Book Reviews

Grassland Ecology

Plant Relations in Pastures. Papers from a symposium, Brisbane, May 1976. JOHN R. WILSON, Ed. Commonwealth Scientific and Industrial Research Organization, East Melbourne, Australia, 1978. xiv, 426 pp., illus. $A25.

This volume of proceedings consists of a keynote address by J. L. Harper, 24 papers under the headings Comparative Ecophysiology, Analysis of Plant Interrelations, and Pasture Ecology and Management, and summative addresses by C. T. de Wit and C. M. Donald. It deals essentially with the ecology and management of plant species in pastures (grasslands), with a strong emphasis, for the first time in a volume on this subject, on genetic and evolutionary themes. The study of pastures has several advantages for population biology over that of wildlands: experimental manipulation is practicable, funding based on agricultural interests is obtainable, and a component of plant breeding can be included. In the present volume botanical composition based on demographic data is emphasized rather than biomass and energetics, which have been an obsession of the International Biological Program grassland biome workers. In the preface four main themes are outlined, namely, species diversity, the role of legumes, plant interrelations (primarily competition), and ecophysiology. Thus the volume deals with topics important in both basic and applied population biology. The contributors are well chosen and the book is attractive and well edited.

In his keynote address Harper reminds us of the value of an analytic approach concerned with the behavior of individual organisms and species, in contrast to the holistic, community-level approach. He has recently begun to focus in his writings on the widespread presence of genetic polymorphisms in plant populations and of rather strong selective forces responsible for rapid evolutionary change as well as for the maintenance of genetic variation. This sounds appealing to a population geneticist, but one should beware of these broad generalities derived from a few selected examples. Similarly, coadaptation among and within species has often been a tempting generalization but is one that requires rather tedious and sophisticated experimental tests. It is to be hoped that Harper is right; the views he presents will spark considerable population genetic research on grasslands, though, curiously enough, they and the renewed emphasis on long-term field studies stand in contrast to the many years of pot experiments for describing niches of related species, treated as genetically homogeneous entities, to which Harper himself made many pioneering contributions. Several other contributors to the present volume (Snaydon and Antonovics among them) do not fully accept evidence for strong selection.

Snaydon's review of genecology, including his own outstanding work on selection under different nutrient regimes, is good. He notes the paucity of long-term studies, remarking that "those of Charles seem to be the only ones to compare the productivity of survivors and original cultivars under sward conditions." Incidentally, the work of Charles, Rhodes, and others on the genetics of pasture plants is not widely cited in writings on population biology, and this volume thus serves to draw attention to additional pasture literature. McWilliam's summary of clinal and other geographical aspects of variation is a fair review of adaptation to climatic factors, but, like many other chapters referring to population genetics, is too sketchy and provides little that is new. The topic of competition in mixtures of genotypes and species is covered in as many as nine contributions. Theoretical ideas as well as statistics are presented clearly by Trenbath, Antonovics, and others along with several interesting "new" results. For instance, Antonovics concludes that "the competitive relationships of two species will not be permanent: theoretical studies invariably predict that they will diverge in resource requirements." This assumes, of course, appropriate genetic variability, but he adds that "competitive ability is a complex trait, and an important fitness component that may be sensitive to inbreeding and have low additive genetic variance." Supporting evidence for these ideas is not presented, however. Trenbath claims that his computer simulation results suggest that reversal of selective advantage of two competing lines during growth (life history stages?) cannot stabilize a mixture. Many of the theoretical details would probably not be understood by the pasture ecologists and managers. Is the notion of filters, another phrase, developed by Torssell and Nicholls, for discussing different stages of life cycles in demographic terms, innovative or just more verbiage? We don't know. Nevertheless, these papers on competition and natural selection raise at least two issues relevant to pasture management: use of mixtures in maintaining diversity for the sake of stability, higher productivity, or both, and monitoring of intraspecific variation to obtain useful products through natural selection. How many strains of subclover are of value in its adaptation and successful pasture use? Is coadaptation common so that selection by breeders should take intergenotype interactions into account? How often are reseeding and reselection likely to pay off? Answering these questions will be among the objectives of applied ecology.

Several authors comment on de Wit's replacement series model as being the most rational and useful. It must be recognized, however, that a diallel study of five or six competitors using de Wit's design of several frequencies and densities pretty soon becomes a large and unwieldy study. And even after lengthy treatment of the de Wit methodology it is not clear why the model is superior. That the interaction term is frequency-dependent, of course, could be detected only by a method utilizing several frequencies. The Lotka-Volterra model allows competition coefficients to be weighted by the products of respective population numbers of the competitors. Graphical methods are more appealing to biologists than equations.

Both papers on the legume-*Rhizobium* symbiosis (by Rovira and by Robson and Loneragan) present good reviews of this newly developing field in experimental population biology. Rovira's paper goes beyond *Rhizobium* to inquire how a better knowledge of other aspects of rhizosphere and microflora (including allelopathy) can allow better pasture management. Most techniques in this area, particularly the genetic analyses of variation in microflora, appear to be in a developmental phase; caution must be exercised in accepting results obtained with them. The evidence for allelopathy in the field environments, for example, is not readily accepted by many workers, in-

cluding Harper. The other papers on ecophysiology, which deal with the responses of plants to light, water, defoliation, and mineral nutrients, are matter-of-fact reviews without many critical, stimulating ideas, and they conclude generally with pleas for field studies. This is an interesting irony, since most field workers in population biology are asked to look into the causal processes underlying their observations by designing precise, controlled laboratory studies. This symposium makes the point that both approaches are needed.

In his summative address de Wit is, as usual, witty and humorous, but he does not attempt a grand synthesis. On the other hand, Baker and Tothill provide excellent reviews of the origin, geographical distribution, broad evolutionary features, and current work aimed at the improvement of pasture species. Several research topics emerge from their surveys: growth habit of perennials versus annuals in adapting to grazing, the role of breeding systems, the population structure of early and late successional species, establishment by seed, species diversity versus intraspecific variation, and rational guidelines for the selection of pasture legumes and grasses for different tropical and temperate grasslands.

The preface includes a comment that "a book of this kind offers the reader a rare opportunity to generalize from the current state of knowledge about a subject." In fact, most population biology writings already have too many generalizations, stated as working hypotheses, firm conclusions, or something in between, depending on the author's taste and circumstance. This volume, too, has its share of cliches about community stability, *r* and *K* strategies, the Gause principle of coexistence, coadaptation, and the genetic structure of inbreeders, but its strength lies in the good reviews it provides of many aspects of pasture (range, grassland) management. Most readers will enjoy and benefit from it through updating their knowledge of work outside their own narrow specialties. It welcomes physiologists and population biologists to an applied field and does it well.

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The History of the Earth's Environment

Evolution of the Atmosphere. JAMES C. G. WALKER. Macmillan, New York, and Collier Macmillan, London, 1977. xiv, 318 pp., illus. $16.95.

A few years ago the need for solutions to environmental problems began to put pressure on various kinds of scientists to pool their resources. Meteorologists, oceanographers, biologists, geochemists, and hydrologists found themselves team-teaching to train students properly. From such associations the scientists began to realize that there is indeed strength in union. Atmospheric scientists were trying to understand the reasons planetary atmospheres have the compositions they do and began to look into the geologic evolution of the planets. They consulted geochemists, who, in turn, realized that the atmospheric scientists could help them. *Evolution of the Atmosphere* is, as far as I know, the first attempt to bring together the products of such scientific weddings. In it J. C. G. Walker admirably melds atmospheric science and geology to give an account of the subject that will surely open a lot of eyes to the incipient power of the combined disciplines.

Is our atmosphere primary or secondary? Has it evolved significantly in its more than three billion years of history? What changes were initiated by the appearance of life? When and why did oxygen appear? What are the feedback systems that prevent great oscillations of atmospheric composition? These are some of the geologic questions raised by Walker and discussed by him in the light of modern atmospheric chemistry and physics.

The book is organized into three parts, totaling seven chapters. Chapter 1 provides background information on the structure and chemical composition of the atmosphere, with, for example, derivations of equations for lapse rate and diffusion time. The chapter includes discussions of the chemistry and structure of the oceans and the crust and a short section on biology and the geologic time scale.

The next three chapters describe the processes that control the composition of the present-day atmosphere—photochemical processes, processes at the bottom of the atmosphere, and processes at the top of the atmosphere. These chapters include rather detailed photochemistry, derivation of equations for escape velocities, and discussion of the interactions of gases with earth materials.

The final three chapters treat the early evolution of the atmosphere—the origin of the atmosphere, its properties prior to the development of life, and its evolution thereafter. Where appropriate, the discussion includes Venus and Mars.

The chapters are uneven in technical level. Chapter 4, "Loss of atmospheric gases to space," is 35 pages largely devoted to the derivation of equations, whereas the three chapters on the ancient atmosphere are largely expository and speculative. This unevenness is an expression of the current state of knowledge. For the reader interested in the cycles of elements or the rise of oxygen, Walker provides the quantitative tools of the modern meteorologist. For the meteorologist, he displays the range of problems that must be solved before the history of life and of the surface environment of the earth can be known even qualitatively. Furthermore, he shows the important role played by atmosphere-earth and atmosphere-ocean interactions in controlling the composition of the atmosphere.

Walker has made a well-balanced presentation of a still poorly defined field. There are many individual items, however, that invite comment. For example, he dismisses climatic effects of CO_2 increase in the atmosphere as unimportant. His stand is interesting in light of the current furor concerning these effects. Also, he concludes that the rate of uptake of CO_2 by chemical weathering of rocks is directly related to the CO_2 pressure of the atmosphere, an idea that became suspect some years ago when it was pointed out that the weathering of rocks is largely controlled by the CO_2 content of the soil atmosphere, which in turn is controlled by the rate of oxidation of soil humus.

Walker uses the "we" style extensively; for example, "We adopt the homogeneous accretion model." Occasionally "we" do not necessarily wish to accept or adopt or describe or assume what Walker does.

Although he carefully gives references and credits others when his discussion draws on their work, I got the impression that I had been invited into Walker's world. In other words, although the book is fully referenced, it is not a review but largely a documented exposition of Walker's views. He has managed to give a good feeling for the lack of constraints on many of the systems he has chosen to