Fine root production and turnover of tree and understorey vegetation in Scots pine, silver birch and Norway spruce stands in SW Sweden

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Abstract

Fine roots contribute to net primary production in forests, but knowledge of fine root longevity and turnover is still incomplete and limited to few tree species. In this study, we used minirhizotrons to compare fine root biomass, longevity and turnover of *Pinus sylvestris* L.*, Betula pendula* Roth and *Picea abies* (L) Karst. in southern Sweden. Minirhizotron tubes were installed in 2006 and root images were taken in 2007-2010. Soil cores were used to estimate fine root biomass. Soil samples were taken from the humus layer and from 0-10 cm, 10-20 cm and 20-30 cm depth in the mineral soil. Only images from the humus layer and the upper 10 cm of mineral soil were included in root analysis.

Spruce has a higher aboveground production than pine and birch in southern Sweden and this was reflected in larger fine root biomass as well as higher fine root biomass production. The annual tree fine root biomass production (humus and 0-30 cm in mineral soil) was 73, 78 and 284g m^{-2} in pine, birch and spruce stands, respectively. Thicker fine roots tended to live longer. The majority of the fine roots were thinner than 0.5 mm in diameter, with a turnover rate (KM) of 0.4 $year^{-1}$. When comparing all fine roots, i.e. all roots 0-2 mm, pine had the highest longevity, 1120 days, compared with 900 days for spruce and 922 days for birch (KM).

Keywords

Picea abies, Pinus sylvestris, Betula pendula, fine root turnover, carbon, minirhizotron

1. Introduction

European forests are important as carbon sinks (e.g. Luyssaert et al., 2010), and a substantial part of the carbon is stored in the soil. Carbon inputs come mainly from leaf and root litter. There have been many studies on fine roots in relation to carbon storage in the last few years (e.g. Gaudinski et al., 2010; Yuan and Chen, 2010; Finér et al., 2011a; Brunner et al., 2012; Yuan and Chen, 2012). Biomass, longevity and turnover rates vary depending on study method (Hendrick and Pregitzer, 1992, 1993; Eissenstat and Yanai, 1997; Tierney and Fahey, 2002; Metcalfe et al., 2007; Gaul et al., 2009; Finér et al., 2011b; Sah et al., 2011), length of study (Strand et al., 2008), species included (Quan et al., 2010; Russell et al., 2010; McCormack et al., 2012), root diameter (Joslin et al., 2006; Gaudinski et al., 2010) and environmental factors (Yuan and Chen, 2010; Finér et al., 2011b). Sequential cores, ingrowth cores, isotopes and minirhizotron studies have been used for estimating fine-root turnover rates (Gaudinski et al., 2001; Finér et al., 2011b; Brunner et al., 2012; Sah et al., 2012). In a comparison of different methods for investigation of root longevity, Hendricks *et al*. (2006) concluded that the minirhizotron technique resulted in the most reliable root production estimates. The negative relationship between minirhizotron and core-based estimates were considered to be caused by core techniques inadequately assessing root production when mortality and production occur simultaneously.

Since tree species differ in root morphology (Pregitzer et al., 2002; Comas and Eissenstat, 2004; Ostonen et al., 2007; Guo et al., 2008b) and turnover rates (Brunner et al., 2012; McCormack et al., 2012), there is a need for further root turnover studies with more than one tree species. In the present study, we used soil coring to estimate fine root biomass and minirhizotrons to estimate fine root longevity, turnover rate and biomass production in adjacent birch, pine and spruce stands in southern Sweden. Birch, pine and spruce are the three most common species in Sweden, together comprising more than 90% of standing volume. In southern Sweden, spruce has the highest production and the relative proportions of standing volume are 45% spruce, 31% pine and 11% birch (Anonymous, 2011). Spruce fine root longevity and turnover rate have previously been estimated (Majdi and Kangas, 1997; Majdi and Andersson, 2005; Gaudinski et al., 2010), but to our knowledge, no one has previously compared fine root production and turnover of these three species under similar conditions. Our aim was to compare species differences in fine root biomass, longevity and turnover. Our starting hypotheses were that i) spruce, with larger above ground production, would have larger fine root biomass than pine and birch ii) fine root longevity would increase and consequently turnover rate decrease with increased root diameter and iii) birch fine roots, with thinner roots than pine and spruce, and more bioturbation in the soil, would turn over faster.

2. Materials and methods

2.1. Study site and experimental design

The study area is located in the Tönnersjöheden Experimental Forest in SW Sweden (56º40-41'N, 13º03-06'E). Mean annual air temperature was 6.4 ºC and mean annual precipitation was 1053 mm for the reference period 1961-1990 (Alexandersson et al., 1991). The soil parent material is of glacifluvial origin. The soils are sandy (>80% sand), with about 40 % coarse material (stones and boulders) (Hansson et al., 2011).

The experimental design included Norway spruce (*Picea abies* (L) Karst.), Scots pine (*Pinus sylvestris* L.) and silver birch (*Betula pendula* Roth) stands, planted in 1951-1963 and replicated in a block design (n=3, except for birch where n=2). Similarly aged stands with different stand density were selected, reflecting the situation in the region, with spruce often having larger basal area per hectare than birch. Average total basal area was 16.3, 21.6 and 29.3 m^2 ha^{-1} for birch, pine and spruce plots, respectively. Spruce stands had no understorey trees or field layer vegetation, whereas understorey trees (*Quercus, Picea, Larix, Fagus, Betula, Frangula* and others), ericoid dwarf shrubs, grasses and forbs were common in the pine and birch stands. The stands are further described in Hansson et al. (2011).

2.2. Fine root biomass

Four samples per plot were taken from the humus layer and from 0-10, 10-20 and 20-30 cm depth in the mineral soil, using a soil corer with 4.1 cm diameter. Samples were stored at -20 °C until preparation.

Roots were removed from the soil by wet-sieving, rinsed to remove soil particles and carefully cleaned and sorted into living and dead roots, based on visual criteria described by Vogt and Persson (1991). Roots were separated into tree and ground vegetation roots. Living tree roots were sorted into fine roots (<2 mm) and coarse roots (>2 mm). The fine root fraction was further sorted into roots with <0.5, 0.5-1 and 1-2 mm diameter. The sorted roots were scanned using Winrhizo Pro 2002 software (Regent Instruments Inc., Quebec) to determine root length. Roots were dried (60 °C) before determination of dry mass. Specific root length (SRL) was calculated by dividing root length by weight.

The data on root biomass of the different stands were statistically analysed according to a split-plot design in blocks, with species as mainplot factor and soil layer as subplot factor, using Proc MIXED in SAS 9.2 software (SAS Institute Inc., Cary, NC, USA). Differences are reported as significant when $P<0.05$.

2.3. Fine root longevity and turnover rate

Fine root longevity and turnover rate of birch, pine, spruce and ground vegetation were estimated. Observations were based on the minirhizotron method and the measurement period comprised four seasons (2007-2010) and contained 14 different sessions.

Five acrylic minirhizotron tubes (5 cm internal diameter, 50 cm length) per stand were installed in April 2006 in pine, spruce and birch stands, three vertically and two horizontally in the humus layer. Image acquisition started in April 2007, one year after tube installation, to allow stabilization of the soil around the tubes. Roots were photographed two to six times during the growing season for four years, until November 2010. For each tube and session, 35-40 images (each image 2.2*1.3 cm) were taken, to approximately 50 cm depth. This was repeated on two opposite sides of the tube, with in total 10 sets of images per plot. In horizontal tubes, the images were taken on the sides, not above and below the tube. All images were taken using the Bartz minirhizotron camera system BTC-2 (Bartz Technology Corporation, Santa Barbara, USA) with the image capture software BTC I-CAP (Bartz Technology Corporation). Five sets of images were selected from each plot. In most cases we used one set of images from each installed tube, but in some cases, when image quality was very bad in one tube, double image sets from another tube were used instead. The images were analysed using WinRHIZO Tron 2007b software (Regent Instruments Inc., Quebec, Canada). For each tube, the humus layer and the upper 10 cm in mineral soil were analysed together. Deeper soil layers were not included in longevity estimates, since a majority of the visible roots in the tubes were in the top soil. For the horizontal tubes, images from the full tube length were analysed. Diameter and length was measured for each root segment. Roots were sorted into pine, spruce, birch and understorey vegetation, the last group including mainly grasses, ericoid shrubs and forbs, but also some undefined understorey tree roots. Tree roots, already suberised in the first session, were excluded from analysis, as were understorey roots (also white when old) without growth between the first and second

session. For each session, roots were classified as alive or disappeared. Live and dead roots are often separated using differences in colour, with white and light brown roots defined as live and roots that have turned black defined as dead (e.g. Majdi and Andersson, 2005). This distinction was not possible in our case, partly due to image quality, but mainly due to large colour variations in live roots depending on mycorrhizal type, with many examples of black roots still growing (see also e.g. Withington et al., 2006; Gaul et al., 2009). Consequently, we did not distinguish between roots that were grazed by soil animals and roots that had died for other reasons. Poor image quality was mainly caused by moisture on tubes, fungal growth on tubes and varying image colour due to technical problems with the camera. A small amount of roots probably disappeared without dying, moving out of sight. However, when this was obvious, the root was excluded from the analysis. When roots die they are sometimes visible for a few months before they disappear after decomposition, which in our case sometimes may have led to an overestimation of root longevity. Preliminary results from a minirhizotron study in Kivalo, in the northern boreal zone in Finland suggest a period of 3-7 months from death to disappearance. Decomposition should be faster in this temperate site in southern Sweden. The northern site has lower temperature and precipitation, shorter growing season, lower heterotrophic respiration rates and no earthworm activity (Olsson et al., 2012). It is therefore reasonable to assume that the bias in this study is in the range of 1-4 months.

The number of roots analysed (considering every root segment as an individual unit) was high. However, the sessions were not evenly distributed over the seasons due to camera problems. Thus, there was a gap of almost a full season (October 2008 to September 2009) in the records.

To shed light on the uncertainty related to the limited number of sessions and other methodological issues, we used two different methods: the Kaplan-Meier product limit method (Kaplan and Meier, 1958), or KM for short, and fitting a Weibull distribution (Weibull, 1951) to the observations. These two approaches are fundamentally different in their assumptions and mathematics, but for infinitely many subjects (roots in the present case) and infinitely many observations they lead to the same asymptotic distribution. Thus, if estimators (median or mean longevity, variance) are similar, then they are reliable and sample size is probably sufficient.

The results were stratified according to tree species plus ground vegetation, and root diameter in discrete classes.

2.3.1. The Kaplan-Meier product limit method

The KM method (Kaplan and Meier, 1958) is a nonparametric method based on the empirical cumulative distribution function. The KM function is always a staircase (see Fig. 1a for an example). The vertical step size is dictated by the number of roots, while a long horizontal plateau may indicate a temporal gap between sessions (here, winters and camera failure). It is common practice to report on the median of the KM function rather than the mean value; the latter is not easy to estimate reliably when the steps are rather coarse (few observations). With regard to censoring, we considered two alternatives: roots still living at the end of the observations (last session) were either considered as censored, or they were considered as dying just then. In that case, there were no censored observations, and KM was equivalent to the empirical cumulative distribution function concerning the median calculation.

2.3.2. Weibull approach

Fitting “time-to-failure” data to a prescribed distribution involves following a parametric approach. Here, we use the approach of Weibull (1951); the basic assumption when using the Weibull distribution is that the failure rate (or death probability) is proportional to time to a certain power. The distribution is attractive for at least two reasons: (1) it is parsimonious since it only has two parameters, the *shape k* and the *scale* λ; (2) it is very flexible – the character of the distribution is radically different depending on the value of k. Figure 1b gives an example of a fit to the Weibull distribution. This is a specially designed plot utilising the fact that the Weibull distribution can be linearised – the fitted distribution always appears as a straight line.Two problems are obvious from the plot, and should in fact be kept in mind with all minirhizotron studies. There are sets of identical values (vertical ‘piles’ of crosses) due to the small number of sessions and thus identical dates; and the long horizontal stretches indicate long temporal distances between the sessions. The mean value estimate may still be robust (small errors), but assessment of the validity of the Weibull assumption is notoriously difficult for this type of data.

The estimates were obtained by nonlinear fitting using the maximum likelihood method. Thus, in addition to the estimates, their Fisher information matrix was also calculated. Inverting it and using the Gaussian

law of error propagation then produced uncertainty estimates for the mean value of the fitted Weibull distribution.

2.3.3. Fine root biomass production

Fine root biomass production was calculated as biomass (g m-2) divided by longevity (years). We used the KM estimations for fine roots 0-2 mm for this calculation, since it was not possible to estimate longevity for pine and birch 1-2 mm roots due to a low number of roots (Table 1).

2.3.4. Mycelia production

Fungal in-growth bags (mesh size 50 µm, allowing in-growth of mycelia, but not of roots) filled with acid-washed sea sand (five in each plot) were left in the forest soil, at the interface between mineral and organic horizons, in October 2006 and collected two years later. The sand was observed under a dissecting microscope and the extent of fungal colonisation was visually estimated on a scale 0-5, with 0 having no visual mycelia and 5 having plenty of mycelia present and sand particles aggregated to a large extent. The sand was then carefully mixed, freeze-dried and samples were taken for analysis of ergosterol content, to provide an estimate of fungal biomass. Ergosterol content was analysed according to Wallander (2011).

3. Results

3.1. Fine root biomass

Total tree fine root biomass down to 30 cm in mineral soil was significantly higher in spruce stands (702 g m^{-2}) than in birch (196 g m^{-2}) and pine (227 g m^{-2}) stands. Fine root distribution followed the same pattern for pine and spruce, with most biomass in the humus layer and decreasing with depth, whereas birch had few roots in the thin humus layer but a greater root biomass in the upper part of the mineral soil (Fig. 2a). SRL for roots with 0-2 mm diameter was significantly higher in pine and birch stands than in spruce stands, 16, 15 and 10 m g^{-1} respectively, *i.e.* pine and birch roots were on average thinner than spruce roots. For pine and spruce, SRL decreased with soil depth, even though the difference was only significant in pine stands (Fig. 3a), whereas there was no clear trend in birch stands. When comparing only the thinnest roots, with 0-0.5 mm diameter, SRL differed significantly between all three species, with SRL 30, 25 and 52 m g^{-1} for pine, spruce and birch, demonstrating that within the 0-0.5 mm fraction, birch roots were significantly thinner than pine and spruce roots.

Total understorey fine root biomass did not differ significantly between pine (205 g m^{-2}) and birch (337 g m^{-2}) stands, but was significantly lower in spruce stands (4 g m^{-2}), which had almost no understorey vegetation except for a moss layer (Hansson et al., 2011). Understorey fine root biomass decreased with soil depth, with most roots in the humus layer in both pine and birch stands (Fig. 2b).

3.2. Fine root longevity, turnover and production

Fine root longevity from birth until disappearance varied from 792 to 1158 days depending on species, root diameter and analysis method (Table 1). Consequently, turnover rate varied from 0.32 to 0.46 $year^{-1}$ (Fig. 4). Within each species (Table 1), coarser roots lived longer. In diameter class 0-0.5 mm, which was the most frequent diameter class, median longevity (KM) was 924 (pine), 917 (birch) and 896 (spruce) days (Table 1). Differences between median longevity (KM) and mean longevity (Weibull) were small for fine roots with 0-0.5 mm diameter, but the difference increased in thicker roots (Table 1).The difference in 1-2 mm spruce roots was 187 days (971 days Weibull; 1158 days KM). For the thickest pine and birch roots (>1mm diameter) it was not possible to estimate longevity, as few measured roots were in this fraction (Table 1) and many thicker roots were still alive at the end of the study period (Fig. 5). Most roots >1 mm diameter lived more than 2 years. When comparing all fine roots, i.e. all roots 0-2 mm, pine had the highest longevity, 1120 days, compared with 900 days for spruce and 922 days for birch (KM).

Longevity of understorey roots did not differ significantly between birch and pine stands. Most understorey roots were 0-0.5 mm in diameter and root longevity (909-916 days) and turnover rate (0.40-0.41 $year^{-1}$) were similar to those of tree roots within that diameter class (Table 1, Fig. 4).

Root growth varied through the growing season with a peak of root birth in late summer (Fig. 3b), with the same pattern for all three tree species. We did not have sufficient data to study seasonal variations in root mortality.

The annual tree fine root biomass production (humus and 0-30 cm in mineral soil) was 73, 78 and 284g m^{-2} in pine, birch and spruce stands, respectively. It was highest in the humus layer for spruce and pine, whereas birch, with a very thin humus layer, had the largest production in the upper part of the mineral soil (Fig. 6).

3.3. Mycelia production

Fungal biomass (ergosterol) was significantly higher in birch stands, 0.26 µg ergosterol g^{-1} sand, compared with 0.13 and 0.08 µg ergosterol g^{-1} for spruce and pine stands, respectively, with the same trend for the visual estimation (Fig. 7).

4. Discussion

The larger fine root biomass in the spruce stands, compared with the birch stands (Fig. 2a) confirmed our first hypothesis. Spruce stands were denser, with larger basal area and higher aboveground litter production (Hansson et al., 2011). Annual tree fine root production estimates were 73, 78 and 285g m^{-2} in pine, birch and spruce stands. Fine root depth distribution and fine root biomass production followed the same pattern

as soil carbon and nitrogen distribution in the stands (Hansson et al., 2011), suggesting a significant contribution of root litter to soil organic matter.

Fine root growth was largest in late summer for all three species (Fig. 3b), a finding consistent with other studies (Burke and Raynal, 1994; Steele et al., 1997; Mainiero et al., 2010; Olesinski et al., 2012).

Recent studies (Joslin et al., 2006; Gaudinski et al., 2010) suggest that fine root populations must contain both short-lived and long-lived roots and our results support this. Longevity was correlated to diameter, with thicker fine roots living longer, confirming our second hypothesis. It was not possible to calculate root longevity for the coarser pine and birch fine roots, as most of them were still alive at the end of the study. When all fine roots are included into one fraction (0-2 mm diameter) root longevity may be overestimated. Differences in longevity and turnover rate depending on root diameter are related to branching orders of the fine roots (Pregitzer et al., 2002; Wang et al., 2006). Naturally, roots with higher branching order live longer, since when a higher-order root dies, all the lower-order laterals also die. However, when using minirhizotrons it is difficult to sort root segments into different branching orders, since the order changes when the root branches and develops laterals, and the root tips are not always visible.
Differences in mycorrhizal colonisation must also be taken into account. In Sweden, more than 90% of the fine roots of both pine and spruce (Taylor et al., 2000) are colonised by mycorrhiza, whereas birch roots in our study tended to have a smaller proportion of mycorrhizal roots, with large morphological variations depending on fungal species. A study on root traits in 23 Chinese temperate tree species (Guo et al., 2008b) found lower mycorrhizal colonisation in birch than in pine roots, but the species were not the same as in our study. They showed that the first three orders of roots often were mycorrhizal, similar in anatomy. The difference between mycorrhizal root tips and long roots is probably at least as important as branching order when considering root longevity. An American study on loblolly pine showed longer lifespan in mycorrhizal roots than in other fine roots (King et al., 2002) and an Australian study on Eucalypt seedlings showed a lower growth rate in ectomycorrhizal fine roots than in non-mycorrhizal roots (Chilvers and Gust, 1982). It has also been shown that fine roots with ectomycorrhizal colonisation decompose more slowly than non-mycorrhizal roots (Langley et al., 2006). A recent study on fine root decomposition in four temperate species (Goebel et al., 2011) report slower decomposition in first- and second-order roots, often heavily colonized by mycorrhiza, compared to third-and fourth-order roots. However, the difference was smaller for *P. sylvestris* than for other studied species (*Acer pseudoplatanus*, *Tilia cordata, Larix decidua*). In the present study, fungal biomass in in-growth bags was larger in birch stands than in spruce and pine stands (Fig. 7). This does not necessarily reflect the extent of mycorrhizal root colonisation, as birch roots tend to be colonised to a lesser extent than pine and spruce roots (pers comm. I Ostonen). More fungal biomass in birch stands may be an indication of more fungal growth, due to bioturbation. When the soil is constantly mixed, the mycelia network is disturbed and more fast-growing fungal species may be favoured (McLean and Parkinson, 2000). Moreover, the ectomycorrhizal community in the mesh bags may not represent the community in the soil (Wallander et al., 2012). Ectomycorrhizal species differ in mycelia production per root tip (Kjøller, 2006), and some species avoid growing in mineral substrates.

Earthworms were much more abundant in the birch stands than in the spruce and pine stands (Olsson et al., 2012), leading to higher bioturbation. *Dendrobaena octaedra* was present in stands of all three species whereas the larger *Lumbricus rubellus* was only found in birch and pine stands. Since L. rubellus are 5-10 times larger than D. octaedra, the earthworm biomass in birch stands was much higher than in pine and spruce stands, and a much larger effect of bioturbation could be expected (Olsson et al., 2012). This disturbance could lead to a faster root turnover in birch stands, but for the finest roots (0-0.5 mm diameter) the difference in turnover rate between species was small (0.39-0.41 $year^{-1}$, KM), and in roots with diameter 0.5-1 mm the spruce roots turned over faster (0.41 $year^{-1}$, KM) than pine and birch (0.32 $year^{-1}$, KM). Thus, our third hypothesis of birch having the fastest fine root turnover rate was not supported by the results.

We followed the same roots for four growing seasons, during which period most of the fine roots with 0-1 mm diameter were gone, enabling a reliable estimation of their turnover rate. Many coarser fine roots (>1mm diameter) were still alive at the end of the study and to get reliable longevity estimates for them, a longer study period would be needed.

Compared to many other minirhizotron studies, our estimates on fine root turnover rate are comparatively low. One reason for this may be that we measured root longevity from birth to disappearance, including both disappearance through grazing of living roots and disappearance of dead roots, partly decomposed before disappearing. We estimated that our longevity values would be from one to four months shorter if we could have analysed root longevity from birth to death. However, other studies have had similar

problems, leading to reporting of longevity based on disappearance (Withington et al., 2006; Gaul et al., 2009) and they still report shorter longevity compared to our study. Our estimate of 1-4 months from death to disappearance was based on visual observations during minirhizotron studies. Goebel et al. (2011) reported a loss of 20% of first- and second-order root mass of many tree species after 36 months of decomposition. However, using mesh-bags may in turn result in underestimates of rates of root decomposition, excluding the impact of soil fauna, especially for the first- and second-order roots (Pregitzer et al., 1997; Dornbush et al., 2002; Stevens et al., 2002; Withington et al., 2006).

Finér et al. (2011b) reviewed fine root production and turnover and they report an average tree fine root turnover rate of 0.90 $year^{-1}$ from minirhizotron studies, compared to 1.88^{-1} from sequential coring data. Earlier minirhizotron studies in Norway spruce stands in Sweden reported a fine root turnover rate of 0.5-1 $year^{-1}$ (Majdi and Kangas, 1997; Majdi and Andersson, 2005). However, these studies only lasted 1-2 years. Strand et al. (2008) showed that longevity estimates increase with study duration, indicating that short time studies underestimate fine root longevity. They concluded that short-term minirhizotron studies may underestimate residence time of fine root biomass by over 300% compared to long-term experiments. Withington et al. (2006) compared fine root life span in 11 different tree species, including Norway spruce and Scots pine. They report a life span of 0.7 and 0.67 years for Scots pine and Norway spruce. These numbers are much lower than ours, but they only include first and second order roots, which have the fastest turnover (Guo et al., 2008a). A recent study (McCormack et al., 2012), comparing fine root lifespan of 12 different American tree species, report a median root lifespan of 95-336 days for first- and second-order roots, with an average diameter of 0.3 mm. Even though we divided the roots into small diameter classes, higher order roots were still present also in the smallest diameter class (0-0.5 mm), which may be one contributing factor to our higher estimates of root longevity.

4.1. Conclusions

Spruce, with larger above ground biomass compared to pine and spruce, also had the largest fine root biomass (g m^{-2}) and production (g m^{-2} $year^{-1}$). Spruce had lower specific root length (m g^{-1}) than pine and birch. The majority of the fine roots were thinner than 0.5 mm in diameter, with a turnover rate (KM) of 0.4 $year^{-1}$. Thicker fine roots had lower turnover rates than roots with a diameter of 0-0.5 mm. 60-100 % of coarser fine roots (1-2 mm) were still alive at the end of the four-year study period, emphasizing the importance of long-term minirhizotron studies to achieve accurate turnover estimates of coarser fine roots.

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Table 1. Fine root lifespan (days), based on Kaplan-Meier (median longevity) and Weibull (mean longevity) analyses, total fine roots 0-2 mm diameter and separated into diameter classes 0-0.5 mm, 0.5-1 mm and 1-2 mm for spruce, pine and birch stands, including understorey vegetation. n=number of analysed root segments

	Spruce			*Pine*			*Birch*		
KM	*n*	*Median*	*KM error*	*n*	*Median*	*KM error*	*n*	*Median*	*KM error*
0-0.5mm	2136	896	± 12	541	924	± 118	1271	917	± 44
0.5-1mm	1915	900	± 4	333	1150	± 6	46	1143	± 115
1-2mm	314	1158	± 23	20			5		
Understorey				1987	909	± 5	639	916	± 12
0-2 mm	4263	900	± 3	885	1120	± 84	1322	922	± 106
Weibull		*Mean*	*Std dev*		*Mean*	*Std dev*		*Mean*	*Std dev*
0-0.5mm		792	± 397		909	± 276		845	± 360
0.5-1mm		866	± 332		1024	± 233		1024	± 165
1-2mm		970	± 301						
Understorey					880	± 277		902	± 233
0-2 mm		843	± 362		956	± 262		851	± 355

Figure captions

Figure 1. a) Uncensored KM function for all birch trees and b) the Weibull plot for all birch trees, the same data as for Fig. 1a. For the lowest and highest 5% of the data, the line is dashed-dotted to indicate "extrapolation" and less reliability.

Figure 2. Differences in fine root (diameter < 2 mm) biomass at different soil depths for a) spruce, pine and birch (n=3 spruce, pine stands, n=2 birch stands; least squares means ± SE) and b) understorey vegetation (n=3 spruce, pine stands, n=2 birch stands; means ± SE). Different letters indicate significant differences between species (P<0.05).

Figure 3. a) (Left) Differences in fine root (diameter < 2 mm) specific root length (SRL) at different soil depths (n=3 spruce, pine stands, n=2 birch stands; least squares means ± SE) and b) birth date for spruce, pine and birch roots, percentage of total fine root length at the end of the study. Different letters indicate significant differences between species (P<0.05).

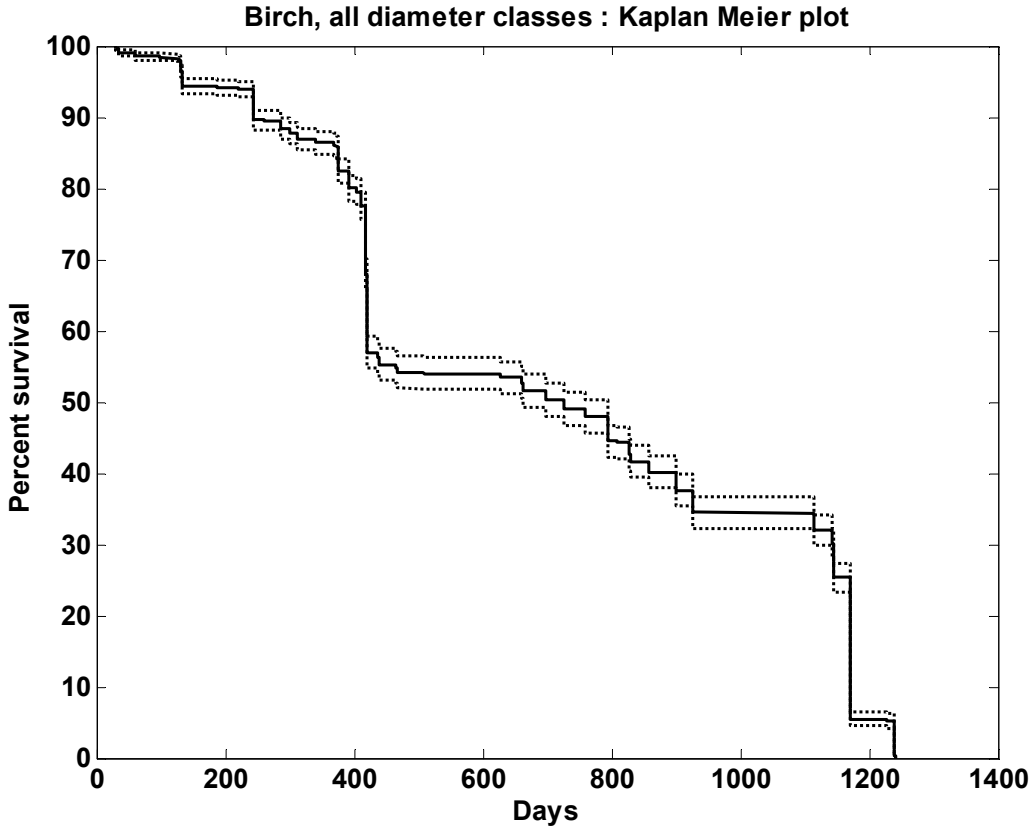
Figure 4. Estimated root turnover rate ($year^{-1}$) for spruce, pine and birch roots sorted into different diameter classes using Kaplan-Meier (median longevity) estimates. In the 1-2 mm fraction, enough data was available only for spruce.

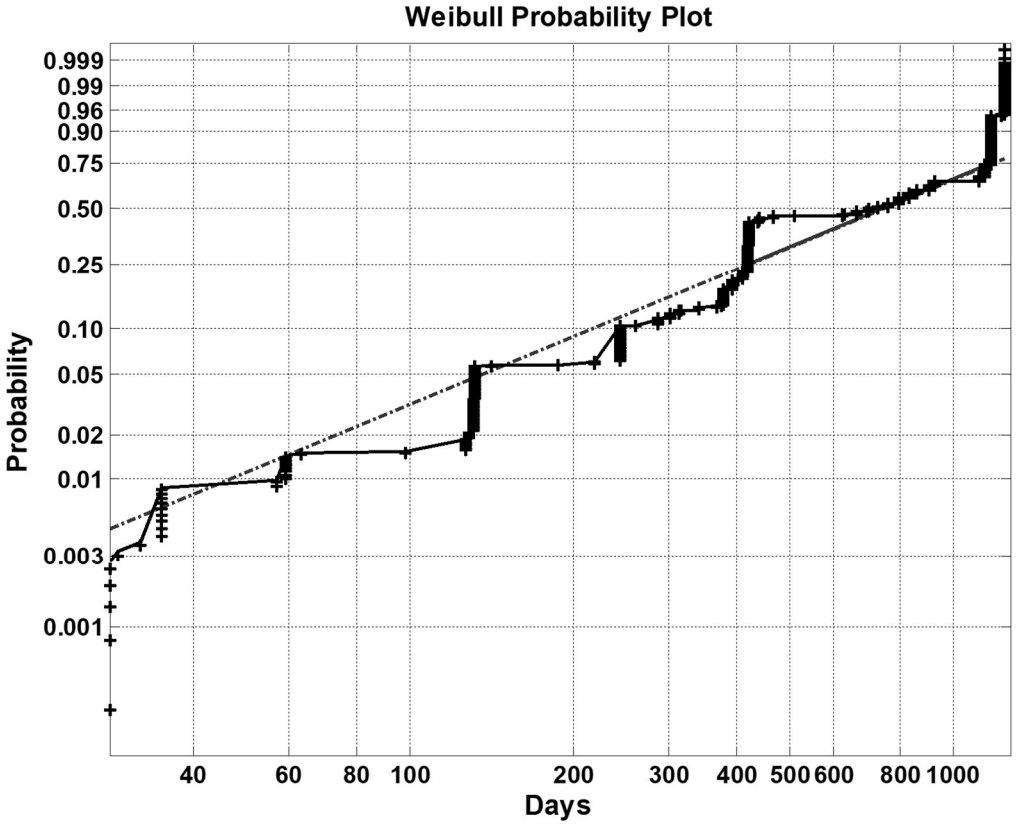
Figure 5. a) (Left) Diameter distribution, sum of all fine roots, length per species (cm) at the end of the minirhizotron study and b) fine roots, % alive at the end of the study, root length per diameter class for each species.

Figure 6. Estimated fine root biomass production (g m^{-2} $year^{-1}$) for spruce, pine and birch roots calculated from turnover rates (0-2 mm diameter) and fine root biomass.

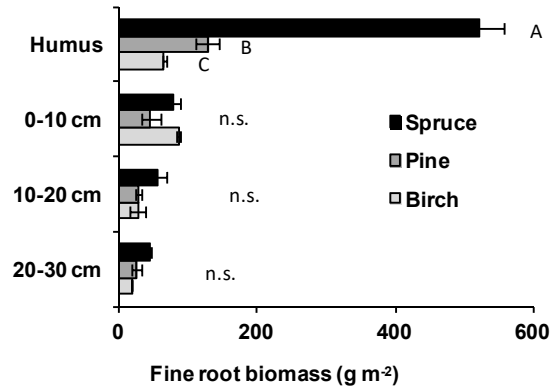
Figure 7. Fungal biomass in mesh bags filled with sand a) ergosterol (µg g-1) and b) estimated on a scale 0-5, using visual
criteria, with 0 having no visual mycelia and 5 having plenty of mycelia present and sand particles aggregated to al large
extent (n=3 spruce, pine stands, n=2 birch stands; least squares means ± SE). Different letters indicate significant differences
between species (P<0.05).

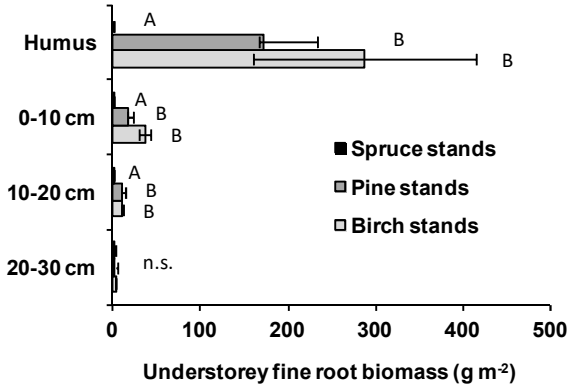
1.


Birch, all diameter classes : Kaplan Meier plot
Percent survival
100
90
80
70
60
50
40
30
20
10
0
0
200
400
600
800
1000
1200
1400
Days

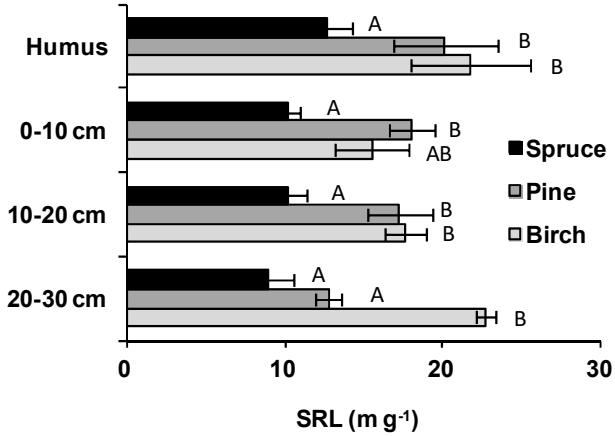

Weibull Probability Plot
Probability
0.999
0.99
0.96
0.90
0.75
0.50
0.25
0.10
0.05
0.02
0.01
0.003
0.001
40
60
80
100
200
300
400
500
600
800
1000
Days

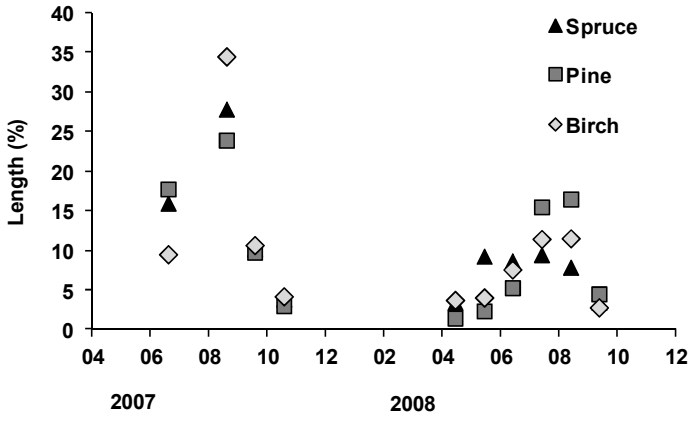
2.


Humus
0-10 cm
10-20 cm
20-30 cm
A
B
C
n.s.
n.s.
n.s.
Spruce
Pine
Birch
0
200
400
600
Fine root biomass (g m-2)

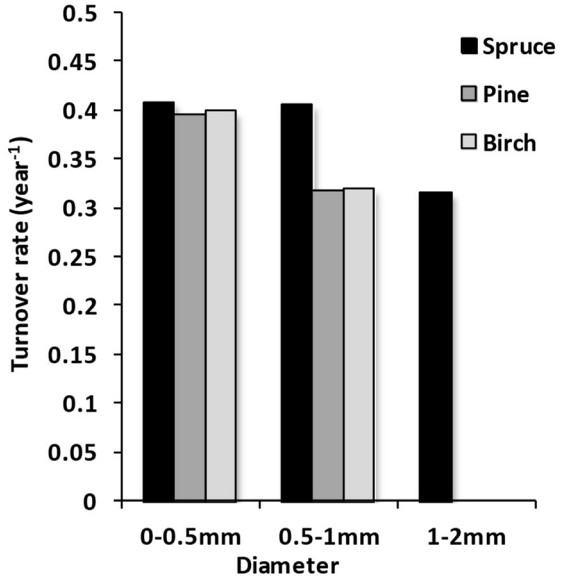

Humus
0-10 cm
10-20 cm
20-30 cm
A
B
B
A
B
B
A
B
B
n.s.
Spruce stands
Pine stands
Birch stands
0
100
200
300
400
500
Understorey fine root biomass (g m-2)

3.

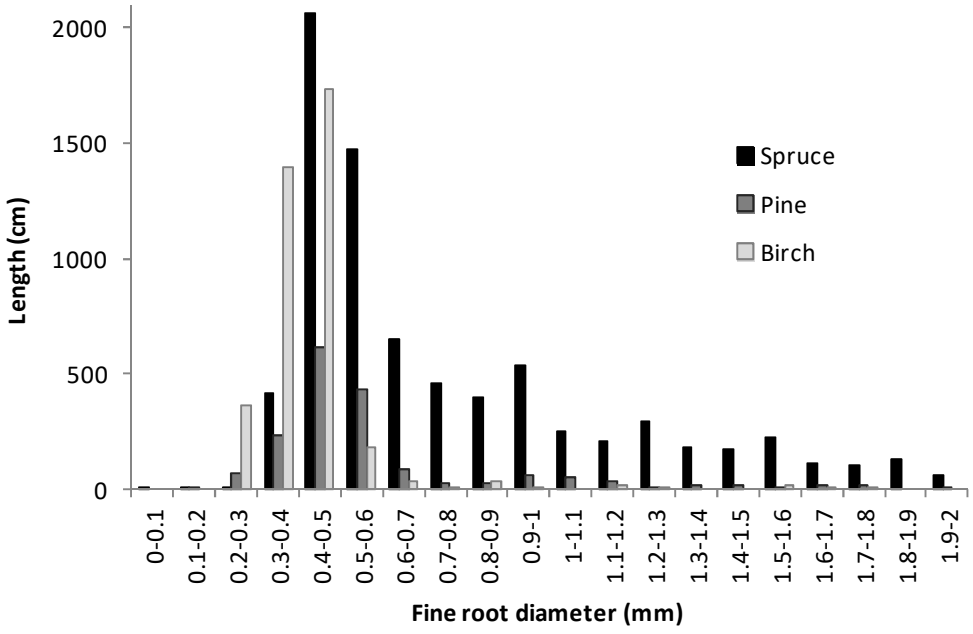

Humus
0-10 cm
10-20 cm
20-30 cm
A
B
B
A
B
AB
A
B
B
A
A
B
Spruce
Pine
Birch
0
10
20
30
SRL (m g-1)

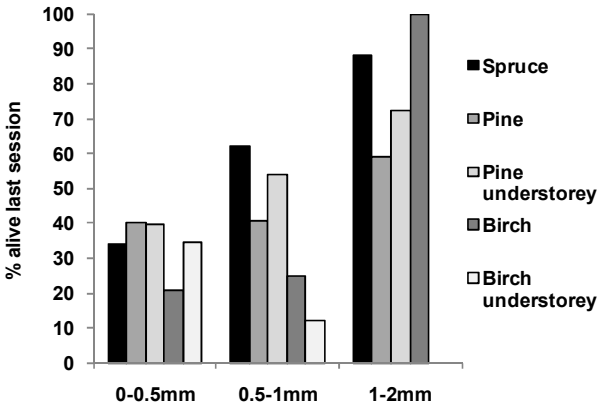

Length (%)
0
5
10
15
20
25
30
35
40
04
06
08
10
12
02
04
06
08
10
12
2007
2008
Spruce
Pine
Birch

4.

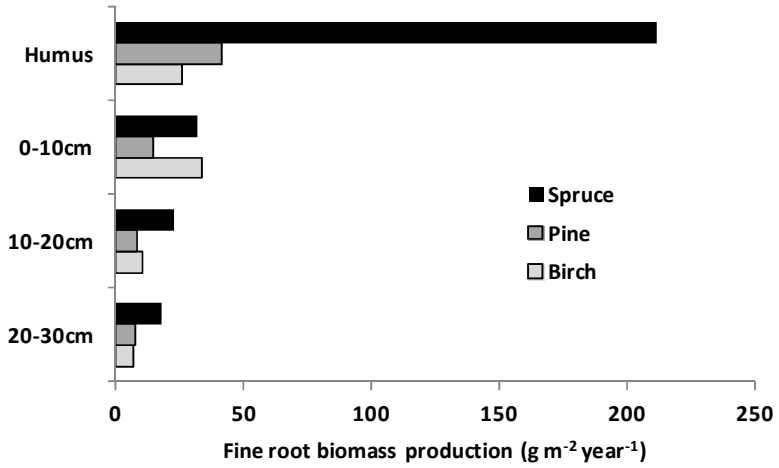

0.5
0.45
0.4
0.35
0.3
0.25
0.2
0.15
0.1
0.05
0
Turnover rate (year-1)
Spruce
Pine
Birch
0-0.5mm
0.5-1mm
1-2mm
Diameter

5.

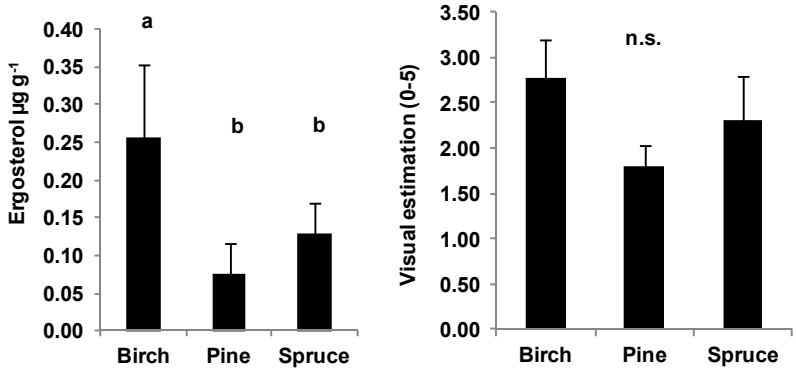

2000
1500
1000
500
0
Length (cm)
Spruce
Pine
Birch
0-0.1
0.1-0.2
0.2-0.3
0.3-0.4
0.4-0.5
0.5-0.6
0.6-0.7
0.7-0.8
0.8-0.9
0.9-1
1-1.1
1.1-1.2
1.2-1.3
1.3-1.4
1.4-1.5
1.5-1.6
1.6-1.7
1.7-1.8
1.8-1.9
1.9-2
Fine root diameter (mm)


100
90
80
70
60
50
40
30
20
10
0
% alive last session
Spruce
Pine
Pine understorey
Birch
Birch understorey
0-0.5mm
0.5-1mm
1-2mm

6.


Humus
0-10cm
10-20cm
20-30cm
Spruce
Pine
Birch
0
50
100
150
200
250
Fine root biomass production (g m-2 year-1)

7.


Ergosterol µg g-1
0.40
0.35
0.30
0.25
0.20
0.15
0.10
0.05
0.00
a
b
b
Birch
Pine
Spruce
Visual estimation (0-5)
3.50
3.00
2.50
2.00
1.50
1.00
0.50
0.00
n.s.
Birch
Pine
Spruce