Book Reviews

Plant Ecology: Matters of Numbers

Population Biology of Plants. JOHN L. HARPER. Academic Press, New York, 1977. xxvi, 892 pp., illus. $58.60.

The publication of the first book devoted to a synthesis of plant population biology is an event that arouses considerable excitement, particularly since the book is authored by John Harper, who has made enormous contributions to our understanding of plant biology. Harper's innovative ideas have led to a whole school of thought and research, one that has spread far beyond his home university in North Wales.

This book was not intended as an introductory textbook to the field of plant population biology but rather as a source book for comparative use by animal population biologists. Its length and cost and the exhaustiveness with which certain topics are covered limit its usefulness for the former purpose. But it will no doubt become a standard reference book for anyone, botanist or zoologist, with interests in population biology.

The field of population biology is generally considered to include information and viewpoints from population genetics, population and physiological ecology, and demography. Three recent symposia in plant population biology (New Orleans, 1976; Wageningen, 1977; Ithaca, 1977) have encompassed these approaches in attempts to synthesize the subject. Harper has taken a much narrower view of the field. His book is devoted primarily to plant demography, with some population ecology, and even this limited perspective has not been developed in the depth the available theoretical framework would permit. These limitations will no doubt disappoint many readers, for they restrict the power with which demographic results can be interpreted.

The study of the biology of plant populations has developed rather slowly. Although there has been considerable progress in our understanding of how individual plants adapt to their environments and how communities and ecosystems function, the study of the structure, operation, and evolution of plant population has lagged, most certainly by comparison with the progress that has been made in animal population biology.

In the initial chapter Harper makes the important point that knowledge of the numbers of individuals of an animal population gives more information than does knowledge of the numbers of plants in a population. This is because of the remarkable plasticity of size most plants possess. That botanists have not come to grips with this problem has impeded the development of plant population biology. Harper suggests that for plants we combine the number of genotypes (N) with the number of construction modules per plant (η), be the module concerned a tiller, a shoot of a tree, or a leaf with its bud of an annual. The plant population size would thus be $N \times \eta$. There is certainly merit in this idea, and no doubt it will be utilized; there will be a great subjectivity in the selection of η units, however, and comparisons between studies will be very difficult.

Harper suggests in other places that solutions to population problems are dependent on the details of the life history of individual species. This is somewhat disheartening, since it would appear that such approaches will not lead to predictive generalities. For example, Harper notes that "neither theoretical nor experimental models of the growth of populations in isolation are sufficient to predict the outcome of a struggle for existence between them. The observer is forced back onto aspects of the natural history of the species to explain their interactions." Later on in the book, in discussions of the dynamics of populations, Harper indicates the need to determine species-specific "life states," which unfortunately, in plants, may be independent of age.

Harper's initial chapter is followed by five main sections: Dispersal, Dormancy and Recruitment; The Effects of Neighbours; The Effects of Predators; The Natural Dynamics of Plant Populations; and Plants, Vegetation and Evolution. Each of the chapters these sections contain has an excellent summary, and many are intensive reviews, citing and discussing virtually every study that has been published on their subjects.

The first section, primarily on seeds, clearly shows the crucial importance of determining the nature and size of soil seed banks and the characteristics of the microsite in which a seed successfully establishes a seedling. Harper also indicates the great difficulty of doing these kinds of studies. He feels strongly that determining the environmental factors responsible for plant distribution by doing correlative analyses of environmental factors and of the distribution of mature plants is of little value, since "the causal events that determine whether a seed forms a seedling or not are usually untraceable when the plant has developed, and the real causes of distribution and abundance will often be missed when mature vegetation is studied."

The section on plant competition surveys the vast literature on the topic, though in this case there is certainly far more information than understanding. Extrapolation from competition experiments in which plants are grown in pots to distribution in the field is generally quite tenuous, since in nature species may partition the resource base, whereas in pots conditions are such that this is not possible. Further, pot experiments simply ascertain competitive outcomes (quite often of shoots only), with little attempt to understand the resource-gathering mechanisms that lead to them, and hence do not give a basis for sound prediction.

Harper deliberately takes a hard and skeptical view of studies of the interactions of plants in nature. He notes that "the interactions between neighbouring plants are so complex, tight and apparently impossible to disentangle that it may be wise to cease to look for simple effects." He is particularly hard on past studies of allelopathy. He thinks that what is called for is the establishment of protocols not unlike Koch's postulates in pathology for the unraveling of the causes of interactions. No doubt such experimental rigor is called for, but it is curious that in later chapters Harper accepts rather uncritically many of the studies of plant-animal interactions, which are often based on correlations and speculation.

In discussing reproduction and growth Harper makes the point several times that energy may be a "superabundant resource for some plants" and that "the green plant may indeed be a pathological overproducer of carbohydrates." Here he has certainly raised a red flag, and no doubt this idea will be the subject of considerable discussion, since there is at

present little hard evidence to support or refute it.

The book is richly illustrated with line drawings. Unfortunately, a surprising number are not readily interpretable without reference to the original source. Errors in the text are relatively few and minor, and since the book is so large I can forgive all of them, except one—Death Valley is in California, not Colorado.

Plant population biology is an emerging discipline. Since the field has so many rapidly developing fronts, Harper's attempt to synthesize and evaluate what we know will certainly occasion some disagreement among workers in the field. There is no doubt, though, that this book will be widely appreciated for what it represents—the laying of a cornerstone for the demographic aspects of this new field.

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Demographics and Subsistence

The Food Crisis in Prehistory. Overpopulation and the Origins of Agriculture. MARK NATHAN COHEN. Yale University Press, New Haven, Conn., 1977. x, 342 pp. $15.

Population-pressure models have enjoyed increasing popularity in anthropology since the economist Boserup turned Malthus upside-down by suggesting that demographic growth leads to agricultural and technological innovation. In recent years population-pressure models have been used to explain a variety of anthropological phenomena from male dominance to the evolution of complex societies.

Cohen's book is the first comprehensive attempt to explain the origins of agriculture on a worldwide basis as a response to population pressure. He tries to answer two basic questions: Why have most human populations abandoned foraging economies for agriculture? and Why did agriculture appear independently and almost simultaneously in diverse parts of the world at the end of the Pleistocene? For Cohen, population pressure provides answers to both questions. Foraging economies were abandoned because they could not sustain growing populations, which had reached a subsistence saturation point, and this point was attained at approximately the same time on all the major continents except Australia.

Cohen makes six basic assumptions: (i) incipient agriculture is not an "invention" but an accumulation of refinements of existing techniques of plant manipulation; (ii) agriculture is not easier nor does it provide a more secure subsistence base than foraging, it simply yields more calories per land unit; (iii) foraging populations do not normally maintain demographic stability, they grow through time; (iv) the preceding assumption notwithstanding, such societies have effective mechanisms for preventing excessive population buildup in local areas, and these led to synchronous buildup over the earth's landmasses and to the emergence of worldwide pressure at the end of the Pleistocene; (v) the worldwide parallels in events leading to agriculture demand a single explanation rather than diverse explanations for each region; and (vi) the archeological record in the Old World and the Americas shows fairly continuous demographic growth in preagricultural times. Each assumption can and undoubtedly will be challenged by other scholars, but on the whole I find them quite persuasive.

Chapters entitled "The theory of population pressure and the origins of agriculture" and "The archaeological measurement of population growth and population pressure" provide the theoretical and practical matrix for Cohen's thesis. They are followed by three chapters that contain demographic and economic surveys of world prehistory. The areas surveyed include Africa, the Near East, Europe, East Asia, North America, Mesoamerica, and South America. In each case the cultural sequences examined extend from the initial occupancy by humans to the establishment of agriculture as the primary subsistence activity.

Interpretations of archeological data on this scale are always fraught with problems related to the quantity and quality of the data. Despite truly impressive advances in the past 30 years, we still do not have adequate information on incipient agricultural societies or their predecessors for any part of the world. The data base is particularly weak for the variables used by Cohen, demography and economy. Archeologists have generally been frustrated in their attempts to estimate areal population size, group size at one point in time, age-sex structures, and other demographic variables for societies lacking historical documentation or close ethnographic analogs. They have also been unable to arrive at realistic estimates of subsistence inputs because of the elusiveness of plant food remains. Cohen is aware of these problems and points out that they are particularly troublesome when one is dealing with the remains of foraging societies. He uses ethnographic analogies to fill in the gaps and to provide a model for archeological interpretations. The analogies are cautious and well drawn but cannot negate the fact that anthropologists have seldom if ever observed pristine foraging or incipient agricultural societies. We may never know to what degree meat was prized by such groups, whether cereal grains were last-choice foods, acceptable only when more highly prized foods were scarce, or whether ancient societies were structurally and demographically similar to their modern counterparts. This is an unfortunate fact anthropologists must simply live with. Given these limitations, Cohen does a superb job interpreting the data available to him. Future investigations should show he is more correct than not.

Cohen's analysis provokes many tantalizing questions. Assuming he is basically correct, why hasn't the human species stabilized demographically? Did the rate of human population growth increase during the millennia prior to the emergence of agriculture, and if so why? Why did aboriginal Australia remain nonagricultural? did it experience population pressure like the rest of the world, and if so how was such pressure dealt with? Why did population pressure build up much more rapidly in the Americas than in the Old World? These and other questions need to be answered and should provide some exciting research in the future.

Archeologists are occasionally pressed to defend their research, particularly when it involves expenditure of public money. They frequently maintain that they are attempting to understand, rather than merely study, the past in order to elucidate the present and predict the future. Cohen's book is certainly relevant in this sense. He has shown that population pressure on basic resources is an integral aspect of most human existence, not merely an Industrial Age phenomenon. He has also shown what one panhuman response to this pressure has been in the past ten millennia. The newspapers remind us daily that the response has not been a permanent solution and that continuing responses are called for. If Cohen is correct, past responses have emphasized increasingly intense exploitation of lower trophic levels. If humans cannot control their fertility in the near future, we may live to see just how far down the trophic pyramid we can go.

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