



A Questioning Life: The Hows and Whys in the Application of Plant Science

Inaugural Professorial Lecture: Professor Chris Atkinson

Wednesday 28 June 2017, 6pm

Inaugural Professorial Lecture Series

A Questioning Life: The Hows and Whys in the Application of Plant Science

by

Professor Christopher J Atkinson

Natural Resources Institute, University of Greenwich

An Inaugural Professorial Lecture

delivered at the University of Greenwich

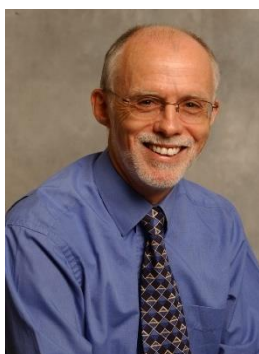
Wednesday 28th June 2017

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FORWARD



Chris Atkinson is a plant scientist at the Natural Resources Institute, University of Greenwich and currently carries out research and teaching in crop science and its application to agriculture and horticulture. Chris's early career saw him working for Unilever Ltd. and for AFRC at the Rothamsted Research Station in Harpenden, where his career was inspired to change direction from analytical chemistry to plant science. On retraining he gained a First Class Honours degree in Applied Biology from the University of London in 1979. His love of 'places wild' and the opportunity to study mountain plants lead him to U.C.N.W. and the School of Plant Biology, Bangor and a Ph.D. on the physiological ecology of montane grasslands (Atkinson, 1982) from the University of Wales. Yes he did take Welsh lessons, but eventually decided it was easier to marry a Welsh-speaker. On finishing his Ph.D. he worked the Dr. Pat Denne in the Department of Forestry, at the University of Wales, learning much about trees that would one day underpin his research. The opportunity arose in 1984 to work with Prof. Harold Mooney and Bill Winner at Stanford University in California and in Virginia at Virginia Polytechnic Institute and State University. The magnificence of living in Appalachia and seeing an 'Appalachian Fall' is a sight never forgotten, but the attraction of 'Lakeland' even greater and the Atkinson's moved to Lancaster. His third and final postdoctoral position came when Prof. Terry Mansfield FRS and Bill Davies, at Lancaster University, invited him to work on a project linked to the chemical control of stomatal behaviour (funded by Shell UK). Six years in Lancaster saw Chris become a Research Fellow as he started writing and delivering his own research proposals. In order to breakout of the post-doctoral cycle of short-term contacts and limited stability, Chris with some reluctance, left Lancaster to come to the warmer and drier south and join Horticulture Research International (HRI) at East Malling, as a Senior Scientific Officer, in the Crop Physiology Department. Those 2 years in forestry had all been worthwhile as he now worked on perennial woody crops (fruit trees). Lots of hard work and the drive to carry out science in manner which would be of use to an industry saw him promoted to Principle Research Scientist, within the Perennial Quality and Biotechnology Team. Further promotions came and he became an Executive Member of East Malling Research's Science Management Team, and was part of the team that achieved privatisation status for the institute in 2006. As Head of Science for the newly privatised organisation he oversaw, with the Group Secretary and Finance Director, East Malling Research balancing its financial books for a number of years. Further changes saw him become the Deputy Chief Executive and Senior Programme Leader (*Resource Use for Sustainable Production*). Chris also became a Fellow of the Chartered Institute of Horticulture and the Royal Society of Biology, before accepting a Chair at NRI, University of Greenwich, in 2012 and is now the Professor of Sustainable Agriculture and Climate Change.

His main research interests focus on understanding the impact of environmental factors on the growth and development of crops, particularly fruits. A major part of his work is on the impacts of drought on crop physiology and production. His research also includes studies of the influence of temperature on the growth and quality of fruit, the impact of autumn temperatures/chilling on the flowering and cropping, and developing strategies to optimise production and examining environmental differences in the ability to set and retain fruit. The tolerance mechanisms of different rootstocks, to drought, have also been a subject for investigation. Recent work is directed at the impacts of soil applied biochar and health benefits of fruit consumption, particularly with respect to agronomic ways to enhance fruit bioactive compounds. His research has also included work on perennial biomass crops, enhancing *Artemisia* production, and pharmaceutical protein production in transformed tobacco.

He has also acted as a peer journal reviewer for a wide range of international plant science journals (>20), for many years, and as the editor of the journal *Plant Growth Regulation*, as well as, a consultant/reviewer for both national and international Research Councils and organisations such as BBSRC, FCT, NERC, DFID, FAO and USDA. His career has resulted in over 250 publications of which over 100 have been in peer-reviewed international journals

OMISSIONS

This of course is only part of my story and my interpretation of the events that not only allowed me to have wonderful life in research, but also to achieve my aspirations. The realisation of my dream could not have been achieved without the input of a large number of people who have helped and encouraged me along the way. Many I have identified through their contribution to my published work and others I have acknowledged at the end of this account. There will of course be others who I have not had time or space to include, so please accept my apologies for any omissions and of course my thanks and gratitude for being part of my story. It should also be made clear that my intentions here have been to cite only the literature that appears in peer-reviewed journals. Much of the great detail of the numerous commissioned project and their reports have had to be excluded along with my literature in the industry press that was published to inform stakeholders and the general public.

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INTRODUCTION

It was only fairly recently that I began to get a strange feeling that my career and life had a 'structure' which I did not feel was a result of my actions and that in some way, may be, fate was involved. It may also be that I have been willing and able to exploit so many opportunities that eventually all would fittingly come together. As a scientist, the evidence suggests that it just takes a lot of enthusiasm and hard work. I should also acknowledge that I often consider, or allow, my life and career to appear as one and the same and that perhaps this is my weakness and my strength. I have, however, been allowed to exploit the boundary between the two, due to an understanding family, and this has much to do with what I have achieved today. I have always felt great excitement and wonder at changing the way we 'think' about things through asking questions, and getting the answers published. For me there can be no end unless the 'questions' and 'answers' are published. This philosophy has been part of my approach in the support of others through guidance and science management, and their career development. What must be acknowledged however is that I have consciously, rightly, or wrongly, taken a broad perspective in my quest for knowledge? The fact that I have done this means that at times my perception of a subject's depth, may well have been limited, but I have sacrificed that for having breadth. I feel that this approach has been justified, particularly in agricultural science where the problems and solutions are complex and cross many traditional boundaries. The great benefit to me has been that my enthusiasm and fascination with plants has never been extinguished. I recall the comments made by John Harper FRS, when I was in Bangor, telling us that specialism was not in fashion and that the world needs scientists that have an integrated vision and understanding (*my words on what I recall of a coffee time edict*). It is now difficult to determine the extent that those words have influenced my thinking, but the problems of our world have never, more than now, required the skills of those who have the capacity to understand the detail and be able integrate that knowledge into solutions. So the challenge here is for me, within this memoir, to knit the strands of 'scientific logic' (*so beloved by the empirical scientist*) into a story that outlines a career and passion for plant science.



Figure 1. A collection of 'firsts' - my school - Noel Park, Wood Green (taken in 1950's), my visit to Greenwich (~1958) and where was my mother? 'Free-climbing', with my Dad, in North Wales (1964).

The intentions of this publication are to provide an insight into what it is I have been doing all these years, whilst enjoying myself, and for the associated presentation to highlight some of the

events and the work carried out. In no particular way is this written account a precise description of the associated presentation.

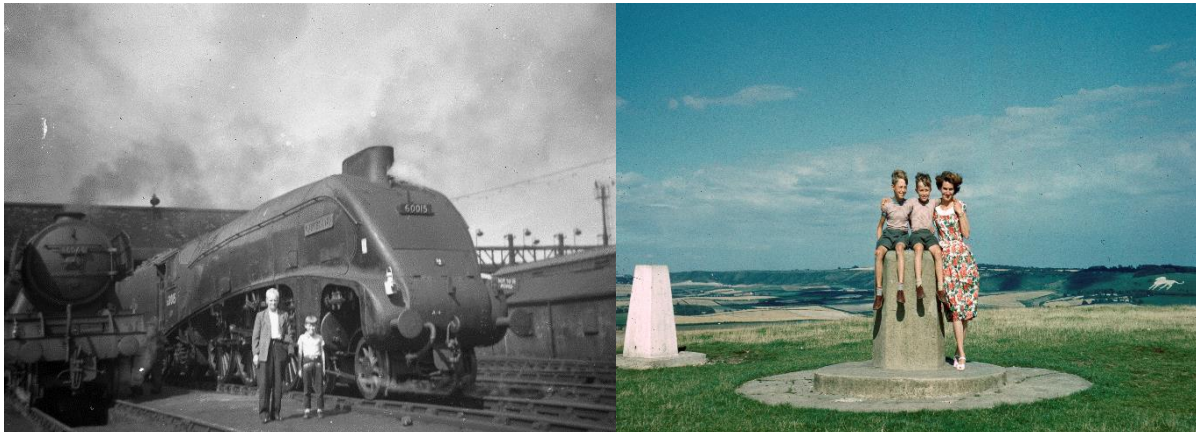


Figure 2. Growing up in London was not all bad, my Grandad was a train driver (image left taken ~1960). Health and Safety would of course not be too keen on this picture so I will not mention driving the train. The effects of blue skies and green grass can be seen on our faces at top of Ivanhoe Beacon, 1960 (right).

SECTION 1: ENGINEERING TO BELLAMY ON BOTANY

I had the great fortune to have been born, at home, in a Victorian terrace house in north east London (N22) in a place called 'Wood Green'. This affluent location only lacked two things, woods and anything green. Just before reaching my eight birthday (just 2 days before) my father had changed jobs and we moved to a 'house in the country', in fact a modern garden city – Stevenage. Everything was new and there were leafy lanes and green woods in great abundance and as boys (I have a brother) we would roam for miles throughout the rural countryside on the freedom of our bicycles. The world of nature was not only on our doorstep, it was in our garden. My mother, and I don't know where she acquired the knowledge, was able to identify a large number of wild plants. I spent most of my time either climbing trees, or scrabbling around in vegetation (*still doing that today*), or playing football, and not doing enough studying and certainly nowhere near as much as my brother. At that stage in our lives we were completely different people and as we grew into teenagers we had little in common, apart from science, eventually. It appeared that I exuded little interest in reading and writing and I was encouraged to turn to my practical side and it looked at one stage as if I was heading for a career in engineering. This is one of those moments when having decided to drop engineering, at the very last moment, I did not realise that all those skills would come back and be vital, particularly when conducting field experiments in remote locations, where you had to understand the workings of the equipment and be able to fix it *in situ* (Atkinson *et al.* 1986). So while in the 6th Form our biology teacher 'disappeared' (*science teachers were hard to find – not much has changed*) and we were taught by the Head Master's wife (Mrs McArthur). She taught at the girl's grammar school and I did extremely well punching out of my league intellectually. I am sure, this was due to her command of her student's (I don't remember any other teacher having that capacity) and of course how she taught. These were the days when school leavers went to work, or a small number to university and of course my brother went to university and I landed, somehow, a job

in an analytical chemistry lab which my dad said was well paid. The beauty of this job was that my employer Unilever paid for my further education and allowed me to have day-release, albeit in analytical chemistry and lots of night classes (including my independent study of 'A levels' in Biology and Chemistry).

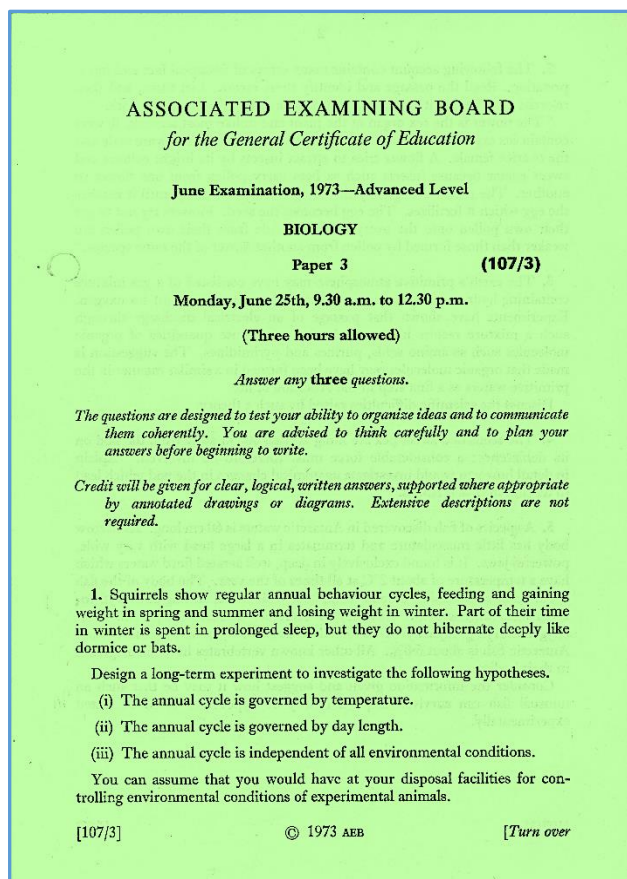


Figure 3. One of my three Biology A level exam papers, the one where you had to think and come up with answers to questions that were purposely not in the curriculum, or the text book.

A pivotal moment in my educational career came when taking 'A level' Biology, at night school. I was made aware by the instructor that given the course ran for one evening a week and for one year she could not teach is all. She did go through my copy of 'Vines and Reece' to highlight all that I had to know that she could not fit into the class (I still have my annotated copy of V&R). That was a tremendous help, particularly as the subject carried 3 examinations, with essay paper 3 being a test of organisation and coherent communication. Not only were the three questions answered expected to reflect an hour each of writing, they were also intended to draw on your ideas and thinking and were not part of the taught

syllabus. I may be wrong, but this is not something that happens these days, despite the fact that, I would suggest, it provides a big insight into the notion of how to do your own thinking.

I finally ended up studying at Hatfield Polytechnic (now the University of Hertfordshire). My boss at Unilever Ltd., Bill Shepherd, taught me many things, including the rigour of doing what you are paid to do; so if you packed up your 'chemistry kit' at 5:10 pm (5:20 pm was home time) he would come along and politely ask 'are you having a half day'. Some of the people I worked with then are not only, still alive, but still turning up to walking reunions and pubbing weekends in remote UK locations. At this time I was beginning to realise that I could be the master of my own destiny, at least up to a point and with my interest in plants growing ever stronger, I decided to make a career change and got a job as an Assistant Scientific Officer (ASO) at Rothamsted, the world's oldest agricultural research station. After carrying out literally thousands of chemical analyses per year on the 'classical experiments' ['Park Grass' and 'Broadbalk'], known around the world, for other research staff, I became aware of several things. Firstly, that anybody could do this, I was doing experimental analyses for others and they were publishing it, and that's what I wanted to do, but I needed to give all this up and retrain. It was also at this point that I discovered the impact of seeing your 'name in print', i.e. having my name in the Rothamsted Annual Review (1973; 1974). I do not remember considering leaving Rothamsted as a big decision and that may be because, I had no responsibilities, I was totally committed to being a

biology undergraduate (and to selling my car) and universities wanted me, and I had all the entry qualifications required, and London University seemed a good choice. As a mature student I had a full grant, unlike the less fortunate students of today.



Figure 4. Manresa Road in Chelsea, London University in the late 1970s. The tower block at the end of the road was my home for my first year as an undergraduate; accommodation went downhill from here. Student accommodation in Victorian terraced houses was affordable, but far from the on-suite opportunities student now have. At least while we were there the gas boiler which hung precariously over the bath never finally came of the wall. The landlord never appeared – somethings don't change. We had little

heating at the weekends and I would wear my duffle coat while writing assignments and laboratory reports. I will not mention the weekend diet of custard creams. Source By Brakspear - Own work, CC BY-SA 3.0, <https://commons.wikimedia.org/w/index.php?curid=20542132>.

I enjoyed every last moment particularly the field biology and had no trouble in achieving my dream. The memory of opening that letter and reading that I had got a first was special and confirmed my intentions to undertake a Ph.D. I had also started my career in publishing, I cannot now remember why I felt it important to publish the outcome of experimental research, but it was probably due to my experiences at Rothamsted and thinking this is something that I can do. So my first direct attempt to publish my work came after an undergraduate residential course in Rhyd-y-Creuau, North Wales, where I looked at the competition between two different leaf gall forming wasps on local oak (*Quercus* spp.). The simple question was when you get these two species egg laying on the same leaf where there measureable size differences in the galls produced when compared to leaves on the same tree in similar positions with the presence on galls of only one species? (*Bulletin of the Amateur Entomological Society* (AES); Atkinson and Julian-Ottie 1980). It was only a journal used by amateur entomologists, but it reinforced my passion to try and report everything I have ever done experimentally through the publication of outputs. I have maintained this philosophy throughout my career and have published at least one peer reviewed publication from every research contract I have ever received.

SECTION 2: CYMRU AM BYTH

The applications and Ph.D. interviews were challenging particularly at Cambridge and Oxford, but eventually, I decided to go to U.C.N.W. Bangor. I did however receive a letter from 'the Master' at Oxford wanting to know why I had not taken up their offer and I explained that Bangor (through John F Farrar) were letting me do what I wanted; not that I knew what I wanted to do for my Ph.D., but I wanted to make that decision (Atkinson 1982; 1983; 1985; Atkinson and Farrar 1983). This was, as I soon found out, not easy; I still remember the concern even now, but it was

one of those ‘character building’ career defining moments, once I knew, the what?, and the how? I still draw on this experience when working with students now. Those that are able to develop skills in separating what’s important from what is not have the potential to undertake the challenges of a career in research. I should say at this point, that being at a Welsh University (Coleg Prifysgol Gogledd Cymru, Prifysgol Cymru), and in the heartland of the Welsh language, it was one the best decisions I have ever made, being a student at Ysgol Llyseieg. Which I should add, when translated into English actually means the ‘School of Vegetables’ [*not the School of Plant Biology as we English understood it*], of course we were far from being vegetables. My first 3 months in Bangor were the making of my research career. Eventually, I decided that I had a subject with a number of relevant scientific questions that I could use to not only get a Ph.D., but also combine my love of botany and mountains, a theme that will reappear in this story. This was of course part of the reasoning behind going to Bangor.



Figure 5. Pen yr Ole Wen viewed from Cwm Idwal looking north to the site of my experimental plot in the Carneddau Mountains of North Wales. The plots were located on the mountain skyline to right of the summit half way down from the peak.

With lots of questioning discussion with John Farrar, my supervisor, I decided that I wanted to explore the realms of plant ecophysiology – i.e. somebody who is interested in understanding how plants function in their environment; a subject that to this day still fascinates me. What I did not know at the time, but quickly found out was that the Head of School of Plant Biology in Bangor, Prof. John Harper FRS, somewhat disliked ecophysiology as a concept and even the people who called themselves ecophysicologists.

After much discussion and a lot of thinking, I decided that I wanted to understand how species co-exist in communities given that they all apparently have similar needs for the resources to survive, e.g. light, nutrition and water. My thinking was that this similarity of resource requirements must generate competition, but in relatively stable communities’ plants have

adaptive strategies which reduce competitive interactions. My hypothesis was very much founded on trying to embed the means (mechanisms) by which plant communities co-exist, at least in part, or an explanation(s) that by having physiological characteristics/functions which reduce the competition with other species in the community. My interests in physiology were integral to the concept that the physiology of co-existing species was in some way complementary to their co-existence. I felt at the time this was a rather heretical approach at Bangor and I recall the attention that Prof. Greg-Smith gave to my hypothesis. His interests and career had focussed on explaining species co-existence in relation to 'describing spatial and temporal vegetation patterns' and the statistical analyses of these associations. This approach had nothing to do with, or apparently require, any knowledge of plant physiology.

As part of the tradition in the School of Plant Biology, all new incoming Ph.D. students had to undertake a Departmental Seminar at which they presented their research ideas, hypotheses and a programme of work for discussion and comment. Having never given a talk in public, let alone a research seminar this was a big deal for me and all my fellow Ph.D. starters. Even worse for me was that as an Atkinson I had to go first, so I had no help from watching others to see what worked and what did not. I recall it being a daunting event, but I got through it. What I still recall vividly was the questions, these of course probed my 'ecophysiological approach' and I became fully aware of Prof. Harpers views. Prof. Greg-Smith then joined in and made it clear that one did not need to understand plant physiology to explain species co-existence it was all to do with 'pattern'. Once the two of them had got enough from me, thankfully, they then turned on each other and we had a Harper, Greg-Smith debate. Despite the rather daunting nature of this type of event it was one of the processes that made Bangor what it was and what I am now, and to some extent, at times, in its absence, this is what I desire - the rigour of debate.

So I had survived the first round and spent what appeared like a lot of time reading around my chosen subject. What became very apparent as I approached the delivery of my seminar was that I had the opportunity to merge my love of mountains and botany by conducting research on a mountain plant community. A physiological understanding of plant co-existence required the use of an experimental plant community which was simple with respect to species composition, i.e. not too many dominant co-existing species. So I wandered around the hills to find an appropriate grassland with a few species; not particularly difficult for those who have visited North Wales and its abundance of poor acidic grasslands. Several locations were proposed from an examination of descriptive plant community publications that I had read. A field trip with John Farrar confirmed a suitable community location with around five co-existing species. This was just a few miles from Bangor and even fewer from my new home (Bethesda – and its famous Penryn Slate Quarry). The one I chose was on the Carneddau ('the cairns') mountains within the National Park, for which I am grateful to the National Trust for allowing assess, and sampling, and monitoring to take place. It was however at 3000 ft. (SI units 1000 m - not so impressive).

Once I had identified the species present (small fine leaved grasses, heavily grazed and rarely flowering – always a challenge), the site was marked out (using small red wooden ground stakes – very difficult to find in Welsh weather, but NT approved as biodegradable). I took my supervisor for a walk to see what I had found, that was the last time he came walking with me. This grassland was dominated by the species *Nardus stricta*, *Festuca ovina*, *Juncus squarrosus* and *Deschampsia flexuosa* all of which have the potential for the storage of energy (carbon) and nutrients in

underground organs (rhizomes and stolons). One the things that I did do with this experimental plot was to measure species abundance (presence and biomass) by making plot measurement every month for a year. For any plant ecologist reading this, they will know the approach of ‘point quadrates’ and the determination of species abundance and seasonal changes. I also quantified this approach, by cutting turves to bring back to the lab, so that I could calculate species biomass (dry weight) in the grassland as it changed with season. Having heard Prof. Greg-Smith feelings on understanding and describing community structure and co-existence, I thought it appropriate to at least be able to describe species changes in community structure over time and see how this related to growth – in my experimental system. This was challenging work and doing it on your knees at 3000 ft. on top of a windswept mountain, generated many questions, not all of them were however scientific.

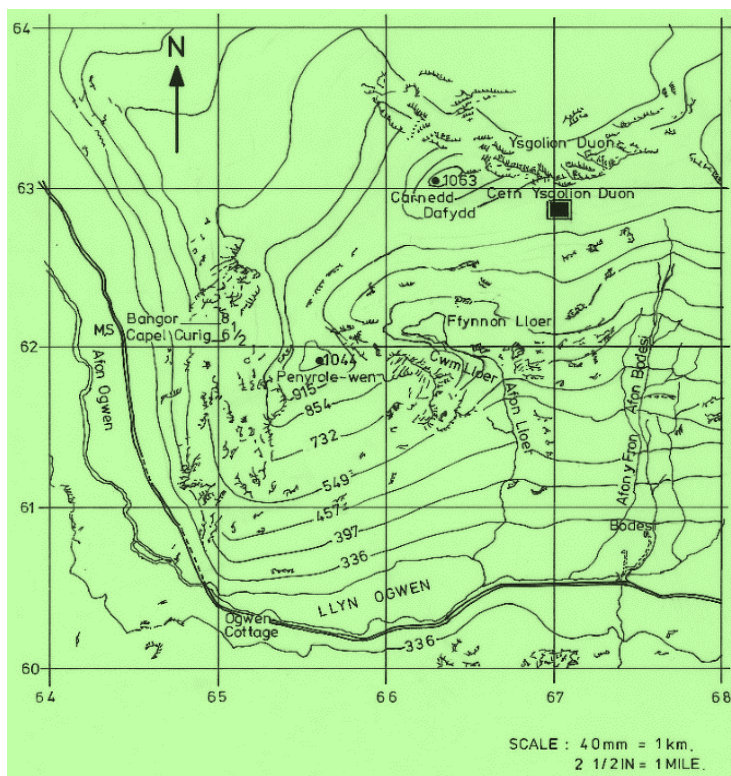


Figure 6. A map drawn by my father that went into my Ph.D. thesis and shows the location on the Carneddau Mountains of North Wales of my experimental plot [■]. The plot was used to collect and remove plants for use in experiments back in the universities glasshouses in Upper Bangor. The plot was also used to determine how grassland species abundance changed throughout the year. This was achieved by carrying out monthly quadrat analyses (Atkinson 1982). The view presented in Figure 5 is looking directly from the bottom of this map northwards.

I still remember the bitter sweet feeling of arriving at the plot, for my November measurements, and finding it covered with a foot of snow. The climb may have been a waste, but at least I did not have to be on my knees for 3 hours or so. Much of the work I did, however, was done by removing plants and growing these at the university glasshouse’s (again thanks to NT for their permission). These slow growing ‘alpine type’ grasses eventually responded as I learned how grow them for my replicated experiments. For the purpose the study, I felt that this type of community would be limited in its vegetative growth (many plants at this altitude do not effectively sexually reproduce) so a key point of focus was what happens when they compete for nitrogen and phosphorus (Atkinson 1982; 1983; 1985; 1986). Working with these nutrients provided an appreciation of not only the species demand for nutrients, but also the possible insights into differences in the process, or their timing with respect to supply and demand which might contribute to explaining the means by which co-existing’s species avoid competition. The important lesson was that through experimentation, a functional, or mechanistic understanding of co-existence could be developed. I was also exposed to a number of techniques that provided

fuel for much of my future research. In particularly, the use of radioactive isotopes to measure plant assimilation and the uptake of carbon and phosphorus with the former initiating my understanding of the process of photosynthesis.

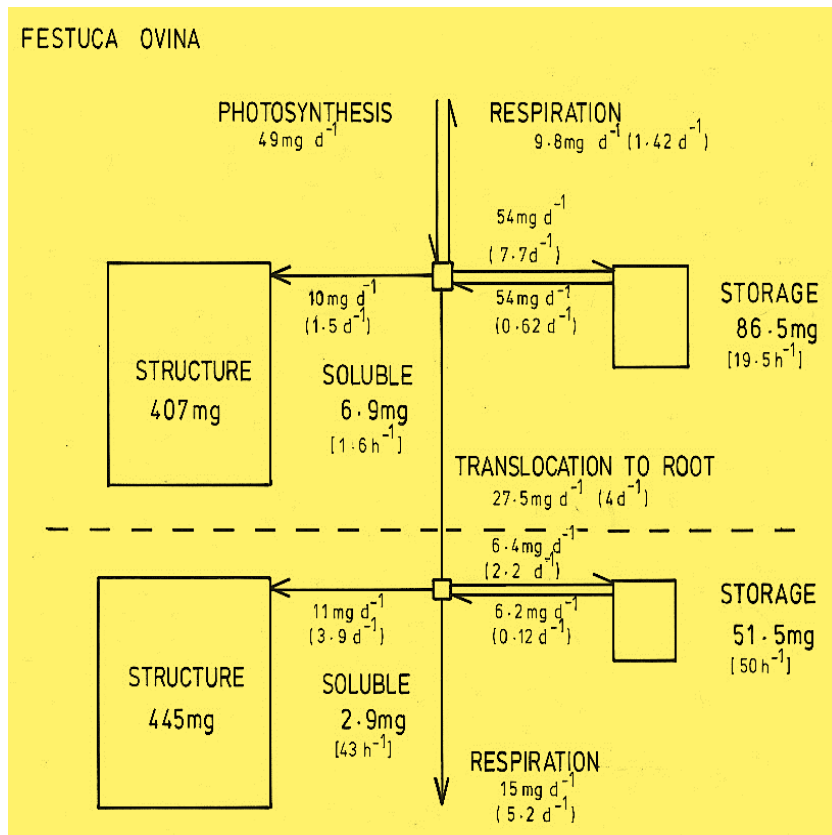


Figure 7. The allocation of photo-synthetically fixed carbon in *F. ovina* to soluble, storage and structural carbohydrates, above and below ground, determined using ¹⁴CO₂ labelling. Pool sizes are shown in proportion (and in text as mg) and the fluxes to the each pool are shown as mg d⁻¹. The directional arrows show the fluxes, or transfer rates from one pool of carbohydrate to another (source CJA Ph.D. thesis drawn by J.L. Atkinson).

A model was constructed from the isotopic and chemical analyses of soluble, storage and structural carbohydrates. The results showed that the soluble pool of carbohydrates was small relative to the storage and structural pools for both species, *F. ovina* and *N. stricta*. The somewhat surprising result was the high flux rates to the 'storage pool'. The naming of the 'storage' pool does not actually agree well with the physiological connotations of the pool descriptor (Atkinson 1992; Atkinson and Farrar 1983).

Bangor was well versed in the use of radioactive isotopes and I was well tutored by Gareth Williams and managed to produce some interesting functional images using autographs of carbon fixation in these species using individual plants and turfs removed from my mountain plots. At this time nobody had used this approach to determine carbon fixation and allocation in these types of plants. The outputs with respect to the autoradiographs were very revealing and suggested that these montane plants did some interesting things with respect to the allocation of newly photosynthetically fixed carbon (Atkinson and Farrar 1983).

This work also involved designing and building a bespoke leaf gas exchange system and leaf chamber for optimising measurements of photosynthesis in these species (*F. ovina* and *D. flexuosa*), which had very thin long leaves, with little photosynthetic area and low rates of carbon fixation. Perhaps the most important and novel element of my thesis was the work of carbon

allocation (Atkinson and Farrar 1983). Again, radioactive carbon was fed to plants ('pulse chase') and its fate (and movement) determined over time with respect to how much was respired or allocated to growth and/or storage. The very interesting outcome was that despite background knowledge and my hypotheses these species actually showed quite dynamic changes in turnover of various pools of carbohydrate particularly the soluble pool from which all other pools were derived. Even the pool of 'storage carbohydrates' was not just a store utilised for seasonal spring regrowth. At the time, and I think it still is, this was considered an unexpected discovery.

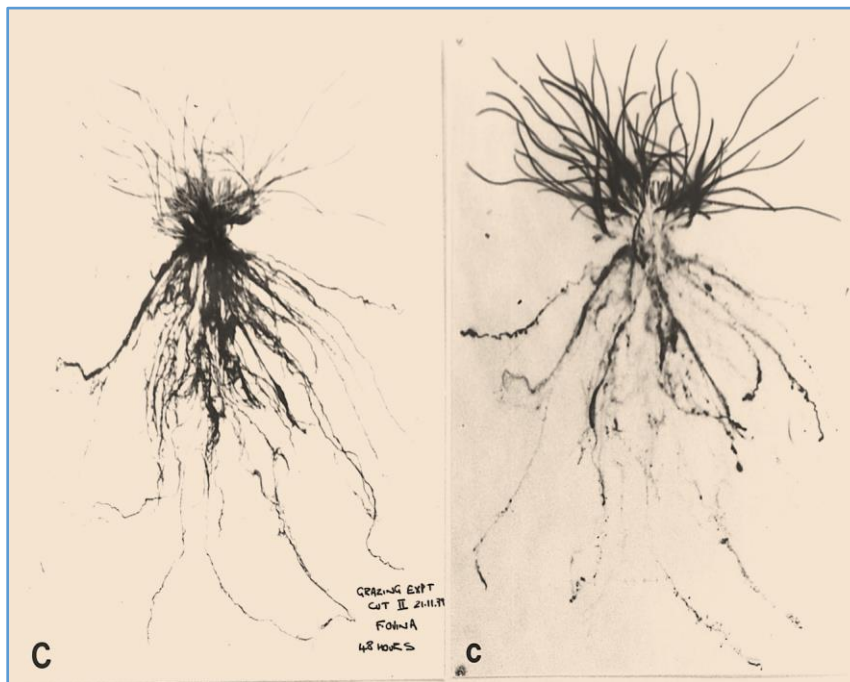


Figure 8. The image on the left shows a photograph of a complete *Festuca ovina* plant, once its roots had been washed out from a pot after being fed radioactive ^{14}C 48 hours earlier. The plant had been subject to clipping to simulate grazing 50 days before the exposure to the ^{14}C radioactive tracer. The image on the right shows an autoradiograph of the same plant.

The interpretation of the autoradiograph highlights (right), with respect to the intensity of the photo blackening, the plant parts which contain radioactive carbon (^{14}C) now fixed by photosynthesis. The young and recently emerged leaves are intensely labelled throughout their length with the isotope and after 48 hours of pulse chase, a number of roots can be seen to contain the translocated isotope (^{14}C) both near to the shoots as well as at their growing ends (radiograph on the right).

The conclusions drawn from this work showed that plant community co-existences can be described using a mechanistically based comparative approach of their physiology. Once my work had been finished, or at least my time was up, we had to choose an external examiner. John and I jointly agreed that we would ask Prof. Terry Mansfield (Lancaster University), as a highly respected all-round plant physiologist, if he could do the job. What I was not aware of at the time was that Terry would become an important character and guiding light in my career development, for which I will always be extremely grateful. I do remember him saying that he would rather avoid coming to North Wales in the winter, so my *viva* was set for spring 1982. All went well, he gave me a shortish list of typos and we said no more about these (Atkinson 1982). For that I was grateful, because in those days theses were typed (thanks to my mum for all her hard work). My recollections of the *viva* focus on the questions and the discussion we had about subjects which were on the periphery of my thesis. I think Terry felt that the thesis showed what

I had done, but he also wanted to explore my thinking behind what was not on paper. I always tell students that the *viva* will not only examine what's in your thesis but also what's not.

SECTION 3: SEE THE WOOD FOR THE TREES

In many ways my love for North Wales and its inhabitants had grown and I desperately wanted to make a life there. I also wanted to carry on with the type of work that I had been doing for my Ph.D. Unfortunately, the political climate of the 1980's was beginning to erode one of the cornerstones of this island's global impact on the UK's science R&D. This decline continues to this day and I fear we will look back in 50 years and regret what we have done and hopefully find a way forward. In 1982 it was all about finding a job and I met with organisations such as the NT and Nature Conservancy Council (now closed), but nobody was engaged in employment. I experienced a short period of unemployment, but then my luck changed as a post-doc in the Department of Forestry in Bangor got a job at Berkeley in California. There was some 2 years left on their research contract and fortune smiled on me and Dr. Pat Denne gave me the vacant position. I knew nothing about trees or their (wood) anatomy, I can only assume that there was very little competition for the post, but did I learn a lot and it was incredibly influential in subsequent jobs, grants applications and my teaching. It also provided me with the time and gave me further impetus to acknowledge that publications are key to a long and happy research career (Atkinson 1984; Denne and Atkinson 1987; Atkinson and Denne 1988).

Pat spent a lot of time passing on her knowledge, which was with respect to UK forestry bodies very unique, nobody seemed to be interested in understanding how trees grew and the implications for this on wood use/quality. I am still amazed about the low level of interests in aspects of tree physiology shown by UK institutes linked to forestry. The NERC grant work involved developing an understanding of the processes which determined xylem (woody tissue produced by secondary thickening) differentiation and growth. Cambial growth within a stem undergoing secondary thickening produces cells which differentiate into xylem, or phloem. It is the processes which determines cell differentiation into different functional types (e.g. vessels, fibres and tracheids etc.) in the woody xylem that determines its structure, physiological functions and use. This was the one of those times which made me aware that science had important implications beyond my fascination of just understanding its workings. We were, and Pat had been doing this throughout her career, trying to understand the processes which determined the fate of cambial initials (first cells differentiating), why did one cambial cell turn into a vessel, while its neighbour differentiated into a parenchyma cell?

The work involved field work, going up ladders into trees to sequentially 'mark' cambial development and then, sometime later, fell these trees to extract and examine, under magnification, the cambial growth in thinly cut sections of woody tissue. It was an art to cut high quality sections of woody tissue once pickled for 6 months, but we had very experienced technical assistants to support the hours spent gazing down our microscopes making measurements of growth and cell type. The work with maturing field grown trees was extremely interesting in that it showed differences in species spring cambial reactivation (Denne and Atkinson 1987; Atkinson and Denne 1988; Denne, Atkinson and Dodd 1994). Convention suggested that spring vessel reactivation, in hardwood trees, takes place in a timed and sequential manner which is linked to the regrowth of the leaf canopy. It is this connection between leaf expansion and cambial vessel differentiation that enable leaves to expand, by

taking up water.

But vessels can only supposedly transport water to the leaf canopy once they have differentiated and gone through cell wall thickening (lignification) which enables them to function (transport water) under negative water potentials and xylem water tension (capillarity). To move water from the roots to the bursting buds in spring suggests that functional xylem is required from the root to the leaf. Our research demonstrated that it was very difficult to show that cambial regeneration was present throughout the tree trunk when spring bud and leaves were rapidly expanding (Denne and Atkinson 1987; Atkinson and Denne 1988; Denne, Atkinson and Dodd 1994).



Figure 9. Anatomical structure of the stained xylem of an ash tree (left). The radial cross-section shows the large early xylem vessels (middle of image) produced in spring (for water transport to the expanding leaves) followed by smaller sized vessels as the annual ring grows during the summer. The 'ray tissue' (rays are transport cells which move sugars laterally in the tree trunk) runs as red bands of cells from the bottom of the image to the top. The production and use of British grown hard woods with their different qualities and uses (right).

If I did not appreciate wood before I met Pat then there is no doubt that it has coloured my life and my work ever since. As many will know I have chunks of wood and sections of xylem tissue throughout my office and my home has more than its fair share of wood products that I have collected or made. As my first post-doctoral position was coming to an end and the likelihood of not getting more money loomed on the horizon I began to face the reality that the possibility of staying in North Wales was ebbing away. Fate again appeared to provide a challenging solution. I received a phone call from the USA from Dr. William (Bill) Winner, who was looking for a research scientist to work in air pollution, he was given my name by Terry Mansfield as a suitable candidate who was looking for a new position. This, when I now look back, was the first time that I was 'head hunted', not that I thought about it in this way at the time.

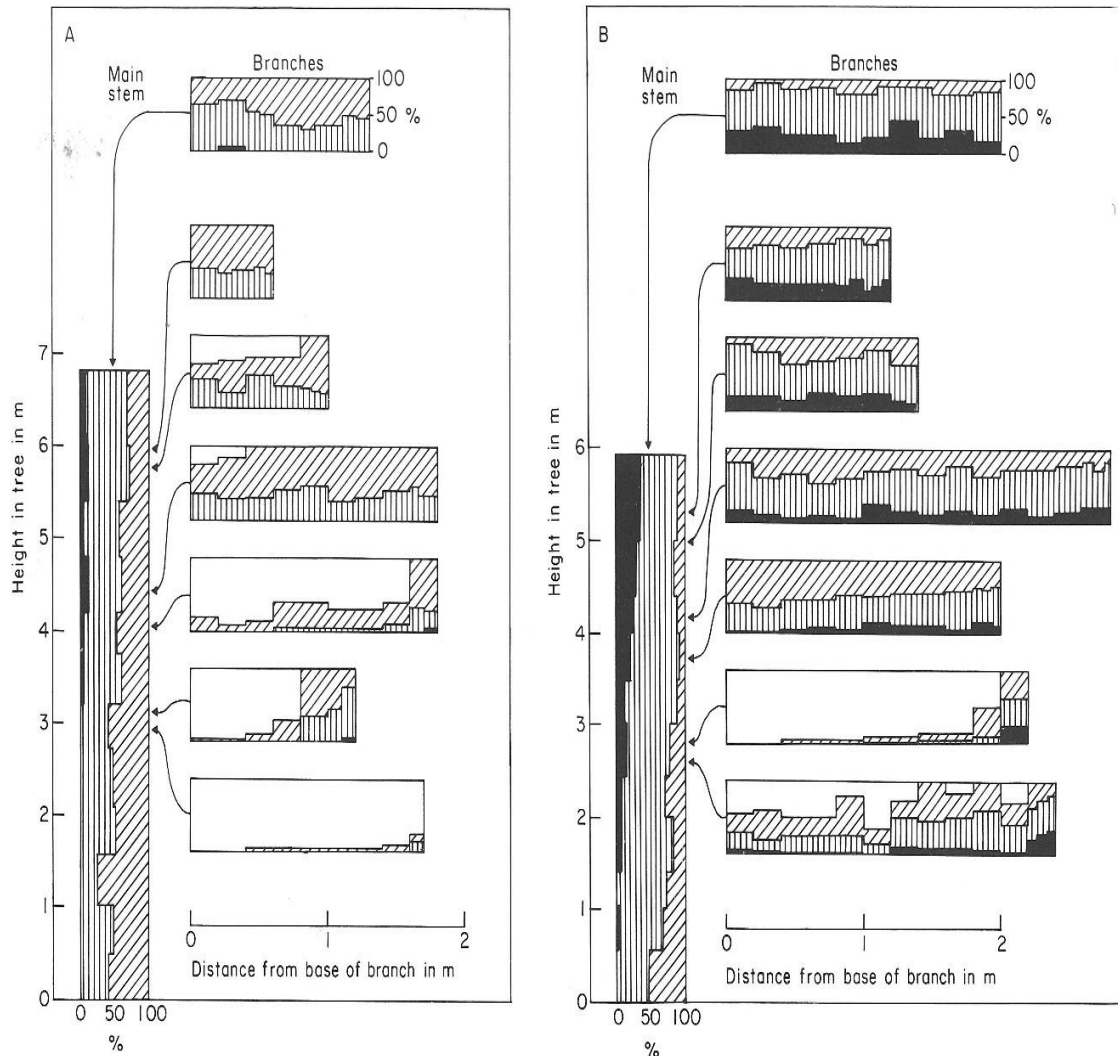


Figure 10. The progression of vessel expansion and maturation in the branches and main stem of two ash trees harvested in early May. The levels of shading in the trunk and branches, which occur at different heights, show the differences in the proportion of lignified functional vessels

Diagram above (Figure 10) shows in part A, trees with retarded bud break and B, shows advanced bud break. Diagonal hatching, is number of expanding vessels as % or potential vessel production in first row of early wood; vertical hatching, number of expanding vessels (lignified but not fully mature) as % of total number in first row of early wood vessels; solid fill, number of fully mature vessels as % of total number in the first row of early wood. These images clearly show that mature functional vessels are not found in the lower main stem until after the beginning of rapid leaf expansion after bud break. This is contrary to previous assumptions about early vessels needing to be functioning before leaf expansion can take place.

SECTION 4: ONCE UPON A TIME IN AMERICA

After a couple of telephone conversations with participants in the USA, I was offered a post-doctoral fellowship and a position as a visiting fellow at Stanford University in California. The

post was particularly attractive in that the position was funded through Stanford, but involved working in Virginia (east coast) and California (west coast). The work also involved working with Prof. Harold Mooney, as I soon learned Hal knew everybody in plant science in the USA and more than half of the top plant biologists were his Ph.D. students and the rest were students of his students; a huge influential legacy. We actually set up home in Virginia and I was also a Research Fellow at Virginia Polytechnic and State University (Virginia Tech). I should come clean and say that we lived in the Blue Ridge Mountains of Virginia. The aim of this work was to build and test a gas exchange system to, for the first time, measure changes in photosynthesis and stomatal conductance, whilst subjecting plants to atmospheric air pollution (Atkinson Winner and Mooney, 1986). California had suffered considerable air pollution in the 60s and 70s due to sulphur dioxide (SO₂) emissions. What was not known at the time was the impact of pollutants such as SO₂ and concentration which were 'chronic' rather than 'acute' with respect to atmospheric dose. The question was directly addressed at what are the impacts on native plant communities particular those of the Chaparral vegetation in California. The Stanford campus was ideally situated close to the foothills of coastal chaparral.



Figure 11. One of several lakes on the Jasper Ridge, Stanford Biological Preserve, near Palo Alto, in California, this one is on the San Andreas Fault (image taken in 1984). I recall being awoken at night by what I thought was a train passing by. It was not until the light of day that I realised that there were no trains in the vicinity and that it was a seismic event due to an earth quake.

I had access to a field site and a house (often as the only occupant) on the Jasper Ridge Biological Preserve, Stanford University. This was the home of bob cats and rattle snakes (only met on two occasions) amongst many others; it was also next to the Stanford linear acceleratory and on the San Andreas Fault. The technical challenges were considerable and fortunately we had the skills of Bill Armstrong an electrical engineer, at Stanford, who designed and built, with my assistance at times, this revolutionary gas exchange system. The aim was for it to be SO₂ proof and field portable. Nobody at this time had gas exchange systems that were able to control and measure and expose plants to ambient concentrations of SO₂, or ozone (O₃). Sulphur dioxide was also a very sticky gas and many materials absorbed it and this made the control of the concentration of the pollutant very difficult. It is also highly corrosive, but I overcame these problems by using only stainless steel parts and had the leaf cuvette, where the measurements of photosynthesis

are made, internally coated with Teflon (Atkinson Winner and Mooney, 1986).

Scientifically our intentions were to focus on two functionally different plant types within the chaparral i.e. *Diplacus aurantiacus* (Sticky Monkey Flower or Orange Bush Monkey) a drought deciduous species and *Heteromeles arbutifolia* (Toyon or Christmas berry) an evergreen drought tolerant perennial shrub. The rather different habits and leaf structures of these two plant species were hypothesised to have potentially important differences linked to pollutant uptake and responses. The field portable system not only enabled pollutant concentrations to be controlled, but also to be delivered at concentrations which were similar to those frequently apparent in the San Francisco Bay region (ambient daily concentrations). To some degree it was 'field portable' albeit it took me half a day to move locations on the Biological Preserve. I worked entirely alone when doing these trips and experiments in the field – issues and risks linked to health and safety were not considered. Clearly things have changed.



Figure 12. The 'portable' leaf gas exchange and pollutant fumigation system I built and tested in operation at the field site on Jasper Ridge within the Stanford University Biological Preserve, California, USA (~image taken in ~1985). A Heteromeles arbutifolia plant is seen with its evergreen leaves on the right with the tripod rig mounting and the leaf cuvette and light source (flood lamp bulb within the Dexion housing). The instrumentation on the left in the electronics controlling the cuvette and the analysers measuring CO₂ and SO₂ concentrations. The mobile generator cannot be seen in this picture.

The novelty and functionality of the system was such that I wrote a paper describing, in some detail, its technical performance (Atkinson, Winner and Mooney 1986). The commutes from lab and glasshouse work in Virginia to California proved very rewarding with respect to publications (Atkinson and Winner 1987; Atkinson Winner and Mooney 1988).

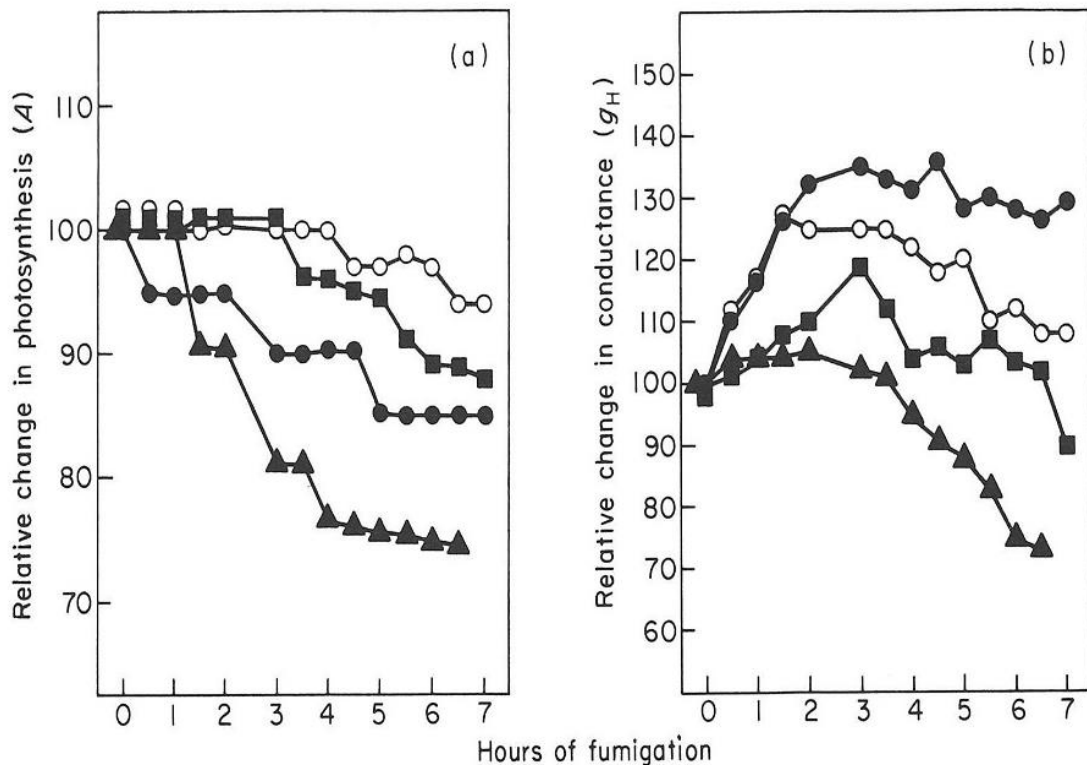


Figure 13. The change in photosynthesis (a) and stomatal conductance to water vapour (b) of a *Heteromeles arbutifolia* leaf expressed relative to the pre-exposure rate and exposed repeatedly to $25 \mu\text{mol SO}_2 \text{ m}^{-3}$ for 7 h on 3 successive days (control day 1 no SO_2 (closed circle), fumigated on day 2 (closed triangle), day 3 (closed square) and day 4 (open circle)).

These publications not only showed the impact of SO_2 on reducing leaf gas exchange of plants growing in their natural environment, via reductions in stomatal conductance, but also the fact that low levels of pollutant concentrations, that were not initially considered particularly harmful, could have chronic effects on photosynthesis and the potential to reduce plant growth (Winner, Atkinson and Mooney 1987).

When not occupied with technical development and field experiments in California, time at Virginia Tech at the Air Pollution Laboratory, provided the opportunity to continue work with SO_2 as well as develop new work linked to the 'up and coming' pollutant of the 80s ozone (O_3). This also included theoretical work on pollutant effects on other related plant types where we knew about their uptake characteristics based on published leaf gas exchange parameters (Winner and Atkinson 1987; Winner, Atkinson and Nash 1988), along with the recognition of our work with review invitations (Winner and Atkinson 1986).

The experimental research in Virginia produced two very novel pieces of work, firstly using the field portable gas exchange system, back in the lab, along with the facilities at Virginia Tech's air pollution lab we were able to demonstrate the differences and severity of exposure to both SO_2 and O_3 at concentrations which were not previously considered detrimental to plant growth and development (Atkinson, Robe and Winner 1988; Atkinson and Winner 1989). That was clearly

not the case with even these low concentrations of pollutants, particularly O_3 had consistently measurable effects on reducing photosynthesis and the accumulation of plant dry matter. We were also thinking more about environmental stress interactions and considering the effects of pollutants are strongly influenced by events such as drought (Atkinson and Winner 1990).

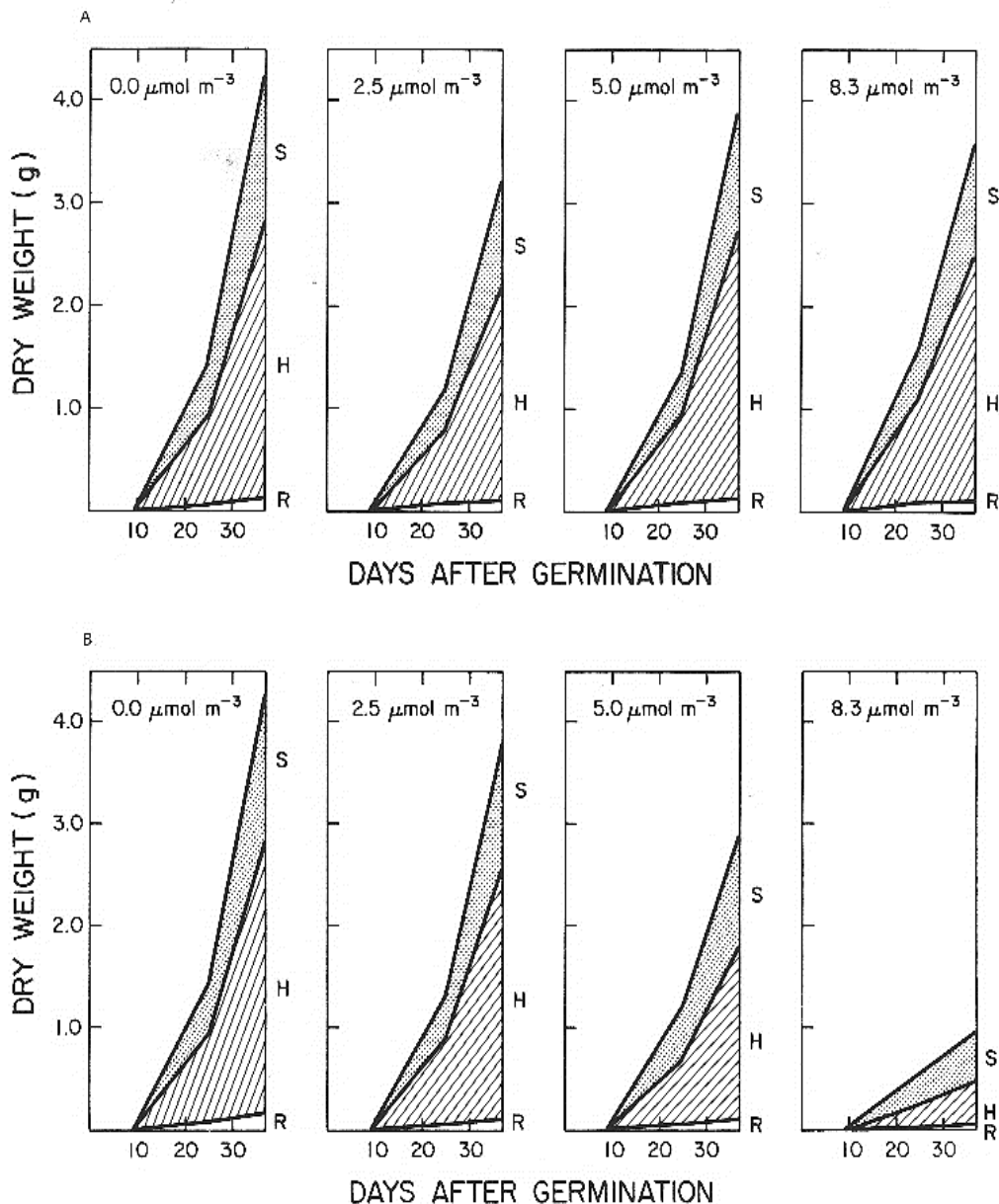


Figure 14. The allocation of dry matter to stems (S), hypocotyl (H) and roots (R) of radish when subject to low concentrations ($\mu\text{mol m}^{-3}$) of the pollutants SO_2 (A) and O_3 (B).

The measured changes in photosynthesis are expressed through a reduction in carbon accumulation (total dry weight) and were much greater for O_3 compared to the same concentrations of SO_2 . The impacts of O_3 on biomass were particularly apparent for hypocotyl (the swollen stem which is consumed) dry matter accumulation, where it was significantly reduced by the presence of O_3 .

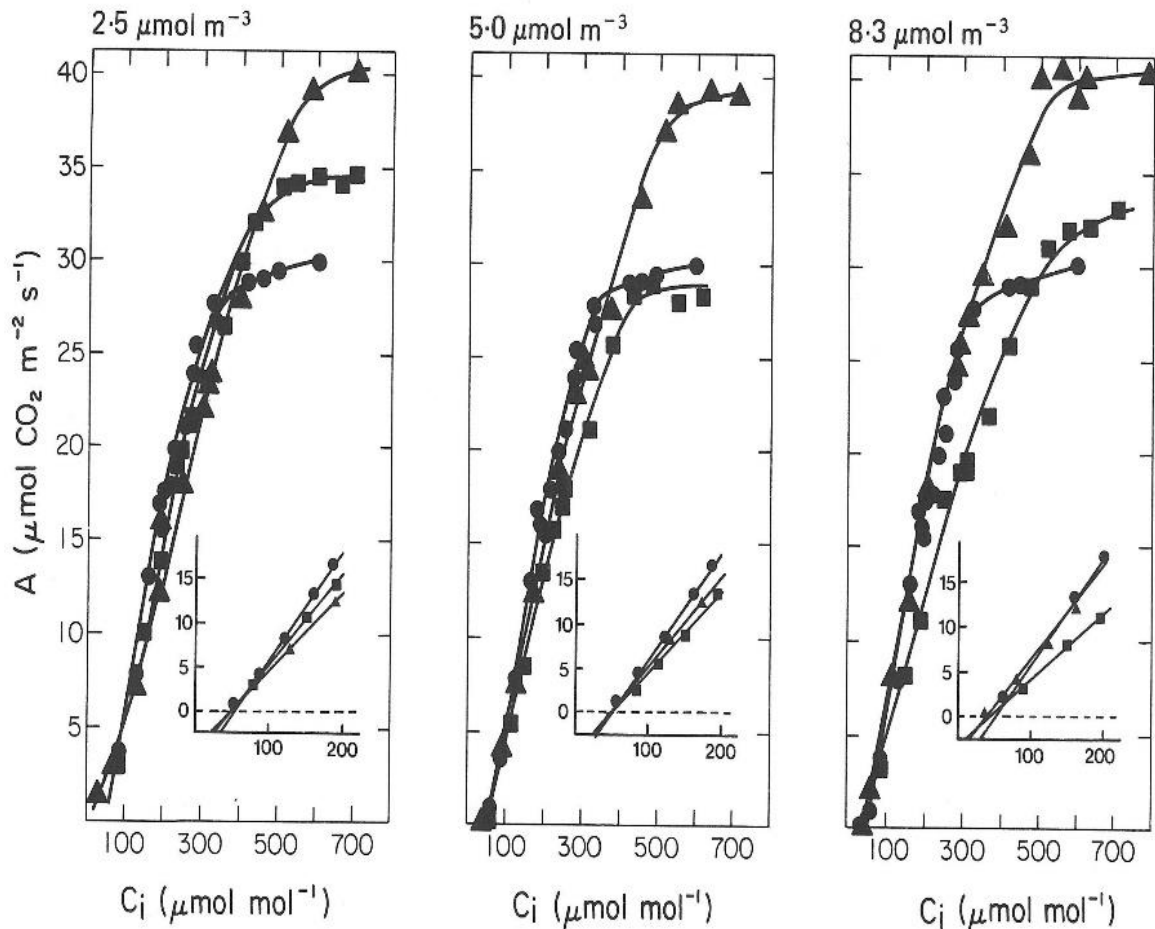


Figure 15. Carbon dioxide, C_i (A/c_i - curve) response curves showing the effects of low concentrations of pollutants on the photosynthesis (A , $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) of radish with respect to carboxylation efficiency (dA/dc_i - the initial slope A/c_i curve) and maximal photosynthesis (J_{max} - the curve asymptote).

Data from experiments with radish, such as that shown above, were able to describe and determine the mechanisms by which low concentrations of pollutant reduced photosynthesis and could reduce plant growth and biomass.

At this time, I was also involved in experiments going on at a field location ('the Horton's' named after our wealthy benefactor) up in the Blue Ridge Mountains of Virginia. This involved, what were then highly fashionable, open top plastic walled chambers which enable plants (even some crops) to grow in local soil, generally in their native atmospheric environments, but the chambers were flushed with charcoal scrubbed (clean air), or polluted air at controlled concentration. Those who were running these experiments on a daily basis were unable to correlate pollutant dose calculations, based on stomatal conductance, with crop response. At the time there was little evidence to contradict the notion that during the dark period leaf stomatal conductance was generally very low for most plant species (there are some exceptions, i.e. CAM plants) and implies that stomata are mostly closed at night and therefore do not take up pollutants at night. The situation was not clear here, however, and as a plant physiologist, I suggested that this notion should actually be tested. It was also becoming apparent that plant responses to O_3 may

differ with respect to topography. Evidence from our pollutant monitoring, at the Air Pollution Laboratory in Blacksburg, showed much lower O₃ concentrations at night compared to those higher up in the mountains at the field site. Apparently, O₃ concentrations are higher at night at elevation because the O₃ migrates upwards. The importance of this point combined with my measurements of stomatal conductance (in the dark) of turnip plants (*Brassica rapa* cv. 'Shogun'), which showed limited stomatal closure at night, enable this work to be published in PNAS (Winner *et al.* 1989).

This was the first and perhaps only time in my career, when the politics of authorship on a publication were very sensitive. I don't know for sure but around this time things in Virginia Tech were become overly political with respect to the management of the Air Pollution Laboratory and we felt that we had to consider either moving on, with respect to seeking a tenure track position in the United States, or a return home. Employment even in the middle of the 80s was still not good and research institutes were still closing (and still the decline continues). However, once again Terry Mansfield, along with Bill Davies at Lancaster University, offered me a job in their laboratory. This would be my third post-doctoral position. There was some consolation here in that post-doctoral positions, particularly overseas were considered somewhat obligatory to career development, but on the downside my age came with a more expensive salary price tag.

SECTION 5: THE FORT ON THE LUNE

If you have not already surmised from the preamble you will now be aware that there are mountains involved with this new location, but the research was very different. Terry and Bill had a contract to explore a historical collection of stomatal 'modifying chemicals' synthesised by Shell UK, Sittingbourne. Shell, back in the mid-80s, had an interest in altering stomatal conductance to influence crop water use. Over a number of years they had been developing and screening chemicals, particularly analogues of abscisic acid [ABA] (a well-known endogenous plant chemical regulator of stomatal opening), for their ability to induce prolonged stomatal closure. In order to undertake this work I needed an appreciation of stomatal physiology and the skills required to undertake stomatal epidermal peel bioassays using *Commelina communis* (Atkinson *et al.* 1989; Mansfield and Atkinson 1989; Atkinson 1991a). Stomatal epidermal bioassay using *Commelina* were, at the time, synonymous with Lancaster and Terry Mansfield.

During my time at Lancaster, not only did I get great support from Terry and Bill, but I had the great pleasure in seeing Terry granted his FRS for pioneering work on stomatal physiology. So after mastering the skills required to grow these plants of *Commelina* from which one could then peel the epidermis (upper adaxial and lower abaxial) from their leaves, I had the tools needed to conduct what I suppose would have been the screening of Shell's chemical ABA analogues. Things, however, did not quite turnout that way, my understanding at the time was that Shell's interests in 'agricultural chemicals' was waning or at least taking another direction. So the idea of looking for an analog of ABA to modify stomatal behaviour was no longer an economic interest of the multi-national company; this was perhaps the beginning of the end of Shell's Research Centre Sittingbourne, in Kent, and its scaling down and closure some years later.

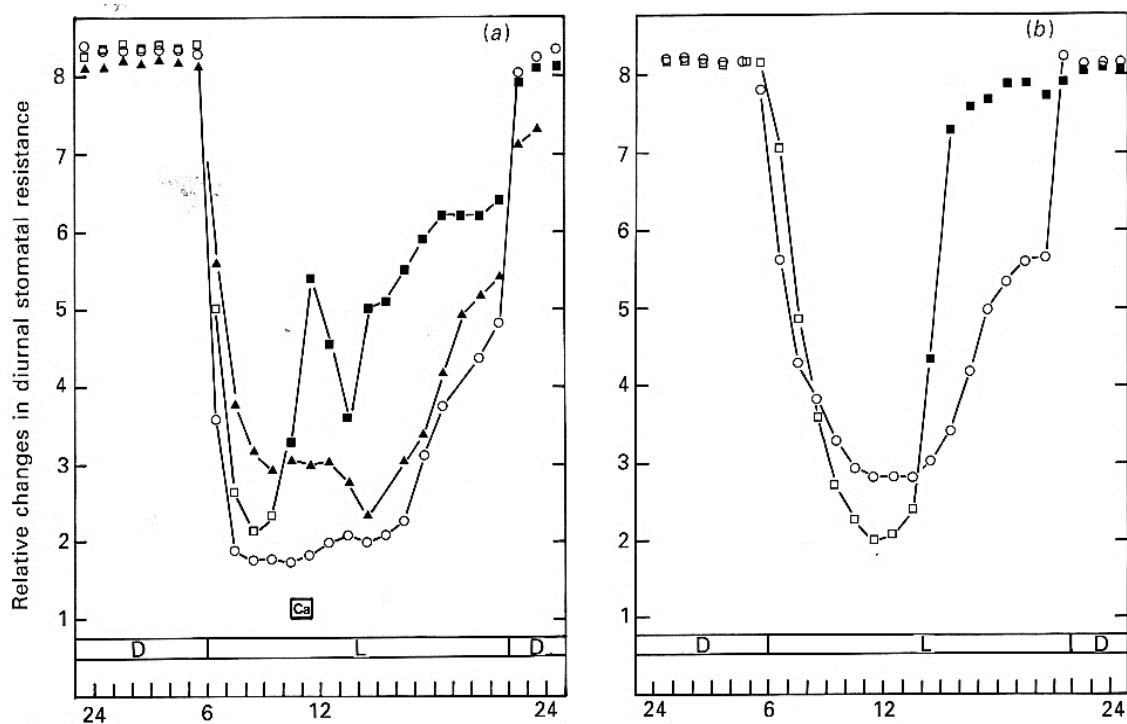


Figure 16. Typical relative change in diurnal stomatal resistance, measured by viscous flow porometry, for *Commelina communis* (a) and *Triticum aestivum* (b) plants. Leaves were fed with $8 \text{ mol m}^{-3} \text{ Ca} (\text{NO}_3)_2$ via a catheter mounted in the mid-rib vein (an approach I developed to feed substances into the transpiration stream of plant and leaves (filled squares). Resistance (the opposite of conductance) is highest when stomata are closed at night.

I am not sure what I would have made of screening a large number of initially obscure chemicals synthesised by Shell over a number of decades. However, fate stepped in and the Shell project manager, Dr. Paul Snaith (former Lancaster student – Ph.D.), ensured us that the project finance would continue as outlined originally, but they (Shell) would be relaxed about what direction the work took. This was now, when I looked back, one of my great opportunities and a moment to make my mark. Clearly, I needed to do something in the area of stomatal physiology and I was particularly interested in a piece of Ph.D. work done by Lionel DeSilva at Lancaster that indicated stomatal function could be modified by calcium (Atkinson, Mansfield and Davies 1990; Atkinson 1991a).

We knew in general that plants have a problem moving calcium around in living cells because if calcium comes into contact with phosphorus (all living cells contain phosphorus) it will form calcium phosphates and that is not good – cells die as these calcium phosphates precipitate out in the cytoplasm of the cell. So I asked myself how do plants cope with needing calcium as a nutrient, but are unable to move it around easily and given that if its leaves are exposed to calcium in their xylem, stomatal closure can occur. I was also asking myself questions about calcium regulation, in the plant water transport system (xylem), an important factor controlling growth (Atkinson 1991a; Ruiz, Atkinson and Mansfield 1993).

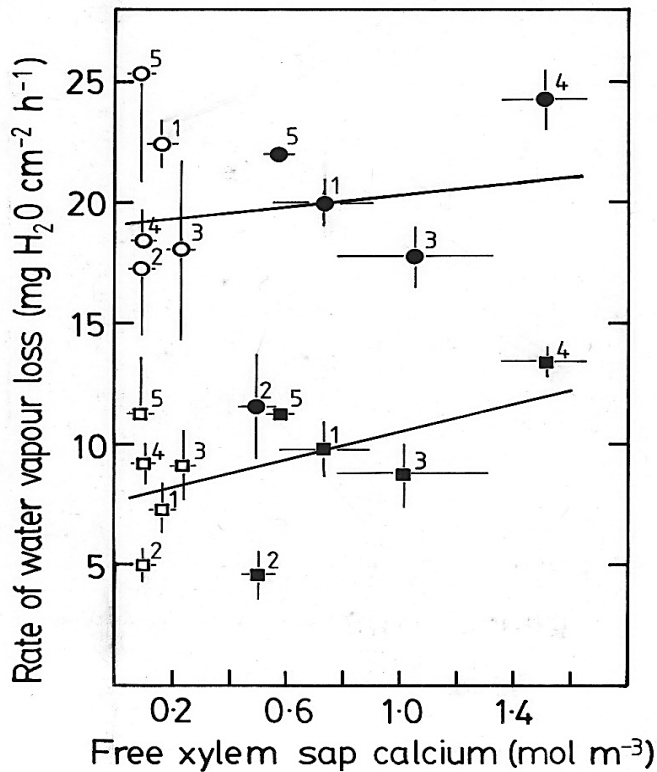


Figure 17. The transpiration rates for detached leaves from lupin are plotted against their respective shoots xylem calcium concentrations. Rates are shown for the distilled water controls (round circles) and the ABA treated leaves (squares) from *Lupinus luteus* plants after 6 h of incubation. Plants were grown on nutrient solution containing 1 mol m⁻³ (open circle and squares) or 8 mol m⁻³ (closed circle and squares) calcium nitrate.

This assay shows a clear response for ABA reducing leaf water loss (transpiration) irrespective of the plants calcium concentration during growth. This indicates that there were no differences in stomatal sensitivity to ABA and no effect of free calcium in the xylem on the ABA response (Atkinson, Ruiz and Mansfield 1992).

A natural extension of this notion was to look for evidence for the regulation of calcium in the transpiration stream (xylem sap) as a determinant of where plants might grow, with respect to the availability of calcium in the soil. Plants are known in ecological and horticultural spheres as 'alkaline liking' (calcicoles) or 'alkaline disliking' (calcifuges). The idea of alkalinity is generally closely linked with the presence of calcium in the soil, or the soil solution. So to me it seemed possible that plants with a distinctive presence, or absence from environments which contained, or do not contain calcium might be due to their ability to regulate calcium uptake into the transpiration stream (xylem sap). The hypothesis was that calcifuges were unable to survive in high calcium environments because of limitations in keeping calcium levels in their xylem sap low enough to avoid stomatal closure. The impacts of prolonged stomatal closure are reduced transpiration and water use, but ultimately limited photosynthesis and therefore reduced growth potential (Atkinson 1991a, b; Atkinson, Ruiz and Mansfield 1992). Undertaking the preliminary development of this idea occupied the next couple of years at Lancaster.

Given that I was a bit older than all of the other post-docs and Ph.D. students in lab, I somehow assumed the unofficial role of the laboratory manager. I was also very much involved in ensuring that the body of post-doctoral workers, at Lancaster, had a voice and were in close communication with those with responsibilities for running the Department of Biological Sciences. This task was shared by my colleague and friend Nigel Paul (now a Lancaster Professor).



Figure 18. A scanning electron microscope (SEM) image of the epidermal tissue of a micro-propagated leaf showing the large number of open stomatal pores and trichomes hairs of the leaf.

This figure shows a high number of large stomata which appear open and would therefore be losing a lot of water via transpiration. Images such as this one led us to start to investigate the reasons why micro-propagated plants had significantly reduced survival rates during the 'weaning' process once removed from the high humidity propagation environment. Many of these stomata appeared not to have the capacity to close and reduce leaf transpiration rate.

As with my life in Bangor, it was not all work, despite what some might say. I joined the Lancaster Fell Walkers; who every Sunday transported us to the Lake District and its environs to enjoy magnificent mountain walks. The club had three levels of walks each weekend and members took it in turn to plan and guide a walk within their group. The group structure was based on endurance (even those that were generally older and often retired members from the C group, they did a 12 to 15 mile hike with at least one climb) and being reasonably fit my endeavours were with the A-team. These born and bred fell walkers also educated me in not only mountain craft, but also in showing me those off the beaten track and places in the Lake District; we never used 'tourist routes' if they could be avoided. I would come back to my wife and young family (after having my away day) late on a Sunday afternoon shattered after trying to keep up with Lancastrian fell walkers, come cyclists, at least 10 years my senior. I still appreciate what a hot bath can do post walking to those tired legs – thanks Lin.

As can be the case when working at institutes which are led by great scientists, which openly engage with everybody, it's not only a wonderful environment for your own work to evolve in, but also to get involved with others and their work. It also provided the opportunity to write with individuals with considerably more experience in the matter of publishing; this was a huge benefit. From collaboration came a raft of publications some of which are still cited (Mansfield, Hetherington and Atkinson, 1990; Mansfield and Atkinson, 1990a, b). It was around this time that the Lancaster laboratory was in what I would call its 'golden-age' in developing an understanding of how plants respond to environmental stress, particularly with respect to the ideas of Bill Davies on soil drying (drought) (Atkinson, Davies and Mansfield, 1989). The lab members in the form of J. Zhang, David Gowing and Gail Taylor (all Ph.D. students) and myself were part of this productive and supportive culture of Terry Mansfield and Bill Davies.

It is perhaps not surprising that my work expanded into crop plants, such as barley and sunflower

looking at their responses to soil drying and ABA (Atkinson Mansfield and Davies 1989; Atkinson and Wookey, 1991; Wookey *et al.* 1991). We also had the opportunity to develop work with industry partners and one fascinating piece work was directed at understanding why micro-propagated plants, when transferred to conventional plant growing systems, failed to survive (Habour *et al.* 1989; Santamaria, Davies and Atkinson 1993). The surprise of this work was not just that the results showed these plants had anatomically adapted (or were conditioned by their responses to the atmospheric environment in micro-propagation, i.e. 100% humidity), but their function with respect to stomatal responses to ABA had changed. Since the work has been published it continues to be cited. The work showed that in the absence of sensitivity to ABA and with a high proportion of stomatal being anatomically abnormal and some which clearly did not function (could not close despite our experimental encouragement) when transferred from micro-propagation (via the process of 'weaning'). Exposure to ABA, or to lower humidity, during micro-propagation did reduce the anatomical changes described at tissue 'vitrification' (Habour *et al.* 1989; Santamaria, Davies and Atkinson 1993).

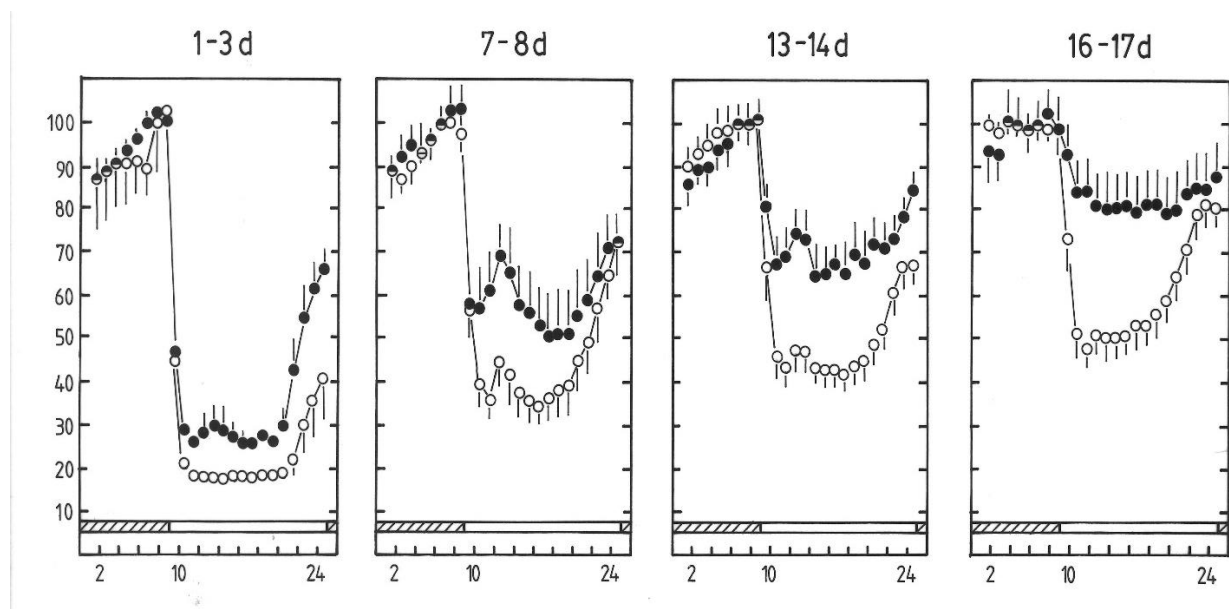


Figure 19. Diurnal changes in stomatal resistance determined by viscous flow porometry for leaves of *Helianthus annuus L. cv. Frankasol*. For well-watered (open circles) and plants with restricted water supply (closed circles).

While at Lancaster, I mastered and built several viscous flow porometers to measure and record long-term changes in stomata resistance of leaves. This original image shows the changes in the leaf resistance of sunflower plants over an experimental period of 17 days with the control treatment well-watered plants (open circles) and those with a restricted water supply (closed circles) (Wookey, Atkinson, Mansfield and Wilkinson, 1991). Changes due to leaf age and drought are clearly apparent.

Albeit I did not work at Lancaster's state-of-the-art air pollution facilities, given my background, it will be no surprise that I found the time to contribute to their programme of activity looking once more at such things as combined stress response (Atkinson, Wookey and Mansfield, 1991; Mansfield *et al.* 1993). In various ways, and with different plant systems, ideas were developed and were being subject to experimental validation to provide a mechanistic understanding of the manner in which plants communicate what is going on in the soil (e.g. drying soil - drought,

changes in ABA or calcium concentration) (Davies, Zhang and Atkinson 1990; Atkinson *et al.* 1990).

As the stomatal work funded by Shell drew to a close, I started to work very closely with Terry Mansfield in preparing a grant application for the NERC to explore my initial interests in addressing questions about the role of xylem sap calcium in controlling growth and development of calcifuges and calcicoles (Atkinson 1991b). Particularly, with respect to questions about, is the regulation of calcium uptake into the root and xylem a determinant of tolerance to soil calcium concentration. This was my first significant experience of grant writing for myself and supporting my own ideas and ultimately my salary. The grant was written primarily by me and for me and I was extremely delighted to win it.

The basic aim of the work was to explore of impacts of differences in root available calcium on the regulation of stomatal behaviour for species which apparently liked, or disliked alkaline high calcium soil environments. To test this hypothesis, I looked at a range of species which were suggested to have different tolerances to soil calcium (Atkinson, Ruiz and Mansfield 1992). These plants were grown in the same environment and rooting medium. When measuring the xylem sap calcium there was considerable interspecific and diurnal variation despite the same growing media. The shoot potential to sequester xylem sap calcium also varied between species and implied that some species regulated the calcium reaching the shoot in the transpiration stream. The long distance transport of calcium did not appear to be solely due to mass flow in the transpiration stream as neither calcium uptake or distribution were linked closely with transpiration (Atkinson, Ruiz and Mansfield 1992). My interest in this work was reinvigorated recently as others asked questions about an explanation for stomatal closure observed after agricultural liming (application of calcium carbonate to correct for soil acidification). This provided me with an opportunity to revisit the developments in this research area and write an invited commentary (Atkinson 2013).

As fate would have it I was not to be a permanent post-doc, and as there were plenty of senior very high quality post-docs in Lancaster who were in what was considered a queue for possible faculty positions, it made sense to consider all opportunities wherever they arose. The ties both with respect to my growing family and our love of Lancaster, and The Lakes, were going to be a hard act to follow. Leaving Lancaster, albeit for a 'permanent job', was one the hardest decisions we (I) have made and I have always missed Lakeland, for me it will always be a very special place with very special people. The timing of our move meant that there was still money left in the grant and the work that I had started was finished through the efforts of an individual whose work had been a source of my initial questioning as he had now returned to Lancaster for a short period (DeSilva *et al.* 1994). I did however take a very strong desire with me, as we moved south, to bring my skills and interests in the processes which linked events belowground with those above in order to bear fruit in the world of horticulture.

SECTION 6: EAST MALLING RESEARCH STATION (EMRS/EMR)

The opportunity for employment security has and will remain an important element within the minds of post docs. This was an opportunity that could not be missed despite some reservations, not just my own, about the durability of horticultural research institutes within the UK. Doubts about the viability of UK research institutes was clearly a real issue, but fortune was to favour a

very productive period of research before the needs of institutional survival came to the forefront.



Figure 20. The East Malling Research/East Malling Trust estate from the south, showing the Network Southeast Railway line in the foreground. The total estate is some 500 ha (240 acres). The laboratory buildings and offices are to the center right with the glasshouse facilities situated to the left of center. The EMWC can be seen on the edge of the glasshouse complex at the top left. Within the surrounded grounds the impression of various field experiments can be seen.

On arrival it became quickly apparent that my predecessor Dr. John Palmer had been gone for nearly a year and there was a contractual gap in research output relative to income. Fortunately, some relevant work had been carried out that had neither been reported, nor published. I was asked to evaluate this work and prepare it for publication. My background knowledge in the area was somewhat limited, but the challenge of a steep learning curve, which was becoming a necessary trade-mark, could not have been achieved without technical input and support from Lorraine Taylor, Drs. Tony Webster and Jim Quinlan to name but a few.

The work on factors which control fruit [*Malus* (apple)] productivity was successfully published (Robbie and Atkinson 1992; Robbie, Atkinson Knight and Moore 1993). These papers showed that fruit tree productivity was very closely linked to the age of the branch on which fruit were borne. This was perhaps something that was not particularly novel with respect to grower's knowledge, but at the time it had not been published, but the second paper was more innovative in that it examined why fruit set was greater when branches were orientated away from the vertical to the horizontal. It was well known that the natural habit of *Malus* was of an upright branch orientation (apically dominant) and it was common management practice to train branches to a more horizontal orientation through weighing or tying down. What this piece of research showed, for the first time, was that the influence of branch orientation on 'fruit set' was a more dynamic response than previously acknowledged. The opportunity to orientate branches to the horizontal and increase fruit set and yield could be done much later than previously known and after the start of regrowth in the spring. The science behind these observations suggested that the flux of the hormone auxin (IAA), derived from branch apical buds, which controls apical dominance, was reduced on branch orientation to the horizontal and that this reduction in auxin flux down the branch could still influence the fate of buds by allowing

the switch from vegetative to reproductive to occur late in the cycle of floral development.

Climate change and fruit growth and development

My first independent opportunity to write and manage a research programme (employing others) came on the back of this work on crop productivity and this was to determine the impacts of climate change on fruit growth, development and productivity (see recent review by Else and Atkinson 2010). This programme of work was funded by the Department of Environment, Food and Rural Affairs (DEFRA) with the intention of determining the impacts of rising temperatures and reduced precipitation - climate change. My intentions were to conduct field experiments (in an established apple orchard) to determine the impacts of a small, but predicted climatic increase in ambient mean air temperatures. This was where my field research on apple (*Malus*) developmental functional crop biology started.



Figure 21. The construction of one of the polytunnels erected over an existing cropping orchard of Cox's Orange Pippin used to determine the effects of a temperature increase and reduced precipitation on fruit growth and development. The central double row of trees was used for measurements of fruit growth. The original rows of trees to the left and right of the experimental row have been removed to enable the polytunnel to be constructed.

It was here through the tremendous help of Lorraine Taylor and Ann Lucas that I developed my knowledge (practical and theoretical) of fruit growth and development. The approach adopted involved the settling up of partial tree covering using conventional polythene tunnels, with some trees being covered for the growing season from spring (post-pollination) onwards. The polythene covers did not extend all the way to the ground but acted like umbrellas over the trees. The intention was that the atmospheric environment would be changed to a minimum. It was hoped that changes in relative humidity and excessive unrealistic, mean air temperature would not be incurred. Uncovered trees were used to act as controls. The design of the irrigation (trickle irrigation applied 3 times a day) experiment was conducted as a direct comparison of uncovered irrigated and unirrigated trees, with the addition of some covered trees being irrigated to compare with covered non-irrigated trees. To undertake these comparisons, a number of similar trees (6 trees) were selected and flowers/fruitlets tagged (360 per treatment) and numbered within each polytunnel.

Background literature reviewing had shown that the critical phase (when fruit cell number was determined) in fruit development occurred early in the season during the period of cell division. The expectations were that temperature elevation would influence the rate, or duration of the cell division phase and that irrigation would impact on the later fruit cell expansion phase closer to maturity/harvest (Atkinson, Taylor and Taylor 1995). A large number of individual fruit were monitored throughout the growing season with the hope that from some a complete description of growth would be obtained.

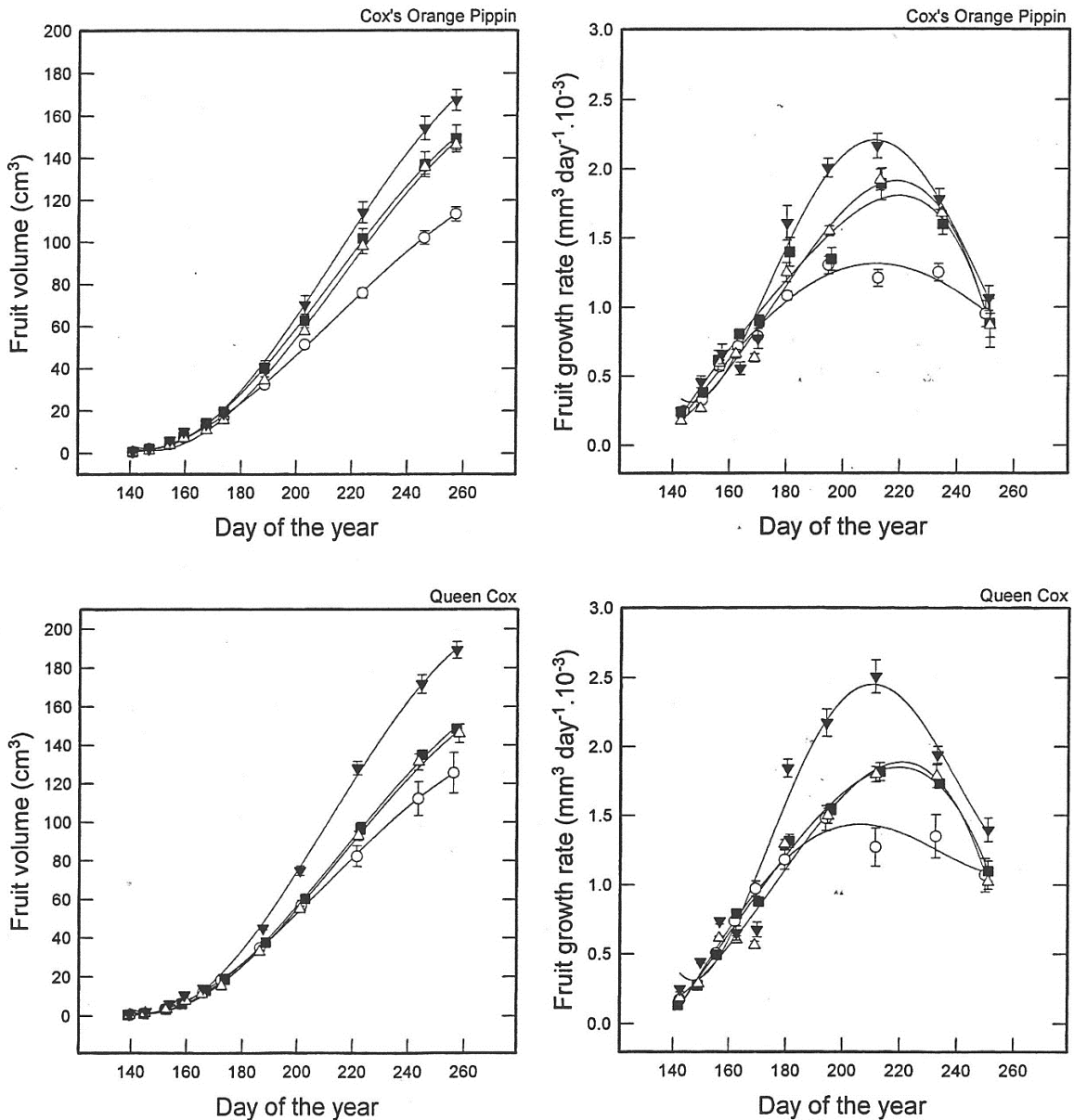


Figure 22. The calculated change in fruit volume (cm³) (left) and absolute fruit growth rate (mm³ d⁻¹ 10⁻³) (right) over the growing season, using a day of the year calendar, for fruit of either 'Cox's Orange Pippin' or 'Queen Cox' on orchard grown trees, in a polytunnel [PT - inverted closed triangle]; a partial polytunnel covering [HP open triangle]; outside with irrigation [OI closed square], and outside in the orchard without irrigation [OU open circle].

The results of this work clearly demonstrated the impacts of elevated temperatures shortening the growing season and the implications for reduced soil water limiting fruit size. Irrigation even in the absence of elevated temperatures and containment within the polytunnel improved fruit size (Atkinson, Taylor, Taylor and Lucas 1998; Atkinson, Taylor and Kingswell, 2001).

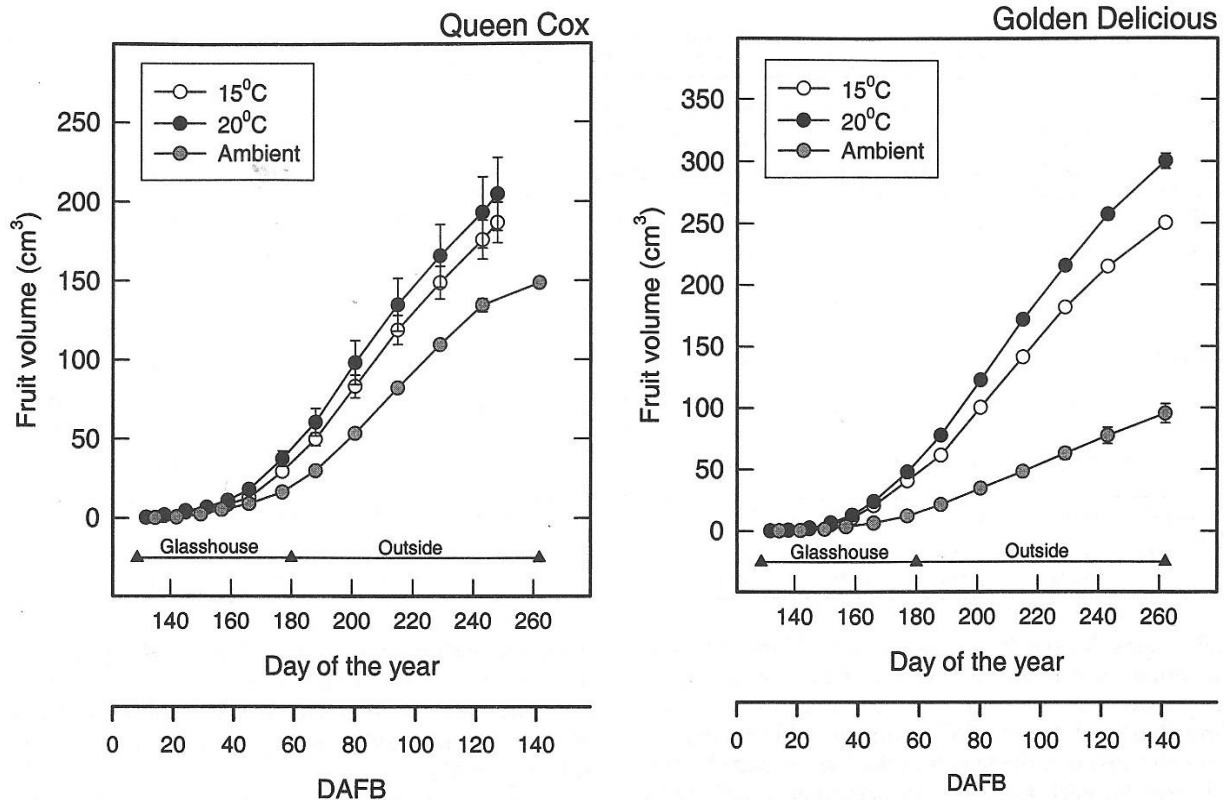


Figure 23. Volumetric fruit growth of 'Queen Cox' and 'Golden Delicious' fruits determined non-destructively throughout the growing season for fruit initially growing at 15°C or 20°C for an eight-week period after flowering. The bars show the time period in the different temperatures as day of the year and days after full bloom (DAFB).

These experiments showed that at the higher temperature 'Golden Delicious' fruit growth was greater than at the initially lower temperature. However these trees set less fruit at the higher temperature, but measurements of fruit anatomy showed that the increase in fruit size at 20°C was not due to temperature increasing cortical cell division. The larger fruit at 20°C were due to the increased size of cortical cells within the fruit.

Climatic winter warming

My interest in climate change was developed further with an idea generated by discussions with Dr. Jim Quinlan (my HoD). There was evidence that climate warming, during the dormant season, might have an impact on flowering time of *Pyrus communis* (pear). The hypothesis being that perennial crops such as apple, pear and cherry require a certain amount of chilling temperature (time above 0°C and around 2-7°C, varying with species) accumulation during the dormant season to complete their synchronised flowering (phenology). Anecdotal evidence suggested that *Pyrus*, because it flowers relatively earlier than that of other perennial crops, was vulnerable to winter warming which caused flowering time disruption. It was at this time it became

apparent that the southern UK was subject to winters that were warmer than the mean 50 year average calculated from East Malling meteorological data.

In the absence of sufficient time at these chilling temperatures flower bud development was being influenced sufficiently to alter flowering date and flower number (and perhaps flower quality - ability to set and retain fruit) and therefore crop productivity. Some earlier studies had used multiple linear regressions of crop yield against climatic variables to show that the cropping potential of *Pyrus* was closely correlated with temperature and in particular with temperatures the year before the year of production, i.e. temperatures during the winter, or dormant season (Browning and Miller 1992).

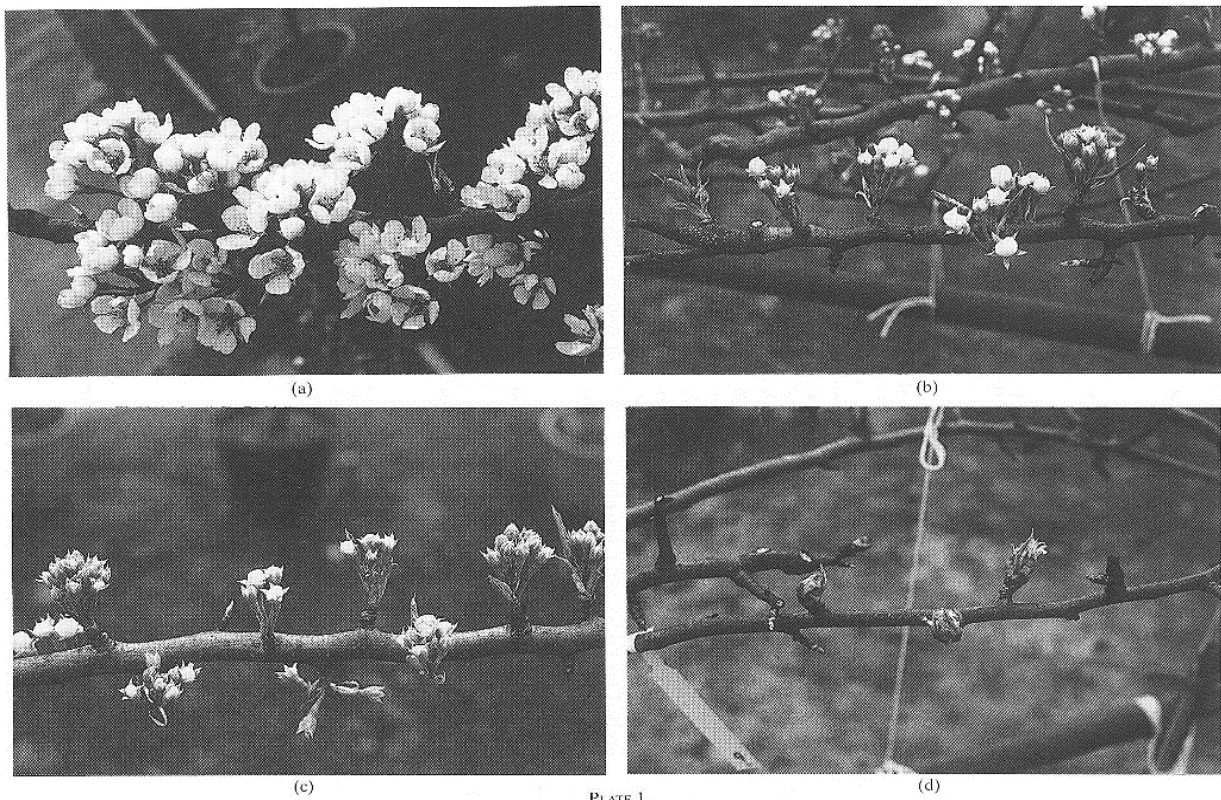


Figure 24. The phenological development of potted Conference pear flowers on Quince C rootstock recorded on 4th April 1993. Control trees at 'full bloom' (a, top left); trees warmed in October in mobile greenhouse at night at 'white bud' (b, top right); trees warmed in November during the day and at night in mobile greenhouse at 'green cluster'(c, bottom left); trees warmed in November, in mobile greenhouse, during the night at 'bud burst (d, bottom right)'.

Potted trees were kept at slightly elevated temperatures during October and November, in mobile heated greenhouses, which were manually moved to cover the trees during the hours of darkness. Some trees were not subject to warming at night in either October, or November, but remained at ambient temperatures. Throughout these experiments temperatures were measured within and outside the mobile greenhouses. When observations were made of flowering phenology the following year in spring there were very distinctive differences in *Pyrus* flowering dates (Atkinson and Taylor 1994). The impacts of warming in either October or November induced a considerable delay in flowering and the later the warming the later the

flowering. These experiments involved the cultivar 'Conference', so in order to determine this was a *Pyrus* response to winter warming a second set of experiments very similar, in nature, to these was undertaken with the cultivar 'Concorde'; a later flowerer than 'Conference'. The result with this cultivar were very similar to those obtained with the cultivar 'Conference' also showing delayed flowering when temperatures were elevated in the autumn (Atkinson and Lucas 1996; Atkinson, Lucas and Taylor 1997). The implications of this work were important in that they showed that not only would autumnal warming influence flowering phenology (delayed due to increased bud dormancy) the following year, but this could influence crop productivity if pollination synchronisation (*Pyrus* requires cross pollination between two compatible *Pyrus* cultivars) were to be reduced. The data also provided a mechanism by which the original statistical analysis of Browning and Miller (1992) could explain the effects of climate change on pear crop productivity (Atkinson, Lucas and Taylor 1997).

This work and the importance of the East Malling data set on flowering phenology, which went back to 1913, along with metrological data and a more recent collection of trees used to measure flowering dates on, was championed by me every year when decisions were made about what experimental plantings needed to be kept or lost. This turned out to be a good decision when we won an open competition from DEFRA to determine the impact and potential implications for climatic winter warming on perennial crops. Growers of hops and blackcurrants were particularly concerned about warm winters reducing chill accumulation and crop productivity. The results of this desk study using several long-term data sets, including those of East Malling Research, showed how important such data are with respect to statistically being able to determine climatic impacts given the natural variation in climate, year-on-year. The analysis showed that winters have been getting warming in the UK particularly in the south relative to the north and it was predicted that the amount of winter chill would continue to decline in response to likely GHG emissions predictions as we progress towards 2080 (Sunley, Jones, Atkinson and Brennan 2006). This led to work to review this research area (Atkinson, Brennan and Jones 2013). Despite expected climatic variation and extreme weather events and interest in climate change, the full impact of warmer winter has yet to be addressed effectively (Else and Atkinson 2010).

Elevated carbon dioxide impacts on growth and development

My interests in climate change were further encouraged by being part of a successful European Union research bid to work with a great group of scientists across the EU looking at the impacts of elevated carbon dioxide (CO₂) concentrations on woody plants. Our part of the programme was to experiment with the effects of elevated CO₂ on the growth and development of oak (*Quercus robur* L. – pedunculated or English oak) and cherry (*Prunus avium* L. x *P. pseudocerasus* – cherry) trees. Working on EU funded science projects was always very enjoyable as you not only worked with the best scientists in Europe, but you also went on long weekend meetings and presented your work annually. This work programme took me to Nancy in France, Budapest in Hungary, Garmisch-Partenkirchen in Germany and Florence in Italy. Not a bad list of places to see and with a free Sunday (cheap flight deals meant that you could not fly back on the Saturday evening) after the two-day working meeting.

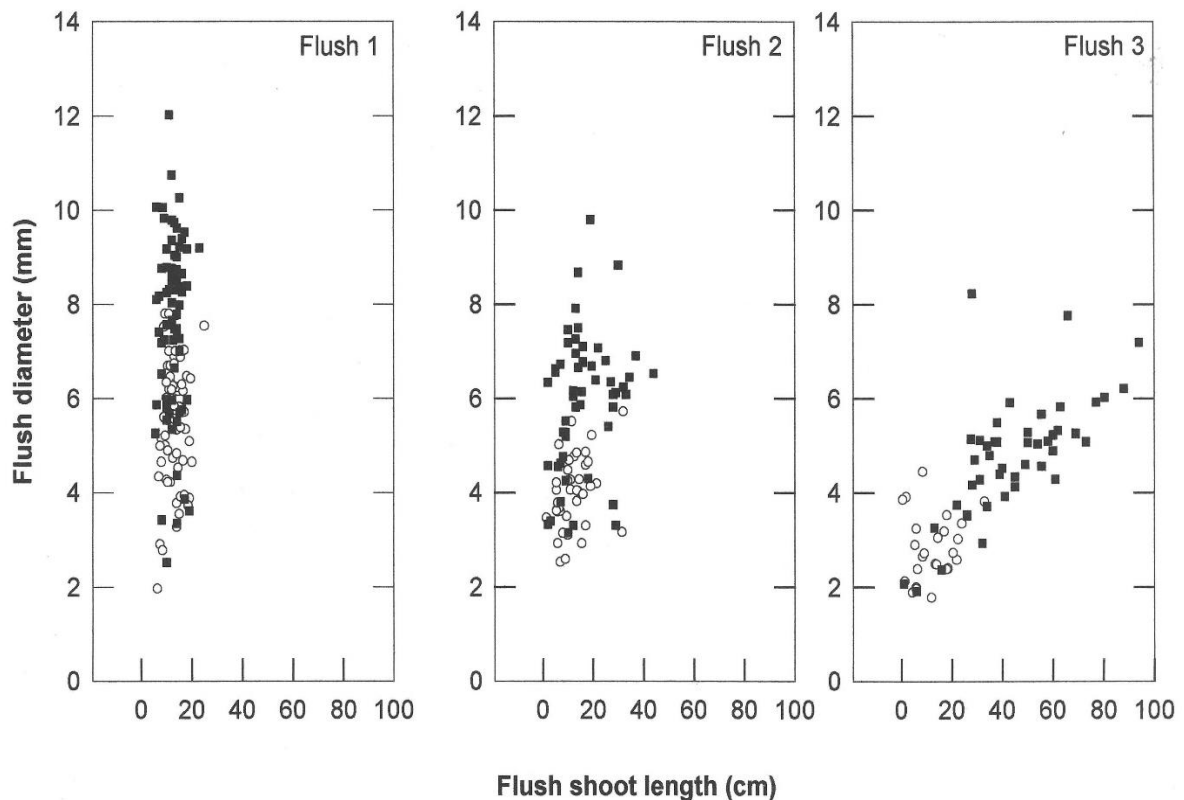


Figure 25. The effects of elevated CO_2 on the relationship between extension growth and stem diameter for three apical shoot flushes of *Quercus* (oak). Shoot length measurements from ambient CO_2 grown seedlings are shown as open squares while those from elevated CO_2 are shown as filled squares. The graph on the left shows the effects of CO_2 on the first shoot flush, while the middle graph shows the effects on second flush and the right hand graph shows the effects on the third shoot flush.

In order to grow trees at elevated CO_2 we had to use the facilities at another site within the parental organisation of the UK's Horticultural Research Institute's. Littlehampton, formally the Glasshouse Crops Research institute (GCRI), was wonderfully accommodating with our research needs and this provided an opportunity to interact with Drs Bob Beresford and Lim Ho, who had been doing a lot of interesting work on the impacts of elevated CO_2 , particularly with glasshouse grown crops. One of our aims was to examine the effects of elevated CO_2 on the structure of xylem (wood) development. Work elsewhere had shown that other plants had the capacity to adapt to elevated CO_2 and this increased their water use efficiency (WUE). The speculation was that this increase in WUE came about due to changes in leaf stomatal conductance and changes in the structural plumbing (xylem) within the plant moving water from the roots to the leaves. Both these focal points utilised my skills and interests in stomatal biology and xylem differentiation already developed at Lancaster and Bangor in the Forestry Department. We attempted to use plant material which included both seedlings and tree saplings as mature as possible, but which could still be able to be grown in large commercial glasshouse where the ambient concentration of CO_2 (350 vpm) was elevated to double ambient (~ 700 vpm). Given the high radiation (sunshine) levels at Littlehampton and the supplementation of CO_2 both the oak and cherry grew very rapidly over a 19 month experiment. It is well known that some oak species

which show recurrent indeterminate growth (determinant – leaf number fixed before bud burst and spring growth) and will go through a number of shoot growth flushes in an annual cycle which appears to be in response to position on the tree and its environment. Such that in good growing years some shoots will produce repeat bud set and bud burst. The seedlings used in these experiments showed in the first shoot flush significantly more shoot extension, but no difference in diametric growth, despite elevated CO₂ (Atkinson and Taylor 1996). While by shoot flush three there were significant differences in shoot length and shoot diameter. This indicates that with *Q. robur* seedlings the benefits of elevated CO₂ initially induced an increase in shoot extension then the allocation pattern of carbon changes with later shoot flushes partitioning more carbon to diametric growth by secondary thickening (stem diametric growth). It was stem secondary thickening that benefited more from elevated CO₂ than initial shoot extension growth (Atkinson and Taylor 1996).

At the end of these experiments trees were harvested and the relationship between leaf area and stem hydraulic function was measured to determine if growth at elevated CO₂ had altered the stem's capacity to meet the transpirational demand of the tree's leaf canopy. Elevated CO₂ had produced significantly larger oak and cherry trees compared to those grown at ambient (Atkinson, Taylor, Wilkins and Besford 1997). Measurement of stem hydraulic conductivity showed it increased linearly with the tree's canopy area it supplied. However, this was not the case with the oak (*Quercus*) grown at elevated CO₂, where there was no change in hydraulic conductivity. This absence of an increase in conductivity was related to changes in total stem vessel area. Despite this increase in total stem vessel area being greater at elevated CO₂ compared to ambient, there was no increase in supplied leaf area. Importantly, this change in the fundamental relationship between leaf area and stem hydraulic conductivity may have a considerable influence on the tree's water balance. The results showed that hydraulic efficiency was changed by elevated CO₂ and that this was most likely due to the measured increase in xylem vessel size (Atkinson and Taylor 1996). The longer-term implications for this work were that such a change may make oak more vulnerable to climatic droughts as larger xylem vessels may transport water more rapidly, but when water is in short supply such larger vessels may embolise and become dysfunctional due to drought (Atkinson and Taylor 1996).

The increase in tree growth in general in response to elevated CO₂ was not unexpected even after only 10 months of growth. The challenge of growing trees within these experiments was that potted trees can become root restricted (reduced root growth) and this can influence total tree growth. It was apparent with cherry that the initial stimulatory growth induced by CO₂ (after 2 months at elevated CO₂) induced by a higher photosynthetic rate was not sustained. After 10 months a decline in photosynthesis suggested that assimilation rate had acclimated to the higher concentration of CO₂. For oak, the amounts of 'Rubisco' (*this is the enzyme that produces plant carbohydrates, from CO₂, for growth and respiration and is the most abundant enzyme on the planet*) and thylakoid-bound protein cytochrome f were higher after 19 months growth at elevated CO₂ compared to the controls at ambient, however in cherry there was less Rubisco at elevated CO₂ (Atkinson, Taylor, Wilkins and Besford 1997). Working in the area of trying to understand the impacts of CO₂ on plant growth provided a number of opportunities to describe and promote the potential impacts of climate change on perennial crops (Jones and Atkinson 1995; Atkinson 1996; 1999).

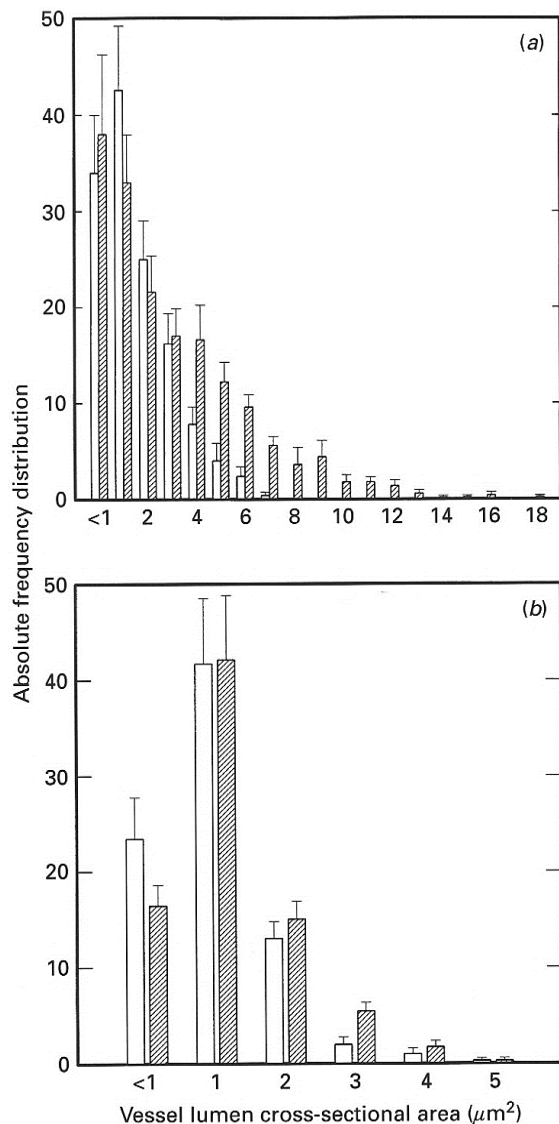


Figure 26. The mean vessel size frequency distribution determined from eight basal main stem segments of oak (*Quercus robur*) (a) and cherry (*Prunus avium* x *pseudocerasus*) (b).

The graph shows that for oak seedlings (grown for 10 months) grown at elevated CO₂ (700 vpm; the hatched bars) there was a significant increase in both mean vessel number and size compared to the growth at ambient CO₂ (350 vpm; the open bars).

These experiments showed, with the exception of oak trees grown at elevated CO₂, that there was a physiologically based linear relationship between transpirational demand (leaf area production) and the stem's transport supply as measured by its hydraulic conductivity. More importantly it also showed that hydraulic efficiency can be changed. The increased growth at elevated CO₂ with oak was achieved by improved hydraulic efficiency through an increase in mean vessel size. Larger vessels move more water, but are more vulnerable to stresses, such as soil water deficits which can cause larger xylem vessels to embolise (contain air bubbles).

Understanding what rootstocks do and how they do it

Right from the start of my involvement with research at East Malling, I had a fascination with the functioning of dwarfing rootstocks and this was supported and encouraged by the generosity of Drs Tony Webster and Jim Quinlan in providing their knowledge and enthusiasm. Modern commercial fruit production relies on the use of composite trees produced by grafting a desirable scion (selected for its fruit characteristics/quality traits) on to a rootstock, of predictable behaviour. Our interest in roots and rootstock has been revived recently as our effort to increase food production in a sustainable manner, to meet the demands of an increasing global population without more resources, while conserving nature and adapting to climate change. There is a huge and as yet untapped potential for roots to be exploited as a means to environmental adaptation and resource capture efficiency (Gregory, Atkinson, Bengough, Else *et al.* 2013).

Rootstocks are selectively bred for a number of reasons and the rootstock has multiple influences on scion growth and development including increased precocity (the fruiting scion

matures and flowers, while the tree is still juvenile, this is not the case with most perennial woody plants) and dwarfing.



Figure 27. The meticulous excavated fruit tree above and below ground which took some 6 months of work to achieve.

Excavations of this type, of which there were many, provided a descriptive analysis of roots and rootstock soil exploitation. They were particularly useful in understanding rootstock differences and the impacts of orchard management practices. If you look closely you can see the small black tags which join roots parted during the excavation.

A dwarfing rootstocks makes the trees fruit more precociously and at a higher efficiency with respect to the conversion of sunlight into fruit and with respect to space and tree canopy size (Atkinson and Else 2001). My earlier work with irrigation and elevated temperature impacts on apple led to work involving differences in rootstock performance during drought stress; this work was supported by several overseas visitors (Atkinson, Policarpo, Webster and Kuden 1997). We were also trying to move away from the more traditional simple approach of measuring a rootstocks performance from a long-term descriptive field trial, at a particularly location, by acquiring knowledge, for example, of how a rootstock responded to environmental stress. This work involved looking at both the planting material – tree age (Webster, Vaughan, Lucas, Spencer and Atkinson 2003) and the management of the root system in the absence of a dwarfing rootstocks, e.g. the application of root restriction by growing non-dwarfing rootstocks in root confining bags (Atkinson, Webster, Vaughan and Lucas 1997; Webster, Atkinson, Lucas, Taylor and Vaughan 2000; Atkinson, Webster, Vaughan, Taylor and Kingswell 2000). It was also extended to cherry with its limited availability (at the time) of rootstocks with any dwarfing capacity (Webster, Atkinson and Vaughan 1997).

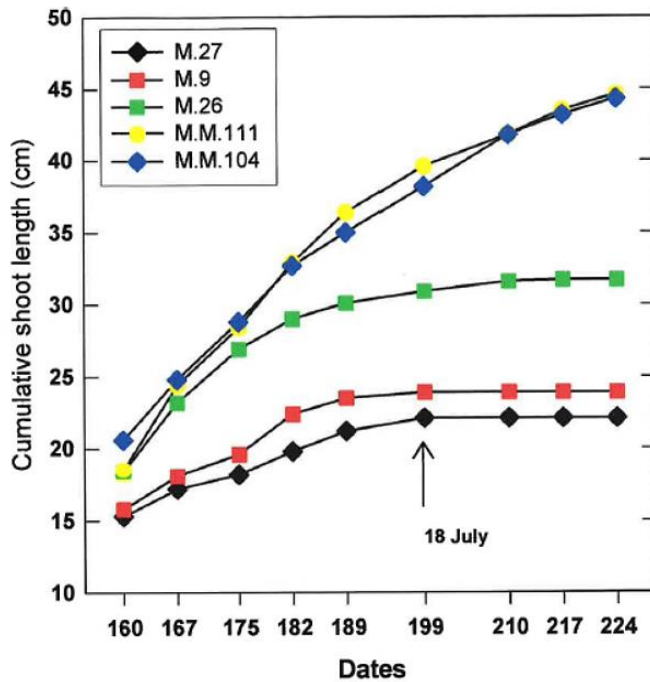


Figure 28. The cumulative seasonal shoot growth (length in cm) of a range of rootstocks from the dwarfing M.27 and M.9 to more invigorating M.M. 111 and M.M.104

One of the many published suggestions was that rootstock dwarfing was due to limitations in water uptake, because dwarfing rootstocks having less root mass than vigorous rootstock and were therefore less able to exploit the soil and cope with drought (Atkinson and Else 2001; Atkinson 2002). Through several experiments we examined the response of a range of rootstocks, with different dwarfing capacities, to cope with a reduced water supply. The first

part of this study described the influence of limitations of water supply on biomass production and its distribution (Atkinson, Policarpo, Webster and Kuden 1999). A second study examined the relationship between the rootstocks water potential and its stomatal conductance. Again, larger negative water potentials (a measure of increasing drought stress), for dwarfing rootstocks, were suggested as a mechanism which causes dwarfing due to its effect on stomatal conductance (Atkinson and Else 2001). Reduced stomatal conductance caused a decline in photosynthesis, as well as, water use (transpiration) and this may explain the reduced growth seen in dwarfing rootstocks (Atkinson, Policarpo, Webster and Kingswell 2000). The union between the scion and rootstock has also been suggested as possible cause of the dwarfing effect through a restriction of the passage of water, or growth determining nutrients from the rootstock into the scion (Atkinson, Else, Taylor and Webster 2001).



Figure 29. Tree stem cross-sectional sections which show typical responses when a grafted fruiting potted tree has had its root system removed when immersed in coloured dye solution and then allowed to transpire for a few hours. Stem tissue cross-sections of the grafted tree are shown at three positions for a dwarfing rootstock. The top three sections show the extent of dye colouration for the rootstock lower 'shank'. The middle larger sections shows staining within the graft union and the bottom three sections show dye staining in the scion.

This type of approach can be used to quantify solution movement across the graft union and between rootstocks. The selectivity of the graft union can be clearly seen as the cross-sectional area of dye staining declines (partial intermittent colouration) moving from the rootstock (top) to the scion (bottom). This classical

method enables a quantitative analysis to be undertaken using mature fruit grafted trees and shows a clear pattern of reduced dye (transpirational water flow) movement across the union and also, but not shown here, the transfer of less dye to the scion as the rootstocks dwarfing capacity increased (Atkinson, Else, Taylor and Dover 2003).

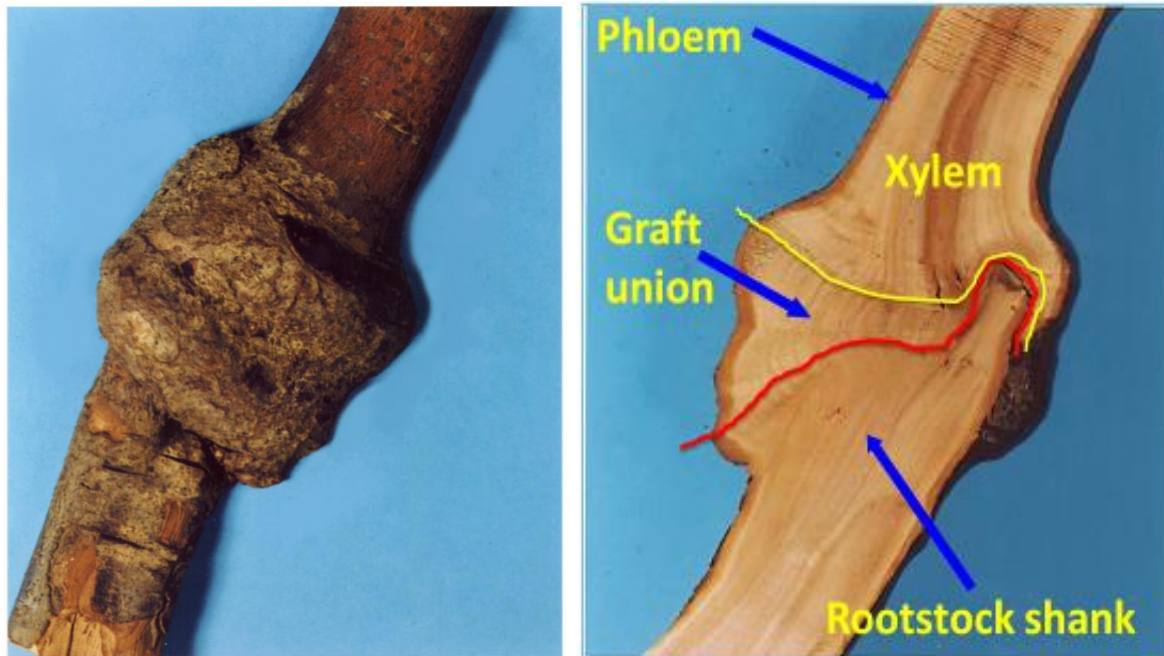


Figure 30. An external image of the root and shoot union of an apple tree scion grafted onto an M.9 rootstock (left). The same graft union cut longitudinally to reveal the internal tissue changes from rootstock shank to union and the scion (right).

The considerable xylem tissue disorganisation observed in the graft union above, may influence the movement of ions and water as well as plant growth altering chemicals; to test this hypothesis measurements were made on 3-year-old grafted apple tree scions (single, same scion used on all) on a range of rootstocks with different dwarfing capacities. The results from measurements of scion hydraulic conductivity were shown to be linked to tree leaf area and rootstock, implying that the rootstock had some control over scion anatomy and its hydraulics. With hydraulic conductivity being greater for the scions grafted on to the more vigorous rootstock and the suggestions that the observed anatomical differences in xylem differentiation, in the graft union, were induced by the rootstock. We concluded, when taking into account factors such as the differences in graft union cross-sectional area, there was a correlative link between graft union increase cross-sectional area and rootstock vigour. The development of the union with respect to its diametrical size was suggested as mechanism to compensate for the union xylem tissue disorganisation and thus not a restriction to the flow of water, or nutrients, from the rootstock to the scion (Atkinson, Else, Taylor and Dover 2003).

Previous studies of root-to-shoot signaling in fruit trees failed to recognise, and account for, the influence that sap flow rates can have on the concentrations of hormones and other solutes in the xylem sap. Sap from trees obtained by removing the scion and collecting sap that exudes under osmotic pressure from the roots, at very slow and highly variable rates within and between rootstocks, can mean that its composition often has very little

resemblance to that flowing in the intact, transpiring tree. To determine accurately the passage of hormones from roots to shoots in the transpiration stream, it is necessary to take samples of xylem sap flowing at rates similar to those present in the intact tree. Information on both the concentration and the delivery rate (concentration multiplied by sap flow rate) of key 'signal molecules' was needed to establish whether changes in the movement of hormones between root and shoot underlie the dwarfing effect.

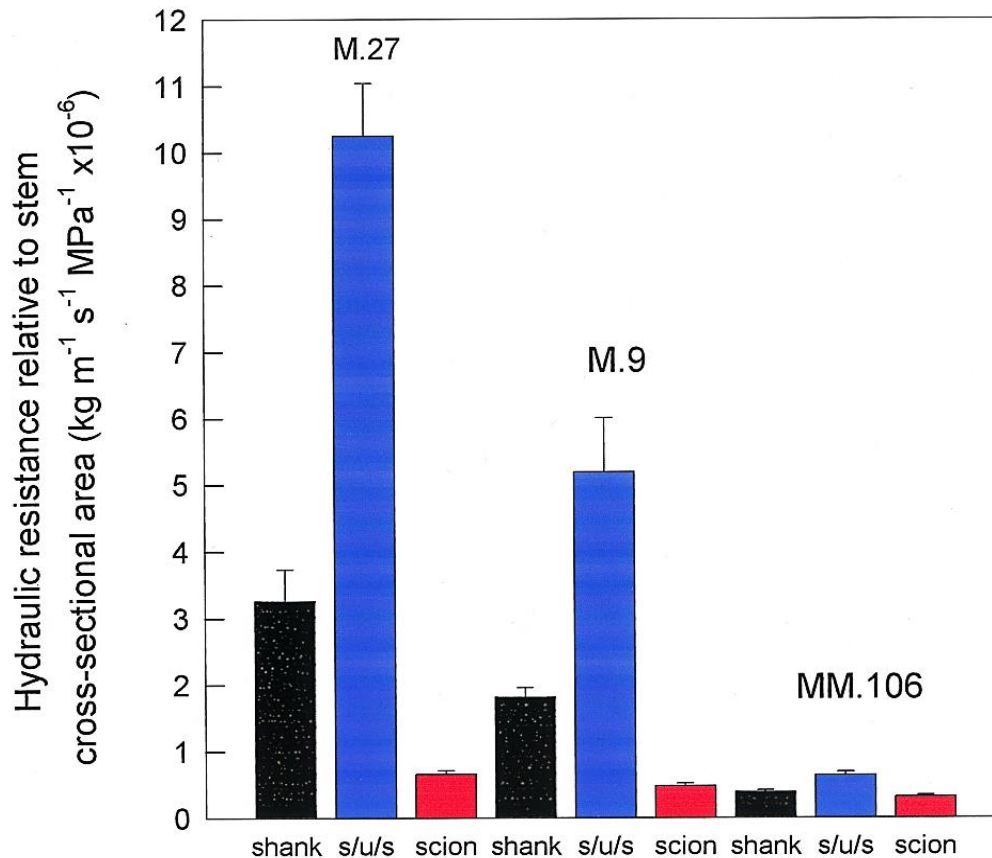


Figure 31. The hydraulic resistance of a range of apple rootstocks with different scion dwarfing/vigour control capacities.

There was a decrease in hydraulic resistance with increasing rootstock vigour as shown by the data measured from the intact rootstock/union and scion (s/u/s - blue bars). A decline in resistance was also present in measurement from the rootstock sections alone (shank). Interestingly, scion resistance also declined with the rootstock measurement which must be due to the influence of the rootstock on the scion as they are genetically all the same.

To explore this notion we quantified the amount and rate at which root-derived substances (mineral ions and hormones) were exported in the xylem from the root, through rootstock and scions stems and into the canopy, and evaluated their importance in determining shoot behaviour. At the time our knowledge of hormone transport studies from roots to shoots emphasized the need to collect samples of xylem sap for hormone analysis at rates similar to those in intact, transpiring trees. This is because of the confounding influences of sap flow rates on the concentrations of solutes in the xylem sap. To achieve this we designed and had

built two unique split-top whole plant pressure chambers which were able contain intact young fruiting trees, with a root volumes up to 25 dm³. By applying a positive pneumatic pressure to the potted roots, we were able to replicate the xylem sap flow rates that we measured in the intact tree. From this the concentrations of hormones and other solutes (cations and anions) in xylem sap samples collected would be the same as those in the transpiration stream of the tree prior to sampling. The key being able to determine whether dwarfing and invigorating rootstocks produce and export different amounts of hormones, and not relying of concentrations alone as these can mislead because they can be dependent on sap flow rates. To take this into account, hormone delivery rates were calculated (concentration multiplied by sap flow rate).



Figure 32. A potted tree within the unique split top pressure chamber which was designed for the extraction of xylem sap from potted fruiting trees (left) and an engineering cross-section of the basic split top pressure chamber principle which allows sap to be collected from intact potted fruiting trees (right). The point at which the tree trunk exits the split top chamber was pressure sealed using quick setting flexible polymer.

The pressure-chamber approach, has shown that the rate of sap flow had a large impact on the xylem sap composition (Else, Taylor, Young and Atkinson, *submitted*). Slow flowing sap concentrated solutes and faster flowing sap diluted solutes. This dilution of solutes was not proportional to the increase in sap flow rates, a doubling of sap flow did not halve the concentrations. An inevitable consequence of this was that solute delivery rates increased with faster flow rates. The slow flowing osmotically-exuding sap concentrated solutes through a lessening of dilution; however, solute delivery rates, from the exuding sap, were still only 4% of those estimated to be passing to the scions in intact trees. Data implied that the use of

this method of sap collection when trying to assign causal status to xylem-borne signalling molecules will likely lead to erroneous conclusions.

Sap osmolality and Ca^{2+} concentrations were reduced by passage through the union of M.9 at low flow. The delivery of anions and cations to the shoot from the roots of M.9 were always similar to those of the MM.106 rootstocks. While the specific root and shoot deliveries of the hormone abscisic acid [ABA] (taking into account the different quantities of root mass and leaf area between M.9 and MM.106) were higher for M.9 compared to MM.106. The hormone ABA is known to reduce stomatal opening [acting as a regulator of water use] and shoot growth. The downward movement of auxin [measured as polar auxin transport – PAT] was lower in the dwarfing rootstock compared with the more vigorous rootstock. This helps explain the reduced root growth and changed xylem anatomy apparent with the dwarfing rootstock union. This is the first integrated understanding of a number of different processes which control tree growth and can be used to explain the dwarfing effect of some rootstocks (Else, Taylor, Young and Atkinson, *submitted*).

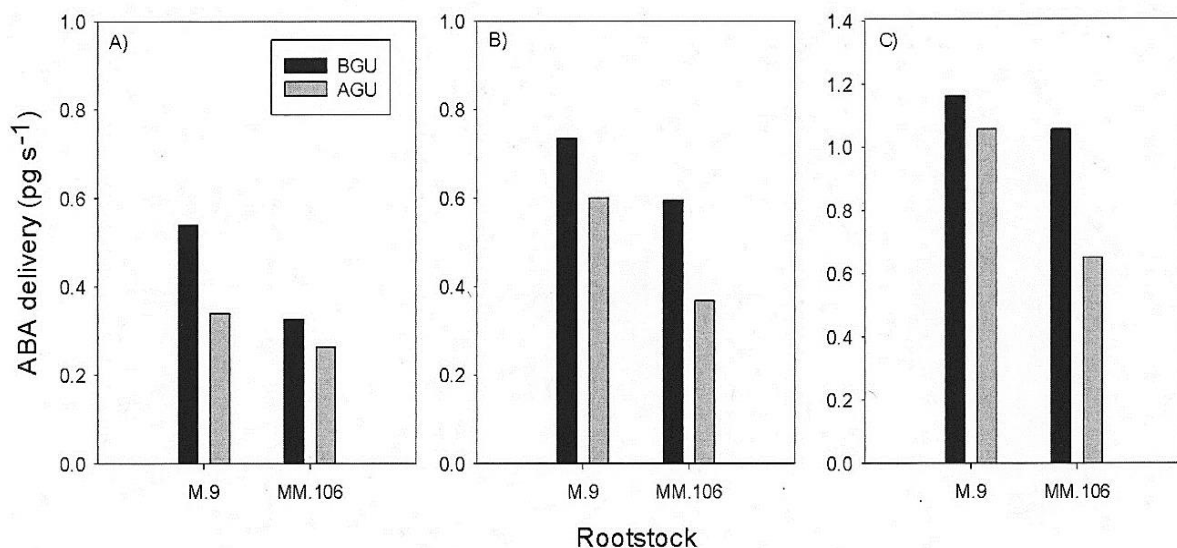


Figure 33. The delivery of ABA below and above the graft union measured from the dwarfing M.9 and more vigorous MM.106 rootstock. Deliveries are shown at three selected xylem sap flow rates for simplicity. The range of xylem sap flow shown includes that measured in the intact trees prior to sampling taking place.

In parallel to this work trying to understand how roots communicate with shoots we were examining the effects of actually over watering (flooding) which causes deprivation of oxygen to the soil (anoxia) which stop roots from respiring and therefore rapidly reduces their capacity to take up water and minerals as they dehydrate – somewhat surprisingly. Using the woody plant *Forsythia* as a model, experiments were developed to show how easy it was to overwater an apparently freely draining potted plant. Even for short periods of some 24 hours of flooding reduced leaf growth was observed. More detailed experiments produced a time course of biochemical changes in the root system and the delivery of the characteristic chemical signal molecules of anoxia, i.e. acetaldehyde and ethanol, in the xylem sap coming from the roots and appearing in the leaves. The time course for the first appearance and the transfer of these root-derived chemicals, in extracted xylem sap, provided a clear ‘cause and effect’

interpretation of the physiological shoot responses, i.e. stomatal closure (Atkinson, Harrison-Murray and Taylor 2008). The start of closure of stomata for *Forsythia* was initially detected around 24 hours after flooding which was a very similar response to that observed in tomato for which we already knew more about mechanistically (Else, Taylor and Atkinson 2006; Else, Franciszek, Atkinson and Jackson 2009).



Figure 34. The entire root system of *Forsythia* plants subject normal watering (top) and flooding (bottom) for 2 days. The flooded root systems shown have reduced dry matter and signs of degradation and darkening/degradation of the root tissues. These changes can be linked to the production, in the roots, of acetaldehyde and ethanol which is transported in the xylem sap to the shoot.

The world of apple research was perhaps my most rewarding for a multitude of reasons. The East Malling Research Station (EMRS) had a reputation for being the global home of perennial fruit tree apple research and it was from here that most of the apple rootstocks used commercially (i.e. M.9) were evaluated and release freely to the world. In the early days of EMRS, Great Britain was supplied with food from an empire (Canada, Australia, South Africa and New Zealand) and it provided its producers with knowledge and plant material to support its growing fruit industries. If only royalties, or breeding rights, were around in those days EMR would not be in the financial situation it now finds itself. Not only did I benefit from working at EMRS, it also enabled me to develop network links with researchers throughout the world. From this collaborative opportunity, came both friends and new colleagues, as well as, the opportunity to travel the world. This also resulted in experimental projects and people coming to EMRS to work with me (Tustin *et al.* 1997; Cahn, Atkinson and Webster 2001; Retamales, Hips and Atkinson, 2004). I also benefited when expert advice was required to answer, or support, governmental questions about an extensive range of issues linked to perennial crops and fruit production. One such digression was to comment on the possible accumulation of radioactive substances in fruit (*a response to the Chernobyl accident 1986*). This led to the publication of an advisory governmental report, which I was able to develop into a critical review of the possible potential routes for radioactive nucleotides getting into fruits (Atkinson and Webster 2000; Atkinson *et al.* 2002; Carini *et al.* 2005), fortunately, this work has remained mostly theoretical.

Why do cherries abscise (runoff) prior to maturity?

In the late 1990s, it had become apparent that cherry production in Kent was subject, at times, to production losses when after fruit set (pollination followed by fertilisation) had initially been good. The phenomenon occurred when a significantly high proportion of the crop would drop (runoff) in a manner which seemed to be literally overnight. This of course was a very disturbing commercial issue given the value and quality of the Kentish cherry crop.



Figure 35. Commercial cherry trees with their abundant floral production (left) and the resultant desired heavy cropping potential (right).

A number of experiments were initiated to determine the cause of this fruit ‘runoff’. These experiments, as with much of my work, started with ‘fact finding’ and carrying out some descriptive experiments to determine what was going on (Atkinson, Else, Stankiewicz and Webster, 2001). The Department of Environment, Food and Rural Affairs (DEFRA), with pressure from an industry that understood the benefits of research and innovation, created a funding scheme called HorticultureLINK for which they provided half the research costs, the remainder coming from industry partner(s). EMR was at the forefront of applying and winning these types of research contracts which contained elements of both novel science and its application for industry use. The philosophy of the programme was the development and application of science to support an industry/business. I was fortunate to win and be involved in a number of these joint science research industry funded projects and a considerable amount of work was achieved during these projects, particularly as they often ran over 5 years. There has always been a need, with perennial crops, to conduct research over a time period which would provide greater certainty with respect to the results obtained, against a background of no one year is ever climatically the same in the UK. The programme ethos also promoted the idea that the researchers worked closely with the farmer/grower and in many cases on the grower’s farm. This enabled experimental inferences to come from real farm situations (field experiments) and under variable climatic and commercial conditions.

We were able to characterise the relationships between the fruit setting potential of a spur (a

flowering unit which may contain several flowers and their associated supporting [spur] leaves) and its position on the tree and its leaf area. Perhaps, not surprisingly, the initial spur leaf area had a positive impact on the setting potential of the flowers within a bud. While the leaves on the growing shoot (extension leaves) were important in maintaining the fruit on the tree after set, i.e. avoiding or reducing runoff. This was an important point at the time as the concept and practice of using growth regulators to inhibit gibberellic acid biosynthesis were being used to control tree growth and size, as sweet cherry had no dwarfing rootstocks to rely on, as was the case with apple. When tree vigour, growth was controlled by paclobutrazol (GA-inhibitor) only very small doses were required to restrict shoot growth considerably. The importance of GAs with respect to function and commercial application was well established (Webster, Spencer, Dover and Atkinson 2006). The impact was however in many practical situation an overly excessive shortening of the space between leaves (stem internode length) and a reduction in leaf number. This effect provided enlightenment to the possible causes of runoff. In field experiments where the supply of photosynthates from spur or extension leaves was reduced, by phloem girdling, it was clear that fruit would not survive to maturity (they ran off).

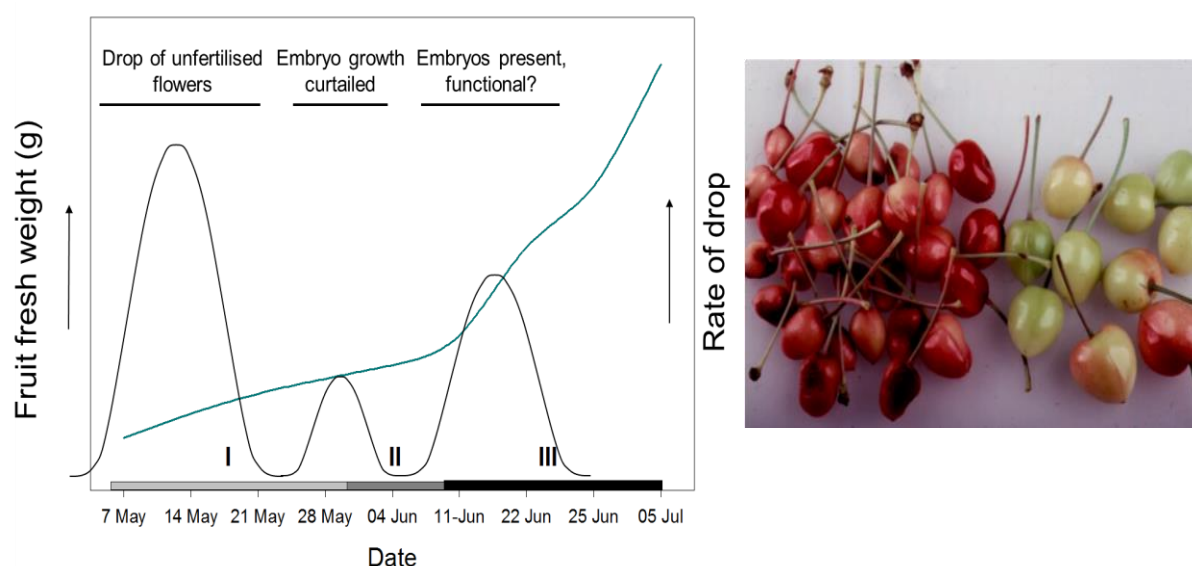


Figure 36. The mean number of fruit abscised per tree per day (left) and the highly coloured runoff fruit compared to the fruit retained (right). The graph shows distinctive peaks where the fruit loss occurs. The first peak corresponds to fruit abscission due unfertilised flowers, the second to fruit not setting fully (and embryo abortion), while the third peak is the 'set fruit' which is running off. The coloured line refers to the change in fruit fresh weight. The intense fruit colouration too early in the normal growth and development cycle is a sign that abscission is about to take place ('the grower nightmare'). The fruit which is developing normally has yet to turn the characteristic red colour of a mature cherry fruit are shown on the right side of the picture.

When spur leaves were girdled fruit set was reduced, while when extension leaves were cut off by girdling fruit runoff could be induced (Atkinson Else, Stankiewicz and Webster, 2002). An examination of climatic factors both at flowering and during the latter part of the fruit development stage (June and July), showed that runoff often occurred, or was more likely to occur when conditions at anthesis (flowering) had promoted heavy fruit set. Then when the subsequent summer did not provided sufficient radiation (sunshine), to supply the fruit

demand (the 'crop load') with adequate photosynthates for fruit growth, the fruit abscised (runoff) (Blanusa, Else, Davies and Atkinson 2006). The lack of photosynthates induced by a typically poor mid-summer implied that fruit were competing for resources (carbohydrates/sugars) that were limiting their growth.

To test this hypothesis we set about doing a series of experiments to see if we could gain insight into how the competition between fruits on the same floral spur was being instigated. The hormone auxin (IAA) is known to be produced by seeds, and exported continuously from fruits, as part of the process in delaying abscission. This therefore provided a good candidate to investigate through an assay of the polar auxin transport (PAT) rate in the tissues linking the fruit to the tree (the peduncle/fruit stalk). PAT activity was shown to be high at the time of flowering and increased further following fertilisation and this equated with IAA export from the fruit via the phloem (the cells that transports sugars in plants) tissue (Else, Stankiewicz, Webster and Atkinson 2004). Further experiments showed that maintaining PAT was integral in keeping fruit on the tree and the application of chemical treatments of known PAT inhibitors caused fruit to abscise (Blanusa, Else and Atkinson 2005).

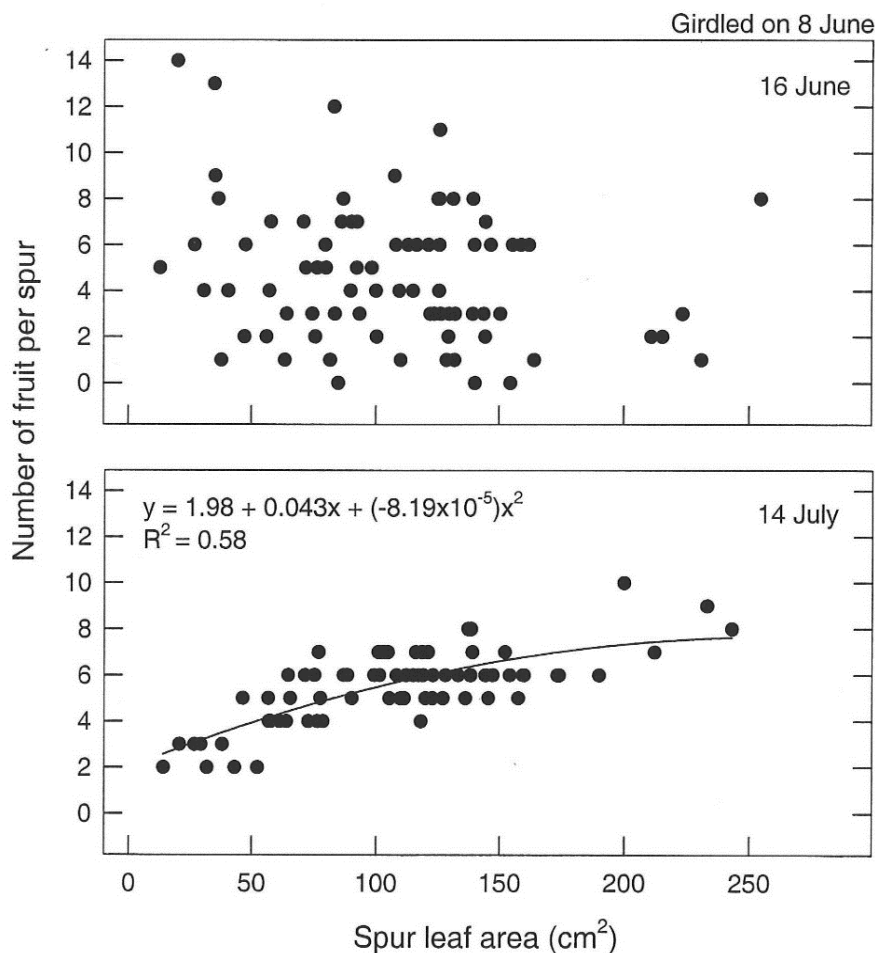


Figure 37. The relationship between spur leaf area (cm²) and number of fruit per spur for spurs girdled on 8th June from sweet cherry 'Lapins' on F1090 rootstock recorded on 16th June and 14th July.

It was apparent that as the spur leaf area declined the number of fruit retained per spur

declined. This suggests that competition for photosynthates might be the cause of runoff. The presence of a larger number of fruit increases the competition for a finite supply of carbohydrates for growth and if the supply rate falls (low level of sunshine) then competition between fruits on the same spur can increase.

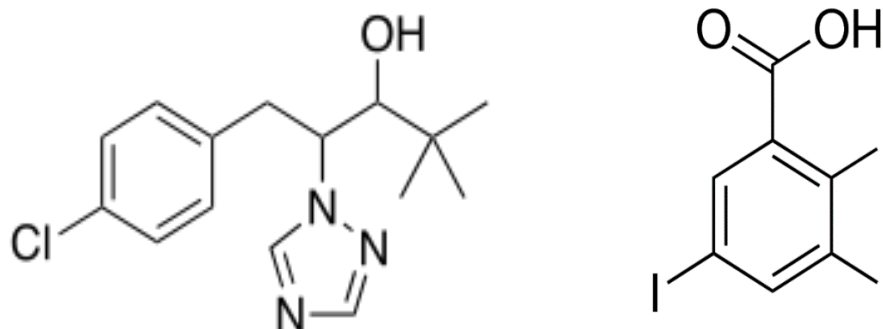


Figure 38. α -tert-Butyl- β -(4-chlorobenzyl)-1H-1,2,4-triazole-1-ethanol (Pacllobutrazol) a GA inhibitor and 2,3,5-Triiodobenzoic acid (TIBA) were used to retard plant growth and inhibit polar auxin transport respectively.

Optimising the production of secondary plant metabolites

My early career background in analytical chemistry has left me with both an interest and the confidence to work both analytically and in the world of chemistry. Plants have been exploited as a major source of chemicals for human use. Many of these chemicals are often described as 'secondary metabolites'. My particular interests began a long time ago when reading about the mechanisms by which plants cope with environmental stress by the production of endogenous chemicals which help protect plant tissues from, heat, cold, UV, high radiation, salinity etc. Many of these secondary compounds are well known and can be characterised as antioxidants. That is a compound able to detoxify the stress produced free radicals which if left unchecked have the potential to initiate cell damage. Humans of course rely on consumption of many plant derived antioxidants and vitamins some of which we are not able to synthesise ourselves. These compounds are generally rich in fruit tissues where they protect the vital DNA within a fruit's seed to ensure its capacity to transfer accurately, the code, into the next generation. Many of these endogenous compounds have been linked, via consumption, to preventive care against a number of cancers (particularly intestinal). It was not long before the opportunity came along where the idea that we might be able to exploit fruits which had intrinsically higher concentrations of these beneficial secondary metabolites (e.g. polyphenol phytochemicals), or even more exciting, increase the concentrations of these compounds in plants by the way they are grown. The idea that we could potentially exploit environmental stress to enhance the concentrations of these compounds and provide consumers with improved dietary intake was part of my thinking (Atkinson, Dodds, Ford, Le Mière, Taylor, Blake and Paul 2006). Being the initiator of this work was important as it provided vital diversification into a new area of work, for EMR, as the more traditional sources of perennial crops research funding began to, decline. It also led on to other interactions and publications (Atkinson, Nestby, Ford, and Dodds 2006), but more importantly future ideas where the manipulation of crop access to resources (nitrogen and water in particular) would be used to invoke environmental stress to gain

benefits, not just from increased concentrations of beneficial compounds but also resource conservation. This area of exploiting stress to control fruit crop growth and development started with the excellent work, which I co-supervised, carried out by Philippa Dodds (Dodds, Taylor, Else, Atkinson and Davies 2007).

We were also part of another LINK project, jointly funded by BBSRC and GlaxoSmithKline, to examine ways to enhance the vitamin C concentration obtainable from *Ribes nigrum* (blackcurrant), which is the primary source of 'Ribena' production. At the start of the project very little was known about vitamin C production in plants despite its importance in human dietary health. We undertook a lot of field work both on farms and set up a number of EMR experiments to understand how the crop might be manipulated to increase fruit concentration of vitamin C. Our experiences with plant stress responses informed our experiments where we looked at manipulating water and nitrogen supply to influence fruit vitamin C.

These field experiments showed clearly that excessive amounts of nitrogen optimised with respect to vegetative growth did not simultaneously maximize fruit vitamin C concentration (Davies, Taylor, Ford, Dodds, Longbottom, Hips and Atkinson 2009). Vitamin C production was reduced at the highest applied nitrogen concentrations. More detailed experiments attempted to address the question where was fruit vitamin C actually made; this was an important question because if we did not know where it was made, it would be difficult to develop and recommend crop management strategies that might influence its production. For example, if it were made in the leaves then reducing leaf number, or plant leaf area, might be expected to have a negative impact of fruit concentrations.

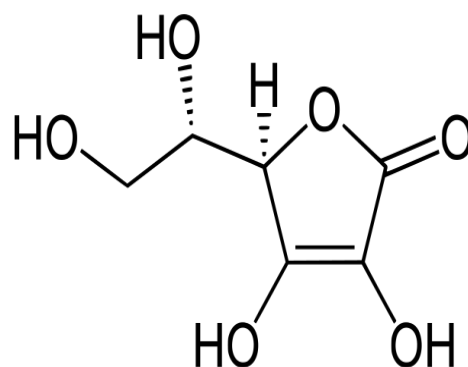


Figure 39. A typical cluster of blackcurrant berries (on the 'strig' or raceme) close to harvest; also evident are the small leaves linked to vitamin C production (left). The molecular structure of vitamin C (right).

A set of experiments was carried out to manipulate the relationship between the potential

‘source’ of vitamin C, the leaves and the ‘sink’ (the fruit) and its size (the number of berries). The results showed that despite being able to manipulate leaf area and assimilate supply via photosynthesis and stored carbohydrates, along with fruit yields, there were only rare effects on fruit vitamin C concentration, showing that vitamin C production in *Ribes* was not coupled directly to assimilate supply. There was equally no evidence that vitamin C production occurred predominantly in leaves and was then transferred to the developing fruits. This led us to conclude that it was the fruit which synthesized vitamin C (Atkinson, Davies, Taylor and Longbottom 2013).

Our profile and capacity to develop and evaluate approaches leading to the optimisation of plant secondary metabolites enabled us to be part of a consortium of researchers looking to the production of the chemical ‘artemisinin’ (a sesquiterpene lactone) from *Artemisia annua* (sweet wormwood, in Chinese its named *Qinghao su*). Extracts from *A. annua* had, in traditional Chinese medicine, been used for at minimum 100s of years to treat apparent cases of malaria caused by *Plasmodium falciparum* and transmitted by mosquitoes. It was not until the 1960s, The West, obtained access to plant samples and a clearer picture of how *Artemisia* might work and that ‘artemisinin’ was the important metabolite in the plant. The secondary metabolite contains a peroxide bond (O-O) which is highly reactive and believed to key to the drugs mode of action in killing the *Plasmodium* in the infected patient.

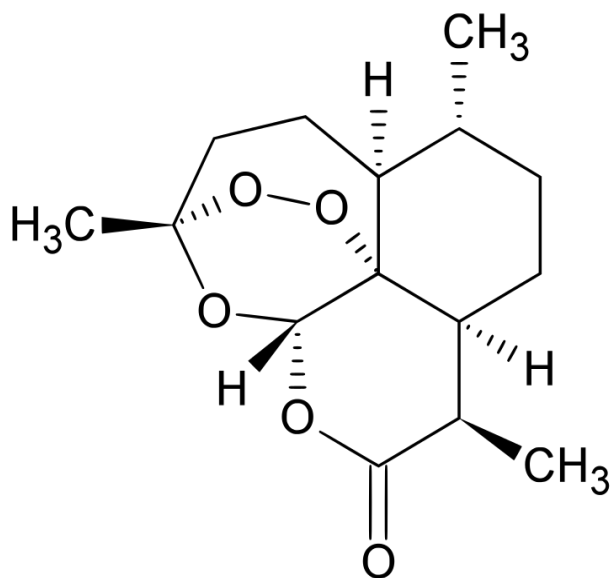


Figure 40. A protected crop of *Artemisia annua* being grown at EMR within the Unigro, GroDome. The chemical structure of the secondary metabolite artemisinin used in the treatment of malaria. The chemical potency is believed due to the highly reactive peroxide bond.

Being able to prevent and treat malaria is a global problem of huge importance and a major killer, particularly of children. The importance of drugs to cure malaria is and continues to be a global challenge, particularly when resistances to several existing drug therapies (e.g. quinine) continues to rise. The opportunity to utilise artemisinin as part of a combined therapy (artemisinin combination therapies – ACT) to reduce the potential for monotherapy resistance was seen as a key target by UK governmental institutes. Concerns were aired that

access to the plant and the chemical were at best erratic and that UK workers and vacationers needed a reliable supply of the drug when in areas where the traditional preventive drugs were failing again due to resistance. It should be noted that at this time there was no acceptable way of synthesizing the chemical in the laboratory. There were also questions about the reliability of the plant-derived product with respect to its quality (the amount of active component), suggesting that the product being marketed overseas, in some regions (Africa in particular), was of limited quality, i.e. contained very little active compound. The UK had no control of access to this drug and our research with partners at NIAB was intended to change that situation.

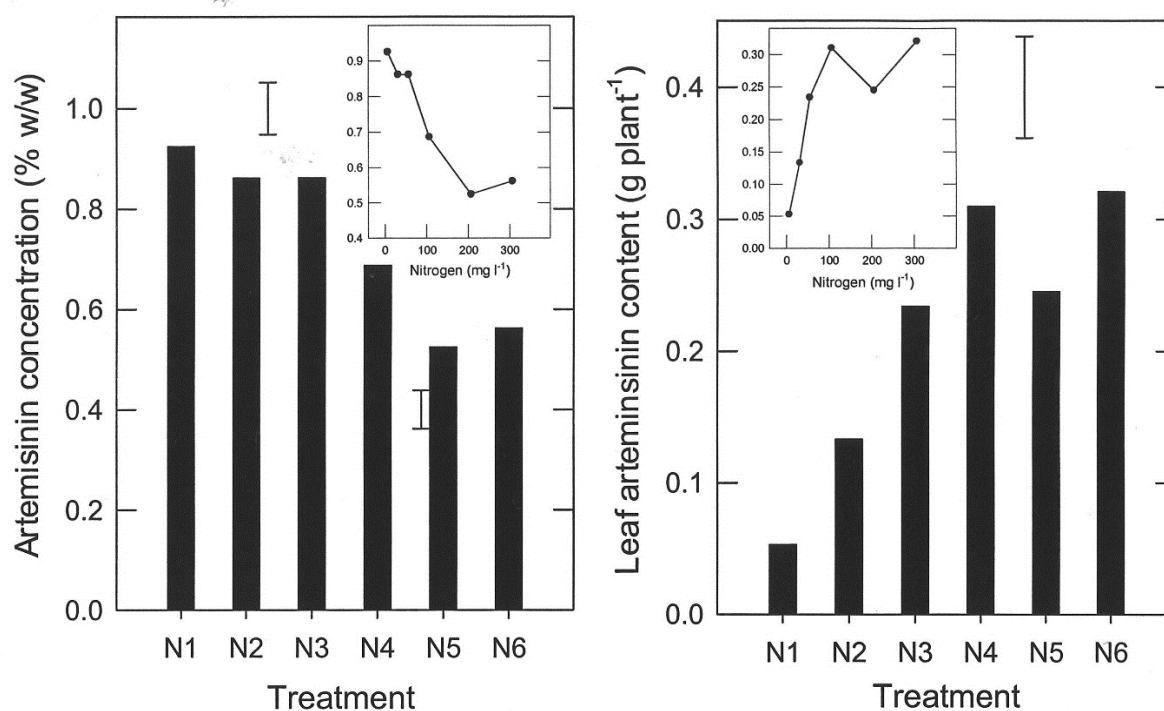


Figure 41. Artemisinin concentration in leaves (left) and total artemisinin content (mineral concentration \times leaf dry weight) at harvest for *Artemisia annua* plants when supplied with differing concentrations of nitrogen (right). Nitrogen concentrations ranged from N1 = 6 mg l⁻¹ to N6 = 306 mg l⁻¹. (Davies, Atkinson*, Burns, Woolley, Hipps, Arroo, Dungey, Robinson, Brown, Flockhart, Hill, Smith and Bentley 2009)

There were a number of objectives within the project but we were asked to firstly contribute to a conventional breeding programme. The challenge and the botanical interest here was that the species only contained very low concentrations of artemisinin (active principal compound 0.1–0.6 % dry weight) and that this was produced almost entirely in trichomes (small cellular hair like structures) borne of the leaf lamina. Existing research had shown that the apparent synthesis of artemisinin changed with crop development and age and that crop handling and harvest could severely reduce the active compound concentration in the leaves. Despite the consortium having access to a good number of accessions of *A. annua* we knew that their flowering was induced by different day-lengths. To carry out conventional plant breeding requires the simultaneous presence of both flowers (the female) of one accession and pollen (the male) from another. We modified a glasshouse to be able to alter the photoperiod of a number of accessions to synchronise flowering and pollen production in this

material. This was particularly successful, initially in getting synchronisation of flowering in most of the accessions used, from this we were able to make crosses (transferring pollen from a male donor to a female flower). The process produced, somewhat to our surprise viable seed which germinated the following year. We were also able to produce viable seed by allowing some plant accessions to 'self' (pollinate their own flowers). The material was used as parental material by NIAB to continue its development and breeding. Importantly, our efforts provided material where the concentration of artemisinin had been doubled (Cockram *et al.* 2012).

Given our knowledge around the manipulation of secondary compounds in fruits, we hypothesised that we should be able to influence artemisinin production by optimising the supply of nutrient resources. The results of several pot experimental studies showed that plant growth, with respect to biomass, could be optimised, in relation to nutrient supplies (e.g. nitrogen and phosphorus). However, the optimal production for artemisinin was always at a lower level of resource supply compared to vegetative biomass. The implications being that when resources for growth are not limiting then secondary metabolite production was not maximal, suggesting an element of the plant's stress response was involved in inducing the production of the metabolite (Davies, Atkinson*, Burns, Woolley, Hipps, Arroo, Dungey, Robinson, Brown, Flockhart, Hill, Smith and Bentley 2009; Davies, Atkinson*, Burns, Arroo and Woolley 2011).



Figure 42. Part of the GroDome facility with fully mature tobacco plants, which have been genetically transformed to produce a therapeutic protein, growing in a hydroponic flow system. Prof Ma and myself discussing experimental issues when being interviewed for an article in the Guardian newspaper.

At EMR we were very fortunate to have plant quarantine growth facilities, which due to their high specification and environmental control, meant that we could use these to not only work on notifiable plant diseases, but also to grow genetically modified plants. This resource provided a great opportunity to collaborate with one of the UK leading immunologist's, Prof Julian Ma working at St George's University of London, in Tooting. Prof Ma had a great conviction and a huge level of enthusiasm for his vision of 'molecular farming' where transformed plants could be used to produce targeted molecules involved in clinical therapies (pharmaceuticals), such as

antibodies and enzymes. The approach, exploiting transformed plants by molecular farming, was envisaged as an alternative technology to current established production approaches which use bacteria, yeast and mammalian cell cultures to produce therapeutic proteins.

We were asked to experimentally contribute to supporting a vision of commercially exploiting the approaches developed in his, and the labs of others, into a proof of production with up-scaling. Given that tobacco (*Nicotiana tabacum*) has a long history of being genetically transformed and it is not a food crop, this was the plant material of choice for this type of work. One of the first things we needed to understand was variability of production on a per plant basis for this production method. The pharmacological and drug regulatory bodies involved in overseeing this type of work needed to have clear and quantitative understanding of drug production variability and its control. Not an unreasonable requirement given the intention was to produce drugs for human use. So I set about designing and converting one of our quarantine compartments within the GroDome to enable plants to be grown hydroponically (no soil - plants are anchored in circulating water/nutrient based rooting environment).

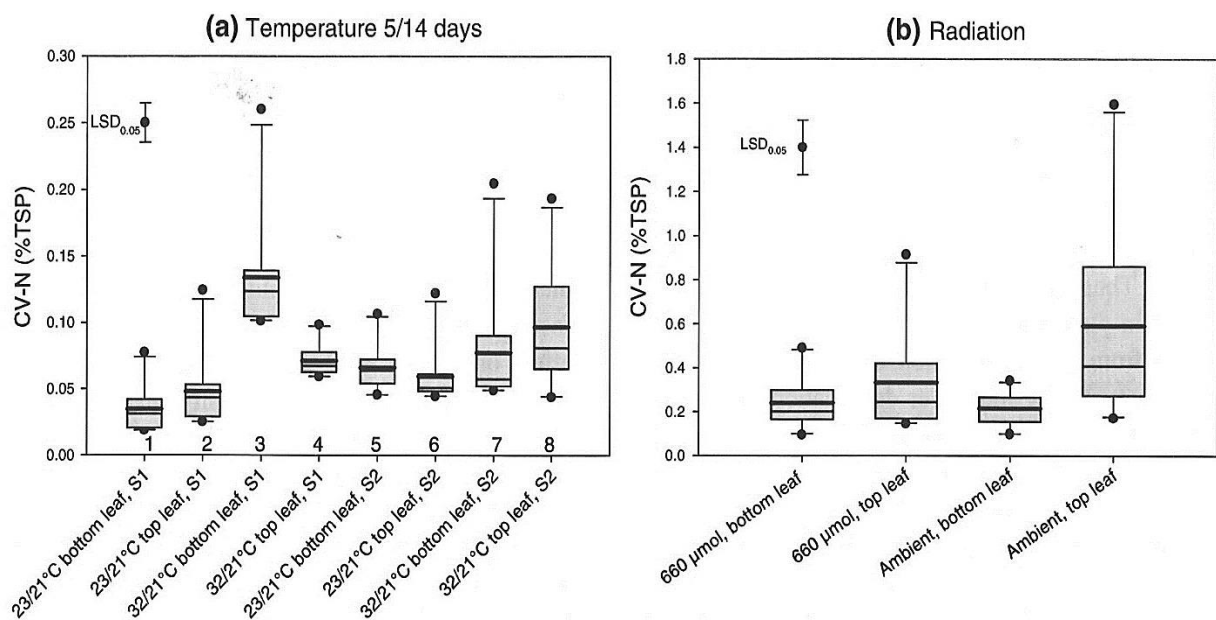


Figure 43. Cultivation condition effects on functional CV-N expression in transgenic tobacco plants grown at two temperature regimes and sampled after 5 (S1) and 14 (S2) days (a); and (b) under supplementary ($660 \mu\text{mol m}^{-2} \text{s}^{-1}$) or ambient light. In each case, data are shown for bottom and top leaf samples. Shaded box represents the 25th and 75th interquartile range and whiskers delineate the 10th and 90th percentile.

The above figure is from transgenic tobacco plants expressing a recombinant cyanobacterial protein (cyanovirin-N or CV-N). This is a protein which shows virucidal activity against a number of viruses and included human immunodeficiency virus (HIV) (Colgan, Atkinson, Paul, Hassan, Drake, Sexton, Santa-Cruz, James, Hamp, Gutteridge and Ma 2010). We devoted a lot of attention to making the environment within the growth facility as uniform as possible and quantifying what the remaining variability was. Particular attention was given to mapping and reducing radiation (light) and temperature variability. We then carried out a number of experiments to measure how the expression of various therapeutic molecules within the plants

varied with leaf position, plant age and location within the GroDome (Colgan, Atkinson, Paul, Hassan, Drake, Sexton, Santa-Cruz, James, Hamp, Gutteridge and Ma 2010). The responses with respect to transgenic protein variability and leaf position were explained as a function of plant age and development caused by a decline or breakdown of the protein. When similar experiments were undertaken with a transgenic protein which accumulates in a different cell location (endoplasmic reticulum - ER) this did not happen. Again, when the non-ER accumulating protein plants were wounded the transgenic protein declined, but did not decline in the ER accumulating protein plants. This work concluded that post-translatory modification of the ER accumulating protein concentration was induced by wounding (Hassan, Colgan, Richard, Atkinson, Sexton, van Dolleweerd, Keshavarz-Moore and Ma 2012). Changes such as this in protein/drug activity are clearly very important in a regulatory situation when considering commercial production.

Optimising water use to control yield and crop quality

The idea that crops, and in particular cropping systems that relied on irrigation, should be made to be more efficient was an idea that I started at EMRS and which led to a very considerable body of profitable research. The initial experiments, which I conducted with Ann Lucas, that are now long superseded, but they showed very clearly that the amount of water supplied to a crop such as containerised strawberry was far greater than what was needed (by the plant) and that the requirement to flush the compost in these bag grown strawberries with frequent over irrigation was unnecessary and wasteful, even for longer growing 'everbearers'.

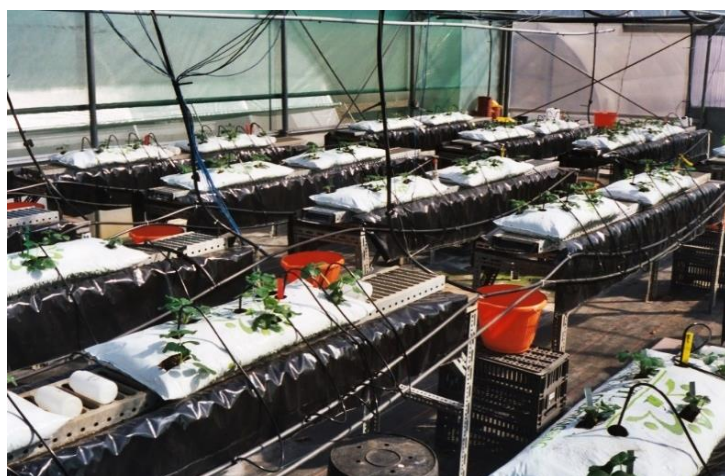


Figure 44. Polytunnel production of strawberry in peat filled bags using trickle irrigation. The experimental system was designed to quantify the water inputs and outputs to the system and the treatments involved different quantities of irrigation. The buckets were used to collect and then weigh the water that ran through the bags and was directed by the trays on which the bags sit.

It became apparent that the build-up of excessive nutrients in the compost did occur to a degree, particularly when the strawberries were grown over two seasons, but this did not influence yield or fruit quality. More importantly yield could be maintained when the quantity of water used was considerably reduced below that of the industry recommendations. Fruit quality and taste were also apparently better when less water was used. The challenge when reducing the volume of water applied was to ensure that it was evenly distributed through the bag to each of the plants within.

Work using resource deprivation initially to influence secondary metabolite concentrations facilitated my involvement in work where plant nurseries had growth variability high on their list of production challenges. Water use and variability with respect to plant uptake were major

issues for the UK hardy nursery stock industry. It has long been apparent that when plants are deprived of water this can have a negative effect of growth, particularly that of the shoot and the leaves. From such knowledge my colleagues working in the area of nursery stock research, where looking at ways to control vegetative growth, reduce nursery water requirements, eliminate water application variability, and schedule irrigation events. The first point needed to make this happen was to understand what the plant's requirements were and how they changed over time and with different environments. In some sense this was relatively achievable when thinking about plants growing in pots. It was possible to measure supply and demand through the process of calculating changes in pot mass before and after irrigation. This simplistic approach, ideal for application in commercial plant nurseries, provided a means by which the idea of imposing a controlled (regulated) and small level of drought could be used to influence (reduce/control) shoot growth.



Figure 45. Demonstrating our nursery water use efficiency work at an industry technology transfer event (left). The size of the problem we were working on in trying to deliver water automatically, uniformly and in response to crop demand over large beds of plants (right).

The extent to which drought was imposed was measured relative to the amount of water needed to replace the total amount of water used by the plant. So the approach is described as regulated deficit irrigation (RDI), less than 100% of a plant's demand for water is provided by the application of irrigation (Cameron, Harrison-Murray, Atkinson and Judd 2006). The benefits to the control of vegetative vigour using RDI where considerable to the nursery industry often with additional benefits of improving flowering intensity and the plants esthetic appeal to the consumer. There was also evidence that exposure to drought via RDI enable plants, on transplanting, to be more robust in coping with the stresses of different environments (Cameron, Harrison-Murray, Fordham, Wilkinson, Davies, Atkinson and Else 2008).

From knowledge of plant demand for water and that of the individual species grown on a nursery, it was possible to optimise irrigation application uniformity to provide water savings and to determine the most suitable method to apply irrigation (overhead sprinklers, trickle irrigation, or bed irrigation) and by what method plant water use can be determined accurately. We carried out a great deal of work in comparing the measured pot compost

moisture content with that of using estimates of evapotranspiration rates (ETp) to determine when and how much irrigation to apply to make savings and control growth (Grant, Davies, Longbottom and Atkinson 2009). Much of the detailed early development work in scheduling irrigation was formulated using irrigation approaches which were based on the application of technology, such as trickle irrigation, which requires pipe work and drippers to deliver water to each plant/pot. Much of the nursery industry has to rely on more economical approaches to delivery water, such as the less water use efficient overhead sprinklers. It therefore seemed appropriate to determine, under some circumstances where the cruder approach to irrigation application efficiency, i.e. cheaper overhead irrigation, could be used to schedule deficit irrigation. Result showed that very different crops (architecture and water use), with respect to water demand could be scheduled using the same system and more importantly deficit irrigation could be applied with the same effectiveness whether trickle, or overhead irrigation systems were used (Davies, Harrison-Murray, Atkinson, Grant 2016).

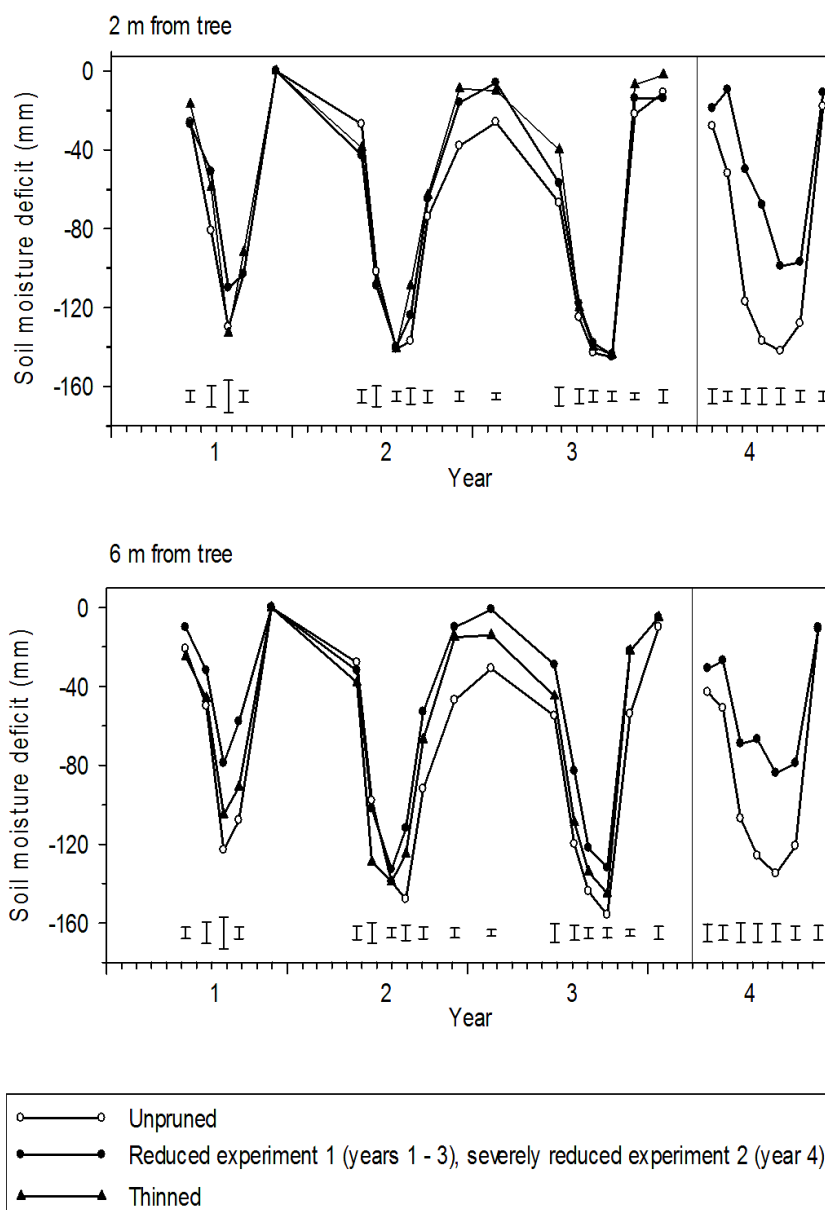
The Agricultural and Horticultural Development Board (AHDB), part funded the designing and production of an experimental nursery stock irrigation facility at East Malling (the East Malling Water Centre - EMWC). The intentions of the facility were to provide a focal point by which the industry could engage and see demonstrated state-of-the-art approaches being used and developed, to promote water conservation, water use efficiency and methods to apply irrigation uniformly. One of the major goals of the approach was not just to evaluate different industry used approaches to irrigation application, but also monitor, quantitatively, how much water was getting to the plant relative to that being lost by various routes (drainage, evaporation or missing the bed). The pot containing beds were lined so that irrigation water could be collected, and quantified, and its chemistry, post-irrigation, could be determined with respect to nutrient wash out.



Figure 46. The construction phase of EMWC (left), showing the main central culvert (left edge of image) where drainage water was to be collected and the EMWC in experimental operation with plant material on the different irrigation beds (right).

It is also appropriate to mention here our work with Association of British Insurers (ABI) aiding them in understanding the causes and remedies of spikes in insurance claims made for apparent subsidence damage to domestic properties (Higgs, Davies, Dunn, Griffiths and Atkinson 2014). These claims were, primarily, from older housing within the London region where properties

where situated on London clay soils. These clays shrink significantly, particularly during the summer, as the soil dries and tree water use increases and this may be part of the cause of the drying. Trees which are close to shallow house foundations are therefore implicated in subsidence claims. Stakeholders throughout the industry needed knowledge to determine firstly, at what level were urban trees responsibly for subsidence and secondly, were current management (tree pruning etc.) approaches, to limit tree water use, effective. All the stakeholders involved did not want to see the removal of trees from the urban landscape, which would have been the simplest solution. A great deal of field work, using a wide range of approaches was carried out during this 5-year project looking at quantifying tree water use in relation to soil moisture content. Many experiments used large trees and ‘Tree Officers’ (tree surgeons) applied industry management practices which were assessed experimentally with respect to changes in tree structure (the leaf canopy) and water use (sap flow).



Figures 47. The effects of canopy manipulation treatments for London plane (*Platanus x acerifolia*) trees on the soil moisture deficits, measured with a neutron probe, at 2 and 6 m from the tree trunk.

This figure shows that the soil under unpruned control trees dries more (the soil moisture deficit being greater) relative to the thinned and reduced trees. The ‘reduced treatment’ trees, which had the largest amount of canopy removed by pruning, conserved the most soil moisture, but there were no significant treatment differences in year 2. The soil moisture conservation effect of the reduced canopy treatments was clearer when some trees were re-pruned in the 4th year of the experiment.

The important conclusions from this work showed that despite the limited esthetical appearance of the trees directly after post-canopy reduction (known as ‘hat racking’), this did reduce tree water use. However, the trees in many cases were able to re-establish their canopy architecture and leaf area (determined by image capture and analysis) much more rapidly through stimulated regrowth. While reductions in tree water use did not last beyond a 2-year cycle of pruning (Hippis, Davies, Dunn, Griffiths and Atkinson 2014). Other less invasive approaches, such as ‘canopy thinning’ (part of the internal canopy branches removed) had only very short-term effects on canopy area and water use. What a research paper often does not demonstrate is the time taken to get this information into the public domain. Some of the content of this paper, when it appeared in the original research report (Hippis, Atkinson, Griffiths, Dunn and Davies 2004) was interpreted in different ways and that has led to a degree of conflict between interested parties outside the project stakeholders. I have also been told that the report is frequently cited in legal subsidence cases.

Bioenergy production

The Department of Environment, Food and Rural Affairs (DEFRA) commissioned me to carry out some work on answering the question why there was little uptake of the opportunity to have a biomass energy generating business in the UK. A large part of this study involved examining published material and trying to consult with interested industry stakeholders. It seemed very appropriate at the time that the content and outcomes of the DEFRA report (NF0439) should be used to produce a peer-reviewed publication outlining the reasoning and challenges faced when contemplating establishing energy crop plantations. The focus of the work was very much on *Miscanthus*, a rhizomatous perennial grass (Atkinson 2009).



Figure 48. Commercially harvested and Miscanthus split rhizomes ready for planting (left), the variability in size and structure was apparent and quality of planted rhizome was analysed as factor determining crop establishment. The presence of rhizomes buds can be seen on the rhizomes in the middle of the image. The impacts of irrigation on the establishment of Miscanthus at EMR (right). Plants of the left side of the picture did not receive irrigation, while those of the right did.

The paper concluded that commercial seed production was not possible and that vegetative

clonal propagation would be required to use selected germplasm. The current process of rhizome production and its subsequent division can limit production even for the potentially small UK industry. For there to be uptake of new germplasm, a cheap and rapid vegetative propagation method was required, particularly when 10,000 to 40,000 plant propagules, per hectare, were required for optimal production economics. It was apparent that it was necessary to have high density plantings to maximise canopy light interception and biomass yields. The slow establishment of *Miscanthus* appeared to be limited by economics; evidence suggests that the cost of rhizomes was the major factor that constrained widespread planting at the right density.

A practical part of the DEFRA commission also included a field trial to determine the best way to establish field grown *Miscanthus* using commercially produced rhizomes. The approach also explored the consequences of rhizome cold storage as it was suggested that rhizomes were at their best with respect to survival if lifted and divided in early spring. Given the fact that the prescribed density of rhizome planting, required to achieve maximum yield per hectare (40,000 plants), meant that a large number of plants had to be lifted and divided before subsequent transport and replanting could take place, this inevitably meant storage of a proportion of the harvested rhizomes would be required. The results from this work showed that rhizome viability was high in March and cold storage had no impact on establishment. There was equally no evidence for differences in rhizome mineral, or carbohydrate concentrations due to storage temperature. Field establishment was improved by the use of compost mulching and the applications of irrigation from May to August. Soil moisture content during establishment was the largest determinant of yield (Davies, Longbottom and Atkinson 2011).

Biochar benefits to agriculture

I sat in on a meeting we were having with an entrepreneurial individual who once owned 'Green and Blacks' chocolate, he spoke passionately about the idea he was going to commercialise the production and development of biochar (type of charcoal produced by pyrolysis – baking in the absence of oxygen). I knew little about the subject at the time. The discovery of the impacts that Amazonia indigenous peoples had had on the improvement of their poor acidic tropical soils, and the benefits to their crop yields, through the application of biochar was considerable and experimentally needed validating in the UK. With my long-term soil scientist, and business manager colleague and friend (Dr. Neil Hipps) we developed a number of proposals to undertake both desk and experimental evaluations of the potential of biochar. At the start we were commissioned to do a commercial desk study specifically for the Southeast Region (Atkinson, Fitzgerald and Hipps, 2011). It seemed to me that this was a great opportunity to write a peer-review update of the situation with the intention of looking at how and why biochar may, or may not work in temperate regions. As they say, the rest is now history. I utilised this initial industry report to produce an extensive science review which was drafted for publication in 'Plant and Soil' and to date the impact of this paper continues to amaze me, as its citation index reaches 800, being my number one cited paper (Atkinson, Fitzgerald and Hipps, 2010).

This stimulated experimental work to evaluate the potential of biochar in field experiments, supported by the East Malling Trust for Horticultural Research. Experiments which used commercial growing approaches for strawberry, potatoes and barley showed over a range of

biochar incorporation rates (1 to 50 t ha⁻¹) that biochar had very few of the productivity benefits described in earlier work (Jay, Fitzgerald, Hipps and Atkinson 2015). The application of some 50 t ha⁻¹ of biochar to the soil was considered a rather extravagant and a highly unlikely quantity of biochar to be able to economically apply. The reasons why there was a limited response to the application of biochar, beyond those of soil alkalinisation and an increase in soil K, irrespective of biochar concentration, were explained by reference to the soil itself. Where biochar had shown crop productivity benefits these occurred most frequently on soils that were nutritionally and physically deficient, i.e. the tropics and their well-documented 'poor soils'.



Figure 49. Application of biochar to part of a field experiment carried out at East Malling Research. Part of a randomised design is shown prior to tractor incorporation. The experiment included strawberry, barley and potatoes. With the strawberry experiment running over two years.

The field experiments at East Malling were not on the best UK soil by long way, but on a soil ('Barming Series') which was agricultural productive and was not particularly degraded. The impacts of biochar at EMR, whether physical, with respect to changes in soil properties, or chemical, with respect to soil available nutrition, were always doing to be less apparent. My interest in biochar continues with a focus of the work now being directed at evaluating biochar specifically in situations where soil quality is poor and water retention is often a major problem. Much has been written about the potential of biochar to improve soil water holding capacity, but there has, until very recently, been very little experimental evidence to support the notion. Again, it is the poor sandy soils of the tropics and arid zones that are more likely to suffer from limited water holding capacity where it could limit crop productivity. More recent work has been developed around this idea of a 'poor soil' focus with respect to exploiting biological wastes as feedstocks of biochar and as a potential soil improver where environmental soil degradation has taken place (Atkinson 2017). Utilisation of biological wastes provides an important added value component to biochar production economics.

Communicating science to non-scientists

I very quickly became even more aware on arrival at EMRS that communication of what you were doing and why was very important. The ethos was very much one of doing science and research for a purpose. The industry for which this work was intended, were supportive and

enquiring, and engaged with great enthusiasm when we talked about our work. In order to achieve this 'technology transfer' as it was called, required a different approach from that of the normal seminar type science research presentation to which I had more familiarity. However, I very much enjoyed engaging and discussing my work with those who potentially might exploit the outputs to aid in the development of their businesses.

One of the recognitionary challenges in the world of science is the publication of scientific papers in appropriate journals. This requires the resources and opportunity to undertake research which asks fundamental scientific questions to evaluate conceptual hypotheses. This is the 'bread and butter' of the research scientist, but often does not rapidly lead to change, or innovation that a business, or industry might instantaneously be able to use. The former provides insight into how our world works, while the latter enables the workings of our world, through the application of science, to be changed. The application of science, or 'applied science' is not perceived in the same manner as that of basic science. Many of the issues within horticulture and agriculture are 'problem orientated' and there may be a challenge in fully researching why more fundamental aspects of scientific understanding are required at all – just solve the problem. It is easy to see why any industry or business might want to cut-to-the-chase and just tell me how to solve my problem; often a problem that they had last year. On a number of occasions I have had discussions, or answered questions related to – why do we need to understand how it happens? My answer to these types of questions has always been if you do not know how something works, or why it happens then any solution to a problem will likely have limited effect and you will have no insight into future solutions and the means to develop further improvements.

The dilemma that EMRS and EMR faced for at least 20 years was that of working for two masters. The scientific institution (Visiting Groups etc.) through internal and external review rightly always focussed on the quality of the scientific outputs and journal rankings in which our research was published, while 'our industry' valued the application of knowledge to solve problems, they were not going to read journal publications. The perceptions of applied science were lower than those of the more fundamental underpinning knowledge gathers. The key to solving this problem, at least at the individual level, was to get the space and develop the capacity to ensure as much of your work contained fundamental question orientated research along with problem solving applied research.

A good example of this approach is shown by work carried out with the intention of providing strawberry plant producers with 'better quality' plants. This requires a better understanding of the processes by which strawberry runners (the 'stolon' which connects daughter plants to the mother plant (see Figure 50) are produced biologically and commercially. The problem that the industry had was that the plants (or ramets) along the stolon differed in their rooting potential, viability and quality with respect to customer acceptance and potential yield.

A series of experiments were conducted to investigate this variability of ramet performance and prescribe approaches that would promote higher rooting potential in the less developed younger ramets. In a scientific sense the project provided the opportunity to understand the physiological processes involved in the hierarchical relationships established between the mother plant and the daughters along the stolon. This worked showed how stolon tissue development and function (rhizome hydraulics) determined the process by which resources,

water and nutrients, were shared by competing ramets on the stolon (Atkinson and Else 2012). The role of auxin transport (PAT) was assayed along the stolon and the movement of this growth regulating chemical was closely correlated with the physiological and developmental changes observed.

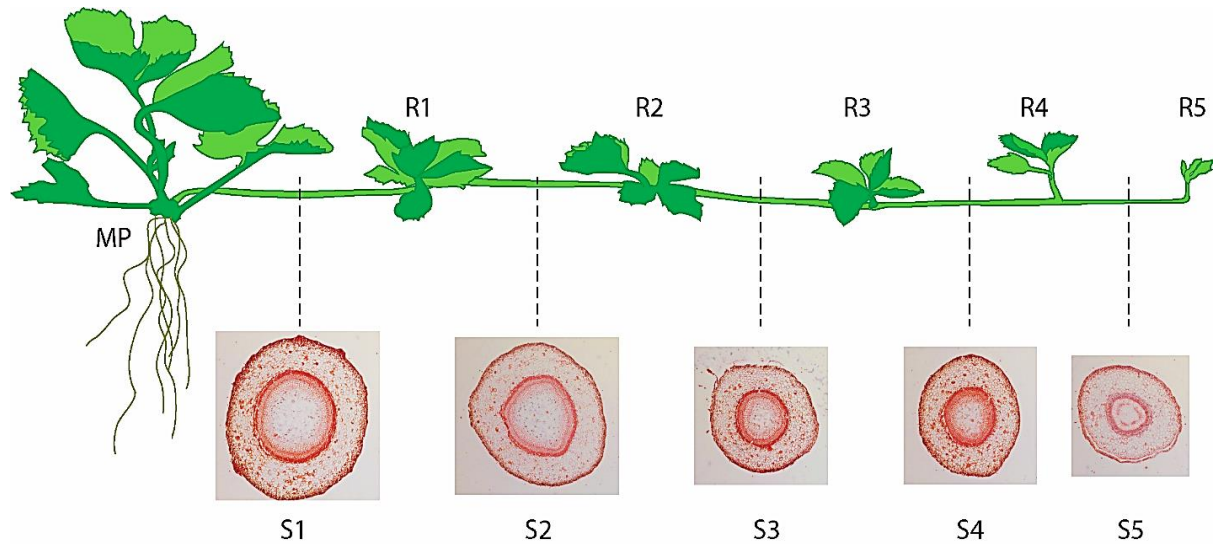


Figure 50. The diagram shows the relationship between structure and position of ramets (R) along the stolon from the mother strawberry plant (MP). This work provided a good example of links between structure and function and the means by which applied problem solving research can also provide insight into the basic biology, in this case, of resource sharing of ramets on stolons (Atkinson and Else 2012).

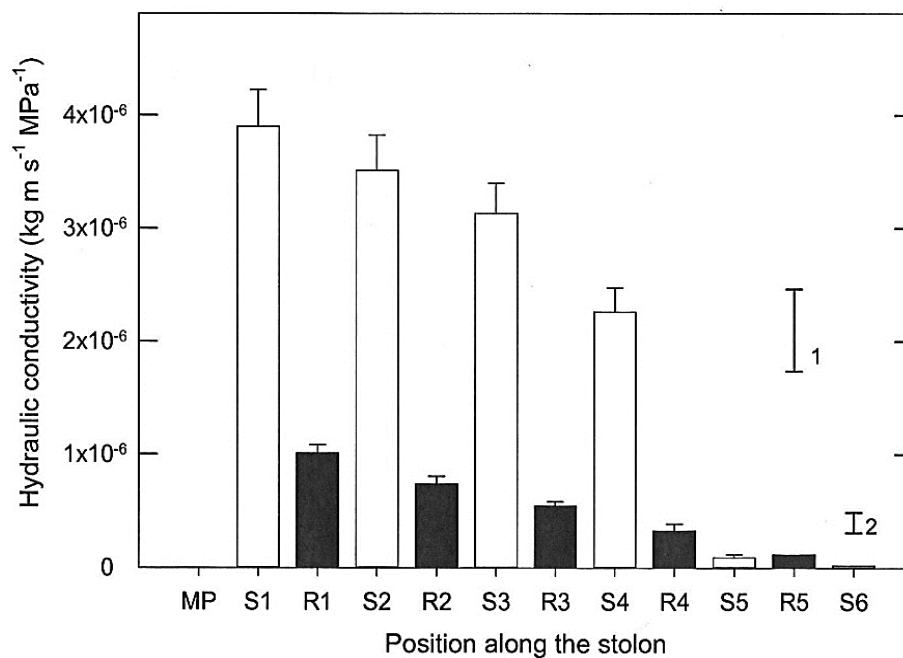


Figure 51. The changes in hydraulic conductance of the strawberry plant 'runner' hierarchical arrangement of the ramets along the stolon. The codes S refer to a stolon measurement and R refer to a ramet. They are present in a hierarchical manner as displayed in Figure 50. (Atkinson and Else 2012).

These data show how the conductivity declines along the stolon and is a reflection of the observed anatomy in Figure 50. It also links with plant water potential data (not shown) to explain how the lower order ramets are able to compete for water with their higher order sibling ramets.

When I arrived at EMRS, I only had peer-reviewed publications to my name, during my tenure I was fortunate to produce more papers directed at understanding ‘how and why’, while contributing to over 150 publications (*technology transfer reports*) specifically written for industry use and uptake. When I was appointed the Head of Science at EMR the opportunity arose to take on-board a leading role in the communication of my science and the vision of what EMR was all about. Not only did I spend a lot of time talking to people interested in hearing about the work being carried out at EMR, but I was able to develop a relationship with local news media that facilitated them seeing EMR as the place to come, to report and film on related horticulture/agriculture and food issues locally and nationally. This was very exciting for me and EMR with respect to frequent publicity broadcasts on national networks. Irrespective of what you might think of the output quality of these broadcasts, they kept coming back for more, in part I think because I was able to help them develop their story-line and I could deliver a clear non-science vocabulary message in the limited time available. Typically they would arrive mid-morning with the intentions of putting the TV piece together on the air at lunchtime and a longer piece for the 6 o’clock news.



Figure 51. Shown here are just a couple of the many events linked to the publication of my work and that of EMR. The filming of Countryfile featuring work on intensive pear production (left) and me talking to Chris Beardshaw during the making of the TV programme - Apples: British to the core.

For me perhaps the most prestigious presentational event of all was the invitation to speak at the Palace of Westminster to MPs and Lords at a meeting of the All Party Parliamentary Group on Science and Technology in Agriculture (APPGSTA 2009-10). I assume that they must have liked something I said about the importance of horticulture, and horticultural research, and it’s inappropriate and unwise demise over the last 10-years, as a couple of years later, I was asked to speak on another subject to this committee.

SECTION 7: NATURAL RESOURCES INSTITUTE AND THE UNIVERSITY OF GREENWICH

Great things were achieved at EMRS (and EMR), for me becoming the Head of Science was very important and a reflection of my contribution to not only research, but also its management and helping to save it from closure after the expressions of Quinquennial Review of 2005. Privatisation under the East Malling Trust for Horticultural Research (now the East Malling Trust), with an extremely able and engaging set of colleagues in the senior management team, enabled us to achieve a balanced research budget for a number of years as a private enterprise. This was not something that had been achieved while we were part of Horticulture Research International (HRI). I was extremely proud and I am still, that this was what we had to do, this was what we were asked to do and this is exactly what we did. I did have some regrets that this work took me away from my love of research which was now going at a slower pace. As is often the way the visions of others suggested alternative ways to develop EMR and when these changes began to be put in place it became very obvious to me that the financial philosophy was not of a type that seemed appropriate to me, or one that would secure the future EMR.

Once again fortune smiled on me; one of my great regrets in my career (and my dream) up to this point was not having the full 'academic experience' and being able to explore my enthusiasm for teaching and learning. There had been several occasions where opportunities had arisen to move into academic jobs, but none were successful. I recall two very prominent universities in the UK doing something that today would not be allowed and even then it was never committed to paper. This was age discrimination; having started by career in research a few years later than the traditional appointment age of a new blood lecturer, and the fact that I would cost more to be employed, irrespective of already having a good publication record, was given as the reason for either not interviewing me, or not appointing me after an interview. Anyway, given my vision of what was going to happen at EMR, the opportunity to move to the Natural Resources Institute, at the University of Greenwich, provided me with a not too difficult decision to make. This was the final piece of my dream, the realisation of the opportunity to spend more time developing the research capacity of others and passing on my knowledge and experience to others. The icing on the cake was the opportunity to work with others both within and outside the university to develop research with a global impact. The global impact that NRI has from its agricultural research delivery is nationally and internationally recognised and reflected in NRI's very high impacts ranking in the 2015 REF exercise. This of course has brought new opportunities and experiences to work in novel areas particularly overseas, including *Jatropha* (de Jesús Osuna Canizalez, Atkinson, Vázquez Alvarado and Barrios, Edwin 2015); rice (Afiukwa, Faluyi, Atkinson, Ubi, Igw and Akinwale 2016) and even pineapple (Williams, Crespo, Atkinson and Essegbey 2017). This has also included teaching and the development of the research potential of a good number of Masters Students on the programmes (Agriculture of Sustainable Development, Sustainable Environmental Management and Applied Plant Sciences) that I lead.

CONCLUSIONS

This is a good point to draw this career account to a close and spend a moment in indulgent reflection. I have been very fortunate to work with a lot of amazing people and to be able to travel and see much of the world. I have also been able to set myself targets and achieve my aspirations. What still astounds me is that every year something new and interesting comes along that makes me stop and think – ‘this is a new challenge’, this is what life is all about. I have also been extremely fortunate to have enjoyed every moment of a long and challenging career. It’s been varied and forever changing, never the same, never dull. I have always enjoyed being able to rise to the challenge of doing something new on the learning curve of life. I am very grateful that ‘work’ continues to feed my thirst for knowledge and the answers to all those questions. If I were to be asked what has been the one critical element in making this happen, it has to be; with the application of effort all obstacles can be overcome.

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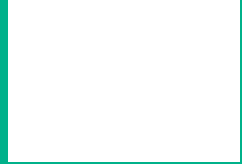
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