

Harper J L. *Population biology of plants*. London: Academic Press, 1977. 892 p.
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"This book attempts to bring together some of our present knowledge of plants that might be relevant to understanding their population biology. It is heavily larded with examples from forestry and agriculture, because these are the sources of most of the facts."¹ [The SCI® indicates that this book has been cited in over 1,660 publications.]

Plant Demography

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Population biology developed as a science mainly in the hands of zoologists and epidemiologists concerned with how the numbers of animals were determined and how they could be manipulated in the control of pests and diseases. An important part of population biology is the demography of organisms, their rates of birth and death; much of the early theory had been developed by actuaries for the life insurance industry. Until the 1960s most of plant ecology was concerned to describe the patterns of distribution of species rather than to count, and then try to explain, the variation in numbers.

In 1874 the distinguished German botanist Carl Wilhelm Naegeli published a theoretical outline of the ways in which two plant species might interact and affect each other's numbers. Although Naegeli was among the most distinguished plant scientists working at that time, his paper was virtually ignored for 60 years.² There are two major problems facing anyone who attempts to count plants. Compared with most animals, plants vary enormously in size, reproduction, and longevity. Counts of the numbers of rabbits in a field give much more information than counting the numbers of plants of a grass. This is because plants grow by branching and their size is rarely determinate (a rabbit has four legs; there is no comparable statement that can be made about the number of leaves or seeds produced by a grass). The second problem is related to the first: many plants grow by producing rooted branches at or below ground level (for example, the strawberry and the bracken fern). Anyone attempting to make a census of a plant population has to decide, for his purposes, what is an "individual." Is it everything that developed from a single seed and so from a single zygote, or is it the unit of structure that forms a shoot above-ground? The problem is at its most extreme with

plants such as duckweeds, in which the whole population of easily countable units in a pond may all be the parts of a single genetic individual that has fallen apart as it grew.

It was, I think, the definition of these two problems that made possible a vigorous science of plant population biology. One reason I could write a rather large monographic treatment of a subject that was still in its infancy was that I knew something of the literature of agronomists and foresters. Hidden in this were marvellous studies that were really fundamental studies of the behaviour of plant populations. The academic snobbery of most "pure" botanists had left this magnificent literature unread. It was enormous fun to bring it into the wider context of a science of plant population biology and to try to place it in the context of evolutionary theory.

That the book and several of my published papers that preceded it^{3,5} were so often cited was undoubtedly because the time was "ripe." Plant ecology was in the doldrums; it was rarely experimental and could not link easily with evolutionary theory. It had little in common intellectually with animal ecology because it lacked a comparable theoretical base. The time was ripe for a new development; when Naegeli was writing the time was definitely unripe!

My role in developing "plant population biology" came about because I had great teachers: Charles Elton and George Varley were animal ecologists who gave me great encouragement when the work was viewed with great suspicion by plant ecologists. Ledyard Stebbins and Bob Allard both forced me to try to think as an evolutionist. I am the son of a grassland farmer, and when I was 13 I counted buttercups along a transect across ridge and furrow grassland on my father's farm!

Many of the studies described in my book were made by an exceptionally able international stream of students who worked with me at Oxford and at Bangor, though rather few were from Britain. Plants, unlike most animals, stand still and wait to be counted—if they are still alive, they are still in the same place next year—but counting and mapping them is very tedious. My students spent day after day, winter and summer, lying in the grass counting and mapping plants and having ideas. On two occasions the drivers of trains on a nearby railway line saw them, thought they were corpses, and alerted the police.

I take special pleasure in the spread of some of the attitudes of plant population biologists back into zoology. Many animals have essentially plantlike growth—that is, they grow by the repeated iteration of modules of construction and remain fixed in position in their habitats. That the corals, bryozoans, many hydroids, and other marine invertebrates are now beginning to be studied in ways developed for plant populations⁶ begins to repay an old debt.

1. Harper J L. Preface. *Population biology of plants*. London: Academic Press, 1977. p. vi.
2. ———. A century in population biology. *Nature* 252:526-7, 1974.
3. ———. A Darwinian approach to plant ecology. *J. Ecology* 55:247-70, 1967. (Cited 240 times.)
4. Harper J L, Lovell P H & Moore K G. The shapes and sizes of seeds. *Annu. Rev. Ecol. Syst.* 1:327-56, 1970. (Cited 285 times.)
5. Harper J L & White J. The demography of plants. *Annu. Rev. Ecol. Syst.* 5:419-63, 1974. (Cited 240 times.)
6. Harper J L, Rosen B R & White J, eds. *The growth and form of modular organisms*. London: Royal Society, 1986. 250 p.