JOHN LANDER HARPER
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Elected FRS 1978

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Born into a farming family, John Harper identified a number of influential figures in his formal education, including his inspirational school master Wilfred Kings, and the plant ecologists Roy Clapham (FRS 1959) and Jack Harley (FRS 1964) and animal ecologists Charles Elton (FRS 1953) and George Varley during his university education at Magdalen College, Oxford. His first academic appointments were in the University of Oxford School of Rural Economy and the Department of Agriculture, where he carried out pioneering research on seed and seedling mortality and the ecology and control of weeds. In 1960 John was appointed to head the Department of Agricultural Botany at the University College of North Wales, Bangor. The departments of Botany and Agricultural Botany merged in 1967 with John as head of the new School of Plant Biology. From this base, he established a research centre that attracted students and visitors from around the world. As one of the most influential of thinkers, John Harper generated a new discipline: plant population biology. In addition, by integrating advances in animal population biology and evolution into his own work, John helped to create a complete master discipline of ecology, as reflected in a textbook Ecology: individuals, populations and communities (Oxford, UK: Blackwell) for which he received (with co-authors Mike Begon and Colin Townsend) an exceptional lifetime achievement award from the British Ecological Society.

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LIFE AND CAREER

John’s family roots include at least six generations of farmers on both his father’s and mother’s side, and his younger brother Peter became a farmer (61)*. His early years were spent, without childhood friends, on a small, isolated farm near Rugby (figure 1a, b).

There was no family history of academic achievement. Joining Lawrence Sheriff School, Rugby, at age eight, John recalled several seminal influences (63). During protracted periods of illness he developed a passion for entomology, keeping various caterpillar ‘farms’, while his taxonomic skills were initiated by his neighbour, Mr Sides, who taught him the Linnaean system. His first use of an ecological transect occurred aged 13 when he counted buttercups of several species across an undulating pasture on his parents’ farm. Buttercups would continue to fascinate him throughout his career. An introduction to pest control of sorts occurred when pupils at his school were sent out to compete in digging out weedy plantains, the prize for the winning class being tea in the headmaster’s garden.

Of overwhelming significance, however, was his deeply inspiring schoolteacher, Wilfred Kings, among whose pupils were two future FRSs—John and A. J. Cain (FRS 1989)—and to whom, much later in life, John dedicated his book, *The population biology of plants* (40): ‘to W.K., Teacher and Friend’; John has written, ‘I owe my career as a biologist almost entirely to him’ (63) (figure 2). John’s account of his life at Laurence Sheriff School focuses particularly on the Natural History Society and on discipline. After complaining to the headmaster that he had been called a liar by the geography teacher and wished never to attend his lessons again, John was surprised that the headmaster agreed to his demands ‘on condition that I did extra biology lessons. Thus are careers born!’ (63). Of his academic achievements he noted that he was regularly towards the bottom of the A stream, but was head boy in his last year.

John entered Magdalen College, Oxford, in 1943, graduating in 1946 with first class honours in botany (figure 1c). The classes were very small, and John was the only student of his year (61). A tutor is reported to have recalled that ‘his prose style was graphic and his quick wit led him to write interesting essays often with wild hypotheses’ (Sagar 1985). Despite his recollection that there were no lectures in ecology, he was rapidly exposed to the subject by ‘total immersion’ in the field classes of A. R. Clapham (FRS 1959), mostly in grassland systems (63). At this stage, plant ecology at Oxford and in most places consisted of listing the plant species and making some subjective assessment of their abundance, but, as John later noted, ‘giving numbers to subjective values did not make them objective’ (63).

Work experience in the vacations at Oxford also had an influence on his subsequent career (61, 63). In the 1944 vacation John was persuaded by W. O. James (FRS 1952) to help with some plant physiological research on cytochrome oxidase and ascorbic acid oxidase. John reports that he did a lot of experiments using ground up barley, but that while his supervisor seemed delighted with what he did, John never fully understood what it was all about. Having also broken two irreplaceable Warburg manometers he concluded that he was not destined to become a physiologist or biochemist. In contrast, part of the summer vacation of 1945 was spent at the Welsh Plant Breeding Station at Aberystwyth, which he remembered as a ‘baptism into a quite new church with enormous influence on my subsequent research activities. There was a way of looking at vegetation that I had never dreamt of’. What he had seen was applied scientists ‘doing wonderful things’ in grassland science that he could use in the pure science of

* Numbers in this form refer to the bibliography at the end of the text.
ecology of natural vegetation. His experience at Aberystwyth was also very helpful in one of his final year practical examinations. On being presented with a piece of a grass sward that had been cut from a field, John knew, from his Aberystwyth experience, exactly how to analyse it. He was told afterwards that this alone could have guaranteed him his first class honours!

In 1946 he was awarded a Senior Mackinnon Scholarship and Department of Scientific and Industrial Research studentship under the supervision of J. L. Harley (FRS 1964) to study for a DPhil on the interactions between microorganisms and plant root systems (1). Mid study, he took up his first academic appointment (1947, see below), continuing research part time, except for a period of six months when he was a full-time salaried microbiologist at the Colonial Microbiological Research Institute, Port of Spain, Trinidad (where much holidaying and partying took place) (63). There he pursued his interest in interactions between microorganisms and plant roots, looking for differences in the rhizosphere flora, and susceptibility of various varieties of banana to Panama disease fungus (2, 3). John had unfond memories of his DPhil studies, eventually combining his work on bananas with an account of the problems that arise in sampling soil microbes to make what he called ‘a very unsatisfactory DPhil thesis’ (63). In 1950 he gained his DPhil as well as an MA, which at Oxford is not a qualification but a rank (no thesis was involved). It is worth mentioning another influence in John’s life at this time; he went to live as a paying guest, en famille, with the botanists G. R. S. (Robin) Snow (FRS 1948) and C. M. (Mary) Snow, who were pioneers in explaining how the leaf arrangement of various plants was determined. Another, particularly important, seminal influence during the latter part of his DPhil studies was the encouragement by Charles Elton (FRS 1953) to attend seminars in Oxford’s Bureau of Animal Populations. John records that contact with animal ecologists ‘affected the whole of his research career—other botanists were not attracted to their “population” approach’ (63; our italics).
Another important event occurred while at Oxford. John, who had a dislike of cricket, found himself explaining the rules of ‘the silly game’ to a lovely young lady, Borgny Lero, a Norwegian working in Oxford (Turkington 2009). Her mother came from a long line of farmers in Fana, Norway (61). John and Borgny married in 1954 and had three children, Belinda, Claire and Jonathan, and subsequently seven grandchildren. John was a keen gardener at home, and had an extensive collection of classical music—his children recall how he would be visibly moved when listening to records in the evenings (Turkington 2009). He also enjoyed walking in the mountains around his home and would don cross country skis every year when the family went to Norway.

John’s first academic appointment, in 1947, was as part-time demonstrator in the School of Rural Economy, Oxford (61, 63). In 1951, having completed his DPhil, he was appointed demonstrator in the Department of Agriculture, where G. E. Blackman (FRS 1959) helped him acquire his own group of DPhil students. From 1953 to 1959 John was a lecturer in the Department of Agriculture. Against a backdrop of his heavy undergraduate teaching load, John pursued two productive lines of research: the influence of the environment on seed and seedling mortality and the ecology and control of weeds.

Before his move to Bangor in 1960, John organized the first symposium of the British Ecological Society: The Biology of Weeds. He took a sabbatical in 1959–1960 as a Rockefeller Foundation Fellow at the University of California, Davis, recalling the great excitement of interactions there between his population ecology approach and the thinking of evolutionists
such as his host G. L. Stebbins (ForMemRS 1999) (63). By the time John’s Oxford period came to an end (figure 3), the foundations of later work had been laid, as exemplified by his keynote contribution ‘Approaches to the study of plant competition’ at the symposium of the Society of Experimental Biology held in 1960 in Southampton, UK (15).

In 1960 John was appointed head of the Department of Agricultural Botany at the University College of North Wales, Bangor. It was a small department with only eight staff, including two demonstrators, but, with Tony Bradshaw (FRS 1982) and Geoff Sagar (figure 4), John created an exciting department with a dynamic and innovative approach to teaching and research. Janis Antonovics (FRS 1988), one of the two demonstrators, recalled ‘His sprightly step and mischievous grin were always energizing. And he was brimming with ideas, enjoyed challenging us, teasing us, cajoling us to think and do better’ (Antonovics 2009).

It was not long before the growing Department of Agricultural Botany merged with the Department of Botany, where Peter Greig-Smith and Paul Richards held chairs. John became head of the new School of Plant Biology in 1967 and brought with him the friendly atmosphere of Agricultural Botany and its informal gatherings over tea and coffee. Lively debates at departmental seminars, particularly involving John and Greig-Smith, were legendary, ‘amidst clouds of tobacco smoke’ (Watkinson 2009). From his base in North Wales, John established a research centre that attracted students and visitors from around the world. He retained the position of head of school until 1982, when he took early retirement as a consequence of political tensions within the university, and became emeritus professor. However, he continued until 1990 as head of the Unit of Population Biology, an autonomous research unit based in the School of Plant Biology. This unit was enabled by a grant from the Barbinder Trust set up by his former landlady, the Oxford botanist Mary Snow (Sackville Hamilton 2009). John
left Wales in 1997 to be close to family in Devon. He served as a visiting professor at the University of Exeter in 1998.

**Research**

*Bacteriology of the rhizosphere*

John’s early work, for his DPhil, concerned the relationships among plant roots, fungi and bacteria. While he never became enamoured with this area, and considered it a dead end, it is worth recording partly to show that even eminent scientists can make decisions they regret and also to identify a link with his later obsessions. John could not remember ever applying for funding for a DPhil but rather drifted into research: ‘it was simply assumed by Magdalen and the Botany Department’ that he would do so (63). J. L. Harley had recently arrived at Magdalen post-war and restarted his research on the way fungi grow in association with plant roots and change root shape and functioning. John was excited by Harley’s enthusiasm and chose him as supervisor. Electing to look at the organisms living in the rhizosphere of plants in a calcareous fen, a decision he described as ‘very, very odd’, he chose, for no
good reason, a common agar medium that favoured bacteria, which necessarily became his main focal organisms. No one in the department was even an amateur in this field: ‘I don’t think anyone else ever tried to study the bacteriology of the rhizosphere’ (63). Much of his DPhil thesis was concerned with the multitude of technical problems that made the research so unproductive. However, his observations of bacterial and fungal colonies on agar plates, some growing over and inhibiting others, served as a forerunner to studying interactions between plants in grassland and led to the experimental plant population biology that dominated his later work.

**Experimental ecology**

Plant ecology had been dominated by the description of vegetation and the autecology of individual species. In contrast, an experimental approach was fundamental to John’s approach throughout his career. He saw the need to move from that essential first step of description to the search for causative mechanisms underlying what had been described. His enthusiasm for this approach derived from his association with animal ecologists. The Botany Department occupied part of the Manley Laboratories on the edge of Oxford’s Botanic Garden. The rest of this building was occupied by two very influential animal ecology research groups—Charles Elton’s Bureau of Animal Populations and David Lack’s Edward Grey Institute for Field Ornithology. The botanists had no links with either group; indeed John recalled that the door from the Botany Department was usually locked. He has written that the botanists ‘were not to know that a large part of animal ecology was being created’ elsewhere in their shared building (63). In the later years of his DPhil research, Charles Elton encouraged John to attend seminars, where he was excited to interact with animal ecologists including Elton, Dennis Chitty, H. N. (‘Mick’) Southern, David Lack (FRS 1951) and George Varley. John acknowledged Elton and Varley as great teachers (who) ‘gave me great encouragement when my work was viewed with great suspicion by plant ecologists’ (59; our italics). Lack and Varley (see Varley 1957) both encouraged John to focus on experimental population studies, an approach that he noted was already ‘quite respectable in agronomic circles’ (61). Certainly, weed and crop seeds provided excellent opportunities for experimental work; they were readily available, and many were annuals so that experiments could be taken through the whole life cycle of a plant. In fact, John had already developed a penchant for the experimental approach in the first year of his DPhil studies when, as departmental demonstrator, he had to design practicals for undergraduates with almost no equipment (not even class microscopes), so he developed a project approach that required no more than a packet of seeds and some pots of soil. His students could design simple experiments to answer questions such as: Does the depth of seed burial affect time of seedling emergence?, or When radish seedlings emerge do they grow more slowly if one of their two seedling leaves is removed? John recalled that he had never been taught science like this, either at school or at university (63). He introduced this same teaching approach when he became head of department in Agricultural Botany at Bangor.

In stark contrast to much of the descriptive plant ecology of the time, from the very beginning John encouraged his research students to carry out experiments under controlled conditions and in the field. One of John’s favourites (Turkington 2015) was the ‘graveyard’ experiment, so called because its arrangement of blocks of plots resembled a graveyard (figure 5), which examined the impact of manipulating soil heterogeneity in a variety of ways on the establishment of plants from seed (20). Many of the experiments that John encouraged
were simple, involving the minimum of materials and equipment. Studies on population regulation and interference, for example, involved growing plants in pots or trays either in monocultures or in mixtures in the greenhouse (e.g. 37, 41, 49) or manipulating densities in the field (43).

Agronomy and weed ecology

John’s next strands of research at Oxford lined up with the foci of Professor Blackman’s Agricultural Research Council Unit of Experimental Agronomy: the development of new crops for British farming and the exploitation of new discoveries in weed control. His interest, of course, reflected an upbringing on a farm, a familiarity with agricultural landscapes and plants, and an early fascination with weeds, those ubiquitous plants of agricultural ecosystems. Buttercups, docks, ragwort, plantains, fat hen, blackgrass, wild oats, groundsel, couch grass, shepherds purse and annual meadow grass were all to be species for study over his career, along with a range of crops, especially maize, and forage plants, such as white clover.

With P. Landragin and J. W. Ludwig, John produced a widely quoted series of eight papers on ‘The influence of the environment on seed and seedling mortality in maize’, at a time when the introduction to Britain of this crop was being examined by Professor Blackman’s unit (Sagar 1985). The survival of seeds depends on having a substrate suitable for germination and thus the soil surface can be viewed as a sieve determining which seeds produce seedlings. The papers explored the influence of factors including time of planting (5) and depth of sowing (8), as well as aspect, temperature, soil moisture and soil colour. Interestingly, this work paralleled the undergraduate practical exercises he designed at Oxford. His work in this area, while highly influential, was not strongly pursued in his later career.

The other research strand, which was to prove much more enduring, concerned weed control. The public emergence of John as a weed biologist and ecologist occurred at the first British Weed Control Conference in Margate, UK, in 1953 (4) at a time when there were
fewer than 10 chemicals available for weed control (Sagar 1985). In fact, his interests rapidly became dominated by weeds because they allowed many interesting ecological questions to be addressed, including the evolution of pesticide resistance. Just over a decade after the introduction of the first modern commercial herbicide, 2,4-dichlorophenoxyacetic acid (2,4-D), John was the first to consider systematically the likelihood of the evolution of herbicide resistance (6), and the earliest examples of resistance occurred just a year later (Gressel 2009; Kraehmer et al. 2014). Indeed, in an addendum to his paper, John noted that since it was written, Hanson (1956) reported that *Erechtites hieracifolia*, which had previously been controlled in sugar cane plantations by applications of 2,4-D, had developed strains resistant to the herbicide.

John also provided early insights into the significance of seed dormancy in weed control (7), noting that most common agricultural weeds have the ability to remain dormant, enhancing the stability of weed populations in the face of herbicide application. He predicted that great advances might occur if chemical means to break weed dormancy could be discovered. In a third influential paper (9), he took an overtly modern ecological approach to the question of weed control, embedding the weed and focal crops in a food web of other plants, fungi and herbivores, as well as predators and parasitoids of the herbivores, noting that knowledge of the biotic relationships of weeds, such as the role of seed-eating birds and herbivorous insects, was ‘deplorably scanty’.

Despite his group making progress in predicting the invasiveness of weeds and in defining how limits on seed production and germination might limit weed infestations (e.g. Naylor 1970, 1972), those studying the ecology of weeds at the time, sadly, failed to make much impact on weed control because herbicides were just too cheap and effective. However, John continued to work on many of these plants long after his main focus of interest had moved on from practical questions concerning weed biology and control. This was in part because they were easy to grow under field and greenhouse conditions, and this made them exceptional experimental organisms. It was only in the 1970s that some in his research group (A. H. L. Huiskes, R. N. Mack, J. C. Noble, A. R. Watkinson) decided to work on dune plants, much to John’s disappointment, and in the 1980s on trees (M. C. Alliende, M. Jones).

**Gause’s hypothesis and species coexistence**

Professor Blackman was exceptionally supportive in helping John to acquire his own group of DPhil students at Oxford: G. R. Sagar and I. H. McNaughton from the Oxford Botany Department and John Clatworthy, a Rhodes Scholar from Rhodesia. A principal focus of the group’s work derived from John’s self-proclaimed obsession with Gause’s hypothesis, to which he was first exposed as an undergraduate in 1944 at a one-day symposium of the British Ecological Society at Cambridge’s Botany School (*The ecology of closely related species*: British Ecological Society 1945). Gause’s pioneering experiments with mixed cultures of protozoa led to his conclusion that two species with ‘the same ecology’ could not persist together, a hypothesis or ‘law’ that, as John put it, ‘begs its own question’ because it forces one to determine the ways their different ecologies may allow persistence (61). His students shared his obsession (Sagar 1985). For John, Gause’s hypothesis was closely tied up with emphasis by Charles Darwin FRS on the similarity between phylogenetically closely related species: ‘it is the most closely allied forms . . . which, from having nearly the same structure, constitution and habits, generally come into the severest competition with each other; consequently, each new variety or species, during the progress of its formation, will generally press hardest on
its nearest kindred, and tend to exterminate them’ (Darwin 1859). Ecology, as a subject, did not exist in Darwin’s day, but John proclaimed that Darwin’s sentence ‘combines ecology, population biology and evolutionary theory in one glorious tantalising cornucopia of lovely questions’ (63).

In a novel and widely cited review of the evolution and ecology of closely related species (14), John and his students meticulously analysed coexistence as it relates specifically to plants (and in contrast to animals), focusing on differences in the biology of higher plants that could make them ecologically complementary in a habitat, including differences in site requirements for seedling establishment, in susceptibility to predators/parasites, in germination time or in requirements for breaking dormancy. This theoretical contribution was rejected by two prestigious journals of the day before being accepted by *Evolution* (Sagar 1985), and it presaged a plethora of publications concerning the comparative biology of closely related species living in the same area, including breeding barriers between *Papaver* species, mechanisms facilitating self-pollination and specific relationships with the principal insect pollinators (10), and inter- and intraspecific interference between and within populations of *Plantago* species (16), *Papaver* species (18), *Trifolium* species (19), *Rumex* species (21), *Avena* species (29), *Ranunculus* species (33), *Agropyron* species (34), *Veronica* species (60), and cultures of *Lemna* spp. and *Salvinia* (17).

*Evolution, life histories and reproductive strategies*

John’s preoccupation with evolutionary questions was fostered during his sabbatical at the University of California, Davis, where he interacted with evolutionists such as G. L. Stebbins and H. Lewis, and geneticists such as M. Lerner and R. W. Allard (61). He recalls how Stebbins and Allard both forced him to try to think as an evolutionist (59). John’s Darwinian approach to plant ecology contrasted with the traditional ‘vegetationalist’ methodology (22), which sought to describe and interpret areas of vegetation. Instead, like Darwin, his focus was on numbers and based on consideration of the consequences of natural selection for individuals and populations (22). He realized that two interlinked properties of higher plants, in contrast to animals, hindered the development of a Darwinian approach to plant ecology: plasticity and vegetative reproduction; these issues are dealt with in a later section. Given John’s focus at the time on weeds and their seeds, plasticity and vegetative reproduction were not so much of an issue, facilitating his predictions about evolution of resistance to herbicides and the studies on closely related species in the same habitat, presumed at least in part to be the result of forces of natural selection.

John’s most significant evolutionary contributions concerned plant life histories and reproductive strategies. In studying the fates of individuals, John inevitably confronted numerous questions about plant life histories, from germination, through seedling establishment, to growth, reproduction and death. He noted that ‘a whole branch of plant ecology lay almost untouched’ with numerous questions to be addressed on the strategy of reproduction, such as whether the proportion of a plant’s output devoted to reproduction is higher in colonizing species, and whether it differs between plants in hazardous climatic conditions as opposed to more stable environments (22). Throughout his career, John addressed significant questions relating to the resources allocated to reproduction (27, 46), to plant breeding systems (11, 12), to abortion (52) and in terms of the shapes and sizes of seeds (28).
Unusually among plant ecologists at the time, John was interested in the allocation of resources to reproduction and growth in terms of the compromises that maximize fitness. This included not only the overall allocation of resources, but also its timing (36), as this had consequences for reproductive value. He also saw it in terms of the modular structure of plants and the ways that meristems were allocated to various activities such as reproduction, growth and defence (57). A perennial habit is thus only possible if some meristems remain in a vegetative condition, while the reproductive schedule of a tree is characterized by a more or less long period in which no meristems are allocated to reproduction followed by slowing of growth as a proportion of meristems end their lives in the lethal act of reproduction. This approach also allowed the extension of existing theory to the evolution of the characteristics of the life histories of clonal organisms, particularly in relation to genet architecture (49) and to r- and K-selection (54).

Population biology

It was John’s Darwinian approach that also provided the impetus for him to work on a wide range of topics relating to the fates of individuals within populations. For many animal population ecologists at this time the driver for research was a desire to explain changing patterns of abundance in space and time. In contrast, John’s approach led him to focus much more on the factors that determine the fate of individuals within populations. As he famously wrote ‘Plants stand still and wait to be counted’ (22), making them, in many ways, easier to study than animals. It was as a result of this detailed demographic approach, focusing on individuals, that he was able to provide insights into not only plant ecology but also plant evolution, as discussed above.

Early in his career much of the focus was on the fate of individual plants as seeds and seedlings in agricultural systems (13, 20). At the same time, he was impressed by the pioneering long-term studies of the Swedish botanist C. O. Tamm on the fate of perennial plants in forests and meadows, showing that many populations were relatively constant in number but displayed a high turnover of individuals (22). He was also struck by the fact that the probability of death was often remarkably constant for many herbaceous perennials after the seedling stage of the life cycle, and that their numbers in the absence of recruitment showed an almost isotope-like constant rate of decay.

Throughout the 1960s and 1970s John scoured the literature and the world for studies on the demography of plants and encouraged his own students to study the fate of individuals over the whole life cycle. This produced a range of reviews (30, 36) and comprehensive studies of the population dynamics of individual species (33, 43).

Building on the pioneering work of T. Kira and K. Yoda in Japan and of C. T. de Wit in The Netherlands (22), John instigated and was involved in a range of studies and reviews that considered how neighbour interactions, both intraspecific and interspecific, affected resource availability and plant performance. Many of the early studies involved single species or two-species mixtures in greenhouse conditions and could be related to agricultural systems, the yield of crops and the effects of weeds on crop yield (35, 37). Later studies, however, increasingly focused on interference in natural populations (43, 45) and on the neighbour relationships of individual plants (41, 49), linked in turn to questions about population regulation and coexistence. The ‘plant’s eye view’ became increasingly important in the Harperian view of population biology (42). The roles of other types of species interaction, such as seed predation, herbivory, parasitism, pathogens and mutualism in the population
biology of plants, received less attention from his own group. However, John produced notable reviews of the role of herbivory in generating vegetational diversity (26) and experimental studies specifically on slug–plant interactions (25, 47) and the grazing of sheep on clover in pastures (38).

Interestingly, despite highlighting the logistic model in the development of his thinking on population growth rates and regulation (22, 40), John did not actively pursue the determination of abundance through population modelling, except for one classic paper on *Lemna* using the logistic model (17). Those of his students who used a modelling perspective to look at abundance did so largely independently (e.g. R. E. L. Naylor, J. Sarukhán (ForMemRS 2003), A. R. Watkinson). He did, though, help to develop a model framework for a size-structured population of genets, in which each genet comprises an age-structured metapopulation of modules (54).

Neither was he particularly focused on spatial aspects of population ecology—colonization and the distribution of species. This was despite the fact that his departmental colleague Peter Greig-Smith was researching the spatial distribution of plants. They were nearly always in conflict in seminars! The paper on the neighbour relations of *Trifolium repens* in the pasture at Aber in North Wales (44) is a rare example of where both the Harperian and Greig-Smith approaches to science coincide. Rather, John’s focus on the individual, whether it was the occupation of biological space (31, 48), a neighbourhood approach (41) or the fate of individual buds (51), led him to look at the ecology of plants at an increasingly fine scale. He was, however, aware of the danger of this (57), given the larger scale questions that were looming on the horizon in areas such as conservation and climate change.

*Modular construction and plasticity*

In his influential presidential address to the British Ecological Society (22), John recognized two interlinked properties of higher plants that had seriously hindered the development of plant demography: plasticity and vegetative reproduction. He tackled both of these topics head on. Both relate to the concept of the individual, a corner stone of the Darwinian approach. The first property, plasticity, relates to the variation in size of individual plants and how even plants of approximately the same age develop substantial variation in size, form and reproductive output (24, 31, 58). The second, vegetative reproduction, relates to the very concept of what constitutes an individual. In time, he rejected the concept of vegetative reproduction, replacing it with ‘clonal growth’ (36). He argued that seeds give rise to genetic individuals (which he termed genets) that then develop through the iteration of modular units (or ramets), which in some plants remain attached, as in the case of annual plants and most trees, while others fall apart, as in the case of two of his early organisms of study, the duckweed (*Lemna*) and buttercups (*Ranunculus*). His concept of plant modularity had a profound impact on the way that his group, and other researchers, considered the fate of individuals within populations.

For those who worked on annual plants, the unit of study remained the genetic individual derived from a seed (41, 43, 60), while the size variation of plants was explored through the differential birth and death rates of modules (39, 53), an individual genetic plant being treated as a population of parts. For herbaceous perennial plants, some studies were carried out on genetic individuals, as in the case of plantains (*Plantago*) (16), some were primarily concerned with the birth and death rates of mixed populations of modules of unknown genetic origin, as in the case of white clover (*Trifolium*) (44, 45), while others considered both genetic and modular units (33) (Soane & Watkinson 1979). John was particularly delighted with the
Figure 6. A diagrammatic life cycle of *Ranunculus repens* (the bicycle) showing the population flux of seeds (left) and rosettes or modules (right) through the year within average quadrats of one metre square in a permanent grassland at Aber in North Wales. The data are taken from Sarukhán (1971), as reproduced in Fig. 19.20c of (40). (Figure used with permission from Elsevier.)

portrayal of a population of buttercups as a bicycle, with one wheel depicting the flux in the number of seeds and the other the flux in the number of modules (figure 6) (40).

In considering individual plants as populations of modules, John increasingly asked questions about the births and deaths of modules, which ultimately led to questions about the fate of buds that would give rise to new modules. This thinking was helped by having the plant morphologist Adrian Bell in his department. John was taking a population perspective not only to the growth of plants, but also to the impact of the birth and death of modules on plant form (49, 51, 55) and the functioning of canopies (56).

BOOKS AND SCIENCE COMMUNICATION

*Population biology of plants*

John Harper outlined his philosophy and approach to plant population biology in his presidential address to the British Ecological Society in 1967 (22). Over the next 10 years, with the aid of a series of 24 lectures (the number of chapters in his subsequent book) given at the University of Massachusetts in 1969 and a sabbatical in Montpellier in 1975, he compiled the information that would allow him to build a comprehensive compendium on the *Population biology of plants*, published by Academic Press in 1977 (40). This not only fleshed out John’s approach to population biology but also provided a virtually complete overview of the relevant literature at the time. Notably he drew extensively on the work of his students and collaborators, including references to virtually all their work, with detailed descriptions of many of their methods. He also drew on a diverse global literature on agriculture,
silviculture and vegetation, enthusiastically endorsing the contributions to population biology from different academic traditions and parts of the world. Population biology of plants was as relevant to those working on arable fields as those working in tropical forests. For a period after publication there was virtually no need for researchers and students to look elsewhere for an understanding of plant population biology. But it was not a swan-song (Sagar 1985); it also set out a research agenda for a new generation of researchers. As Norris noted (Norris 2009): ‘John Harper’s 1977 book on plant population biology is probably the single most tattered book in my personal library collection, attesting to the many times that I used it or loaned it to students.’

Science communication
John was just as committed to the communication of ideas as he was to research. This is evident from the innovative experimental approach he developed for undergraduate practical teaching while still a DPhil student, his membership in the 1960s of the Nuffield Science Teaching Project (a programme to develop a better approach to teaching science in British secondary schools), his contribution to the British Ecological Society symposium on teaching (23) and his article in the Journal of Biological Education about the value of project teaching in university courses and the manner in which projects should be assessed (32). His eccentric manner of interacting with his students in Bangor’s Botany Department is also fondly remembered by many research students. Ogden (2009) recalls how John became so engrossed in discussing his results that he gradually slid down the wall until sitting on the floor; followed by a 20-minute discussion while people passed to and fro in the corridor between John and his student. Sackville Hamilton (2009) also recalls this habit, ‘of squatting down, pipe in hand, while bemused visitors changed between standing, bending, half-crouching and squatting right down beside him, as they wondered how to react’! These memorable times must certainly have left their educational mark. John’s predilection for wild hypotheses, first noted when he was an undergraduate, was also evident in Friday afternoon seminars when he encouraged the audience to shoot them down. Anything that passed this test was ready for a broader audience (N. R. Sackville Hamilton, personal communication).

Ecology: individuals, populations and communities
John’s understanding of ecology as a whole, not just plant ecology, and the way it should be taught, reached its widest audience with publication in 1996 of an advanced ecology textbook, Ecology: individuals, populations and communities, with M. Begon and C. R. Townsend (50), and a more elementary version in 2000, Essentials of ecology (62). More editions were to follow, with translations into Russian, German, Spanish, Italian, Chinese, Japanese, Korean, Czech and Portuguese. Its success can be gauged by the more than 13 000 citations the book (all editions) has garnered in the primary ecological literature, and the Exceptional Lifetime Achievement Award the authors all received from the British Ecological Society in 2007. Begon (Begon & Townsend 2009) has written: ‘John already knew what an ecology textbook should be, and Colin and I bought into his vision. We had responsibilities, he insisted, to our young (and not so young) readers: not to patronize them by pretending things were simpler or more certain than they really were; to make them think, make them question; and to make them feel that our subject was alive and waiting for them to make their own contribution.’
LEGACY

As one of the most influential of thinkers, John Harper generated a new discipline: plant population biology. He taught us a new way to study plants and arguably had a greater impact on the development of plant ecology as a modern science than any other ecologist in the twentieth century (Turkington 2015). But he did much more than this. By assimilating advances in animal population biology and evolution and integrating these with his own work, John helped to create a complete master discipline, as reflected in the textbook *Ecology: individuals, populations and communities* (50), which was the first to set out to give equal prominence to all living organisms.

All those who learned ‘Harperian’ ecology from him were privileged to be ramets derived from John as genet (Porter 2009). His influence on students and visitors is by no means always evident from a review of the literature; for example, he was not identified as an author on many of his students’ papers—claiming, incorrectly, that he had not made sufficient contribution to their work. One of his many distinguished visitors, the American pathologist J. H. Andrews, came to Bangor for a sabbatical to explore how John’s ideas about plant population biology might apply to the world of microbes. He produced an influential book on the *Comparative ecology of microorganisms and macroorganisms* (Andrews 1991), another example of John’s contribution to the unification of ecological disciplines.

John had a great love of words. Take, for example, his book chapter (57) that begins: ‘Apophasis was a process used by theologians to describe the nature of God by defining the extent of their ignorance. This chapter attempts an apophasis of plant population biology.’ John always emphasized, in his research and textbooks, that the beginning of knowledge is the awareness of ignorance. He was also obsessed with the careful definition of terms. He strongly promoted the ditching of the word adaptation, with its Latin prefix implying purpose, and changing it to abaptation, correctly implying ‘the result of’ the natural selection of ancestors. Naylor (2009) points out that this predates the perspective of Richard Dawkins (FRS 2001) by some decades that the individual phenotype reflects the history of previous environmental exposure. In *Ecology: individuals, populations and communities* (50) the word abaptation is promoted, and indeed appears in the first three editions, but disappears in the fourth because it had not found common favour, despite being the more appropriate term. John also railed against the fuzzy definition of terms and helped the ecological community sort out what was really meant by competition, strategy and stress. He particularly disliked the term vegetative reproduction, noting: ‘If a tree spreads vertically we call it growth, but if a clover spreads laterally we call it vegetative reproduction—nonsense.’ His preferred term, clonal growth, has become widely accepted and, because it incorporates animal clonal growth, once again serves the purpose of an all-encompassing science of ecology.

AWARDS AND APPOINTMENTS

**Distinctions**

| Year     | Title                                                                 |
|----------|----------------------------------------------------------------------|
| 1966–1968| President of the British Ecological Society                          |
| 1978     | Fellow of the Royal Society                                         |
| 1981     | Honorary Associate of the Swedish Society for Phytogeography         |
| 1984     | Foreign Associate of the National Academy of Sciences USA            |
1984 Distinguished Ecologist Award of the Ecological Society of America
1984 Honorary DSc, University of Sussex
1989 Commander of the British Empire (CBE), Queen’s Birthday Honours
1990 Darwin Medal of the Royal Society
1993–1995 President of the European Society for Evolutionary Biology
1996 Doctor Honoris Causa, National Autonomous University of Mexico
1999 Millennium Botany Award, International Botanical Congress
1999 Marsh Ecology Award, British Ecological Society
2008 ‘Harper Prize’ inaugurated by the British Ecological Society (annually for best paper in *Journal of Ecology* by an early career author)

**Memberships**

1971–1981 Member of the Natural Environment Research Council, UK
1980–1990 Member of the Agriculture and Food Research Council, UK
1984–1990 Member of the Management Committee, Centre d’Études Phytosociologiques et Écologiques, CNRS, France
1990–1998 Member of the Joint Nature Conservation Committee, UK
1990–1998 Trustee of the British Museum of Natural History

**Editorial roles**

1974–1981 Editor-in-Chief of *Agroecosystems*
1980–1982 Associate Editor of the *Proceedings of the Royal Society*
1982–1994 Co-Editor of *Oecologia*
1989–1992 Editorial Board member of *Acta Oecologica*
1990–1992 Editorial Board member of the *Philosophical Transactions of the Royal Society*
1992–1998 Editor of the *Proceedings of the Royal Society B*

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**AUTHOR PROFILES**

*Colin Townsend FRSNZ*

Colin Townsend is emeritus professor in the Department of Zoology at the University of Otago, New Zealand. He obtained his first degree and DPhil at the University of Sussex, before taking up teaching appointments at Oxford, the University of East Anglia (UEA), UK, and the University of Otago, New Zealand. He is a fellow of the Royal Society of New Zealand and a fellow of the Cawthron Institute.

Colin’s research has explored the effects of flow-related disturbance, invasive species and multiple agricultural stressors on aquatic food webs. For more than 30 years he was co-editor in chief of *Freshwater biology*. He received the 2013 Award of Excellence from the Society for Freshwater Sciences and the 2014 Medal of Excellence from...
the New Zealand Freshwater Sciences Society. Colin has co-authored or sole-authored ecology textbooks that have been adopted by universities around the world and translated into nine languages. The most successful of these was co-authored with John Harper (and Mike Begon, University of Liverpool). In 2007 these three authors received the Exceptional Lifetime Achievement Award from the British Ecological Society.

Andrew Watkinson

Andrew Watkinson is emeritus professor of ecology at the UEA. He took his first degree in biology at the University of York before undertaking, from 1972 to 1975, a PhD in plant population biology with John Harper at the University College of North Wales, Bangor. His PhD, on ‘The population biology of Valpia membranacea’, laid the foundation for work on the population dynamics of plants at the UEA, where research initially focused on population regulation and the factors determining the abundance and dynamics of annual plants. As his research interests in ecology broadened, he moved from the School of Biological Sciences to Environmental Sciences. He was one of the founding members of the Tyndall Centre for Climate Change Research in 2000, becoming its director in 2007 before moving on to become director of Living With Environmental Change (LWEC), a joint Research Council and UK government initiative led by the Natural Environment Research Council. He retired in 2015 but continues as emeritus professor at UEA and as emeritus research fellow at the Centre for Environment, Fisheries and Aquaculture Science, an agency of the UK government’s Department of Environment, Food and Rural Affairs.

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