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ADAPTATION AND GENETIC VARIATION IN POPULATIONS

INTRODUCTION

EVOLUTION is fundamentally a genetic phenomenon. Genes provide the continuity of living matter over time: seeds, sporophytes, gametes, and gametophytes all have limited lifespans, even when viewed as populations of dividing cells. But survival of genes depends on the characteristics of the various phenotypes that the plant assumes throughout ontogeny and phylogeny and the ability of those phenotypes to capture resources and convert them into offspring in the face of competition and environmental constraints. Consequently, genes and the phenotypic structures they indirectly produce are intimately connected through a series of feedbacks during development and through the action of natural selection.

The genetically inclined population biologist is interested in ascertaining the frequency of genes and genotypes throughout the life cycle, the changes that take place in those frequencies, and the underlying causal factors (Figure 1). Such a goal, however, is unattainable at present for a variety of technical and conceptual reasons. Two factors are paramount. The first is the very limited knowledge that we presently possess regarding the process of development. Although it is possible in many instances to predict fairly accurately the genic composition of the population of gametes and zygotes from a knowledge of the phenotype of the parent plant population (provided the inheritance mechanism of the character is understood), it is not possible to predict the phenotype of a population of mature plants from knowledge of the genic composition of the zygote population, because we have a very limited understanding of how genes and environmental factors interact in development (Lewontin, 1974). The second reason is the technical problem of actually identifying genes and alleles. The technique of characterizing alleles by their primary gene products (allozymes) through gel

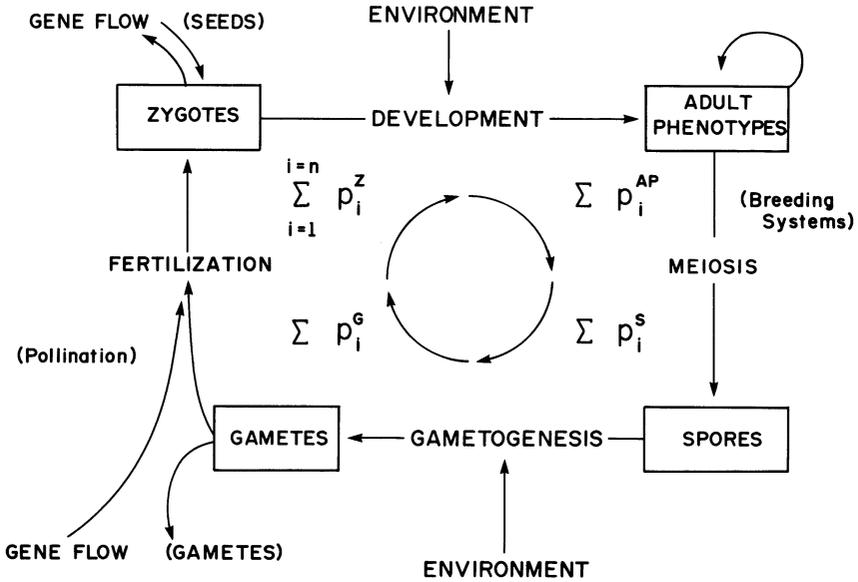


Figure 1. Generalized genetic model of the life cycle. The information of concern here is the gene frequency ($\sum p_i$) at different stages of the life cycle and the effect of external factors (environment, breeding systems, pollination) on gene frequency change.

electrophoresis has provided a means of obtaining empirical data on gene frequencies in populations. However, as Johnson points out in this volume (article 3), the problems of biochemical regulation during development put in question the validity of evolutionary studies based on the monitoring of allele frequency changes of single genes in populations. Nevertheless, preliminary conclusions can be drawn in certain instances, as Hamrick (article 4) shows in correlating gene frequency with lifespan in plants.

Two factors influencing changes in gene frequency distributions are the breeding system and the details of pollination and fertilization. Solbrig (article 5) presents a cost-benefit analysis of recombination. One of the unresolved paradoxes of modern population biology is the apparent high level of heterozygosity in populations, which is impossible to account for under present single-gene models with selection. Plants, with their great variety of breeding

systems, are ideal for testing costs and benefits of inbreeding and outbreeding.

Donald Levin (article 6) presents some novel ideas regarding pollinator behavior and interspecific hybridization, as well as the way that pollinators affect and are affected by the genetic structure of the population. The matter of gametic selection is not addressed in this section, but the interested reader is referred to Mulcahy's (1976) recent book.

But are models of plant evolution based on optimality arguments justified? Horn, in the introductory article (2), presents arguments in favor of an optimality view of evolution, although cautioning against circular and tautological thinking. He also presents the tantalizing view that botanists and zoologists have developed different outlooks as a result of being involved in the study of primarily sedentary and mobile organisms, respectively.