The Study of Plant Populations

Topics in Plant Population Biology. Papers from a conference, Ithaca, N.Y., June 1977. OTTO T. SOLBRIG, SUBODH JAIN, GEORGE B. JOHNSON, and PETER H. RAVEN, Eds. Columbia University Press, New York, 1979. xviii, 590 pp., illus. $25.

The most important event in the field of ecology over the past decade has been the development of plant population biology into a vigorous and challenging discipline. Finally we seem to be escaping from an ecology that has been dominated by a descriptive-correlative approach to plant communities and an evolutionary biology that has all too often been reduced to an aide-de-camp of plant taxonomy. The growth of plant population biology, which was firmly established by John Harper and his co-workers in Britain, was catalyzed in this country in the early '70's by the integration of theoretical approaches of population ecology and population genetics. The focus of this integration has been the life history, because the schedule of births and deaths determines in large measure both the overall population size and the fitness of the component genotypes. And plants, because of their experimental tractability and their convenience for demographic accounting ("they stand still and wait to be counted," as Harper put it), are providing a rich hunting ground for workers interested in exploring the interactions of ecology and genetics. It is no wonder that in the present book there are contributions from at least three people whose backgrounds are primarily zoological.

The book is a collection of papers that, as Solbrig states in the introduction, is "an attempt by a generation of American plant population biologists in their 30's and 40's to present their view of the field." In terms of age, it could not have been otherwise, since the field has as yet not accumulated any grand old men. The dedication and opening eulogy of the book are to George Ledyard Stebbins, undoubtedly the intellectual powerhouse and grand old man of the plant evolutionary biologists of the 1960's and '60's. Stebbins himself opens the book with a paper entitled "Fifty years of plant evolution." While the content will be of interest to a newcomer to the field, many of its sections seem to belong to another world from the chapters that follow.

These chapters are grouped into three sections: Adaptation and Genetic Variation in Populations, Life-Cycle Parameters, and Energy Harvest and Nutrient Capture. The first section is, like its subject, high on ideas and low on data. The data that do exist on electrophoretic genetic variation in plant populations are elegantly summarized by Hamrick, but, as he points out, we are now beyond the era of such "find-and-grind" surveys where the ecology is ignored and the biochemistry remains mysterious. Yet intriguing questions emerge, such as what is it that makes trees the world's most genetically variable organisms. Johnson continues this theme when he exhorts, "We must address the proper phenotype. Little is accomplished by studying conveniently assayed but functionally unrelated enzymes." He argues that we must look at multiple-locus genotypes, where the loci under study affect a known metabolic pathway and hence a known phenotype. Yet the realization of this goal seems far away, and one has to hope that the phrase "multilocus genotype" will not become another empty substitute for that mysterious UFO of evolutionary biology, the "co-adapted gene complex."

The other papers in this section illustrate the role "optimality thinking" plays in current evolutionary thought. As Horn discusses, this approach presumes an optimum; it also presumes many trade-offs. But to judge from the papers by Solbrig and Levin (and from papers in subsequent sections by Mooney and Gulmon and by Givnish), its power in stimulating testable hypotheses is unquestionable. Certainly, the approach of examining the costs and benefits of variation in a trait is a big improvement over assuming a trait to have some particular "role" or, worse, an "adaptive significance." However, these papers (and, as Jain laments, such studies in general) inadequately discuss the genetic basis of such trade-offs and how costs and benefits can be translated into gains and losses in fitness. The reader may be left wondering why benefits have to have costs and confused about what constitutes the legal currencies in such discussions. Benefits have costs because directional selection on a pair of characters contributing to fitness will leave substantial genetic variance in those characters only if they are negatively correlated. And the analysis of such genetic (as opposed to phenotypic) correlations and trade-offs is a prerequisite for proper prediction of evolutionary direction in cost-benefit models. Moreover, the measures of such costs and benefits (whether in calories, growth, or fecundity) should be ultimately translatable into fitness defined as lifetime contribution to subsequent generations.

The section on life-cycle parameters begins with a paper by Jain, who explores the concept of a "strategy" as much (he admits) to convince himself as to convince the reader of the usefulness of this concept. I came away agreeing with the plant physiologist Paul Kramer, who has remarked that "the use of the word strategy is best left to the military." What Jain does convince us of is that generalized models of evolutionary processes have a real part to play in furthering our understanding of the evolution of complex life-history traits. Yet the notion of "adaptive strategy" diverts our attention from analysis of process to argument about goals (what should the strategy maximize or minimize), which are nonexistent in evolution.

The papers that follow in this section are as important in pointing out what we don't as what we do know. Angevine and Chabot's final message that "we are profoundly ignorant of the actual patterns of seed germination in space and time for seeds as components of field populations" seems more important than their tentative classification of germination patterns based on a paucity of just such data. Cook points out that we know nothing about whether the high juvenile mortality in plants is selective or not. Are the few surviving individuals supergenotypes that are the victors in a battle to survive, and if so do they represent only temporary gene combinations that will be disrupted in the next generation? His own data may have helped generate these questions but do not help answer them. Werner in her introduction reminds us that the idea of competition in plant populations has been a product of faith and not a deduction from experiments, since "there are few studies which demonstrate the relationship between potential distributions of a population and actual distribution given the absence of competitors." She describes studies that suggest directions for future work on this question, though they do not address it directly. The whole volume is in fact rather frustrating in that it points to gaps in our knowledge yet tantalizes us with data that are only tangential to these gaps. It is essential to be patient when reading it: the unanswered questions become exciting when we realize that they will form the focus for studies over the next decade.

Submerged in this section, yet almost deserving one on its own, is a paper by Gottlieb on the recent origin of a new species. Here we clearly see the separation of the new population biology from the old. Like much of the recent work on speciation in *Drosophila*, the analysis combines genetics, developmental studies, physiology, and ecology. We are shown that the speciation process is almost certainly the result of limited genetic changes in response to relatively simple selection forces. I was left with an excitement that was greater than if speciation events had been more grandiose, since at last we see the speciation process as experimentally approachable by the methods of population biology.

The last section of the book is an attempt to bring physiological ecology under the wing of population biology. Physiological ecology has always struck me as a science without a home. Its techniques seem never sophisticated enough to satisfy the physiologist yet always too impracticable for the "real world" ecologist. Its paradigm seems to have been that an understanding of the physiological characteristics of a plant will help us understand species abundance and distribution. Yet how such characteristics might be related to individual fitness is perceived only dimly. In that plant population biology encompasses a rigorous and unified view of evolution and abundance, it will provide physiological ecology with some direction and clarification of its basic tenets. A theme that recurs throughout the present volume is that to understand populations we need to have more studies that complete the pathway from gene to phenotype to environment and so to fitness. Physiological ecology is rightly posited as playing an important role here, and this section of the book is a step, albeit a very uneasy one, toward the marriage with population biology. Thus whereas Mooney and Gulmon present models that are disquieting to the evolutionary biologist because they maximize photosynthetic rates, Givnish provides the healthy warning that "selection probably no more actually favors maximal carbon gain in plants than economic competition actually favors short-term profits in business and monopolies." The papers by Teeri and by Chabot and Bunce illustrate both the power and the dangers of a purely correlational approach. In both cases the authors look at how particular physiological characters correlate with plant distribution. The problem with this approach is that these correlations may come to be treated as "explanations" rather than as sources of hypotheses to be tested. Thus whereas Teeri calls for more information on the genetics and evolutionary processes that led to the independent evolution of the C_4 pathway in many plants, Chabot and Bunce presume that a perfect correlation should exist between drought tolerance and distribution, in order to derive the combination of attributes that "most completely explain" the ecological behavior. This comes mighty close to the "adaptive story-telling" Gould and Lewontin have warned against. I also felt uneasy with the paper by Miller and Stoner, which though providing a good account of a "heritage of canopy simulation models" never clearly points out that measures on a per unit area basis, while of relevance for the production ecologist, are quite the wrong measures for a population biologist interested in individual selection.

I was glad two other aspects were included. The first is leaf shape, treated in a paper by Givnish. Leaf shape is one of those morphological features that are given the multitude of technical names that commonly befuddle the beginner in local floristics, and I always get a thrill out of realizing that such characters are indeed of relevance to the biology of the individual. The second is root systems, treated in a paper by Caldwell. The numerous virtues of plants for population biology are easy to extol, and it was good to find that this volume has not ignored their one big disadvantage, namely the black box that constitutes their underground activities. Caldwell's paper vividly reminds us of a world down there that has hardly been explored. Consideration of localized depletion of nutrients (and perhaps water) around roots not only may be important in understanding continued root growth, root branching patterns, and root deciduousness but may throw much light on why in many plants the outcome of competition seems often to be dictated by the maxim that possession is nine-tenths of the law.

On the whole this is not a book for the beginner in the field or for a zoologist interested in broaching the subject of plant population biology for the first time. Such a reader would do better to attack the more disciplined and elegant *Population Biology of Plants* by Harper (Academic Press). As with any attempt by many people to conceptualize one subject, there is much chaff among the wheat, and the book could have benefited from more editorial winnowing. But if the reader is prepared to scream ("water is a nutrient") and groan ("the leaves and roots constitute an integrated system in the ultimate sense"), as well as cheer ("the best measures of environmental quality are those that include the response of the plant"), then this book will be stimulating and will have done its job.

My main criticism of the volume is that the papers seem to be not so much held together by as ensnared in a web of confusion about adaptation. When we speak of a character state as being adaptive we subsume two possibilities: the character state may be the product of past selection, or it may be of importance in conferring differential fitness in present-day populations. There is a crucial difference in how these possibilities are assessed. In the case of past selection, we can only assess adaptation indirectly, by a process of inference. Though Hickman in this volume rightly warns against the dangers of deducing past evolutionary processes from their outcomes ("post selection mortality patterns cannot provide critical evidence for or against the selective effects of mortality patterns"), we frequently have no alternative. In the case of present-day populations, on the other hand, we can make and test the prediction that a character state will be associated with differential contribution or fitness—though, as many people have pointed out with respect to enzyme polymorphisms, inferences about causality may remain problematic. Abandonment of the word "adaptation" would have helped avoid obfuscation concerning these distinctions.

The book has two major omissions. Treatment of plant-animal interactions, an important aspect of the subject, was deliberately excluded. Nor do the papers in the book make any tangible connection with the agricultural sciences. In Europe, Australia, and Japan the growth of plant population biology has been closely tied to those sciences, yet in this volume we see nothing about their rich contributions to such aspects of population biology as yield component analysis, quantitative genetics, competition designs, and growth modeling. While

Raven in his summary predicts that plant population biology "will have profound implications for human welfare and survival" we see nothing in the present volume of what these implications might be. There are no sections, for example, on the importance of plant demography for weed control and plant conservation, on the relation of fitness to yield, or on the significance of genetic variation for yield stability. This unfortunate dichotomy within botanical sciences is undoubtedly the result of the exclusion of students of plant populations from funding (except for a recent trickle) by the U.S. Department of Agriculture. Until this is rectified, pure and applied botanical sciences will both be the losers. This volume exposes a real need (reiterated by several contributors) for a multidisciplinary approach to plant population biology. This need has been recognized in Holland, where ambitious team projects are under way, but such efforts remain a pipe dream here.

In the summary, Raven produces a masterly analysis of the current issues and future problems in this field. He warns against coevolutionary studies' becoming stagnant and descriptive; he puzzles why phenotypic plasticity has rarely been investigated with much success; he pleads for more critical studies of selection at the population level, especially with regard to physiological traits; and he still wonders what accounts for the maintenance of those "wide ranging units that we recognize as species." He recognizes that there is "an explosion of experimentation and thought." He talks of new methodologies and how the new population biology is seeking to counter the historical legacy of a "300-year-old encyclopedic mentality which leads us to believe instinctively that it is best to study many kinds of organisms descriptively and relatively superfically rather than a few in depth as systems." In fact I suspect he understates the case, and that we are in the middle of a Kuhnian-type revolution in ecology and evolution, where old methodologies are being replaced by new standards of explanation, new conceptualizations, and new paradigms. It is clear that in the next decade the population biology approach will come to pervade and merge the disciplines of evolutionary biology, physiological ecology, and ecology under a broad umbrella of similar goals and similar experimental methodologies.

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Theoretical Particle Physics

Recent Developments in Gravitation. Proceedings of an institute, Cargèse, Corsica, July 1978. MAURICE LÉVY and S. DESER, Eds. Plenum, New York, 1979. viii, 596 pp. $69.50. NATO Advanced Study Institute Series B, vol. 44.

The last two decades have seen gravitation return to the mainstream of fundamental particle physics because of precise physical observations and important technical and conceptual advances in both general relativity and particle physics. Once the emphasis in general relativity shifted from general coordinate covariance to gauge invariance, general relativity became a paradigm for non-Abelian gauge theories that have been tremendously fruitful in quantum flavor dynamics (weak and electromagnetic interactions) and quantum chromodynamics (strong interactions). The renormalizability of unified electroweak interactions has emboldened particle physicists to attempt a grand unification of electroweak and strong interactions and to look toward an ultimate superunification of all interactions with gravity. Meanwhile, quantum gravity theorists succeeded in renormalizing pure gravity through the one-loop approximation. Although beyond experimental or cosmological test, this limited success with a gauge theory much more difficult than the Yang-Mills theory suggests the promise (and the problems) of supersymmetry and supergravity.

This set of Cargèse lectures begins with reviews of classical general relativity by B. Bertotti, Y. Choquet-Bruhat, and B. Carter. The emphasis here is on the exterior calculus, Lie differentiation on differentiable manifolds, fiber bundles, group structure, and representation theory. A later paper by B. Zumino also contains an excellent treatment of differential geometry, preparatory to a discussion of the geometry of superspace specified by tangent group and torsion constraints. Spinors are useful in gravity theory even when half-integral spins are not present; they are even more natural in supergravity.

In a long section on quantum gravity, D. G. Boulware and L. Parker treat the quantized electromagnetic and charged scalar fields in a background curved space-time using the Schwinger-deWitt proper time formalism, functional integration, Wick rotation, and Riemann normal coordinates. The problem here is to define the vacuum for particles whose wavelength exceeds the space-time curvature: Is the quantum field tied to the geometry (induced polarization) or to radiation propagating independent of geometry? The quantum field theory is renormalizable (by Pauli-Villars regularization, point splitting, or dimensional continuation) because the creation, propagation, and annihilation of particles are all described in tree approximation by local terms. These terms are polynomials in the action and not only are renormalizable but also serve to renormalize the nonlocal terms. The most interesting quantum effect is that general covariance together with local conservation laws requires that the trace of the renormalized energy-momentum tensor be nonvanishing. Parker shows the relation between this trace anomaly and particle creation in asymptotically static Friedman-Robertson-Walker universes.

B. S. DeWitt contrasts the different low- and high-energy properties of Yang-Mills and quantum gravity gauge theories. Yang-Mills theories are renormalizable because they generate only four primitive ultraviolet divergences; although new infrared divergences appear in the coupling of gluons to other massless fields, they can be removed. Their removal appears to be connected with quark confinement and dynamical symmetry breaking in quantum chromodynamics and quantum flavor dynamics. In quantum gravity, no new infrared divergences appear, but the ultraviolet divergences cannot be compensated for beyond the one-loop approximation or in the presence of matter. This is the important difference between Yang-Mills and quantum gravity, although the latter's gauge structure is still not completely unraveled.

The recent developments in supersymmetry and supergravity seem destined to be important to particle physics. As is explained by Zumino, P. Van Nieuwenhuizen, and S. Ferrara, supersymmetry is the graded extension of Poincaré symmetry. This leads to a supergroup whose even and odd (anticommuting) parameters are elements of a Grossmann algebra. The supermultiplets, supersymmetry representations by one-particle states containing both fermions and bosons, have spins 1 and $1/2$ in the supersymmetric Yang-Mills case and spins 2 and $3/2$ in the simple supergravity case. Even in simple supergravity (only one spinorial charge) these spin $3/2$ gravitinos dramatically improve the theory's convergence. In the case of extended supergravity (several spinor charges transforming under some internal symmetry