Progress in Genetics

Proceedings of the Second International Conference on Quantitative Genetics. (Raleigh, NC, May–June 1987.) BRUCE S. WEIR, EUGENE J. EISEN, MAJOR M. GOODMAN, and GENE NAMKOONG, Eds. Sinauer, Sunderland, MA, 1988. xii, 724 pp., illus. $60; paper, $38.50.

The genetics of quantitative characters had its scientific beginnings in the mathematical work of R. A. Fisher and Sewall Wright. The theory was applied to livestock breeding by J. L. Lush of Iowa State University and, because of his wide influence and many students, spread rapidly. The Lush school of quantitative genetics dominated animal breeding for several decades. In Britain the scientific leadership was supplied by Alan Robertson and his colleagues in Edinburgh. There has been a similar growth of quantitative methods in plant breeding, although they have been less dominating because of the greater ease of genetic manipulation in plants (owing to self-fertilization, polyploidy, cytogenetics, and vegetative reproduction) and frequent instances where a single gene is important.

This volume contains the papers given at the second international conference on quantitative genetics, held at North Carolina State University in 1987. The first conference was held at Iowa State University in 1976. Comparisons are in order.

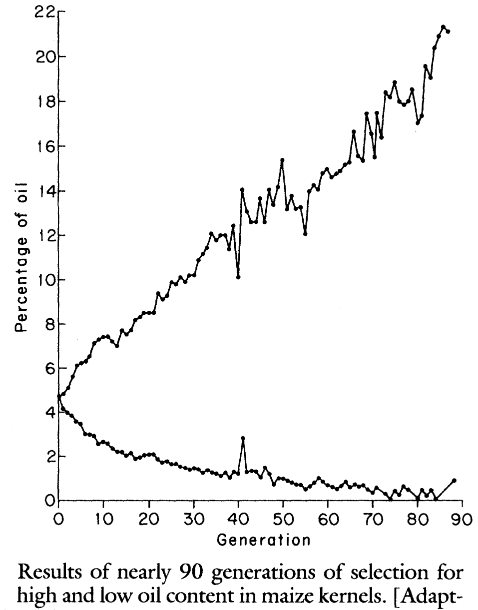
First, personalities. Both volumes include group photographs of the participants. Appropriately positioned in center-front of the 1976 picture are Sewall Wright and J. L. Lush. They are missing from the 1987 program. An era has ended. A new generation—a more varied group of statisticians, computer experts, geneticists, breeders, and molecular biologists—has come forward.

Second, subject matter. As a consequence of the greater diversity of background among the participants, the current volume is considerably more varied than its predecessor. For example, the application of quantitative genetic methodology to human genetics and to the evolution of quantitative traits in natural populations had little emphasis in the earlier conference but is prominent in the later one.

Third, techniques. Computers are prominent in both conferences but play a much more central role in the later one. Furthermore, although statistical methods have always been at the heart of quantitative genetics, more sophisticated methods—largely the result of computing power—are now the rule.

In the 1976 conference there were predictions of the future importance of molecular methods. Yet Oscar Kempthorne found it "fair to say that molecular biology in spite of its great advances, has had essentially no impact on theoretical quantitative genetics and surely nearly no impact on applied quantitative genetics." In the 1987 conference, in contrast, there was much discussion of possibilities for molecular intervention in livestock and plant breeding. Several papers were devoted to molecular markers and to gene transfer. The marriage of molecular biology and quantitative genetics has occurred, but the issue are still gestating. But molecular techniques have had indirect effects, both genetic and environmental: disease and frost resistance increase crop yields; hormone treatment enhances milk production.

This volume is notable for being comprehensive and diverse. A sampling of the subjects dealt with can give some idea of the scope: human population structure, genetic epidemiology, macroevolution, biochemical markers, retrovirus insertion, multigene families, transposable elements as a source of quantitative variation, statistical methods in livestock breeding, new techniques in animal breeding, finding and inserting genes affecting quantitative traits, new sources of genetic variation, human blood pressure and lipoproteins, endosperm traits, analysis of heterosis and epistasis, future prospects for farm animals and plants, environmental stress, nontraditional species and their potential for agriculture, selection in fish, forestry genetics, developing better inbred lines, and more—55 papers in all. An excellent structural feature of the book comes from the organization of the conference itself. Each session was chaired by a senior worker who was asked to review the past decade's progress, and these summaries are regularly spaced throughout the book. The reader gets a broad, current picture of quantitative genetics.



Results of nearly 90 generations of selection for high and low oil content in maize kernels. [Adapted from E. Pollak, O. Kempthorne, and T. B. Bailey, Jr., Eds., *Proceedings of the International Conference on Quantitative Genetics*, Iowa State University Press, 1977; J. W. Dudley has kindly supplied newer data not reported in that volume]

The most important applications have been in agriculture. One effect of this book, and its predecessor, is to reinforce one's faith in the power of selection based on additive genetic variance. The classical example is selection for oil content of maize at the University of Illinois, summarized in the 1976 conference (see graph). This experiment started in the 19th century, prior to the rediscovery of Mendel's laws. After nearly 90 generations the oil content in the line selected for increased amount is almost five times (and 20 standard deviations) above the starting value. There is no hint that genetic variability is running out, despite the fact that the original selected groups consisted of only 12 ears. Whether mutation during the process has played a significant role is an unanswered question.

For most important performance characteristics there is good evidence that progress is nowhere near its limit. (Obvious exceptions are traits with a natural limit, such as zero in downward selection for oil content in maize and 365 eggs per year for poultry.) As reported in the current volume, improvement in milk production in dairy cattle has continued for many years; recently the rate of change, rather than declining, is accelerating. There are several reasons: more intense selection through the use of frozen semen; systems for record-keeping that aid in identifying superior genotypes; greater statistical power through the use of computers; and, of course, management improvements. Milk production would seem to be an ideal candidate for a trait that is unresponsive to selection—a long history of unidirectional selection, a phenotype expressed in one sex only, and antagonisms between greater milk yield and other desirable traits. Yet a great deal of additive genetic variance is present. That there is room for continued selective advance is illustrated dramatically by the fact that the very best cows produce about five times as much as the national average (25,000 as compared to 5500 kilograms per lactation).

Nevertheless, although the improvement is striking, it is only about half as rapid as would be expected if the most efficient selection had been practiced. And in much of the Third World there has been very little genetic improvement of native strains.

For decades breeders have tried, with almost no success, to identify individual genes that affect production traits. Molecular markers will surely advance this hunting expedition. This book includes one outstanding example of a monogenic trait of great economic importance, the multiple-birth gene, *F*, in Booroola Merino sheep. The effect on litter size is roughly additive (+/+, 1.5; *F*/+, 2.2; *F*/*F*, 2.7). During each generation of selection for increased litter size, females of the selected Booroola strain were mated to introduced males from another strain. If the trait were polygenic, such selection would not succeed, because of the 50 percent dilution with each generation of outcrossing. Selection during backcrossing was long ago suggested by Sewall Wright as a way of finding and isolating a major gene; the Australian sheep breeders were unwittingly doing just this.

The current volume is substantially improved over its predecessor in several small but important ways. The printing and page format are better, there is an index, and the references for all the papers are pooled into a single list. Understanding some of the papers requires familiarity with statistics and matrix manipulations, but the majority are accessible to general geneticists. Here is a way to find out what is happening in the far from quiescent field of quantitative genetics.

The book is appropriately dedicated to Clark Cockerham, a student of Lush's and a leading statistical geneticist.

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Directions for Limnology

Complex Interactions in Lake Communities. STEPHEN R. CARPENTER, Ed. Springer-Verlag, New York, 1988. xviii, 283 pp., illus. $64. From a workshop, Notre Dame, IN, March 1987.

This book results from a workshop initiated by the National Science Foundation Ecology Program "to rethink research on community ecology of lakes" and "to set the tone of community level research in lakes for the next 5 to 10 years." It is clear this document is designed to support the establishment of a research center. The result is a view of community ecology that showcases the idea that organisms at the "top" of the food web are largely responsible for the observed species distributions at lower levels. Such a simplistic view is difficult to support given the available data, however, and the term "complex interactions" is proposed as a unifying theme. The idea is that recognition of the complexity should lead to greater care in experimental design and interpretation of results. Of course, it also leads to the conclusion that one investigator cannot hope to cover all the bases, hence the necessity for research centers (four are actually suggested).

The first half of the book is devoted to a set of eight plenary papers that present a series of examples of complex interactions. Three papers deal with pelagic food webs. Mills and Forney conclude that consumer forces control biological structure and producer forces regulate production at each trophic level (the latter is clearly unavoidable, given the direction of energy flow). One repeated theme is the idea of "bottlenecks" in food webs. In eutrophic Oneida Lake the bottleneck results from the inability of zooplankton to exploit large phytoplankton species in late summer, and in oligotrophic Gwendolyn Lake it results from the recruitment of juvenile midge larvae. Neill makes the excellent point that graded perturbations, rather than all-or-none, are most useful for understanding the limits of various interactions. Persson *et al.* decry the traditional schism between aquatic ecologists and fisheries biologists and also call into question the regression approach to understanding food webs. They offer an alternative approach that relies on determining the number of trophic levels along a productivity gradient. The lack of consideration of microbial interactions or trophic shifts by many species illustrates just how simplistic the model is.

Two contributions deal with the potential importance of microbial processes in food webs. The energetics question of how much of the carbon fixed by algae is burned up by the respiration of microbes and how much is transferred to higher trophic levels is raised. The role of *Daphnia* as a keystone species in this transfer process is championed in both papers. Some new and innovative techniques for measuring interactions among these small organisms are obviously required.

Two additional papers, based on models, deal with effects of time scale on food web processes. The model of Bartell *et al.* is particularly irritating in its unrealistic assumptions and parameters and reliance on dichotomies. The authors' explicit goal was to identify "particular circumstances where competition or predation dominate control" of community structure. I cannot perceive how such a result would be useful in a system of complex interactions. Concepts such as "control" and "direction" should be replaced with that of relative turnover rates. Carpenter emphasizes the importance of processes acting on the time scale of the lifespan of the dominant predator. Curiously, humans as the dominant predators in many aquatic systems are not considered.

I found the five group discussion chapters to be the most interesting part of the book, probably because they are more reasonable in tone than some of the plenary papers. The goal was to identify recent advances, current problems, and research needs with respect to food web interactions, size-structured interactions, habitat interactions, microbial interactions, and scale in design and interpretation of community structure. It is obvious that lakes are an ideal place to investigate many of the basic issues in community ecology. The food web group emphasizes the usefulness of gradient experiments and cautions against extreme manipulations that "may achieve statistically significant results of little ecological significance." Size structure is broadly useful as a scaling factor, and it is suggested that size-structured bottlenecks deserve study and that the physiological and reproductive potential of dominant species must be well known. Lakes are complex, heterogeneous spaces, so habitat interactions usually cannot be neglected. This group considers biogeochemical interactions to be important and actually mentions parasitism. Refreshingly, differential effects along gradients are a major theme. The microbial interaction group sees an undeveloped opportunity to take advantage of the fast time scales of microbial communities to examine many general theories in ecology. The group dealing with problems of scale is concerned mainly with experimental design from test tubes to comparisons across lakes. Many useful warnings are included.

Unfortunately, the theme of "top down" vs. "bottom up" control of community structure pervades these discussions. I have never seen the usefulness of an either-or conceptualization for processes that operate along a set of continuums governed by relative rate processes. The fact is that both growth and loss rates are involved in determining the abundances of species. In my opinion, it is counterproductive to ask which is "more important" for any particular species or trophic level. It would be better to try to develop ways to determine some of these rate processes more accurately and to include turnover rates in food web models.