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PERSONAL VIEW

On becoming a plant ecologist

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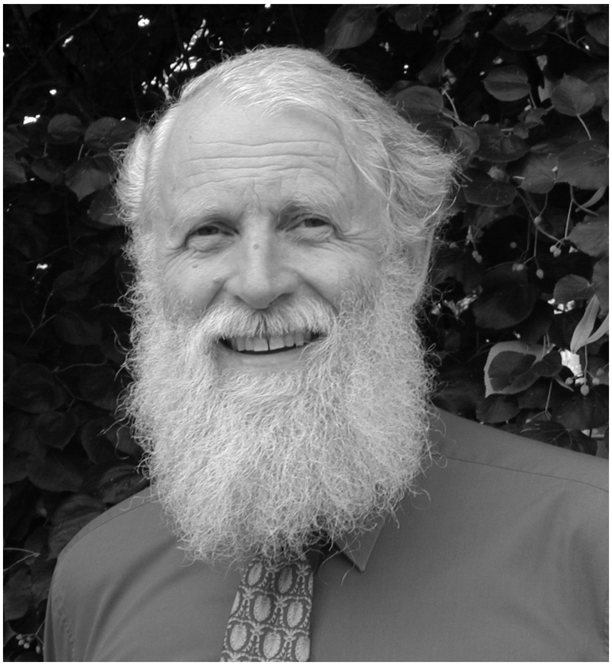

Peter J. Grubb

Introduction

Many scientists take time to find the field in which they are most productive, but I think it is fair to say that I took longer than most. I spent many years as a physiologist and as a researcher into cryptogamic botany, especially bryology, before becoming a fully fledged ecologist. Expeditions to far places, especially two to tropical South America, paved the way for my conversion, which was sealed during my first sabbatical leave when I worked in Australia and visited still more tropical countries. As an ecologist I first worked my way through various classical fields: phytosociological description of vegetation where the flora is well known, characterization of vegetation in terms of structure and physiognomy in wilder regions where the flora is unknown, plant–soil relations and microclimatology. All this time I was fascinated by vegetational dynamics, not the classical study of succession but the study of regeneration processes whereby a community is maintained despite the coming and going of individuals, and the relative abundances of species are determined. But I could not see my way to formulating any new generalizing ideas. Then, on my second sabbatical leave, at the age of 35, spent mainly in Papua New Guinea, I finally came up with an idea that caught the imagination of plant ecologists worldwide – the 'regeneration niche'.

During the 1970s and 1980s, while my children were growing up, I chose to work chiefly in Britain and continental Europe, particularly on grasslands and scrub on soils over limestone, although I also became involved in work on mediterranean-climate vegetation in Europe and Australia. The maintenance of diversity and control of relative abundance were my major interests, but I began to be involved in arguments about 'plant strategies' (cf. Grubb, 1998) and made studies on the effects of plants on soil pH and fertility which were significant in the context of conservation. At the end of the 1980s, I returned to tropical rainforests as my major system for study; there followed an immensely rewarding decade, my last in employment. During this time seed science research became a major theme for me, and I gained particular pleasure from the work reported by Marañón and Grubb (1993), Grubb and Metcalfe (1996), Grubb and Coomes (1997) and Grubb *et al.* (1998). My final fling, in the late 1990s, was to become seriously involved in research on semi-deserts, especially in southern Africa, where I was amazed by the lessons I still had to learn. During my life I was lucky enough to be guided and inspired by a number of outstanding characters, and helped to exploit my

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ideas by many splendid students, only a few of whom get any mention in the following account.

To keep my account within bounds, I am confining it to the time leading up my publication of the regeneration niche idea, and the immediate aftermath.

School days

I was born in 1935 in Ilford, on the east side of London; my father was a clerk on the Stock Exchange, and my mother had been a buyer for a cloths shop in London. Both had left school at 14. On both sides of the family, I go back to humble folk in East Anglia.

In 1937 we moved to a newly developed suburb about 10 miles (16 km) east of the City of London, and by 1945 I had shown my first interest in natural history, collecting butterflies and moths in local gardens. I cannot recall how this interest started. At first my interest in insects ran alongside collecting postage stamps, cigarette packets and the numbers of railway engines, but gradually these other interests were left behind. In my later teens I spent many hours 'setting' specimens, and by the age of 19, when I left school, I had a large collection of Lepidoptera from the county of Essex. It was displayed on the walls of my bedroom in glass-fronted cases made by my father.

My first effort at studying plants came when I was nearly 16, and rashly agreed to produce a list of species of phanerogams in the school grounds. There was no user-friendly colour guide to British flowering plants then, and I learnt the thrill of using keys and Latin names through the then still-standard flora of Bentham and Hooker (1886), revised a little by A.B. Rendle in 1924 and reprinted in 1943.

When I started at the local state grammar school in Romford in September 1946 at the age of 11, I could not have imagined that, when I left, I would hold an open scholarship to a Cambridge college and stand on the brink of a lifetime in biology. Luckily for me, the Headmaster, Mr G.H.R. Newth, was very ambitious for his pupils, and ensured that countless boys got the chance in life that they deserved. Halfway through the fifth year, some months before the state-run 'O' level' exams, the school ran its own 'mock O levels', and then Mr Newth spotted those with academic potential. In my case he had to work hard to persuade my father, who had a very modest income, that I could get to university at all, that I could actually get into Cambridge, and that – with a scholarship – I could afford to go. My parents had to make very real sacrifices at that stage for me to get on. A sense of the period is given by the fact that I worked in a shop on Saturdays selling clocks for a whole term in order to earn the train fare to Cambridge to take the scholarship exam, and to pay the exam fee and cost of accommodation.

Another enormous piece of good luck for me was the arrival of a new biology master, Monty Faithfull, just before I took 'O' levels. He had recently graduated from the Botany Department at University College London, one of the best Botany Departments in Britain at the time. It was headed by W.H. Pearsall, a pioneer ecologist. Monty's approach inspired me and gave me confidence, and he passed on to me convictions that I still hold strongly. He insisted that any worthwhile study in biology must consider *both* the physiological *and* the evolutionary aspects; any essay that failed to do this was bound to receive a liberal covering of green ink. He regarded every aspect of biology from the ecological to the biochemical as self-evidently interesting and equally deserving of study. More than that, the scientist was to be interested in matters cultural, and his hero was that lion of the Renaissance, Leonardo da Vinci.

Undergraduate years in Cambridge (1954–1957)

I found that many of the lectures offered in botany were out-of-date and uninspiring, and large areas of important work were simply not covered. However, the Botany Department – always known as 'the Botany School' – was a very friendly place, and most members of staff were happy to give up hours to help interested students. On Saturday afternoons in the winter terms, there were excursions by bicycle, to enable students to get to know the local angiosperm flora (with Max Walters) and bryophytes (with Harold Whitehouse). One important message that came through consistently from lectures, practicals and excursions was that you could never be a 'real botanist' if you didn't get to know plants in other parts of the world, and in particular the huge variety of plants in tropical rainforest. For many of us, the most inspiring lecturer was E.J.H. Corner, who had worked in Singapore in the 1930s and survived the Second World War there, and then had a spell in Latin America. It is ironic that some of those who are most inspiring can be the most wildly wrong in their theories. He got us all to be enthusiastic about his 'Durian theory' for the origin of flowering plants (Corner, 1949) but, of course, it is generally rejected now. However, he also provoked interest in many topics simply not covered in the textbooks, such as the development of the palm leaf and the early development of flowers. He was full of memorable aphorisms. Frustrated by the emerging emphasis on laboratory studies, he would say 'You can't study a banana plant in a Petri dish'. His clarion call was 'For goodness sake, get off the tramlines of conventional thinking.'

In the 1950s there was a tremendous increase in the number of 'expeditions' undertaken by groups of students from British universities. Luckily there were several charitable funds that made it possible for those of us without much money to become involved. The trick was to learn how to sell yourself to them. With various colleagues I went in successive summers to Floröfjord in Norway, to the Prokletije mountains on the Albanian border of Serbia (now in Kosovo) and to the Colombian Andes. On the last of these, we climbed the highest peak in the Sierra Nevada del Cocuy, Alto Ritacuba Blanco (5493 m), considerably higher than the highest peak in Europe (Mont Blanc, 4810 m). We also collected a good number of species new to science, new to Colombia or new to that part of the country. More importantly for my subsequent teaching and research, I saw for myself many new life-forms of plants, some of which I had read about, such as the little-branched trees of *Espeletia* in the tropic–alpine zone, but some of which were surprises, such as the extremely hard mound-forming angiosperms in alpine valley mires. I actually broke the blade of strong knife trying to extract a specimen from a metre-wide mound of *Distichia*, an aberrant member of the *Juncaceae*. Most importantly, I saw the impacts on the vegetation of very steep gradients in rainfall superimposed on gentler gradients in temperature. In a few tens of kilometres, you could pass from dense rainforest to thorn woodland. Such effects are very much a feature of the Andes, being less marked in East Africa, and virtually absent in the high mountains of Indonesia and Papua New Guinea. I object profoundly to the 'life zone' classification of vegetation put forward by Holdridge (1947), and used so widely in North American papers on the tropics, because it is based on a dogmatic classification of climates and not on objective description of vegetation, but I do understand why Holdridge was inspired to come up with some such scheme by his experiences in the Andes in the Second World War.

A traumatic first attempt at research

It was common at Cambridge for 'clever' students of botany to do a Ph.D. in plant physiology, whatever speciality they followed later on. Unusually for a British student, I chose my own topic, combining physiology and the study of mosses – an interest encouraged by Monty Faithfull when I was at school, which had blossomed under the guidance of Harold Whitehouse at Cambridge. I studied the translocation of mineral ions in *Polytrichum formosum* Hedw., a moss about 5–8 cm tall, which is common on acidic soils in the moister parts of Eurasia and North America. The basis for interest was its possession of a subterranean rhizome system with a somewhat endodermis-like layer, and of tissues resembling xylem and phloem (hydrome and leptome) in its rhizomes, aerial stems and leaves. Did the rhizomes effect selective uptake and concentrate the nutrients into the transpiration stream, and did the leptome act like phloem in redistributing some ions from ageing tissues to growing parts? I used the then newly available radioactive isotopes. As some were short-lived, I often worked alone in the lab through the night on the day of delivery, something unthinkable now. Being a research student was different from the present time in other ways too. All of the little relevant literature on bryophytes was in German, and it was taken for granted that I could and would read it. My supervisor, Professor G.E. Briggs FRS, who was Head of Department and generally perceived to be rather fierce, was immensely kind to me personally and very encouraging, but he insisted that he could not comment on my draft dissertation. 'If I were to try to improve your use of English, Grubb, I might incidentally affect your scientific interpretation, and then it wouldn't be yours!'

In fact, the dissertation was passed by the Ph.D. examiners with almost no criticism of consequence, and won a prestigious and valuable biennial prize at Oxford, the Rolleston Memorial Prize, open to students at Oxford or Cambridge in 'animal or vegetable anatomy or physiology'. But the interpretations it contained were false, and the results had been accepted by me (and others) essentially because they agreed with the views of my supervisor. We did not question them as we should have done. I found no selective effect of the rhizome on uptake, and no evidence of recirculation of nutrient ions from the leaves to the growing sporophyte. These results fitted all too well with my supervisor's view of ion movements in the plant, which involved a minimal role for metabolically driven active transport. Only my friend from University College London, Dicky Clymo, now the world's expert on *Sphagnum*, asked gently if perhaps the plants in my experiments were failing to behave normally for some reason. Gradually, I realized that he was right, and I spent a lot of time over the next several years doing a better set of experiments, which showed that indeed the rhizome was selective in its uptake, and yes, there was phloem-like activity translocating useful ions from the older leaves to the young ones and from leaves to sporophyte. Sadly, the whole story was published only in notes in the *Transactions of the British Bryological Society* (Grubb, 1961, 1965, 1968).

This experience was indeed traumatic, leading me to question a system that could award a prestigious prize (and the academic positions that I was given at the end of my research studentship) for unsound work. Of course, there was not the slightest question of my having cheated, only of my being unwise in my failure to question my results. It was a hard lesson about the nature of 'the scientific method'.

One of the worst features of the Botany School during my early years was the lack of emphasis on prompt publication of results. While on a mule trail on the eastern side of the Andes in 1957, I spotted on a rocky slope a small fern that I believed (hoped!) would be a new genus. When I showed it to the British fern expert of the day, A.H.G. Alston, he said simply 'Quite new'. In fact, he had forgotten the one previous collection from a different part of Colombia (represented in the British Museum), which had been given the manuscript name *Nephopteris* ('cloud fern') by the very distinguished American pteridologist, W.R. Maxon, who had died before publishing it formally. I thought his name unhelpful, and wrote a description for *Trifoliofilix*, as it had clover-like leaves, but did not give publication a high priority, and it became clear that a young American intended to publish Maxon's name. *Nephopteris* was eventually described by Lellinger (1966). I had squandered a splendid opportunity.

I persisted with work on bryophytes until about 1970, and had another hard lesson to learn in that connection. I became interested in hepatics, which had underground parts and xylem-like hydrome, and I made a critical study of the morphology, anatomy and water relations of *Haplomitrium* and *Takakia* (Grubb, 1970). Unlike the moss *Polytrichum*, these hepatics have colourless organs that grow downward into the soil (not just horizontally below the soil surface), branch to a degree dependent on species, and form a mucilaginous cap over the apex easing its way through the soil. I called these organs 'roots', and indeed they are as much like the roots of vascular plants as the 'stems' and 'leaves' of bryophytes are like those of vascular plants. Professor Sinske Hattori, who first described *Takakia*, kindly agreed that they are roots, but they are still not treated as such in the textbooks. The lesson I had to learn was that, however reasonable the case you make, you mustn't expect people to be rational and accept your view! So often, prejudice rules the day.

Getting nearer to being an ecologist

Expeditioning continued. I revisited the Prokletije Mountains in Serbia in 1959 and 1962, on the last trip making comparisons on Mt. Musalla in Bulgaria (the highest peak in the Balkans at 2925 m) and Mt. Olympos in Greece (2911 m). But the most important expedition was to Ecuador in 1960. Two Oxford undergraduates, Rob Lloyd (who has had a distinguished career in teaching biology) and Terry Pennington (now the world expert on *Meliaceae* and *Sapotaceae*) dreamed up an expedition that would visit the Andes and the lowlands of the Oriente, and needed a graduate to be Leader, in order for the operation to be a candidate for the highly desirable title of 'Oxford *University* Expedition to … '. I agreed, on condition that they also accepted my friend Tim Whitmore, who – though we could not know it – was to become the most prolific writer on tropical rainforests in our generation. The medical officer, Ralph Hudson Johnson, became a consultant neurosurgeon, and the 'organizer', Michael Emerson, became a highly distinguished economist and Head of Delegation of the European Communities to the CIS in Moscow. As a result of exemplary teamwork and detailed planning (a Whitmore speciality), the expedition was immensely successful.

The chief plant-ecological project was a comparison of montane and lowland rainforests. Exactly how did they differ in structure, physiognomy and floristics? Was it true that the montane forest, swathed in epiphytes, was hardly ever exposed to drying air? Did the temperature regime control the distribution of forest types? Did the forests differ in the relative importance of sunflecks in the light reaching the forest floor? We were inspired in this work, like so many students of our generation in Britain and in North America, by the relatively recently published book, *The tropical rain forest* (Richards, 1952). We produced three papers in the *Journal of Ecology* (Grubb *et al*., 1963; Grubb and Whitmore, 1966, 1967). These have been cited 84, 63 and 20 times, respectively, and are still being cited – not bad for a student expedition! Because of my traumatic experience in my Ph.D. work, these were my first three real publications.

First steps on the academic ladder

I had been made a sort of junior research fellow of my college (Magdalene) after 1 year of research. That enabled me to enjoy the heady life of High Table. The Magdalene fellowship was small (about 20), but included a number of wonderful conversationalists, the most notable being C.S. Lewis, Professor of Medieval and Renaissance English. Guests familiar with his books on popular theology were surprised to see him get through two large glasses of port and two cigarettes after dinner, before he retired to his room to make a pot of tea and write the next episode in the 'Narnia' series.

On 1 January 1961, I became a university demonstrator in botany, responsible chiefly for first-year classes, and a staff fellow of Magdalene College. Professor H. Godwin (later Sir Harry), had taken over as Head of Department and given me my job, which was to last 5 years, after which I expected to be thrown on the market. Early on I went to see him, meaning to ask if I might gain some experience in lecturing, but I never got that far, as he emphasized the enormously demanding nature of being in charge of the practical classes. I was to know the name of every student, and how they were progressing, lest their college tutor rang me to enquire. I left the room duly humbled, but in fact I was asked, only 2 years later, to contribute to a new course on lower green plants, which I had helped Godwin formulate. Because of my tropical experience, I was asked to give nine lectures on pteridophytes. I managed to give the first six without using a note, but by the seventh I was writing the lecture the night before and had to swallow my pride and take notes into the lecture room!

The definitive conversion to ecology

Expecting to be thrown out after 5 years, I asked to take sabbatical leave in my eighth term as a demonstrator (the northern summer of 1963). Godwin had a wonderful way of giving the best advice for the craziest reason. He had just been lecturing in Canberra, and rightly said that it would be better for me to go to Australia than to the United States. But his reason was that there were more ways of getting money to go to Australia. This was manifestly untrue, there being many funds available in respect of the States and only two at that time for Australia. Luckily, I succeeded with one of those, obtaining a Royal Society and Nuffield Bursary.

I was still deemed to be primarily a physiologist, even though I had no substantial publication in that area, and I went to work in Adelaide with Professor R.N. Robertson (later Sir Rutherford), known to everyone as Bob. My topic was the ionic relations of young roots of the salt bush *Atriplex vesicaria*, a dominant over vast areas of semi-desert in South Australia, and my stay was to last 5 months. Bob Robertson was keen on my project, but it soon became clear that he was not in the least intent on squeezing out of me a lot of new experimental results. Rather, he wished me to visit a number of vegetation types, and talk to a wide range of the liveliest plant people in Australia at that time, be they physiologists or ecologists, or some other sort of botanist. I was utterly absorbed by the Australian vegetation, with its xeromorphic appearance and its dominance by fire, both features making such a contrast with the temperate deciduous forest zone of Europe, and I was greatly taken by the beauty of the arid centre – the Flinders and the Macdonnell Ranges, with their red soils in the foreground and blue mountains behind. The trip also gave me further experience in rainforest, in Malaya and Singapore on the way out, in south-east Queensland, and in the Solomon Islands with Tim Whitmore on the way home.

Taken together, the great range of vegetation types I had seen, and the exciting possibilities of investigating them, inspired me finally to throw in my lot with the ecologists. This decision coincided with my unexpectedly getting a permanent job at Cambridge. C.D. Pigott left in 1964 to become the founding Head of Biology at the new University of Lancaster, and I was given his lectureship. That meant teaching ecology to the third year, as well as lower green plants to the second, and – most importantly – teaching a brand new integrated course of physiology, anatomy, morphology and ecology to the first year.

In Adelaide I also met my wife-to-be, Anne Hall, who was setting up a pollen analysis lab from scratch, to learn about vegetational history from one of the few peat deposits in the state of South Australia (E.A.A. Grubb, 1978). Previously she had worked on a classic study of the recovery of semi-desert over 36 years, when sheep were removed from the worst-grazed paddocks on the most over-grazed property in South Australia (Hall *et al.*, 1964).

The influence of A.S. Watt

A.S. Watt was by far the biggest influence on me, once I became a committed ecologist. In particular, it was he who taught me to ask on visiting any site what it was like 10 or 100 years ago, and what was it going to be like in 10 or 100 years time. It was the forester's approach applied to all vegetation.

At this stage it is worth going back to Watt's lectures to the third year, to see how they influenced my thinking. Three themes were particularly important. First, he was at pains to show that soils could be as important as climate in determining vegetation type. He had been especially impressed by what he had seen in the southern half of Australia in 1950–51. In the wettest climates, dense rainforest occupies the richer soils and open eucalypt forest the poor soils, while in seasonally dry areas grassy eucalypt forest or woodland occupies the richer soils and shrubby forest or woodland the poor soils, and in the driest climates the semi-desert is dominated by grey 'salt bushes' on richer soils and by spiny hummock-forming 'spinifex' grasses on poor soils (Beadle, 1981). It was this background that led me, in my first-ever book review for the *Journal of Ecology* (Grubb, 1963), to dismiss out of hand the Holdridge scheme, in which climate is supposed to determine vegetation type.

The problem persists. I suggest that the concept of 'biome' has been the single greatest impediment to understanding vegetation–environment relations in southern Africa, as shown in the volume edited by Cowling *et al.* (1997). There, the very extensive and fascinating 'renosterveld' vegetation, characteristic of richer soils under a mediterranean type of climate, receives only two paragraphs because it doesn't fit neatly into an account of the 'fynbos biome', which takes its name from the well-known heathland of very poor soils. The account of the semi-deserts ('karoo') doesn't mention that grasslands dominated by C_4 grasses (generally associated with summer rainfall) 'transgress' over large areas in the winter-rainfall region, where their ability to tolerate sandy soils poor in N becomes the most important determining factor. Walter's textbooks (1964, 1972) were important for me in emphasizing the role of soil texture rather than fertility in determining vegetation type in arid regions.

The second Wattian theme of great importance was 'What is a plant community' (cf. Watt, 1964). In the mid-fifties the great excitement was over the extent to which vegetation consisted of distinct communities, or a continuum of varying composition. The key players – Poore (1955) and Whittaker (1956) – emphasized continua in different ways. Poore introduced the idea of recognizing reference points in the continuum ('noda'), while Whittaker introduced 'direct gradient analysis'. Poore's papers were the stimulus for our efforts in phytosociology in the Prokletije mountains. Whittaker came in for stick from Watt. 'How absurd', he said, to mix, in one analysis, stands with abundant birch near the tree line, where other species cannot tolerate the conditions, and stands lower down, where birch is abundant because there has been some recent disturbance. Much later Daubenmire (1966) emphasized this problem in the primitive ordinations offered by Curtis (1959).

Watt's most distinctive contribution was his concern with dynamics. His paper on 'Pattern and process' (Watt, 1947), which was appreciated only after a long delay in North America and in continental Europe, made a deep impression on my generation in Britain.

I first put into practice the Watt approach when I re-examined, in Grubb *et al.* (1963), the concept of 'stratification' of forests. At that time P.W. Richards and others used the number of 'strata of trees' to classify forests. I argued that this practice was unsound. You must separate 'stratification of individuals' and 'stratification of species', and you cannot expect to determine whether or not there are strata of species by looking at profile diagrams (like that in Fig. 1), in which you see individuals that have grown to various proportions of their mature height.

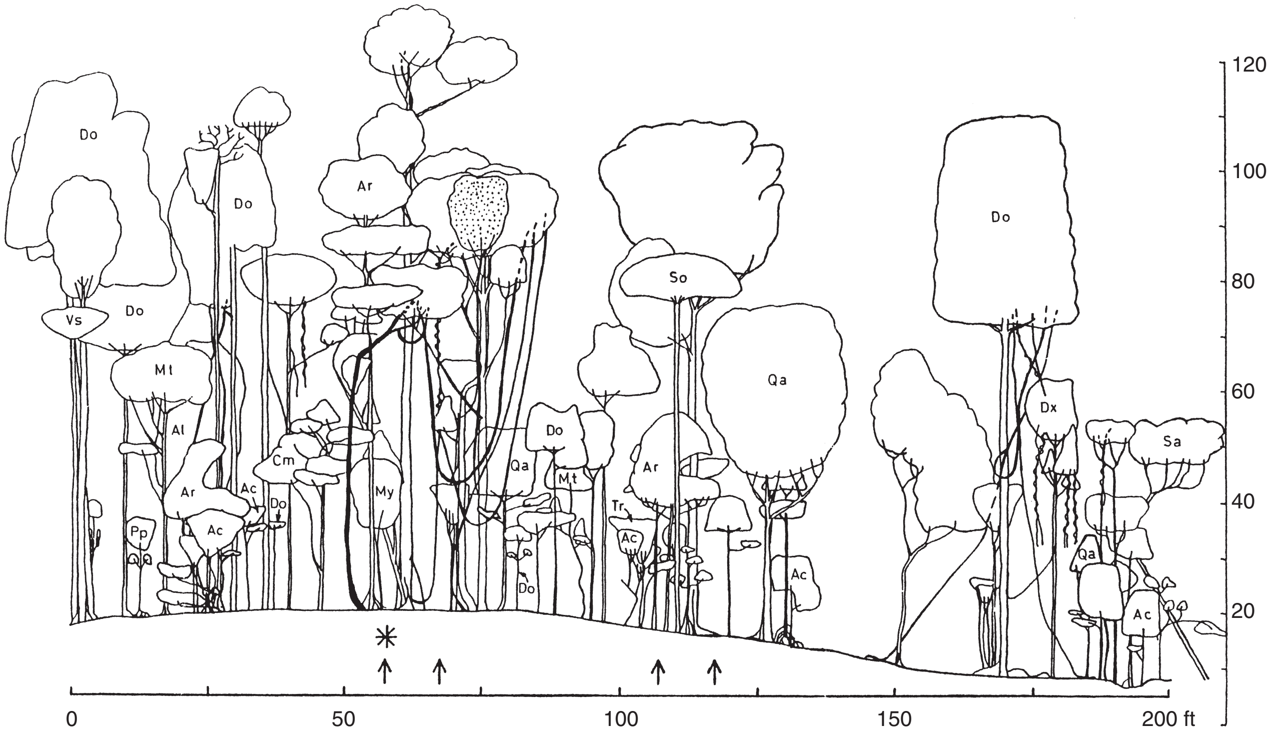

Figure 1. Profile diagram of lowland rainforest in Ecuador (from Grubb *et al.*, 1963). Reproduced with permission of Blackwell Science.

I next applied the Watt approach in my first serious effort at plant ecology in Britain. The 'calcicole–calcifuge problem' was a focus of much interest at that time, and I studied the peculiar community called 'chalk heath', which contains an intimate mixture of the two sorts of plant. It is found in southern Britain on shallow, slightly acidic soils over chalk. Tansley and Rankin (1911) supposed that the mixture was made possible by the calcifuges rooting in the acidic topsoil and the calcicoles in the calcareous subsoil, but this idea did not allow for the regeneration of the calcicoles. In fact, the correct interpretation – argued by Grubb *et al.* (1969) – is that the middling pH values of the topsoil (5–6) are within the ranges known from physiological studies to be tolerable by both calcicoles (>4.8) and calcifuges (<6.5).

The situation in the field was complicated by the fact that since myxomatosis had struck the British rabbit population in 1954, the turf had changed radically, from one about 2–5 cm tall over wide areas to one 20–30 cm tall; the eaten-down heather (*Calluna vulgaris*) had grown into scattered sizeable bushes, and the community had been invaded by gorse (*Ulex*), formerly confined to rough edges. The bushes of both *Calluna* and *Ulex* had acidified the topsoil under them very quickly, from 5–6 down to 3.6–4.5 in a decade (Fig. 2). This was perhaps not surprising for *Calluna*, generally recognized as forming mor humus, but it was unexpected for *Ulex* – known to foresters as a 'soil improver'. We went on to analyse the processes involved in acidification, and found incidentally that cast-forming earthworms can use soil of pH down to 3.8–4.2, i.e. within the range normally associated with mor humus, provided it is under *Ulex* rather than *Calluna*, and presumably rich in micro-organisms (Grubb and Suter, 1971). This fact is too inconvenient to be noted in the textbooks.

Another rewarding spin-off from this project was the chance to give the first analytical account of the vegetation of ant heaps, which were abundant at our study site. The plants are profoundly and differentially affected by the continual addition of new subsoil to the top of the heap. We also found that, without the intervention of *Calluna* or *Ulex*, the newly deposited subsoil was leached of its content of calcium carbonate remarkably quickly.

The follow-up on tropical montane rainforests

Grubb and Whitmore (1966) had argued that tropical montane rainforests (MRFs) were distributed in relation to cloud cover, not temperature regime, the incidence of both regular cloud cover and MRFs being much higher on larger mountain ranges – the so-called tropical *Massenerhebung* effect. I developed the idea that the cloud cover worked through a reduction in nitrogen supply, an inevitable consequence of the rate of mineralization being low where the soils were excessively wet. Reduced nitrogen supply was supposed to explain the lower stature and xeromorphic leaves of MRFs. This is the one thesis that I know came to me while lying in the bath. It was published in *Nature* (Grubb, 1971), and was one of the items picked up that week from *Nature* by *The Times*. By then, I was in Papua New Guinea with Peter Edwards, making a study of nutrient capital and nutrient cycling in a magnificent lower montane rainforest at *c.* 2500 m, where we were finding that the

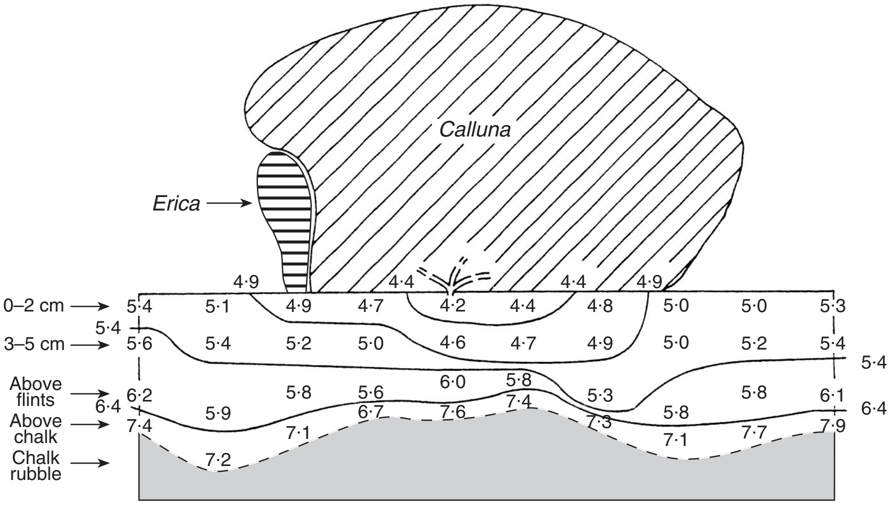

Figure 2. Section through a bush of heather (*Calluna vulgaris*), showing acidification of the topsoil within a decade of removing the rabbit population by infection with myxomatosis, which allowed the bush to grow freely (from Grubb *et al.*, 1969). Reproduced with permission of Blackwell Science.

amount of nitrogen in circulation was indeed less than in lowland forest, but this was not true of other major nutrients (Edwards, 1982). The work was aided enormously by the taxonomist Peter Stevens, then based at Lae, with whom I wrote a very full review of New Guinean montane and subalpine forests in order to put into perspective our work on nutrient cycling and plant form at one complex of sites – written mostly in 1974 and eventually published 11 years later (Grubb and Stevens, 1985).

There is not room here to finish off the MRF story, but some flavour of it is given by Grubb (1977a, 1989a). In 1973, Edmund Tanner began a superbly successful study of MRFs in Jamaica under my direction, and when he joined the staff in 1979, I passed over to him this field of research. One very general point emerges from our research on MRFs – just how much 'one man and a dog' can achieve on minimal funding if the research is appropriately focused and planned. I would confidently pitch the contributions of Grubb, Edwards and Tanner against the patchy and unsatisfactory account of the ecology of montane rainforests in Puerto Rico in the 1597-page volume edited by Odum and Pigeon (1970), which was produced with massive funding from the US Atomic Energy Commission.

The regeneration niche: birth, development, rejection and acceptance

Students of my generation at Cambridge never had it put to them that the long-term persistence of many species together in one community of plants provides a problem because it seems to contravene the Darwinian theory of the evolution of the fittest, and the dictum of 'one niche, one species'. I cannot remember thinking about it until provoked by such papers as that of Putwain and Harper (1970). To my shame I had missed the important paper of Whittaker (1965). My interest was really kindled during a lively discussion involving John Harper and Edward Newman that took place on a fine summer evening at the British Ecological Society Symposium held at Norwich in July 1970. The problem lay in the back of my mind during the following 9 months as I worked through the rainforests of Japan and Malaysia, and established my project in New Guinea.

By June 1971, I had for the first time got to know a tropical rainforest of reasonable diversity really thoroughly. Sadly, a wonderful virgin forest was being clear-felled around our working area. Scrambling through the fallen trees each week, I got to know very well the flora of about 150 species of tree, treelet and shrub, about 120 species of vascular epiphytes, and about 40 species each of herbs and climbers or scramblers. Walking through the as-yet untouched forest, I looked for juveniles of all the species. In this context, the idea of the 'regeneration niche' somehow came to me – the idea that the regeneration requirements of all the species in a community might be different. It wasn't just a matter of different-sized gaps favouring different species, but all sorts of properties of gaps, which varied on different scales of time and space. The ability to fill a gap could also be seen to depend on the extent to which sound seed was produced and transported to it.

As I travelled back from Papua New Guinea to Britain in August–September 1971, I put my idea of the 'regeneration niche' to various ecologists in Australia, New Zealand, Canada and the United States, but none seemed very excited about it. In 1973 John Dickie started with me as a research student, exploring the idea for perennials in chalk grassland. There was a certain amount of sniping in the department about this doubtful idea that Grubb had. The writing of my own papers was greatly inhibited in 1972–1977 by my co-editing the *Journal of Ecology*, but steadily I built up from the literature more and more examples of differentiation between species in their requirements at various stages of the life cycle. In April 1976 I submitted a long paper to *Science*, intended to take off from Whittaker's 1965 paper in that journal. Within 2 months I received a polite reply from the editor, saying that he was advised that the idea was interesting, but didn't merit such a long treatment. He would keep the figures and await a shorter text.

I disagreed, believing that a full account of the background issues was needed, as well as my summary of the available evidence. I was on the editorial board of *Biological Reviews*, and asked the editor, Nevill Willmer, whether he would take the article, showing him the *Science* referee's report. He did so at once (Grubb, 1977b), and the way in which he edited my paper made me feel as though as I was back at school again, such was his mastery of the technique of writing. I wrote to *Science* asking for my figures back, and was rung at home by an assistant, who said that the editor had changed his mind and would take the paper as I had submitted it. I had to explain that that was no longer possible. Thus, *Science* lost a paper that has been cited over 1000 times in the 25 years since publication, and I gained a much better written account of my thesis.

Do I regret anything about the paper now? I greatly regret two omissions. I did not make clear that, within a gap, conditions may vary enormously at the scale of a newly germinated seedling or newly established plant. Others soon took that point up. I also failed to apply my idea explicitly to fire-prone systems, where four variables in the fire regime are important: frequency, intensity, season and extent

(Grubb and Hopkins, 1986). To be fair, the application of the regeneration niche idea to fire-prone systems became much clearer in the 1980s through the research of William Bond in the fynbos of South Africa. He showed how species could be lost if fires were not sufficiently frequent (Bond, 1980), were of the wrong intensity (Bond *et al.*, 1990) or at the wrong time of year (Bond *et al.*, 1984; see Fig. 3). It is precisely in this kind of system that a student can see easily that the regeneration niche is not just some fancy theoretical idea, but absolutely basic to management.

The most obvious limitation of the 1977 paper was that it did not provide a mathematical model defining the conditions under which differentiation in the regeneration niche will lead to long-term coexistence. Unfortunately, I lack the appropriate mathematical skills, and it was, therefore, thrilling for me to see the necessary analysis provided by Chesson and Warner (1981). Much later, it was immensely exciting to see the idea of the regeneration niche illustrated so beautifully in the field-calibrated, individual-based model for regeneration of deciduous forest in the north-east of the USA, produced by Pacala *et al.* (1996).

As to the use of the regeneration niche idea by others, I am only sorry that so many have thought of it simply as defining the kind of gap a species needs. In fact, I emphasized from the start the importance of what is now called the 'supply side' – the variation from year to year in the propagules available to fill any gap (cf. Fig. 4).

My impression is that in no vegetation type has anyone found that any two species have the same regeneration niche. The bigger issue has become whether or not species need different niches for 'coexistence'.

Impacts of sparsity and patchiness

By 1979, it was plain to me that something very important was missing from my 1977 paper. It takes for granted that all species in a community are effectively in competition with one another. In 1978, I had set up what was to be a 20-year study of the populations of nine species of short-lived plants in permanent transects at a chalk grassland site (cf. Grubb *et al.*, 1982). After a year, I could easily see that the sparser species were simply not encountering each other very often, even as newly germinated seedlings. The adults were not sufficiently fecund to provide seeds to reach every suitable gap, and, in any case, there were losses of seeds to predators and dispersibility was limited. I set out this revised perspective in Grubb (1984) and Grubb (1986). Benzing (1981) had put forward an essentially similar idea for the special case of epiphytes, and with more emphasis on the difficulties of establishment.

Unfortunately, the idea of recruitment limitation was not formalized mathematically until a decade later (Hurtt and Pacala, 1995), but then it was elegantly illustrated in tropical rainforest by Dalling *et al.* (1998). Now there is plentiful evidence of its importance in that kind of system (Wright, 2002). Our studies in a very different system, that of diminutive annuals on sand dunes in Britain, have also yielded evidence of limited impact of one species on another (Rees *et al.*, 1996; Coomes *et al.*, 2002).

Control of relative abundance

Even more inspiring to me than Watt's paper on pattern and process was a passage in his review (Watt, 1961, p. 125), which ran 'as far as I am aware, no

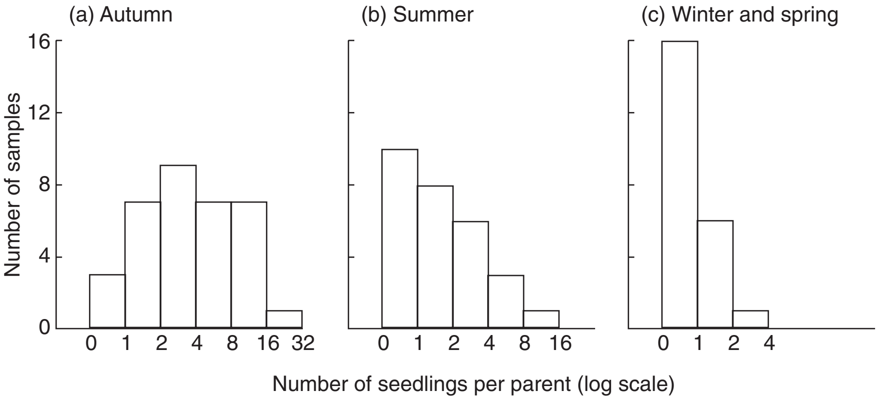

Figure 3. Success of establishment of all serotinous *Proteaceae* combined is dependent on the fire season: autumn fires are most favourable, and winter fires least favourable (reproduced with permission from Bond *et al.*, 1984). Reproduced with permission of Blackwell Science.

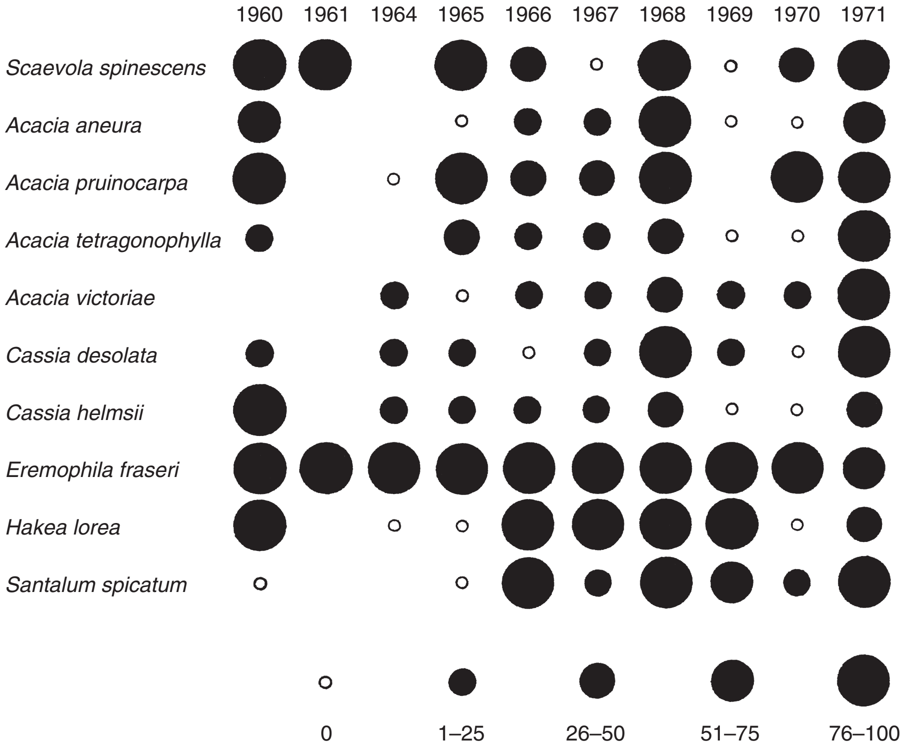

Figure 4. Year-to-year variation in seed production by shrubs and trees in a semi-arid part of Western Australia (from Davies, 1976). Reproduced with permission of Blackwell Science.

critical examination has been made to find out why, in a given plant community some species are rare, some common, some constant (even if rare or occasional only and others sporadic).' Immediately on reading these words in 1964, I was convinced of the importance of tackling the question, but I could make no progress until I had sorted out in my mind the concept of the regeneration niche. As models like that of Pacala *et al.* (1996) show, the relative adundances of woody plants without much vegetative spread can be explained in terms of their regeneration niches and the disturbance history of a site. In grasslands, where individual plants may be as long-lived as trees in a forest, but the shoots die back each year, characteristics of the species effective in each growing season and summarized in their 'competitive ability' may be as important as conditions needed for establishment and onward growth, or even more important.

I was especially pleased to be able to present to Watt, on his ninetieth birthday, our essay on control of relative abundance in herbaceous communities (Grubb *et al.*, 1982), and in the following years I believe we came up with a reasonable basis for understanding of the control of relative abundance in chalk grassland, which is notable for constancy of the hierarchy of abundance among perennials (Mitchley and Grubb, 1986; Grubb *et al.*, 1997).

In all I have written, the single most embarrassing sentence is 'What is significantly different about the rainforest trees, compared with chalk grassland perennials, is that they show no hierarchy of abundance among the species in any one forest type if this is sampled at sites several kilometres apart, and in this respect they resemble the interstitial short-lived plants of chalk grassland … ' (Grubb, 1986, p. 224). I wrote that under the influence of Steve Hubbell's findings in Panama. Now we know that where there is minimal variation in soil and climate over large areas, and where the impacts of human disturbance have been modest, as in parts of western Amazonia, there can be a remarkably constant hierarchy of abundance over very large distances (Pitman *et al.*, 2001). The contrast with the situation in Panama, now made explicit by Condit *et al*. (2002), probably results from the steep gradients in climate on the Isthmus of Panama, appreciable variation in soil type, and the impacts of disturbance by humans over several millennia.

Closing thoughts

All three of my leading mentors at Cambridge (E.J.H. Corner, G.E. Briggs and A.S. Watt) encouraged me to challenge the received views of the day, and to have the confidence to set forth my own views. Perhaps they 'sowed their seed' on fertile ground. During the general election of 1951, our headmaster allowed the school to hold a mock election. I stood as an independent candidate and received four votes out of more than 300. Fortunately, most of my ecological ideas have received proportionately more support than my primitive offerings in politics!

Ecologists are constantly seeking the 'principles' of their science, or what I prefer to call 'generalizations' (Grubb, 1989b). Yet ecologists, like all those who study, are becoming ever more specialized in their research. Those who seek to generalize must read widely, but the trouble is that the literature is often misleading or downright wrong. When it comes to formulating generalizing ideas that have a good chance of standing the test of time, there is no substitute for personal experience in a wide variety of systems. Not every ecologist can have the privilege of travelling as widely as I have, but I do urge ecologists who are setting out on their careers at the present time to gain experience early on in a number of contrasted vegetation types, and – if possible – climatic zones. You will not regret it!

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Seed Dispersal and Frugivory:
Ecology, Evolution and Conservation

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Until recently, the production of fruits by plants, their consumption by animals (frugivory) and the relevance of these to seed dispersal have attracted less attention than topics such as pollination biology. However, since the 1970s they have started to gain more prominence and now give rise to more research funding, seminal papers and international symposiums. This book contains chapters adapted from the Third International Symposium-Workshop on Frugivores and Seed Dispersal held in August 2000 in Rio Quente, Brazil.

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