter and summer: the greatest fluctuations are found on the high-slope positions. These latter results contrast with Vetaas (1986) who found higher temperature means on the high-slope positions. However, Vetaas' results were taken during a short ten-day summer period and, as he admits, this may have been due to the calm and sunny weather that prevailed during the measurement period.

In winter, the present results suggest that the differences in the temperature fluctuations, across the moraines, are associated primarily with differences in snow duration: high-slope positions on the moraines emerging from snow cover long before low-slope positions (Figs. 3.20 – 3.25). During the summer, the differences are likely to be associated with differential wind exposure and differential solar heat absorption caused by differences in vegetation cover. The differences, between high-slope and low-slope positions, are also experienced by the distal and proximal sides of the moraine. The proximal sides have greater fluctuations in temperature during the year, they have lower average winter temperatures, and they emerge from the snow at an earlier date. The temperature data show that microtopography has a significant effect on prevailing temperatures, largely as a result of differential snow-lie and/or exposure, and these results provide additional elucidation for those studies that emphasise the importance of snow duration on vegetation patterns (e.g. Evans and Fonda, 1990; Benedict, 1990a, 1990b, 1991; Auerbach and Halfpenny, 1991; Kudo, 1991, 1992; Kudo and Ito, 1992; Komárková, 1993; Scherff, et al., 1994; Stanton, et al, 1994). The temperature results support those of Evans and Fonda (1990) who found that soil temperature parallels the time of snow release. Furthermore, the work of Auerbach and Halfpenny (1991) is also supported in so much as they showed that winter ground temperatures are least stable where snow cover is least stable. The results supplement the previous work (most of which have not made any temperature measurements) by indicating that the influence of temperature, on the prevailing vegetation patterns, arises from differences in the *range* and *extremes* of temperature fluctuation and not from differences in average temperatures *per se*.

Much of the previous research, reviewed in chapter (1), simplifies the influence of microtopography because of the type of site being studied. For example, those researchers investigating snowbeds tend to emphasise the limiting effects of long snow duration on the vegetation growth on older ground (e.g. Benedict, 1990a; Stanton et al. 1994) while those investigating glacial moraines emphasise the limiting effects of exposure on the vegetation growth on older ground (e.g. Elven, 1975; Whittaker, 1985; Vetaas, 1986). Those studying vegetation succession tend to suggest that the effect of microtopography is not important on young terrain and is likely to be most important on ground of intermediate age, with an intermediate vegetation cover (e.g. Jochimsen, 1963, 1970; Zollitsch, 1969; Elven, 1975, 1978; Vetaas, 1986; Schubiger-Bossard, 1988). In contrast, the present results differ from most of the previous work in the following four ways: a) the effect of microtopography is seen to be important on all terrain-ages; b) high-slope as well as low-slope positions may have a limiting effect on vegetation and soil development (but see Scott, 1974); c) the way in which microtopography is related to age is not consistent between forelands (see Fig. 7.2); d) differences in the relative influence of microtopography on the vegetation patterns are related to both age and altitude. These complicated relationships are described in Fig. 7.2 and are discussed in greater detail in the following paragraphs.

The individual foreland correlation results (Tables 5.17-5.24 and Table 5.27) show that on the subalpine forelands only the *"Age factor complex"* is important on axis (1). The effect of microtopography on the alpine forelands is more important than on the subalpine forelands, so that members of the *"Microtopographic factor complex"* are a significant influence on both axes (1) and (2). On most of the low-alpine forelands, on DCA axis (1), high-slope positions are related to younger ground, suggesting that the exposed crests of the moraines are likely to be the most disturbed sites with the lowest vegetation cover. On DCA axis (2) the opposite is true with the lowest positions, disturbed by fluvial activity or late-lying snow, being related to the younger ground. From this it is suggested that exposure is the most important microtopographic effect on the low-alpine forelands while fluvial activity or late snow-lie are of secondary importance. In contrast, on the mid-alpine forelands, low-slope positions are related to the younger ground and the high-slope positions are related to the mature lichen heaths on DCA axis (1). On DCA axis (2) the high-slope positions are related to the younger ground and the low-slope positions are related to mature late-snow heath. From this it may be suggested that late-snow-lie (and perhaps fluvial activity) is a more influential microtopographic effect than exposure on the mid-alpine forelands. It should be noted, however, that although late-snow duration and fluvial activity appear to be the dominant microtopographic influence on mid-alpine forelands it is likely that exposure is also an important influence. This notion is supported by the high eigenvalues for both axes (1) and (2) shown by the mid-alpine ordination results. The relationship between the most important environmental parameters and DCA axes (1) and (2) are summarised, for both the individual and combined foreland data sets, in Table 7.1. The relationships, described above, can be seen by looking at the relative location of the age-related and microtopography-related parameters at either end of each axis.

As can be seen in Table 7.1 the combined data set ordination results on DCA axis (1) show that high-slope positions are related to the poorly vegetated younger ground, with a high proportion of bare-ground gravels and boulders, poor soil development, low snow duration, high frost activity and high pH (at higher altitudes). Low-slope positions, on axis (1), are related to the well-vegetated, oldest terrain with well-developed soils, low proportions of bare ground and longer snow duration during the winter period (at lower altitudes). On axis (2), low-slope positions are related to the younger ground, with high fluvial activity, long snow duration, high proportions of bare ground boulders and an easterly aspect. The high-slope positions, on axis (2), are related to the well-vegetated mature heaths with low snow duration, well-developed soils, low moisture and a westerly aspect. From this it would seem that the overall influence of microtopography across the forelands is dominated by relative exposure, although the limiting influences of late snow-lie and fluvial activity, on vegetation patterns, are also significant. It should be noted that the effects of aspect, shown on the combined foreland axis (2) have been ignored because: a) the different orientations of the moraines and forelands within the present study make objective between-foreland comparisons difficult; b) the individual foreland data tend to show little significance with respect to the aspect data; c) the results are contradictory - easterly aspect, on axis (2), is associated with longer snow-lie, fluvial disturbance and bare ground, and not with greater vegetation cover, as would be expected from aspect-related snow-distribution patterns (e.g. Evans et al, 1989). It is therefore possible that the results concerning aspect may be meaningless. Fig. 7.2 summarises the relative influence of microtopography with age, on both axes (1) and (2), for the combined data set (see also Fig. 6.16).

The effect of microtopography on micro-environmental parameters, as shown by the results of the present thesis, has been elucidated and is summarised as follows:

1. A "*Microtopography - exposure - snow-lie - frost - moisture - fluvial activity - factor complex*" occurs.
2. The relationship between microtopography and micro-environmental parameters is complex: low vegetation cover and soil development can be associated with both high- and low-slope positions. Exposure is the most important microtopographic effect on the low-alpine forelands, significant on DCA axis (1)) while late snow-lie is quite an important microtopographic effect (significant on DCA axis (2)). Late snow-lie is the most important microtopographic effect on the mid-alpine forelands (significant on axis (1)), although exposure is also an important microtopographic effect (significant on DCA axis (2)). The combined data set shows that exposure is, overall, the most significant microtopographic effect across all the forelands.
3. High-slope positions are related to low snow duration; low moisture; increases in the proportions of gravels and boulders; and increases in frost activity. Solifluction is greatest on slope sides, while fluvial activity is greatest at the bases of moraines.

4. The effect of microtopography, on temperature, is to influence the degree of temperature fluctuation: high-slope and proximal positions experience greater fluctuations in winter and summer.
5. The review (in chapter (1)) showed that microtopography-related parameters are snow-lie, exposure, nutrient-rich water supplies, disturbance factors, texture, clast size and aspect. These findings are in general agreement with those of the present study. However, the results, of the present study, differ from the previous work in a number of ways: a) microtopography is an important influence on all terrain-ages; b) high- and low-slope positions can have a limiting effect on vegetation and soil development; c) age is not related to microtopography in a consistent manner, from foreland to foreland; d) the relative effect of microtopography on vegetation patterns is related to altitude and age.

7.3 Effects of environmental factors on vegetation patterns

This section includes a discussion of the distribution of TWINSPAN "final species groups" in relation to the factor complexes. The intention is to highlight the most representative assemblages-types associated with microtopography, terrain-age and altitude (and their respective factor complexes) by using the TWINSPAN "final species groups". The TWINSPAN "final site groups" will be used in the more general discussion of successional sequences in section 7.4. The combined foreland data is used in the discussion of the relative influence of altitude on vegetation patterns. However, both the combined and individual foreland data sets are used for discussion of the relative influence of age and microtopography because the combined data set results are more difficult to interpret.

7.3.1 The *"Altitude factor complex"*

The ordination results for the combined data set, summarised in Table 7.1, show that the positive end of axis (1) is most associated with low altitude, vegetation cover, root depth, soil depth, humus depth and older terrain and suggests that vegetation and soil develop faster at lower altitudes. These results correspond with much of the previous research (e.g. Sommerville et al., 1982; Grace and Unsworth, 1988; Burrows, 1990). The TWINSPAN "final species groups" (Table 6.4) display a clear altitude gradient, along the DCA ordination axes, from the mid-alpine lichen heaths, at the negative end of axis (1), to the low-alpine lichen and low-growing shrub heaths, at the centre of the axis, to the subalpine woodland at the positive end of the axis. Superimposed upon the altitudinal gradient are time and microtopography gradients which are discussed in sections 7.3.2 and 7.3.3.

The ordination results, described in chapter (6), show that the "final species group" assemblages are generally not faithful to one particular altitudinal zone (i.e. mid-, low- and subalpine) but occur in two out of the three zones (see Fig. 6.15). In fact only three of the assemblages are exclusive to one altitudinal zone and this suggests that there is an altitudinal gradient of assemblages. However an interesting pattern emerges by examining the relative location of particular assemblages shared between two altitudinal zones.

All the assemblages, dominant in the mid-alpine zone, are found in one other altitudinal zone. It appears that assemblages found at low-slope positions, in the mid-alpine zone, are found at high-slope positions or younger ground in the low-alpine zone. In the previous section it was shown that conditions become more extreme with increases in altitude (e.g. Green and Harding, 1980; Crawford, 1989; Burrows, 1990). It is therefore suggested that as temperature drops and wind increases the assemblages found on high-slope positions or younger ground, at lower altitudes, can only prevail on low-slope positions and older ground, at the higher altitudes. The only exception is an assemblage ("final species group" 30) found widely across older and intermediate sites at low-alpine altitudes. Species group (30) is found on low-slope positions at the subalpine altitude, possibly due to the strong modifying effect of the woodland canopy on the environment below (Khil'mi, 1962).

These patterns therefore suggest that most of the assemblages span across several altitudinal zones and change the type of site that they occur in, possibly according to the prevailing environment (both biotically and abiotically conditioned) found at that site. It is likely that the members of each of the assemblages have certain environmental requirements but that it is not possible to define most assemblages as being representative of certain types of microtopographic position (i.e. toe-slope, crest, etc.). This conclusion supports Matthews and Whittaker (1987) who proposed that similarities in population pattern between species suggests common roles within succession and responses to resources. Given that the prevailing environmental conditions at a site may determine the assemblage found at that site, it is possible that with detailed environmental monitoring it may be possible to draw a relationship between an assemblage (or at least some of dominant members) and its environmental range. These results support the "*Dynamical Systems Perspective*" outlined by Roberts (1987: 30), which proposes that environment can influence vegetation, but vegetation can influence environment, and each species will grow within an environmental subspace "*delimited at its perimeter by the minimum requirements of the species*".

It is well known that assemblages change with altitude (e.g. Gjærevoll and Jørgensen, 1978; Matthews, 1992) and Matthews suggests altitude is the most important influence on succession. Roberts (1987) suggests that the relationship between vegetation and environment is dynamic and this is particularly well illustrated by the effect of altitude on the vegetation and environmental patterns. Vegetation cover (and biomass) decreases with altitude and so the effect of vegetation on the environment is less at higher altitudes. However, environmental factors, such as lower temperatures and higher wind speeds, are likely to be the cause of the changes in vegetation cover and plant biomass. Therefore an endless *Environment → Vegetation → Environment → Vegetation .....* chain of influence can be seen, which confirms Robert's (1987: 32) hypothesis that "*the relationship between vegetation and environment is relational rather than functional*". The present results, outlining the combined effects of altitude and microtopography using a comparable methodology, and summarised in Fig. 7.3, are, as far as the author is aware, original.

The likely influence of the *"Altitude factor complex"* on vegetation patterns as shown by the results of the present thesis may be summarised as follows:

1. The most important influence on species separation on the combined foreland DCA ordination axis (1) is altitude and the *"Altitude factor complex"* so that mid- and low-alpine assemblages occur at the positive end and subalpine assemblages at the negative end. The positive end, of axis (1), is associated with high vegetation cover and soil development; the negative end is associated with high frost activity, exposure (low snow cover) and bare ground.
2. The TWINSPAN "final species groups" are generally found in two altitudinal zones, with lower altitude high-slope exposure-tolerating assemblages being found on more sheltered low-slope sites at higher altitudes. This suggests that environmental conditions determine the pattern of assemblages so that assemblages are not faithful to particular microtopographical positions at different altitude.
3. Detailed environmental monitoring, to determine the range of a distinct assemblage or its dominant member-species, could provide a basis for the use of some assemblages as environmental indicators.

7.3.2 The *"Age factor complex"*

According to the results from the combined data set (Fig. 6.17 and Table 6.5), age of substrate is, after altitude, the most important influence on the prevailing environment and vegetation patterns. This supports Elven (1975, 1978), Vetaas (1986), Whittaker (1985, 1989) and Crouch (1992), who, in their work on glacier foreland chronosequences, found age to be the most significant influence and microtopography to be a lesser, but still significant, influence. In section 7.2 it was proposed that the relative influence of age is greater on the subalpine forelands than on the alpine forelands and that the effect of age decreases as the effect of microtopography becomes more important with increasing altitude. This pattern is supported by the patterns of assemblages described by both the individual and combined data sets and is summarised in Fig. 7.3. This is also clearly seen by referring to Fig. 6.15 where the most age-related assemblages can be determined by referring to their preferred site-type - i.e. most of the subalpine assemblages are defined by age of ground while most of the mid-alpine assemblages are defined by microtopography and age. However, one important element of the relative influence of age on the prevailing environment was not detected by the examination of the environmental results in the previous section. The pioneer assemblage, "final species group" (35), (Fig. 6.15) occurs on young terrain at all three altitudes, and also on some low-slope positions on older ground. From this it is suggested that age of ground is the most important influence on the composition of pioneer assemblages and this hypothesis is further supported by the occurrence of this assemblage only on older ground undergoing some form of severe disturbance. The distinctness of this assemblage also discredits the "initial floristic composition" (IFC) model (Egler, 1954), which suggests succession is a change of dominance of species that colonise simultaneously.

The present work supports those authors who recognise pioneer assemblages as comprising plant species which are specially adapted to the colonisation of environmentally stressed terrain (e.g. Walker et al., 1986; Chapin, 1993; Chapin et al., 1994) and the present results suggest that only a relatively small group of plant species are so adapted. Pioneers are adapted to environmental stress (including fluctuations in temperature, moisture and exposure), but are not adapted to competition (e.g. Elven and Ryvarden, 1975; Bazzaz, 1987; Walker, 1993; Whittaker, 1993). It is logical that the pioneers are found at a wider range of altitudes than other species because, as shown by the results (see chapter 3), all the pioneer (or disturbed) ground suffers relatively similar conditions (only more extreme at higher altitudes). This is supported by Bazzaz (1987) who suggests that disturbance selects for broad niches due to larger fluctuations in resources, water, light, and temperature than in later successional stages. In contrast, the results (see chapter 3) show that the differences in microclimate found in a subalpine birch woodland are more stable (in terms of exposure, snowlie and moisture) than those found on the mature midalpine lichen heaths. It therefore follows that, as proposed in Fig. 7.3, the influence of altitude on assemblage make-up can be considered to increase with age.

These results emphasise the distinctness of the pioneer assemblages (cf. Rydin and Borgegård, 1991).. Furthermore, the individual foreland results suggest that microtopographically induced differences in microenvironmental factors (such as moisture, substrate texture and frost activity) on the youngest terrain are enough to cause some differentation of pioneer assemblages. Faegri (1933) also noted that substrate texture and moisture had a significant influence on pioneer assemblage distribution but, despite this, he suggested that members of different pioneer assemblages are interchangeable and therefore assemblage differentiation does not start on pioneer terrain. In many ways the results of the present study agree with Faegri in so much as the members of pioneers (as well as all other assemblages) are considered, by the present author, interchangeable. Furthermore, the occurrence of only one pioneer assemblage within the combined data set would suggest that the pioneer assemblages have interchangeable members. Nevertheless, all assemblages are considered to have interchangeable members and interchangeability is not considered as evidence for lack of differentiation. Elven (1975) also suggests that differentiation does not occur on the youngest terrain, according to microtopography, despite his proposition that early pioneer assemblages occur on flushes and also early extreme snowbeds (thus suggesting microtopography-related differentiation). Despite previous claims of non-differentiation on the youngest terrain, the overall pattern (including the individual foreland data sets) from the present study suggests that pioneer assemblages (as well as the later assemblages) differentiate, at least to some extent, according to microtopography. It is therefore proposed that factors (in addition to time), relating to microtopography and/or disturbance, have some influence on the distribution of pioneers plants. This premise is supported by Stöcklin and Bäumler (1996) who found that pioneer seeds have a high germination success but depend on microtopography and moisture.

By referring to Tables 4.10 and 5.26, and Figs. 4.18-92, the relationship between terrain-age, the assemblages and the *"Age factor complex"* can be seen. At Austerdalsbreen and Fåbergstølsbreen, the majority of the TWINSPAN "final species groups" are concentrated on less than four out of six moraines of a particular age-range (i.e. young, intermediate, or old terrain). These findings contrast with Vetaas (1986) who suggested that the majority of species grow on all the moraines at Bødalsbreen. DCA ordination of the subalpine data sets shows that age and the *"Age factor complex"* is important on both axes and position is only important on axis (2) at Austerdalsbreen. The present results also appear to differ from Fægri (1933), studying at Nigardsbreen, and Vetaas (1986), studying at Bødalsbreen, who found that cryptogams and dwarf shrubs colonise the bare substrate (rather than the combination of grasses, herbs and total bryophytes, found by the present study). However, the present results agree with them with regard to an intermediate heath phase being slowly overgrown by *Betula pubescens* shrubs and, on the oldest ground, by *Betula pubescens* woodland, at least at Fåbergstølsbreen. However at Austerdalsbreen, the oldest terrain is dominated by a *Vaccinium myrtillus* heath (Fig. 6.13), and not *Betula pubescens,* possibly due to a heavier past grazing regime than that found at Fåbergstølsbreen (J.R. Petch, pers. comm.). This suggests that the assemblages found at all successional stages on the subalpine forelands may be more difficult to predict than previous work has suggested (e.g. Fægri, 1933; Vetaas, 1986) and is dependent on a wide range of disturbance factors. Microtopography may have some influence but only within a narrow age-range.

According to Tables 4.10 and Figs. 4.39-69, the majority of the TWINSPAN "final species groups", on the low-alpine forelands, are found on at least four out of the six moraines suggesting that age is less important than on the subalpine forelands and many of the assemblages have separated according to a combination of microtopographic effects and age. However, the low-alpine assemblages tend to be faithful to particular terrain-ages, and it is suggested that age is a more important influence on the assemblage location than position and this supports previous work in the region (e.g. Whittaker, 1987; Crouch, 1993). This is born out by the relative importance of age and the *"Age factor complex"* on axis (1) of the low-alpine DCA ordinations shown in Table 5.26. At Svellnosbreen, position appears to be more important on axis (1) than age, but it is suggested that this is due to a number of causes including: a) the foreland is steep; b) fluvial activity is severe; c) the altitudinal range is large; d) the oldest terrain consists of a gully. Despite this, the results of the ordination on axis (2), at Svellnosbreen, are related to age and the eigenvalues for both axis (1) and (2) are relatively high (0.442 and 0.357 respectively) suggesting that the sequences on both axes are meaningful. The mature assemblages on the low-alpine forelands fall into two categories: the mature heath assemblages; and the snowbed or late-snow heath assemblages. The intermediate ground assemblages fall into three main groups: the exposed lichen heath assemblages; the intermediate widespread heath assemblage; the late-snow intermediate heath or snowbed assemblages. The pioneer and younger ground, at Svellnosbreen, is represented by the outliers *Cerastium cerastoides* and *Deschampsia alpina*, where fluvial disturbance is greatest, but otherwise pioneer species are found on older ground, where disturbed. These results are in line with Matthews (1979d), and confirmed by Matthews and Whittaker (1987), who proposed a three-stage low-alpine sequence from a pioneer assemblage (postulated to be the same as the mid-alpine *Cerastium cerastoides - Poa alpina* assemblage) to an intermediate, *Phyllodoce caerulea - Salix spp,* assemblage, proceeding to a well-developed heath, *Betula nana - Vaccinium spp,* assemblage. However, it can be seen that this simplistic scheme is complicated by the effect of microtopography.

According to Table 4.10 and Figs. 4.70-92, many of the TWINSPAN "final species groups", at mid-alpine altitudes, are found across a wide range of moraines and it is clear that position is important on all terrain-ages. The mature and intermediate assemblages can be divided into three main categories: lichen heath; late-snow or widespread heath; and snowbed. The young terrain is less differentiated in the mid-alpine zone and is dominated by one pioneer assemblage comprising many of the same pioneer species found at lower altitudes. Nevertheless members of later assemblages, made up especially of snowbed species, are also found at low-slope positions on the youngest terrain. Despite the obvious importance of position on the mid-alpine foreland, Table 5.26 shows that age and the *"Age factor complex"* is still the most important influence on the separation of the assemblages on axis (1) of the individual data sets, and this suggests that age is the most important influence across each of the individual forelands. Matthews (1992: 221), comparing the work of various authors, found that successions within the alpine zone tend to have *"fewer stages and smaller vegetational differences between pioneer and mature stages. Pioneer communities have the same physiognomy and some of the same species as pioneer stages in the subalpine zone"*. These suggestions are supported by those of the present study, although the present results suggest that there are greater similarities between pioneer assemblages at the subalpine and alpine altitudes than there are between the pioneer and mature assemblages at the mid-alpine altitude. Matthews and Whittaker (1987) suggest that the pioneers, within the low-alpine heath succession, are completely replaced by heath species on the older ground, whereas within the mid-alpine snowbed succession the pioneers persist to the oldest ground. However, the results from the present study suggest that disturbance, for example caused by long snow duration, fluvial activity, wind abrasion or frost activity, allows the persistence of pioneer species on the older ground. This suggests that disturbance creates "younger ground" disturbed sites on the older ground where pioneer species can colonise. Such disturbed-site assemblages on the older ground have more in common with pioneer assemblages and should be considered separate from the dominant mature assemblages found on the older terrain. The results suggest that the pioneer species exist as a distinct assemblage, even at the mid-alpine altitude, and generally occur on disturbed or newly exposed ground.

The likely influence of the *"Age factor complex"* on vegetation pattern, as shown by the results of the present thesis, are summarised as follows:

1. The *"Age factor complex"* appears to be the most important influence on vegetation patterns across most of the forelands. Its influence is greatest on the subalpine forelands and least on the mid-alpine forelands
2. Subalpine TWINSPAN "final species groups" proceed from cryptogams, herbs and grasses to taller shrubs and trees. The sequence of assemblages may, however, be modified by disturbance. Microtopography has a consistent influence only within a narrow age-range, so that few microtopography-influenced assemblages occur across a sequence of moraines. It is difficult to make a

detailed prediction of subalpine assemblage composition on the basis of research at other locations of similar altitude.

3. Low-alpine TWINSPAN "final species groups" are located across a broader age-range, according to microtopography, than on the subalpine forelands, i.e. many of the assemblages occur across a sequence of moraines at particular slope positions. The simplistic scheme outlined in Matthews and Whittaker (1987) is augmented by the present study's investigation of microtopographic effects on vegetation patterns. Uncertainties at Svellnosbreen (i.e. the dominance of microtopography on DCA axis (1)) may be caused by severe fluvial activity on the young terrain and the sampling of a gully, on the oldest terrain, rather than a till ridge, which may have exaggerated the influence of fluvial activity in the individual foreland data set.
4. In the mid-alpine zone, the importance of time as an influence on the separation of TWINSPAN "final species groups" has diminished further. The pioneer assemblages have separated from a combination of the intermediate and mature assemblages. Many of the assemblages, which have separated from the pioneers, occur across a large number of moraines on older and intermediate terrain, at particular microtopographical positions.
5. Pioneer assemblages occur on young ground and their existence is most influenced by terrain-age and the "*Age-factor-complex*". However, pioneers are also associated with disturbed sites on older ground. Terrain-age is the most important influence on the pioneer TWINSPAN "final species groups" (more important than altitude): pioneers tend to be faithful to young ground and the combined foreland TWINSPAN "final species group" (35) occurs on the youngest terrain in all three altitudinal zones.

7.3.3 The *"Microtopographic factor complex"*

The results of the present study do not indicate any noticeable directional trend in the relative influence of microtopography on assemblage composition through time, so that microtopography is an important influence on all terrain-ages, including the youngest terrain (see previous section for discussion). However, the influence of microtopography on vegetation patterns appears to increase with altitude (see section 7.2.1). It is suggested that exposure is, in general, a more significant microtopographic effect on the vegetation patterns than late-lying snow, but by referring to the individual data sets (Table 5.26) it can also be seen that late-lying snow becomes more important, than exposure, at higher altitudes. No other study has attempted to elucidate the relative influence of microtopography-related exposure and snow-lie with altitude and so these results cannot be upheld by reference to previous work. However, as discussed in section 7.2.1, greater proportions of terrain at higher altitudes are blown clear of snow and snow accumulates in hollows for long periods. It would be logical that the assemblages at higher altitudes may therefore be better adapted to exposed conditions with a short snow duration_(chionophobous species) (cf. Jonasson, 1981). The gradient between the exposed ridges and snow-bound hollows is therefore likely to be much steeper and few species can survive in the hollows that suffer long snow-duration (hence snow cover is a more limiting influence than exposure). Conversely, at lower altitudes, snow duration in the hollows has a shorter duration and therefore the sheltered conditions in the hollow is beneficial for plant species (hence snow cover has a more positive influence at the lower altitudes). This suggestion is partly supported by Scott (1974a) who emphasised the limiting effect both of exposure and of late snow duration on alpine plant community composition and distribution. These results suggest that the relative effect of microtopography on vegetation patterns tends to increase with altitude and furthermore the way in which microtopographical controls act upon the vegetation patterns change with altitude (see Fig. 7.3 and Table 5.26).

According to Tables 4.10, 5.26, and Figs. 4.18-38, the subalpine TWINSPAN "final species groups" (individual data sets) are only weakly associated with microtopographic position and these include the snowbed assemblages, related to low-slope or fluvially disturbed sites, and a few lichen heath assemblages on the most exposed crests of the moraines, with the shortest snow duration, low moisture and a high proportion of boulders and gravels. Although the time sequence, from the present study, partly corresponds with that of Vetaas (1986), results corresponding to microtopographic-related patterns contrast with those of Vetaas in that he found wind direction to be an important influence across Bødalsbreen foreland, with significant differences in assemblage patterns between the distal and proximal sides of the moraine. In addition, he found that the *Betula - Vaccinium* assemblages expand up the moraine slopes, more slowly on the proximal sides, suggesting a greater microtopographic influence on the subalpine forelands than that found in the present study. It may be that the sampling design of the present study, which used the line of optimally developed vegetation across each moraine, may have caused the differences between the present study and Vetaas' work. Sukachev and Dylis (1964) suggested that the ability of plant species to modify their environment is proportional to their biomass, stature and metabolism. In other words, canopy species, or large shrubs, are likely to cause the greatest modifications to their environment and it is likely that this influence would nullify the influence of microtopography where the vegetation is dense (cf. Birks, 1980). It is possible that the transects used for sampling on the subalpine forelands within the present study were better vegetated than those used in Vetaas' study.

On the low-alpine forelands (Tables 4.10, 5.26; and Figs. 4.39-69) microtopography appears to be important on all terrain-ages, although the assemblages tend to be faithful to particular terrain-ages. This causes a larger number of assemblages than those found at the mid-alpine altitude and many of the assemblages (and their site-type) correspond with previous regional research (e.g. Matthews, 1976; Elven 1978; Whittaker, 1985; and Crouch, 1992). On the oldest and late intermediate terrain the assemblages are divided into two categories, according to position: a) the mature heath assemblages (high-slope); and b) snowbed assemblages or late-snow heath assemblages (low-slope) (cf. Nordhagen, 1943). On the intermediate-aged ground the assemblages are divided into three assemblage-types, according to position: a) exposed lichen heath assemblages (high-slope); b) the intermediate widespread heath assemblages (general and mid-slope); and c) the late-snow intermediate heath or snowbed (low-slope). Low-alpine pioneer species correspond with the distinct pioneer assemblages described for the other altitudinal zones as well as the combined data set (TWINSPAN species "final groups"). According to the DCA ordination centroid plots (TWINSPAN "final species groups") for the low-alpine forelands (Figs. 5.27 to 5.29), relative exposure has a more significant limiting influence on the vegetation cover than late-lying snow on axis (1): the crests of the 1900 through to the 1750 moraines comprise exposed lichen heath assemblages which are associated with low vegetation and the younger ground. This therefore suggests that many of the mature low-alpine assemblages are not tolerant of high winds and exposure. However, some of the moraine bases suffer disturbance, from fluvial activity and/or late-lying snow, so that members of pioneer snowbed assemblages, associated with low vegetation cover and younger ground, are also found on low-slope positions of the 1900 through to the 1750 moraines. The limiting influence of fluvial activity and late-snow-lie is prominent on DCA ordination axis (2) on the low-alpine forelands.

On the mid-alpine forelands (Table 4.10, 5.26, and Figs. 4.70-92) the relationship between microtopography and assemblage composition and structure is much simpler (cf. Archer, 1973; Elven, 1975; Matthews, 1979a,b; Sommerville et al., 1982). Although vegetation cover increases with age, the assemblage composition on the oldest and intermediate terrain is fairly similar, with many of the assemblages occurring across a sequence of moraines. The assemblages that tend to be found on the intermediate ground on low-alpine forelands are dominant across the mid-alpine forelands, including the oldest terrain. In agreement with Elven (1975, 1978) on the oldest and intermediate terrain, there are three main categories of assemblage which have separated according to position: a) lichen heath (high-slope); b) late-snow or widespread heath (general or mid-slope); and c) snowbed (low-slope). A widespread, *Stereocaulon spp - Solorina crocea,* assemblage is found across the forelands on most sites. Elven (1978) suggests that *Stereocaulon alpinum*, along with *Salix herbacea* is widely distributed, but especially ground with a late snow melt, which corresponds with the present results. The lichen heath assemblages are most strongly associated, on DCA axis (1), with the oldest terrain and a short snow duration, which suggests that the mature assemblages at the mid-alpine zone are well adapted to high winds and exposure. A late-snow or widespread heath assemblage, which is especially dominant on the less exposed oldest terrain, and snowbed assemblages occur on sheltered low-slope sites. The assemblages appear to be strongly differentiated, according to microtopography, and long snow duration (and fluvial activity), rather than exposure, is considered to have the greatest limiting microtopographical effect on the vegetation (see section 1.3.2). The young terrain is represented by species found on the youngest ground at the lower altitudes. These findings are partly in line with those of Matthews (1979d) who proposed a 2-stage succession for the mid-alpine zone at Storbreen consisting of a pioneer, *Poa alpina - Cerastium spp,* assemblage proceeding to a snowbed, *Salix herbacea - Polygonum viviparum,* assemblage. However, it is suggested that Matthews' proposal is too simplistic, as he did not take microtopography into consideration - i.e. within the present study the pioneer assemblage is replaced by three assemblage types at the mid-alpine altitude.

The likely influence of the *"Microtopographic factor complex"* on vegetation pattern, is summarised as follows:

1. Microtopography appears to be important on all terrain-ages, contradicting previous researchers who suggest that it is most important on ground of intermediate age. However, the relative importance of microtopography appears to increase with altitude.
2. Age and microtopographic effects are confounded, on DCA axis (1) and (2), thus complicating the relationship between these factors and the vegetation patterns.
3. On subalpine forelands, assemblages are largely defined by age - i.e. they are either characteristic of the oldest terrain; intermediate terrain; or young terrain.
4. In the low-alpine zone the assemblages tend to be defined by a combination of age- and microtopography-related factors. For example, on the oldest terrain the dominant assemblages are: heath assemblages on high-slope positions; and late-snow heath and snowbed assemblages on the low-slope positions. Exposure has the strongest limiting microtopographical effect on the low-alpine assemblages.
5. There are fewer assemblages in the mid-alpine zone and they tend to occur across a broad age-range, at particular microtopographical positions. For example, lichen heath assemblages occur on the high-slope positions on older terrain, while late-snow heath and snowbed assemblages occur on the low-slope positions on older terrain. The most important limiting influence on the vegetation patterns, at the mid-alpine zone, is long snow duration.

7.3.4 Other influences on vegetation pattern

According to the DCA centroid plots (Figs. 5.1-16 and 6.17-18), for both the individual foreland data sets and the combined data sets, another important influence on the vegetation patterns is fluvial activity. The results show that fluvial activity is prevalent, at low-slope positions, at the base of the three youngest moraines on six out of eight of the foreland sequences and it is prevalent at the base of older moraines on five out of eight of the foreland sequences (see Figs. 3.55-62). Species, generally associated with young terrain or snowbeds, are found on older ground in association with fluvial disturbance. In agreement with Rydin and Borgegård (1991), the results show that pioneer assemblages are distinct and generally fairly exclusive to young sites and this is supported by Elven (1978) who, in a review of pioneer assemblages on glacier forelands, showed species similarities between pioneer assemblages in North America, Scandinavia and Alps. The occurrence of pioneer assemblages on older ground therefore suggests that fluvial activity can cause the disturbance necessary for the predominance of pioneer species on older sites (cf. Tisdale et al, 1966; Zollitsch 1969; Whittaker, 1993). The use of a gully on the oldest terrain at Svellnosbreen could have been partly responsible for the increased influence of fluvial activity shown across this foreland.

At Fåbergstølsbreen, a debris flow, occurring in 1979 (Ballantyne and Benn, 1994), swept across the 1930 moraine causing disturbance that allowed the re-colonisation of pioneer species, associated with young, disturbed, moist and bare terrain, such as *Cerastium spp, Oxyria digyna, Saxifraga stellaris* and

Deschampsia alpina, and thus providing evidence for retrogressive succession (see section 7.4.3). On the 1930 moraine at Austerdalsbreen, intermediate heath assemblages are dominant across the entire moraine which suggests that the vegetation on the 1930 moraine at Fåbergstølsbreen should also comprise intermediate assemblages. It is likely that any disturbances which cause patches of bare ground, such as debris flowage, overgrazing or trampling, would also cause a reinvasion and predominance of pioneer species, although detailed investigation of this particular question was not within the scope of the present study.

The individual foreland results are confirmed by the combined DCA ordination results (see Table. 7.1), which show fluvial activity to be the most important parameter at the positive end of axis (2). The results show that fluvial activity is not related to altitude but is significantly related to age on axis (2). Despite this, fluvial disturbance was not included within the *"Age factor complex"* as it was not an important age-related factor on axis (1) and furthermore the results suggest that fluvial activity is more dependent on topography than age and thus it is included within the *"Microtopographic factor complex"*. The importance of fluvial disturbance and its relationship both to microtopography and age has been partly responsible for the confounding of age and microtopography within many of the ordination data sets. Some of these findings agree with Whittaker (1985) who suggests that overall disturbance decreases with age of ground, although he did not distinguish whether the disturbance was fluvial. Crouch (1992) distinguished fluvial activity, on an ordinal scale, but only found a weak correlation with pH and soil moisture - the lack of significance shown by fluvial disturbance in her results is possibly due to her sampling strategy. In other words, Crouch may not have had enough fluvially-disturbed low-slope position sites in her sample. Previous work has also shown disturbance to be an important influence on vegetation patterns (e.g. Tisdale et al., 1966; Archer, 1973; Jonasson, 1986; Arnalds, 1987; Walker and Chapin, 1987; Chambers et al., 1990; Chapin et al., 1994; Matthews, 1998) and it is suggested that the most obvious disturbance variables at a site (e.g. grazing, trampling, fluvial activity, frost heave and solifluction) should always be investigated separately in order to achieve the most ecologically meaningful results.

The likely influence of disturbance on vegetation pattern, as shown by the results of the present thesis, are summarised as follows:

1. Fluvial activity is an important influence on vegetation patterns on seven out of eight forelands and so it is suggested that fluvial activity is, in general, an important variable. Fluvial activity, and other major disturbance factors, can cause retrogression, providing suitable conditions for pioneer or earlier species in the succession, and therefore such species should not be considered as part of the mature assemblage patterns.
2. Fluvial activity is not influenced by altitude but appears to be influenced by age and microtopography, occurring to a greater extent on younger terrain at low-slope positions. It is included within the *"Microtopographic factor complex"*.

3. The importance of fluvial activity, and its close relationship with both age and microtopography, has been partly responsible for the confounding of these parameters on DCA axes (1) and (2) for both the individual and combined data sets.

7.4 Environmental influences on vegetation succession

The relative effects of the meso-environmental parameters on vegetation patterns and succession can be seen most clearly by referring to the results of the TWINSPAN "final site group" separations from both the individual foreland and combined data set in chapters (4), (5) and (6). The specific relationship between the vegetation succession and the environmental factor complexes, emphasising microtopography, is elucidated here.

7.4.1 The importance of microtopography in successional pathways

The individual foreland results in chapter (4) show that the influence of microtopography on succession increases with altitude and this is revealed by the increasing number of assemblages that are associated with particular microtopographic positions at lower TWINSPAN levels of subdivision -i.e. levels (3) and (4) (see profile diagrams Figs. 4.2-9). According to the succession diagram (Fig. 4.10), at Austerdalsbreen, microtopography is most influential on the pioneer and oldest terrain: there is slight convergence to intermediate terrain and then slight divergence to the oldest terrain, where there is assemblage differentiation. The pathway at Fåbergstølsbreen is complex (Fig. 4.11), with a debris flow causing suitable conditions for pioneer species. The oldest terrain is not differentiated, as it is at Austerdalsbreen, possibly due to the occurrence of birch woodland across the entire profile and this supports the premise that woodland causes a convergence of assemblages (e.g. Fægri, 1933; Elven, 1975; Vetaas, 1986). The pathway across the Storbreen low (1) moraines are similar but slightly different to the "replicate" sequence Storbreen low (2) (Figs. 4.12-13): the difference may be due to the size and shape of the moraines causing a different snow-lie and exposure regime across the profiles. The low-alpine pathways at Storbreen display parallel succession (Fig. 4.14) and then slight divergence. The pathway at Svellnosbreen is distorted by an outlier pioneer assemblage so that the majority of "ecologically meaningful" assemblages, along the pathway, are separated at a high level of subdivision making them appear to be less distinct than they are likely to be. The pathway at Svellnosbreen shows convergence then divergence. The mid-alpine pathways (Figs. 4.15-17) display slight convergence at Storbreen and, at Høgvaglbreen and Bøverbreen, convergence followed by divergence. The pathways at Høgvaglbreen and Bøverbreen are likely to be caused by the occurrence of small intermediate moraines that sustain a lengthy snow duration across their entire profiles.

The results from the combined data set (section 6.3.6; Fig. 6.2, Table 6.1) support those of the individual foreland data sets although some of the important details shown by the individual foreland data sets is absent. The combined data set shows a number of general patterns of succession for each altitudinal zone:

a) on the subalpine forelands the pathways are complex and unpredictable, although the main trend is one of convergence, except where disturbance occurs, and a lack of significant microtopographic influence; b) on the low-alpine forelands early intermediate pathways (not pioneer) are fairly unpredictable but the pathways become more predictable with age so that the pathways show a slight divergence to a slight convergence to a parallel development, that is influenced by microtopography; and c) on the mid-alpine forelands the pathways are relatively predictable and are mainly divergent or parallel, with microtopography being a significant factor.

The individual foreland and combined foreland results (see Figs. 4.10-18, and Fig. 6.2) support the premise that there is more than one assemblage on the oldest terrain and thus the traditional view of convergence to a monoclimax (*sensu*: Clements, 1916) is rejected. Matthews (1979d) suggests that an increase in the distinctness of assemblages with time shows a divergent succession, but within the present study there appear to be several distinct TWINSPAN "final site groups" at the pioneer stage as well as the mature stage, corresponding with the results of Crouch (1993). These findings contrast with the results of Matthews (1979d) and Elven (1975, 1978) who found a divergence, in the strict sense of the word, from one pioneer assemblage to several mature types. The pioneer "final site groups" have been separated by TWINSPAN at a low level of subdivision and this suggests that the separation of the pioneer "final site groups" are meaningful and the assemblages themselves are distinct. The separation of several pioneer TWINSPAN "final site groups" contrasts with the evidence from the combined TWINSPAN "final species groups" (as there is only one pioneer "species group 35") but not with all the individual foreland "final species groups" (see Table 4.10) which show that, on some forelands, there are several pioneer assemblages. Because of the larger number of disturbed or young-ground sites than pioneer species it was possible to meaningfully separate the sites according to age as well as microtopography. This therefore causes the successional pathways (based on "final site groups") to show a parallel type rather than a strongly divergent type and shows considerable agreement with the work of Schubiger-Bossard (1988) who indicated a tendency for parallel development on the Rhone Glacier foreland.

The review of succession in section 1.3.3, indicates that most research (e.g. Churchille and Hanson, 1958; Viereck, 1966; Zollitsch, 1969; Sommerville et al., 1982; Burrows, 1990; Helm and Allen, 1995) shows a continuous succession of different plant assemblages across glacier forelands. The successions usually progress from a dominance of herb, low shrub and moss species through to taller shrub, lichen and tree species that can progress in stages or in steps and the present study agrees with this finding. The results also support those who suggest that primary succession is more complex (e.g. Matthews, 1979a; Whittaker, 1985; Grubb, 1987; Burrows, 1990; Crouch, 1992; Del Moral, 1993; Miles and Walton, 1993; Chapin, 1994) than previously thought (e.g. Odum, 1975; Connel and Slatyer, 1977). The pathways, are more complex and difficult to predict than previously acknowledged due to factors that have only recently started to be investigated, notably microtopography and disturbance. In addition, traditional differences in the characteristics of pioneers and later colonisers have been found to be simplistic. Grubb (1987), argues that the traditional view (i.e. the confusion between r-selected opportunists and early colonisers) of the characteristics of pioneers, as easily dispersed and short lived species, is a simplification. He suggests "*At unstable sites the pioneers are also usually long-lived; some have large disseminules, and others invade by vegetative spread. ... All these cases contrast with the common type of primary succession* [my underlining] *on stable sites with relatively large supplies of water and nutrients, in which shorter-lived plants are the pioneers ...*" Grubb (1987: 98). Due to the mosaic of disturbed and more stable patches on the young ground (and most terrain-ages) within the present study, small-scale differences in microtopography and disturbance shows that a "*common type of primary succession*" is unlikely to exist, at least on glacier forelands, and thus Grubb's view is possibly a more generalised phenomenon than he suggested. Furthermore, generalisations concerning the characteristics of colonisers on pioneer sites are likely to be misleading. If it is necessary to generalise about the characteristics of pioneers and later colonisers, it is necessary to understand colonisation of all the pioneer terrain and thus a study of both microtopography and disturbed terrain is necessary. Chapin (1993: 176) attempted to supply a list of coloniser traits and exceptions. However, his list is likely to be too general in that the "*major exceptions*" appear to refer to ecosystems, whereas it is more likely that "*major exceptions*" can occur on an unstable patch within a more stable area (within a particular ecosystem). This further highlights the usefulness of studying microtopographical (and disturbance) effects on vegetation succession.

The results from the present study show that the glacier foreland successions involve several pathways that are mainly influenced by time but are also significantly affected by microtopographic and environmental factors, the most important being snow-lie, exposure and disturbance. Divergence, convergence and parallel pathways are shown to be involved in the course of succession across most of the glacier forelands and convergence to one mature assemblage does not appear to occur. Generally the pathways appear to be simpler across environmentally stressed glacier forelands (i.e. at higher altitudes) and, as expected, divergence tends to be related to microtopography.

The description and comparison of the successional pathways, shown by the combined and individual data sets, is one of the more complex aspects of the present thesis and these results are best further elaborated by briefly answering a number of important questions:

1. *Does microtopography affect the assemblages found along the foreland chronosequences?*
   Microtopography, and associated factors within the "*Microtopographic factor complex*", appears to affect the types of assemblages found along foreland chronosequences by influencing the prevailing environmental conditions at different topographical positions. It is probable that the most important micro-environmental influences on the vegetation are snow-lie, exposure, fluvial activity and available moisture (cf. Billings and Bliss, 1959; Billings, 1974; Miller, 1982; Alexander, 1986; Whittaker, 1987; Kudo and Ito, 1992; Walker et al., 1993). It is likely that microtopography affects the type of assemblage at all successional stages so that, at low-slope positions, there are pioneer snowbed

assemblages proceeding to intermediate late-snow heath assemblages and mature snowbed assemblages; and on high-slope positions there are exposed pioneer assemblages followed by exposed intermediate lichen heath assemblages and mature heath assemblages (cf. Schubiger-Bossard, 1988).

2. Does the relative effect of microtopography on successional pathways change with either time or altitude?

The results show that microtopography has a minimal effect where woodland is prevalent on the older terrain on the subalpine forelands, possibly due to an evening out of conditions across microtopographic features (cf. Elven, 1975; Vetaas, 1986). The results (section 3.3.1) show that winter snow cover is more uniform on the subalpine forelands and a long snow duration generally does not occur at the bases of moraines (maybe due to higher spring temperatures and an earlier spring melt) so that late snow-lie is not necessarily associated with all low-slope sites. The unbroken succession of snowbed assemblages from younger moraines to older moraines is therefore not as pronounced as it is on the low- and mid-alpine forelands. For this reason assemblages associated with microtopographic position (and marked differences in snow distribution patterns), on the subalpine forelands, tend to be found on isolated moraines and not across a sequence of moraines. On the subalpine forelands, as woodlands develop, the effect of microtopography appears to decrease and thus an overall trend of convergence with age can be determined (cf Fægri, 1933; Birks, 1980; Vetaas, 1986, 1994; Matthews, 1992). However, it has also been shown that the subalpine assemblages are most influenced by microtopography on the young terrain, and on the oldest terrain (possibly due to previous grazing regimes or fluvial activity), which counteracts this trend to some extent.

On the low- and mid-alpine forelands microtopography is an important influence on the pathways at all stages of succession, with certain assemblage types occurring across a sequence of moraines at particular microtopographic positions. The sequence on the low-alpine forelands is slightly more complex than the mid-alpine sequence, with a greater number of assemblages occurring within the sequence (cf. Matthews, 1979b). Age therefore does not appear to affect the relative influence of microtopography on the assemblage separation. However microtopography does appear to have an increased influence on the successional pathways, at higher altitudes. Another interesting finding, displayed in Fig. 7.3, appears to be that the influence of altitude on the separation of assemblages is greater on the oldest terrain, and less on the youngest ground, so that pioneer assemblages tend to occur across a wider altitudinal range than the mature assemblages.

3. Do the successional pathways diverge as a result of microtopography?

If fewer pioneer assemblages are replaced by a greater number of assemblages the pathways are said to diverge and it is apparent that divergence of assemblages, within a successional sequence, can be related to microtopography (cf. Elven, 1975, 1978; Matthews, 1979b; Alexander, 1986; Whittaker, 1993). A distinct environmental gradient across a major microtopographic feature, such as a moraine, will cause the differences in assemblage-types between the crest and low-slope positions of the moraine leading to divergence. Convergence, on the other hand, is generally related to a similarity of environmental conditions between the crest and low-slope positions of major microtopographic features (caused, for example, by woodland), or to other, more homogeneous, types of landscape (e.g. Faegri, 1933; Vetass, 1994). Divergence, as a result of microtopography, was found to occur on all forelands within the present study, but to a greater extent on the alpine forelands.

4. Is the relative divergence or convergence of assemblages influenced by terrain-age or altitude?

Summarised in general terms the TWINSPAN "final site group" results (Figs. 4.10-18 and Fig. 6.2) show that the clarity and simplicity of the successional pathways is greater on the low- and mid-alpine forelands than on the subalpine forelands. The pathways described within the present study, across all altitudinal zones, showed divergence, convergence and parallel successions which are likely to be related to a combination of many different factors, such as size of moraine, disturbance, prevailing wind, snow duration, vegetation type and cover and so on. It is therefore not possible to generalise as to whether pathways diverge or converge through time. However a general trend, with regard to the effect of altitude on the time trends, was shown by the individual and combined data sets. The subalpine forelands, in the present study, showed a general convergence from pioneer to mature (cf. Faegri, 1933; Vetaas, 1994), although the pathways across the two forelands had rather different characteristics. The subalpine trend is likely to be most influenced by the occurrence of woodland (dominated by *Betula pubescens ssp tortuosa,* Fig. 6.14) or low shrub (dominated by *Vaccinium myrtillus,* Fig. 6.13) across most of the oldest till-ridge profiles, as well as a more even cover of winter snow.

The low-alpine forelands showed a general trend of parallel succession or a slight divergence, on the older ground, possibly due to the stronger environmental gradients across the moraines, caused by divergent snow duration, than that found on the subalpine forelands. The results on the alpine forelands compare with those of Schubiger-Bossard (1988), who found a trend of parallel successional pathways and Jochimsen (1970) who found a variety of convergent or divergent pathways are possible on pioneer ground. The results also compare with Zollitsch (1969), who found a noticeable divergence of assemblages onto the intermediate ground, followed by convergence. The lack of *Betula pubescens* and the lower cover of *Vaccinium myrtillus,* on the oldest low-alpine sites, may also be the cause of divergent environmental conditions across microtopographic features. Nevertheless, the dominance of low shrubs such as *Betula nana* and *Empetrum nigrum,* on the oldest terrain of the low-alpine forelands (Figs. 6.5, 6.10), provides a denser and more protective vegetation cover than the prostrate shrubs and lichens on the oldest terrain on the mid-alpine forelands. The hypothesis that different types of vegetation cover have a strong influence on the prevailing micro-environment is supported by the work of Khil'mi (1962) and Sukachev & Dylis (1964).

On the mid-alpine forelands the general trend is one of parallel succession and divergence. The environmental gradients across the moraines are more distinct, with the snow-lie patterns having a significant influence on the distribution of the assemblages. The mature assemblages tend to be dominated by prostrate species of vascular plants or lichens, such as *Arctostaphylos alpina, Arctostaphylos uva-ursi*, *Cetraria nivalis* and *Cetraria ericetorum* (Fig. 6.3) which are unlikely to influence the microclimate, in terms of reduced wind and increased moisture, to such a degree as the low-alpine shrubs might (cf. Khil'mi,1962; Sukachev & Dylis, 1964). It appears, that divergence of assemblages onto the oldest terrain, as a result of microtopography, may be more prevalent within successional pathways at altitudes above the tree line and increasingly so with higher altitudes and increased environmental stress. It is likely, however, that on the subalpine forelands the occurrence of divergent trends in succession is related to a combination of factors, such as grazing regime and disturbance, and that the effects of microtopography on the divergence of assemblages can either be indirect (e.g. due to increased grazing pressure at the base of the moraine or increased trampling on the crest).or direct (due to the influence of the *"Microtopographic factor complex"*). It should be noted that little comparison with previous work can be made (i.e. on successional pathways at different altitudes) because very few studies have been carried out on this particular area of interest.

5. Can the pattern of assemblages on the oldest terrain (i.e. the end-point of succession) be described as "Climax"?

It has been shown that there is usually more than one assemblage on the oldest terrain of each foreland and that many of these assemblages have evolved along different pathways, which would suggest that they can be considered as being part of a mosaic of assemblages, rather than being variations of the same assemblage (cf. Schubiger-Bossard, 1988; Matthews, 1979c; Whittaker, 1993). Interestingly, analysis showed that, across all altitudinal zones, the most distinct assemblages tended to be those found on either the young terrain or the oldest terrain. This further supports the premise that the term "climax" for the vegetation within any particular landscape should not be used and the term "mature assemblage", within a mosaic of several mature assemblages, is preferred (sensu: Burrows, 1990).

The probable influence of microtopography on successional pathways are summarised as follows:

1. The dominant influence on successional pathways is the *"Age factor complex"*.
2. At higher altitudes, the successional pathways are simpler and most assemblages reflect microtopographic influence at lower levels of subdivision. The influence of microtopography therefore appears to be greater at higher altitudes.
3. There is always more than one mature assemblage, but there is usually more than one pioneer assemblage so that a straightforward divergence hypothesis is too simplistic.
4. The present study agrees with most of the more recent research in the following ways: a) the same general pathways have been elucidated; b) the pathways are complex from intermediate to mature; and c) the effect of microtopography is important.

5. The present study disagrees with most of the previous work, however, in several ways: a) pioneer assemblages are predictable; b) pioneer assemblages are distinct; c) microtopographic effects on successional pathways are more complex than previously thought; and d) succession can follow convergence, divergence or parallel successional pathways due to a diversity of factors.

7.4.2 The influence of microtopography on assemblage gradients and the relationship between assemblage members.

An important question, central to successional theory, is whether or not the defined assemblages are distinct within the landscape, and, if so, whether the most distinct assemblages appear to be so as a result of the *"Microtopographic factor complex"* and/or other factor complexes. By referring to the review chapter (1), it can be seen that there has long been considerable disagreement over the occurrence of discrete successional and climax communities (e.g. Clements, 1936; Gleason, 1939; Whittaker, 1951, 1953; Churchill & Hanson, 1958; McCormick, 1968; Odum, 1969; Drury and Nisbet, 1973; McIntosh, 1981; Jonasson, 1981; Kershaw and Looney, 1985; Matthews and Whittaker, 1987). By discussing the relative distinctness of assemblages, and by looking for particular patterns of distinctness, further elucidation of the relationship between species within the assemblages can be made. Table 7.1 summarises the most distinct TWINSPAN "final groups", for both the individual foreland and combined data sets, as described by the DCA ordination rank diagrams (Tables 5.1-16 and 6.4). The relationship between the assemblages and the environmental parameters is also shown so that the relative influence of the factor complexes can be seen.

The combined data set tends to confirm the individual foreland data which contends that the most distinct assemblages are the pioneer and snowbed assemblages, the lichen heath assemblages, and the subalpine late-intermediate or mature woodland assemblages (cf. Sommerville et al, 1982; Crouch, 1993; Evans et al, 1989). Pioneer assemblages are distinct on all forelands, possibly because they comprise species adapted to disturbance processes associated with bare ground but do not tolerate competition for light, nutrients or browsing (e.g. Whittaker, 1993). The main influence on the distinctness of pioneer assemblages is likely to be time (see Elven, 1978) and factors associated with the *"Age-Factor-Complex"* highlighted within this thesis. Lichen heath assemblages are distinct on alpine forelands, possibly because they comprise species adapted to exposed sites. They are chionophobus, and are more tolerant of the repeated freeze thaw regime found on moraine crests (cf. Jonasson, 1981; Jonasson and Sköld, 1983), lower nutrient availability and drought (e.g. Miller, 1982; Wijk, 1986). Snowbed assemblages are also distinct on all forelands, possibly because they comprise species adapted to lengthy snow duration, a short growing season, saturated soil conditions and heavy winter browsing regimes but are not tolerant of exposure (cf. Emanuelsson, 1984; Auerbach and Halfpenny, 1991; Walker et al, 1993). The main influence on the distinctness of lichen heath and snowbed assemblages is likely to be the steepness of the topographically-related snow distribution gradients (e.g. Jonasson, 1981; Kudo and Ito, 1992; Stanton et al, 1994). It appears that age causes the separation of the most distinct assemblages on the subalpine forelands but a combination of age and microtopography influence the separation on the alpine forelands. On most of the forelands mature assemblages tend to be distinct due to a number of possible reasons, for example, an individual species, within each mature assemblage, has to adapt to a fairly narrow resource gradient caused by competition with other species (Tilman, 1985; Bazzaz, 1987; Whittaker, 1993). By referring to Table 6.3, it can be seen that the assemblages that are most characteristic of particular site-types, are the alpine lichen heath assemblages (red), found on high-slope positions, and the pioneer assemblages (pink) found on young or disturbed sites. It must be emphasised, however, that despite such distinctness they should not be regarded as true communities until this is confirmed by experimental study.

Despite the distinctness of a minority of assemblages on each foreland there is considerable overlap between most assemblages (including the most distinct) suggesting that demarcated zones tend not to occur and that the assemblages tend to grade into one another. This premise supports, among others the conclusions of Matthews (1976), Whittaker (1985) and Crouch (1992). The rank diagrams (Tables 5.1-5.16 and Table 6.4) show that most of the assemblages, described by the TWINSPAN analysis, are not distinct and so can only be regarded as loose assemblages along a gentle gradient of gradually changing environmental parameters. It is unusual for most of the members of loose assemblages to remain constant, between forelands, and therefore they cannot be considered as distinct communities. Rather, it is likely that the distribution of member species, within the majority of assemblages, are caused by common preferences for particular environmental resources and requirements (cf. Parrish and Bazzaz, 1982; Tilman, 1985; Matthews and Whittaker, 1987).

The evidence suggests that both age and microtopography are important influences on the relative distinctness of the assemblages. However, according to Table 7.1, it appears that altitude does not have a significant influence on the distinctness of assemblages since the most distinct assemblages can be found on forelands within both the subalpine and alpine altitudinal zones. Their relative influence varies between the forelands, thus supporting the notion that the influence of age and microtopography, on assemblage patterns and distinctness, is complex and relatively unpredictable. These results support the individualistic concept of vegetation (described in Moravec, 1989: 29) in so much as "*plant communities (phytocoenoses) are not natural objects (wholes) as such but merely mixtures of plant individuals co-existing on the same site as a result of migration and environmental selection*". However, Moravec continues that supporters of the individualistic concept hold that "*the classification of vegetation is quite arbitrary if not pseudoscientific*". The present results show that some of the species appear to occur together in what may be distinct environmental pockets, such as: young ground; exposed alpine ridges; the mature heathland; mature woodland; or areas of long snow duration (cf. Jonasson, 1981; Walker, 1993). Therefore the division of species into assemblages cannot be considered as arbitrary although the pattern may not necessarily be biotically induced. The results of this study are in complete agreement with Crouch (1993: 133) who suggested "*there is evidence for much individualistic behaviour of species on the Storbreen glacier foreland supporting the validity of a population approach. Yet many species exhibit similarity in* *their distribution patterns, which suggests that a community approach is not inappropriate*". Furthermore a model that explains vegetation patterns in terms of both the effect of environment on vegetation, as well as the effect of vegetation on environment, as subscribed by Roberts (1987), would do much to explain the patterns and relative distinctness of many of the assemblages described in the present study.

The results relating to the influence of microtopography on assemblage gradients, and the affinity between assemblage members, are summarised as follows:

1. On all forelands there is a considerable overlap between assemblages supporting the notion that demarcated zones are not distinct and that gradients of assemblages are more realistic.
2. There appears to be a considerable difference in the distinctness of assemblages found across the forelands. The most distinct assemblage types tend to be lichen heath, pioneer, snowbed and mature woodland on each of the forelands and there is considerable correspondence in member species of these assemblage types between-forelands. It is also suggested that the assemblages are distinct for a range of reasons including tolerance to environmentally stressed conditions such as exposure.
3. Although some assemblages, especially the lichen heath and pioneer assemblages, appear to be distinct, it is necessary to investigate experimentally the relationship between constituent species before these assemblages can be regarded as "communities" (i.e. where members of the assemblage are associated through some kind of interdependence).
4. The evidence suggests that species show considerable individualistic behaviour and thus a population approach can be justified. However, a "community approach" is also considered valid due to the obvious alliances (either interdependent or coincidental) shown between the member species of many of the assemblages. The "community" approach, is also considered more pragmatic with regard to analysing large data sets.
5. A combination of assemblage eigenvalues (derived from TWINSPAN) and rank diagrams are useful in showing assemblage distinctness across the forelands. By using an approach that uses both "community" or assemblage data (i.e. the DCA centroid plots), as well as charts which display individual species distributions (both spatially and also in relation to the environmental parameters on the ordination axes), it is possible to combine the individualistic and community approaches. A greater understanding of the processes underlying succession can therefore be provided.

7.4.3 Problems of retrogression, "climax", and the mechanisms of succession

Retrogression, considered to be where outside factors bring about a replacement of a "higher" by a "lower" type of plant community (Tansley, 1920), has been denied by some researchers (e.g. Clements, 1916; Philips, 1934-5; Moravec, 1969) and defended by others (Cowles, 1919; Cooper, 1916; Gleason, 1917, 1927; Tansley, 1935). By referring to the individual foreland succession diagrams (Figs. 4.10-18), it can be seen that retrogression appears to occur on some of the forelands, especially where major disturbances on older ground occurs. For example, the debris flow at Fåbergstølsbreen, which swept across the 1930 moraine (Ballantyne and Benn, 1994) caused disturbance that allowed the re-colonisation of pioneer species on terrain that should (as suggested by the assemblages found on the 1930 moraine at Austerdalsbreen) comprise early intermediate heath or snowbed assemblages. Across the Storbreen high and Svellnosbreen sequences, there is also some evidence for retrogression: a pioneer snowbed assemblage (TWINSPAN "final site group" 6) is found at low-slope distal sites on the 1750 moraine at Storbreen high; and a late snow heath (TWINSPAN "final site group" 21) found on M5, at Svellnosbreen, is also found at low-slope sites on M1-3. It is likely that either fluvial disturbance or long snow-lie are responsible for the pattern of the assemblages, on the low-alpine forelands, and this is confirmed by referring to the DCA ordination centroid plots (Figs. 5.5 and 5.6).

There is no doubt that pioneer assemblages can replace intermediate or mature assemblages. However, the main question is whether retrogressive succession can be considered as a "*turning back at an angle, in a direction different from the original development*" (Whittaker, 1953: 47) when the main cause of retrogression appears to be disturbance. It would therefore seem unlikely that the pattern of change would always be a gradual retrogressive degeneration in a similar way to succession as gradual progressive development: at Fåbergstølsbreen the debris flow caused an abrupt change in the assemblage types that cannot be regarded as a classic retrogression. According to Moravec (1969) "*if such a process* [i.e. retrogression] *takes place in nature, then it is only by the influence of factors outside the ecosystem, the action of which is antagonistic to the community and usually destroys the habitat (e.g. erosion). Such a process has, however, a different nature and a different cause and according to Tansley (1920) "is only to be brought into the concept of succession in a very broad and general way"* ... ". Because Moravec believes that succession is driven by the plants themselves (i.e. autogenic succession) he dismissed the concept of retrogression outright. However, to simply dismiss retrogression as a non-successional process is too simplistic. Twelve years of direct measurement of succession, across the Storbreen foreland, showed progressive succession on terrain aged 20 to 50 years but retrogression on the older ground, possibly due to disturbance (Matthews and Whittaker, 1987). The authors did not specify the type of disturbance but it appears that the change in assemblage types was gradual rather than abrupt, supporting the view that retrogression can take place. Johnson et al (1990) suggest that soil development may be progressive (e.g. to deeper and organised into profiles) or regressive (e.g. to simpler shallower profiles). They suggest that regression may occur due to factors including: profile shallowing due to losses (e.g. erosion); addition of "rejuvenating" materials, normally found in young profiles (e.g. base-rich organic matter or divalent cations); and surface sedimentation so that profile development cannot keep up. These findings are particularly useful in understanding the possible influences on the retrogression of vegetation within an area (or small patch of ground).

It is probably best to investigate retrogression with specific reference to the prevailing disturbance factors. If the disturbance factors are extreme and abrupt, so that the vegetation and soil is all but completely destroyed (e.g. by a debris flow or severe fluvial activity), then this cannot be referred to as retrogression and the resultant succession needs to be referred to as some form of renewed, or disturbance-related, succession. However, where the disturbance is persistent and relatively long-term (as in the case of intermediate fluvial activity, grazing or trampling) and the deterioration of the soil and vegetation is gradual, then *"Retrogression may be in some cases a useful term to describe changes occurring in a community changes "retrogressive" by definition, and perhaps most significantly involving decrease in community productivity"* (Whittaker, 1953: 47-8). With regard to the question of whether there is a relationship between retrogression and microtopography, it is probable that retrogression is dependent on the influence of disturbance which in turn may occasionally be determined by microtopography (e.g. fluvial activity on low-slope positions).

As discussed in section 1.3.1, "climax" is another problematic term and because it carries so many controversial and varied meanings it was decided to use the term "mature" as it is a less controversial and more general defining name for assemblages found on the oldest ground (Whittaker, 1985, 1993; Burrows, 1990). The trends outlined in section 4.3, support the notion, similar to the climax pattern hypothesis first suggested by Whittaker (1953), that the oldest terrain consists of a pattern of populations similarly related to one another, corresponding to a pattern of environmental gradients. The hypothesis that the oldest terrain comprises vegetation that appears to be a relatively stable and self-maintaining successional stage, which contrasts with unstable and relatively short-term successional stages, has been accepted by most authors and has been shown to exist in this study. The results of this study, however, do not support that all vegetation progresses to a mature successional stage, or end point, because of the constantly changing circumstances (climatic, physical or biotic - including human effects) that can cause retrogression or further succession. This notion is highlighted by the similarity between some mature assemblages and pioneer, or early intermediate assemblages, on a number of forelands including Svellnosbreen. These results suggest that, due to the importance of disturbance factors, the so-called end-point to any successional sequence should be considered as being dynamic rather than static (cf. Whittaker, 1953; Churchill and Hanson, 1958; Williamson, 1987; Roberts, 1987; Burrows, 1990). The results of this study support Tansley (1939) in that climax is considered to be a partially stabilised community steady-state that is adapted to the maximum utilisation of environmental resources. Most popular ecology text books define the term "climax" as a stable end-point to succession (e.g. Odum, 1975; Slingsby and Cook, 1986; Begon, Harper and Townsend, 1996; Allaby, 1994, 1998), whether it is a mosaic (*sensu*: Whittaker, 1951) or monoclimax (*sensu*: Clements, 1916). Confusion therefore arises over the use of the term if the plant populations (and assemblages) are spatially dynamic. This further promotes the use of the term "mature" in preference to the term "climax".

The mechanisms of succession, touched upon in chapter (1), generally need to be specifically tested (Connell and Slatyer, 1977) using specially designed experiments. Thus, it is not within the scope of this study to contribute in a detailed way to the understanding of actual mechanisms of succession at work on each foreland. However, this study shows that microtopography influences the pattern of assemblages and this would suggest that there are mechanisms, other than facilitation, that are driving succession. This study therefore views that there is not just one mechanism of succession at work but a combination of factors which are driving succession at the population and individual level, a notion which is defended by many authors (e.g. Gleason, 1927; Billings, 1952; Finegan, 1984; Gibson and Brown, 1985; Picket et al, 1987; Burrows, 1990; Miles and Walton, 1993). The differences shown in the results with regard to the influence of microtopography, age and altitude on succession (section 7.4.1), therefore support Peet and Christensen (1980) in their recommendation of an individualistic, population-based approach to succession, and endorses the population-based approach adopted by Whittaker at Storbreen (Whittaker, 1985, 1991,1993). However for large-scale studies, such as the present one, which attempt to summarise the effect of meso-scale and micro-scale environmental gradients on successional pathways on a number of glacier forelands, the individualistic population-based approach is not practical and an assemblage- (or "community"-) based approach is considered more realistic (cf. Matthews and Whittaker, 1987; Crouch, 1992).

Roberts (1987) proposed a dynamical systems approach that attempts to combine the individualistic concepts with those of the holists (i.e. using an assemblage-based approach) by suggesting that not only does environment effect vegetation patterns but vegetation effects environment. This hypothesis is supported by the results of the present study which indicate environmental effects on vegetation (e.g. the effects of snow duration and exposure). Furthermore, it is supported by the effects of vegetation on environment such as the likely effects of woodland canopy on the underlying environment and the proposed decreasing effect of vegetation on moraine microclimate with altitude. As described earlier, this dynamical systems hypothesis suggests a continuous chain of influence between environment and vegetation and, if an effective methodology could be found, this might go a long way to finding the true relationship between vegetation and environment (cf. Matthews, 1996). The geoecological approach (*sensu*: Matthews, 1992), is used to investigate vegetation patterns by considering all aspects of plants, space, time and environment and has been shown to provide comparable vegetation data for both holistic, "community" approaches (Matthews, 1976; Whittaker, 1985; Crouch, 1992; and the present thesis), as well as individualistic, population-based approaches (Whittaker, 1985, 1993), to the interpretation of successional pathways and mechanisms. The geoecological approach, combined with the dynamical systems approach, proposed by Roberts (1987), would go a long way to understanding the complex relationships between vegetation and environment so that researchers, as well as conservation managers, would be in a better position to understand and predict vegetation patterns, given a particular set of variables (both biotic and abiotic).

The relevance of the results with regard to some of the fundamental questions associated with succession, including retrogression, "climax", and the mechanisms of succession, may be summarised as follows:

1. Retrogression occurs but should be investigated in relation to the prevailing disturbance factors. If disturbance is mild and persistent then retrogression is likely to occur, but if disturbance is extreme it may cause secondary or even primary succession.

2. Retrogression is more likely to be associated with disturbance than microtopography, but the disturbance factor itself (e.g. fluvial activity) may be related to microtopography.
3. The concept of a multi-assemblage mature vegetation, which forms a relatively stable end-point to succession, (previously referred to in polyclimax or climax-pattern hypotheses) has been supported. However it is suggested that disturbance, or a multitude of other factors, may cause the vegetation to either regress or to develop to another vegetation type. The concept of monoclimax is dismissed.
4. A combination of the geoecological approach (*sensu*: Matthews, 1992) and the dynamical systems approach (*sensu*: Roberts, 1987), could provide a sound basis for future research into the relationship between environmental and vegetation patterns during succession.

7.5 Methodological and technical implications

A wide range of methodologies and presentation techniques have been used within the present thesis. Some methods and techniques are original, while others are a further development from other researchers in the field. All the methods and presentation methods are summarised, along with their sources, in Appendices (7) and (8). The main methodological and technical contributions, of the present thesis, are discussed below.

7.5.1 Individual foreland data sets versus a combined foreland data set

The author considered that valuable information would be lost if only an interpretation of the combined data set was carried out and so it was decided to run analyses on each of the individual data sets and compare the results with those of a combined data set run. This needs justification. In particular, three main questions need to be answered:

1. What are the advantages of the individual foreland analysis runs over the combined foreland run?
2. What are the advantages of the combined foreland analysis run over the individual foreland runs?
3. Can a large combined foreland data set be used for the analysis of data instead of a series of individual foreland data sets or should both types of analysis run be performed?

The main problem with the combined data set was a) the large size and b) the confounding of the influence of the major factor-complexes on the vegetation patterns. For example the DCA centroids of TWINSPAN species scores for the combined data set (Fig. 6.17) were very close together at the centre of the diagram and it was necessary to display the centroids on a large scale diagram (Fig. 6.18), omitting the environmental parameters. Although the positioning of these centroids are ecologically meaningful (cf. Whittaker, 1987; Kent and Coker, 1992), showing that it is worth examining the pattern of DCA centroids on the axis, it was necessary to check the interpretation of this diagram by referring to the individual foreland data set. It was felt that where the data points are cramped it is possible that slight distortion (van Groenewoud, 1992; and Palmer, 1993) may cause the points to be misplaced within a particular sequence, whereas the individual foreland data points are generally better spread out so that the major trends displayed are likely to be more reliable. In addition, the TWINSPAN site data, which provided useful information from the individual foreland rank diagrams (Tables 5.1-8), was too cumbersome for the provision of combined foreland rank diagrams.

The combined foreland ordination data (see Tables 6.4-5 and Fig. 6.17) show that position is a relatively insignificant influence on both axis (1) and (2), but that snow-lie and fluvial activity are highly significant. Although both of these parameters can be related to microtopographic position this calls into question the relative importance of position. However, the individual foreland ordination data show that position is an important influence on every foreland except the subalpine forelands and Bøverbreen. It is possible that position may not have been shown to be important at Bøverbreen because of small intermediate moraines, entirely snow-covered during most of the winter and possibly causing snow to be a more significant influence than position. The combined data set therefore averaged out, or obscured, the results to the extent that an important influence on particular forelands could not be adequately elucidated. Without the individual data set analyses the relative influence of position on vegetation pattern may have been considered to be of minor importance. Position is considered to be an important component of the *"Microtopographic factor complex"* and thus such a finding may have seriously undermined the main aims of the thesis. This emphasises the need for careful interpretation of the results to find ecological meaning within the data sets. This is especially true, for the large data sets (both the individual and combined data) used within the present thesis, because statistical significance may not provide a representative rendering of the results (cf. Gauch, 1982; Greig-Smith, 1983; Whittaker, 1987). Another important finding from the individual foreland data sets was the changing relative microtopographic effects of exposure and late-snow-lie, which limited vegetation and soil development, at different altitudes. Thus, exposure is the more important microtopographic effect at lower altitudes, whereas late snow duration is more important at higher altitudes. The combined data set, however, only showed exposure to be the most important microtopographic effect across all the forelands - another "averaging out" effect of the combined data set.

Despite the advantages of using individual data sets for analysis, the combined data analysis shows clear advantages over the individual data sets. Most obvious is that the combined data set clarifies the effect of altitude on the vegetation patterns. Especially interesting results concern the relationship of assemblages, between forelands. For example, the Storbreen high TWINSPAN "final site group" data (Fig. 6.1f) consists of: mid-alpine assemblages on the oldest terrain; mainly low-alpine assemblages (including some mature) on the intermediate terrain; and pioneer assemblages that are found at all the altitudes within the survey. Furthermore, the most distinct assemblages, namely the alpine lichen heath assemblages and the (subalpine and alpine) pioneer assemblages, would not have been so apparent without analysis of the combined data set. Additionally, without the combined data set, it would not be possible to draw relationships between the united effects of altitude, age and microtopography on vegetation patterns (plus associated micro-environmental patterns) at a regional scale across the foreland sequences. Neither would it have been possible to construct the *"Altitude factor complex"*. The combined data set also enabled a confirmation of the main trends found by the individual data sets - for example that altitude is the most important influence on vegetation patterns, followed by age and microtopography; that exposure is the most important microtopographic effect overall. Thus the combined data set, as well as acting as a back-up to the individual foreland conclusions, led to the detection of a decline in the relative influence of age with altitude as the importance of microtopography increases.

7.5.2 Other technical contributions

The thesis has used a number of new methodologies and adapted a large number of others. A prototype capacitance probe, from the Institute of Hydrology, Wallingford (see section 2.6.2.1), was used to provide an alternative, quantitative, measure of moisture as well as to test the relative accuracy of the finger test method. The results from these measurements suggest that although the finger test method is useful as an approximate measure of moisture, it should not be considered as a reliable method of moisture measurement and a more quantitative method should be sought. A number of scales were developed for use within the study: a) a position scale of 1 (toe slope) to 5 (crest) was developed to provide the location of the sites across each moraine; b) two aspect scales, which entered the aspect of moraine slopes onto two specially developed circular scales for northerliness and easterliness, on scales of 1 to 5 respectively; and c) an age scale was developed which divided the age of the terrain into 11 successively older age-classes - each of the classes represents 25 years except for scale 11 which represents ground older than 250 years. Frequency of many environmental parameters (1/25 small squares) was used in preference to the use of a subjectively defined scale of none (0) to severe (3) (e.g. Crouch, 1992). Frequency was considered to be a more quantitative assessment and was used for most of the disturbance variables, including frost heave, fluvial activity, solifluction, trampling and grazing.

By referring to Appendix (8), it can be seen that the thesis has used a number of useful new presentation methods for the classification and ordination results and it is proposed that these form an important contribution in themselves. Many of the presentation methods are completely new while others are modifications of previous presentation methods. Many researchers put long hours of labour into data collection and analysis but then do not attempt to elucidate their findings by using new methods of presentation. The profile diagrams (Figs 4.2 to 4.10 and Figs. 6.1a-i) were developed to allow the examination of the TWINSPAN "site groups", along each of the moraine sequences, at all levels of subdivision so that the influence of the meso-environmental variables on the TWINSPAN site separation can be examined. From this the most ecologically meaningful site groups (or TWINSPAN "final site groups") were distinguished and separated. Colour is used to differentiate the "site group" separations at the different levels and is especially useful for any study which uses transects placed along a landscape profile.

The TWINSPAN "final species groups" were defined using the final tables produced by the TWINSPAN programme itself. The "final species groups" were then placed onto species charts, which showed the distribution and % cover of the species members of each of the groups across the individual forelands (Figs. 4.18-92) and combined forelands (Figs. 6.3-14). These charts are a very useful way of presenting the data because the location of TWINSPAN "final species groups" can be defined (Table 4.10 and Fig. 6.15) and related to the TWINSPAN "site groups". Colour has been used to represent each "final species group", with different colours representing a generalised description of each of the assemblage-types (e.g. red for lichen heath assemblages; pink for pioneer assemblages; purple for widespread assemblages). By investigating both the site and species data it is possible to double check the conclusions and provide a more reliable prediction of the location of the different assemblages. Furthermore, the use of "final groups", which were taken from several levels of subdivision, was considered to be a more ecologically meaningful separation of assemblage types (cf. Kent and Coker, 1992). The use of "final groups" contrasts with the previous work (e.g. Matthews, 1976; Whittaker, 1985; Crouch, 1992) which described all the assemblages separated at each level of subdivision. Despite the recent criticism of TWINSPAN (e.g. van Groenewoud, 1992) the TWINSPAN results have been shown to produce highly comparable results (i.e. between the forelands) at both high and low levels of subdivision and, most importantly, the results are generally ecologically meaningful.

DCA ordination was used in order to organise the data along a series and provide a comparable means of investigating the data of both the individual and combined data sets. The main presentation methods allow a direct comparison of the TWINSPAN and DCA results by superimposing the TWINSPAN "final group" data onto the ordination data. This is known as complementary analysis and is outlined in Kent and Ballard (1988). One of the techniques, namely DCA centroids of TWINSPAN "final group" scores and environmental parameter biplots (Figs. 5.1-16 and Figs. 6.17-18), has been used before (e.g. Crouch, 1992). The other, using the rank lists with the colour TWINSPAN species and site "final groups" superimposed onto axes (1) and (2), was developed for this study and are referred to as rank tables (Tables 5.1 to 5.16 and Table 6.4). The rank tables show the distinctness of the individual foreland TWINSPAN "final groups" along each ordination axis, as well as how they relate to each other and the environmental parameters. The rank tables provide a clear presentation of the complex individual foreland data and they can also lend support to the eigenvalues - i.e. whether or not assemblages are distinct. Although eigenvalues are generally a fairly safe guide as to the distinctness of "final groups" sometimes they are unreliable. A combination of rank tables and eigenvalues are therefore useful in order to elucidate the most distinct and meaningful "final groups". From the rank tables it was possible to construct sequence diagrams (Figs. 5.17 to 5.32; Tables 5.25 to 5.26; and Fig. 6.16) which show how the TWINSPAN "final groups" are related to one another and also to the prevailing environmental parameters on the DCA ordination axes (1) and (2). The newly developed presentation methods, in combination with earlier methods, provide an exhaustive approach to elucidating the patterns shown by TWINSPAN and DCA ordination analysis. Despite criticism concerning these techniques (e.g. van Groenewoud, 1992; Tausch et al., 1995) this author has found these techniques to provide comparable and ecologically meaningful results, for both medium-sized individual foreland and large combined foreland data sets, that have furthered our knowledge of the relationship between environmental and vegetation patterns on subalpine and alpine glacier forelands.

The presentation methods used within the present thesis were originally produced for the author to make full use of all the TWINSPAN and DCA output. However, it is proposed that the profile diagrams and rank tables are a useful method of presentation for those using TWINSPAN and DCA to investigate the relationship between vegetation and micro-environmental patterns along meso-environmental gradients.

The methodological contributions of the thesis may be summarised as follows:

1. The combined foreland data set showed certain **disadvantages** over the individual foreland data set: a) difficulties in identifying vegetation and environmental patterns on the DCA centroid plots and rank tables where the effects of altitude, age and microtopography interact; b) the combined rank table for sites was too cumbersome to use; c) the combined data set averages out the general effects of parameters and thus may obscure significant relationships involving particular environmental parameters; and d) the varying relationship, involving altitude, between the microtopographic influences of long snow duration and severe exposure, was not elucidated by analysis of the combined data set.
2. The combined foreland data set showed certain **advantages** over the individual foreland data set: a) it is possible to demonstrate the effect of altitude and construct an *"Altitude factor complex"* involving other environmental parameters associated with altitude; b) it is possible to show how the vegetation and environmental patterns are related between forelands, a major advantage; c) it summarises the main trends; and d) it is relatively quick to perform.
3. The three main aims of the thesis, concerning the general effects of microtopography on vegetation patterns and environment, were fulfilled using the results from the combined foreland data set (i.e. different glacier forelands). However, the combined data set results are complex and benefit from additional back-up from less complex data (i.e. individual glacier foreland data sets) in order to provide a deeper, and more reliable, understanding of the processes at work on the forelands. It is therefore suggested that both individual foreland and combined data set analyses should be carried out for a detailed and reliable account of the effects of environment on vegetation patterns at a number of different glacier forelands.
4. A range of scales and methodologies are recommended.
5. New techniques included the use of a prototype capacitance probe to measure moisture; the development of new scales for the measurement of position, aspect and age; and the use of ordinal-scale estimates of disturbance variables including frost, fluvial activity, solifluction, trampling and grazing, based on frequency counts.
6. The use of a classification and an ordination technique to analyse the data thoroughly, as well as exhaustive presentation techniques to display the information derived from these techniques, is

recommended in order to provide a thorough and ecologically meaningful interpretation of the results, and this suggestion is supported by other researchers (e.g. Matthews, 1976; Whittaker, 1985; Crouch, 1992; Kent and Coker, 1992).

7. A number of new presentation methods, summarised in Appendix (8), were developed the most notable being the profile diagrams and the use of "final groups" in, for example, summary tables and rank diagrams.

7.6 Limitations and proposals for future research

Within any study there is always room for improvement and the present study is no exception. Some of the sampling procedures would have given a clearer view of the prevailing environment had they been of an even more comprehensive nature. Although great effort was put into recording the environment, certain parameters need, ideally, to be studied further, using more reliable and refined methods, such as that attempted for quantitative moisture measurement using the prototype capacitance probe. More detailed work on the relationship between the most important environmental parameters, associated with the "*Microtopography - exposure - snow-lie - frost - moisture - fluvial activity - factor complex*" (as found by the present study), and topography is needed. The results of the present thesis suggest that the factors associated with microtopography change noticeably along slope gradients and yet, as outlined in chapter (1), very little previous work has been carried out on these relationships. The present study provides a starting point for work on the relationship between topography-related plant distribution patterns and moisture, snowlie and exposure gradients, during succession at a range of altitudes. However, most of the methods used to record the environmental parameters, within the microtopographic factor complex, were carried out using ordinal scale measurements. The use of these methodologies has been adequately justified, and two of the methods (i.e. the finger test, using the capacitance probe; and the frequency of frost heave evidence, using dowel heave) have been supported by the use of quantitative measurements. Nevertheless, further tests of their accuracy using quantitative recording techniques would provide further support for the utilisation of these simple, efficient and cheap methods of environmental evaluation. Further work on the snow duration (% black : green lichens) and exposure (position) scales is especially recommended. Previous research (e.g. Haines-Young, 1983, 1985; Elven, 1975; Vetaas, 1986) can be used to support the use of these methodologies, but their use for the specific purpose of estimating snow duration or exposure has, as yet, to be confirmed.

The present work is considered as a starting point for work on the effects of altitude and microtopography on plant (and micro-environmental) patterns during succession, and thus it is suggested that further work should be carried out in order to provide a more comprehensive understanding of these relationships. For example, further testing of reliable methods of moisture assessment and then the use of these methods to carry out detailed investigations into the relationship between moisture and plant assemblage patterns or individual species distributions, would be of great interest and use. Results from the present study show an unimportant relationship between terrain-age and moisture, but a strong relationship between moisture and microtopography and this supports the work of some (e.g. Whittaker, 1985), but refutes others (e.g. Crouch, 1992). It would therefore be useful to investigate further the relationship between altitude, terrain age, soil development, assemblage patterns, other abiotic factors (such as snow patterns and duration, and exposure to wind) and moisture. Recently, an increasing number of researchers are using Geographic Information Systems (GIS) to investigate these relationships (cf. Walker et al, 1989; Walker et al, 1993; Price and Heywood, 1994) and the use of a geoecological approach for micro- and meso-scale data collection, in combination with GIS to aid interpretation on a wider scale, would be of particular interest. Practical applications of such studies would include the provision of a sound understanding of natural successional sequences on glacier forelands (and surroundings) so that realistic interpretation and prediction can be made of the vegetation pattern and succession within large-scale degraded arctic or alpine landscapes.

For a complete understanding of succession, all factors that affect the sequence of plant assemblages need to be investigated, including the influence of human activity as well as wild animals. Grazing and trampling are parameters that are difficult to estimate easily. Although other studies have found both these parameters, especially grazing, to have a highly significant and widespread influence on vegetation patterns (e.g. Emanuelsson, 1984; Magnusson and Magnusson, 1992; Hik et al, 1992; Bock et al, 1995), it was not within the scope of the present study to demonstrate their significance adequately. Emanuelsson (1984) showed that rodents are highly selective in the way in which they influence dwarf shrub species, especially as a result of winter grazing under snow. Emanuelsson's study has important implications for researchers interested in understanding successional sequences, in arctic and alpine landscapes, and the effects of rodents (and other widespread, but relatively inconspicuous, grazers such as birds and insects) need to be considered to a much greater extent than previously. The sampling methodology, using sections of moraine with optimal vegetation, mitigated against the sampling of sites exposed to large amounts of trampling or grazing. The measurement of grazing and trampling, for present study purposes, was only able to highlight patches of heavy trampling or grazing. This permitted the explanation of some anomalies in the data set and was therefore useful but not comprehensive. Future research into the effects of grazing and trampling on the glacier forelands, in relation to altitude, age and microtopography, would be of great interest and use, especially with regard to the conservation of areas that may be sensitive to these disturbance factors. A number of possibilities exist with regard to questions concerning the role of grazing (of domestic livestock) and trampling (human or livestock) across the forelands in relation to microtopography, age and altitude. For example: Is there any pattern of livestock grazing and trampling with regard to landscape variations and age? Do the grazers show preference for certain species so that succession is diverted in another direction to areas which are ungrazed? Does the pattern of grazing appear to be more related to preference for certain species or to accessibility or position (i.e. the need for shelter or a vantage point)? Bock et al., (1995) emphasise the need for further investigation of the relationship between ungulates and higher plant evolution (i.e. possible causes of genetic change), which would also be of relevance to developing the theme within the present thesis.

A number of elements were left out of the thesis, not because they were considered to be unimportant, but because their inclusion would have caused certain difficulties. Although an attempt was made to choose moraines of similar size and shape it should be possible to incorporate measures of these diverse parameters in future studies. Several measures of size using height, volume or a height/transect length ratio were attempted by the present author but preliminary results showed the measurements to be misleading as they did not take shape into consideration. Instead the profile diagrams (drawn to scale) were used to provide an accurate visual assessment of the size and shape of the moraines and these provided a meaningful and easily interpretable method of assessment. The results suggest that, on certain forelands, size and shape of moraine have a considerable influence on vegetation patterns (see section 7.4.1). Although no other studies, as far as the author is aware, have investigated this problem, Alexander (1986) investigated micro-scale soil variability at crest positions along a short moraine ridge. His results showed that microtopography is sufficient to cause differences in micro-climate, along the ridge crest, causing differences in vegetation and soil development. This suggests that size and shape of the moraine can cause variability in vegetation and soil development along its length. He suggested that the differences could be caused by differences in snow-lie and exposure. The possibility that size and shape of moraine influences vegetation patterns (and the prevailing micro-environment) suggests that a specific investigation could be made of the relationship between size and shape of the microtopographic feature and the prevailing vegetation and environmental patterns. The implications of such a study would be to provide valuable information especially with regard to an understanding of the use of so-called homogenous and heterogeneous landscapes for successional studies. Once an efficient and practical method of assessing the size and shape of microtopographical features has been found, examples of questions to be answered would include: Given that microtopography has an influence on environmental and vegetation patterns and successional pathways, how does the size and shape of glacial moraines influence these factors across a sequence of moraines of increasing age? Does altitude affect the relative influence of moraine size and shape on environmental and vegetation patterns and successional sequences?

Another important component that was left out of the data set were the bryophytes (except for the recording of total cover of all bryophyte species). Bryophytes have been found to be important environmental indicators (Crouch, 1992) and would have been useful within the present study. The main reason for not including them was the time that would have been required for their inclusion within the data sets. The cryptogams are difficult to identify and so the lichens, which have also been found to be important micro-environmental indicators (Flock, 1978; Longton, 1988; Crouch, 1992), were used to represent the cryptogam component. It was considered more important to include a larger number of sites, at various altitudes, at the expense of investigating the effects of microtopography on the bryophytes. Future researchers carrying out detailed studies on aspects of the effects of microtopography on plant distribution patterns and associated environmental patterns (some such studies have been outlined above), should include the environmentally sensitive bryophytic component within their data sets.

There are always special problems associated with ecological fieldwork on glacier forelands in arctic and alpine environments (Crouch, 1992). The low-alpine foreland sequences (at Storbreen and Svellnosbreen) have young terrain at the mid-alpine altitude and this has been a problem for previous researchers, especially at Storbreen where most of the previous vegetation work, in this region, has been carried out. A certain amount of common sense has to be used when interpreting the data and the inclusion of altitude and age, within the data sets, does much to prevent the results from being misleading. Interestingly there are considerable similarities between the pioneer assemblages found on the subalpine forelands and on the mid-alpine forelands (see Fig. 7.3) and so it is suggested that an early low-alpine pioneer assemblage could also comprise species similar to those found on the sub- and mid-alpine forelands. To corroborate the findings of the present study it would be helpful to find a low-alpine foreland that has low-alpine pioneer assemblages. At the same time it would also be useful to sample further sequences from one or two forelands within the 700 to 1100 m altitudinal zone to complete the altitudinal sequence described within the present study. And lastly, future work could provide additional information especially concerning low-alpine pioneer assemblages as well as the assemblages within the subalpine - low-alpine transition zone.

Some specific limitations of the present study and proposals for future research following from them are summarised as follows:

1. The finger test method is only an approximate measure of soil moisture and a more accurate, quantitative approach should be sought.
2. The sampling design fulfilled the intention of the study to pinpoint anomalies of vegetation pattern caused by heavy trampling or grazing. However, as grazing and trampling are likely to be a significant influence on vegetation and environmental patterns, it is suggested that further work should be carried out on the relative effect of these disturbance factors.
3. The use of profile diagrams to elucidate the size and shape of moraines in relation to vegetation patterns, and associated environmental patterns was considered to be satisfactory for the purposes of the present study. However, size and shape of moraine are likely to be a significant influence on the relative effects of microtopography, and future work, on the specific effects of these factors, is recommended.
4. Although the total cover of bryophytes was recorded, individual species were not. The total cover measurement was useful for present study purposes, but the measurement of bryophytes, due to their environmental sensitivity, is recommended for those intending to carry out detailed work on the relationships between certain environmental factors and vegetation patterns, in order to obtain a more complete knowledge of the vegetation in glacier foreland environments.
5. Sampling in the field often requires a certain amount of compromise since the sampling situation may not be perfect. Further work, to investigate low-alpine pioneer assemblages, as well as sequences from the 700 to 1100 m altitude would be useful to corroborate the findings of the present study.

7.7 Final word

This study has followed J.A. Matthews, R.J. Whittaker, H. Crouch, and others, in the fascinating pursuit of knowledge and understanding of primary succession on recently deglaciated terrain. The study has been successful in its attempt to investigate the effects of microtopography on vegetation patterns on a number of glacier forelands using a variety of different methods. It has answered the three main aims of the thesis: by analysing the specific environmental parameters comprising the microtopographic gradients; by describing the distribution of individual species and plant assemblages across microtopographic gradients of similar type (i.e. moraine slopes) but different ages and altitudes; and by interrelating the vegetational and environmental variation and hence providing an explanation of the vegetation in terms of both successional stage and environmental factors. The study has provided some interesting and, sometimes, original results and conclusions, and the wide-ranging nature of the thesis opens up an endless array of avenues for further and deeper investigation.

REFERENCES

Alexander, E.B., and Burt, R. (1996). Soil development on moraines of Mendenhall Glacier, southeast Alaska. 1. The moraines and soil morphology. *Geoderma*, **72**, 1-17.

Alexander, M.J. (1983). Soil development at Engabredal, Holandsfjord, north Norway. In: J. Rose (Ed.), *Okstindan Research Project Preliminary Report 1980-1981*. Reading University, England, pp. 1-23.

Alexander, M.J. (1986). Micro-scale soil variability along a short moraine ridge at Okstindan, northern Norway. *Geoderma*. **37**, 341-360.

Allaby, M. (1994). *The Concise Oxford Dictionary of Ecology*. Oxford University Press.

Allaby, M. (1998). *The Oxford Dictionary of Plant Sciences*. Oxford University Press.

Anderson, H.W. (1947). Soil freezing and thawing as related to some vegetation, climatic and soil variables. *J. For.*, **45**, 95-101.

Archer, A.C. (1973). Soils and vegetation of the lateral moraine at Malte Brun, Mount Cook Region, New Zealand. *New Zealand J. Bot.*, **11**, 23-48.

Arnalds, A. (1984). Eolian nature and erosion of some Icelandic soils. *J. Agri. Res. Iceland*, **16**, 21-35.

Arnalds, A. (1987). Ecosystem disturbance in Iceland. *Arc. Alp. Res.*, **19** (4), 508-513.

Auerback, N.A. and Halfpenny, J.C. (1991). Snowpack and the subnivean environment for different aspects of an open meadow in Jackson Hole, Wyoming, U.S.A. *Arc. Alp. Res.*, **23** (1), 41-44.

Ballantyne, C.K. & Matthews, J.A. (1983). Desiccation cracking and sorted polygon development, Jotunheimen, Norway. *Arc. Alp. Res.*, **15**(3), 339-349

Barclay-Estrup, P. (1971). The description and interpretation of cyclical processes in a heath. *J.Ecol.*, **59**, 143-166.

Bateson, S.R. (1970). Preliminary observations on vegetation succession and environmental influences in front of a glacier. *Horizon (J. KCL & LSE)*, **19**, 56-66.

Battey, M.H. (1975). (unpublished). The geology of the area around Storbreen. (Report of the 1974 Jotunheim Research Expedition).

Bazzaz, F.A. (1987). Experimental studies on the evolution of niche in successional plant populations. In: *Colonisation, Succession and Stability*. 26th Symposium of "The British Ecological Society", eds: Gray et al., **26**, 245-272, Oxford: Blackwell.

Begon, M., Harper, J.L., and Townsend, C.R. (1996). *Ecology*. 3rd Edition. Blackwell, Oxford.

Bell, J.P. (1976). Neutron probe practice. *Institute of Hydrology Report No. 19.*

Bell, J.P., Dean, T.J., and Hodnett, M.G. (1987). Soil measurement by an improved capacitance technique, part II. Field techniques, evaluation and calibration. *J. Hydrol*, **93**, 79-90.

Benedict, J.B. (1990a). Lichen mortality due to late-lying snow: results of a transplant study. *Arc. Alp. Res.*, **22** (1), 81-89.

Benedict, J.B. (1990b). Experiments in lichen growth. I. Seasonal patterns and environmental controls. *Arc. Alp. Res.*, **22** (3), 244-254.

Benedict, J.B. (1991). Experiments on lichen growth II. Effects of a seasonal snow cover. *Arc. Alp. Res.*, **23** (2), 189-199.

Bickerton, R.W., and Matthews, J.A. (1992). On the accuracy of lichenometric dates: an assessment based on the "Little Ice Age" moraine sequence of Nigardsbreen, southern Norway. *The Holocene*, **2**, 227-237.

Bickerton, R.W., and Matthews, J.A. (1993). "Little Ice Age" variations of outlet glaciers from the Jostedalsbreen ice-cap, S. Norway: a regional lichenometric-dating study of ice-marginal moraine sequences and their climatic significance. *J. Quat. Sci.*, **8**(1), 45-66.

Billings, W.D. (1952). The environmental complex in relation to plant growth and distribution. *Quat. Rev. Biol.*, **27**(3), 253-265.

Billings, W.D. (1974). Arctic and alpine vegetation plant adaptations to cold climates. In *Arctic & Alpine environments*. Eds: J.D. Ives & R.G. Barry. pp. 403-443

Billings, W.D. and Bliss, L.C. (1959). An alpine snowbank environment and its effects on vegetation, plant development, and productivity. *Ecology*, **40** (3), 388-97.

Birkeland, P.W. (1984). Holocene soil chronofunctions, Southern Alps, New Zealand. *Geoderma*, **34**, 115-134.

Birkeland, P.W., and Burke, R.M. (1988). Soil catena chronosequences on E. Sierra Nevada moraines, California, U.S.A. *Arc. Alp. Res.*, **20** (4), 473-484.

Birks, H.J.B. (1980). The present flora and vegetation of the moraines of the Klutlan Glacier Yukon Territory, Canada. *Quaternary Research*, **14**, 60-86.

Biswell, H.H., Schultz, A.M., Hendrick, D.W. and Mallory, J.L. (1953). Frost heaving of grass and brush seedlings on burned chamise brushlands in California. *J. Range Manage.* **6** (3), 172-180.

Bormann, B.T. and Sidle, R.C. (1990). Changes in productivity and distribution of nutrients in a chronosequence at Glacier Bay National Park, Alaska. *J. Ecol.*, **78**, 561-578.

Bowman, W.D. (1992). Inputs and storage of nitrogen in winter snowpack in an alpine ecosystem. *Arc. Alp. Res.*, **24**, 211-215.

Brandani A.A. (1983). Glacial processes and disturbance in vegetation richness. In *Tills and related deposits*, eds. E.B. Evenson, Ch. Schlüchter & J. Rabassa, 403-10. Roterdam: Balkema.

Braun, E.L. (1936). Forests of the Illinoian till plain of southwestern Ohio. *Ecol. Monogr.*, **6**, 89-149.

Braun, E.L. (1956). The development of association and climax concepts: Their use in interpretation of deciduous forests. *Amer. J. Bot.*, **43**, 906-911.

Brink, V.C., Mackay, J.R., Freyman, S and Pearce, D.G. (1967). Needle ice and seedling establishment in southwestern British Columbia. *Can. J. Plant Sci.*, **47**, 135-139.

Broady, P.A., Given, D., Greenfield, L.G. and Thompson, K. (1987). The biota and environment of fumaroles on Mount Melbourne, northern Victoria Land. *Polar Biology*, 7, 97-113.

Burrows, C.J. (1990). *Processes of Vegetation Change*. London: Unwin Hyman.

Burt, R., and Alexander, E.B. (1996). Soil development on moraines of Mendenhall Glacier, southeast Alaska. 2. Chemical transformations and soil micromorphology. *Geoderma*, **72**, 19-36.

Canada Soil Survey Committee. (1978). *The Canadian System of Soil Classification*. Ottawa: Supply & Service Canada. (Canada Department of Agriculture, Publication No. 1646)

Carleton, T.J., Stitt, R.H. & Nieppola, J. (1996). Constrained indicator species analysis (COINSPAN): an extension of TWINSPAN. *J. Veg. Sci.*, 7, 125-130.

Caseldine, C.J. (1989). Pollen assemblage-plant community relationships on the Storbreen glacier foreland, Jotunheimen mountains, southern Norway. *New Phytologist*, **III**, 105-118.

Chambers, J.C., MacMahon, J.A., and Brown, R.A. (1990). Alpine seedling establishment: the influence of disturbance type. *Ecology*, **71**, 1323-1341.

Chapin III, F.S. (1993). Physiological controls over plant establishment in primary succession. In *Primary Succession on Land*, eds. J. Miles and D.H. Walton, Oxford: Blackwell Scientific Publications (in press).

Chapin III, F.S., Walker, L:R., Fastie, C.L. and Sharman, L.C. (1994). Mechanisms of post-glacial primary succession at Glacier Bay, Alaska. *Ecol. Mono.*, **64**, 149-175.

Chapin, D.M. (1996). Nitrogen mineralisation, nitrification, and denitrification in a high Arctic lowland ecosystem, Devon Island, N.W.T., Canada. *Arc. Alp. Res.*, **28**(19), 85-92.

Christensen, N.L. and Peet, R.K. (1984). Convergence during secondary forest succession. *J. Ecol.*, **72**, 25-36.

Churchill, E.D. and Hanson, H.C. (1958). The concept of climax in Arctic and Alpine Vegetation. *Botanical Review*, **24**, 127-191.

Clements, F.E. (1916). *Plant succession: an analysis of the development of vegetation*. Washington D.C: Carnegie Institution of Washington.

Clements, F.E. (1936). Nature and structure of the climax. *J. Ecol.*, **24**, 252-84.

Coker, P.D. (1988). *Some aspects of the biogeography of the Høfjellet with special reference to Høyrokampen, Bøverdal, Southern Norway*. Thesis submitted for the M.Phil. degree University College, London, January 1988.

Coker, P.D. (1994). Plant communities and environ-mental relationships, Høydal, Jotunheimen, S Norway. *Coll. Phyt.*, **23**, 339-358.

Colinvaux, P.A. (1973). *Introduction to Ecology*. New York: Wiley.

Connell, J.H. and Slatyer, R.O. (1977). Mechanisms of succession in natural communities and their role in community stability and organisation. *American Naturalist*, **111**, 1119-44.

Coombe, D.E. and White, F. (1951). Notes on calcicolous communities and peat formation in Norwegian Lappland. *J. Ecol.*, **39**, 33-62.

Cooper, W.S. (1916). Plant succession in the Mount Robson region, British Columbia. *The Plant World*, **19**, 211-38.

Cooper, W.S. (1923a). The recent ecological history of Glacier Bay, Alaska: I. The interglacial forests of Glacier Bay. *Ecology*, **4** (2), 93-128

Cooper, W.S. (1923b). The recent ecological history of Glacier Bay, Alaska: II. The present vegetation cycle. *Ecology*, **4**, 223-46.

Cooper, W.S. (1923c). The recent ecological history of Glacier Bay, Alaska: III. Permanent quadrats at Glacier Bay : An initial report upon a long-period study. *Ecology*, **4**, 355-65.

Cooper, W.S. (1926). The fundamentals of vegetation change. *Ecology*, **7**, 391-413.

Cooper, W.S. (1931). A third expedition to Glacier Bay, Alaska. *Ecology*, **12**, 61-95.

Cooper, W.S. (1939). A fourth expedition to Glacier Bay, Alaska. *Ecology*, **20**, 130-55.

Cooper, W.S. (1942). Vegetation of the Prince William Sound region, Alaska; with a brief excursion into post-Pleistocene climatic history. *Ecol. Monog.*, **12**, 1-22.

Cowles, H.C. (1919). Review of Clements' "Plant Succession". *Bot. Gaz.*, **68**, 477-478.

Crawford, R.M.M. (1989). *Studies in plant survival.* Oxford: Blackwell.

Crocker, R.L. and Major, J. (1955). Soil development in relation to vegetation and surface age at Glacier Bay, Alaska. *J. Ecol.*, **43**, 427-48.

Crocker, R.L., and Dickson, B.A. (1957). Soil development on the recessional moraines of the Herbert and Mendenhall Glaciers, south-eastern Alaska. *J. Ecol*, **45**, 169-85.

Crouch, H. (1992). *Cryptogam distribution patterns and successional sequences on a glacier foreland in southern Norway.* Ph.D. thesis, University of Greenwich, U.K.

Crouch, H. (1993). Plant distribution patterns and primary succession on a glacier foreland: A comparative study of cryptogams and higher plants. In *Primary Succession on Land,* eds. J. Miles and D.W.H. Walton, pp 133-145. Oxford: Blackwell Scientific Publications.

Dahl, E. (1956). Rondane: mountain vegetation in south Norway and its relation to environment. *Skrifter utgitt av det Norske Videnskaps Academie i Oslo. Matematisk-naturvidenskapelig klasse*, **3**, 1- 374.

Dahl, E., and Krog, H. (1973). Macrolichens. Universitetsforlaget.

Dean, T.J. (1994). The IH capacitance probe for measurement of soil water content. *IH Report No. 125.*

Decker, H.F. (1966) Plants. In *Soil development and Ecological Succession in a Deglaciated Area of Muir Inlet, Southeast Alaska*, ed. A. Mirsky, pp. 73-95. Columbus, Ohio: Ohio State University Research Foundation. (Institute of Polar Studies, Report No. 20)

Del Moral, R. (1993). Mechanisms of primary succession on volcanoes: a view from Mt. St Helens. In *Primary Succession on Land*, eds. J. Miles and D.W.H. Walton, pp 79-100. Oxford: Blackwell Scientific Publications.

Dobson, F.S. (1979). *Lichens, an illustrated guide*, Richmond, Surrey.

Douglas, G.W. (1972). Subalpine plant communities of the western North Cascades, Washington. *Arc. Alp. Res.*, **4**, 147-166.

Douglas, G.W. and Bliss, L.C. (1977). Alpine and high subalpine plant communities of the North Cascades Range, Washington and British Colombia. *Ecol. Monogr.*, **47**, 113-150.

Drury, W.H. and Nisbet, I.C.T. (1973). Succession. *J. Arn. Arb.*, **54**, 331 - 68.

Durocher, M.J. (1847). Étudees sur les glaciers du nord et du centre de l'Europe. *Annales des mines, Série 4,* 12, 3-142 (Paris).

Egler, F.E. (1954). Vegetation Science Concepts. 1. Initial floristic composition: a factor in old-field vegetation development. *Vegetatio*, **4**, 412-417.

Egler, F.E. (1970). *The way of Science. A philosophy of Ecology for the Layman.* Hafner, New York.

Ellis, S. (1979). The identification of some Norwegian mountain soil types. *Norsk Geografisk Tidsskrift*, **33**, 205-12.

Ellis, S. (1980). Soil-environmental relationships in the Okstindan mountains, north Norway. *Norsk Geografisk Tidsskrift*, **34**, 167-176.

Elven, R. (1975). Plant communities on recently deglaciated moraines at Finse, southern Norway. In *IBP in Norway, Methods and Results Section PT-UM Grazing Project, Hardangervidda Botanical Investigations. Appendix I*, eds. Norwegian National IBP Committee, 381-467. Oslo: Norwegian National IBP Committee. (Norwegian National IBP Committee, Annual Report for 1974)

Elven, R. (1978) Association analysis of moraine vegetation at the glacier Hardangerjøkulen, Finse, South Norway. *Norwegian Journal of Botany*, **25**,171-91.

Elven, R., and Ryvarden, L. (1975). Dispersal and primary establishment of vegetation. *Ecol. Studies. Fenn. Tundra Ecosystems*. **16** (1), 82-85.

Emanuelsson, U. (1984a). I. Dynamics of dwarf shrub heaths in relation to grazing of small rodents in the Torneträsk area, northern Sweden. 45 pp. In: *Ecological effects of grazing and trampling on mountain vegetation in northern Sweden*. Ph.D. thesis, University of Lund, Sweden.

Emanuelsson, U. (1984b). II. Short-term effects of trampling in subalpine and alpine ecosystems in the Torneträsk area, northern Sweden. 72 pp. In: *Ecological effects of grazing and trampling on mountain vegetation in northern Sweden*. Ph.D. thesis, University of Lund, Sweden.

Emanuelsson, U. (1984c). III. Vegetation zonation on tracks through dwarf shrub heaths in the Torneträsk area, northern Sweden. 40 pp. In: *Ecological effects of grazing and trampling on mountain vegetation in northern Sweden*. Ph.D. thesis, University of Lund, Sweden.

Erikstad, L. and Sollid, J. L. (1986). Neoglaciation in South Norway using lichenometric methods. *Norsk Geografisk Tidsskrift*, **40**, 85-105.

Evans, B.M., Walker, D.A., Benson, C.A., Nordstrand, E.A., and Petersen, G.W. (1989). Spatial relationships between terrain, snow distribution and vegetation patterns at an arctic foothills site in Alaska. *Holarctic Ecology*, **12**, 270-278.

Evans, R.D. and Fonda, R.W. (1990). The influence of snow on subalpine meadow community pattern, North Cascades, Washington. *Can. J. Bot.*, **68**, 212-220.

Fægri, K. (1933). Über die Längenvariationen einiger Gletscher des Jostedalsbre und die dadurch bedingten Pflanzensukzessionen. *Bergens Museums Årbok 1933, Naturvidenskapelig rekke*, 7, 1-255.

Fægri, K. (1937). Some recent publications on phytogeography in Sweden. *Bot. Rev.*, **3**, 425-456.

Finegan, B. (1984). Forest Succession. *Nature*, **312**, 109-14.

Fitter, A. (1984). Succession theory is too reductionist. *Nature*, **312**, 705.

Fitter, A.H., and Parsons, W.F.J. (1987). Changes in phosphorous and nitrogen availability on recessional moraines of the Athabasca glacier, Alberta. *Can. J. Bot.*, **65**, 210-213.

FitzPatrick, E.A. (1974). *An introduction to soil science*. Oliver and Boyd, Edinburgh.

Flock, J.W. (1978). Lichen-bryophyte distribution along a snow-cover-soil-moisture gradient, Niwot ridge, Colorado.

Fox, J.F. (1981). Intermediate levels of soil disturbance maximise alpine plant diversity. *Nature,* **293**, 564-565.

Frenot, Y., et al. (1995). Particle translocation and initial soil development on a glacier foreland, Kerguelen Isls, subantarctic. *Arc. Alp. Res.*, **27**(2), 107-115.

Friðriksson, S., & Magnússon, B. (1992). Development of the ecosystem on Surtsey with references to Anak Krakatau. *Geojournal*, **28**, 287-291.

Gauch, H.G., Jr. (1982). *Multivariate Analysis in Community Ecology.* Cambridge Studies in Ecology 1. Cambridge University Press, Cambridge.

Gauch, H.G. & Whittaker, R.H. (1981). Hierarchical classification of community data. *J. Ecol.*, **69**, 135-52.

Gellatly, A.F. (1986). Establishment of soil cover on tills of variable texture and implications for interpreting paleosols - a discussion. *Int. Geom.*, Part II, 775-785

Gelting, P. (1955). A west Greenland *Dryas integrifolia* community rich in lichens. *Svensk Bot. Tidsk.* **49**, 295-313.

Gittins, R. (1965). Multivariate approaches to a limestone grassland community. III. A comparative study of ordination and association analysis. J. Ecol. 53. pp. 411-425.

Gjærevoll, O. (1950). The snow-bed vegetation in the surroundings of Lake Torneträsk, Swedish Lappland. *Svensk Bot. Tidsk.* **44**, 387-440.

Gjærevoll, O. (1952). Botanik og vegbygging I høgfjellet. *Syn og Segn.*, 1-8 pp.

Gjærevoll, O. (1954). Kobresieto- Dryadion in Alaska. *Nytt Mag. Bot.* **3**, 51-54.

Gjærevoll, O. (1956). The plant communities of Scandinavian alpine snow-beds. *Det Kongelige Norske Videnskabers Selskabs Skrifter for 1956*, **1**, 1-406.

Gjærevoll, O. and Jørgensen, R. (1978). *Mountain Flowers of Scandinavia.* Keller and Toft: Trondheim.

Gleason, H.A. (1917). The structure and development of the plant association. *Bulletin of the Torrey Botanical Club*, **44**, 463-81.

Gleason, H.A. (1927). Further views of the succession concept. *Ecology*, **8**, 299-326.

Gleason, H.A. (1936). Twenty-five years of ecology, 1910-1935. *Memoirs of the Brooklyn Botanical Club,* **4**, 41-49.

Gleason, H.A. (1939). The individualistic concept of the plant association. *The American Midland Naturalist*, **21**, 92-110.

Goulet, F. (1995). Frost heaving of forest tree seedlings: A review. *New forests*, **9**, 67-94.

Grace, J., & Unsworth, M.H. (1988). Climate and microclimate of the uplands. In: *Ecological change in the uplands.* eds: Usher & Thompson, Special publications series of the British Ecological Society 7: 137-150. Oxford: Blackwell.

Gray, A.J. (1987). Genetic change during succession in plants. In: *Colonisation, Succession and Stability.* 26th Symposium of "The British Ecological Society", eds: Gray et al., **26**, 273-293 Oxford: Blackwell.

Gray, A.J., Crawley, M.J., and Edwards, P.J. (1987). *Colonisation, Succession and Stability.* 26th Symposium of "The British Ecological Society". Oxford: Blackwell.

Green, F.H. & Harding, R.J. (1980). Altitudinal gradients of air temperature in S. Norway. *Geogr. Ann.*, **62A** (1-2), 29-36.

Greig-Smith, P. (1983). *Quantitative Plant Ecology.* 3rd ed., Studies in Ecology, Vol. 9, Blackwell Scientific, Oxford.

Griffey, N.J. and Matthews, J.A. (1978). Major neoglacial glacier expansion episodes in S Norway: evidence from moraine ridge stratigraphy. *Geog. Annals*, **60**A(1-2): 73-90

Grove, J.M. (1988). *The Little Ice Age.* London: Methuen.

Grubb, P.J. (1987). Some generalising ideas about colonisation and succession in green plants and fungi. In . *Colonisation, Succession and Stability.* eds. A.J. Gray, M.J. Crawley, and P.J. Edwards, pp. 81-102. Oxford: Blackwell Scientific Publications.

Gunnlaugsdóttir, E. (1985). Composition and dynamical status of heathland communities in Iceland in relation to recovery measures. *Acta Pyhtogeographica Suecica*, **75**, 84pp.

Haines-Young, R.H. (1983). Size variation of *Rhizocarpon* on moraine slopes in S. Norway. *Arc. Alp. Res.*, **15** (3), 295-305.

Haines-Young, R.H. (1985). Discussion of "size variation of *Rhizocarpon...*": A reply. *Arc. Alp. Res.*, **17**, 212-216.

Haines-Young, R.H. (1988). Size-frequency and size-density relationships in populations from the *Rhizocarpon sub-genus Cern.* *J. Biogeog.*, **15**, 863-878.

Hanson, H.C. (1950). Vegetation and soil profiles in some solifluction and mound areas in Alaska. *Ecology*, **31**, 606-630.

Hanson, H.C. (1951). Characteristics of some grassland, marsh, and other plant communities in western Alaska. *Ecol. Monog.*, **8**, 317-378.

Hanson, H.C. (1953). Vegetation types in northwestern Alaska and comparisons with communities in other arctic regions. *Ecology*, **34**, 111-140.

Harper, J.L. (1987). *Population Biology of Plants.* London: Academic Press.

Hastings, S.J., Luchessa, S.A., Oechel, W.C. and Tenhunen, J.D. (1989). Standing biomass and production in water drainages of the foothills of the Philip Smith Mountains, Alaska. *Holarctic Ecology.* **12**, 304-311.

Hedberg, O, Martensson, O., and Rudberg, S. (1952). Botanical investigations in the Paltsa region of northernmost Sweden. *Bot. Not.*, Supl. **3**, 1-209.

Heilbronn, T.D. and Walton, D.W. (1984). Plant colonisation of actively sorted stone stripes in the Subantarctic. *Arctic and Alpine Research*, **16** (2), 161-172.

Helm, D.J., and Allen, E.B. (1995). Vegetation chronosequence near Exit Glacier, Kenai Fjords National Park, Alaska, USA. *Arc. Alp. Res.*, **27** (3), 246-257.

Helm, D.J., Allen, E.B., and Trappe, J.M. (1996). Mycorrhizal chronosequence near Exit Glacier, Alaska. *Can. J. Bot.*, **74**, 1496-1506.

Hibbs, D.E. (1983). Forty years of forest succession in central New England. *Ecology*, **64**, 1394-401.

Hik, D.S., Jefferies, R.L., and Sinclair, A.R.E., (1992). Foraging by geese, isostatic uplift and asymmetry in the development of salt-marsh plant communities. *J. Ecol*, **80**, 395-406.

Hill, M.O. (1979a). *DECORANA - a FORTRAN Program for Detrended Correspondence Analysis and Reciprocal Averaging.* Cornell University, Department of Ecology and Systematics, Ithaca, New York.

Hill, M.O. (1979b). *TWINSPAN - a FORTRAN Program for arranging Multivariate Data in an ordered Two Way Table by classification of the Individuals and the Attributes.* Cornell University, Department of Ecology and Systematics, Ithaca, New York.

Hill, M.O., and Gauch, H.G. (1980). Detrended correspondence analysis, an improved ordination technique. *Vegetatio*, **42**, 47-58.

Hoel, A., and Werenskiold, W. (1962). Glaciers and snowfields in Norway. *Norske Polarinst. Skrift.* **114**, 1-291.

Holtmeier, F, and Broll, G. (1992). The influence of tree islands and microtopography on pedoecological conditions in the forest-alpine tundra ecotone on Niwot Ridge, Colorado Front Range, USA. *Arc. Alp. Res.*, **24** (3), 216-228.

Hopkins, D.M. and Sigafoos, R.S. (1951). Frost action and vegetation patterns on Seward Peninsula, Alaska. *U.S. Geol. Survey, Bull.* **974C**, 51-101.

Hopkins, D.M. and Sigafoos, R.S. (1954). Role of frost thrusting in the formation of tussocks. *Amer. Jour. Sci.*, **252**, 55-59.

Horn, H.S. (1974). The ecology of secondary succession. *Annual Review of Ecology and Systematics*, **5**, 25-37.

Hurlbert, S.H. (1984). Pseudoreplication and the design of ecological field experiments. *Ecological Monographs*, **54**, 187-211.

Innes, J.L. (1985). Moisture availability and lichen growth: effects of snow-cover and streams on lichenometric measurements. *Arc. Alp. Res.*, **17** (4), 417-424.

Jacobson, G.L. Jnr and Birks, H.J.B. (1980). Soil development on recent end moraines of the Klutlan Glacier, Yukon Territory, Canada. *Quaternary Research*, **14**, 87-100.

Jahns, H.M. (1980). *Collins guide to the Ferns, Mosses and Lichens of Britain and Northern and Central Europe.* Collins, Grafton St, London.

Jenny, H. (1980). *The soil resource: Origin and Behaviour.* New York: Springer Verlag.

Jobbágy, E.G., Parvelo, J.M., and Leon, R.J.C. (1996). Vegetation heterogeneity and diversity in flat and mountain landscapes of Patagonia (Argentina). *J. Veg. Sci.*, **7** (4), 599-608.

Jochimsen, M. (1963). Vegetationsentwicklung im hochalpinen Neuland. *Bericht das Naturwissenschaftlich-medizinischen Vereins in Innsbruck*, **53**, 109-23.

Jochimsen, M. (1970). Die Vegetationsentwicklung auf moränenboden in Abhängigkeit von einigen Umweltfaktoren. *Veröffentlichungen der Universität Innsbruck*, **46**, 1-22.

Johnson, D.L., Keller, E.A., and Rockwell, T.K. (1990). Dynamic pedogenesis: New views on some key soil concepts, and a model for interpreting Quaternary soils. *Quat. Res.*, **33**, 306-319

Jonasson, S. (1981). Plant communities and species distribution of low alpine *Betula nana* heaths in northernmost Sweden. *Vegetatio*, **44**, 51-64.

Jonasson, S. (1986). Influence of frost-heaving on soil chemistry and on the distribution of plant growth forms. *Geografisker Annaler*, **68** (A), 185-195.

Jonasson, S., and Sköld, S.E. (1983). Influences of frost heaving on vegetation and nutrient regime of polygon-patterned ground. *Vegetatio*, **53**, 97-112.

Jongman, R.H.G., ter Braak, C.J.G. & van Tongeren, O.F.R. (1987) *Data Analysis in Community and Landscape Ecology*. Pudoc, Wageningen.

Leach, W., and Polunin, N. (1932). Observations on the vegetation of Finmark. *J. Ecol.*, **20**, 416-430.

Leader-Williams, N., Smith, R.I.L., & Rothery, P. (1987). Influence of introduced reindeer on the vegetation of South Georgia: Results from a long-term exclusion experiment. *J. Appl. Ecol.*, **24**, 801-822.

Longton, R.E. (1988). *Biology of Polar Bryophytes and Lichens*. Cambridge: Cambridge University Press.

Lynch, A.J.J., and Kirkpatrick, J.B. (1995). Pattern and process in alpine vegetation and landforms at Hill One, S range, Tasmania. *Aust. J. Bot.*, **43**, 537-554.

Kasser, P. (1973). *Fluctuations of glaciers* 1960-1965. International Commission on Snow and Ice of the International Association of Hydrological Sciences and UNESCO:

Kent, M., and Ballard, J. (1988). Trends and problems in the application of classification and ordination methods in plant ecology. *Vegetatio* **78**, 109-24.

Kent, M., and Coker, P. (1992). *Vegetation Description and Analysis*. London: Belhaven Press.

Kershaw, K.A., and Looney, J.H. (1985). *Quantitative and Dynamic Plant Ecology*. London: Edward Arnold.

Kershaw, K.A. and Rouse, W.R. (1973). Studies on lichen-dominated systems. V. A primary survey of a raised-beach system in NW Ontario. *Can. J. Bot.*, **51**, 1285-1307.

Khil'mi, G.F. (1962). Theoretical forest biophysics. Transl. from Russian by R. Levin-Nadel. Israel Program for Scientific Translation, Jerusalem.

Kicuchi, T., and Miura, O. (1993). Vegetation patterns in relation to micro-scale landforms in hilly land regions. *Vegetatio*, **106**, 147-154.

Knight, D.H., Rogers, B.R., and Kyte, C.R. (1977). Understory plant growth in relation to snow duration in Wyoming sub-alpine forest. *Bul. Tor. Bot. Club.* **104**(4), 314-319.

Komárková, V. (1993). Vegetation type hierarchies and landform disturbance in arctic Alaska and alpine Colorado with emphasis on snowpatches. *Vegetatio*, **106**, 155-185.

Krebs, C.J. (1978). *Ecology - The Experimental Analysis of Distribution and Abundance*. New York: Harper International.

Kudo, G. (1991). Effects of snow-free period on the phenology of alpine plants inhabiting snow patches. *Arc. Alp. Res.*, **23**, 436-443.

Kudo, G., and Ito, K. (1992). Plant distribution in relation to the length of the growing season in a snow-bed in the Taisetsu Mountains, northern Japan. *Vegetatio*, **98**: 165-174.

Kvillner , E., and Sonesson, M. (1980). Plant distribution and environment of a subarctic mire. *Ecol. Bull. Stockholm*, **30**, 97-111.

Lamb, H.H. (1988). Climate and life during the Middle Ages, studied especially in the mountains of Europe. In: *Weather, climate and human affairs - A book of essays and other papers,* ed. H.H. Lamb, pp. 40-74. London and New York: Routledge.

Lambert, J.D.H. (1972). Plant succession on tundra mudflows; preliminary observations. *Arctic,* **25**, 99-106.

Larson, D.W., and Kershaw, K.A. (1974). Studies on lichen-dominated systems. VII. Interaction of the general lichen-heath with edaphic factors.

Lawrence, D.B., Schoenike, R.E., Quispel, A., & Bond, G. (1967). The role of Dryas drummondii in vegetation development following ice recession at Glacier Bay, Alaska, with special reference to its nitrogen fixation by root nodules. *J.Ecol.*, **55**, 793-813.

Lawrence, D.B. (1979). Primary versus secondary succession at Glacier Bay National Monument, southeastern Alaska. *Proceedings 1st Conference on Scientific Research in the National Parks,* pp. 213-24. United States Department of the Interior, National Parks Service, Transactions and Proceedings Series No. 5. (U.S. Government Printing Office Stock No. 024-005-00743-1)

Leach, W., and Polunin, N. (1932). Observations on the vegetation of Finmark. *J. Ecol.*, **20**, 416-430.

Lid, D.T., and Gjærevoll, O. (1985). *Norske, Svensk, Finsk Flora.* Det Norske Samlaget, Oslo.

Lindröth, C.H. (1965). Skaftafell, Iceland: a living refugium. *Oikos* Supplementum, **6**, 1-142.

Luken, J.O. (1990). *Directing Ecological Change.* 251 pp. London: Chapman and Hall.

Lynch, A.J.J. & Kirkpatrick, J.B. (1995). Pattern and process in Alpine vegetation and landforms at Hill One, S. range, Tasmania. *Aust. J. Bot.*, **43**, 537-554

Lüdi, W. (1921) Die Pflanzengesellschaften des Lauterbrunnentales und ihre Sukzession. *Beiträge zur Geobotanischen Landesaufnahme*, **9**, 1-364.

MacKinney, A.L. (1929). Effects of forest litter on soil temperature and soil freezing in autumn and winter. *Ecology,* **10**, 312-321.

MacMahon, J.A. (1980). Ecosystems over time: Succession and other types of change. In: *Forests: Fresh perspectives from ecosystem analyses,* ed. R. Waring, pp. 27-58. Oregon State University Press.

MacNaughton, S.J. (1983). Physiological and ecological implications of herbivory. *In Encyclopaedia of plant physiology,* **12** (c), 657-677. Springier Verlag, Berlin.

Magnússon, B., & Magnússon, S. (1992). Rannsóknir á gróðri og plöntuvali sauðfjár í beitartilraun á Auðkúluheiði. (Vegetation and plant preferences of sheep in a grazing trial on an alpine heathland range in northern Iceland). *Fjölrit Rala,* **159**. 106 pp.

Magnússon, B., Magnússon, S., & Guðmundsson, J. (1996). Gróðurframvinda í Surtsey. Búvísindi, *Icel. Agri. Sci.*, **10**, 253-272.

Magnússon, S., & Magnússon, B. (1990). Studies in the grazing of a drained lowland fen in Iceland. II. Plant preferences of horses during summer. *Búvísindi,* **4**, 109-124.

Magnússon, S. (1994a). Vegetation, seed bank and field germination at different successional stages following soil erosion in the highlands of S. Iceland. I. 33pp. In *Plant colonization of eroded areas in Iceland.* Ph.D. thesis, University of Lund, Sweden.

Magnússon, S. (1994b). Effects of vegetation and soil surface morphology on accumulation of seeds in an eroded area in the highlands of S Iceland. II: 19pp. In *Plant colonization of eroded areas in Iceland.* Ph.D. thesis, University of Lund, Sweden.

Margalef, R. (1968). *Perspectives in ecological theory.* University of Chicago Press, Chicago. 111 pp.

Matthews, J.A. (1974). Families of lichenometric dating curves from Storbreen gletschervorfeld, Jotunheimen, Norway. *Norsk geografisk Tidsskrift,* **28**, 215-235.

Matthews, J.A. (1975). Experiments on the reproducibility and reliability of lichenometric dates, Storbreen gletschervorfeld, Jotunheimen, Norway. *Norsk geografisk Tidsskrift,* **29**, 97-109.

Matthews, J.A. (1976). *A phytogeography of a Gletschervorfeld: Storbreen-i-Leirdalen, Jotunheimen, Norway.* Ph.D. thesis, University of London (Kings College).

Matthews, J.A. (1977). A lichenometric test of the 1750 end-moraine hypothesis: Storbreen gletschervorfeld, S. Norway. *Norsk geografisk Tidsskrift,* **31**, 129-136.

Matthews, J. A. (1978a). An application of non-metric multidimensional scaling (NMDS) to the construction of an improved species plexus. *J. Ecol.*, **66**, 157-173.

Matthews, J. A. (1978b). Plant colonisation patterns on a gletschervorfeld, S. Norway: a mesoscale geographical approach to vegetation change and phytometric dating. *Boreas*, 7, 155-178.

Matthews, J. A. (1979a). Plant colonisation patterns on gletschervorfeld, southern Norway, I. Introduction and approaches involving classification. *J. Biogeog.*, **6**, 17-47.

Matthews, J. A. (1979b). The vegetation of the Storbreen gletschervorfeld, Jotunheimen, Norway, II. Approaches involving ordination and general conclusions. *J. Biogeog.*, **6**, 133-67.

Matthews, J. A. (1979c). A study of the variability of some successional and climax assemblage types using multiple discriminant analysis. *J. Ecol.*, **67**, 255-71.

Matthews, J. A. (1979d). Refutation of convergence in a vegetation succession. *Naturwissenschaften*, **66**, 47-9.

Matthews, J.A. (1981). Vegetation Studies. In *Quantitative Geography - A British View,* eds. N. Wrigley & R.J. Bennett, pp. 294-308. London: Routledge & Kegan Paul.

Matthews, J.A. (1991). The late neoglacial ("Little Ice Age") glacier maximum in southern Norway: new carbon-dating evidence new carbon-dating evidence and climatic implications. *Holocene*, **1** (3), 219-233.

Matthews, J.A. (1992). *The Ecology of Recently Deglaciated Terrain: A geoecological approach to glacier forelands and primary succession.* Cambridge: Cambridge Studies in Ecology.

Matthews, J.A. (1996). Classics in physical geography revisited. *Progress in Physical Geography,* **20** (2), 193-203.

Matthews, J.A. (1998). Disturbance regimes and ecosystem response on recently-deglaciated substrates. In Walker, L.R. (ed.) *Ecosystems of disturbed Ground.* Elsevier Science, Amsterdam, *in press.*

Matthews, J.A., Dawson, A.G., and Shakesby, R.A. (1986). Lake shoreline development, frost weathering and rock platform erosion in an aline periglacial environment. *Boreas*, **15**, 33-50.

Matthews, J. A. and Whittaker, R.J. (1987). Vegetation succession on the Storbreen glacier foreland, Jotunheimen, Norway: a review. *Arc. Alp. Res.*, **19**, 385-95.

Matthews, J.A., Shakesby, R.A. and McCarroll, D. (1995). Contemporary terminal-moraine ridge formation at a temperate glacier: Styggedalsbreen, Jotunheim, Norway. *Boreas*, **24**, 129-139.

Matthews, J.A., Shakesby, R.A., Berrisford, M.S., and McEwen, L.J. (in press) Periglacial patterned ground on the Styggedalsbreen glacier foreland, Jotunheimen, southern Norway: microtopographic, paraglacial and geoecological controls. In: *Permafrost and Periglacial Processes*. 9(2).

McCarrol, D., and Ware, M. (1989). The variability of soil development on Preboreal moraine ridge crests, Breiseterdalen, southern Norway. *Norsk Geog. Tids.*, **43**, 31-36.

McCormick, J. (1968). Succession. *Via*, **1**, 22-35 and 131-132.

McIntosh, R.P. (1981). Succession and Ecological Theory. In: *Forest Succession: Concepts and Applications*, eds. D.C. West, H.H. Shugart and D.B. Botkin, pp 10 - 23. New York: Springer Verlag.

McIntosh, R.P. (1980). The relationship between succession and the recovery process in ecosystems. In: *The recovery process in damaged ecosystems*, ed. J. Cairns Jnr, pp 11-62. Ann Arbor Sci. Inc., Ann Arbor, Michigan.

Mellor, A. (1985). Soil chronosequences on Neoglacial moraine ridges, Jostedalsbreen and Jotunheimen, southern Norway: a quantitative pedogenic approach. In *geomorphology and soils*, eds. K.S. Richards, R.R. Arnett and S. Ellis, pp. 289-308. London: George Allen and Unwin.

Mellor, A. (1987). A pedogenic investigation of some soil chronosequences on Neoglacial moraine ridges, southern Norway: examination of soil chemical data using principal components analysis. *Catena*, **14**, 315-59.

Messer, A.C. (1984). *A Geographical Investigation of Soil Development on Glacier Forelands in South-central Norway*. Ph.D. Thesis, University of Wales (University College Cardiff).

Messer, A.C. (1988). Regional variations in rates of pedogenesis and the influence of climatic factors on moraine chronosequences, southern Norway. *Arctic and Alpine Research*, **20**, 31-9.

Messer, A.C. (1989). An alternative approach to the study of pedogenic chronosequences. *Norsk Geografisk Tidsskrift*, **43**, 221-9.

Miles, J. (1987). Vegetation succession: past and present perceptions. In *Colonisation, Succession and Stability*, eds. A.J. Gray, M.J. Crawley and P.J. Edwards, pp. 1-29. Oxford: Blackwell Scientific Publications.

Miles, J., and Walton, D.W.H. (1993). Primary succession revisited. In *Primary Succession on Land*. eds. J. Miles and D.W.H. Walton, pp 295-302. Oxford: Blackwell Scientific Publications.

Miller, P.C. (1982). Environmental and vegetational variation across a snow accumulation area in montane tundra in central Alaska. *Holarctic Ecology*, **5**, 85-98.

Milne, G. (1935). Composite units for the mapping of complex soil associations. *Transactions 3rd International Congress of Soil Science*, **1**, 345 -7.

Mirskey, A. (ed.) (1966). *Soil development and ecological succession in a deglaciated area of Muir Inlet, Southwest Alaska*. Rep. No. 20 Ohio State University Institute of Polar Studies, Columbus, Ohio.

Moberg, R. & Holmåsen, I. (1982). *Lavar: en fälthandbok*. Interpublishing, Stockholm

Moore, P.D. & Chapman, S.B. (1986) *Methods in Plant Ecology*. Blackwell, Oxford.

Moravec, J. (1969). Succession of plant communities and soil development. *Folia Geobotanica et Phytotaxonomica*, **4**, 133-64.

Moravec, J. (1989). Influences of the individualistic concept of vegetation on syntaxonomy. *Vegetatio*, **81**, 29-39.

Murray, C. and Miller, P.C. (1982). Phenological observations of major plant growth forms and species in montane and *Eriophorum vaginatum* tussock tundra in central Alaska. - *Holarctic Ecology*, **5**, 109-116.

Müller, F. (1977). *Fluctuations of glaciers* 1970-1975. International Commission on Snow and Ice of the International Association of Hydrological Sciences and UNESCO:

Naumann, C.F. (1824). *Beyträge zur Kentiss Norwegens gesammelt auf Wanderungen der Summermonate der jahre 1821 und 1822, Volume 2.* Leipzig.

Nesje, A. (1989). Glacier front variations of outlet glaciers and climate in the Jostedalsbreen region, W. Norway (1901-80). *Norsk Geografisk Tidsskrift*, **43**, 3-17.

Nesje, A. (1991). Younger Dryas and Holocene glacier fluctuations and equilibrium-line altitude variations in the Jostedalsbre region, W Norway. *Climate dynamics*. **6**: 221-227

Nesje, A., et al. (1987). The vertical extent of the late Weichselian ice sheet in the Nordfjord-Møre area, W Norway. *Nors. Geol. Tids.* **67**: 125-141.

Nesje, A. & Dahl, S.O. (1990). Autochthonous block fields in S Norway: implications for the ... isostatic loading of the Late Weichselian Scandinavian ice sheet. *J. Quat. Sci.*, **5** (3): 225-234.

Nesje, A, and Kvamme, M. (1991) Holocene glacier and climatic variations in western Norway: evidence for early Holocene glacier demise and multiple Neoglacial events. *Geology*, **19**, 610-612.

Nitychoruk, J. and Dzierzek, J. (1988). Morphological features of talus cones in northwestern Wedel Jarlsberg Land, Spitzbergen. *Polish Polar Research*, **9**, 73-85.

Noble, P.L. and Alexander, R.R. (1977). Environmental factors affecting natural regeneration of Engelmann Spruce in the Central Rocky Mountains. *For. Sci.*, **23**, 420-429.

Noble, I.R., and Slatyer, R.O. (1980). The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbances. *Vegetatio*, **43**, 5-21.

Noble, M.G., Lawrence, D.B. and Streveler, G.P. (1984). *Sphagnum* invasion beneath an evergreen forest canopy in southeastern Alaska. *The Bryologist*, **87**, 119-127.

Nordhagen, R. (1943). Sikilsdalen og Norges fjellbeiter. En plantsosiologisk monografi. Griegs Boktryh. 607 pp.

Nordhagen, R. (1954). Vegetation units in the mountain areas of Scandinavia - *Veröff. des Geobot. Inst.* Rübel in Zürich. No. **29**.

Oberbauer, S. and Miller, P.C. (1979). Plant water relations in montane and tussock tundra vegetation types in Alaska. *Arctic and Alpine Research*, 1, 69-81.

Odum, E.P. (1969). The structure of ecosystem development. *Science*, **164**, 262-70.

Odum, E.P. (1975). *Ecology*. London: Holt Saunders

Odum, H.T. (1971). *Environment, Power and Society*. New York: John Wiley and Sons.

Oechel, W.C. (1989). Nutrient and water flux in a small arctic watershed: an overview. *Holarctic Ecology*, **12**, 229-237.

Oliver, C.D., Adams, A.B., and Zozoski, R.J. (1985). Disturbance patterns and forest development in a recently deglaciated valley in the northwestern Cascade Range of Washington, U.S.A. *Can. J. For. Res.*, **15**, 221-232.

Olson, J.S. (1958). Rates of succession and soil changes on southern Lake Michigan sand dunes. *Botanical Gazette*, **119**, 125-70.

Palmer, M.W. (1993). Putting things in even better order: The advantages of canonical correspondence analysis. *Ecology*, **74** (8), 2215-2230.

Palmer, W.H. and Miller, A.K. (1961). Botanical evidence for the recession of a glacier. *Oikos*, **12**, 75-86.

Parkinson, R.J., and Gellatly, A. (1991). Soil formation on Holocene moraines in the cirque de Troumous, Pyrenees. *Pirineos.* **138**, 69-92.

Parkinson, R.J., and Roberts, A.H. (1985). Microtopographical control of soil development in the Okstindan region, N. Norway. *Okstindan Research Project Preliminary Report for 1983*, eds. J. Rose and C.A. Whiteman, pp1-9. London: University of London, Birkbeck College.

Parrish, J.A.D. & Bazzaz, F.A. (1982). Competitive interactions in plant communities of different successional ages. *Ecology*, **63**(2), 314-320

Pearsall, W.H. (1950). *Mountains and Moorlands.* The Fontana New Naturalist Series (1970 edition).

Persson, Å. (1964). The vegetation at the margin of a receding glacier Skaftafellsjökull, southeastern Iceland. *Botaniska Notiser*, **117**, 323-54.

Philips, J.F.V. (1934-5). Succession, development, the climax, and the complex organism: an analysis of concepts. Parts I-III. *J. Ecol.*, **22**, 554-571; **23**, 210-246, 488-508.

Pickett, S.T.A., Collins, S.L., and Armesto, J.J. (1987). Models, Mechanisms and Pathways of Succession. *Bot. Rev.* **53**, 335 - 371.

Price, M., and Heywood, I. (1994). Mountain environments and Geographic Information Systems. zz

Randall, R.E. (1978). Theories and techniques in vegetation analysis. Oxford University Press, Oxford.

Raup, H.M. (1971). The vegetational relations of weathering, frost action and patterned ground processes in the Mesters Vig district northeast Greenland. *Meddr. Grønland Bd.* **194** (1), 92 pp.

Raven, J., and Walters, M. (1956). *Mountain Flowers.* Fontana.

Rekstad, J. (1902). Lagttagelser fra braeer i Sogn og Nordfjord. Norges Geologiske Undersøgelses Aarbog 1902, **3**, 1-48.

Reiners, W.A., Worley, I.A., and Lawrence, D.B. (1971). Plant diversity in a chronosequence at Glacier Bay, Alaska. *Ecology*, **52**, 55-69.

Rekstad, J. (1900). Periodiske forandringer hos norske bræer. *Norges geol., Unders*, **28**(4), 1-15.

Rekstad, J. (1901). Iagttagelser fra bræer i Sogn og Nordfjord. *Norges geol., Unders*, **34**(3), 1-48.

Roberts, D.W. (1987). A dynamical systems perspective on vegetation theory. *Vegetatio*, **69**, 27-33.

Robinson, M., and Dean, T.J. (1993). Measurement of near surface soil water content using a capacitance probe. *Hydrological processes*, **7**, 77-86.

Rose, C.J. & Hawkesworth, D.L. (1981). Lichen recolonisation in London's cleaner air. *Nature*, **289**, 289-292.

Rose, J. (1990). Subarial modification of glacier bedforms immediately following ice wastage. *Norsk Geografik Tidsskrift*, **45**, 143-153.

Russell, E.W. (1973). *Soil conditions and plant growth.* Longman (10th edition).

Rydin, H., and Borgegård, S. (1991) Plant characteristics over a century of primary succession on islands: Lake Hjälmaren. *Ecology*, **72**(3), 1089-1101.

Sampson, H.C. (1930). The mixed mesophytic forest community of north-eastern Ohio. *Ohio Journal of Science*. **30**, 358-367.

Schell, D.M., and Alexander, V. (1973). Nitrogen fixation in Arctic coastal tundra in relation to vegetation and micro-relief. *Arctic*. **26**, 130-137.

Scherff, E.J., Galen, C., and Stanton, M.L. (1994). Seed dispersal, seedling survival and habitat affinity in a snowbed plant: limits to the distribution of the snow buttercup, *Ranunculus adoneus*. *Oikos*, **69**, 405-413.

Schubert, G.H. (1970). Ponderosa pine regeneration problems in the southwest, pp. 1-4. In: *Regeneration Ponderosa Pine Symposium*, Corvallis, Oregon.

Schubiger-Bossard, C.M. (1988). Die Vegetation des Rhonegletschervorfeldes, Ihre Sukzession und Naturräumliche Gliederung. *Beiträge zur Geobotanischen Landesaufnahme der Schweiz*, **64**, 1-228. (Teufen AR, Switzerland: F. Flück-Wirth).

Scott, R.W. (1974a). The effect of snow duration on alpine plant community composition and distribution. In *Icefields Ranges Research Project, Scientific Results: Volume 4*, eds. V.C. Bushnell and M.G. Marcus, pp. 307-18. New York and Montreal: American Geographical Society and Arctic Institute of North America.

Scott, R.W. (1974b). Successional patterns on moraines and outwash of the Frederica Glacier, Alaska. In *Icefields Ranges Research Project, Scientific Results: Volume 4*, eds. V.C. Bushnell and M.G. Marcus, pp. 319-29. New York and Montreal: American Geographical Society and Arctic Institute of North America.

Shaw, C.H. (1909). The causes of the timberline on mountains: The role of snow. *Plant World*, **12**, 169-180.

Sjörs, H. (1965). Northern mires. Regional ecology of mire sites and vegetation. *Acta phytogeographica Suecica*, **50**, 180-188.

Slingsby, D., and Cook, C. (1986). *Practical Ecology*. Macmillan Eduacation, London

Sochting, U. & Johnsen, I. (1974). Changes in the distribution of epiphytic lichens in the Copenhagen area from 1936 to 1972. *Botaniske Tiddskrift*, **69**, 60-63.

Sochting, U. & Johnsen, I. (1978). Lichen transplants as biological indicators of SO_2 air pollution in Copenhagen. *Bull. Env. Cont. and Tox.*, **19**, 1-7.

Sommerville, P., Mark, A.F. and Wilson, J.B. (1982). Plant succession on moraines of the upper Dart Valley, southern South Island, New Zealand. *N. Z. J. Bot.*, **20**, 227-44.

Sondheim, M.W., and Standish, J.T. (1983). Numerical analysis of a chronosequence including an assessment of variability. *Can. J. Soil Sci.*, **63**, 501-517.

Sorensen, T. (1945). Summary of the botanical investigations in northeast Greenland. *Meddel. om Grønland,* **144** (3), 1-48.

Stanton, M.L., Rejmánek, M. and Galen, C. (1994). Changes in vegetation and soil fertility along a predictable snowmelt gradient in the Mosquito range, Colorado, U.S.A. *Arc. Alp. Res.*, **26** (4), 364-374.

Steere, W.C. (1954). The cryptogamic flora of the Arctic: v. Bryophytes. *Bot. Rev.*, **20**, 425-450.

Stork, A. (1963). Plant immigration in front of retreating glaciers, with examples from the Kebnekajse area, northern Sweden. *Geografiska Annaler*, **45**, 1-22.

Stöcklin, J. and Bäumler, E. (1996). Seed rain, seedling establishment and clonal growth strategies on a glacier foreland. *Journal of Vegetation Science*, **7**, 45-56.

Sturges, D.L. (1989). Response of Mountain Big Sagebrush to induced snow accumulation. *J. Appl. Ecol.*, **26**, 1035-1041.

Sukachev, V. & Dylis, N, N. (1964). Fundamentals of forest biocoenology. Transl. from Russian by J.M. McLennan. Oliver and Boyd, London.

Sveinbjörnsson, J.D. (1995). Soil carbon and nitrogen mineralisation at different elevations in the Chugach Mts of south-central Alaska, USA. *Arc. Alp. Res.* **27** (1), 29-37.

Tansley, A. G. (1920). The classification of vegetation and the concept of development. *J. Ecol.*, **8**, 118-49.

Tansley, A.G. (1935). The use and abuse of vegetational concepts and terms. *Ecology*, **16**, 284-307.

Tausch, R.J., Charlet, D.A., Weixelman, D.A. & Zamudio, D.C. (1995). Patterns of ordination and classification instability resulting from changes in input data order. *J. Vege. Sci.*, **6**, 897-902.

Taylor, B.W. (1955). Terrace formation on Macquarie Island. *J. Ecol.*, **43**, 133-137.

Tilman, D. (1985). The resource-ratio hypothesis of plant succession. *American Naturalist*, **125**, 827-52.

Tisdale, E.W., Fosberg, M.A. and Poulton, C.E. (1966). Vegetation and soil development on a recently glaciated area near Mount Robson, British Columbia. *Ecology*, **47**, 517-23.

Trolander, H.W., Case, D.A., and Harruff, R.W. (1971). Reproducibility, stability and linearization of thermistor resistance thermometers. 5th Symposium on Temperature, Washington D.C.

Ugolini, F.C. (1968). Soil development and alder invasion in a recently deglaciated area of Glacier Bay, Alaska. In *The Biology of Alder*, eds. J. M. Trappe, J. F. Franklin, R. F. Tarrant and G. M. Hansen, pp. 115-40. Portland, Oregon: United States Forestry Service.

van Groenewoud, H. (1992). The robustness of Correspondence, Detrended Correspondence, and TWINSPAN Analysis. *J. Vege. Sci.*, **3**, 239-246.

Vetaas, O. (1986). *Økologiske Faktorer i en Primærsuksesjon på Daterte Endmorener i Bødalen, Stryn.* Ph.D. thesis, University of Bergen. (Botanical Institute)

Vetaas, O. (1994). Primary succession of plant assemblages on a glacier foreland - Bødalsbreen, S Norway. *J. Biogeog.*, **21**, 297-308.

Viereck, L.A. (1966). Plant succession and soil development on gravel outwash of the Muldrow Glacier, Alaska. *Ecological Monographs*, **36**, 181-99.

Walker, L.R. (1993). Nitrogen fixers and species replacements in primary succession. . In *Primary Succession on Land,* eds. J. Miles and D.W.H. Walton, pp 249-272. Oxford: Blackwell Scientific Publications.

Walker, D.A., Binnian, E., Evans, B.M., Lederer, N.D., Nordstrand, E., and Webber, P.J. (1989). Terrain, vegetation and landscape evolution of the R4D research site, Brook Range Foothills, Alaska. *Holarctic Ecology*, **12**, 238-261.

Walker, L.R. and Chapin, III, F.S. (1986). Physiological controls over seedling growth in primary succession on an Alaskan floodplain. *Ecology*, **67** (6), 1508-1523.

Walker, L.R. and Chapin, III, F.S. (1987). Interactions amongst processes controlling successional change. *Oikos*, **50**, 131-5.

Walker, D.A., Halfpenny, J.C., Walker, M.D., and Wessman, C.A. (1993). Long-term studies of snow-vegetation interactions. *Bioscience*, **43**, 287-301.

Walker, L.R., Zasada, J.C., and Chapin III, F.S. (1986). The role of life history processes in primary succession on an Alaskan floodplain. *Ecology*, **67**, 1243-53.

Ward, M.R. (1970). The colonisation of "annual moraines", eastern lobe, Austre Okstindbreen. *In: Worsely, P. (ed.): Okstindan Research Project 1970, Preliminary report,* Reading: pp 39-45

Wartenberg, D., Ferson, S., and Rohlf, F.J. (1987). Putting things in order: a critique of detrended correspondence analysis. *American Naturalist*, **129**, 434-448.

Watt, A.S. (1940). Studies in the ecology of Breckland. IV. The grass heath. *J.Ecol.*, **17**, 173-70.

Watt, A.S. (1947). Pattern and process in the plant community. *J.Ecol.*, **35**, 1-22.

Westman, L. (1975). Air pollution and vegetation around a sulphite mill at Ornskoldsvik, north Sweden. Pollutants and plant communities on exposed rocks. *Wahlenbergia*, **2**, 17-31.

Whittaker, R.H. (1951). A criticism of the plant association and climatic climax concepts. *Northwest Science*, **25**, 17-31.

Whittaker, R.H. (1953). A consideration of climax theory: the climax as a population and pattern. *Ecological Monographs*, **23**, 41-78.

Whittaker, R. J. (1985). *Plant Community and Plant Population Studies of a Successional Sequence: Storbreen Glacier Foreland, Jotunheimen, Norway.* Ph.D. thesis, University of Wales. (University College Cardiff)

Whittaker, R. J. (1987). An application of DCA and NMDS to the identification and analysis of environmental factor complexes and vegetation structures. *J.Ecol.*, **75**, 363-376.

Whittaker, R. J. (1989). The vegetation of the Storbreen Gletschervorfeld, Jotunheimen, Norway. III. Vegetation-environment relationships. *J.Biog.*, **16**, 413-433.

Whittaker, R.J. (1991). The vegetation of the Storbreen gletschervorfeld, Jotunheimen, Norway. IV. Short-term vegetation change. *J. Biogeog.*, **18**, 41-52.

Whittaker, R. J. (1993). Plant population patterns in a glacier foreland succession: pioneer herbs and later-colonising shrubs. *Ecography*, **16**, 117-136.

Whittaker, R.J., & Bush, M.B. (1993). Dispersal and establishment of tropical forest assemblages, Krakatoa, Indonesia. In *Primary Succession on Land,* eds. J. Miles and D.W.H. Walton, pp 147-160. Oxford: Blackwell Scientific Publications.

Whittow, J. (1984). *The Penguin Dictionary of Physical Geography.* Penguin Reference.

Wiggins, I.L. (1951). The distribution of vascular plants on polygonal ground near Point Barrow, Alaska. *Contr. Dudley Herb*, **4**, 41-56.

Wijk, S. (1986a). performance of *Salix herbacea* in an alpine snow-bed gradient. *J. Ecol.*, **74**, 675-684

Wijk, S. (1986b). Influence of climate and age on annual shoot increment in *Salix herbacea. J. Ecol.*, **74**, 685-692.

Williamson, M. (1987). Are communities ever stable? In . *Colonisation, Succession and Stability.* eds. A.J. Gray, M.J. Crawley, and P.J. Edwards, pp. 353-371. Oxford: Blackwell Scientific Publications.

Worley, I.A. (1973). The "black crust" phenomenon in Upper Glacier Bay, Alaska. *Northwest Sciences*, **47** (1), 20-29.

Zollitsch, B. (1969). Die Vegetationsentwicklung im Pasterzenvorfeld. *Wissenschaftliche Alpenvereinsheft* (München), **21**, 267-90.

GLOSSARY

AGE: Unless otherwise stated, “age” or “time” refers to terrain-age i.e. the period of time since the retreat of the glacier from the site, as shown by lichenometry or other means of dating.

ALTITUDINAL ZONE: A large scale grouping of the landscape, according to height above sea level, based on the prevailing species (Gjærevoll and Jørgensen, 1978), into subalpine (below the tree line), low-alpine (up to the highest limit of *Vaccinium myrtillus*) and mid-alpine (up to areas dominated by ice, snow, rocks and scree).

ASSEMBLAGE: A group of species growing together; it does not imply any statistical association between the species. It is preferred to the term “community” which has implications of functional interrelationships and/or integration.

ATYPICAL ASSEMBLAGE: An assemblage and/or group of sites that deviates from the general trends shown by previous research in the region. Atypical assemblages tend to be mixtures of two typical assemblages e.g. heath and snowbed. see typical assemblage

CENTROID: Average scores, found by DCA ordination, for individual members of the TWINSPAN species groups and the TWINSPAN site (sample) groups. Centroids are used in complementary analysis.

CLIMAX: “*the terminal community said to be achieved when a sere achieves dynamic equilibrium with its environment and in particular with its prevailing climate*” (Whittow, 1984: 98). The term “climax” has been rejected by many (e.g. Burrows, 1990) as it is not universally applicable and for the purposes of the present study the term “mature assemblage” is preferred.

COMBINED FORELAND DATA SET: Comprises the data from all the individual foreland data sets, combined together into one large data set.

COMMUNITY: “*An organised group of plants or animals, generally of distinctive character and related to a particular set of environmental requirements*” (Whittow, 1984: 106). This is a popular definition and because of the inferred relationship between members of a community, suggested by the definition, the term assemblage is preferred.

COMPLEMENTARY ANALYSIS: Where ordination and classification are performed on the same data (cf. Kent and Ballard, 1988; Matthews, 1979b).

CONFOUNDED RELATIONSHIPS: These are relationships between environmental variables that exist coincidentally, for example between age and altitude, but they have no ecological meaning (especially relevant when interpreting the results of an ordination).

CONVERGENCE: Matthews (1979d) states that convergence is a transformation of vegetation from a varied conformation, in early stages, to uniformity in later successional stages. Convergence results in climax types that are similar and indistinct, while early successional stages are dissimilar and distinct.

CUT LEVEL: Used to divide the cover values of each species into groups of similar cover value.

DEFAULT OPTION: The normal analysis options recommended by the computer programmer.

DISTINCT ASSEMBLAGES: Assemblages that have higher eigenvalues and thus are considered least variable between sites. The centroids of distinct assemblages are well dispersed across a DCA ordination plot and the species belonging to distinct assemblages are distributed close to each other on the DCA rank tables with superimposed TWINSPAN groups.

DIVERGENCE: A term summarising the pattern of vegetational trajectories during succession. "*A relatively monotonous* [vegetation] *landscape in the early stages becomes a relatively heterogeneous one, with relatively clear altitudinal zonation of vegetation and relatively distinct vegetation zones related to microtopography on older terrain*" (Matthews, 1992: 207).

DYNAMICAL SYSTEMS APPROACH: A conceptual model developed by Roberts (1987:27) to "*characterise the influence of environment, the effect of vegetation on environment, and the subsequent response of vegetation to the modified environment*".

EARLY-INTERMEDIATE ASSEMBLAGE: An assemblage which occurs on areas of the glacier foreland deglaciated between AD 1810 and 1900.

ECOLOGICALLY MEANINGFUL: In classification and ordination, if the separation of TWINSPAN groups or the distribution of species and samples along the ordination axes is compatible with the interpretation of environmental patterns, then the data is considered as ecologically meaningful.

EIGENVALUE: "*Eigenvalues are values that represent the relative contribution of each component to the explanation of the total variation in the data. There is one eigenvalue for each component, and the size of the eigenvalue for a component is a direct indication of the importance of that component in explaining the total variation within the data set*" (Kent and Coker, 1992: 187)

EXPOSED POSITIONS: Microtopographical positions on the crests of moraines, or on the proximal side of young moraines. Such positions are believed to experience greater wind speeds, and thus a more severe microenvironment, than sheltered positions.

FINAL GROUP: Kent and Coker (1992) state "*Not all groups have to be taken from one* [TWINSPAN] *level. If further subdivisions of a large group make more ecological sense, then it should be subdivided by looking at the next level. If two subdivisions of a small group seem to produce artificial sub-groups, then it may make sense to amalgamate them again.*" Such groups, defined within the present thesis as final groups, are considered to be ecologically meaningful.

GEOECOLOGICAL APPROACH: It investigates vegetation patterns by considering all aspects of plants, space, time and environment together. The approach was developed by Matthews (1992) and emphasises the environmental effects in vegetation succession.

GLACIER FORELAND: The area in front of a glacier which has emerged since the end of the "Little Ice Age".

HEATH: Assemblage-type characterised by shrubby vegetation (Whittow, 1984) dominated by such species as *Phyllodoce caerula* and *Salix spp* on intermediate-aged sites; and *Betula nana* and *Vaccinium spp* on older, mature, sites (cf. Matthews, 1976).

HOLOCENE: This is the most recent geological period, of approximately 10,000 years duration, that followed the last Ice Age. It is also referred to as the "Recent" or "Post-Glacial" epoch.

IMPORTANT ENVIRONMENTAL PARAMETERS: Those parameters located at the furthest positions along or between the DCA ordination axes and considered to have the greatest influence on species and site separation. They are represented by arrows on the ordination plots.

INDICATOR SPECIES: These are the strongly differentiated preferential species defined by the TWINSPAN divisions and are "*designed to provide a simple criterion for re-identification of the groups*" (Hill, 1979b).

INDIVIDUAL FORELAND DATA SET: A data set from one of the eight glacier foreland sequences used for the present study. The individual foreland data sets contrast with the combined foreland data set.

LATE SNOW HEATH: An assemblage associated with late snow-lie and generally occupying low-slope positions on moraines and consisting mainly of heath (cf. Matthews, 1978b) and lichen species.

LATE-INTERMEDIATE ASSEMBLAGE: An assemblage which occurs on areas of the glacier foreland exposed before AD 1810, but deglaciated since the Little Ice Age maximum.

LITTLE ICE AGE: A period of cooler climatic conditions said to have occurred between the late middle-ages and the middle of the eighteenth century (Grove, 1988).

LOOSE DISTRIBUTION: A TWINSPAN group, characterised by species or sites that have a scattered or dispersed distribution across the TWINSPAN final tables or on the DCA ordination rank tables. A loose distribution suggests that the assemblage is not distinct and that the species are not strongly associated.

MACRO-SCALE: Scale, used within the present study to refer to between-foreland and regional differences in vegetation and environment .

MATURE ASSEMBLAGE: An assemblage on terrain that remained uncovered by the glaciers during the Little Ice Age. Assemblages previously known as "climax" are referred to as "mature" in order to avoid the assumption of stable vegetation in a final equilibrium state.

MESO-CLIMATE: Climate at a within-foreland scale, e.g. associated with glacier wind or valley-side differences.

MESO-ENVIRONMENT: Environment at a within-foreland scale (for present study purposes).

MESO-SCALE: Variations in vegetation or environment at a scale greater than a moraine, but smaller than a mountain, valley or region (e.g. within a foreland, or part of a mountain side).

MICRO-CLIMATE: The climatic features of a moraine, site or quadrat.

MICRO-ENVIRONMENT: The environment of a moraine, site or quadrat (for present study purposes).

MICRO-SCALE: Scale used, within the present study, to define small features or areas (e.g. moraine, site or quadrat).

MORAINE: A ridge in the landscape formed directly by a glacier, in terms of pushing, dumping and other mechanisms of depositing the glacial debris. Within this study the mature till ridge is labelled M1, and the outermost, terminal, moraine (generally formed around 1750, at the end of the Little Ice Age) is labelled M2. Progressively younger moraines, across each glacier foreland, are labelled with increasingly higher numbers (M3, M4 ... etc.), with the highest numbers on the youngest ground.

PARAMETER GROUP: It is a general term including site (sample) groups, the species groups and environmental factors.

PIONEER ASSEMBLAGE: An assemblage composed of the earliest colonising species, characteristic of the earliest stages of succession found on the most recently deposited terrain.

POSITION: The topographic position of quadrats on a moraines, including toe-slope, base-slope, mid-slope, shoulder-slope and crest. Toe and base-slope (and mid-slope) positions may be collectively described as low-slope positions, sites or quadrats; and, conversely, the shoulder-slope and crest (and mid-) positions may be described as high-slope positions, sites or quadrats.

PRE-BOREAL: Written in mixed case sentences as pre-Boreal (Allaby, 1994), this refers to a climatic period, during the early part of the Holocene (*circa* 10,300 to 9600 BP), of rapid forest expansion in post-glacial times. This term is not to be confused with Pre-Boreal which refers to climatic conditions (Allaby, 1994).

PREFERENTIAL SPECIES: Species that tend to be found with particular TWINSPAN site groups, but are not exclusive to the group.

PRIMARY INDICATOR: TWINSPAN separates the sites, in a hierarchical manner, so that a differentiation in assemblage types is brought about. Two species that are the most strongly differentiated and have been defined, in TWINSPAN, as indicator species and are used to identify the TWINSPAN site groups. Where TWINSPAN has not defined indicator species for a particular group, the author uses preferential species instead.

PRIMARY SUCCESSION: "*The ecological succession which begins as a "pioneer" on a surface that has not been previously occupied by a community of organisms, i.e. on a lava flow or a newly exposed glaciated rock surface*" (Whittow, 1984: 422). For the purposes of the present thesis, all references to succession will normally concern primary succession. see also secondary succession.

PSEUDOSPECIES: "TWINSPAN employs the idea of a pseudospecies whereby the presence of a species at different predetermined levels of abundance is used." (Kent and Coker, 1992: 279). In TWINSPAN the percentage cover scale is divided into cut levels, and within the present study nine cut levels were used (0%; 2%; 5%; 10%; 20%; 30%; 45%, 60; 80%) for each species.

QUADRAT: A 1m□ grid quadrat was used throughout this study.

REGIONAL CLIMATE: Generally defined by areas of similar latitude, longitude and altitude at scales greater than that of the foreland.

SAMPLE SCORES: Scores of the sites depending on where they are placed on the ordination axes. Sites with similar vegetation receive similar scores.

SECONDARY SUCCESSION: Ecological succession following the disturbance of established vegetation. The change in succession generally occurs as a result of a major environmental disturbance, such as fire or logging, but, unlike in primary succession, the previous vegetation is not altogether destroyed.

SHELTERED POSITIONS: Low-slope microtopographical positions on moraines, or possibly higher slope positions on the distal side of moraines in more favourable locations. Such positions are believed to experience lower wind speeds, and thus a more sheltered microenvironment, than exposed positions.

SITE GROUPS: Groups of sites which possess common species in TWINSPAN analysis. The assemblages occurring on these groups of sites are known as site assemblages which are represented by indicator and preferential species. As the site assemblages are not exclusive, the preferential and indicator species can be found in more than one group.

SITE: Two replicate quadrats (each of $1m^2$) which occupy the same position on a moraine.

SLOPE POSITION: see position

SNOWBED ASSEMBLAGE: An assemblage, generally on low-slope positions on the moraine, is subject to late-lying snow. Snowbed assemblages are generally dominated by forbs, bryophytes and graminoid species and/or the low growing dwarf willow, *Salix herbacea.*

SPECIES GROUPS: Groups of species which possess common sites in TWINSPAN analysis. The assemblages occurring within these groups of sites are defined as species assemblages.

SPECIES SCORES: The score of a species on an ordination axis reflects the importance of the species as a contributor to the axis and the degree of association of the species with the axis.

SUCCESSION: a change of vegetation composition through time that is broadly directional and predictable and may be caused by both autogenic and allogenic controls. Succession can be progressive, following a sequence of vegetation towards mature vegetation types; cyclic, following a repeating pattern of building, mature and degenerative phases of vegetation types; or retrogressive, returning to the vegetation of preceding stages.

TIGHT DISTRIBUTION: A TWINSPAN group, characterised by species or sites that occur in close proximity to each other across the TWINSPAN final tables or on the DCA ordination rank tables. A tight distribution suggests that the assemblage is distinct and that the members are strongly associated.

TYPICAL ASSEMBLAGE: TWINSPAN species or site groups that correspond with those defined by previous researchers, especially regionally (e.g. Matthews, 1976; Whittaker, 1985; Crouch, 1992). see atypical assemblage.

Appendix 1 (sheet 1) List of full species names

(Each number is that used within the combined data set)

Abbreviation	Species name
1. Emp nig	*Empetrum nigrum*
2. Phy cae	*Phyllodoce caerula*
3. Cal vul	*Calluna vulgaris*
4. Sal gla	*Salix glauca*
5. Bet pub	*Betula pubescens*
6. Vac uli	*Vaccinium uliginosum*
7. Vac myr	*Vaccinium myrtillus*
8. Cor sue	*Cornus suecica*
9. Mel syl	*Melampyrum sylvaticum*
10. Ath dis	*Athyrium distentifolium*
11. Jun fil	*Juncus filiformis*
12. Vio bif	*Viola biflora*
13. Pot cra	*Potentilla crantzii*
14. Ant odo	*Anthoxanthum odoratum*
15. Des fle	*Deschampsia flexuosa*
16. Tri eur	*Trientalis europaea*
17. Rum ace	*Rumex acetosa*
18. Des alp	*Deschampsia alpina*
19. Luz arc	*Luzula arcuata*
20. Gym dry	*Gymnocarpium dryopteris*
21. Lyc cla	*Lycopodium clavatum*
22. Nar str	*Nardus stricta*
23. Sor auc	*Sorbus aucuparia*
24. Cla hyd	*Cladonia spp* (not identified)
25. Cet isl	*Cetraria islandica*
26. Cla squ	*Cladonia squamosa*
27. Cla gra	*Cladonia gracilis*
28. Sor cup	*Cladonia spp* (not identified)
29. Cla lon	*Cladonia spp* (not identified)
30. Cla fim	*Cladonia fimbriata*
31. Alc alp	*Alchemilla alpina*
32. Oxa ace	*Oxalis acetosella*
33. Gna nor	*Gnaphalium norvegicum*
34. Sal her	*Salix herbacea*
35. Pyr min	*Pyrola minor*
36. Leo aut	*Leontodon autumnalis*
37. Sib pro	*Sibbaldia procumbens*
38. Sol vir	*Solidago virgaurea*
39. Fes ovi	*Festuca ovina*
40. Bet nan	*Betula nana*
41. Ran spp	*Ranunculus spp*
42. Sal phy	*Salix phylicifolia*
43. Mel pra	*Melampyrum pratense*
44. Ste alp	*Stereocaulon alpinum*
45. Cla por	*Cladonia portentosa*
46. Cla chl	*Cladonia chlorophaea*
47. Cla con	*Cladonia coniocraea*
48. Cla dig	*Cladonia digitata*
49. Cla unc	*Cladonia uncialis*
50. Lyc sel	*Lycopodium selago*
51. Eup hel	*Euphorbia helioscopia*
52. Lis cor	*Listera cordata*
53. Lyc ann	*Lycopodium annotinum*
54. Jun tri	*Juncus trifidus*
55. Vac vit	*Vaccinium vitis-idaea*
56. Pin vul	*Pinguicula vulgaris*
57. Arc alp	*Arctostaphylos alpina*
58. Car spp	*Carex spp*
59. Cet eri	*Cetraria ericetorum*
60. Ste con	*Stereocaulon condensatum*
61. Lou pro	*Louiseleuria procumbens*
62. Cla car	*Cladonia cariosa*
63. Cla cer	*Cladonia cervicornis*
64. Cla ver	*Cladonia verticillata*
65. Sol cro	*Solorina crocea*
66. Cla ran	*Cladonia rangiformis*
67. Cla arb	*Cladonia arbuscula*
68. Cla def	*Cladonia deformis*
69. Cla pix	*Cladonia pyxidata*
70. Cla ama	*Cladonia amaurocraea*
71. Cla bel	*Cladonia bellidiflora*
72. Cla sul	*Cladonia sulphurina*
73. Cla ple	*Cladonia pleurota*
74. Cla cri	*Cladonia crispata*
75. Pel pol	*Peltigera polydactyla*
76. Des ces	*Deschampsia cespitosa*
77. Cla arb	*Cladonia arbuscula*
78. Sal lan	*Salix lanata*
79. Lot cor	*Lotus corniculatus*
80. Ath dis	*Athyrium distentifolium* *
81. Ste bot	*Stereocaulon botryosum*
82. Oxy dig	*Oxyria digyna*
83. Phl alp	*Phleum alpinum*
84. Sax ste	*Saxifraga stellaris*
85. Sax aiz	*Saxifraga aizoides*
86. Ste ves	*Stereocaulon vesuvianum*
87. Ver alp	*Veronica alpina*
88. Pyr nor	*Pyrola norvegicum*
89. Aln glu	*Alnus glutinosa*
90. Jun com	*Juniperis communis*
91. Par pal	*Parnassia palustris*
92. Pol viv	*Polygonum viviparum*
93. Ger syl	*Geranium sylvaticum*
94. Alc glo	*Alchemilla glomerulans*
95. Ort sec	*Orthilia secunda*
96. Pri spp	*Primula spp.*

Appendix 1 (sheet 2) List of full species names

(Each number is that used within the combined data set)

Abbreviation	Species name
97. Rub ida	*Rubus idaeus*
98. Cer spp	*Cerastium spp.*
99. Str cup	*Cladonia spp* (not identified)
100. Cla coc	*Cladonia coccifera*
101. Cla con	*Cladonia coniocraea* *
102. Cla sub	*Cladonia subfurcata*
103. Cla cer	*Cladonia cervicornis*
104. Cla fur	*Cladonia furcata*
105. Cla ste	*Cladonia stellaris*
106. Bro cup	*Cladonia spp* (not identified)
107. Ste pas	*Stereocaulon paschale*
108. Cet cuc	*Cetraria cucullata*
109. Bla cup	*Cladonia spp* (not identified)
110. Cer cer	*Cerastium cerastoides*
111. Gna sup	*Gnaphalium supinum*
112. Cry cri	*Cryptogramma crispa*
113. Hie spp	*Hieracium spp*
114. Agr ten	*Agrostis tenuis*
115. Sag sag	*Sagina saginoides*
116. Luz spi	*Luzula spicata*
117. Ulm gla	*Ulmus glabra*
118. Epi als	*Epilobium alsinifolium*
119. Epi ang	*Epilobium angustifolium*
120. Rus spp	*Rush* (not identified)
121. Cer alp	*Cerastium alpinum*
122. Cas hyp	*Cassiope hypnoides*
123. Sed ros	*Sedum rosea*
124. Hie alp	*Hieracium alpinum*
125. Ant alp	*Antennaria alpina*
126. Des ces	*Deschampsia cespitosa* *
127. Lyc alp	*Lychnis alpina*
128. Cet niv	*Cetraria nivalis*
129. Cet ste	*Cetraria stellaris*
130. Cet del	*Cetraria delisei*
131. Tha ver	*Thamnolia vermicularis*
132. Cor acu	*Cornicularia aculeata*
133. Sph glo	*Sphaerophorus globosus*
134. Nep arc	*Nephroma arcticum*
135. Cla alp	*Cladonia alpestris*
136. Arc alp	*Arctostaphylos alpina*
137. Arc uva	*Arctostaphylos uva-ursi*
138. Eup fri	*Euphrasia frigida*
139. Tar spp	*Taraxacum spp* *
140. Hie alp	*Hieracium alpinum* *
141. Ran acr	*Ranunculus acris*
142. Cam rot	*Campanula rotundifolia*
143. Bar alp	*Bartsia alpina*
144. Poa alp	*Poa alpina*
145. Ale cha	*Alectoria chalybeiformis*
146. Pso hyp	*Psorama hypnorum*
147. Sil aca	*Silene acaulis*
148. Pet fri	*Petasites frigidus*
149. Tof pus	*Tofieldia pusilla*
150. Ped lap	*Pedicularis lapponica*
151. Coe vir	*Coeloglossum viride*
152. Cor div	*Cornicularia divergens*
153. Ale och	*Alectoria ochroleuca*
154. Tri spi	*Trisetum spicatum*
155. Cla pyx	*Cladonia pyxidata* *
156. Sph fra	*Sphaerophorus fragilis*
157. Pan pez	*Pannaria pezizoides*
158. Ale nig	*Alectoria nigricans*
159. Car pet	*Cardaminopsis petraea*
160. Des ces	*Deschampsia cespitosa* *
161. Cla cen	*Cladonia cenotea*
162. Cla sym	*Cladonia symphycarpa*
163. Car bel	*Cardamine bellidifolia*
164. Sph mel	*Sphaerophorus melanocarpus*
165. Phs spp	*Physcia spp*
166. Jun spp	*Juncus spp*
167. Tar spp	*Taraxacum spp* *
168. Ped spp	*Pedicularis spp*
169. Luz tri	*Luzula triflora*
170. War gra	*Cladonia spp* (not identified)
171. Far red	*Cladonia* (not identified)
172. Mel rub	*Melandrium rubrum*
173. Sau alp	*Saussurea alpina*
174. Ran pyg	*Ranunculus pygmaeus*
175. Pel pol	*Peltigera polydactyla*
176. Squ cup	*Cladonia spp* (not identified)
177. Tof pus	*Tofieldia pusilla* *
178. Ste spp	*Stereocaulon spp*
179. Lyc sol	*Lycopodium selago*
180. Gre cla	*Cladonia spp* (not identified)
181. Dry oct	*Dryas octopetala*
182. Cla fri	*Cladonia spp* (not identified)
183. Ant dio	*Antennaria dioica*
184. Ane ver	*Anemone vernalis*
185. Ran niv	*Ranunculus nivalis*
186. Leo spp	*Leontodon spp*
187. Rum ari	*Rumex arifolius*
188. Cet del	*Cetraria delisei* *
189. Cor aca	*Cornicularia aculeata* *
190. Sal myr	*Salix myrsinites*
191. Sax opp	*Saxifraga oppositifolia*
192. Sax cer	*Saxifraga cernua*

Appendix 1 (sheet 3) List of full species names

(Each number is that used within the combined data set)

Abbreviation	Species name
193. Vis alp	*Viscaria alpina*
194. Dra alp	*Draba alpina*
195. Sal ret	*Salix reticulata*
196. Ara alp	*Arabis alpina*
197. Lyc spp	*Lychnis spp*
198. Dry exp	*Dryopteris expansa*
199. Pyr spp	*Pyrola spp*
200. Phy sch	*Physconia schiastra*
201. Ran alp	*Ranunculus alpina*
202. Lec qua	*Lecidea quadricolor*
203. Och fri	*Ochrolechia frigida*
204. Ale spp	*Alectoria spp*
205. Woo alp	*Woodsia alpina*
206. Sax ces	*Saxifraga cespitosa*
207. Ran gla	*Ranunculus glacialis*
208. Nar spp	*Nardus spp*
209. Unn cup	*Cladonia spp* (not identified)
210. War red	*Cladonia spp* (not identified) *

Notes: The combined data set is constructed from the individual foreland data sets and so there are some accidental repetitions of certain species and these are marked "*". A number of small lichens (all Cladonia spp) were not identified - these are listed as Cladonia spp.

Appendix 2 List of full glacier foreland names

Abbreviation	Glacier foreland
AUSF	Austerdalsbreen
FÅSF	Fåbergstølsbreen
STLF1	Storbreen low sequence (1) (the first sequence of moraines recorded across the low-alpine section of the foreland)
STLF2	Storbreen low sequence (2) (the second sequence of moraines recorded across the low-alpine section of the foreland)
SVLF	Svellnosbreen
STHF	Storbreen high (the sequence of moraines recorded across the mid-alpine section of the foreland)
HØHF	Høgvaglbreen
BØHF	Bøverbreen

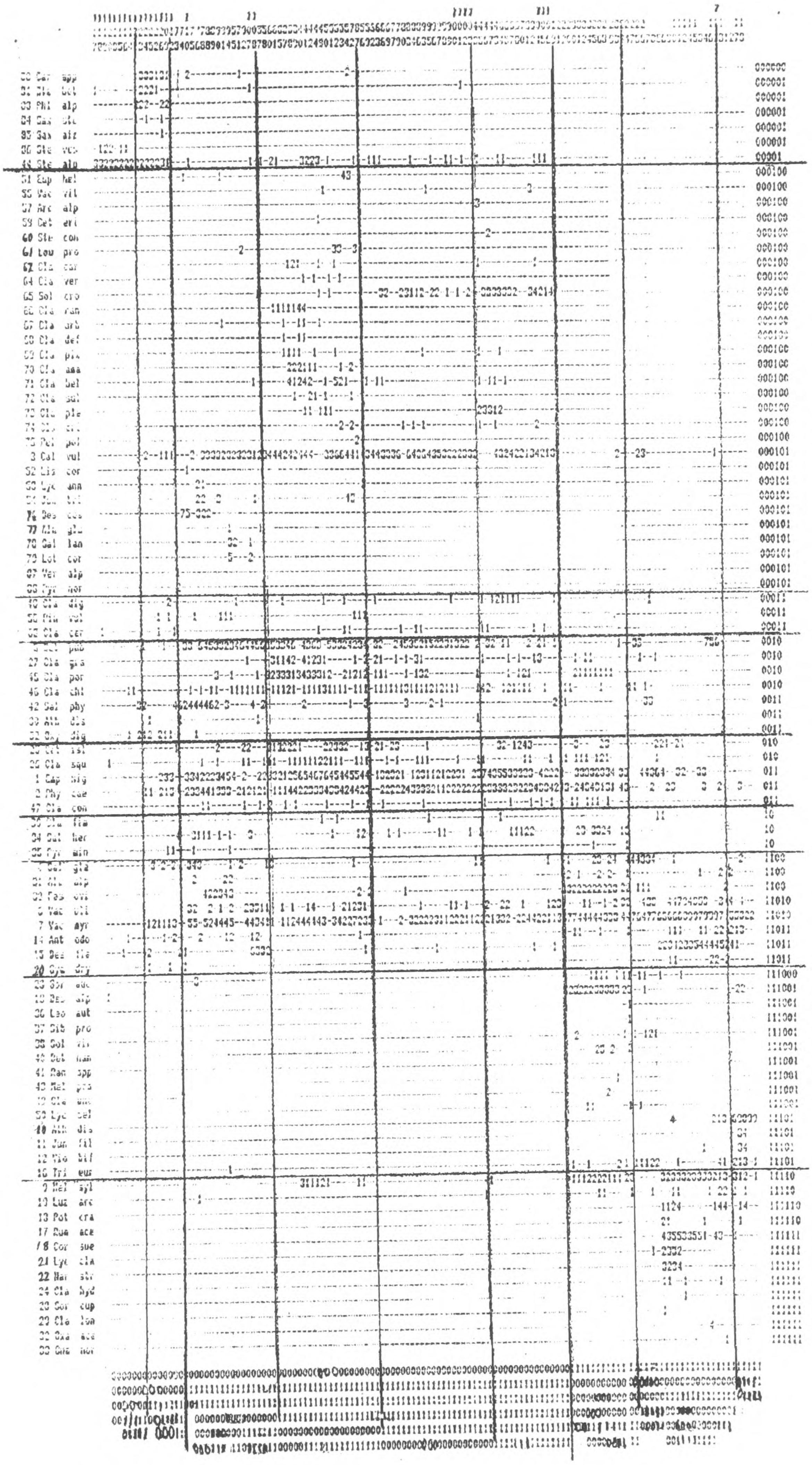
Appendix 3 List of full environmental parameter names

(Each number is that used within all data sets)

Abbreviations	**Environmental parameter** (and measurement criteria)
1. Sno lie	Snow duration: percentage ratio of the black crustose lichen (*Umbilicaria spp*) to the green crustose lichen (*Rhizocarpon spp*), a high ratio signifying short snow duration
2. Pos env	Position: on an ordinal scale of 1 (toe-slope) to 5 (crest)
3. Fro hve	Frost heave: frequency (1/25) of evidence of frost activity (e.g. stripes, polygons, cracks, nubbins and larger clasts on surface)
4. Dow els	Dowel heave: quantitative measure of mean heave (cm) of nine dowels (match sticks) emplaced for one year.
5. Moi tre	Moisture: "finger test" method used to estimate moisture on an ordinal scale of 1 (wet) to 5 (dry). Three readings (surface, 2.5 cm and 5 cm) were combined to make a 3 (wet) to 15 (dry) scale that was entered into the data set.
6. Flu via	Fluvial: frequency (1/25) of evidence of fluvial activity (e.g. stream flow or channels)
7. Slo pe*	Slope: quantitative measurement (°)
8. Sol flu	Solifluction: frequency (1/25) of evidence of solifluction (e.g. lobes, ripples and scars)
9. Asp ect	Northerly aspect: on an ordinal scale of 1 (north) to 5 (south)
10. Tra mpl	Trampling: frequency (1/25) of evidence of trampling (e.g. broken plants, paths and foot prints)
11. Ani inf	Animal influence: frequency (1/25) of evidence of grazing (e.g. nibbled plants or dung)
12. Soi tex	Soil texture: on an ordinal scale of 1 (sand); 2 (sandy loam); 3 (loamy sand); 4 (loam).
13. pH* ***	pH: quantitative measurement to two decimal places
14. Hum dep	Humus depth: quantitative measurement of the depth of the organic horizon (Ao, Aoo)
15. Sta dep	Soil depth: quantitative measurement of the depth of the soil (*"the total depth of organic staining (Bh horizon) or of organic material within a mixed organic-inorganic horizon - whichever is greater"* - Whittaker, 1989)
16. Roo dep	Root depth: quantitative measurement of the depth of representative root penetration
17. Bar bou	Bare ground boulders: quantitative measurement of the percentage proportion of boulders on bare ground within each quadrat
18. Bar gra	Bare ground gravels: quantitative measurement of the percentage proportion of gravels and cobbles on bare ground within each quadrat
19. Bar fin	Bare ground fines: quantitative measurement of the percentage proportion of fines on bare ground within each quadrat
20. Veg cov	Total vegetation cover: percentage cover and frequency
21. Bry cov	Total bryophyte cover: percentage cover and frequency
22. Asp eas	Easterly aspect: on an ordinal scale of 1 (east) to 5 (west)
23. Alt tud	Altitude: quantitative measurement (m)
24. Age mor	Terrain age: measurement on an ordinal scale of 1 (<25 years) to 11 (>250 years) (each point on the scale represents 25 years and the last point represents terrain older than 250 years)

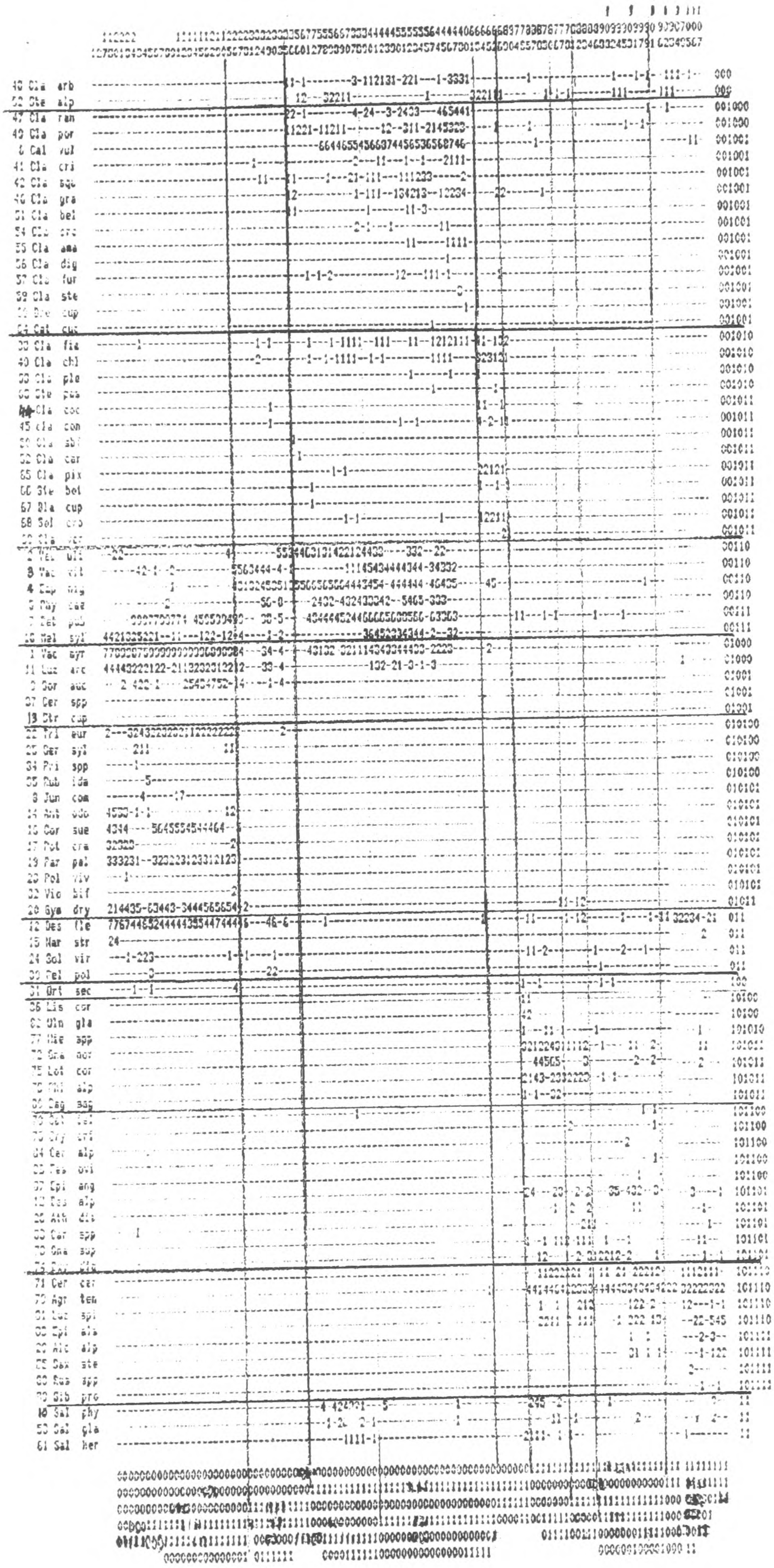
Appendix 4.1 Copy of original TWINSPAN Final Table for Austerdalsbreen

(Please excuse poor quality of print out, unfortunately original table, on disk, is lost)



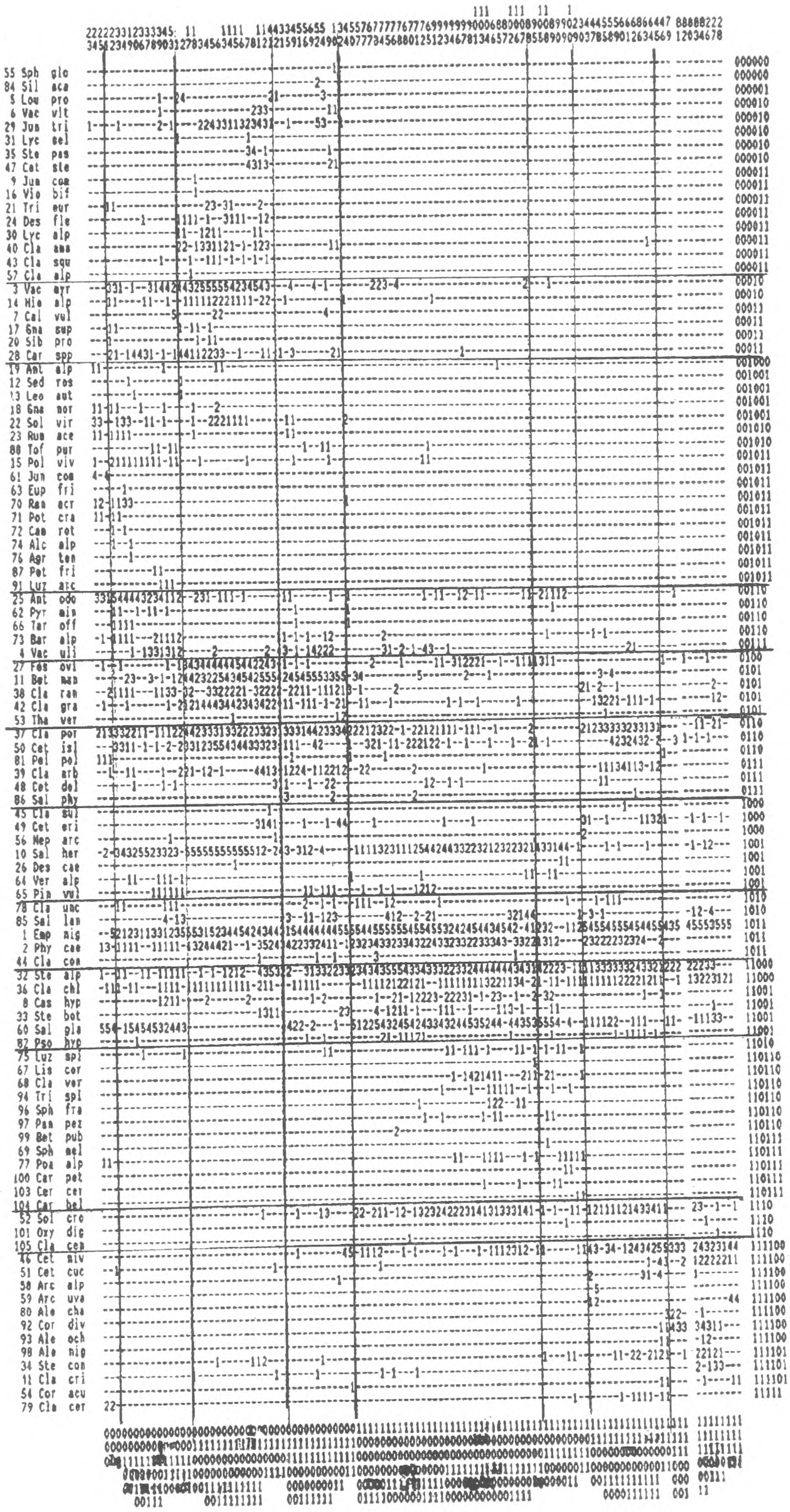
Appendix 4.2 Copy of original TWINSPAN Final Table for Fåbergstølsbreen

(Please excuse poor quality of print out, unfortunately original table, on disk, is lost)



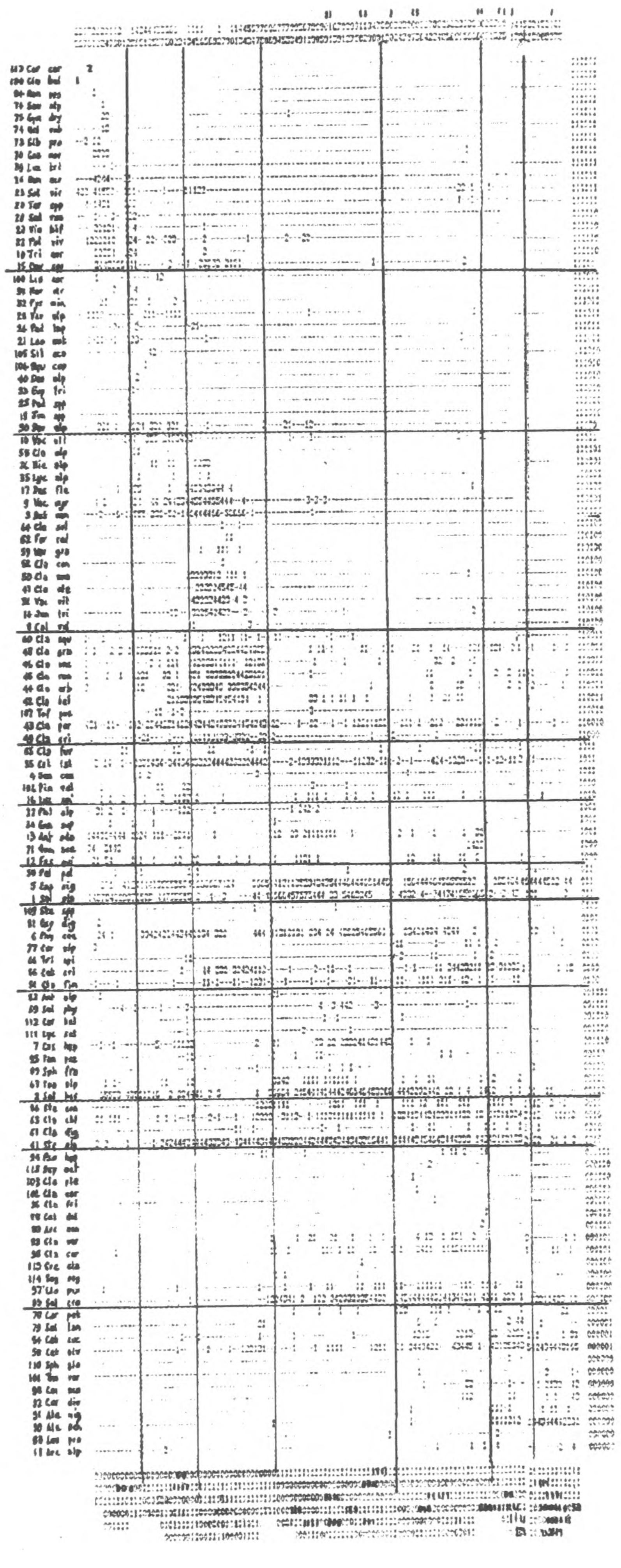
Appendix 4.3 Copy of original TWINSPAN Final Table for Storbreen low (1)

(Please excuse poor quality of print out, unfortunately original table, on disk, is lost)



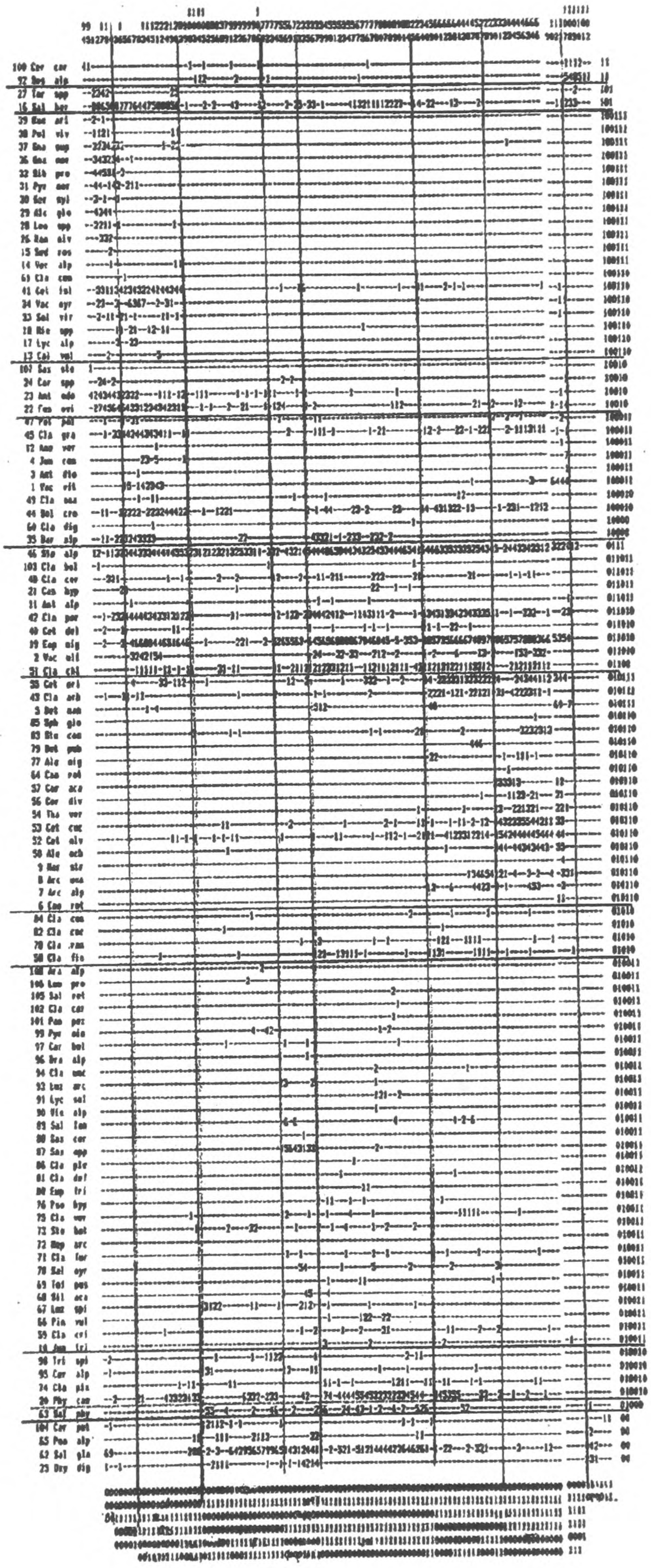
Appendix 4.4 Copy of original TWINSPAN Final Table for Storbreen low (2)

(Please excuse poor quality of print out, unfortunately original table, on disk, is lost)



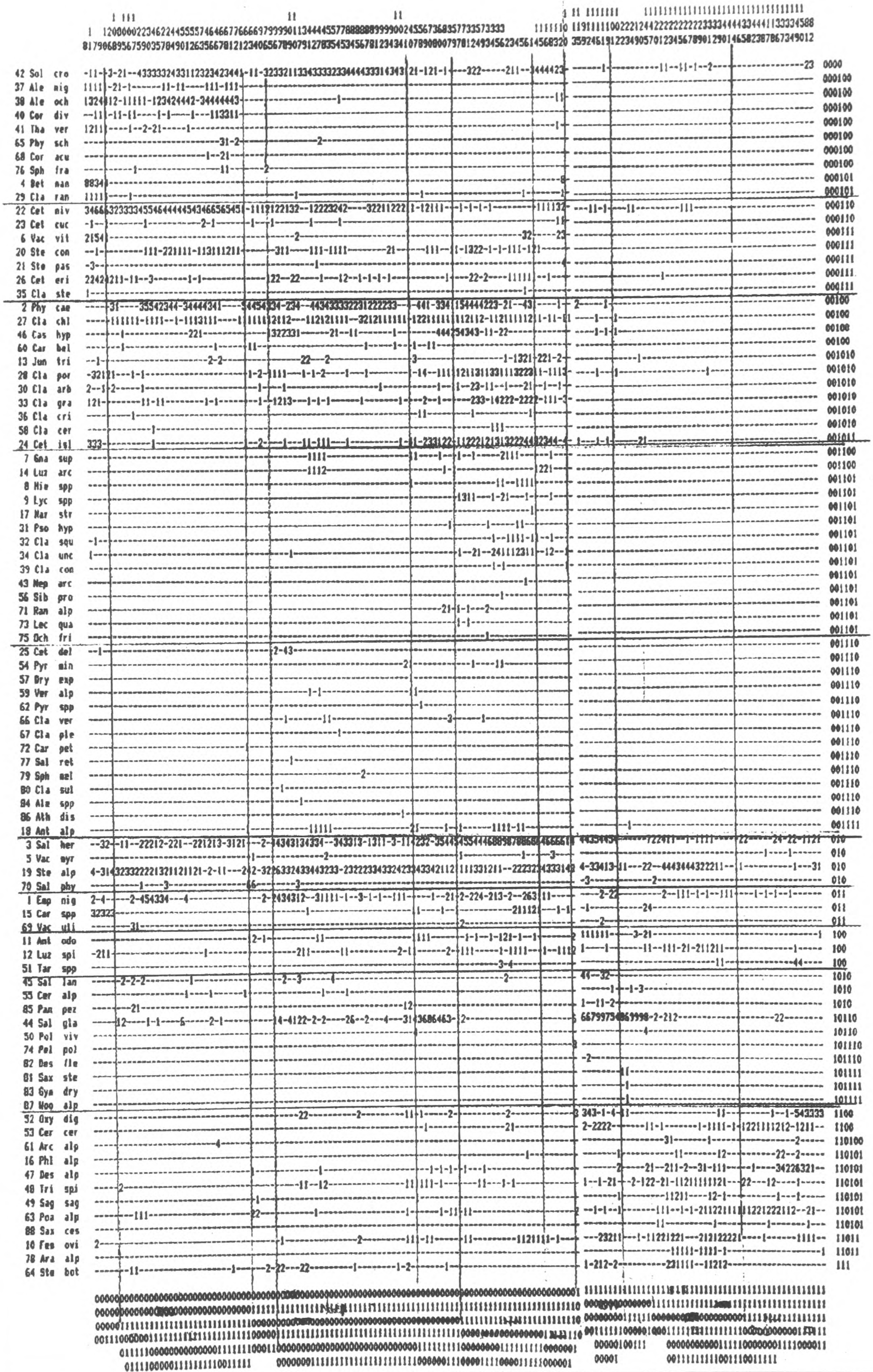
Appendix 4.5 Copy of original TWINSPAN Final Table for Svellnosbreen

(Please excuse poor quality of print out, unfortunately original table, on disk, is lost)



Appendix 4.6 Copy of original TWINSPAN Final Table for Storbreen High

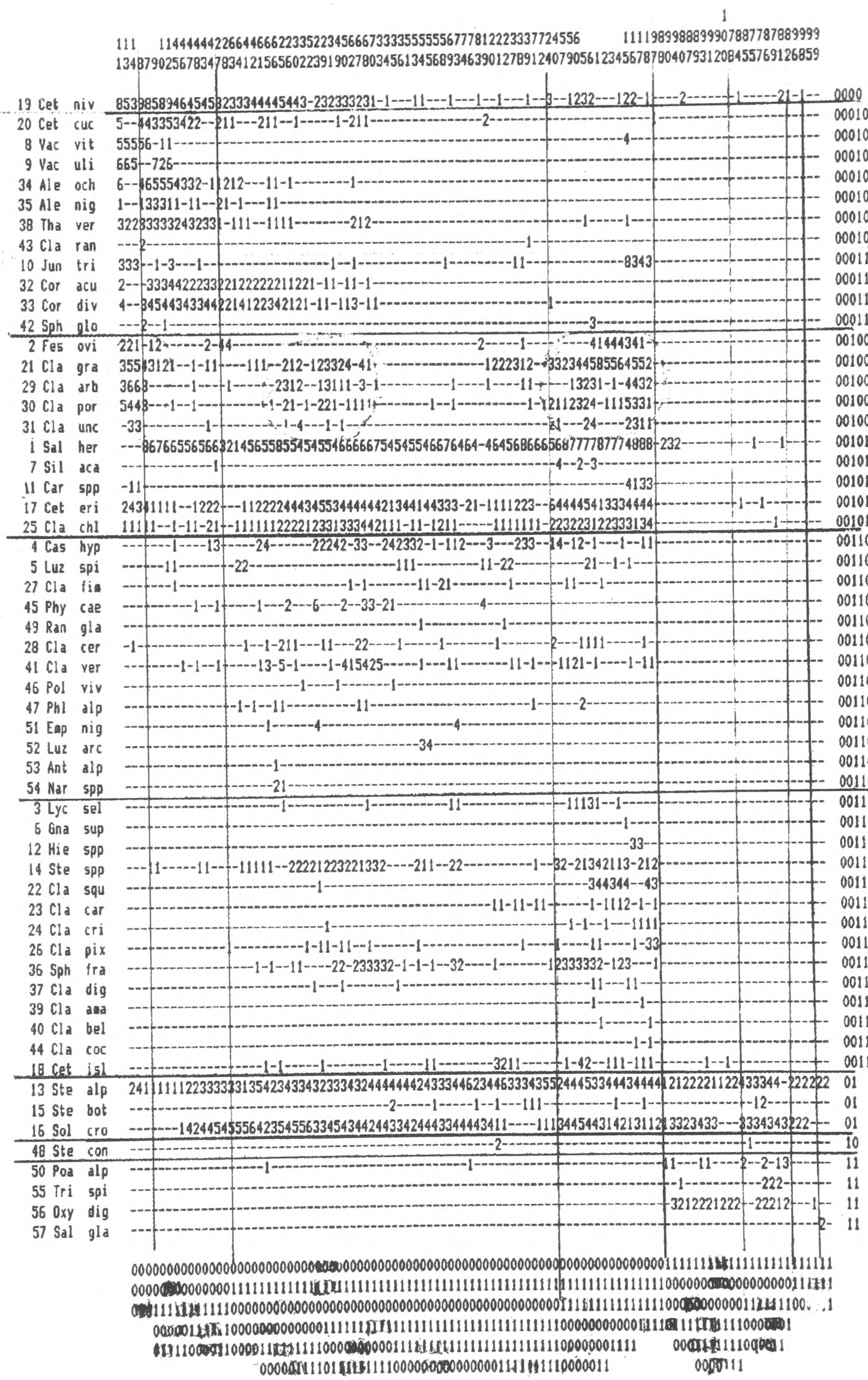
(Please excuse poor quality of print out, unfortunately original table, on disk, is lost)



```
42 Sol cro   0000
37 Ale nig   000100
38 Ale och   000100
40 Cor div   000100
41 Tha ver   000100
65 Phy sch   000100
68 Cor acu   000100
76 Sph fra   000100
 4 Bet nan   000101
29 Cla ran   000101
22 Cet niv   000110
23 Cet cuc   000110
 6 Vac vit   000111
20 Ste con   000111
21 Ste pas   000111
26 Cet eri   000111
35 Cla ste   000111
 2 Phy cae   00100
27 Cla chl   00100
46 Cas hyp   00100
60 Car bel   00100
13 Jun tri   001010
28 Cla por   001010
30 Cla arb   001010
33 Cla gra   001010
36 Cla cri   001010
58 Cla cer   001010
24 Cet isl   001011
 7 Gna sup   001100
14 Luz arc   001100
 8 Hie spp   001101
 9 Lyc spp   001101
17 Nar str   001101
31 Pso hyp   001101
32 Cla squ   001101
34 Cla unc   001101
39 Cla con   001101
43 Nep arc   001101
56 Sib pro   001101
71 Ran alp   001101
73 Lec qua   001101
75 Och fri   001101
25 Cet del   001110
54 Pyr min   001110
57 Bry exp   001110
59 Ver alp   001110
62 Pyr spp   001110
66 Cla ver   001110
67 Cla ple   001110
72 Car pet   001110
77 Sal ret   001110
79 Sph mel   001110
80 Cla sul   001110
84 Ale spp   001110
86 Ath dis   001110
18 Ant alp   001111
 3 Sal her   010
 5 Vac myr   010
19 Ste alp   010
70 Sal phy   010
 1 Emp nig   011
15 Car spp   011
69 Vac uli   011
11 Ant odo   100
12 Luz spi   100
51 Tar spp   100
45 Sal lan   1010
55 Cer alp   1010
85 Pan pez   1010
44 Sal gla   10110
50 Pol viv   10110
74 Pol pol   101110
82 Des fle   101110
81 Sax ste   101111
83 Gya dry   101111
87 Woo alp   101111
52 Oxy dig   1100
53 Cer cer   1100
61 Arc alp   110100
16 Phl alp   110101
47 Des alp   110101
48 Tri spi   110101
49 Sag sag   110101
63 Poa alp   110101
88 Sax ces   110101
10 Fes ovi   11011
78 Ara alp   11011
64 Ste bot   111
```

Appendix 4.7 Copy of original TWINSPAN Final Table for Høgvaglbreen

(Please excuse poor quality of print out, unfortunately original table, on disk, is lost)



```
                                                                                           1
             111   11444444226644666223352234566673333555556777812223337724556        1111989988899907887787889999
             1348790256783478341215656022391902780345613456893463901278912407905612345678780407931208455769126859

  19 Cet niv 8539858946454582333444445443-232333231-1---11---1---1--1---1--3--1232---122-1---2------1-----21-1--  0000
  20 Cet cuc 5--443353422--211---211--1-----1-211---------------2---------------------------------------------  000100
   8 Vac vit 55556-11------------------------------------------------------4----------------------------------  000101
   9 Vac uli 665--726---------------------------------------------------------------------------------------  000101
  34 Ale och 6--465554332-11212---11-1--------1-------------------------------------------------------------  000101
  35 Ale nig 1--133311-11--21-1---11--------------------------------------------------------------------------  000101
  38 Tha ver 322833332432331-111--1111--------212----------------------------1-----1------------------------  000101
  43 Cla ran ---2------------------------------------------------1------------------------------------------  000101
  10 Jun tri 333--1-3---1-----------------1--1-----------1---------11------------8343------------------------  00011
  32 Cor acu 2---3334422233212222222211221-11-11-1------------------------------------------------------------  00011
  33 Cor div 4--345443433442214122342121-11-113-11------------------------1------------------------------------  00011
  42 Sph glo ---2--1--------------------------------------------------------3---------------------------------  00011
   2 Fes ovi 221-12-------2-44-------------------------2-----1---------41444341--------------------------------  001000
  21 Cla gra 3554312l--1-11----111--212-123324-41--------------1222312--332344585564552-------------------------  001000
  29 Cla arb 3668-------1----1------2312--13111-3-1----------1----1----11----13231-1-4432-----------------------  001001
  30 Cla por 5448---1--1-----------1-21-1-221-1111--------1--1----------1-12112324-1115331----------------------  001001
  31 Cla unc -33---------1----------1-4---1-1----------------------------21---24----2311------------------------  001001
   1 Sal her ---8676655656663214565585545455466666754545546676464-46456866656877787774888-232--------1---1------  001010
   7 Sil aca ----------------1------------------------------------------4--2-3----------------------------------  001011
  11 Car spp -11------------------------------------------------------------4133--------------------------------  001011
  17 Cet eri 24311111--1222---1122224443455344444421344144333-21-1111223--644445413334444------------1--1-------  001011
  25 Cla chl 11111--1-11-21--111111222212331333442111-11-1211-----1111111-223223122333134-------------1--------  001011
   4 Cas hyp ---------1----13-----24------22242-33--242332-1-112---3---233--14-12-1---1--11---------------------  001100
   5 Luz spi -------11--------22-----------------------111----------11-22------------21--1-1-------------------  001100
  27 Cla fim ---------1------------------------1-1-------11-21---------1--------11---1--------------------------  001100
  45 Phy cae -----------1--1-----1---2---6---2--33-21------------4---------------------------------------------  001100
  49 Ran gla ------------------------------------------1-----------1-------------------------------------------  001100
  28 Cla cer -1-----------------1--1-211---11---22----1-----1-------1--------2---1111-----1--------------------  001101
  41 Cla ver ----------1-1--1-----13-5-1----1-415425-----1---11-------11-1---1121-1----1-11--------------------  001101
  46 Pol viv ----------------------------1----1-------1----------------------------------------------------------  001101
  47 Phl alp -------------------1-1--11----------11----------------------1------2--------------------------------  001101
  51 Emp nig ------------------------1------4--------------------4----------------------------------------------  001101
  52 Luz arc ------------------------------------------34------------------------------------------------------  001101
  53 Ant alp -------------------------1--------------------------------------------------------------------------  001101
  54 Nar spp -------------------------21------------------------------------------------------------------------  001101
   3 Lyc sel -------------------------1-----------1-----------11-----------------11131--1-----------------------  001110
   6 Gna sup ------------------------------------------------------------------------1--------------------------  001110
  12 Hie spp -------------------------------------------------------------------------33------------------------  001110
  14 Ste spp ---11-----11----11111--22221223221332----211--22----------1--32-21342113-212----------------------  001110
  22 Cla squ ----------------------------1------------------------------344344--43------------------------------  001110
  23 Cla car ----------------------------------------------------11-11-11------1-1112-1-1-----------------------  001110
  24 Cla cri ----------------------------1---------------------------------1-1--1---1111------------------------  001110
  26 Cla pix ----------------------1-11-11--1------1---------------1----1----11----1-33-------------------------  001110
  36 Sph fra ------------------1-1--11----22-233332-1-1-1--32----1-------12333332-123---1-----------------------  001110
  37 Cla dig ---------------------------1---1-------1-----------------------11---11----------------------------  001110
  39 Cla ama ---------------------------------------------------------------1------1----------------------------  001110
  40 Cla bel ----------------------------------------------------------------1------1---------------------------  001110
  44 Cla coc ------------------------------------------------------------------------1-1------------------------  001110
  18 Cet isl --------------------1-1-----1--------1-----11---------3211------1-42--111-111------1--1-------------  001111
  13 Ste alp 24111111223333331354234334323334324444444243334462344633343552444533444344441212222112243334 4-222222  01
  15 Ste bot ---------------------------------2-----1-----1--1---111------------1---1-----------------12--------  01
  16 Sol cro -------14244545556423545563345434424433424443344443411----1113445443142131121 3323433---3334343222---  01
  48 Ste con -------------------------------------------------2------------------------------------1------------  10
  50 Poa alp --------------------1----------------------1---------------------------11---11----2--2-13----------  11
  55 Tri spi --------------------------------------------------------------------------1-----------222----------  11
  56 Oxy dig --------------------------------------------------------------------------3212221222--22212---1----  11
  57 Sal gla --------------------------------------------------------------------------------------------------2-  11

             0000000000000000000000000000000000000000000000000000000000000000000000000000000111111111111111111111
             0000000000000000011111111111111111111111111111111111111111111111111111111111111000000000000000001111
             0001111111111111111000000000000000000000000000000000000000000000001111111111111111000000000000011111100. .1
               0000011111100000000000000000111111111111111111111111111111111111100000000000011111111111110000001
               0111100001100001111111110000000000111111111111111111111111111100000001111     0001111111100001
                         0000111110111111111000000000000000001111111111110000011           0000111
```

Appendix 4.8 Copy of original TWINSPAN Final Table for Bøverbreen

(Please excuse poor quality of print out, unfortunately original table, on disk, is lost)

```
                                                                                    11  111 11            1   11  11         1
             444442244 1223244    11  111112233  1122342335333355555567566666666866500770009007888788787881778007 119999999990
             6345778189059062956781234345690412127812803790345612356789090123456378434125680797045912496780586123 123451267890

37 Sph  glo  -----1----1----------------------------------------------------------------------------------------- ------------  000000
38 Ale  och  133444334434231----1--------------------------------------1-1--------------------------------------- ------------  000000
40 Cor  acu  -322343223221121----------------------112-------------------1--------------------------------------- ------------  000000
41 Cor  div  --11-22325341211-----------------------11-1--------------------------------------------------------- ------------  000000
39 Ale  nig  -2143-1--211121---------------------------------------------1--------------------------------------- ------------  000001
60 Arc  alp  --2------------------------------------------------------------------------------------------------- ------------  000001
 1 Emp  nig  ----3--------------1-3------------------------------------------------------------------------------ ------------  000010
 9 Hie  spp  ---------21-1-----------------2-1------------1------------------------------------------------------ ------------  000010
21 Cet  niv  -4425325499542544666644-111-----2-111--1-231331---------13--1-1---------------1--------------------- ------------  000010
58 Jun  tri  -2------------2------------------------------------------------------------------------------------- ------------  000010
22 Cet  cuc  1-21---4-1133-2-3111--1----------1------11-1---------------1-12-1---------------------------1------- ------------  000011
32 Cla  ama  ---------12------22112--2---1--1-------------------------------------------------------------------- ------------  00010
42 Tha  ver  -1-------2328----32322---1-----1---1---------------------------------------------------------------- ------------  00010
 4 Car  spp  ---------34------1-234--4231-----1---1-------------------------------------------------------------- ------------  00011
44 Unn  cup  ----------1---------1---11-------------------------------------------------------------------------- ------------  00011
54 Cla  cri  -----------2-------------------1-------2------------------------------------------------------------ ------------  00011
18 Ste  bot  ---------------12--1--121---1112211--1--2--211----12--11---2----11-1-------------------------1------ --1---------  001000
49 Gna  sup  -----------------------------1-------1------2--2211--------------1-1-------------------------------- ------------  001000
53 Cla  cer  ------------1-121-----------11111----11--11-----211--11-----1--11---------------------------1------- ------------  001000
 3 Phy  cae  -----------------------------------2--------3-------2-1-113----------------------------------------- ------------  001001
11 Lyc  sel  --------------------1------------------------------------1-------1---------------------------------- ------------  001001
36 Cla  fur  -------------------1-----------1-----------1------1------------------------------------------------- ------------  001001
48 Cas  hyp  -------------------------------1-----22----2--------112--------------------------------------------- ------------  001001
55 Cla  dig  ------------1-------------------------------------------------1---1--------------------------------- ------------  001001
57 Pso  hyp  --------------------------------1-----------1-1----------------------------------------------------- ------------  001001
 6 Luz  spi  -1--1--1-------------2-----1-11---1111----1-11--221------------------------------------------------- ------------  001010
16 Ste  con  -1111--221-22-221222221232222211241-232221222221-11-1-111--1-22-13--1-------------2-----------1----- ------------  001010
23 Sph  fra  --12-------13-223---------2322423--3322--3213222-333--1--------1---1-------------------------------- ------------  001010
24 Cla  chl  1121---211112-3122322432344334332332344222122321--221112311331341211221----------------------------- ------------  001010
26 Cla  fim  ----------1-------1---1---------11-----------1--1---1-1---1----1------------------------------------ ------------  001010
30 Cla  ran  ---------12-1-1--1-1133-1-------11------------------------------------------------------------------ ------------  001011
43 Pel  pol  ----------1---------21--1--1------------------------------------------------------------------------ ------------  001011
20 Cet  eri  -11-1--311211-4336564445445344444442325443322411--23321------1-1-1---1------------------------------ ------------  001100
19 Cet  isl  -------3---11-41142232321443332234334332343342-3122--1---------------------------------------------- --------1---  001101
25 Cla  pix  ---------1--1---11111112233121-1111-12-1--1-1----11-------1-----1----------------------------------- ------------  001101
27 Cla  squ  ------------1---111-1211132224311-434222--1--12122222----------------------------------------------- ------------  001101
33 Cla  gra  ---------1111-12445454455444544444664344443121344-2211------------1--------------------------------- ------------  001101
35 Cla  ver  ------------1---21-11111----1----1---1---------1--------2------------------------------------------- ------------  001101
62 Cet  del  ---------------------------------------2--1--------------------------------------------------------- ------------  001101
10 Vac  vit  --------------------44------------------------------------------------------------------------------ ------------  001110
12 Ran  gla  -----------------------------------1---------------------------------------------------------------- ------------  001110
13 Nep  arc  -------------------------2-------------------------------------------------------------------------- ------------  001110
17 Ste  spp  ----------------11-1111---11-1---1------------------------------------------------------------------ ------------  001110
28 Cla  por  ---------22-1--12333344333332444541-1-12--1--11---1-1-1--------------------------------------------- ------------  001110
31 Cla  unc  ---------11-----1222233-1-354222241------1---------------------------------------------------------- ------------  001110
34 Cla  car  ------------------11---1---112---11-1-1------------------------------------------------------------- ------------  001110
45 Cla  ste  --------------------1-------------1----------------------------------------------------------------- ------------  001110
46 Cla  bel  ------------------------1--------------------------------------------------------------------------- ------------  001110
47 Pan  pez  ---------------------------1------------------------------------------------------------------------ ------------  001110
51 Sag  sag  ------------------------------1--------------------------------------------------------------------- ------------  001110
56 War  red  ---------------------------------------------------------------------------------------------------- ------------  001110
29 Cla  arb  -11------33-2-11-34543333433323444-11--2-1---------------------------------------------------------- ------------  001111
 2 Sal  her  -3--154646666-5565575663566665666676646665665655566555666655566565355555--4314232354342-2322-1443323 1-23-11111--  01
 5 Fes  ovi  --1---1--2111-4----2323--1211--22131-1-1--2---12-----------------2-33323------1--2222------2---22--- --1---1-----  01
 8 Ant  alp  ----------11-1----1---------------11----------------1---------1-11-----------------------1---------- ------------  01
15 Ste  alp  --1-1--231326-44433461244342333554342244448335333265655546646243144455584-112221323444233212232334421 112221133321  10
50 Tri  spi  2-21---------121---------------111------1--222-1221--1-11331-1111121-----------2-----------------1-- --222--122--  10
63 Sal  gla  ----------------------------------------------------1-----------------1----------------------------- ------------  10
14 Sol  cro  -12-112312-33-43323--2244445453343323434141533211212--21--4324114341121-1-2333224432332-1444454222- --21---2221-  110
 7 Poa  alp  ---1-----------------------------11-----1---1----1--1111-1-1--1--111-2111--1-11-1322232311223-333331 223434433333  1110
52 Oxy  dig  -------------------------------------------22-2--1-----------------2---1--1---2222-211--323433323342 3244445312--  1110
61 Des  alp  -------------------------------------------------3---------------2---------------1--11--21221-22-433 33-2-1------  1110
64 Cer  cer  ------------------------------------------------------------------------------1--2---1--22222-222--- --2--22-----  1110
59 Cer  alp  ------------------------------------------------------------------2-------------1121222---------1--- ------------  1111

             0000000000000000000000000000000000000000000000000000000000000000000001111111111111111111111111111111 111111111111
             0000000000001111111111111111111111111111111111111111111111111111111110000000000000000111111111111111 111111111111
             0111[illegible]111000000000000000000000000000111111111111111111111111111111[illegible]1111[illegible]1111110000000000000 00111[illegible]1111
              000[illegible]0001[illegible]0000[illegible]001111111[illegible]111111111111111100000000000011111111111111111   0[illegible]00001[illegible]1000[illegible]0001[illegible] 110[illegible]01[illegible]
              000[illegible]111   0000[illegible]0[illegible]1[illegible]111111111111111111100001111111000000000111111111   06[illegible]1100[illegible]14000000111001 110001100011
              000[illegible]111 00000[illegible]1[illegible]1111[illegible]111111111111111100001111110000000001111111111
                        00111     0000[illegible]000001[illegible]111   000011100000011000000011       000111      001111
```

Appendix 5.1

Coordinates for Fig. 5.1 ("final site group" centroid plot, Austerdalsbreen)

	axis 1	axis 2
1 Sno lie	-273	-127
2 Pos env	-114	-207
3 Fro hve	-472	-11
4 Dow els	-190	80
5 Moi tre	-196	-51
6 Flu via	428	120
7 Slo pe*	-84	-3
8 Sol flu	-23	-177
9 Asp ect	-36	-73
10 Tra mp	-176	-116
11 Ani inf	-126	-22
12 Soi tex	525	-188
13 pH* ***	-39	370
14 Hum d	746	-144
15 Sta de	602	-280
16 Roo de	882	-154
20 Bar bo	-369	24
21 Bar gra	-320	326
22 Bar fin	-303	11
23 Veg cc	517	-236
24 Bry co	-584	134
25 Asp ea	-36	18
26 Alt tud	-257	575
27 Age m	764	-335
Group 7	336.2	16.4
Group 8	-157.4	254.1
Group 9	-62.7	449.1
Group 10	11.5	295.5
Group 13	168.1	-0.4
Group 22	-8.5	33.6
Group 24	46.5	-41.4
Group 25	53	19.6
Group 46	-65.7	-34.5
Group 47	-74.2	-37.7

Appendix 5.2

Coordinates for Fig. 5.9 ("final species group" centroid plot, Austerdalsbreen)

	axis 1	axis 2
1 Sno lie	-273	-127
2 Pos env	-114	-207
3 Fro hve	-472	-11
4 Dow els	-190	80
5 Moi tre	-196	-51
6 Flu via	428	120
7 Slo pe*	-84	-3
8 Sol flu	-23	-177
9 Asp ect	-36	-73
10 Tra mp	-176	-116
11 Ani inf	-128	-22
12 Soi tex	525	-188
13 pH* ***	-39	370
14 Hum d	746	-144
15 Sta de	602	-280
16 Roo de	882	-154
20 Bar bo	-369	24
21 Bar gra	-320	326
22 Bar fin	-303	11
23 Veg cc	517	-236
24 Bry co	-584	134
25 Asp ea	-36	18
26 Alt tud	-257	575
27 Age m	764	-335
Group 8	-77.3	333.1
Group 9	-36.4	89.1
Group 68	-63.8	-34.5
Group 69	-0.9	86.9
Group 35	-54.7	53.3
Group 5	-32	-25.4
Group 6	1.7	13.3
Group 14	69.6	34.6
Group 30	111.4	-9.1
Group 31	158.9	-31.6

Appendix 5.3

Coordinates for Fig. 5.2 ("final site group" centroid plot, Fåberstølsbreen)

	axis 1	axis 2
1 Sno lie	-71	247
2 Pos env	-136	80
3 Fro hve	414	-37
4 Dow els	461	-14
5 Moi tre	-108	323
6 Flu via	721	91
7 Slo pe*	-153	-265
8 Sol flu	102	-82
9 Asp ect	130	75
10 Tra mp	259	12
11 Ani inf	-80	-284
12 Soi tex	-89	-174
13 pH* ***	352	82
14 Hum d	-616	-358
15 Sta de	-879	-110
16 Roo de	-657	-352
20 Bar bo	561	100
21 Bar gra	682	89
22 Bar fin	386	-11
23 Veg cc	-456	-89
24 Bry co	-376	-258
25 Asp ea	186	-316
26 Alt tud	302	-46
27 Age m	-648	-346
Group 7	167.6	-4.3
Group 9	-47.4	-5.1
Group 11	-25.3	72
Group 12	225.1	8
Group 16	-46.2	-155.2
Group 17	-47.2	-128.7
Group 20	-32.4	28.2
Group 21	-42.4	114.1
Group 26	227.8	-17
Group 27	246.2	1.5

Appendix 5.4

Coordinates for Fig. 5.10 ("final species group" centroid plot, Fåberstølsbreen)

	axis 1	axis 2
1 Sno lie	-71	247
2 Pos env	-136	80
3 Fro hve	414	-37
4 Dow els	461	-14
5 Moi tre	-108	323
6 Flu via	721	91
7 Slo pe*	-153	-265
8 Sol flu	102	-82
9 Asp ect	130	75
10 Tra mp	259	12
11 Ani inf	-80	-284
12 Soi tex	-89	-174
13 pH* ***	352	82
14 Hum d	-616	-358
15 Sta de	-879	-110
16 Roo de	-657	-352
20 Bar bo	561	100
21 Bar gra	682	89
22 Bar fin	386	-11
23 Veg cc	-456	-89
24 Bry co	-376	-258
25 Asp ea	186	-316
26 Alt tud	302	-46
27 Age m	-648	-346
Group 8	21	66
Group 36	-42.3	125.5
Group 37	-34.3	77.6
Group 19	-43.3	36.5
Group 20	-47.4	-33.2
Group 21	-43.5	-137.2
Group 11	7.7	-78.7
Group 26	208.6	3.4
Group 27	211.7	-1.5
Group 7	71.3	19.3

Appendix 5.5

Coordinates for Fig. 5.3 ("final site group" centroid plot, Storbreen low (1))

	axis 1	axis 2
1 Sno lie	230	-150
2 Pos env	310	-160
3 Fro hve	136	-210
4 Dow els	176	25
5 Moi tre	412	-48
6 Flu via	-63	76
7 Slo pe*	88	127
8 Sol flu	-284	-246
9 Asp ect	75	133
10 Tra mp	239	67
12 Soi tex	-204	-218
13 pH* ***	221	60
14 Hum d	-447	-50
15 Sta de	-479	-75
16 Roo de	-181	215
20 Bar bo	151	214
21 Bar gra	258	154
22 Bar fin	73	127
23 Veg cc	-236	-167
24 Bry co	96	-11
25 Asp ea	-38	-5
26 Alt tud	59	110
27 Age m	-395	-182
Group 4	-50.9	70.3
Group 10	-66.4	-36.5
Group 11	-15.25	-39.4
Group 12	30.7	17.8
Group 13	34.2	65.9
Group 14	63.1	-29.1
Group 15	116.2	2.3

Appendix 5.6

Coordinates for Fig. 5.11 ("final species group" centroid plot, Storbreen low (1))

	axis 1	axis 2
1 Sno lie	230	-150
2 Pos env	310	-160
3 Fro hve	136	-210
4 Dow els	176	25
5 Moi tre	412	-48
6 Flu via	-63	76
7 Slo pe*	88	127
8 Sol flu	-284	-246
9 Asp ect	75	133
10 Tra mp	239	67
12 Soi tex	-204	-218
13 pH* ***	221	60
14 Hum d	-447	-50
15 Sta de	-479	-75
16 Roo de	-181	215
20 Bar bo	151	214
21 Bar gra	258	154
22 Bar fin	73	127
23 Veg cc	-236	-167
24 Bry co	96	-11
25 Asp ea	-38	-5
26 Alt tud	59	110
27 Age m	-395	-182
Group 8	-15.4	-11.6
Group 9	-14.4	23.7
Group 10	-7.2	-13.8
Group 11	-1.8	-1.8
Group 12	-1	-2
Group 13	3.6	-1.2
Group 28	6.3	2.7
Group 29	8.1	19.1
Group 30	15.3	9
Group 31	24.5	-4.1

Appendix 5.7
Coordinates for Fig. 5.4 ("final site group" centroid plot, Storbreen low (2))

	axis 1	axis 2
1 Sno lie	524	-204
2 Pos env	468	-230
3 Fro hve	767	7
4 Dow els	291	-120
5 Moi tre	594	-132
6 Flu via	-61	268
7 Slo pe*	338	84
8 Sol flu	112	-237
9 Asp ect	281	-87
10 Tra mp	290	49
11 Ani inf	240	-58
12 Soi tex	-716	-170
13 pH* ***	-91	-89
14 Hum d	-746	55
15 Sta de	-715	-226
16 Roo de	-787	-51
20 Bar bo	307	341
21 Bar gr	793	132
22 Bar fin	501	42
23 Veg c	-746	-286
24 Bry co	-94	109
25 Asp ea	-124	-200
26 Alt tud	738	204
27 Age m	-713	-100
Group 4	-93.5	216.3
Group 7	173.4	0.65
Group 10	-73.1	32
Group 11	-84.4	-119.3
Group 12	43.5	13.7
Group 13	73.9	4.1

Appendix 5.8
Coordinates for Fig. 5.12 ("final species group" centroid plot, Storbreen low (2))

	axis 1	axis 2
1 Sno lie	524	-204
2 Pos env	468	-230
3 Fro hve	767	7
4 Dow els	291	-120
5 Moi tre	594	-132
6 Flu via	-61	268
7 Slo pe*	338	84
8 Sol flu	112	-237
9 Asp ect	281	-87
10 Tra mp	290	49
11 Ani inf	240	-58
12 Soi tex	-716	-170
13 pH* ***	-91	-89
14 Hum d	-746	55
15 Sta de	-715	-226
16 Roo de	-787	-51
20 Bar bo	307	341
21 Bar gr	793	132
22 Bar fin	501	42
23 Veg c	-746	-286
24 Bry co	-94	109
25 Asp ea	-124	-200
26 Alt tud	738	204
27 Age m	-713	-100
Group 30	-114.1	190.2
Group 31	-106.2	47.8
Group 14	-81	-66.1
Group 6	-30.7	61.6
Group 10	22.6	12.9
Group 11	-2.3	23.3
Group 18	56.5	-16.5
Group 19	24.8	33.2
Group 16	147.3	1
Group 17	68.2	10.8

Appendix 5.9
Coordinates for Fig. 5.5 ("final site group" centroid plot, Svellnosbreen)

	axis 1	axis2
1 Sno lie	-654	-108
2 Pos env	-598	-83
3 Fro hve	-578	-245
4 Dow els	-258	-110
5 Moi tre	-439	171
6 Flu via	286	89
7 Slo pe*	22	235
8 Sol flu	-166	434
9 Asp ect	-210	-263
10 Tra mp	159	-192
11 Ani inf	20	145
12 Soi tex	-279	383
13 pH* ***	55	-584
14 Hum d	270	669
15 Sta de	194	648
16 Roo de	148	635
20 Bar bo	153	-335
21 Bar gr	147	-436
22 Bar fin	-177	-117
23 Veg c	-164	521
24 Bry co	169	-105
25 Asp ea	117	-48
26 Alt tud	61	-229
27 Age m	-326	666
Group 3	510	38.5
Group 8	230.5	-48.5
Group 9	43	140.2
Group 20	120.9	-124.4
Group 21	24.5	-73.4
Group 22	-60.3	-15.3
Group 23	131.9	9.9

Appendix 5.10
Coordinates for Fig. 5.13 ("final species group" centroid plot, Svellnosbreen)

	axis 1	axis 2
1 Sno lie	-654	-108
2 Pos env	-598	-83
3 Fro hve	-578	-245
4 Dow els	-258	-110
5 Moi tre	-439	171
6 Flu via	286	89
7 Slo pe*	22	235
8 Sol flu	-166	434
9 Asp ect	-210	-263
10 Tra mp	159	-192
11 Ani inf	20	145
12 Soi tex	-279	383
13 pH* ***	55	-584
14 Hum d	270	669
15 Sta de	194	648
16 Roo de	148	635
20 Bar bo	153	-335
21 Bar gr	147	-436
22 Bar fin	-177	-117
23 Veg c	-164	521
24 Bry co	169	-105
25 Asp ea	117	-48
26 Alt tud	61	-229
27 Age m	-326	666
Group 7	359.5	-18.5
Group 13	92	126.5
Group 25	82.8	179.8
Group 24	-17.7	54.1
Group 11	6.2	-8.4
Group 42	-20	-49.2
Group 43	-115.5	-4
Group 83	53.2	-81.2
Group 84	31.1	-76.6
Group 40	62	-107
Group 4	141.2	-84.7

Appendix 5.11
Coordinates for Fig. 5.6 ("final site group" centroid plot, Storbreen high)

	axis 1	axis 2
1 Sno lie	-486	78
2 Pos env	-496	97
3 Fro hve	-230	209
4 Dow els	-169	-116
5 Moi tre	-456	188
6 Flu via	480	62
7 Slo pe*	-199	221
8 Sol flu	-24	23
9 Asp ect	87	4
10 Tra mp	233	-97
12 Soi tex	-463	-296
13 pH* ***	304	-122
14 Hum d	18	-445
15 Sta de	-213	-603
16 Roo de	7	-437
20 Bar bo	-34	355
21 Bar gr	-54	325
22 Bar fin	226	122
23 Veg c	30	-453
24 Bry co	-94	160
25 Asp ea	106	77
26 Alt tud	-79	-176
27 Age m	-552	-408
Group 6	115.9	128.4
Group 8	-107.6	-182.8
Group 9	-100.1	63.3
Group 10	-20.3	54.4
Group 11	-25.9	-91.6
Group 14	147.2	-91
Group 15	260.2	-2.4

Appendix 5.12
Coordinates for Fig. 5.14 ("final species group" centroid plot, Storbreen high)

	axis 1	axis 2
1 Sno lie	-486	78
2 Pos env	-496	97
3 Fro hve	-230	209
4 Dow els	-169	-116
5 Moi tre	-456	188
6 Flu via	480	62
7 Slo pe*	-199	221
8 Sol flu	-24	23
9 Asp ect	87	4
10 Tra mp	233	-97
12 Soi tex	-463	-296
13 pH* ***	304	-122
14 Hum d	18	-445
15 Sta de	-213	-603
16 Roo de	7	-437
20 Bar bo	-34	355
21 Bar gr	-54	325
22 Bar fin	226	122
23 Veg c	30	-453
24 Bry co	-94	160
25 Asp ea	106	77
26 Alt tud	-79	-176
27 Age m	-552	-408
Group 16	-46	32
Group 17	-90.3	-48.9
Group 18	-28.1	-23.9
Group 38	-14.3	-95.4
Group 39	-3	30.7
Group 5	3.7	-21.7
Group 6	80.4	107.9
Group 7	146.7	-25.6

Appendix 5.13
Coordinates for Fig. 5.7 ("final site group" centroid plot, Høgvaglbreen)

	axis 1	axis 2
1 Sno lie	-563	-371
2 Pos env	-455	-414
3 Fro hve	-172	-289
4 Dow els	-219	-350
5 Moi tre	-123	-338
6 Flu via	454	20
7 Slo pe*	-249	268
8 Sol flu	-205	76
9 Asp ect	-135	-74
10 Tra mp	-388	16
11 Ani inf	188	-55
12 Soi tex	-406	339
13 pH* ***	406	-688
14 Hum d	-112	606
15 Sta de	-269	685
16 Roo de	-232	588
20 Bar bo	334	-127
21 Bar gr	388	-532
22 Bar fin	0	-156
23 Veg co	-518	527
24 Bry co	49	-138
25 Alt eas	-114	98
26 Alt tud	616	-553
27 Age m	-586	480
Group 4	-10.3	-1.8
Group 6	34.4	-0.9
Group 7	13.8	-3.2
Group 11	0.2	9.7
Group 20	-2.8	-9.5
Group 21	3.5	-2.1

Appendix 5.14
Coordinates for Fig. 5.15 ("final species group" centroid plot, Høgvaglbreen)

	axis 1	axis 2
1 Sno lie	-563	-371
2 Pos env	-455	-414
3 Fro hve	-172	-289
4 Dow els	-219	-350
5 Moi tre	-123	-338
6 Flu via	454	20
7 Slo pe*	-249	268
8 Sol flu	-205	76
9 Asp ect	-135	-74
10 Tra mp	-388	16
11 Ani inf	188	-55
12 Soi tex	-406	339
13 pH* ***	406	-688
14 Hum d	-112	606
15 Sta de	-269	685
16 Roo de	-232	588
20 Bar bo	334	-127
21 Bar gr	388	-532
22 Bar fin	0	-156
23 Veg co	-518	527
24 Bry co	49	-138
25 Alt eas	-114	98
26 Alt tud	616	-553
27 Age m	-586	480
Group 8	-8.3	0.5
Group 36	-2.8	8.8
Group 37	-0.4	5
Group 38	0.6	-4.3
Group 39	0.1	8.8
Group 5	6.7	-0.3
Group 3	24.2	0

Appendix 5.15
Coordinates for Fig. 5.8 ("final site group" centroid plot, Bøverbreen)

	axis 1	axis 2
1 Sno lie	-261	591
2 Pos env	97	82
3 Fro hve	70	74
4 Dow els	209	161
5 Moi tre	-14	336
6 Flu via	394	-48
7 Slo pe*	-12	131
8 Sol flu	205	77
9 Asp ect	-73	-170
11 Ani inf	-119	81
12 Soi tex	-120	-154
13 pH* ***	-93	-1
14 Hum d	-439	-400
15 Sta de	-547	-561
16 Roo de	-552	-373
20 Bar bo	-76	316
21 Bar gr	428	398
22 Bar fin	328	183
23 Veg co	-168	-430
24 Bry co	35	-447
25 Asô ea	26	57
26 Alt tud	62	51
27 Age m	-809	-187
Group 4	-72.7	257.2
Group 6	115.6	-21
Group 7	233.9	4.3
Group 10	-57.4	-53.2
Group 11	11.6	25.8

Appendix 5.16
Coordinates for Fig. 5.16 ("final species group" centroid plot, Bøverbreen)

	axis 1	axis 2
1 Sno lie	-261	591
2 Pos env	97	82
3 Fro hve	70	74
4 Dow els	209	161
5 Moi tre	-14	336
6 Flu via	394	-48
7 Slo pe*	-12	131
8 Sol flu	205	77
9 Asp ect	-73	-170
11 Ani inf	-119	81
12 Soi tex	-120	-154
13 pH* ***	-93	-1
14 Hum d	-439	-400
15 Sta de	-547	-561
16 Roo de	-552	-373
20 Bar bo	-76	316
21 Bar gr	428	398
22 Bar fin	328	183
23 Veg co	-168	-430
24 Bry co	35	-447
25 Asô ea	26	57
26 Alt tud	62	51
27 Age m	-809	-187
Group 16	-67.4	149.5
Group 17	-70.8	-24.4
Group 36	-16.2	-5.7
Group 37	-47.7	-22.9
Group 19	-57.7	-59.6
Group 5	3.7	8.7
Group 6	44.3	15
Group 7	164.8	-4.7

Appendix 6.2

Coordinates for Fig. 6.17 and 6.18 ("final site group" centroid plot, combined data set)

Environmental parameters

	axis (1)	axis (2)
1 Sno lie	-299	-215
2 Pos env	-86	-95
3 Fro hve	-392	-89
4 Dow els	-137	-41
5 Moi tre	-67	-99
6 Flu via	-11	281
7 Slo pe*	49	-49
8 Sol flu	-11	-26
9 Asp ect	60	-19
10 Tra mpl	-84	-21
11 Ani inf	106	11
12 Soi tex	95	-41
13 pH* ***	-145	46
14 Hum de	271	-30
15 Sta dep	246	-122
16 Roo de	321	-46
17 Bar bou	-162	35
18 Bar gra	-421	5
19 Bar fin	-136	21
20 Veg co	343	-89
21 Bry cov	205	-30
22 Asp ea	2	28
23 Alt tud	-581	-21
24 Age mc	121	-258

"final species groups"

	axis (1)	axis (2)
Group 32	-8.518519	-8.777778
Group 33	-5.666667	1.222222
Group 34	0.808824	2.970588
Group 35	-3.266667	40.6
Group 18	-0.4	17.4
Group 19	-3.555556	-3.888889
Group 5	3.538462	6.615385
Group 6	5.142857	-0.857143
Group 14	3	15.5
Group 30	11.55556	20.22222
Group 62	33.59091	7.090909
Group 63	18.41176	-2.882353

Appendix 7 (sheet 1) Summary of data collection methods used within thesis

METHODS	REASON FOR MEASUREMENT	ORIGINAL SOURCE	METHOD USED BY	COMMENTS (mainly modifications or innovations)
Forelands, at a number of altitudes, were chosen for the study.	*To show how location and altitude influences the effect of microtopography on vegetation pattern.*	*Mellor (1985) and Messer (1988) studied soil chronosequences at a number of forelands, vegetation patterns have not been studied at a wide range of forelands.*	*None*	*The effect of altitude on vegetation succession is rarely studied and its effect on microtopographically induced vegetation patterns within a chronosequence has never been studied before.*
Moraine sequence - a series of the best developed and well-spaced moraines were chosen for investigation.	The moraines, in the present study, present microtopographical features, of relatively consistent size and shape and known age, that are covered by vegetation at various stages of development.	Moraines have been widely used for succession studies on glacier forelands e.g. Birks (1980)	e.g. Lutz (1930); Sommerville et al (1982) Fitter and Parsons (1987);	
Moraine transect - placed on the "optimally" vegetated section across the moraine	Well vegetated transects are chosen so that the foreland sequences are comparable. Sections of moraine with high proportions of boulders or scree are ignored.	Messer (1988) used optimally vegetated sites for soil analysis on her moraines.	Messer (1988)	Many authors use common physiognomic structures (e.g. Vetaas, 1994) or homogeneous vegetation types to determine sampling site, but such methods are inappropriate here.
Site - nine sites (2m²) across each moraine are chosen according to position	*Each site represents a particular microtopographical position: Distal (D)and proximal (P) toe; D & P low; D & P mid; D & P shoulder; and crest.*	*NONE - developed for present study*	*Some similarities to Walker et al (1989); Vetaas (1986); Larson and Kershaw (1974).*	*As far as the author is aware there are no other studies that have used the same site sampling strategy.*
Quadrat - each site was made up of two 1m² quadrats that were next to one another at the same position across the moraine.	*Each quadrat acted as a "replicate" of the other and the data from each quadrat was entered separately. The 1m² quadrat is considered adequately large enough to describe the vegetation (e.g. Crouch, 1992).*	*NONE - developed for present study.*	*NONE - developed for present study*	*Many chronosequence studies do not divulge their precise sampling technique. None appear to be similar to this study except Larson and Kershaw (1974).*
Species record - % cover and frequency (1/25) of all vascular plants and soil-growing lichens, ferns and club-mosses	To show vegetation patterns as effected by the environmental parameters associated with microtopography, age and altitude. Vascular plants were recorded as they represent the most obvious component of the vegetation. Lichens, as representatives of the cryptogams, are useful to record as they have been found to be sensitive to small-scale environmental gradients (Crouch, 1992)	The use of % cover and frequency of plant species is a standard recording method	e.g. Matthews (1976), Whittaker (1985), Crouch (1992)	Only total cover of the bryophyte species was recorded because the recording of lichen species was considered a sufficient representation of the cryptogams. The collection of data from a large number of sites was considered more important.
% Black : Green lichens on nearby rocks at each site	Elucidation of snow duration: high black : green suggests a short snow duration (Benedict, 1990a; Crouch, 1992).	Crouch (1992)	Crouch (1992)	Crouch used % Green : Black
Position on a scale of 1 (toe-slope positions) to 5 (crest position) at each quadrat	*Microtopographical location across the moraines with quadrats placed according to position.*	*NONE - developed for present study*	*Follows similar methodology used by Walker et al (1989)*	*NEW METHOD*
Frost heave - presence of frost evidence in 1/25 small squares at each quadrat.	Evidence of frost activity in terms of the presence of nubbins, heaved vegetation, ripples and frost sorting etc.	Whittaker (1985),	Whittaker (1985), Crouch (1992)	Frequency scale (1/25) has not been used before for frost evidence
Dowels - 9 match sticks placed into the ground and tops, protruding from the ground, are spray painted at each site.	The amount of heave of the dowels, the following field season, is recorded as evidence for frost heave at that site.	Whittaker (1985, 1989) - small sample	e.g. Jonasson (1986)	Dowels were placed at each site on every foreland providing a more extensive survey of frost activity.
Moisture - finger test method on a scale of 1 (wet - pool forms) to 5 (dry)	The amount of moisture in the soil at 3 depths - surface, 2.5 cm depth and 5 cm depth. The 3 measurements were combined to form a scale of 3 (wet) to 15 (very dry).	Crouch (1992)	Crouch (1992)	Crouch used a 1 (dry) to 5 (wet) (scale) and did not combine the scores into a 3 to 15 scale.
Moisture - Capacitance probe for measurement of soil water content	This prototype instrument was used to provide an alternative, quantitative measure of moisture as well as to test the relative accuracy of the "finger test" method	Institute of Hydrology, Wallingford, UK.	Prototype described in Dean (1994)	Unfortunately the device failed so that it could only be used for test runs and one foreland sequence.

Appendix 7 (sheet 2).

Fluvial - presence of fluvial activity in 1/25 small squares at each quadrat.	Evidence of fluvial activity in terms of the presence of water flow or evidence of water flow.	Crouch (1992) - scale of 0 (none) to 3 (severe)	Crouch (1992)	Frequency scale (1/25) has not been used before for fluvial activity
Slope - slope angle of site and slope angles at 2m intervals along the moraine transect..	To provide slope angles for each site so that the influence of slope on vegetation pattern could be ascertained and also to provide slope angles, every 2 metres, for the moraine profile diagrams.	Whittaker (1985), Crouch (1992) recorded slope angle at each site	Whittaker (1985), Crouch (1992)	The sampling strategy, using transect profiles, differs from the random approach used by Crouch and Whittaker.
Solifluction - presence of solifluction in 1/25 small squares at each quadrat.	Evidence of solifluction in terms of the presence of lobes, crinkles and cracks caused by the downward surface movement of soil.	Whittaker (1985), Crouch (1992) - scales of none to severe.	Whittaker (1985), Crouch (1992)	Frequency scale (1/25) has not been used before for solifluction
Aspect - measured to the nearest degree at each site	*Aspect of the moraine slope was recorded and then the measurement was set onto two circular measurement (1 to 5) scales according to northerliness and easterliness.*	*The recording of aspect is a standard scientific measurement*	*e.g. Matthews (1976), Whittaker (1985), Crouch (1992).*	*The circular northerliness and easterliness scales for the data input of aspect are, as far as the author is aware, new.*
Trampling - presence of trampling in 1/25 small squares at each quadrat.	Evidence of trampling in terms of the presence of broken branches, flattened plants, path-like bare patches or foot prints	Crouch (1992) - scale of 0 (none) to 3 (severe)	Crouch (1992)	Frequency scale (1/25) has not been used before for trampling
Grazing - presence of grazing in 1/25 small squares at each quadrat.	*Evidence of grazing in terms of the presence of broken bitten-off branches, leaves or stems and evidence of droppings.*	*None - new for the present study*	*None - new for the present study*	*Frequency scale (1/25) has not been used before for grazing*
Soil texture - scaled from course sand (1) to fine loam (4) at each site.	To show the coarseness of the soil a scale of 1 for sand; 2 for loamy sand; 3 for sandy loam; and 4 for loam.	Crouch (1992) - used a finer scale of 1 to 7 for soil texture.	Crouch (1992)	Scale of 1 to 4 not used before.
pH - to two decimal places	To show the relative acidity of the soil	The recording of pH is a standard scientific measurement	e.g. Crouch (1992)	Great care was taken to use a comparable methodology for the pH sampling
Humus depth - in cm at each site	To show the depth of the blackened organic Ao and Aoo horizons.	Whittaker (1989) called this a litter horizon and also included both Ao and Aoo horizons	Many others have measured the various soil horizons.	This measurement is synonymous with the surface organic material
Soil depth - in cm (stain depth) at each site	To show soil depth: "*the total depth of organic staining (Bh horizon) or of organic material within a mixed organic-inorganic horizon - whichever is greater*" (Whittaker, 1989)	Whittaker (1985, 1989)	Most authors measure the soil horizons separately	This measure of soil depth, as defined in Whittaker (1989) is considered more convenient than horizon measurement.
Root depth - in cm at each site	To show the average depth of root penetration - an indication of the relative growth of the prevailing vegetation	Whittaker (1985, 1989)	e.g. Miller (1982); Hastings (1989); Holtmeier and Broll (1992)	
Bare ground boulders - proportion of boulders on bare ground within each quadrat	To show the percentage and frequency of boulders (> 256 mm) that make up the unvegetated substrate.	Crouch (1992) - her largest clast size was cobbles (60 mm +) - estimate of stoniness	Most authors that investigate particle size use the time-consuming sieving method	The present author made a special category for boulders (> 256 mm)
Bare ground gravels - proportion of gravels and cobbles on bare ground within each quadrat	To show the percentage and frequency of gravels and cobbles (2 - 256 mm) that make up the unvegetated substrate.	Crouch (1992) - she had a category for course gravels (20 - 60 mm) -estimate of stoniness	Most authors that investigate particle size use the time-consuming sieving method	The present author made a special category for gravels and cobbles (2 - 256 mm)
Bare ground fines - proportion of fines on bare ground within each quadrat	To show the percentage and frequency of fines (< 2 mm) that make up the unvegetated substrate.	Crouch (1992) - she had a category for fine gravels (2 - 20 mm) - estimate of stoniness	Most authors that investigate particle size use the time-consuming sieving method	The present author made a special category for fines (< 2 mm)
Total vegetation cover - percentage cover and frequency	To show the total cover of all vegetation at a site - this is an important factor to measure as vegetation acts as an environmental factor.	This is a standard scientific measurement for succession studies	This is a standard scientific measurement for succession studies	
Total bryophyte cover - percentage cover and frequency	Bryophytes are known to be sensitive environmental indicators and it is important to include their total cover in the analysis	Crouch (1992) measured total bryophyte cover	Crouch (1992)	

Appendix 7 (sheet 3).

Altitude - measurement	Altitude is probably the most important influence on environmental and vegetation patterns and it is necessary to have an accurate representation of this in the data set.	Matthews (1976), Whittaker (1985) and Crouch (1992) - at Storbreen	Few compare altitudes e.g. Sommerville et al (1982); Emmanuelsson (1984b)	This study is different from the others because a large altitudinal range was used (i.e. 290m to 1550m).
Age - measurement on a 1 to 11 scale.	*An accurate representation of age is necessary - each point represents 25 years and the last point representing greater than 250 years*	*Not used before*	*Not used before*	*New method of entering age.*
TWINSPAN - classification technique	A useful technique for organising the species and site data into hierarchical groups so that the relationships between species and between site-types, as well as the relationship between species and sites, can be examined	Crouch (1992) used this programme and on the basis of her findings this programme was considered to be an appropriate analysis technique	It is a widely used method and its use is reviewed and supported by Kent and Coker (1992) and Crouch (1992)	The present study has used various new methods to present the TWINSPAN data in such a way that maximum information can be derived from the data at a glance (see Appendix 8)
DCA - indirect ordination technique	A useful technique for organising the vegetation and site data along a ranked sequence so that the relationships between species and between site-types, as well as the relationship between species and sites, can be examined. The influence of environmental parameters on the site and species ranks can also be elucidated	Whittaker (1985) and Crouch (1992) used this programme and on the basis of their findings this programme was considered to be an appropriate analysis technique.	It is a widely used method and its use is reviewed and supported by Whittaker (1985, 1989), Crouch (1992), and Kent and Coker (1992)	The present study has used various new methods to present the DCA data in such a way that maximum information can be derived from the data at a glance (see Appendix 8)
Pearson's product moment correlation coefficient (r)	The correlation matrices have been constructed for each foreland in order to further elucidate the relationship between different environmental variables and the ordination axes. It is a parametric technique and therefore most appropriate to normal data and thus only stringent significance levels should be used (Crouch, 1992)	Crouch (1992) used this programme and on the basis of her findings this programme was considered to be an appropriate analysis technique	Crouch (1992)	Following Crouch (1992) only the intercorrelations significant at $p<0.001$ should be considered important
"t" test statistic was used to calculate the number of measurements needed to get a consistent measurement using the Capacitance Probe.	$\sqrt{n-1} = \frac{t.s}{CI}$ KEY: **n** - number of measurements needed **t** - "t" statistic for sample of 50 at 95% CI; **C.I.** - Confidence interval of 0.05 **s** - Standard Deviation for 50 measurements	John Matthews, Swansea University	Appears to be a modified t test	
Spearman's rank correlation coefficient for moisture measurements.	To show whether there is significant correspondence between the measurements from the finger test and the capacitance probe.	SPSS programme in WINDOWS	Standard statistical procedure	
Descriptive statistics - for temperature reading.	To show how much the average temperature readings taken from two-weekly and five-day periods fluctuated within those time periods.	By hand and also in Microsoft Excel.	Standard statistical procedure	
Population correlation coefficient - for thermistor readings.	To show divergence or similarities between the temperature readings taken by the thermistor recorders.	Correlation in Microsoft Excel: returns the covariance of two data sets.	Standard statistical procedure	
Regression - for temperature readings from the Norwegian Meteorological Office	To show the general decrease in temperature with altitude.	in Matthews (1992) covering data from 1930 to 1960	also Green and Harding (1980)	A regression has not been done for the regional data from 1960 to 1990.
Kendall's "tau" and Spearman's rank correlation	To investigate the degree of correspondence between vegetation and environmental data collected at the same sites over 3 years.	In Microsoft Excel.	Matthews (1976) and Whittaker (1985) performed rigorous tests to investigate recorder variance because they used many assistants.	Only the author of the present thesis collected data and so the only test necessary was between-year variations in data recording.

Appendix 8 (sheet 1). Summary of data presentation approaches used within the present thesis

Note: New presentation methods, especially developed for the present study, are in italics.

TECHNIQUE	**FIGURE OR TABLE LABEL** (and whether in Black and White or Colour)	**SOURCE OF TECHNIQUE**	**RESEARCHERS USING APPROACH FOR SAME PURPOSES**	**APPROACH USED TO ELUCIDATE WHAT?**	**COMMENTS**
Chapter 1					
Climate charts and soil profile diagrams	Figs. 1.1-2 and Table 1.1	Standard technique of display.	Many authors use this method	To elucidate effect of altitude on temperature and regional soil profile types.	The latest temperature data (1960-1990) has been used.
Chapter 2					
Regional and foreland maps	Figs. 2.1-2	Standard technique of display	Many authors use this method, including Whittaker, 1989.	The location of the forelands and weather stations within the region; and the location of moraines across each forelands.	The region is well documented in Matthews (1992) and the maps are copied from other authors.
Photograph	Fig. 2.3	Standard technique of display	Many authors use this method, including Matthews, 1992.	Snow duration at Høgvaglbreen through to mid- July.	Only one photograph has been used because the figures are considered to provide superior displays.
Diagrams to show the distribution of sites and thermistors across moraines	Figs. 2.4-8	Standard technique of display	Many authors use this method, including Matthews, 1992.	Position scale and siting of thermistors	The position scale is new, but the method of display is not
TWINSPAN hierarchy to show how the programme divides the groups.	Fig 2.9 (B&W)	Similar diagram used in Kent and Coker (1992)	Not many authors provide a detailed diagram of the various levels and groups	It is necessary to show exactly what is meant by using terms "level" and "group" within the TWINSPAN hierarchy	The present author has slightly modified the terminology used for the TWINSPAN groups.
Tables displaying environmental parameters and correlation results	Table 2.1-7	Standard technique of display	Many authors use this method, including Matthews, 1992.	Tables are usually able to elucidate relationships more clearly than text descriptions	In this thesis, results are both described in the text and summarised in tabular form.
Chapter 3					
Charts and graphs to show distribution of measured environmental parameters across the forelands (individual foreland data sets)	Figs. 3.1 to 3.118 (B&W and Colour)	Standard technique of graphical display.	e.g. in Kent and Coker (1992); Kershaw and Looney (1985)	To show distribution of environmental parameters along the foreland sequences	The relatively new advances in computer software has made the preparation of multiple complex charts much easier than before.
Temperature charts	Figs. 3.20 – 3.30	Standard technique of graphical display	Many authors use this method	To show differences in the degree of temperature fluctuations across moraines	A large number of readings allowed the standard deviation of temperature readings to be found.
Tables to elucidate information concerning the microenvironmental parameters and meso-environmental influences (individual foreland data sets).	Tables 3.1 to 3.15 (B&W)	Standard technique of display	Many authors use this method	To summarise relationships and information in a small space.	Tables have been widely used in this thesis to summarise the large number of complex relationships
Chapter 4					
Key to Profile diagrams	*Fig. 4.1 (Colour)*	*New type of colour diagram developed for the present study*	*NEW METHOD*	*This key explains the profile diagrams in chapters 4 and 6.*	*The profile diagrams allow examination of the site group divisions, along each of the moraine sequences, at all levels of division.*

Appendix 8 (sheet 2).

Profile diagrams for the individual forelands	*Figs. 4.2 to 4.9 (Colour)*	*New method*	*NEW METHOD*	*To show the TWINSPAN site divisions for each foreland individually*	*Shows clearly how the sites are related to each other within each foreland.*
Succession pathways, based on the individual foreland TWINSPAN site group data	Figs. 4.10 to 4.17 (Colour)	Many succession studies produce succession diagrams e.g. in Matthews (1992)	Few succession studies provide a succession scheme which takes microtopography into account.	To show the influence of microtopography and age on vegetation patterns across 8 foreland sequences.	These diagrams are also unusual in that they show how the site groups are related to one another.
Species charts - based on the individual foreland TWINSPAN "final species group" data	Figs. 4.18 to 4.92 (B&W)	Many succession studies produce species charts e.g. in Kershaw and Looney (1985)	Few studies provide charts showing microtopography-related patterns of TWINSPAN species groups.	To show how the TWINSPAN species groups are distributed across each of the moraines along the foreland sequences.	These charts allow us to see if the TWINSPAN species divisions are ecologically meaningful.
Table to show TWINSPAN site groups for each individual foreland.	Tables 4.1 to 4.8 (B&W)	Few studies provide details of the TWINSPAN site divisions	None, as far as the author is aware.	To summarise each of the individual foreland TWINSPAN site groups - their size, location and constituent indicator and preferential species.	The tables allow us to examine all the TWINSPAN site groups at all levels so that the relationships between the site groups can be seen.
Summary table of individual foreland TWINSPAN "final site groups" (refer to profile diagrams)	Table 4.9 (Colour)	Few studies provide details of the TWINSPAN site divisions and show how the groups compare between locations	None, as far as the author is aware.	To compare the distinctness of the individual foreland TWINSPAN site groups, and their preferred location, between each of the forelands.	This table displays the ecologically meaningful final groups and how their number, distinctness and location compares.
Summary of TWINSPAN "final species groups" from all the individual foreland data sets (colour-coded location based on species charts)	Table 4.10 (Colour)	Few studies provide details of the TWINSPAN "final species groups" and show how the groups compare between locations	None, as far as the author is aware.	To compare the distinctness of the individual foreland TWINSPAN "final species groups", and their preferred location, between each of the forelands.	This table is a very useful summary of the TWINSPAN "final species groups" that shows between-foreland differences and similarities at a glance.
Chapter 5					
DCA centroids of TWINSPAN "final group" scores and environmental parameter biplot scores.	Figs. 5.1 to 5.16 (B&W)	Kent and Ballard (1988)	Where both classification and ordination is used e.g. Crouch (1992); Magnusson (1994a).	To relate the TWINSPAN site and species groups to the ordination axes (+ prevailing environmental parameters if entered)	This is known as complementary analysis Kent and Ballard (1988).
Sequence diagrams of TWINSPAN "final groups" on the individual foreland DCA ordination axes (1) and (2)	*Figs. 5.17 to 5.32 (B&W)*	*New method of presentation*	*NEW METHOD*	*To show how the TWINSPAN "final groups" are related to one another and elucidate their relationship to the prevailing environmental parameters.*	*These diagrams are based on the colour rank tables (Tables 5.1 to 5.16)*
Individual foreland rank tables of the sites and species on DCA ordination axes (1) and (2) with superimposed colour-coded TWINSPAN "final groups".	*Tables 5.1 to 5.16 (Colour)*	*New method of presenting the ordination rank tables*	*NEW METHOD*	*Shows how distinct the individual foreland TWINSPAN "final groups" are along the axes, as well as how they relate to each other and the environmental parameters.*	*The rank tables provide a clear presentation of the complex individual foreland data at a glance.*
Matrices for Pearson's product moment correlation coefficient (r)	Tables 5.17 to 5.24 (B&W)	Correlation matrices are standard presentation methods.	e.g. Crouch (1992); in Kent and Coker (1992)	Relates environmental parameters to ordination axes, and to each other, in order to relate the defined environmental factor complexes to the vegetation patterns.	Pearson's is parametric (thus requiring normal data), so high significance levels are used to support rather than to prove.
Summary table of the sequence diagrams for the individual foreland TWINSPAN "final group" data on the DCA ordination axes (1) and (2).	*Tables 5.25 and 5.26 (B&W)*	*New method of presentation*	*NEW METHOD*	*To compare how the TWINSPAN "final groups", on DCA axes (1) & (2), are related and are influenced by the environmental factors on each foreland.*	*These summary tables provide a clear presentation of the complex individual foreland data at a glance.*

Appendix 8 (sheet 3).

Summary table of the relationship between age and position and microenvironmental parameters.	*Table 5.27 and 5.28 (B&W)*	*New method of presentation but based on the "Factor complex" hypothesis developed by Whittaker (1985)*	*NEW METHOD*	*To show the meso-environmental parameters that have the most influence on each of the forelands, according to the correlation matrices.*	*Table 5.27 shows the micro-environmental parameters that form environmental factor complexes associated with age or position.*
Chapter 6					
Profile diagrams for the combined forelands (including hierarchy to show separation)	*Figs. 6.1a-h and 6.1i (hierarchy diagram) (Colour)*	*New method*	*NEW METHOD*	*To show the TWINSPAN site divisions for the combined data set*	*Shows clearly how the sites are related to each other between each foreland.*
Succession pathways, based on the combined foreland TWINSPAN "final site group" data, colour-coded according to the "final groups" on the profile diagrams.	Fig 6.2 (Colour)	Many succession studies produce succession diagrams e.g. in Matthews (1992)	Few succession studies provide a succession scheme which considers microtopography and altitude	To show the influence of microtopography age and altitude on vegetation patterns across 8 foreland sequences.	These diagrams are also unusual in that they show how the "final site groups" are related to one another.
Species charts - based on the combined foreland TWINSPAN "final species groups", dominant species in colour within each group	Figs. 6.3 to 6.14 (Colour)	Many succession studies produce species charts e.g. in Kershaw and Looney (1985)	Few studies provide charts showing the distribution of TWINSPAN species groups across a number of sequences at increasing altitude.	To display the combined foreland TWINSPAN "final species groups" distributions across the moraines of each of the foreland sequences.	These charts allow us to see if the TWINSPAN species divisions are ecologically meaningful.
Summary diagram to show the general location of the TWINSPAN "final species groups" (based on the species charts)	Fig. 6.15 (B&W)	Many succession studies produce species charts e.g. in Kershaw and Looney (1985)	Few studies provide charts showing the distribution of TWINSPAN species groups across a number of sequences at increasing altitude.	To compare how the combined foreland TWINSPAN "final species groups" are distributed across the moraines of each of the foreland sequences.	This chart is more approximate than the succession diagrams based on the "final site groups" because "final species groups" are more widely dispersed.
Sequence diagram of TWINSPAN species groups on the combined foreland DCA ordination axes (1) and (2)(Based on species ranks (Tables 6.5)	*Fig. 6.16 (B&W)*	*New method of presentation*	*NEW METHOD*	*To show how the TWINSPAN "final species groups" are related and elucidate their relationship to the prevailing environmental parameters.*	*These diagrams are based on the colour rank table (Table 6.4)*
DCA centroids of TWINSPAN species scores and environmental parameter biplot scores.	Figs. 6.17 and 6.18 (B&W)	Kent and Ballard (1988)	Where both classification and ordination is used e.g. Crouch (1992); Magnusson (1994a).	To relate the TWINSPAN site and species groups to the ordination axes (+ prevailing environmental parameters if entered)	Fig 6.18 is a blow-up of 6.17, without the environmental parameters
Table to show TWINSPAN site groups for combined data set, colour coded in relation to the combined foreland profile diagrams.	Table 6.1 (Colour)	Few studies provide details of the TWINSPAN site divisions	None, as far as the author is aware.	To summarise each of the combined TWINSPAN site groups - their name, distinctness, location, constituent indicator species and main influences on separation.	The table allows us to examine all the TWINSPAN site groups at all levels so that the relationships between the site groups can be seen.
Summary table of combined foreland TWINSPAN "final species groups" (colour-coded location based on species charts)	Table 6.2 (Colour)	Few studies provide easily accessible details of the TWINSPAN species divisions	None, as far as the author is aware.	To compare the distinctness of the combined foreland TWINSPAN species groups, and their preferred location, between each of the forelands.	This table is a very useful summary of the TWINSPAN "final species groups".
Summary table of the colour-coded combined foreland TWINSPAN "final species groups" and how they compare to those of the individual foreland assemblages	*Table 6.3 (Colour)*	*New presentation method*	*NEW METHOD*	*This shows how constituent species of the combined and individual foreland assemblages compare in order to show which species tend to form the most distinct assemblages.*	*This table elucidates the most distinct species groups at a number of altitudes. It also elucidates how the constituent species, of particular group-types, change with altitude.*

Appendix 8 (sheet 4).

Summary table to show DCA ordination species ranks, on AXIS (1) and 2, for the combined data set (with superimposed TWINSPAN "final species groups")	*Table 6.4 (Colour)*	*New method of presenting the ordination rank tables*	*NEW METHOD*	*Shows how distinct the combined foreland TWINSPAN "final species groups" are along the axes, as well as how they relate to each other and the environmental parameters.*	*The rank tables provide a clear presentation of the complex combined foreland data at a glance.*
Matrices for Pearson's product moment correlation coefficient (r)	Table 6.5 (B&W)	Correlation matrices are standard presentation methods.	e.g. Crouch (1992); in Kent and Coker (1992)	Relates environmental parameters to ordination axes, and to each other, in order to relate the defined environmental factor complexes to the vegetation patterns.	Pearson's is parametric (thus requiring normal data), so high significance levels were used to support rather than to prove.
Summary table of the relationship between age and position and microenvironmental parameters.	*Table 6.6 (B&W)*	*New method of presentation but based on the "Factor complex" hypothesis developed by Whittaker (1985)*	*NEW METHOD*	*To elucidate the relative importance of the meso-environmental parameters on all selected forelands, according to the correlation matrices.*	*Table 6.7 shows the micro-environmental parameters that form environmental factor complexes with altitude, age or position.*
Chapter 7					
Summary of the influence of altitude on micro-environmental parameters.	*Fig. 7.1 (B&W)*	*The relationship between altitude and micro-environmental factors has not been elucidated before*	*NEW PRESENTATION*	*This figure summarises the results in relation to the effects of altitude and microtopography on microenvironment.*	
Summary of the relationship between microtopography and time on DCA axes (1) and (2) (combined data set).	*Fig. 7.2*	*The complexity of the relationship between time and microtopography has not been elucidated before.*	*NEW PRESENTATION*	*This figure summarises the results in relation to the effects of age and microtopography on microenvironment.*	
Generalised relationship between altitude, age and microtopography on the separation of TWINSPAN assemblages.	*Fig 7.3*	*The combined effect of these meso-environmental factors on assemblage separation has not been elucidated before.*	*NEW PRESENTATION*	*This figure summarises how the effects of altitude, age and microtopography are interrelated and how they may influence vegetation patterns.*	
Summary table displaying the most distinct TWINSPAN site and species assemblages, on DCA axes (1) and (2), for all data sets.	*Table 7.1*	*New method of presentation*	*NEW METHOD*	*This table provides details of the most distinct assemblages, and their relationship to the environmental factors, on axes (1) & (2) of all data sets.*	