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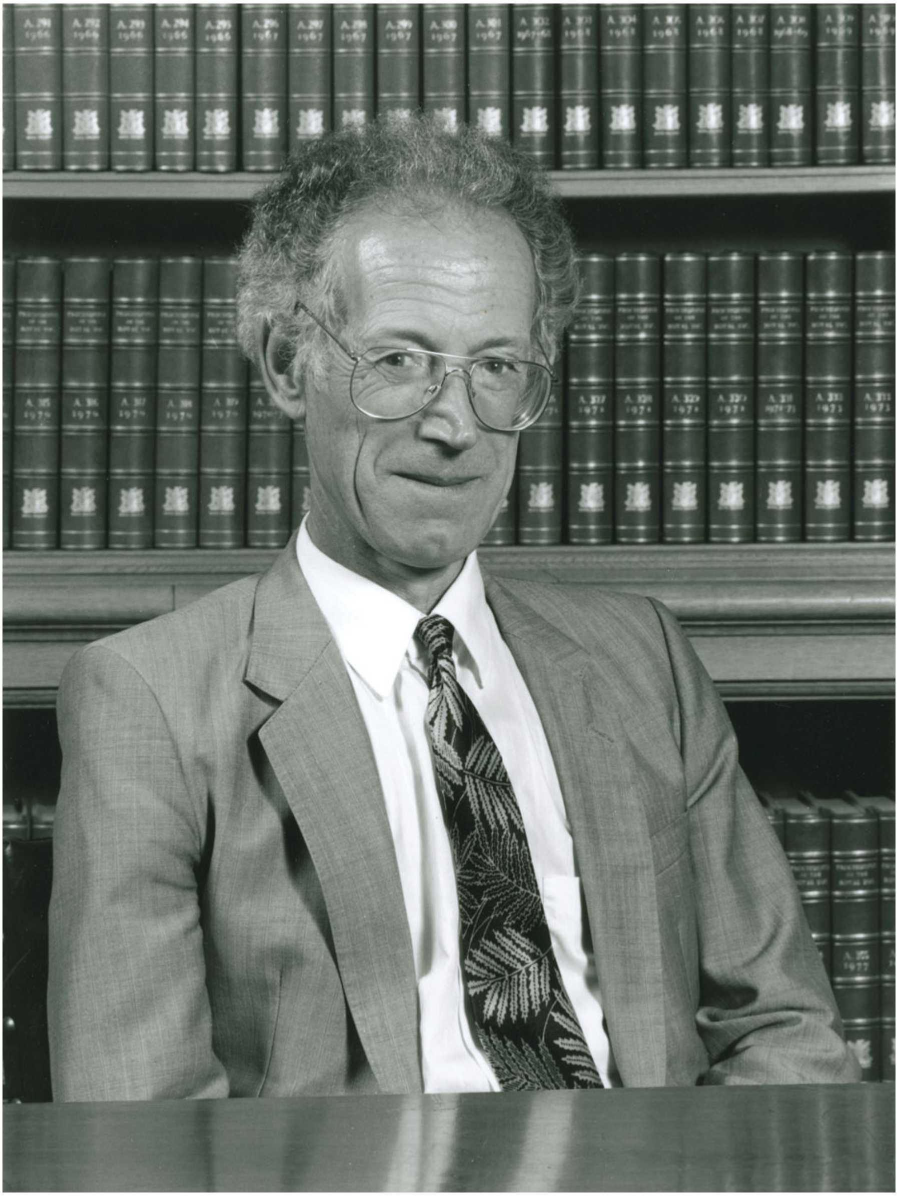

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Elected FRS 1997

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Paul Gordon Jarvis was a widely known and well-respected plant ecologist and physiologist, who pioneered the scientific analysis of the exchange of water and carbon dioxide between forests and the atmosphere, and laid the foundations for decades of study on the interplay between forests and the climate system. He was one of the first to measure directly the photosynthesis and transpiration of forests, and leading from this, his analysis of the relationships between the physiology of plants and the weather has informed and inspired a generation of young scientists. In particular, he was one of the first to address the linkage between knowledge gained at the microscopic scale of stomata and the landscape scale of forests, and the implications of that linkage for the climate system.

Early life

Paul was the son of a farmer from Hertfordshire. His father was an aviator who flew the Sopwith Camel, the famous single-seat biplane fighter of World War I. The aircraft had a large rotary engine, giving it an almost uncontrollable torque, and many novice pilots crashed on take-off. However, his father survived, and later became a founding member of the Royal Air Force Regiment. Paul's mother was the secretary of Karl Pearson FRS, the renowned statistician who held the Galton Chair of Eugenics at University College, London.

Paul was born in Tunbridge Wells. His childhood was evidently a happy one. With his two brothers, Brion and Richard, he enjoyed rural pursuits. In later life he was fond of telling colleagues about his boyish adventures: for example, making a raft for the pond and paddling

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a canoe on the river. He attended Sir Anthony Brown's School in Brentwood, Essex (school motto: 'Virtue, Learning and Manners'). Paul showed an early academic talent and went to Oriel College, Oxford University, to read Forestry, later changing to Botany. His tutors included W. O. James (FRS 1952), E. F. Warburg and J. L. Harley (FRS 1964). Paul was a keen student, but a lot of his time and energy was spent rowing for his college and working as the Secretary of Boats. It was at Oxford that he met his future wife Margaret. They were married three months after graduating with BA degrees in botany (figure 1).

Sheffield 1957–1960

Paul and Margaret went on to graduate studies in the Botany Department of the University of Sheffield, at a time when the Department was expanding its teaching and research in both ecology and plant physiology under the astute leadership of Professor A. R. Clapham (FRS 1959). Supervised by C. D. Piggott, Paul worked on the ecology of sessile oak, *Quercus petraea*, whilst Margaret investigated the influence of climatic factors on the distribution of selected Derbyshire plants, including the mossy saxifrage, *Saxifraga hypnoides*, near its southern limit in the British Isles. They often did fieldwork together, at sites which were a short car journey from the university. They travelled around in an old (1937) Hillman van. Margaret recalls its dubious brakes. Paul carried out a detailed experimental analysis of growth of oak seedlings at Padley Wood, relating growth rates to the light intensity, and showing that competition with the roots of other plants was also an important factor. Paul and Margaret were awarded their PhDs in 1960.

Uppsala 1960–1964

After finishing their PhDs, and thanks to two NATO fellowships, Margaret and Paul moved to the Institute of Physiological Botany at the University of Uppsala in Sweden, joining Professor Nils Fries and Drs Henry Rufelt, Olle Björkman and Paul Holmgren. The original arrangement was that Paul would work on the mycorrhizal requirements of trees with Elias Melin whilst Margaret would investigate the water relations of tree seedlings with Henry Rufelt. But Paul had become more interested in photosynthesis and its relation to the state of water in plants, and in the end the mycorrhizal line was not followed. Instead, Paul and Margaret worked together. Importantly, Paul learned how to measure rates of photosynthesis through collaboration with Björkman and Holmgren, who at that time were clear world-leaders in the subject. Henry and Olle could measure the quantum efficiency of photosynthesis and the rates of gas diffusion into leaves, and they could characterize the carboxylation reaction. This sort of work was ground-breaking, and certainly had not been possible in Sheffield. At that time, the areas of research in which Paul would eventually become a major player, i.e. energy-based concepts of plant–water relations, and the use of electrical analogues to model water transport in the soil–plant–atmosphere, were only just developing in a few centres in the USA, Australia and The Netherlands (Gaastra 1959). The UK lagged far behind these countries through poor funding, especially for forestry research, although John Monteith (FRS 1971) at Rothamsted and later at Nottingham was already advancing a biophysical approach in relation to field crops. Only Jack Rutter at Imperial College was progressing on the water

Figure 1. Paul and Margaret Jarvis, Oxford days.

relations of forests, a topic which Paul was beginning to think about. Paul made contact with these two scientists and remained friends until their death.

Paul and Margaret made many Swedish friends and became fluent in Swedish. They translated the work of the Swedish ecologist M. G. Stalfelt into English, *Stalfelt's plant ecology*, thus making it available to the entire English-speaking world.

In five landmark papers, Paul and Margaret wrote jointly on the water relations of tree seedlings (1–4, 6)* and later Paul published with Holmgren on the measurement of resistances to water and carbon dioxide diffusion in leaves from plants of differing ecological types (7).

One of the most memorable of the husband-and-wife collaborations resulted in a publication on the 'Growth rates of woody plants' (5). They noted that woody plants do not grow as fast, or have such high rates of photosynthesis, as herbaceous species. They asked 'Why?' The answer to this seemingly simple enquiry was not simple, especially in those days when relevant published data were scarce. After an exhaustive review the authors were forced to conclude 'A number of possible explanations are considered, but a lack of knowledge about the physiological bases for differences in assimilative ability prevents a conclusion.' On re-reading and looking at the subsequent citations, it is clear that the question they had posed of why plants with different life-forms had contrasting capacity for photosynthesis sparked widespread interest and led to many further investigations spanning several decades (see Mooney 1972; Wright *et al*. 2004). It is generally true that the leaves of trees have a lower nitrogen content and lower area per mass than herbaceous plants, which may explain why their photosynthetic rates are generally lower, but this is not the whole story. And the topic remains alive today, as Earth system modellers search for physiological and structural definitions of plant functional types to include in their representations of the global carbon cycle (Wullschleger *et al*. 2014).

These years spent in Sweden must have been very stimulating, and much of Paul's subsequent work can be seen as springing from his Uppsala days—most notably the interest in leaf gas exchange as well as the exposure to research into the physiology of forests were topics almost unknown in the UK. He saw scientists developing completely new measurement techniques, mostly for use in the laboratory, but these techniques certainly had the potential to be used in the field.

In Uppsala, the highly supportive Head of Institute, Nils Fries, suggested that Paul should submit the results of his work for another doctorate, the Fil. Dr., equivalent to a PhD in the UK. This he did, and he was successful. It meant that he was now judged as 'competent' in the Swedish system and he duly became a Senior Lecturer in the Department of Plant Physiology at the Royal College of Agriculture in Uppsala. When their first child Eric was born in 1964, Paul's and Margaret's life changed somewhat (figure 2). Margaret began working as scientific editor and translator, working on Pergamon's abstracting journal *Current Advances in Ecological Science*.

Impressively, Paul and Margaret published ten joint papers in their four years in Uppsala.

During the time in Sweden, several overseas conferences were to influence Paul's career. Perhaps the most important was the 1963 symposium 'Water Stress in Plants', held in Prague, at which Paul and Margaret each presented their work. Michal Marek recalls a 'vigorous invasion' by the young British ecologist, who contributed and enlivened the discussions at that meeting (yes, Paul was both loved and feared for his incisive questions at the end

* Numbers in this form refer to the bibliography at the end of the text.

Figure 2. Paul Jarvis with baby Eric. (Online version in colour.)

of conference presentations, and, although he did mellow somewhat later in life, he never lost the knack). Paul became quite associated with scientific developments in what is now the Czech Republic, through collaborations with Šesták and Čatský in the 1971 book *Plant photosynthetic production: manual of methods* (10). This book became a standard text for anyone trying to measure gas exchange of plants. Some called it the Bible. It deals with all aspects in over 800 pages, ranging from the design of leaf chambers to the various corrections required for temperature and pressure. Paul became a member of the editorial board of *Photosynthetica*, a new journal launched in 1967 by the Czech Academy of Sciences to accommodate this growing field of eco-physiological research. Later, Paul was awarded the Gregor Mendel Medal of the Czech Academy to mark his contributions. The connection and continuing commitment to Czech science is remarkable as it occurred at the time of the Iron Curtain, and collaboration between the UK and any of the Iron Curtain countries seemed impossible. Diplomatic relations were frosty and funding was non-existent, a situation which remained until the Iron Curtain finally fell in 1991. Paul of course was not concerned with political divisions: he struggled to bring Czech scientists to the UK, finding ingenious methods to facilitate their travel. Later, in the period after 1991 he was keen to bring his

Czech colleagues into the mainstream of European science by encouraging them to participate in European funding initiatives. Even later (November 2014) a new laboratory building at the CzechGlobe Global Change Research Centre in Brno was named in memory of Paul.

A second important conference of that period, also in 1963, was the UNESCO Arid Zone Research Symposium, held in Montpellier. Here, Paul met Ralph Slatyer (FRS 1975)—a leading Australian scientist from the Commonwealth Scientific and Industrial Research Organisation (CSIRO). Slatyer was the chief of CSIRO's Division of Land Research and Regional Survey in Canberra, tasked with the job of assessing whether a particular region of Australia had potential for agriculture. He was known as a man of great good judgement, later becoming Australia's first Chief Government Scientist and Australia's Ambassador to UNESCO. He was at that time attempting to connect climate, water use and plant production, by combining physiological ideas with fundamental physical concepts. On this occasion, his judgement was that Paul Jarvis would be an excellent appointment for CSIRO, and he was able to offer Paul the position of Visiting Scientist.

Canberra 1964–1966

CSIRO at that time was surely 'the place to be' for anyone interested in the water relations of plants at a large scale. Ralph Slatyer was proposing the new biophysical approach of water transport using an Ohm's Law analogue whereby water is simply transferred between flow resistances along a continuum from soil to atmosphere along a gradient of water potential—a term which expresses the availability of water in units of energy. Also at CSIRO were several young scientists who would later become well known for their work on aspects of drought in arid regions, including John Begg, Calvin Rose, Gavin Byrne and Tom Denmead. Paul worked especially on the gas exchange of leaves, publishing with Rose and Begg (9) and in *Science* with Ralph Slatyer (8). The Slatyer & Jarvis paper illustrates Paul's continuing fascination with the technical aspects of measurement. In that paper the authors describe a new instrument for measuring the diffusion of gases into leaves (the stomatal conductance), which used nitrous oxide as a tracer. Paul would return to the design of the porometer (so-called because water vapour diffuses through the stomatal pores) during his Aberdeen years.

Aberdeen 1966–1975

Paul had met Professor Paul Weatherley (FRS 1973) in 1963 at the Prague Symposium. They had a lot in common. Both were called Paul and had married women called Margaret, and both had a farming connection. Both were experimentalists at heart, and both were interested in water. Weatherley's special interest was the relation between water and solutes—obviously important because when water is drawn into plants the nutrients in the soil solution are swept in too. And so it was that Paul received a letter inviting him to a position in the University of Aberdeen. By now, the family had increased in size (with the addition of Kathryn, born in Canberra, 1965), and when the family moved to Aberdeen they lived at first in the University's cottage in Old Aberdeen and then moved to a new property in the nearby Cults.

Paul applied for funds to the Natural Environment Research Council (NERC) for an extremely large research programme on the gas exchange of a forest. Paul saw that forests are, to a first approximation, merely a collection of leaves, and so the same principles should hold.

Why not see if a knowledge of the leaf gas exchange can be used to find the water and carbon dioxide exchange of the forest as a whole? Why not try to continuously measure the forest's gas exchange, to see how the weather influences the fundamental process, and to understand the mechanisms? It had not been done before in forestry, but elsewhere agronomists were already starting this work. His application succeeded; the project was funded with the largest grant ever awarded by NERC.

Fetteresso forest was a 20-year-old Sitka spruce (*Picea sitchensis*) plantation near Aberdeen, typical of the coniferous forest being planted throughout the UK and especially in Scotland. At this site he established a field laboratory with canopy access. Although somewhat primitive by modern standards, Paul's skills in do-it-yourself were applied to good effect to make a working environment. An old caravan, a diesel generator, ladders and planks were the basic components. And rope, of course. Building human capacity was also one of his talents. He built a research team of students, postdocs, technicians and visiting scientists. Accommodation within the university tested Paul's creative capacity. Somehow, he took over an old woolshed between the Botany and Forestry departments, which became 'Jarvisland' for his scientific family. The results were remarkable, and mostly came out as a series of papers in the *Journal of Applied Ecology.* Under the brilliant editorship of Harold Woolhouse this journal was gaining a reputation for publishing fundamental research, somewhat contrary to the journal's name. Ten papers were published in the series entitled 'Photosynthesis in Sitka spruce (*Picea sitchensis* (Bong.) Carr.)', most of them on the physiology of photosynthesis. In a short time we knew more about Sitka spruce than about any other tree species on the planet.

Looking at these papers today, what is remarkable is that many of the discoveries were overlooked by the research community at the time. For example, in the first paper (11) we see the clear demonstration that spruce shoots have a higher rate of photosynthesis in diffuse light than in direct light. This simple experimental observation was almost completely ignored, and began to be examined much later when it was realized that atmospheric aerosols derived from pollution or volcanoes are scattering solar radiation and changing the ratio of direct to diffuse light (Gu *et al*. 2003). This turns out to be very important when models are used to estimate the photosynthesis or evapotranspiration of the entire planet, as a number of authors have reported (e.g. Farquhar & Roderick 2003).

Paul's group was assembled on an ad hoc basis, taking the opportunities for funding that arose more or less at random, yet the recruits were all highly talented individuals. Where did they all come from? John Norman came from the University of Minnesota, Merv Ludlow from the University of Queensland, Neil Turner from CSIRO Canberra, Joe Landsberg from South Africa, and Sune Linder from Sweden. It was a truly international group, quite rare in those days. Sune Linder recalls:

> the first time I visited Paul's group in Aberdeen was in August 1968. That was the same year as Joe moved with his family to Aberdeen. I spent most of the month soldering thermocouples which we later inserted in the tree stems. I benefited a lot from the open and lively discussions within the group and the friendship that developed with Paul, Margaret and many members of the group. From then on I visited Paul's group at least once a year, first in Aberdeen and from 1975 and onwards in Edinburgh.

Paul spent much time and energy developing a system to measure the flux of CO_2 and H_2O over the forest. He adopted the micrometeorological approach which was already being used in the 1960s for field crops. This requires accurate measurement of gradients of CO_2 and H_2O concentrations and wind speed over the canopy, and calculation through application of diffusion theory by what became known as the ‘flux-gradient’ method. What he had not reckoned with is the fact that the concentration differences to be measured are much smaller over the aerodynamically rough surfaces of forests than they are over the relatively smooth surfaces of field crops. These differences are typically just a few parts per million of CO_2 over forest whereas for field crops they are larger by an order of magnitude. Gas analysers of the day were much less sensitive than they are now, and differences of one part per million were close to the limit of resolution. Moreover, the data had to be recorded by an inked ribbon on an analogue chart recorder, laboriously read off by the researcher and keyed onto punched tape for storage. Ten years later data loggers became widely available. But the whole concept of estimating fluxes from concentration gradients measured over forests was called into question when it became clear that the flux would sometimes apparently occur in the wrong direction, i.e. from low to high concentration, because of the large scale of turbulence and the presence of large parcels of air which moved up and down. The CO_2 flux data from this work were thus not published until 1994, but important lessons had been learned and Paul would return to the matter in the years to come.

Paul always had a deep interest in stomata, the microscopic pores on leaf surfaces, gateways through which H_2O and CO_2 molecules diffuse. In Aberdeen he was fascinated by the work of his young colleagues. Michael Penny was using a microprobe to investigate electrochemical gradients in and around stomatal guard cells (Penny & Bowling 1974) and Christopher Jeffree was using scanning electron microscopy to study the wax crystals that seemed to be blocking the stomatal aperture (12). But Paul wanted to understand stomatal behaviour in the natural environment, and suitable field equipment at this time was not available. In those days several of us made our own porometers (most science departments in the UK had excellent workshops). At the heart of the instrument was a humidity sensor, consisting of a piece of polystyrene that had been boiled in sulfuric acid. The surface of such a homemade chip was hygroscopic and its electrical resistance depended on the humidity of the air. But the calibration was unstable and this was not good enough for Paul. He designed an instrument called the null-balance porometer. This used an entirely new principle which did not require the humidity sensor to be exactly calibrated. His Aberdeen null-balance porometer simply bled dried air into the leaf chamber, and measured the flow rate of dried air required to exactly balance the water vapour that was being given off by the leaf (13). The sensor’s calibration was thus not critical; one only needed to detect the ‘no change’ condition. The calculation of conductance required the accurate measurement of the flow rate, which was easy to achieve using off-the-shelf components.

Paul’s fondness of water relations of plants was enhanced in 1970 by a visit to Aberdeen from the young US researcher Richard (‘Dick’) Waring. He came with the Scholander Pressure Chamber, a device to measure the water status of leaves (Waring & Cleary 1967). Paul, in turn, was later to bring the methodology to Edinburgh where it was put to good use. Dick Waring remained a life-long friend.

Another line of work from the Aberdeen days was the collaboration with John Stewart of the Institute of Hydrology (IoH) at Thetford Forest. The IoH wanted to know the rate of water usage by coniferous forests and they established a project between 1968 and 1976 in a very large plantation at Thetford Forest in the east of England (East Anglia). They collaborated with Paul in an attempt to measure evapotranspiration by applying the micrometeorological approaches that Paul was developing at Fetteresso. In the Edinburgh years, this line of work would be developed further.

All this work on stomatal conductance and water potential culminated in one of Paul's most important papers, delivered at a Royal Society Discussion Meeting in January 1975, organized by John Monteith and Paul Weatherley (16). He used a statistical approach to summarize the response of stomata to light, temperature, humidity, plant water potential and carbon dioxide. It was controversial. John Monteith, in summing up, said:

> Dr Jarvis has suggested a statistical method by which relationships derived in the laboratory and growth room can be fitted to observations in the field. I am convinced that a sensible alternation of experiments in natural and controlled conditions can be most rewarding in ecological studies but until Dr Jarvis can improve the fit between his formulae and his measurements, I shall reserve judgement about the value of nonlinear regression techniques in this context.

Delivered to an audience of fellow scientists and later published verbatim, this seems harsh. But Monteith's scepticism was ill-founded. The Jarvis approach has been fruitful and is still being used, despite the availability of several rival models.

Edinburgh 1975–2013

Paul's arrival in Edinburgh in 1975 as Professor of Forestry and Natural Resources and *ipso facto* Head of Department was viewed by colleagues with some trepidation. What changes would he make? He had a reputation of being a strong researcher, and arrived with a large group. Some of the existing staff were not research-active, had rarely applied for grants, and held the view that teaching 'came first'. Moreover, most of the staff had a background in management subjects (the Department of Forestry and Natural Resources had been a traditional Forestry Department until 1970, when it was broadened and began to teach an ecology degree). For the first year he made no changes at all, watching and learning. After that, he began to show his mettle. He introduced a high degree of rigour to undergraduate teaching. Nowhere was this more evident than in the practical classes for the Ecological Science degree. Students worked with instruments borrowed from the research laboratory, and needed a good grasp of the latest concepts of plant water status (see especially (14)). Moreover, work was to be written up immediately and to a high standard. No undergraduate was ever harmed by this and some even said they had enjoyed the challenge.

In Edinburgh, Paul and Margaret purchased a large Victorian house, 'Belmont', with associated buildings (formerly the stable) and a croquet lawn in the nearby town of Dalkeith. When they bought it, the whole place needed redecoration, which they mostly did themselves, room by room. The bathroom was an exquisite example from the Victorian era, sporting a bath and shower with much brass-work, and nozzles that could direct water to many parts of the body. Visitors loved it. Paul and Margaret kept the house's Victorian appearance, and for some time ran a small bed-and-breakfast business, aided by other members of their family. They hosted parties for students at graduation, and invited colleagues and friends every Boxing Day. Visiting scientists often stayed for months in the refurbished stable.

Paul's rigour was applied to everything he did. He was a tough editor, a stickler for the exact use of English and for the proper use of units of measurement. This applied as much to the setting of examination questions as it did to reviewing manuscripts. He always corrected the many scientists and journalists who talked about 'levels of carbon dioxide in the atmosphere', pointing out that *level* might possibly be used to talk about water in a reservoir, whereas for CO_2 it is the *concentration* or *partial pressure* that is the relevant quantity. Moreover, the concentration should be expressed as a mole fraction, not the usual (and ambiguous) parts per million. He frequently criticized colleagues for their misuse of units and quantities, even for units firmly fixed in the literature: for example, he didn't like the use of litres as a measure of volume, as strictly speaking it is not a Standard International Unit. He kept copies of the Royal Society's booklet on *Quantities, units and symbols* to be handed out to his students when they transgressed.

Paul did have a sense of humour but he could over-react to things he did not like. It was our habit to drink beer in the student union on Friday evenings, after work had finished. Several of Paul's colleagues, secretaries and most of the research students would fill the student union bar at the King's Buildings campus. There was little room for anyone else. It became a highlight of the week—an opportunity to talk over events of the last five days and 'have a laugh' at misfortunes. Whilst some people needed to leave early to attend to matters at home, many stayed until late. One Friday we found the bar had been redecorated. The walls had been painted green. Paul reacted strongly, and questioned the wisdom of this 'act of desecration' which had been carried out without consultation with us, the members. A stand-off between Paul and the bar manager ensued. Paul announced that we would never be coming again, and so it was that we transferred our custom to an off-campus hostelry known as Leslie's Bar, more tastefully decorated with walls in the traditional pale shade of brown. They sold good cheese toasties and so Leslie's became our regular haunt.

In 1978 Paul was a co-founder of the journal *Plant, Cell and Environment*. His fellow-editors were Harry Smith (Nottingham), David Jennings (Liverpool), and John Raven (FRS 1990) (University of Dundee). The journal was published in Oxford by Blackwell's, headed by the enthusiastic Bob Campbell. It rapidly became one of the top journals in eco-physiology. Paul believed that only world class material deserved to be published and he punished authors severely for the poor use of English, using his red ballpoint pen on their manuscripts with such conviction that the ink frequently came through to the other side of the page. The journal has retained its high standards and continues today as one of the best in its field.

One of the best things Paul did during his early years at Edinburgh was to organize meetings, bringing together some of the best physiologists and ecologists of the time. One such meeting was an international symposium, 'Plants and Their Atmospheric Environment', aided by David Ford and John Grace. It was to be the 21st Symposium of the British Ecological Society. Invitees included John Monteith, Jack Rutter, Gerald Stanhill, Ian Woodward, Harry Smith, Christian Körner, Mel Tyree, Olle Bjorkman, Hanno Richter and Joe Landsberg. The meeting was held on 26–30 March 1979. The weather was unusually wintry with heavy snow. However, all went well: it cemented relationships, produced a book which is still consulted by researchers (17) and marked Edinburgh as an international centre of expertise.

Paul's research developed rapidly and his group grew. The work on plantation forests at Fetteresso, Roseisle and Thetford attracted visitors and research funds. David Whitehead, who later became the Chief Scientist at Landcare in New Zealand, worked with Paul on the scaling of sapwood with leaf area—a topic first developed in Japan as 'pipe-model theory'. Ross Edwards, also from New Zealand—a technical wizard—developed new techniques for measuring water in tree stems. Dick Waring from Oregon State University brought radiotracer technology and modelling ideas to Edinburgh. But it was not 'all work and no play'. Paul would take the entire group to the Highlands each spring holiday, staying at a youth hostel and walking the hills. Both Paul and Margaret were keen hillwalkers, enthusiastic about Scotland and liked to show visitors its flora, fauna and landscape.

He would also make sure young researchers had chances to attend conferences, especially the Annual Conference of the Society for Experimental Biology (SEB). With his friends Lynton Incoll from Leeds and Bill Davies from Lancaster, Paul was instrumental in forming the Environmental Physiology Group of the SEB and he served as President of the SEB from 1993 to 1995. Uniquely, this group was shared between the SEB and the British Ecological Society. It is still active.

Paul's interest in photosynthesis of forest canopies produced a stream of publications spread over three decades. When he began his work at Fetteresso forest in the 1960s it was usual to represent plant canopies as homogeneous layers of leaves in order to estimate how much solar energy they absorbed, as a means of estimating canopy photosynthesis. The approach goes back to work by the Japanese researchers of the 1950s (Monsi & Saeki 1953). They provided the basic idea, but one that could be implemented only after digital computers arrived in the 1960s (de Wit 1965; Duncan *et al*. 1967). The computation began by considering the attenuation of a beam of light as it passed through the top layer, taking account of the leaf angles and the optical properties of randomly dispersed leaves, and assuming that each layer obeyed the Beer–Lambert Law as if it were a chlorophyll solution. After several iterations, the light absorbed by all layers in the canopy could be calculated, and the resulting rates of photosynthesis of all layers could be estimated. This was clearly simplistic, but did seem to produce the correct results in field crops. However, a walk in any forest reveals that the canopy structure is highly complex, and the leaves are far from randomly arranged. Properly estimating the rate of photosynthesis of such a structure would indeed be difficult.

Help came from the USA in the form of John Norman, who worked with Paul as a postdoctoral assistant in Aberdeen from March 1971 to May 1972. John was a highly energetic and talented young scientist, who had already made his mark by developing a novel light sensor (Norman *et al*. 1969). Paul and John made great progress in both measuring and modelling the light interception of the spruce canopy (15). A wire carrying a light sensor ran through the forest, measuring and recording the intricate patterns of sun and shade. When John returned to the USA he engaged a clever Masters student, Jon Welles, who worked on radiation attenuation in an orchard. Jon's work resulted in code that could, in principle, be used to calculate the energy absorbed by an array of trees. Later, Jon joined the staff of the US instrument company Li-Cor, and helped develop the highly successful Canopy Analyser that most researchers use today.

Meanwhile, Paul still wanted to develop a model for coniferous canopies. In 1982 he visited Forest Research in New Zealand, and collaborated with Jenny Grace. Jenny's work was on *Pinus radiata*, an exotic tree from the west coast of North America. It grows wonderfully well when planted in New Zealand, and produces a fine timber when its lower branches are cut away. She was interested in understanding how the spacing of the tree could affect the timber yield of the plantation. Paul obtained the Jon Welles code, and Jenny built a Fortran model in which the trees were represented by three-dimensional ellipsoids. Back in Edinburgh, Paul wanted a version that would work on Sitka spruce. Along came a Chinese student, from the Beijing Forestry University (figure 3). Overcoming the language problems, and helped also by Paul's postdoc Andrew Sandford, Ying Ping survived the culture shock, even learning to enjoy

Figure 3. Paul Jarvis with Ying Ping Wang in 2004: Melbourne, Australia. (Online version in colour.)

Leslie's Bar (then the nearest pub to the University's King's Buildings), and produced a new model. Paul was very pleased and he called the model MAESTRO, which we believe stood for Multi Array Evaporation Stand Tree Radiation Orgy. Ying Ping camped at Tummel Forest for many days with a light sensor and so was able to verify the model (20,21). This was a huge step forward. A little later, in 1985, Paul went to Canberra and worked with Ross McMurtrie, who was developing a somewhat similar model. Through Ross, further data for verifying MAESTRO became available. Belinda Medlyn came from Ross's group to Edinburgh and quickly became the resident expert on the huge Fortran program that Ying Ping had left on the main-frame computer. She revised it, corrected a few mistakes and made it more user-friendly. The model underwent a gender change: she re-christened it MAESTRA, and opened it up to anyone who cared to visit Paul and Belinda. Elsewhere, she tells the full story (Medlyn 2004).

What became of all these scientists? They became part of the great Jarvis diaspora. Ying Ping Wang is now a chief research scientist in CSIRO where he is one of three scientists responsible for developing the Australian land surface model CABLE. Jenny Grace continues as a research scientist at the New Zealand Forest Research Institute. Jon Welles went to work for Lambda Instruments in Nebraska, a company making scientific instruments, which later metamorphosed into the world-leading Li-Cor Biosciences, Inc. Ying Ping's friend Andrew Sandford followed a somewhat similar career path, joining the Utah-based company Campbell Scientific, and now is the Technical Director of Campbell Scientific at the UK office.

Belinda Medlyn is a Professor at Western Sydney University, working on how forests respond to increasing atmospheric carbon dioxide and climate change. John Norman developed a detailed plant–environment model named CUPID, with applications to agriculture, ecology, forestry and meteorology. He collaborated with Li-Cor in the development of much of their instrumentation and is now Emeritus Professor at the University of Wisconsin.

In his early days at Edinburgh, Paul built a state-of-the-art photosynthesis laboratory, and, aided by technician Jeremy Landless and research students Andrew Sandford, Chris Beadle, Peter Ng, James Morison, Pedro Aphalo and Jerry Leverenz, he could learn everything he needed to know about the response of stomata to environmental variables. The precision of these measurements enabled quite subtle differences to be detected and the results could be used to interpret the much coarser field data collected in spruce and pine forests. He realized that there was a fundamental discrepancy between the widely held and reasonable-sounding views of plant physiologists which were being reiterated by lecturers in botany departments everywhere, namely that stomatal opening and closing controlled the water loss by plants, and the quite different perceptions of meteorologists. Their view was that water use by vegetation is controlled by climatological factors, especially the supply of radiant energy. To some extent these views had already been reconciled by Monteith's seminal 1965 paper, in which evapotranspiration was shown to be determined partly by the supply of energy (the net radiation) and partly by humidity and an important wind-speed-dependent term that Monteith called 'the external diffusion resistance in the air surrounding the leaf', shortly afterwards abbreviated to 'the aerodynamic resistance' (Monteith 1965). Paul was fascinated by this aspect of Monteith's work, especially as applied to short versus tall vegetation, and wrote review papers that made Monteith's contribution more accessible to ecologists and physiologists. Most researchers had placed their leaves in well-stirred chambers, often forgetting that in the natural state these same leaves, and the canopies of which they are part, are surrounded by layers of rather still air in which water vapour tends to accumulate, setting up a negative-feedback process. Paul wrote a comprehensive review of the subject with Keith McNaughton for *Advances in Ecological Research*, in which they put forward the idea of a coupling factor known as Omega, which can vary between $\Omega = 0$ and $\Omega = 1$, to indicate the extent to which vegetation is *coupled* to the atmospheric environment (18,22). This work was widely read, and, as of 2018, the first of these two papers (18) has been cited well over a thousand times. Citation continues at a rate of about fifty times per year.

How did this fruitful collaboration come about? Keith McNaughton takes up the story:

> Back in Edinburgh we talked about it again (the issue of scale—leaf or landscape—as it relates to the prediction of evapotranspiration), and Paul said 'Let's do it.' With 10 days of my stay remaining I was a little taken aback. I don't usually work at that speed. Fortunately it was university vacation time and there were few around to interrupt us. Paul and I would map out our next tasks, then go to our respective offices and write, longhand, the next few pages. Drafts were swapped and red-ink applied every hour or two, and Anne (I think her name was), whose office was in the middle, typed each of the drafts as it landed on her desk. By the time I left we had a fairly advanced draft of the paper that went to *Advances in Ecological Research*, and Paul tidied it up over the next few weeks.

The reasons for the success of the work may have been that it was published at a time when plant physiologists were starting to address truly global issues.

Paul often travelled abroad. Once he went to Australia and New Zealand for a whole year (1981/2). He did short-term consultancy work with Alcoa in Western Australia before travelling to CSIRO's Division of Forest Research in Canberra, of which Joe Landsberg was then the Chief. It was during that time that Paul met and worked with Ross McMurtrie. Later he went to the Division of Plant Industry, where he visited John Passioura and Neil Turner and began working with Keith McNaughton (DSIR Plant Physiology Division at Palmerston North, New Zealand). He attended many conferences organized by the Union of Forestry Research Organisations. At one of them, in Knoxville 1985, he met Dennis Baldocchi (then at the National Oceanic and Atmospheric Administration, Oak Ridge, Tennessee) and invited Dennis to Edinburgh, thus forming an important friendship which was to last until Paul's death. Dennis was later to establish FluxNet, a huge global network of all those researchers measuring fluxes of gases and energy over terrestrial vegetation.

Several times Paul participated in major international research campaigns, notably the Hydrologic Atmospheric Pilot EXperiment in the Sahel (HAPEX-Sahel) (1991–1992) in western Niger and the Boreal Ecosystem–Atmosphere Study (BOREAS) in Canada (1993–1994). He loved field work, whether it was part of a huge international programme or simply a departmental field course for undergraduates. Often, travel involved meeting close friends and frequent collaborators Sune Linder, Joe Landsberg and Richard Waring, a group referred to as 'the Club'. It was during a meeting of the Club that Paul received the news of his election to the Royal Society. According to Sune Linder, two bottles of champagne were ordered.

In the 1990s Paul became very interested in the measurement of CO_2 fluxes above vegetation and the role of forests in the carbon cycle, a topic which he had started to work on in the Aberdeen days. To what extent are forests a 'sink' of CO_2, absorbing the ever-increasing emissions from fossil-fuel burning? And to what extent are forests growing faster (and thus becoming a stronger sink) as a result of the fertilization effect of elevated CO_2. These huge questions became a main research agenda for many of us in that period, and Paul was one of the leading authorities. He had already delivered an important paper at a discussion meeting of the Royal Society in 1988 organized with John Monteith, James Shuttleworth and Michael Unsworth (19). He tried to bring together all that he had been learning from studying CO_2 by forests and their foliage, in field and laboratory. The paper contained a huge amount of information (perhaps too much for some of the audience) and it was to be the springboard for new projects mostly funded by the European Union. The discussion after the talk highlights some of the questions that would occupy Paul's mind for many years to come. For example, the palaeobotanist William Chaloner FRS and the plant physiologist Hamlyn Jones asked more about the long-term adaptation (or acclimation) to CO_2 that plants might develop, and James Morison questioned Paul about the role of forests in the global oscillations in CO_2 concentration.

It was clear that sustained long-term measurements of CO_2 fluxes over forests were required. Although Paul had pioneered this theme at Fetteresso, the methodology of the day had been inadequate. So now he worked with colleagues John Moncrieff and Robert Clement to develop a new system for measuring CO_2 fluxes. With these colleagues, he took this eddy covariance system to the Sahel and to Canada to measure fluxes over contrasting vegetation as part of the HAPEX-Sahel and BOREAS programmes. Nearer to home, he established a permanent CO_2 flux station at Griffin Forest near to Aberfeldy, which became part of the European networks EuroFlux and CarboEurope and the global network FluxNet. The measurements showed that a Sitka spruce plantation (Griffin Forest, near Aberfeldy in central Scotland) was absorbing about seven tonnes of carbon per hectare per year, much more than comparable forests in other parts of Europe. Paul was very pleased about that, and was quick to show the result to foresters in the UK.

For all of us at this time, European funding opened new opportunities. We all made scientific friendships, visited far-away sites and tirelessly applied for funds to keep our projects going. We collaborated and published with some of the best institutes, and benefited from numerous exchanges.

By the early 1990s it was becoming clear that the story of carbon would not be complete without knowledge of the behaviour of the nitrogen cycle. It was known from the Swedish work that European forests responded to experimental fertilization with ammonium. Paul kept a slice of wood on his desk, brought from a Swedish spruce forest by Sune Linder, where the result of such an experiment was dramatically recorded in the annual growth rings. Coming from The Netherlands, Bart Kruijt worked with Paul on how this scarce resource, nitrogen, was distributed in the leaf canopy. Bart was joined in this endeavour by Olevi Kull from Estonia and Patrick Meir. The work showed how nitrogen is distributed in the canopy in such a way that the most brightly illuminated leaves are supplied with most nitrogen and those in the shaded lower regions of the trees receive least—strong support for the 'optimal nitrogen distribution' hypothesis.

In 1993 Paul obtained European funding for a new project to expose trees to twice-normal CO_2 to discover how they would respond to elevated CO_2 in the future. In this project he consolidated his scientific links in Europe, involving scientists from Belgium, the Czech Republic, Finland, France, Germany, Italy and Sweden. The Edinburgh team had far more researchers than could be funded by the grant, as once more he had numerous visitors and students who were eager to participate. Moreover, they were from several countries: Helen Lee, Craig Barton, and Lynn Evans from the UK, Roger Pettersson from Sweden, Mauro Centritto from Italy, Ana Rey from Spain, Shirong Liu from China, later to be joined by Belinda Medlyn from Australia. The results are summarized in a 370-page book, *European forests and global change* (23).

In the few years before he retired Paul spent much time and energy in his advocacy of forests as carbon sinks (figure 4). He worked on this especially with his long-time friend and colleague Sune Linder in Uppsala (24). He also brought to publication some older data sets on CO_2 flux which had accumulated over many years: from Africa (25), and Thetford (26) and Griffin (27) forests.

Retirement 2001

Paul retired in April 2001. His colleagues held a retiral conference in Edinburgh, attended by many of his collaborators (Mencuccini *et al*. 2004). He retired but he did not give up. He continued on local, national and international committees, including the National Trust for Scotland. But the most significant activity that he kept going was his advocacy of carbon forestry. He gave lectures and played a major role in preparing a report for the Forestry Commission: *Combating climate change—a role for UK forests*. This report was edited by Sir David Read (then Vice President of the Royal Society). In the first version of the report, Paul's chapter was by far the longest and the most detailed (see Read *et al*. 2009). Later,

Figure 4. Paul estimating the girth of an *Auracaria* tree in Chile. (Online version in colour.)

for use by non-specialists including members of both Houses of Parliament, a much-reduced *Synthesis report* was produced.

Paul and Margaret moved away from Edinburgh to a smaller property near to Aberfeldy in Perthshire, immediately adjacent to Griffin Forest (figure 5). The property had land attached,

Figure 5. Margaret and Paul relax on the summit of Schiehallion, June 2010. The mountain is a 20 minute drive from their retirement cottage near Aberfeldy, Perthshire, Scotland. Schiehallion is where the Royal Society expedition of 1774 determined the density of the Earth (and by extension, its mass) by observing the minute deflection of a pendulum suspended at the side of the mountain. (Online version in colour.)

and Paul and Margaret created an arboretum of several hundred trees. Their house became a staging post for young researchers visiting the research facility.

Paul's life touched and influenced a huge number of young scientists, most of whom now occupy prominent positions all over the world. He had a highly retentive mind, and he often reminisced about these people, decades later. He kept in contact. The efforts of his research group have increased knowledge of how trees and the atmosphere influence each other, and advanced our understanding of how forests will respond to a future climate. His career is summarized succinctly in Dennis Baldocchi's message of condolence to Margaret: 'he has almost single-handedly formed the field that links plant physiology, ecology and micrometeorology'. His influence was timely, coming in the years when the world was waking up to realize that forests are more valuable than the wood they produce.

Honours and distinctions

1979 Fellow of the Royal Society of Edinburgh
1988 Fellow of the Institute of Chartered Foresters

1988	Fellow of the Institute of Biology
1993	Fellow of the Royal Society of Sciences, Uppsala, Sweden
1996	Fellow of the Royal Swedish Academy of Agriculture and Forestry
1997	Fellow of the Royal Society
2000	G. J. Mendel Honorary Medal for Merit in the Biological Sciences, Academy of Sciences of the Czech Republic

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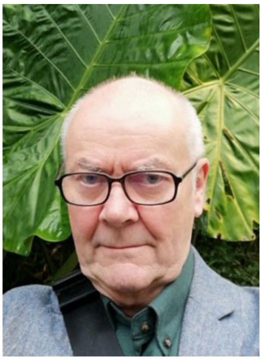
The frontispiece portrait was taken in 1997 and is copyright © The Royal Society.

Author profile

John Grace



John Grace is Emeritus Professor in the School of GeoSciences at the University of Edinburgh, and worked as a colleague alongside Paul Jarvis for 26 years, collaborating in teaching programmes including field courses for undergraduates, co-supervising postgraduate students and working in research programmes. John Grace received his academic degrees from the University of Sheffield, UK. His research interests are: ecophysiology, especially water and carbon relations, forest ecology, fluxes of greenhouse gases, global change, urban flora. He is a past President of the British Ecological Society and of the Botanical Society of Scotland. He was the co-founding editor of the British Ecological Society's journal *Functional Ecology*.

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