

John L. Harper FRS, CBE

1925–2009

Photo by Peter Davis

Professor John Lander Harper revolutionized plant ecology and had perhaps a greater impact on its development as a modern science than anyone else since Darwin. John brought population biology and experimental approaches into the forefront of plant ecology, linking demography and selection, and therefore ecology and evolution. He will be remembered with great affection and gratitude by plant ecologists throughout the world.

John was born on 27 May 1925 into a farming family, and he developed an early interest in natural history at the Lawrence Sheriff Boys' Grammar School in Rugby, England. He was profoundly inspired by his teacher, Wilfred Kings, to whom, much later in life, he dedicated *Population Biology of Plants*: "To W.K., Teacher and Friend." In 1943 John entered Magdalen College, Oxford, and graduated with a First Class Honours in Botany in 1946, followed by an M.A. and a D. Phil. in 1950 under the supervision of Dr. J. L. Harley. At this time, Professor G. E. Blackman was searching for a keen botanist with enthusiasm for research. John was formally interviewed and appointed as a Demonstrator in 1951, and from 1953 to 1959 was Lecturer in the Department of Agriculture at Oxford University. Although John's development as an ecologist was strongly influenced by reading Charles Darwin, it was during his time with Blackman that he developed his distinctive blend of research involving natural selection, theory, and experimentation (Sagar 1985). In an e-mail message to me dated 22 November 2003, John said:



It is fascinating for me to trace the history of my concern with grassland. My Prof in Oxford was T.G.B. Osborn who is almost unknown, but it was he who took me and one or two others to London to hear a BES meeting on Gause's hypothesis on the ecology of closely related species and who suggested that I spend a summer at the Welsh Plant Breeding Station, Aberystwyth. These two

episodes had enormous influence starting me thinking. Osborn was a splendid example of a scientist who had powerful influence by being a teacher and creating a new scientific generation while being almost unremembered in his own.

Another significant event happened to John while at Oxford. When visiting the Harpers in 2006 John told me: “I had a great dislike for cricket and didn’t really understand the game, but one evening I spotted a lovely young lady watching a cricket match. I did my best to explain the rules of the silly game to her.” The young lady was Borgny Lero, a Norwegian working in Oxford, and John and Borgny were married in 1954. They have three children, Belinda, Claire and Jonathan, and seven grandchildren.

John and Borgny provided a very enriching environment for their children that embraced living in North Wales, learning Welsh, exploring the mountains and beaches, and playing in the continually evolving garden. The children write:

In our teenage years we would catch the bus into town to socialize and dance, and our father would always be there to pick us up if we missed the last bus home. Our parents gave us a great deal of trust and patience, they gave us the space to make mistakes and learn from them. We were introduced to a high level of culture, including visits to London to the theatre and to seminal art exhibitions such as Giacometti and Picasso. Our father was a very creative man and imparted such an ease and enjoyment out of all the activities he took part in, he loved to make things with us, transforming walnut shells into birds, making papier-mache, folding origami; he would listen to his extensive collection of classical music in the evenings which he was visibly moved by, make the lightest cheese soufflé you have ever tasted and recite the “daftest” poems. He was never sporty, yet we went back to Norway every year and donned cross-country skis. We would often walk in the mountains around the house in North Wales, though gradually the garden took precedence; both parents were passionate gardeners.

John spent a sabbatical in Davis, California, from 1959 to 1960, and returned to Britain, specifically to North Wales, and to the jaw-breakingly delightful home address: Glan-y-Coed Park, Dwygyfylchi, Penmaenmawr, Gwynedd, North Wales, where he was appointed Professor of Agricultural Botany at University College of North Wales, Bangor. In 1967 his Department merged with the Department of Botany to form the new School of Plant Biology, of which he became Head. It was from this base that he established a research center that attracted students and visitors from all over the world. During the 1970s, in particular, the famous and the want-to-be famous made pilgrimages to SPB at UCNW. Recently, I sent e-mails to 60 of John’s former students, colleagues, visitors, and collaborators based in different countries throughout the world, and within four days I had 51 responses from 15 countries carrying warm words of affection and memories of JLH.

The School of Plant Biology, and JLH, became identified with almost everything new emerging in the field of plant population ecology. John had already established his credentials as an agricultural botanist and weed ecologist, and trained a number of students in those fields. But it was from Bangor that many seminal and influential papers were published. He produced more than 150 publications over 40 years, including three books. Opinions differ on his most influential publications, but high on the list are the series with McNaughton and others on “The comparative biology of closely related species

living in the same area,” “Factors controlling plant numbers” (Harper 1960), “Approaches to the study of plant competition” (Harper 1961), “The individual in the population” (Harper 1964), “A Darwinian approach to plant ecology” (Harper 1967; his Presidential Address to the British Ecological Society), “The shapes and sizes of seeds” (Harper et al. 1970), and of course his 892-page *Population Biology of Plants* (1977), affectionately known as “The gospel according to St. John.” But John himself once told me that he wanted to be remembered for the so-called graveyard experiment, the first in a series on “The behaviour of seed in soil” (Harper et al. 1965). These papers, and the man himself, revolutionized plant ecology by transforming it from descriptive, correlative natural history to a quantitative, process-oriented subject. In a review of *Population Biology of Plants*, Harold Mooney (1978) wrote “... John Harper has made enormous contributions to our understanding of plant biology. Harper’s innovative ideas have led to a whole school of thought and research that is spread far beyond his home University.” Stanley Woodell (1977) noted that “there are enough ideas to keep several workers busy for a lifetime.” Finally, the Begon, Harper, and Townsend textbooks have had a profound influence on a generation of undergraduates, being called a nouvelle cuisine when first published, and currently having been translated into six languages.

John was ruthless when faced with fuzzy thinking and had an abhorrence of sloppy terminology. In “After description” (Harper 1982) he attacks usage of the words stress, strategy, and adaptation. In *Ecology: Individuals, Populations and Communities* (Begon et al. 1986), and *Essentials of Ecology* (Townsend et al. 2000), the word adaptation is dismissed in the early pages and apparently not used again. In my last conversation with John in 2006, he said, with that unique Harperian twinkle in his eye “I’m not sure that Mike (Begon) or Colin (Townsend) know that the word has been removed.” He particularly disliked the term vegetative reproduction: “if a tree spreads vertically we call it growth, but if a clover spreads laterally we call it reproduction—nonsense.” So on his 50th birthday in 1975, students and visitors posted adverts for a spoof Departmental seminar with the title “Vegetative reproduction as an adaptative strategy in stressful environments,” and the speaker was J. L. Harper!

Harper’s accomplishments and authority in the field of plant population biology gained him much international recognition. From 1971 to 1998 he served in various advisory roles for bodies including the Natural Environment Research Council, the Royal Society, the Agricultural and Food Research Council, the Comité de Direction, C.E.P.E. (CNRS), the Joint Nature Conservation Committee, and as a Trustee of the British Museum of Natural History. He also held various editorial roles including Editor-in-Chief of *Agroecosystems* (1974–1981), Co-Editor of *Oecologia* (1982–1994), Assistant Editor, *Philosophical Transactions of the Royal Society B*, (1990–1992), Assistant Editor, *Proceedings of the Royal Society B* (1980–1982), and Editor, *Proceedings of the Royal Society of London B* (1992–1998). He was President of the British Ecological Society (1966–1967), elected to the Royal Society of London (1978), an Honorary Associate of the Swedish Society for Phytogeography (1981), a Foreign Associate of the U.S. National Academy of Sciences (1984), and in 1981 was named “Eminent Ecologist” by the Ecological Society of America. He was awarded Honorary Doctorates at the University of Sussex in 1984, and the Universidad Nacional Autónoma de México (UNAM) in 1986, a CBE in 1989, and the Royal Society Darwin Medal in 1990. In 1999, the International Botanical Congress awarded him the Millennial Medal, and the British Ecological Society gave him the Marsh Award in 2000—not bad for one lifetime!

John was also proud of the legacy of his many students. He left a profound ecological footprint, especially in Mexico, the United States, Canada, and parts of Europe. Two of his former students, José Sarukhán and Rodolfo Dirzo, were elected as foreign associates of the U.S. National Academy, and Sarukhán was also elected a foreign member of the Royal Society. As far as I can determine, 18 of his former students hold faculty positions in universities throughout the world. One of them, Lesley Clegg (now Lovett-Doust), is Vice-President of Michigan Technical University at Houghton, Michigan. For a number of years Sarukhán was President of the largest university in the world (UNAM), in Mexico City.

John Harper also had a mischievous sense of humour, a rapier-sharp wit, and an equally sharp intellect. He loved to debate and often provoked the unsuspecting into extremely defensive situations. To those who did not know JLH this was often seen, incorrectly, as arrogance, but for those of us who knew him—well, we knew better! Many of us will remember tea time in the foyer of SPB where JLH's unique mannerisms were always on display. John would swivel around, poke you in the chest with his pipe, and ask a thought-provoking question; if the dialogue were prolonged he would squat down with his back against a wall. During my recent visit to him in 2006 he was still debating allelopathy and $-3/2$. Six of my e-mail respondents stated “he was the smartest man I ever met.” He will be remembered for many of his so-called “Harperisms” such as: “plants stand still and wait to be counted”; “counting the number of legs in a herd of cows gives a sufficient measure of the size of the population of cows; counting the number of leaves in a population of white clover does not”; “plants make excellent research material for zoologists”; “PCA is a formalized description of consequences”; “stress is what I don't think I would like if I were a buttercup”; “plants are merely the mechanism by which seeds produce more seeds”,.....

John was more than just a researcher; he was also a teacher and Head of Department. One undergraduate records that “Professor Harper was very clued-in to each of us as undergrads! If we skipped a class, he would have a light-hearted response in the next class that we attended. ‘Welcome back!’ he would say with that impish sparkle in his eye!” Another undergraduate student commented that “It was the power of the man and his ability to strike an intellectual match in the brain of young biologists that was one of his very great skills.” He never recycled lectures. Every lecture in every year was custom-made for each particular class, and he would say, “To get the best out of undergraduates, you must leave them with more questions than answers.” And from other departmental colleagues I am told that at the time when the School of Plant Biology was booming with population biologists, faculty who were doing other things, such as physiology or microbiology, did not feel in any way that they were lesser beings. JLH as Head of the School was just as generous, supportive, and enthusiastic about their research activities as of his own. He was an excellent Head, an excellent communicator, he had his finger on the Departmental pulse, he made sure all staff were highly valued, and he had an innate ability to get the best out of people. It was a stimulating place in which to work.

John Harper retired in 1982, and on the day of his retirement one of his first acts was to remove his “Prof. J. L. Harper PRIVATE PARKING” sign from the Departmental parking lot. He gave the sign to me in 1986 and it is still hanging on my office wall at the University of British Columbia, in Canada! John and Borgny left Wales in 1997 to live near their family in Exeter.

John Harper taught us a whole new discipline and a whole new way to study plants. To undergraduates he was Professor Harper, to graduate students he was Prof, and while he wanted most other people to call him John, most simply called him Prof or JLH. He was a teacher, mentor, friend and colleague to generations of plant population ecologists.

I thank Peter Brindley, Chris Wood, Chris Marshall, John Porter, Paul Cavers, Janis Antonovics, Glenn Matlack, Mike Hutchings, and John's children for providing me with information. A detailed profile of John's life until 1985 is provided by Sagar (1985).

This obituary was reprinted, with permission, from the *Journal of Ecology* 97(5):835–837.

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