21. AN APOPHASIS OF PLANT POPULATION BIOLOGY

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Apophasis was a process used by theologians to describe the nature of God by defining the extent of their ignorance. This chapter attempts an apophasis of plant population biology. This may be worthwhile if it is true that the beginning of knowledge is the awareness of ignorance.

A population biologist seeks to explain and then hopes to predict the abundance of organisms. There are clearly two quite different types of explanation—proximal and ultimate (final). Proximal explanations are made by showing how the present properties of organisms place limits on the range of environments that they discover and exploit and the speed with which they do so. Ultimate explanations invoke evolutionary forces (e.g. natural selection) to explain how the organisms came to have those present properties that impose those present limits on their behaviour, abundance and distribution. It is very easy to confuse these types of explanation, especially when the same word 'adaptation' is used to describe *both* the present match between organisms and their environments *and* the process by which the match is supposed to have evolved.

There is of course no reason why we should suppose that the ultimate forces that led to the evolution of the present properties of organisms bear any close relationship to the present consequences of those properties. Unfortunately, most of the evidence for the nature of forces that have governed the direction of evolution (and so the source of ultimate explanations) comes from observations of proximal events. We make the assumption that the forces that shaped the past were essentially the same as those we can observe today.

Sex is an example of a property that has certain clear present consequences in the behaviour of individuals, populations and species. It is hard to resist the temptation to explain the evolution of sex in terms of its present consequences. However it may be just one of many properties that, having been acquired by populations during odd episodes of history, are irreversible and hang like millstones round the necks of evolving populations. Proximal explanations of the consequences of sex (and other properties) may have little to do with ultimate explanations of its evolution (see e.g. Gouyon, Gliddon & Couvet, 1988). An apophasis of plant population biology needs to stress that we are ignorant of how far we can obtain ultimate explanations of biological phenomena by examining their proximal consequences. True ultimate explanations might need to show how the present behaviour of organisms has become limited within narrow specializations rather than how they have become perfected fits to their present environments.

All known organisms are specialists, capable of growth and reproduction in only a limited range of conditions. Environments are patchy in space and time. The abundance of any particular type of organism depends on the abundance and distribution of patches in which its special requirements are met and whether it disperses to and is able to colonize these patches. The result is that only tiny subsets of the world's flora are present in any area we choose to study. The overwhelming characteristic of the flora of a region is the absence of all species but for a few egregious oddities. The specializations that distinguish taxa are responsible for excluding them from most of the world's habitats.

Darwin's evolutionary optimism saw the process of natural selection as a perfecting force, creating '. . . from the war of nature, from famine and death, the most exalted object which we are capable of conceiving . . .'. This attitude finds itself expressed in Sewall Wright's adaptive landscapes in which populations are envisaged as moving, under natural selection, across contours of genetic variation to the tops of hills—adaptive peaks (Wright 1931, 1932, 1935). An alternative view, an evolutionary pessimism, is that of Huffaker (1964) who saw instead specialization as 'a deepening rut in evolution'. The appropriate evolutionary landscape would then be of pits and troughs, with populations more or less deeply embedded in them; some indeed descending deep on their way to extinction! It may be that sex itself is a deep rut in the evolutionary process, from which it is very difficult to escape. We may be paying too much attention to trying to find the forces that lead to the evolution of sex—the more important question may often be what are the forces that constrain populations from losing the sexual habit. The answers may be quite different in higher plants (in which apomixis offers the opportunity for easy escape from outbreeding, without inbreeding depression) and in animals in which the formation of a zygote so often seems to be an obligatory condition for the start of a new life-cycle.

In this volume, Antonovics reexamines Haldane's dictum that the population size of a species will only be affected by changes in genotypes if the resultant phenotypes respond differently to density-dependent factors. He concludes that this may be true only under very specialized 'perfect' conditions. If the evolution of specializations, forced by fitness differentials, may have the effect of reducing population size, an adaptive landscape of troughs and ruts may be the most realistic picture of the real world. However Antonovics points out that '. . . we have no data or developed methodology that can provide even a tentative answer to the question of whether the "genetic component" does or does not influence population size.' This is one example of a part of the science of population biology that is defined at present by the extent of our ignorance.

Plasticity

The genotype of a plant acts on its development by determining how it interacts with the environment. Many specializations represent narrow limits within which phenotypes may vary—this is especially true of the form of insect–pollinated flowers. Other organs may vary widely in form in different parts of the same plant (e.g. leaves of aquatic *Ranunculus* spp., juvenile and adult leaves of many *Eucalyptus* spp., *Acacia* spp., *Valeriana dioica*) or between plants of the same species or clone. This phenomenon of plasticity is especially well known in higher plants (see e.g. Bradshaw, 1965) but is probably characteristic of all modular organisms (Harper, Rosen & White 1986).

All organisms that grow by the branching iteration of their modular parts have an inherent plasticity in the number of these parts. The size of an oak tree, a strawberry clone or a coral is determined by the number of its modules. The number usually increases with age, but is profoundly influenced by environmental conditions of irradiance, nutrient and water supply and by the effect of neighbours on the availability of these resources. As a result the size (and hence usually the extent and sometimes even the timing of reproduction) of modular organisms becomes phenotypically highly plastic. Weiner (1988) reviews the literature on plant to plant variation in size that occurs within populations and results in hierarchies of reproductive output. Gottlieb (1977) has shown that much of this variation in fitness between individuals may have no genetic base and may indeed blur and slow the effects of selective forces in shaping evolutionary change.

At the level of the module however, it is not at all clear that phenotypic plasticity is more strongly developed among plants than among animals. The shapes and sizes of leaves, flowers, fruits and seeds may not, on average, be phenotypically more plastic than body size in *Drosophila*, rabbits or snails. In higher plants it is as if the tight control of development has been shifted from the genetic individual to its parts. Nevertheless there remain intriguing variations in the plasticity of modular parts. The flowers of annual cornfield poppies (*Papaver rhoeas* and *P. dubium*) are highly plastic, the length of petals and the number of stamens per flower varying at least five-fold. However in *Ranunculus* spp., e.g. *R. bulbosus*, petal size scarcely varies and in other species of Ranunculaceae, e.g. *Aquilegia* spp., stamen number has become rigidly canalized.

Levin 1988 argues that the ability to respond to different environments by phenotypic plasticity lessens the forces of selection (and drift) that operate within populations and so slows the pace of evolutionary change and divergence. How then does natural selection act on plasticity itself? By slowing down the speed of evolutionary response to a given selective force the risk of becoming trapped in an evolutionary rut is reduced. Over the long term, populations of individuals with high phenotypic plasticity may be less likely to go extinct, though, over the short term, those individuals with a precise canalized response to their immediate environment may often be fitter. Studies of comparative plasticity between and within species and within individual plants are still extremely rare (an exception is Marshall, Levin & Fowler 1986). We are still in almost complete ignorance of the genetic control of plasticity and homeostasis of the modules of higher plants. The great interest stimulated among animal breeders by the work of Lerner (1958) on homeostasis seems to have had little impact in the plant sciences.

Plants grow in environments that are patchy in space and time. The theoreticians' vision of panmictic populations in homogeneous environments developing to equilibrial conditions was created to make it easier to do sums; not because it represents the real world. Hubbell (1979) and Hubbell & Foster (1986) have argued from studies of a Panamanian forest, that in such patchy environments the composition of the forest is determined by populations of species (or at least guilds of species) that vary randomly—the ecological equivalent of genetic drift. However, Fowler (1988) argues that there is a variety of scenarios in which competition—and frequency-dependent interactions—may occur in plant communities yet be very difficult to detect or measure in the field (although they are easy to demonstrate in deliberately constructed experimental communities).

It is extremely difficult to design the appropriate experiments that might reveal how much of the composition of natural communities is determined by forces such as density and frequency dependence and how much by unrecognized heterogeneity in the communities over space and time. The boundaries of our ignorance of even the most general principles are drawn by the sheer limitation in the number of appropriately designed studies. As Fowler points out, proving Hubbell's hypothesis is extremely difficult as it is a null hypothesis. If we fail to find pattern and order in systems it may be that we have simply failed to search in the right way or that there are quite simple processes that govern the population dynamics which in their operation give results indistinguishable from chaos (May 1981). It is not certain what is the appropriate scientific method that resolves this situation—presumably only continuing the search for causation and continuing to adopt random processes as a fall-back position until or unless we discover causation.

Somatic mutation

A number of population biologists have become excited about the role of somatic mutation as a source of variation on which natural selection may act and as a source of variation within single clones (genetic mosaics) that might give protection against disease and other hazards. It is remarkable that this enthusiasm for naturally occurring somatic mutation is found among ecologists and not among plant breeders. Three sets of evidence are frequently cited for the importance of somatic change in natural systems. Durrant's work (Durrant 1958, 1962, 1971) established beyond dispute that heritable changes could be induced in flax (*Linum usitatissimum*). What is extraordinary in this case is that the phenomenon seems to be almost entirely restricted to a very few species. There is simply no evidence that the phenomenon is widespread in the plant kingdom. If the phenomenon were at all frequent it would have served as a powerful tool for plant breeders! This has not happened. The other two frequently cited papers are those of Whitham & Slobodchikoff (1981) and Gill (1986). Both papers give convincing evidence that different parts of the same genet behave differently. However in neither case is there evidence that the observed differences between plant parts involve changes in the genome.

There are many alternative explanations of differences in behaviour between plant parts. It is for example rather easy to ensure that different branches on the same tree bear their main fruit crops in different years by inhibiting fruiting for 1 year on selected branches. Asynchronous fruiting between the branches then continues for several years. It is a commercial procedure that may be used to prevent alternating years of high and low fruit production. A common source of what may look like somatic variation occurs as a result of virus infection producing quite different morphologies and physiologies on different parts of the same genet. The history of virus disease within potato varieties (which are single genets) is ample proof of this source of somatic variation. Differences in susceptibility to disease in parts of the same genet have been claimed to be the result of genetic mosaicism—but virus infection may have the same result. Indeed Gibbs (1980) showed that seedlings of *Kennedya rubicunda* infected with yellow mosaic virus suffered less from grazing by rabbits than healthy seedlings and that in palatability trials infected plant material was consumed at a significantly lower rate than healthy material. It is technically quite a laborious procedure to prove that viruses are not responsible for somatic variation within plants. Even the demonstration that the somatic change is transmitted through gametes to progeny does not rule out viruses as the cause because of the ease with which some viruses are pollen- or ovule-transmitted.

Another source of evidence that somatic mutation is an important element in plant evolution comes from the known origin of horticultural cultivars from vegetative 'sports'. Some of these are certainly viral infections. Indeed the first records of somatic 'mutation' that proved to be virus infection are the illustrations of broken-flowered tulips in the works of Dutch realist painters. The extent of viral infections of plants in nature is virtually unknown. Attention has been concentrated almost entirely on crop plants and the most recent survey of virus distributions in natural populations is that of MacClement & Richards (1956), which reports natural incidence of infection as high as 10% and in one genus, *Plantago*, above 64% of the individuals were infected in nine study sites in England. Mackenzie (1985) found virus infections in seven out of fourteen populations of *Primula vulgaris* sampled in North Wales. The effects of virus infections are likely to be reported as somatic mutations if only part of a genet is infected.

For most of the somatic cultural 'sports' in horticultural plants there is no evidence at all that they involve changes in the genome or that they contribute genes to the population gene pool. This is the crucial test of whether they are material on which natural selection acts.

Of course somatic variants may easily be obtained from plant material that has passed through tissue culture–somaclonal variation (e.g. Evans & Sharp 1983). The formation of callus appears to be a necessary step in eliciting this variation. The abnormalities are generated only during passage through the disorganized condition of callus culture and appear to be a product of the treatment: regeneration from wound callus has long been known as a procedure that can generate polyploids and other genetic changes in the karyotype. It may be that somatic mutation is extremely rare or absent in organized multicellular meristems, or that it is a common occurrence but that diplontic selection weeds out mutant cells. It is perhaps significant that some of the strongest evidence of somatic variation without an intervening callus stage is that of Klekowski, Kazarinova-Fukshansky & Mohr (1985) from studies of ferns. It is in such plants with single apical cells that the opportunity for diplontic selection would be expected to be least. If somatic mutation is a common feature within plants it should be especially common in mosses where the haploid tissues should immediately display even recessive mutations.

Antolin & Strobeck (1985) have modelled the ways in which somatic mutation might influence the variation that is exposed to natural selection—but the value of their model awaits the critical data that show whether the phenomenon is real or not (and if it is real, whether it is of significant magnitude). Schaal (1988) contributes some of the strongest evidence for somatic mutation as a real phenomenon in flowering plants. Her data were obtained from careful analysis of ribosomal DNA in *Solidago altissima* and *Brassica campestris*. Despite the strength of her evidence, she is extremely guarded in her conclusions: '. . . whether this somatic variation is inherited and enters into the gene pool remains to be determined . . . The significance of these processes in population biology is yet to be determined.' Perhaps the most important experiments needed in this area are not those that examine whether or not somatic mutation occurs, but whether it makes a significant contribution to the genetic variation on which selection may act. The crucial experiments are those that will give us measures of the relative contributions made to *genetic* variance by variation between and within genets.

The problem of the role of somatic mutation is a good illustration of apophasis. The extent of our ignorance is not easily mapped if exciting ideas are rapidly assimilated into a body of literature before they have become more than ideas or hypotheses. The risk is greater because authors are unwilling to report, and editors reluctant to publish, purely negative results from hypothesis testing. The boundaries of ignorance are set by knowledge—not by hypotheses.

Life-cycles and growth form

The life-time activity of mobile unitary animals can be seen as a partitioning of time and resources between a variety of activities such as hunting for food and mates, competing with other individuals, escaping from enemies and rearing offspring. Arber (1950) pointed out that almost every activity of an animal that is related to its ability to move is achieved by plants through some aspect of growth or form. It is not surprising therefore that plant population biologists are increasingly concerned with the ways in which form is determined—both its canalization and its plasticity.

In the case of mobile animals it is often convenient to compare the 'costs' of various activities in terms of the ways in which some resource, usually energy, is partitioned. Energy spent in searching for food is energy that is not available for escaping from enemies or for some other activity. Natural selection may be seen as acting on the ways in which limited resources are allocated between the variety of activities, each of which brings rewards but also incurs costs. This same approach may be followed for plants, e.g. Harper

& Ogden (1970) (though currencies other than energy or carbon may then be appropriate).

An alternative approach for plants and other modular organisms is to compare the ways in which modules of structure are allocated to various activities such as reproduction, growth, defence, etc. Higher plants grow by the iteration of modular units of structure which are generated from meristems. Meristems may be allocated to growth, reproductive or other structures. The very form of the plant is therefore the consequence of the ways in which meristems have been allocated. The time schedules of growth and of reproduction are locked together because of the dependence of both on a limited resource of meristems. Thus the annual plant may be annual because it switches all its available meristems to reproduction and so puts an end to further growth. A perennial habit is possible only if some meristems remain in a vegetative condition.

The reproductive schedule of a tree is characterized by a more or less long period in which no meristems are allocated to reproduction (the juvenile phase) followed by a sudden or gradual slowing of growth as a proportion of meristems end their lives in a lethal act of reproduction. The timing of changes in the patterns of allocation of meristems largely defines the reproductive schedule of a plant and can quite readily respond to selection over generations or as phenotypic change in the life of an individual. The switch of meristems from continuing production of new modules and meristems to a lethal reproductive fate is often a response to photoperiodic stimulus as, for example, in annual cereals.

The responsiveness of the switch mechanism to selection has been dramatically illustrated by the selection of rapid-cycling populations of *Brassica* spp. The commercial brassica crops and their wild relatives normally require 6 months or more to complete their life-cycle from seed to seed. A period of innate seed dormancy is normally added to this so that the life-history is completed only once in a year. Williams & Hill (1986) selected and interpollinated early flowering forms from a world collection of brassicas and radish (*Raphanus*) and repeatedly selected for (1) minimum time from sowing to flowering, (2) rapid seed maturation, (3) absence of seed dormancy, (4) small plant size and (5) high female fertility. This gave populations of *B. campestris* that can flower 16 days after sowing, complete the whole life-cycle in 36 days and are capable of completing ten whole life-cycles in a year!

The placement of reproductive as opposed to vegetative meristems is a major determinant of form and accounts for much of the variation in the structure of plant canopies: plants with terminal floral and axillary vegetative meristems clearly produce a different canopy structure from those that bear axillary floral and terminal vegetative meristems. Such differences in the pattern of meristem allocation account for much of the variation in tree form that has been summarized in a classification of the shapes of tropical trees (Hallé 1986; Hallé & Oldemann 1970; Hallé, Oldemann & Tomlinson 1978). It would be of great interest to know the levels of heritability of factors controlling the allocation of meristems in wild species. The effects of both reproductive schedules and form on the population biology of plants are clearly potentially very profound. We need to know much more about the degree of plasticity and the genetic canalization of the processes in different species. In particular we need to know much more about the heritability of morphology and life-history properties in different species. Is it the case that in some species the properties are readily selected and in others they are resistant to microevolutionary change?

Form is, however, more than just the result of the allocation of meristems to different fates (to survive or die, to generate more vegatative meristems or reproductive organs); the lengths of internodes and angles of branching also make a major contribution to the way in which a canopy is displayed to light, flowers are displayed to pollinators and seeds are poised for dispersal. Clearly the resources used in making long internodes are costs to the plants—they might have been used in making other organs. One consequence of bearing short internodes is that the plant acquires a compact 'phalanx' growth form, with more or less tightly packed modules. As a consequence the modules may enter into each other's resource depletion zones (Harper 1985)—tightly packed leaves on a plant are more likely to shade each other and tightly packed roots on a single plant are more likely to deprive each other of access to water and nutrients. A compensating effect is that the territory of phalanx plants may be extremely resistant to invasion by other individuals of the same or different species. Typical phalanx growth forms among herbs are tussock grasses (e.g. *Deschampsia caespitosa* is an extreme example among temperate species), the dense clones formed by some clonal herbs (e.g. *Mercurialis perennis*) and shrubs (e.g. *Gaultheria shallon*) and the dense canopies of some trees (e.g. *Cupressus* spp, *Taxus baccata, Abies* and *Picea* spp.).

Plants with internodes that are long relative to the size of the leaves or shoots that they bear, (whether on aerial shoots or on rhizomes), develop a canopy with more widely dispersed leaves and shoots, that enter less severely into each others resource-depletion zones and so produce less intense competition for resources within the individual plant. However, as a consequence the canopies are more invadable and the shoots, though more effective as invaders of new resource zones, are more easily penetrated and invaded by the shoots of individuals of the same or of other species. The strawberry (*Fragaria vesca*), *Potentilla reptans* and rhizomatous grasses (e.g.

Agropyron repens and *Agrostis stolonifera*) are examples of extreme guerilla forms among herbs. However, guerilla growth forms can also be recognized in the canopy forms of trees. Species such as *Acer pseudoplatanus* and to a lesser extent *Quercus robur* and *Fagus sylvatica* are capable of extending long internodes (and so branches) into light gaps, giving them exploratory qualities that are denied to the more tightly canalized phalanx growth forms of, e.g. *Picea* and *Abies* spp. The branches of a sycamore wander and explore gaps in a canopy—the branches of a fir may die if they find themselves in shade but are under too tight a programme of development to grow out and 'wander' into light gaps.

The physiology of individuals in populations

There is a clear contrast between species in which the form of the whole genet is under tight developmental control and those in which there is opportunistic local response to the environmental conditions experienced by the parts. At one extreme is the firmly canalized growth form of trees like *Picea* and *Abies* in which strong forces of correlative inhibition keep the expression of form of the genet within narrow limits. At the other extreme are species such as the aquatics *Lemna* spp., *Pistia stratiotes, Salvinia* spp., in which physical connection and all opportunity for developmental coordination of the modules is rapidly lost. In most plants, even though the integrity of physical connection is maintained, the individual parts have a high degree of physiological autonomy (Watson 1984; Watson & Casper 1984). Hutchings & Slade (1988) discuss the ways in which the balance between autonomy and regulation acts to control growth form and resource capture in the woodland herb *Glechoma hederacea*. Experiments of this sort are rare and they emphasise how ignorant we are of the physiology of plants in real environments.

The overwhelming majority of studies made by plant physiologists use isolated plants or plant parts (leaves, roots, etc.). Yet in the real world most plants grow with neighbours—and these determine much of the quality of the local environment. There is of course a well-developed science of the physiology of natural, agricultural and forest ecosystems—concerned with the carbon assimilation, water balance and nutrient cycling of areas of vegetation—but these studies almost inevitably neglect the behaviour of individual plants within the systems. The result is that we know a great deal about the physiology of individual plants outside their communities and a great deal about the physiology of communities without reference to the behaviour of individual plants. The physiology of *the individual in the population* is a wide open area of ignorance. Rozema *et al.* argue this case in the present volume and they also indicate the importance of competition between organisms for limiting resources as a major force in plant population biology.

In most studies of the reaction of individual plants to the presence of neighbours their behaviour is usually interpreted as *either* the withdrawal by one of the resources that could have allowed the faster growth of the other (competition); *or* the provision by one of the resources that allow the faster growth of one another (e.g. nitrogen fixation by legumes in a population of grasses); *or* the creation by one of physical conditions (e.g. humidity) that hinder the growth of another; *or* the production by one of chemicals that suppress the growth of another as in the still strictly unproved case of allelopathy.

There is another important way in which plants may respond to the presence of neighbours; this is the reaction to environmental cues from neighbours which change their behaviour and so minimize competition. The enforcement of seed dormancy by canopy-filtered radiation has the effect of preventing seeds from developing into seedlings in environments that would be likely to prove lethal. The demonstration by Deregibus *et al.* (1985) that the development of grass tillers may be inhibited by canopy-filtered radiation is another example of potential competition between plants or plant parts that is 'anticipated' by cues and then avoided. The growth and branching of white clover (*Trifolium repens*) appears to be regulated by canopy-filtered radiation in the same way so that the plants respond not just to reduced photosynthetically active radiation in shade but also to the nature of the shade cast specifically by leaves (Solangaarachchi & Harper 1987). Mechanisms like these may be as important in regulating the intensity of competition between plants as territorial behaviour is in animals—the processes have much in common.

Patchiness

We know a great deal about the effects of the density of populations, of pure and mixed species, on the growth of plants in experimental models and in agronomic practice. We still know extraordinarily little about how these effects are produced. Moreover, most of what we know comes from experiments in which spacing and mixing are designed to give more or less homogeneous populations: edge effects are usually excluded in the protocol of experimental design. One of the great areas of ignorance is of the effects of patchiness in populations and what happens at edges. Most of the natural world is patchy and most of the exciting things probably happen at edges. It is unfortunate that the literature concerned with pattern (patchiness) in vegetation has been concerned to describe the patchiness of species distribution (e.g. Greig-Smith 1983) and not with the much more difficult description of the patchy distribution of individuals or genets. This makes it impossible to use the existing elegant data on pattern in plant communities for important exercises like the measurement of genetic areas or for purely demographic studies. The science of plant population biology needs different procedures if we are to gain an understanding of the effects of patchiness on population dynamics comparable to its known effects in some animals (see e.g. Hassell 1981).

The patchiness of natural populations makes for some obvious comparisons with the patchy occurrence of diseases. The older science of epidemiology may indeed have much to offer to plant population biology. Areas of land become 'infected' by colonizing plants and these areas may become foci for infection of neighbouring areas. Areas of land may develop vegetation that confers 'immunity' against further infection. Newly susceptible land areas become available for infection and the chance that this will occur depends on the proximity of these 'habitable areas' to those already infected. It seems likely that whole blocks of formal epidemiological theory might usefully be absorbed into plant population biology and the approach of Carter & Prince (1988) may help to discover the missing link between plant population dynamics and more classical studies of the dynamics of vegetation.

Parasitism, predation and mutualism: major forces or minor complications in the biology of plant populations

Much of the early development of plant population biology as an experimental science was concerned to establish relationships between plant density and performance in pure stands and in mixtures. Relationships such as the Law of Constant Final Yield and the −3/2 thinning law were described by Japanese workers (e.g. Kira, Ogawa & Shinozaki 1953; Yoda *et al.* 1963) mainly for single species stands, and de Wit (1960) developed replacement series models that allowed the behaviour of two species mixtures to be analysed and described. Such models, in which the ecological world is composed solely of higher plants interacting with each other in an otherwise wholly physical environment, have developed greatly in sophistication. But the real world is a great deal more complex as evidenced by the chapters in this volume by Augspurger on the role of plant pathogens, Crawley on herbivory, and Turkington on the microorganisms of the rhizosphere. Watkinson adds another dimension to the plant–plant interactions by discussing the parasitic interactions between higher plants.

We simply do not know whether it is the direct density- and frequency-dependent interactions between higher plants coupled with physical heterogeneity in the environment and mediated by dispersal phenomena that account for the greater part of the character of natural vegetation—in which case all these other phenomena of predation, parasitism etc. are just noise in the system. However it may be that, in the majority of natural communities, it is these parasites, predators and mutualists that are the real determinants of community structure. It may be that it is competitive interactions between higher plants that are the forces that confuse the picture.

It is a worry for those who expect science to produce simplifying generalizations of nature, that research seems continually to expose new elements that need to be taken into consideration in accounting for the character of the natural world. New complications keep emerging, rather than a simpler story. Agronomists are well aware that plant viruses, nematodes and possible virus–nematode interactions are often major determinants of plant performance in the field. These are two extra forces (with their potential further interactions!) to add to those that are already being studied by population biologists.

It is not just that population biologists keep discovering new forces that may need to be considered as possible explanations of population phenomena; it is perhaps even more worrying that so many studies reveal highly species-specific interactions. Indeed, in the case of pathogens, the interactions are commonly specific at the race, or even individual genotype level (see e.g. Burdon 1987). Is it the case that plant population biology is developing by the accumulation of ever more individualistic special cases. The problem is not of course peculiar to the study of plants—a recent book on human evolutionary ecology (Foley 1987) is, perhaps cynically, titled *Another Unique Species*! If this is how the science is developing, the boundaries of our ignorance are becoming defined by a cloud of unique spots of knowledge, rather than by broad sweeping lines of generalization.

Grime *et al.* (1987) describe an experiment in which they established microcosms of many species of higher plant with and without VA mycorrhiza. After a year, a mycorrhizal network of interspecies connections appeared to have established: the species diversity of the microcosms was quite different in the presence and absence of the mycorrhiza. Most notably the dominant species (*Festuca ovina*) was strongly suppressed in the mycorrhizal microcosms. It may be that in this case *Festuca* reacted to the fungus as a pathogen and the increased diversity of the mycorrhizal microcosms reflected the reduced competitive force from the dominant. However, whatever the mechanisms involved, it is no longer realistic to neglect the role of other organisms in the population biology of higher plants. It may be that it was natural selection from the animal (and microbial) kingdom that provides the ultimate explanation of the variety in the plant kingdom that we know today; it may be these same kingdoms that retain proximal responsibility for the present patterns of abundance among the diversity that they created.

The dynamics of plant populations

Plant population biologists are concerned to explain patterns in the numbers of plants over space and time. Some of these patterns develop over intervals of time that are long compared to the life of humans. The life-span of genets of rhizomatous plants and of trees commonly exceed that of humans and it is not surprising that we have few records over long enough time-spans to contain the essential elements of their population dynamics. The dynamics of *Pinus strobus* populations in New England appears to be determined essentially by fires and hurricanes. A major fire occurred in forests in New Hampshire in 1665 and a series of hurricanes in 1635, 1898, 1909 and 1929 (Henry and Swan 1974). In this case it was possible to reconstruct some of the dynamics of the populations from data frozen in fallen tree trunks—but few research programmes would have included the experience of such crucial events within their time-span.

We depend for much of our information about natural population dynamics on those individuals who have set up permanent recording sites and made arrangements for repeated census after they stopped making them themselves. White (1985) has reviewed the history of long-term studies—they are relatively few and may have given us a biased view of the dynamics of natural vegetation. A partial substitute for long-term studies is possible when communities in which different stages in community development can be found as a mosaic in space at the same time. This allows the dynamics of the whole to be inferred from its parts. Much of what we know about the population dynamics of tropical rainforest comes from this type of analysis and is illustrated by Whitmore (1988).

Perhaps the most important developments in plant population biology and vegetation science in the past 20 years have stemmed from the belated appreciation of the work of Watt (1947). He emphasized that communities are mosaics in space and time—that the apparently stable mixtures of species in a community are really space–time mosaics of replacements, local extinctions and colonizations (the regeneration niche of Grubb 1977). Martínez-Ramos, Sarukhán & Piñero (1988) describe this process for Mexican forests and also describe ways in which the annual 'tree', *Kochia trichophylla*, may be used to explore intimate 'tree-to-tree' relationships in experimental patches. The emphasis on patchiness in the chapters of both

Whitmore & Martínez-Ramos, Sarukhán & Piñero again stresses that most of the exciting phenomena in plant population biology occur at edges—where interactions between plants, and the elements in population processes can be followed in the performance of individuals. The patchiness may in itself allow density- and frequency-dependent processes to be operating within the fine scale of a mosaic, yet not be detectable in the larger scale of the community (Fowler 1988).

It might be expected that, if generalizations are to appear in plant population biology, it will be the study of annual plants that contributes most. This is because it is clearly easy to follow whole life-cycles of several generations in relatively short research programmes and because they are especially suited to experimental population studies. The most extensive data set is that of Symonides (1988). Her data show that a whole variety of population dynamics may be found among annual plants—the only feature they seem to have in common is that the generation time is short. Perhaps the important point is that, 20 years ago, it would have been quite impossible to recognize similarities and differences in the population dynamics of different groups of plants. Data sets for the natural dynamics are now beginning to be assembled and it is at last possible to see commonalities beginning to emerge—though perhaps not across the groupings where they might have been expected.

Data sets of the quality of those obtained by Symonides are needed in much greater numbers if generalizations are to emerge. There are few technological advances that substitute for immensely laborious field census-compiling. There are few funding bodies prepared to invest in research programmes of appropriate length. The science of population biology depends on committed individuals, often working over long periods and often in their spare time, to produce the data sets that justify the activities of the experimentalists and theoreticians. At present the balance between those producing data about population processes in the real world and those attempting interpretation appears to be grossly unbalanced. Sadly, a century of phytogeography and descriptive community studies has assembled records of the world flora that are virtually useless to those who wish to interpret how populations behave and how vegetation comes to be what it is.

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