Gaps in the programme were filled by impromptu papers from volunteers recruited on the spot. The success of the meeting owes much to their contributions, as well as to the excellent quality of the papers from speakers who could attend.

Many people contributed to organizing the meeting and the final production of this book. We particularly wish to single out a few for their outstanding support: Sheila Wilson, who assisted during this whole process; and the producers from CAB International, particularly Rachel Robinson, Claire Gwilt and Rebecca Stubbs, who very patiently listened to the editors while they were making up their minds during the production process. We also thank our sponsors, Campbell Scientific, Delta-T Devices, Li-Cor, ADC BioScientific, PP Systems and The Royal Society of Edinburgh. Finally, a big vote of thanks to all the contributors to this volume and to all those who corresponded with us at several stages with useful information.

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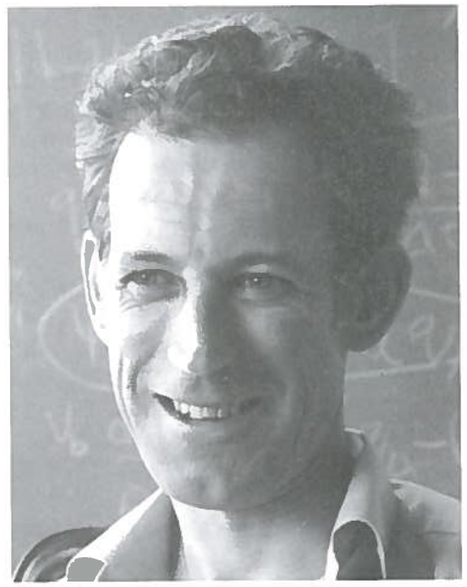
Foreword



Professor Paul Gordon Jarvis retired in April 2001 after 26 years as Professor of Forestry and Natural Resources at the University of Edinburgh, and after more than four decades as one of the world's most prominent plant ecophysiologists. His particular specialty is the exchanges of water and CO_2 between forest trees and the atmosphere. During his career Paul stayed at the forefront as this field changed from a minor topic on the margins of forestry and ecophysiology into a major focus of international research with implications for the future of the whole earth and its climate. For his achievements Paul Jarvis received one of science's highest honours when, in 1997, he was elected a Fellow of the Royal Society.

Paul was born on 23 May 1935 in Tunbridge Wells, Kent. His father had joined the Royal Flying Corp and flown Sopwith Camels in World War I. Later, in World War II, he was a founder member of the Royal Air Force Regiment, looking after aerodrome defences throughout the UK. When not serving in the RAF, Paul's father was a farmer and in the post-war period had a milk round, delivering milk from a pony and trap. Later he became an agricultural adviser, subsequently returning to farming in Hertfordshire. Paul's mother had been

secretary to the geneticist Karl Pearson at University College, London. Paul and his two brothers Brion and Richard, therefore, had a rural upbringing – but with an academic slant to it: they built a raft to use on the farm pond and they became interested in the wildlife on the farm. Paul and his younger brother Richard attended Sir Anthony Brown's School in Brentwood, Essex. Paul was academically gifted and went to Oriel College, Oxford, where he read Botany and rowed.

Many careers are built on a number of important events, some planned and some arising by accident. For Paul, a very important event was undoubtedly his marriage to Margaret, in September 1957, just 3 months after both had graduated with BA degrees in Botany. They moved to Sheffield, and together began graduate studies at the university. Paul's research concerned the growth and regeneration of sessile oak, *Quercus petraea*, in nearby relict native woods, while Margaret investigated environmental limits to the geographical distribution of *Prunus padus* and other northern and southern species. They received their PhDs in 1961 and were ready to explore the wider world.

Two research careers required two research positions, so their next move was to the Institute of Plant Physiology at the University of Uppsala, for which both had been awarded NATO fellowships. Paul was to study the mycorrhizal requirements of oak and pine with Elias Melin while Margaret would work with Henry Rufelt on the water relations of tree seedlings and their relationships to environmental conditions. Paul soon decided that Margaret's line of work was the more interesting, so they teamed up. This brought Paul to the field that was to become his particular specialty. Together with Henry Rufelt they compared the growth and transpiration responses of tree seedlings to water stress. Significantly, they began using the leaf chambers developed by Olle Björkmann and Paul Holmgren to study the transport of CO_2 and water vapour to and from leaves. When the NATO fellowships ran out they continued, supporting themselves on local grants and a half-time research assistantship for Paul with Carl-Olof Tamm at the Royal College of Forestry in Stockholm. At the suggestion of Nils Fries, their very supportive Head of the Institute, Paul then submitted his Swedish work to Uppsala University, gaining a second doctorate (Fil. dr) and his 'competence' to teach at Swedish Universities, whereupon he became a senior lecturer in the Department of Plant Physiology at the Royal College of Agriculture in Uppsala. Together Paul and Margaret produced an impressive ten joint papers in these 4 years. Paul and Margaret's partnership entered a new phase when their son Eric was born in 1964. Margaret remained active in science as a scientific editor and translator, notably translating *Stålfelt's Plant Ecology*, with Paul's assistance, published in 1972.

In 1963 Paul attended two scientific meetings that significantly affected his career. The first was a Symposium on Water Stress in Plants, held in Prague. Michal Marek recalls the 'vigorous invasion' by a young fellow from the UK who took part in many discussions with much enthusiasm, and considerably contributed to the success of this meeting. Those who know Paul will understand exactly what Michal means. Paul subsequently joined the editorial board of *Photosynthetica*, and reviewed an endless stream of manuscripts for them. In this way Paul helped many young scientists from Eastern Europe to maintain

international standards during the Soviet era of isolation. When the barriers were removed Paul helped them back into the mainstream of European science, working with Michal Marek to design a Czech project to study the effect of increasing CO_2 concentration on forests and to find EU funding for it. Paul also helped them to set up their large semi-open chambers and to carry out the long-term experiments. This unstinting support over many years reveals something of the man beneath Paul's 'vigorous' exterior. For his contributions to Czech plant physiology, Paul received the Gregorius J. Mendel medal of the Czech Academy of Sciences in October 2000. But such honours were for the distant future. More importantly for Paul's immediate future, at the Prague symposium he also impressed Paul Weatherly, then Professor of Botany at the University in Aberdeen, who offered him a lectureship at Aberdeen a few years later.

The second significant meeting in 1963 was a UNESCO Arid Zone Research symposium, held in Montpellier. There Paul met Ralph Slatyer, with whom he had corresponded. In those days the CSIRO Division of Land Research and Regional Survey in Canberra kept a full position for visiting scientists and this had just fallen vacant. Ralph Slatyer wasted no time in offering it to Paul, who accepted and moved there the following year. It was a good choice as their interests overlapped splendidly. Ralph Slatyer's research interests had evolved through ecoclimatology to a heavy involvement in micrometeorology and then to environmental plant physiology. By the early 1960s he was attempting to set plant/water relationships into a full environmental context and was using leaf chambers to gain crucial information. Paul's interest had evolved out of botanical ecology, but he had arrived at the same point with an equal desire to apply the exact methods of the physical sciences to the problems of understanding how plants interact with their environment. In that group, which included such notable scientists as Calvin Rose and John Begg, Paul began to measure stomatal conductance in the field using portable diffusion porometers, and learned how to measure fluxes of water and CO_2 using micrometeorological techniques. This combination of laboratory and field research was to become a feature of Paul's scientific research.

The Aberdeen Years, 1966–1975

A letter from Paul Weatherly, offering a lectureship in the then vibrant (now extinct) Botany Department at the University of Aberdeen brought Paul back to Britain. He arrived in 1966 with his family, now increased by the arrival of Kathryn in Australia. He was filled with enthusiasm to apply the Australian approach to ecophysiology to a Scottish forest: he wanted to understand its exchanges of water and CO_2, and so ultimately its growth, by building upwards from a detailed knowledge of the functioning of its needles. In particular he wanted to match up the layer-by-layer transpiration and CO_2 assimilation calculated from physiological models with the gross sources and sinks calculated from the humidity and CO_2 concentration profiles in the canopy air space. It was a bold plan and with his characteristic drive he won from NERC the largest research grant they had made up to that time to carry it out.

A field site was chosen in a stand of Sitka spruce at Fetteresso Forest, about 30 km from the University, where they worked from a caravan powered by a diesel generator. His university laboratory was in an old woolshed between the Botany and Forestry departments. Much time was spent travelling back and forth between the field and lab in a canvas-topped Land Rover, which made for chilly travel in winter. On the site, access to the upper canopy was by a plank between two ladders lashed to trees in adjacent rows. Rope handrails ran between the ladders a little higher up to give a sense of security, but even so this arrangement was a bit tricky when there was ice on the planks. Strong winds, lightning and mice added to the difficulties of maintaining the measurements. His lab in the woolshed became known as 'Jarvisland' by others in the Botany department. In it Paul built his tight-knit team from a progression of students, post docs, technicians and visitors. Merv Ludlow was his first physiologist and Joe Landsberg his first micrometeorologist. John Norman and Neil Turner soon followed, as did Lubosh Nátr from Czechoslovakia, Stan Tajchman from Germany, and many more.

Some of Paul's ambitions exceeded the technology and understanding available at that time. For example, use of the Bowen ratio approach to measure water and CO_2 fluxes over forest canopies was in its infancy, requiring accuracy of measurement to be at least an order of magnitude higher than over crops. Thus, most of the micrometeorological flux measurements were never published, but from it all Paul produced a landmark study and some enduring innovations. Diffusion porometers suitable for use on conifer twigs did not exist, so Paul, with Mike Beardsell and Ewan Neilson, developed the 'Dingbat' porometer. It introduced the null-balance principle that has become the standard today. His study with John Norman of the effect of canopy architecture on radiation penetration into the canopy was highly influential and laid the foundation for the later MAESTRO model. With Brian James and Joe Landsberg he made some of the earliest measurements of CO_2 fluxes over a forest, and from their work they learned enough to write a review that remains a standard work today. Little was known at the time about the physiology of Sitka spruce, despite its pre-eminent place in commercial forestry in the UK. In parallel with the micromet approach in the forest, Paul developed a strong programme of leaf, root and whole plant physiology of Sitka spruce in the laboratory. Together with the micromet work, this led ultimately to 30 publications and five Ph.D. theses on Sitka spruce.

One wonders how Paul fitted it all in. Aside from his research work, Paul developed his Czechoslovakian connection further, co-editing *A Manual of Photosynthetic Methods* with Zdanek Sestak and Jiri Catsky. In a personal tour de force, he co-authored six of its chapters. Despite these commitments, Paul maintained a strong presence in the lab., contributing good ideas of his own and, equally importantly, listening to the good ideas from his team, shaping them and backing them with resources. In discussion Paul was often challenging, but his team came to recognize this as one of his strongest traits. As John Norman put it 'We could both pour our best efforts into the discussions with great intensity, without any personal animosity and with a kind of enjoyment that goes with being able to concentrate on the problem in hand, unencumbered by protocol'. This could be daunting to students, but they came to understand Paul's underlying generosity of spirit and his concern for their success. It is a tribute to Paul's qualities as an educator that of the more than 30 PhD students that he supervised in his career, all completed their degrees successfully. His post docs were similarly fortunate. He taught them to ask significant questions, to be quantitative and rigorous in pursuit of answers and, when writing their papers or theses, to state the question at the beginning and answer it at the end. Not least, he taught them to write science using symbols and quantities in the SI-approved manner! Even when he was away for long periods the cooperative spirit and the close loyalties Paul had built up within the team carried them along, and the work went on as usual.

This part of Paul's career ended with a period of leave from the University, to spend time in Seattle as a consultant to the US Coniferous Forest Biome component of the International Biological Program. This 'integrative' period produced some of his most influential papers. With Ken Read, he developed a phenomenological model of photosynthesis in relation to environment, using an optimization approach. Based on that approach, he formulated the 'Jarvis model' of the response of stomatal conductance to leaf water potential, saturation deficit, light temperature and atmospheric CO_2 concentration. This became the standard phenomenological model of stomatal responses to environment. Also whilst in Seattle he wrote an influential review of hydraulic transport mechanisms in plants, extending the resistance model by adding a resistance law for conduction in the xylem. Together these made it possible to model water vapour and CO_2 exchanges from whole forests – a tremendous achievement in just 9 years.

The Edinburgh Years, 1975–2001

While still in Seattle Paul was recruited by the University of Edinburgh to become its Professor of Forestry and Natural Resources. He moved there in 1975. As Professor he automatically became Head of Department. Previously, he had had no significant administrative experience, except as the leader of a research group. The Department was medium-sized by the standards of the day, with a strong forestry tradition. However, what had been the Department of Forestry in 1968 had become the Department of Forestry and Natural Resources, and the forestry degree had become Ecological Science with Honours streams that also included Resource Management and Wildlife Management. It now taught courses in animal ecology, remote sensing and hydrology as well as plant science and forestry. Only two members of staff had ever met Paul, but his reputation preceded him, and the Edinburgh colleagues braced themselves, expecting him to deprecate some of the activities and especially the management-related teaching that had evolved over many years. Paul must have sensed the unease, and when asked what changes he would be making, replied 'I want to see how it all works first'. For that one sentence he gained huge respect.

However, he soon set about introducing rigour into teaching, and especially into practical classes. He had the departmental workshop constructing

batches of Scholander pressure chambers, and second year students were required to make, and fully analyse, pressure–volume relationships of leaves. This was an excellent experience, involving some comparative ecology (leaves from sun and shade, different life forms, different treatments), manipulative skills, conceptual understanding, and data handling. Most students rose to the challenge and were able to infer the elastic modulus of the cell walls from pressure–volume curves, even though they were only second year students. In his Honours teaching, students would construct and calibrate thermocouples, and his first undergraduate lectures on the Omega factor preceded publication of his paper introducing Omega to the rest of the world. Amazingly, the students mostly took to Omega like ducks to water.

Paul was also enthusiastic about undergraduate field courses, and decided to take the second year field course to Bettyhill on the north coast of Scotland, staying in an old school house belonging to Aberdeen University, and sometimes taking his younger daughter to act as cook. It was very handy for visits to the Flow Country, a vast area of blanket bog with very controversial private plantations of conifers. The weather in late September was generally 'bracing' but the coastal scenery was quite magnificent, providing a habitat for rare plants such as *Primula scotica*. This was never blooming when the course ran, but it didn't seem to matter, as Paul's pride and joy was a stand of *huge* Sitka spruce trees grown on a local estate. Bettyhill was almost a day's journey from Edinburgh, and after several years was abandoned in favour of Firbush, the University's outdoor centre on Loch Tay. Paul's enthusiasm for field courses has persisted into his retirement and he still goes to the Firbush field course – always with a good idea for a student project on trees.

On their move to Edinburgh Paul and Margaret saw advertised a large stone house named Belmont, in Dalkeith just 5 miles south of the university. It was described as having 'fourteen rooms but no kitchen'. Belmont was in a poor state. Despite some misgivings, they bought it and began its repair and improvement – a project that lasted most of their 26 years in Edinburgh. They were very generous with this house, so that Belmont became a base for many of Paul's old colleagues and students on their visits to Edinburgh. One of its endearing features was the shower: a Victorian masterpiece of engineering with seven taps, by which one could direct water to any chosen region of the body. No-one had seen anything like it, not even in museums. The house had flower beds, a prolific vegetable patch, several *Eucalyptus* trees raised from seed brought from Australia (a symbol perhaps of the Aussie connection), and a large lawn where croquet was played. At the end of the academic year Paul would invite colleagues (with families) and Honours students to a party at Belmont. Wine flowed, dogs became excited, croquet was played, and speeches were made. A good time was had by all. He and Margaret also held an annual party on Boxing day, where relatives, neighbours, colleagues and visitors could meet each other. There was always a gigantic jigsaw puzzle in progress, so the more introverted could escape from the crowd and work on the sky.

Paul brought people, equipment and ideas with him to Edinburgh. This influx invigorated the Department and increased its size and output. Most of Paul's efforts in the Edinburgh years went into his research – he loved to be in

the field, and he loved to receive visitors. A favourite annual event for members of his group and the visitors and their families was a trip to the highlands in the spring, staying in a Youth Hostel and walking the hills. Paul was always very fit and an extremely strong walker (he, Margaret and Eric ran marathons). His research interests in the early years included: the mechanism of stomatal function, the response of stomata to humidity, sap flow in trees, photosynthesis, light interception by foliage. He established a photosynthesis laboratory and a water relations laboratory; and the departmental workshop was much-excercised in making various pieces of equipment to satisfy Paul's desire for technical excellence. He extended his modelling work, developing the MAESTRO model of radiation penetration and absorption in plant canopies with Jenny Grace and Yingping Wang. He interacted with his research group through morning coffee and Friday evening sessions in Lesley's bar, and he successfully balanced the role of being Head of Department with that of being leader of the group, although there were inevitable conflicts of interest. One of his pleasures was to escape the tedium of administrative duties and join his team at their field base: the caravan this time being in Roseisle Forest near Elgin. Paul's review of plant hydraulics had proposed a theory of homeostasis in water-conducting properties as stands developed. Paul built a team to test this. David Whitehead and John Roberts, of the Institute of Hydrology, were the main researchers, and Dick and Doris Waring joined in during their year's visit. Sometimes being department head had its advantages, as when there was a rush to strip hundreds of bags of branches from the forest, which were starting to grow mouldy in storage. Paul not only joined in the task but commandeered research and administrative personnel to help as well!

After 6 years Paul decided he would rather not be Head of Department any more. He duly went to the Dean and made his position clear. To Paul's surprise the Dean agreed to release him from the position, instigating the scheme of 'rotating Headship', which caught on fast, and has prevailed throughout the university ever since.

To mark his renewed focus on research Paul took a sabbatical year, visiting old colleagues Joe Landsberg, at the time Chief of CSIRO Forestry Division, Neil Turner, then at CSIRO Division of Plant Industry in Canberra, and Jenny Grace and David Whitehead, at the Forest Research Institute in Rotorua, New Zealand. He also spent 3 months in Palmerston North where his brother, Brion, lectured in microbiology at Massey University. Paul had arranged a desk at DSIR Plant Physiology Division and Keith McNaughton was assigned to be his minder. No collaboration was planned but they hit it off immediately. Keith was a micrometeorologist with an interest in evaporation and the theory of advection. They wrote a review of evaporation from catchments, *for the first time* treating the ground vegetation and the boundary layer above as one interactive system. Keith McNaughton visited Edinburgh for a month in 1984 and the work was extended to a discussion of 'scaling-up'. This paper appeared just when the likelihood of man-induced climate change was becoming generally recognized and their work allowed ecophysiologists to see how information on single leaves, single trees and small stands of trees could project upwards onto the regional and global scales. The 'Omega factor' from those papers is now

permanently linked with Paul's name. Through this work Paul led the way as the principal concerns of environmental physiology changed from the economic productivity of crops and forests in individual fields and stands to their ability to adapt to a world with higher atmospheric CO_2 concentrations. With Derek Eamus, he wrote the first comprehensive review of the effects of CO_2 fertilization on tree growth. This helped set the research agenda as the field grew dramatically.

With the improvement of eddy covariance for measuring fluxes over canopies, the science that he had started back in his Aberdeen days had become much easier. One could collect data continuously rather than in short campaigns, and this allowed understanding of seasonal changes in the control of gaseous exchanges between forests and the atmosphere, and subsequently total fluxes to be compared between years. Paul returned to Sitka spruce, selecting a stand near Aberfeldy where he also had a cottage (the first cottage was shared with his brother, the second cottage is at the edge of the forest). At that time NERC was starting a thematic programme TIGER (Terrestrial Initiative in Global Environmental Research), and he tapped NERC funds to participate in BOREAS. He loved participating in international projects – and there were many. He especially enjoyed BOREAS; it was a chance to 'get away from it all' and immerse himself in his research in the 'field'. The comradeship and contact with old friends was part of the appeal. He was also involved in the HAPEX-Sahel experiment and a whole string of European projects, and was a leading player in EUROFLUX, a project to measure fluxes of CO_2 and water vapour over forests throughout Europe.

At the same time, he was making a huge effort as co-ordinator of ECOCRAFT to evaluate the response of trees to elevated CO_2 by using open-top chambers, branch-bags and other facilities at almost every European site where forest research was active. In this period his capacity to aid, encourage and inspire younger scientists was especially evident. ECOCRAFT laid the foundation for modelling forest response to rising CO_2 concentration and temperature across Europe and was the forerunner for the subsequent suite of projects in CarboEurope. It provided the launching pad into climate change and carbon cycle research for many young scientists across Europe. Yes, he was often away, but when available he was uncommonly good value.

Paul also enjoyed editing. With Harry Smith and John Raven, he co-founded *Plant Cell and Environment*, which rapidly became one of the top journals in plant sciences, and still is. He would always exercise full 'Jarvisian rigour' in dealing with submitted papers, and sometimes his critical comments incurred the wrath of authors. Distinguished scientists would visit Paul to discuss their science and sometimes the matter of Paul's comments on their manuscripts would be raised. Not all authors could bear Paul's robust style of discussion: on one occasion a very senior Harvard professor required post-Paul therapy in John Grace's office. A stiff cup of tea in the Atholl Room was required to achieve full recovery. On other occasions, discussion frequently continued over 'a pint' in the local pub.

During his Edinburgh years Paul led substantial research teams working on a range of topics from the role of vegetation type in catchment water balances,

through stomatal behaviour in the field and physiology of stomatal action, boundary layer properties of leaves and canopies, water transport in plants, agroforestry, carbon balance and growth of vegetation, nitrogen supply rate, growth, photosynthesis and carbon allocation, to scaling up CO_2 and water exchange processes from leaf to regional scale. This work involved collaborations with the Institute of Hydrology, the Institute of Terrestrial Ecology, the Forestry Commission and the Macaulay Land Use Research Institute, as well as laboratories in Belgium, France, Germany, Italy, the Czech Republic, Sweden and Finland. He was international co-ordinator for an IGBP/GCTE Core Project studying the impact of elevated CO_2 and temperature on European Forests (ECOCRAFT). He was involved in the BOREAS with over 200 scientists, largely from North America. With colleagues in the Institute of Ecology and Resource Management he set up the Edinburgh University Biosphere–Atmosphere Programme (EUBAP), which had three major components of impact studies, modelling and flux measurements. His most exciting recent development is a theoretical analysis of the role of spatial scale in exchange of water and carbon by plants, crops – natural and semi-natural vegetation. The analysis leads to far-reaching consequences with respect to our fundamental ideas about use of controlled environments, water use, vegetation types, experimental design and such questions as the likely long-term effects of rising atmospheric CO_2 on vegetation.

Some measure of Paul's success and prominence can be gauged by the formal honours he has received and the prestigious positions he has held. He was elected to Fellow of the Royal Society, the Royal Society of Edinburgh, the Royal Swedish Academy of Agriculture and Forestry, the Royal Science Society of Uppsala, the Institute of Chartered Foresters, and the Institute of Biology, and was awarded the Gregorius J. Mendel Medal of the Academy of Sciences of the Czech Republic. He has served as President and on the Council of the Society for Experimental Biology, on the Natural Environment Research Council Terrestrial and Freshwater Sciences Technology Board, as a Commissioner for the Countryside Commission in Scotland, on the AGBP/BAHC Scientific Steering Committee of the International Geosphere–Biosphere Programme, on the John Muir Trust, and on the committees of many other national bodies. He was co-founder and Sectional Editor of the journal *Plant Cell and Environment*, and served on the Review Boards of *Photosynthetica*, *Tree Physiology* and *Agricultural and Forest Meteorology*.

Retirement in Aberfeldy

Before he retired Paul and Margaret had bought a small farmhouse with 5 acres of land in the shadow of Griffin Forest, near Aberfeldy, and had begun to plant an arboretum and improve the house during weekend visits. On retirement they sold Belmont and moved there permanently. Paul's new interests include a practical project concerned with restoration of native woodland on severely over-browsed hill land. Paul and Margaret also win prizes at local horticultural shows for the fruit and vegetables from their garden. They are now

grandparents and visit their younger daughter, Alice, and her family in Namibia as often as they can.

This does not mean that Paul has entirely adopted the lifestyle of a retired country gentleman. In 2000 Paul became a 'Director' of the Edinburgh Centre for Carbon Management, a small company located near the University, concerned in part with carbon sequestration by forests to meet 'Kyoto goals' and is now able to take a more active part in the business. He maintains an office at the university and comes in weekly, when not out of the country, attending seminars and discussing research. Paul still has research results to digest and papers to publish. His involvement with EU projects continued through 2003 as his last graduate students complete their degrees. Paul also continues on as Principal Investigator of a NERC project with John Moncrieff and Keith McNaughton. Also, with Griffin Forest on his doorstep, Paul is keen to see the next stage of the work there, the thinning experiment, go ahead and he is doing what he can to assist that.

So 'retirement' is a relative term for Paul. He has diverted some of his boundless energy into new directions, but most of his old interests remain. We will see his name in print again, and scientists throughout physiological ecology will continue to feel his influence for many years to come. We wish Paul and Margaret a long, happy and *productive* retirement.

Keith McNaughton
John Grace

1

Stomatal Control of Transpiration: a Major Dilemma 100 Years Ago

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The important role of stomata in facilitating the gas exchange of leaves had already been recognized in the second half of the 19th century, but nevertheless there remained a great deal of confusion about the extent of the control that they could exert. The very influential textbook by Strasburger *et al.* (1903) left the question of the degree of the control of transpiration unresolved:

> The cell walls of all living organisms are saturated with water, and, when the cuticle of the epidermis is not too strongly developed, water is constantly evaporated, even from uninjured cells... Evaporation is also promoted by the numerous Stomata (Air-pores) which penetrate the epidermis, and which give the air, saturated with watery vapour, an opportunity to escape from the intercellular spaces.

This clearly suggests that a significant proportion of transpiration is outside the control of the stomata, a conclusion that appeared to be supported by a lot of contemporary experimental evidence. Although we now have a clear picture of the significance of stomatal control, and we view stomata as being of central importance in the evolution of land plants (Edwards *et al.*, 1998), it is right to acknowledge the contribution of one plant scientist in particular, J.V.G. Loftfield, made over 80 years ago. It is salutary to recall that Einstein had introduced his special theory of relativity in 1905 and his general theory of relativity in 1915, and yet the full significance of the role of stomata – something so indispensable to our understanding of living systems on earth – remained unresolved until 1921.

At the Close of the 19th Century

One of the most influential early papers on stomatal physiology was that of Francis Darwin (1898), and it serves as a convenient point from which to start this brief historical survey. Darwin gave a comprehensive account of some

 Forests at the Land–Atmosphere Interface (eds M. Mencuccini, J. Grace, J. Moncrieff and K.G. McNaughton)