

Spatial Heterogeneity at Small Scales and How Plants Respond to It

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I. Introduction

The lives of plants are strongly influenced by their being rooted in place and having to endure their local situation without being able to seek more favorable conditions (Bradshaw, 1965). Plants must respond to minute-to-minute fluxes in insolation, change in temperature and humidity from day to night, day-to-day variation in precipitation, seasonal cycles of nutrient availability, annual variation in the length of the growing season, and countless similar elements of environmental variation. Both the variety and the functional significance of such responses to temporal variation in the environment are amply documented in this book. Despite being rooted in place, plants experience not only temporal but also spatial variation in their environment. As a plant grows and extends into adjacent areas (Caldwell, Chapter 12, and Fitter, Chapter 11, this volume), it is likely to encounter different conditions—in other words, the plant's "perception" of environmental variation extends beyond the scale of the individual. Nor is the extent of these spatial effects limited to the scale of roots and rhizomes. As pollen and seeds disperse, the effects of spatial variance at even greater distances are "perceived" by the plant as variation in its success in transmitting genes through progeny to subsequent generations in the local population. This makes spatial structure in the local environment, as well as temporal variation, important to the study of plant responses to environmental heterogeneity. We might estimate environmental heterogeneity with instrumental measures of the physical and chemical environment, by quantitative descrip-

tion of the biota, or by the response of bioassays using standardized test plants. Such data on environmental heterogeneity may be interpreted from various points of view (Addicott *et al.*, 1987; Wiens, 1989; Kolasa and Rollo, 1991), but we will be concerned here with the spatial pattern of microenvironmental patches at scales ranging from that of individual plants to that of plant populations. One of our goals in this chapter is to illustrate how plants respond to environmental heterogeneity at the scale of the population. We shall argue that it is necessary to judge plant responses to environmental heterogeneity not only at the scale of the individual plant, but also at the scale of the plant population.

The most straightforward response of a plant to adversity is to die or, less dramatically, to set little or no seed. If this were generally the case, most populations of plants would comprise a large number of specialized types, each flourishing within a narrow range of environmental conditions and perishing elsewhere. At large spatial scales, this is often true: We find different species of plants in different habitats. Whether comparable specialization to a locale mosaic of different environments can also account for genetic diversity within populations (references in Bell 1990a,b, 1991a,b) and species diversity within communities (references in Bazzaz, 1991) is less certain. There is some evidence for such genetic specialization from field experiments that compare the performance of plants from the same genetic stock in their native site and in more or less distant sites. Such reciprocal-transplant experiments have consistently shown that incomers are less successful than residents (Schoen *et al.*, 1986; Antonovics *et al.*, 1987; Kadmon and Shmida, 1990; Platenkamp, 1990; Platenkamp and Foin, 1990). Other evidence of specific local adaptation includes the findings that the direction in which selection acts on given phenotypic characters can vary among sites separated by only a few meters (Stewart and Schoen, 1987; Argyres and Schmitt, 1991), and that crosses within natural populations tend to be more productive between parents that are growing close together than between parents that are separated by a few tens of meters (Schmitt and Gamble, 1990; McCall *et al.*, 1991).

Though these results show that there is often some degree of microenvironmental specialization or local adaptation within plant populations, it can scarcely be concluded that individual plants have the potential to grow successfully only in a very narrowly circumscribed range of conditions. Many of the papers in this volume demonstrate the contrary view, that individual plants can maintain high levels of performance over a wide range of conditions. Given the relative immobility of individual plants and the ubiquity of environmental heterogeneity, it is reasonable to infer that plants will have evolved sufficient plasticity to grow successfully over a range of conditions. The available data, especially at small

spatial scales (representing the distances traveled by pollen and seeds) and at small genetic scales (within populations of a single species), do not suggest that either specialization or plasticity predominates. Some balance of specialization and plasticity among individuals in plant populations, perhaps shifting in response to local environmental heterogeneity, seems more likely.

This is not an issue that we can resolve by studying the responses of groups of genetically uniform plants to carefully controlled environmental variation under laboratory conditions. The variation expressed in controlled-environment studies will depend on the range and nature of the test environments selected. Similarly, our assessment of the degree of variation among genotypes depends on the breadth of our sampling: Larger samples of genotypes, or tests across a wider range of environments, may always reveal unusual individual responses that substantially increase our overall estimates of variation in a trait. These problems may not be of much concern to breeders concerned with plant performance in managed environments (Mayo, 1987), but they can be seriously misleading in studies of plants in natural environments (Lawrence, 1982). The appropriate approach in studies of wild plants is to describe the patterns of environmental heterogeneity that exist and the responses that plants have evolved while growing under these conditions, that is, to study the nature and selection of plasticity under natural conditions. In this chapter we shall also suggest methods for carrying out such studies and point out some promising directions for research on the evolution of plasticity in natural populations.

II. Interrelated Concepts of Plasticity

Concepts of plasticity differ from discipline to discipline, leading to confusion when reading the diverse literature on plant responses to environmental heterogeneity. The usage of the word "plasticity" is not consistently well defined across disciplines, and there are often subtle differences in the operational definition of plasticity even within disciplines. Plasticity is gauged in one way or another by the degree of variation found in traits describing plant form or function. At the simplest level, the variance around the mean of replicate measures of a trait provides a measure of plasticity. Depending on the purpose and scale of the investigation, that variance may be estimated from measurements on single individuals repeated over time, from clonal replicates of individuals grown in different environments, or from individuals randomly sampled in one or more local populations and grown in one or more experimental environments. In all of these cases, a trait with greater variance

would be considered, generally speaking, more plastic. This usage is rooted in the colloquial meaning of plastic, the idea that some basic stock is malleable and can readily take various forms. We emphasize, however, that plants that are able to make broad physiological adjustments to different environments, and that therefore express a large amount of plasticity with respect to physiological characters, will be able to survive and reproduce successfully across this range of environments, and will therefore express a small amount of plasticity with respect to characters related to fitness. Plasticity at the level of physiology is likely to be accompanied by stability at the level of fitness. This point is taken up again in Section IX.

Confusion in the literature of plasticity arises from three sources. First, the variation studied may range from individual plants varying over time to interspecific variation among geographically separated populations. Second, studies do not consistently distinguish, and sometimes do not even recognize, the genetic and environmental components of phenotypic variation. Third, depending on the purpose of the study, there can be substantial differences in the temporal scale at which traits are defined and variation is considered. Generally speaking, evolutionary ecologists tend to measure plasticity as the variation among plants in particular genetically defined stocks growing in different experimental test environments. They view plasticity in terms of the mean environmental variance estimated in experiments that allow the variation among individuals to be partitioned into genetic and environmental components. Physiological ecologists, on the other hand, tend to view plasticity more in terms of the adjustments that plants make in response to changing environmental conditions. They measure plasticity by changing form or function without particular regard to its genetic basis. It is useful to elaborate the nature of these contrasting points of view.

Botanists in general, and physiological ecologists in particular, usually use the term "plasticity" to suggest adjustments in the form or function of an individual plant subjected to changing environmental conditions (Jennings and Trewavas, 1986; Kuiper and Kuiper, 1988). Their concern is with phenotypic variability, not with the genetic processes that underlie that variability. More often than not, plasticity is studied and described as an attribute of the population or species rather than of the individual, despite the fact that the measurements are made on individual plants. In this sense, plasticity is illustrated by the heterophylly of submerged versus emergent leaves on an aquatic *Ranunculus*, or by the acclimation of the photosynthetic light response in *Trillium* leaves as the tree canopy closes in at the end of spring. Many of the ecophysiological processes discussed in this book emphasize such plastic changes, with the plasticity being variously referred to as physiological, developmental, or ontoge-

netic. In this botanical view, plasticity is characterized by the amount of change, the pattern of that change, and the temporal scale over which the change is expressed in individual plants (Kuiper and Kuiper, 1988).

Evolutionary ecologists are equally concerned with the amount and pattern of plasticity, but less attention has been given to the response time of plastic changes (Schlichting, 1986; Thompson, 1991). Evolutionary ecologists study the responses of individuals, but usually do not take into account plasticity in individual plants over time. Their focus is on traits that can be readily measured on individuals that characterize the longer-term functional adaptation of a plant to its environment. They favor traits closely linked to plant survival and reproduction, that is, to components of fitness (Lechowicz and Blais, 1988). For example, they might estimate seed production in preference to maximal stomatal conductance, or total vegetative biomass in preference to the partitioning coefficient for investment in leaf biomass. They use these data on individuals, together with techniques adopted from quantitative genetics, to analyze the genetic and environmental basis of the phenotypic variability among individuals of known genetic relationship sampled from a range of environments (see Lawrence, 1982, Via, 1987). Their focus is on the phenotypic and genetic variability *among* individuals in plant populations rather than on the plastic variation of individual plants (Schlichting, 1986, 1989; Sultan, 1987; Stearns, 1989; Thompson, 1991). There is more concern with spatial heterogeneity as a source of plastic response, or with temporal variation between generations, than with the effects of temporal variation over the life of individual plants.

Differences in the way that studies of plasticity approach temporal variation can be an especially perplexing source of confusion. In deciding how a plant response will be characterized when studying its plasticity, a clear conceptual line has to be drawn between dynamic regulatory processes such as stomatal opening and closing and characteristic variables that define the functional set points in a regulatory system. Most would consider the maximal stomatal conductance as a trait characterizing stomatal regulatory strategy and subject to plastic variation; conversely, most would consider the moment-to-moment changes in stomatal conductance as regulated dynamics, and not as plasticity. This can become a source of confusion because a trait that is chosen for a study of plasticity may vary on several different time scales. For example, an evolutionary ecologist may choose to investigate variation in photosynthetic capacity among plants in a population by assaying maximum photosynthetic rates under favorable test conditions at a single time period during the season. A physiological ecologist would be concerned that this estimate of photosynthetic capacity will vary seasonally, as well as with conditions immediately before and during the assay. In other words,

the variability among individuals can be confounded with variability within individual plants if traits are not appropriately chosen and measured. Evolutionary ecologists strive to choose traits that do not vary much from time to time when measured on the same individual, so that they can better estimate the variability among individuals—variability within an individual plant is unwanted noise. Physiological ecologists, on the contrary, plan explicitly to study the variability of an individual as its environment changes on time scales from seconds to weeks or months—variability among individuals is unwelcome noise that makes the definition of representative response patterns more difficult.

III. Evolutionary Ecology of Plasticity

Natural populations may comprise not many highly specialized genotypes, but one or a few generalists able to cope with the modest amounts of environmental variance found at small spatial scales. Both extreme points of view, narrow genetic specialization and virtually unlimited phenotypic plasticity, are contradicted by the most mundane observations. A more reasonable approach is to recognize both genetic variation in performance and the environmental constraints within which this variation is expressed. We can then recognize that phenotypic plasticity is not merely an arbitrary attribute of plants, but instead a property that evolves through the natural selection of genotypes that determine a more or less plastic response to environments that vary in space and in time. The crucial concept that we wish to advance here is that the amount of environmental variance expressed by plants grown under different conditions is itself a character under genetic control, that is, plasticity is heritable. This fact has been recognized for a long time (Bradshaw, 1965; Schlichting, 1986), but without receiving the attention it deserves (Stearns, 1989; Thompson, 1991).

The concepts of plasticity and its heritability can be given precise statistical meaning in experiments where several genotypes or families are each grown and scored in several environments (Lawrence, 1982; Falconer, 1986). The variance of average scores among the genotypes is a genetic variance (s_G^2); The variance of average scores among the environments is an environmental variance (s_E^2). These two components sum to the total variance, provided that each genotype responds in the same way to differences among environments. However, if genotypes respond differently when the environment changes, a third source of variance will be contributed by genotype–environment interaction ($s_{G \times E}^2$). We consider the environmental variance, s_E^2 , as a good measure of plasticity for studies in evolutionary ecology—the greater this environ-

mental variance, the more plastic is the character. It should be noted that there are alternative opinions among evolutionary ecologists on exactly which variance components should be considered the measure of plasticity. Scheiner and Goodnight (1984) prefer the sum of s_E^2 and $s_{G \times E}^2$ as a definition of plasticity, whereas Thompson (1991) considers plasticity to be defined by the interaction effect ($s_{G \times E}^2$) alone. We prefer to keep the concept of the mean phenotypic plasticity (s_E^2) separate from that of the genetic variance of phenotypic plasticity ($s_{G \times E}^2$). This $s_{G \times E}^2$ can be thought of as the heritable portion of the total environmental variance. It has been discussed theoretically by Via (1987), Via and Lande (1985), and Lyman (1989, 1991), in an experimental context by Bell (1990a,b), and in the field situation by Via (1991).

To the extent that the quantity of environmental variance can be inherited, it can evolve under natural selection, if a greater or lesser sensitivity to environmental variation is advantageous. The environmental variance ties the phenotypic variation we observe to its environmental basis, and is therefore a good measure of plasticity. But if the phenotypic variation is due to s_E^2 alone, then there is no potential for differential selection favoring the degree of plastic response exhibited by the fittest individuals in the population. In that case, the plants do respond to environmental variation, but there is no opportunity for improving the magnitude or direction of this response through selection of greater or lesser plasticity. Without some genetic component to the plastic response, selection of that response is impossible. The environmental heterogeneity that a plant "perceives" and responds to from an ecological point of view will only be relevant from an evolutionary point of view if there is heritable variation in plasticity. This argument applies to any plant trait or response, but we shall be interested primarily in reproductive success, or in characters that are highly correlated with reproductive success. The concern with the evolution of plasticity, rather than merely its description, necessarily shifts the focus of investigations of plasticity from the individual plant to the population.

IV. Implications for Physiological Ecology

The preceding chapters have been concerned mainly with the mechanisms by which individual plants exploit gaps, patches, and resource-rich microsites. This emphasis is consistent with the long tradition in physiological ecology of studying plant responses to environmental gradients. The shift from early experimental definition of, for example, equilibrium photosynthetic rates along a gradient from 0 to 2000 $\mu\text{moles photons/m}^2/\text{s}$ to the transient response to sunflecks is a natural one. It

is a shift from an ecophysiological perspective focused on stable acclimation to experimental gradients to one that takes more account of the spatial and temporal heterogeneity of resources in natural environments, and leads to a view of plasticity gauged by changes in traits during the life of a single individual (Kuiper and Kuiper, 1988). This shift engenders studies of plant responses to experimentally manipulated resource patches, rather than along gradients. Our mechanistic understanding of plant responses has been much enriched by these investigations.

This new ecophysiological approach, with which this book has been largely concerned, is nonetheless incomplete. In most mechanistic investigations, individual variation is considered only as a nuisance that increases the number of replicates necessary to get a good estimate of the response. In fact, this variation among individuals in a population is a reflection of the effects of environmental heterogeneity at the population level and is of interest in its own right. Such variation among individuals in a plant population has important implications both for ecological patterns (Bazzaz and Sultan, 1987; Tilman, 1990; Turkington and Mehrhoff, 1990; Bazzaz, 1991), and for evolutionary processes (Bradshaw, 1965; Antonovics *et al.*, 1987; Stearns, 1989; Bell, 1990a, 1991a; Cohen and Levin, 1991). It is also of interest to agronomists and plant breeders, who are often concerned with developing strains of crop plants that perform well over a wide range of environments, and may be willing to sacrifice exceptionally high levels of performance in particular environments in order to do so (Mayo, 1987). In this context, we can ask how variability in plant traits maps onto variability in the environment over the relevant spatial and temporal scales. Do plants respond to the same levels of environmental heterogeneity that we might measure instrumentally, or do they buffer or filter the variation in some way? Are the levels and patterns of plastic responses to environmental heterogeneity similar or different among traits? What is the balance of genetic and environmental effects that account for the range and pattern of phenotypic variation across a range of heterogeneous environments? The notion that phenotypic plasticity is a heritable trait exposed to selection gives us a powerful general principle for approaching these and other questions.

V. A Fine-Scale Survey of Maple Seedlings

In the body of this chapter we shall put forward a number of generalizations concerning environmental variation and how plants respond to it. We shall be particularly concerned with spatial pattern in native populations of plants growing in undisturbed natural environments at very small spatial scales, of the order of dispersal over a single generation. This

is the scale that is most relevant to the evolution of plasticity, although it has been largely ignored by both ecologists and plant physiologists. Many of the suggestions that we shall make are speculative and are intended as hypotheses to be tested rather than as assertions of ascertained fact. The empirical basis for these speculations has been provided by work at the McGill Field Station at Mont St. Hilaire in southern Quebec, the published part of which will be cited in the appropriate following sections.

To provide a concrete example of phenotypic variation in a natural population, we shall analyze an unpublished survey of seedling sugar maples (*Acer saccharum* Marsh) growing in the understory of old-growth forest at Mont St. Hilaire. Most of these seedlings became established after damage from a glaze ice storm in December 1983 had increased insolation on the forest floor (Melancon and Lechowicz, 1987). Even in this single locality, which we refer to as the Lake Hill site, the seedlings are likely to differ from one another genetically (Perry and Knowles, 1991), and we can describe only the phenotypic variation among these individuals without partitioning its genetic and environmental basis. This is sufficient for our present purposes, but limits our discussion to a strictly ecological rather than an evolutionary perspective. We are essentially concerned with comparing the range and nature of phenotypic variation in different traits of the seedling maples growing at this forest site.

To quantify the spatial pattern in this population, we randomly harvested five seedlings in each of 198 meter-square plots randomly located within a 50 × 50-m grid. We aged each seedling by counting terminal bud scars and calculated its mean annual production of woody tissue (NAP: g/year); both aboveground and belowground woody tissues were included. The NAP is a good index of seedling fitness in this canopy tree that survives long periods of suppression in the understory (Canham, 1988). We also measured the area and mass of leaves on each seedling to calculate its specific leaf mass (SLM: mg/cm²). The SLM is central to the functional organization of leaves (Gutschick, 1987), including those of sugar maple (Lei and Lechowicz, 1990; Ellsworth and Riech, 1992), and is known to respond strongly to light regime (Givnish, 1988). Figure 1 shows the spatial distribution of these two seedling traits within the sampling grid.

VI. Physical Environment in the Forest Understory

We are concerned to relate phenotypic variation among these maple seedlings to fine-scale environmental heterogeneity in this habitat. The simplest approach to measuring environmental variance is to record the readings of instruments that are sensitive to environmental factors, such as insolation or the concentrations of inorganic ions, at different points

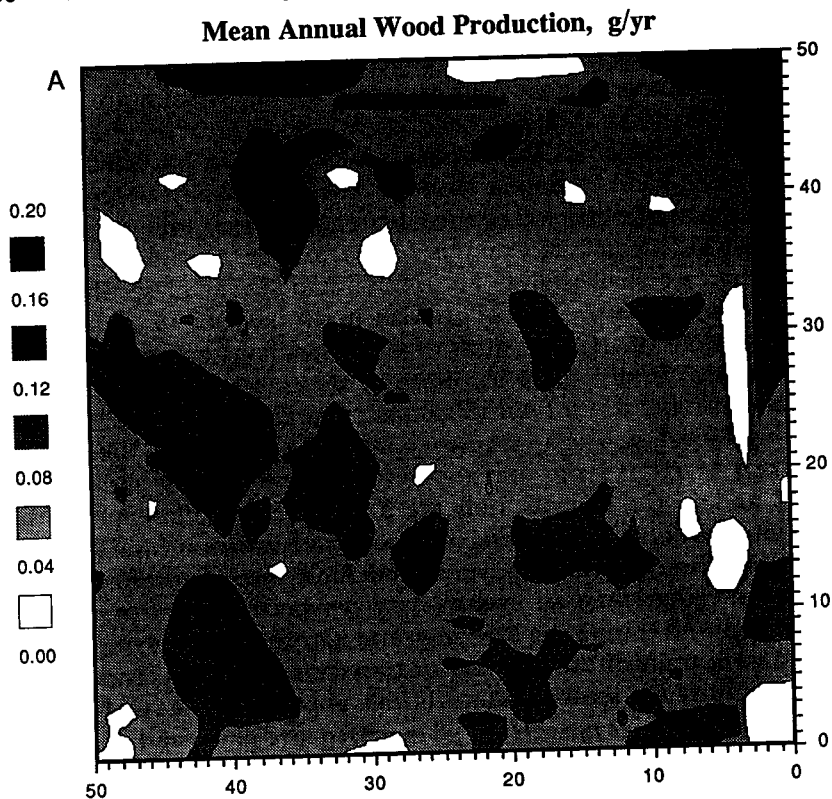
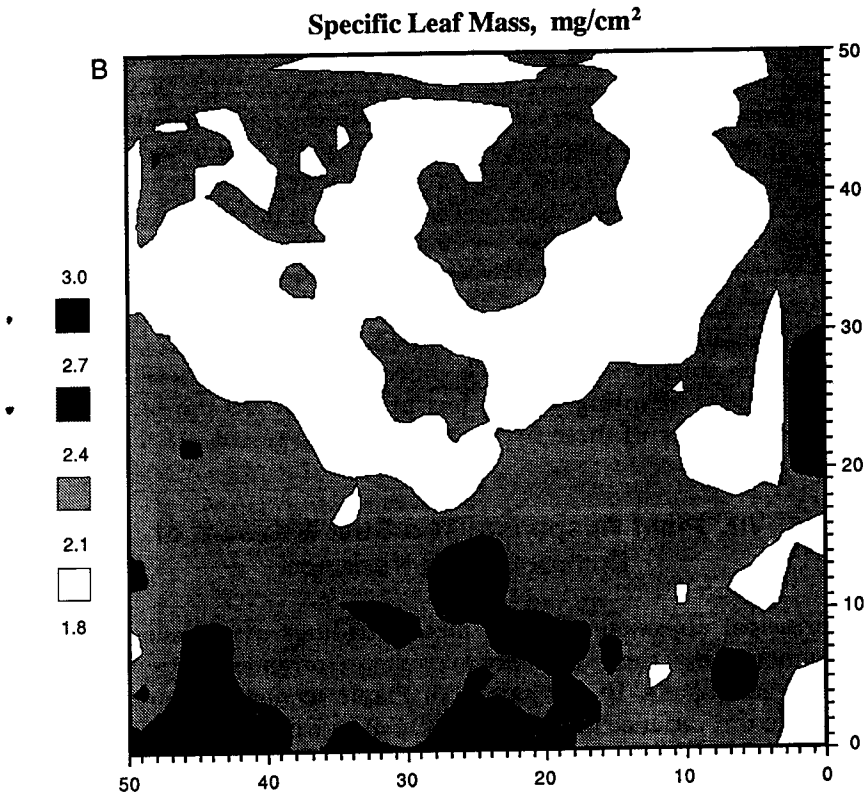


Figure 1 Contour plots of (A) the mean annual wood production (g/year) and (B) the specific leaf mass (mg/cm^2) of sugar maple seedlings sampled in 198 meter-square plots in the understory of a mature forest with *Fagus grandifolia* and *Acer saccharum* codominant in the canopy. The canopy at this Lake Hill site was heavily damaged by an ice storm in the winter of 1983–1984 but had largely closed in when these samples were taken in 1991 (Melancon and Lechowicz, 1987).

within the sampling area. By replicating measurements at each sampling point the error variance (confounding true measurement error with unanalyzable spatial variation at the sampling point) can be estimated; the remaining variance component is an estimate of the variance among sampling points. We do not yet have data of this sort for the Lake Hill grid, but we have found substantial variation among sites within a similar $50 \times 50\text{-m}$ grid nearby on the mountain for soil pH, nitrogen, and potassium (Lechowicz and Bell, 1991). Even at very small spatial scales, the physical environment is not uniform, and we can expect selection for plasticity within this local population of sugar maples.

When the sampling area is extended, a greater range of recognizably



distinct habitats will be included, and it is reasonable to expect that the estimate of environmental variance will tend to increase. A plot of the environmental variance among a set of sites against the average distance separating the sites expresses spatial pattern (for technical discussion of the statistical procedures involved, see Burrough, 1983; Webster, 1985; Trangmar *et al.*, 1985; Robertson, 1987). If the regression has zero slope the sites are uncorrelated, and as much variance can be found within a smaller as within a larger area. If the regression has positive slope then nearby sites are positively correlated, and conditions of growth will become steadily less predictable as one moves away from any given point. The variance of physical features of the environment increases with distance even within 50 × 50-m grids at Mont St. Hilaire (Lechowicz and Bell, 1991), and similar results have been reported in less undisturbed environments (Palmer, 1990; Robertson, 1987; Robertson *et al.*, 1988; Moloney, 1988). Surveys at larger spatial scales have led us to propose the general rule that variance increases continuously with distance at all

scales (G. Bell *et al.*, unpublished). This suggests two possible generalizations about the evolution of plasticity. First, species of plants that disperse their propagules more widely will display less phenotypic plasticity (or greater phenotypic stability) with respect to fitness when challenged with a range of deliberately manipulated environments. This is because their offspring, as a group, will encounter a greater quantity of environmental variance, and selection will therefore have favored physiologically plastic genotypes, which because they are able to survive and reproduce over a wide range of environmental conditions will express relatively little variation in fitness. Second, any given species will display less plasticity (greater stability) for fitness toward physical variables whose variance increases less steeply with distance, since the levels of these variables encountered by offspring will be less predictable. To the best of our knowledge, neither of these hypotheses has been tested.

VII. Plant Response: The Best Measure of Environmental Variance

The principal objection to using meter readings as measures of the environment is that their relevance to plant performance is often difficult to define adequately. In our survey of maple seedlings, we would like to describe the variance of the environment in which they are growing. We might begin by deciding that the most relevant environmental factor for NAP and SLM is insolation, but that would arbitrarily ignore covariant changes in soil nutrients, water, and similar factors (Bazzaz and Wayne, Chapter 13, this volume). Even if we accepted the simplification that plastic responses in NAP and SLM were dominated by variation in insolation, how could we quantify variation in insolation? Given the immense temporal and spatial heterogeneity of insolation in the understory of deciduous forests (Baldochi and Collineau, Chapter 2, this volume), do we place a recording instrument at each of our seedlings throughout the growing season? If we had these numerous records second by second throughout the growing season, how would we summarize the variance in insolation? Given the effects of plant acclimation to previous insolation (Percy and Sims, Chapter 5, this volume), neither the simple variance nor even a power analysis of the time-series would provide a complete and biologically meaningful summary of the variance in insolation across all the seedling microsites. We are forced to conclude that the routine measurement of spatial and temporal heterogeneity in this single environmental factor, let alone all the covarying factors that can influence plant response, is at best impracticable, and may be impossible even in principle. We must turn to some alternative measure of environmental heterogeneity against which to gauge plant responses.

One alternative is the "phytometer" method, first introduced by Clements early in this century (Clements and Goldsmith, 1924) and recently revived by Antonovics and his associates (see Antonovics *et al.*, 1987). Clonally propagated plantlets transplanted into the natural environment serve as a bioassay of conditions throughout a study site. Bell and Lechowicz (1991) have referred to this design as an "implant" to distinguish it from "explant" trials, which have a similar purpose. In an explant trial, the bioassay is conducted using samples (soil cores, for instance) removed to a common test environment, in which they can be arranged randomly in order to destroy any purely spatial covariance. Implant trials estimate the full range of biotic and physical sources of environmental heterogeneity, but their interpretation can be complicated, or restricted to certain characters or test species, by high levels of transplant mortality. Explant trials circumvent this difficulty, but at the expense of assaying only some of the sources of environmental heterogeneity. Both approaches have the advantage that the environmental variation is measurable in units directly relevant to plant fitness: size or seed production, for example. These methods have been used to demonstrate the existence of spatial heterogeneity that influences plant fitness at scales from 10^{-1} to 10^2 m both in pristine environments at Mont St. Hilaire (Bell and Lechowicz, 1991; Bell *et al.*, 1991) and in more disturbed habitats (Antonovics *et al.*, 1987).

VIII. Separation as an Estimate of Environmental Similarity or Difference

Another method of studying environmental variance through plant response is to use *in situ* measurements of unmanipulated native plants. This approach uses the distance separating sampled plants as a basis for inferring the degree of difference in their microenvironments. We commonly suppose that two microenvironments close together are more similar than two that are farther apart, and this has been shown to be the case in forest understory (Palmer, 1990; Bell and Lechowicz, 1991; Lechowicz and Bell, 1991; Bell *et al.*, 1991) as well as more generally in other habitats (Robertson, 1987; Robertson *et al.*, 1988; Moloney, 1988). We can confidently predict that any two of our sampled seedlings separated by a meter should on average be more similar than two separated by 10 m. In other words, the variance of NAP (or SLM) among all pairs of seedlings separated by 1 m should be less than that among all pairs separated by 10 m. A graph of the variance of any factor on the distance apart of sampling sites is a description of the structure, or pattern, of the environment. This approach can readily be extended to partition

phenotypic variance into its genetic and environmental components by analyzing the spatially patterned responses of replicate plants that are genetically characterized and planted out over the spatial grid in this natural environment. Such an analysis would provide measures of plasticity and its heritability unambiguously relevant to natural selection in this maple population.

There are some problems, however, with using variance as a measure of plant variability in comparisons of this sort. First, any measure of variance is dependent on the sampling interval on which it is based. If photosynthesis fluctuates from near zero to near maximum in response to sunflecks in a matter of seconds, but our infrared gas analysis system responds to changing rates only on the order of minutes, then we have artificially damped the real variance in photosynthesis. Only good technology and thoughtful sampling design can account for such effects of sampling interval on estimates of variance in a character. Second, because variance is calculated as squared deviations from the mean, any changes in units or measuring scales will change the variance, just as it will change the mean. If we measure nocturnal tissue pH of a CAM plant on a scale of pH units (logarithms of hydrogen ion concentration), the variance (and the mean) will be far smaller than if we measured hydrogen ion concentration itself. The same is true if we log-transform a measured variable to meet the requirements of a statistical analysis. To compare the relation of variance to distance among different characters, it is often useful to use the *z*-standardization (normalization) that adjusts the sampled values so that they have a mean of zero and a standard deviation of one (Zar, 1974). Unless the initial distribution of the data is very far from normal, this standardization removes the unwanted effects of scale and units of measurement without altering the pattern of plant variability over distance. We use the normalized phenotypic scores of the maple seedlings to describe the spatial pattern of NAP and SLM throughout this small area of forest floor (Figure 2).

The sampling design and our lack of genetic information about the sampled individuals place some limits on our discussion. Our estimate of the error variance is the variance among the five sampled seedlings within each square meter, so that we cannot analyze spatial variance at scales of 1 m or less. The remaining variance is our estimate of the overall environmental variance at scales exceeding 1 m within the 50 × 50-m sampling area. This estimate is substantial and highly significant for both characters: for SLM, environmental variance $s^2_E = 2.28 \times 10^{-2}$ (error variance $s^2_e = 2.59 \times 10^{-2}$, $P = 0.0001$ for $H_0: s^2_E = 0$); for NAP, $s^2_E = 2.80 \times 10^{-4}$ ($s^2_e = 6.91 \times 10^{-4}$, $P = 0.0001$). We emphasize again that these values, based on individuals of unknown genetic relationship, are not pure estimates of the environmental variance; they include

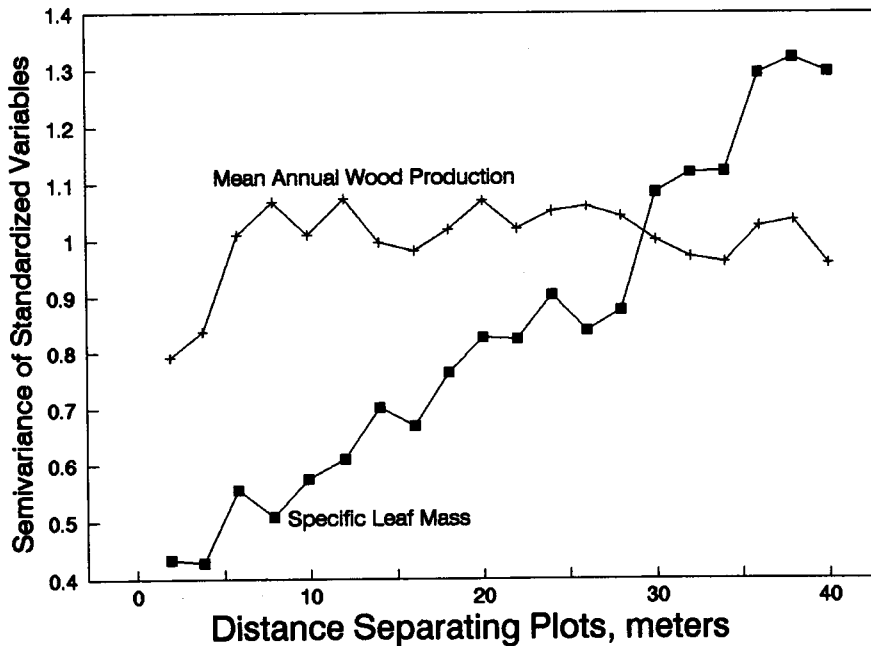


Figure 2 Semivariograms for standardized values of specific leaf mass and mean annual wood production for the seedling sugar maples sampled at the Lake Hill site (cf. Figure 1).

portions of the genetic and genotype–environment interaction variances, as well as genotype–environment covariance. However, experiments at Mont St. Hilaire using the understory herb *Impatiens pallida* from similar old-growth forests have shown that the environmental component of variance is much larger than the genotypic components (Bell *et al.*, 1991; Schoen *et al.*, in press), and we are confident that for our present purpose these estimates can be interpreted as a measure of plasticity.

The variance of SLM, which increases steadily with distance, illustrates the use of *in situ* plants separated by known distances to gauge patterns of environmental heterogeneity (Figure 2). The spatial response of this particular trait undoubtedly arises from the correlation between nearby points with respect to the physical factors to which variation in SLM represents a response—for example, nearby points will tend to have similar light regimes. However, it is the plant response itself that provides both the simplest and the most appropriate integration of these physical factors. Explant studies using genetically uniform material of *Arabidopsis* and *Hordeum* have likewise shown substantial small-scale environmental variance and pattern for similar areas at Mont St. Hilaire, in trials where

genotypic sources of variance can be excluded (Bell and Lechowicz, 1991). However, these sources of variance were not absent: Different genotypes of the test species showed different patterns. A plant's "perception" of local variation in the environment depends on its genotype as well as on the trait being monitored. In either explant or implant trials, it is preferable to use a range of defined genotypes; the precision of estimates is not thereby compromised, and their generality is greatly extended. The existence of some heritable differences in plant response to this forest understory environment only emphasizes the potential for selection to act on plasticity within the range of conditions found in this small area.

IX. Nature of Plastic Responses to Environmental Heterogeneity

A plastic type varies physiologically in response to variation in the external environment. If plasticity has evolved under selection, plastic variation is likely to be functionally appropriate, in the sense of tending to increase expected survival or reproductive success, rather than being a mere passive fluctuation. Physiological processes may then vary as widely, or even more widely, as the environmental factors to which they are a response. However, we expect that the eventual output of these underlying physiological processes, lifetime reproductive success, will vary much less. This is because any lineage within a population that inhabits a heterogeneous environment will encounter different conditions in different generations. The environment perceived by the line descending from any given family will change through time, as members of the lineage are dispersed in successive generations to a succession of different sites. The long-term fitness of a lineage in these circumstances will depend on its geometric mean rate of increase and will therefore be greater when its environmental variance of fitness is less (Gillespie, 1977). Selection in a heterogeneous environment for *plasticity* of physiological response will therefore result in a *stabilization* of reproductive output.

This is little more than a simple principle of general homeostasis, but it is not quite as straightforward to test as might appear. It is not immediately clear how the data should be transformed to make different environmental and trait scores comparable. In a few instances a direct approach to the comparison of biotic and physical variation may be possible when the same variable can be meaningfully scored for both plant and environment. For example, we might predict that the rate of increase of variance with distance will be less for plant tissue potassium concentration than for soil potassium concentration. Whether any such

comparisons are valid is questionable: Even if potassium is expressed in the same apparent units (g/g) in both plant and soil, there is no assurance that the mass of potassium relative to soil is truly comparable with the mass of potassium relative to plant tissue. The difficulty is compounded because the magnitude of the variance for untransformed scores will depend on the units of measurement, as explained earlier. The z-transformation, which we have used in Figure 2, forces the overall variances of all scores to be equal, which will not always be appropriate; there is no compelling theoretical rationale either for any particular scalar transformation or for scaling on the mean. However, environmental *pattern*, as expressed by the rate of increase in variance with distance, does not encounter these difficulties. We therefore suggest that in general the rate of increase of variance with distance will be less for functionally important plant responses than for the physical environment. The rate of increase of variance can be estimated as the slope of the regression of log variance on log distance.

Given that the rate of increase in variance over distance allows us to compare plasticity in different traits, we can ask whether different traits show different patterns of plasticity in the same range of environments. To show that this may happen, we have compared the amount of variation in NAP and SLM as a function of distance in the seedling maple population at Mont St. Hilaire (Figure 2). We might expect a priori that the amount of variation in both traits would increase with distance at nearly the same rate as more different microenvironments are encountered, but in fact this was not the case. The patterns of phenotypic variability in NAP and SLM of the sugar maple seedlings in this population are not alike. The variance of SLM increases steeply and continuously with distance, but NAP shows a quite different pattern: Variance increases from 0 to about 5 m separation, but thereafter remains at nearly the same level, so that the correlation between sites is nearly zero for distances in excess of 5 m. Put another way, both SLM and NAP are plastic traits, but the plasticity of SLM is directly coupled to increases in environmental heterogeneity and that of NAP is not. NAP is a less plastic trait, or a more stable trait, than SLM in the face of increasing environmental heterogeneity. This is to some extent an artefact of the arithmetic scale that we have used; if we were to sample plots several kilometers distant, there is little doubt that a greater variance in NAP would be found. Nevertheless, the two variables are clearly patterned in different ways, which we might express by saying that SLM measures a coarse-grained environment whereas NAP measures a fine-grained environment, or alternatively by saying that NAP is a more stable character than SLM. This difference in the environmental grain of the two plant responses is shown graphically by the contour plots of these data (Figure 1).

Since different characters will give different estimates of environmental variance and pattern, can we predict which characters will be more plastic and which less? It follows from the argument at the head of this section that characters that are more highly correlated with fitness will be less plastic, or more stable. The slope of log variance on log distance, which provides a convenient measure of plasticity, will be smaller for characters that are more highly correlated with fitness. The prediction is valid either for *in situ* surveys or for implant experiments using native plants. Insofar as selection favors plasticity, rather than leading to genetic specialization, it will favor genotypes with mediocre reproductive success sustained over a wide range of environments with different physical characteristics. However, this may require quite different physiological mechanisms in different circumstances. To give a hypothetical example, an umbellifer growing in full sun might be adequately defended against invertebrate herbivores by modest investments in photoactivated toxins but require high water-use efficiency to deal with its drought-prone water regime; conversely, at a nearby shaded site, water-use efficiency may be less important while investments in antiherbivore defenses may be much greater. The proximate physiological mechanisms involved in dealing with the physical environment would thereby retain much of the spatial correlation exhibited by physical variables, while selection would erode this correlation at the level of their eventual outcome, reproductive success. This is an evolutionary argument and applies only to native plants sampled in the environment they have evolved in; it would not necessarily apply, for example, to explant studies using exotic species as bioassays. The maple seedlings may provide an example of this principle, since the likelihood of eventual growth to reproductive maturity will be much more highly correlated with NAP than with SLM.

X. Artificial Selection for Phenotypic Plasticity

The most valuable technique for investigating these aspects of phenotypic plasticity in the laboratory is the selection experiment. Despite the recent increase of interest in plasticity, we know of very few attempts to manipulate the plastic response of plants by selection over many generations, using reproductive success itself as the character under selection; a partial exception, using plant height, is Jinks *et al.* (1977). A brief review of related work on morphological characters in *Drosophila* is given by Scheiner and Lyman (1991). The most straightforward experiment would be to select directly for plasticity by testing a range of genotypes in each generation and selecting those with the least environmental variance in fitness. This scheme might not work, because it would be likely

to cause selection for genotypes that had low variance because they had very low fitness in any environment, as the result of deleterious mutations. It would be preferable instead to base selection on the geometric mean of fitness over environments. This is equal to $\bar{x} - \frac{1}{2} \sigma^2_E$, where \bar{x} is the arithmetic mean and σ^2_E the variance over environments, for any given genotype. This design would address two fundamental questions.

First, what is the cost of plasticity? Since plasticity is limited, and reaches different limits in different species, it is presumed that acquiring a greater degree of plasticity entails some cost, but the nature and magnitude of this cost remain unknown. In the selection experiment, a cost would reveal itself as a correlated response of mean fitness: as the environmental variance of fitness fell, arithmetic mean fitness would also fall, if genotypes can express high levels of plasticity only at the cost of a reduction in mean fitness. Second, is plasticity dissociable? We have argued earlier that plants may display different levels of plasticity with respect to different physical variables; this assumes that selection can act independently on the responses to different variables, rather than simply reducing overall sensitivity to the physical environment. There is evidence for such differential plastic responses across key functional traits in herbaceous plants (Lechowicz and Blais, 1988; Macdonald *et al.*, 1988; Schlichting, 1989). In the selection experiment, this means that selection lines in which plasticity with respect to (say) temperature had been increased would not necessarily exhibit greater plasticity with respect to other variables, such as nutrient concentration. It is even possible that different plastic responses are antagonistic, so that increased plasticity with respect to temperature tends to be accompanied by greater sensitivity to variation in nutrient concentration; this would act as a further constraint on the evolution of plasticity with respect to any given physical variable.

A different but equally valuable approach is to select indirectly for greater plasticity. Since it is supposed that plasticity is an adaptation to variation in the physical environment, populations that are maintained over many generations in a diverse environment should evolve greater plasticity (with respect to the particular variables contributing to that diversity) than comparable populations maintained in a uniform environment.

XI. Conclusions

We have attempted to describe how plants respond to environmental heterogeneity not only as individuals but also more extensively on the scale of the local population. Both natural and managed environments often have great spatial and temporal heterogeneity with respect to fac-

tors that influence plant growth and reproduction at all scales, from less than that of the individual plant to greater than that of the habitat as a whole. The progeny produced by a plant, being dispersed away from the parental site, will encounter a range of environments, and any individual plant must therefore be able to grow successfully over a range of conditions. Selection will direct the evolution of an appropriate degree of plasticity. In studying the mechanisms by which individual plants adjust to temporal changes in their immediate microenvironment, we should not lose sight of the importance of larger-scale environmental heterogeneity in the evolution of plasticity.

Plant physiologists usually study the acclimation of individual plants to conditions of growth that vary in time. The reasons for this are largely methodological. In this chapter we have described a quite different perspective, which comes from studying populations of plants whose conditions of growth vary in space. Our arguments are statistical rather than deterministic, and evolutionary rather than physiological. Although these two points of view are quite different, and are normally pursued by different groups of scientists using different techniques, we see them as complementary rather than antagonistic; eventually, each will be necessary for the success of the other, as the validation of the evolutionary arguments requires physiologically informed experiments, while the generalization of the physiological work requires an evolutionary interpretation. The principal suggestions that we have made, all requiring further investigation, are as follows.

1. Phenotypic plasticity is a heritable trait that evolves under natural selection and that can be manipulated by artificial selection.
2. There is substantial physical environmental variance at the spatial scale of plant dispersal; selection will therefore act on plasticity even within local populations of plants.
3. Environmental variance increases with distance; the rate of increase of environmental variance with distance supplies a measure of environmental structure. Species that disperse their propagules farther will be more plastic. Any given species will be less plastic more stable with respect to physical variables whose variance increases less steeply with distance.
4. The most appropriate measure of environmental variance is plant response, as measured by implant, explant, or *in situ* studies. Plants vary less than their physical environment, at least for functionally critical traits.
5. Characters that are more highly correlated with fitness (reproductive success) display less environmental variance, as the outcome of the evolution of plasticity.

6. Selection experiments offer the best approach to the genetic architecture of phenotypic plasticity. The main objects of selection experiments should be to demonstrate and quantify the cost of plasticity, to investigate the independence of the plastic response to different environmental variables, and to test the hypothesis that plasticity evolves in heterogeneous environments.

The genetics of phenotypic plasticity have been neglected in the past, because geneticists prefer to work on highly stable characters, whereas physiologists and ecologists tend to ignore individual variation. This neglect accounts for the fact that many of the propositions that we have advanced are highly tentative, or even highly contentious. However, a Darwinian approach to the plastic response is long overdue, and our main object in writing this chapter has been the hope that evolutionary arguments will contribute more prominently to the next generation of research.

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