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## HABITAT SELECTION IN PLANTS

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*Abstract.*—Habitat-selection concepts have rarely been explicitly used for plants, perhaps because the majority of them are immobile. For plants, habitat selection results from evolutionary adjustment of species to environmental factors so that the species functions better in some habitats than in others. Habitat choice refers to the ability of a plant to disperse, in space or time, to preferred patches. Habitat specialization means that a species performs best in a small subset of patches in a given location.

The modular structure of plants and their flexible growth response to the patterns of resource availability allow individuals to occupy large areas, exposing them to much spatial and temporal heterogeneity. Modular structure, to a large extent, determines the options available, as well as the constraints, for plants choosing habitats. Choice, however, may be made by the habitat rather than by the plant. That is, the characteristics of the habitat determine which species of the plants that disperse into the habitat become established in that particular habitat. For plants, it is likely that choice is made proximally by the habitat but ultimately by the plants through natural selection.

“Choice” habitats for plants (1) supply resources (e.g., light, water, nutrients, etc.) in sufficient quantities for growth and reproduction; (2) provide pollinators, dispersers, and other symbionts; and (3) have few herbivores, predators, and pathogens, except those that afflict their competitors. Because similar individuals prefer these sites, there can be intense competition among neighbors. Thus, the forces of preference for these choice habitats and habitat selection to reduce competition may oppose one another.

Plants have several mechanisms that improve their ability to reach appropriate habitats and have evolved several attributes that allow them to function in a changing local environment despite their immobility. These mechanisms include (1) wide dispersal of many propagules, (2) targeted dispersal to favorable habitats or away from unfavorable ones, (3) dispersal with a supply of some required resource(s), (4) location of foraging organs in habitat patches where resources are less contested by neighbors, (5) morphological and physiological integration of several patch types, and (6) actual movement to choice habitats by clonal spread and fragmentation. The above mechanisms are forms of spatial habitat choice.

Habitat choice occurs temporally also. Plant life-history events are timed to

coincide with the availability of necessary resources for growth. For example, separation of seasonal and daily flowering phenology between species that require, and may compete for, specific pollinators may be a form of habitat selection. Other mechanisms of temporal habitat choice include (1) the controls on seed dormancy and germination, (2) the evolution of secondary dormancy in plants of unpredictable habitats, (3) the germination of certain desert species only when enough rain for the completion of the life cycle has fallen, and (4) the timing of fruit ripening to coincide with the arrival of their dispersers.

Lacking mobility, and therefore being unable to move to a more hospitable location, many plants have evolved high acclimation potential and phenotypic plasticity to deal with local environmental variability. These attributes, together with ontogenetic response shifts, lessen the need for precise habitat choice. Habitat selection is intimately tied to niche differentiation and coexistence in plant communities, a controversial area of ecology and evolutionary biology. Therefore, progress in one area will invariably lead to a better understanding of the other.

When Gordon Orians invited me to participate in this symposium and to discuss habitat selection among plants, I gladly accepted his invitation. I anticipated an enjoyable and easy task because I thought I knew the meaning of the words "plants," "habitat," and "selection." But when I began to think seriously about what to say, I discovered that I was unsure what the term "habitat selection" meant for plants, and whether it is the habitat or the plant that does the choosing! I consulted ecology textbooks to find out how different authors defined the term and read some key papers that had "habitat selection" in their title. I quickly discovered an ambiguity in the literature. Moreover, except on rare occasions, plant ecologists have not explicitly used the term "habitat selection"; for example, it does not appear in the indexes of recent textbooks such as Begon et al. (1990) and Silvertown (1987).

Animal ecologists use a variety of terms to describe this phenomenon: "habitat selection," "habitat choice," "habitat preference," and "habitat specialization." Moreover, much of the theory about habitat selection and its relation to foraging, species packing, coexistence, and community organization was developed for unitary animals. Higher plants, however, have certain features that set them apart from such animals (see Harper 1977), and the present theory may not be entirely applicable to them. In this article, taking the plant's point of view, I relate plant responses to these concepts and assess whether they are appropriate for plants. I begin with some definitions.

"Habitat selection" results from evolutionary adjustment of species to environmental factors (including the physical environment, competition, herbivores, predators and pathogens, pollinators, dispersers, and symbionts) such that the species function better in these habitats relative to other habitats. "Habitat specialization" means that a species performs best in a small subset of patches in a given location. "Habitat choice" refers only to the ability to disperse to preferred patches. Proximal habitat choice and preference may lead evolutionarily to habitat selection. Habitat specialization results from strong and consistent selection

by the environment; competition may play a role in generating habitat specialization.

For plants there are "choice habitats" that share several common attributes. (1) They supply resources (e.g., light, water, nutrients, etc.) in sufficient quantities and balanced proportions for plants to grow and reproduce. (2) They provide mates, pollinators, dispersers, and symbionts. (3) They are relatively free of herbivores, predators, and pathogens, except for those that afflict their competitors. However, because all individuals do better in these sites, there can be intense competition among neighbors. Thus, the opposing forces of preference for these choice habitats and specialization to reduce competition come into play. Ecologists have strongly debated both the strength and the consequences of competition with regard to differential growth and reproduction within populations and among species. They have developed both verbal and mathematical models to express these interactions and have speculated widely about their evolutionary consequences with regard to response divergence and convergence and niche relations.

Plants differ from higher animals in several attributes that have direct relevance to habitat selection. Plants are characterized by (1) a modular body structure and a less canalized vegetative morphology; (2) a great similarity in required resources (e.g., light, water, nutrients, and carbon dioxide); (3) little mobility, except during the seed and pollen stages; (4) no specific germ line (i.e., somatic and germ-cell lines are not initially differentiated); (5) dependence on morphological and chemical defenses; although individuals may differ in apparency (in the sense of Feeny 1976), they cannot hide! These attributes, to a large degree, determine the options available for plants to choose their habitats.

The modular structure of plants has consequences for their size, patterns of growth, and response to resource availability. Regulation of populations, including recruitment and death in response to density and other factors, occurs at both the module and the whole-plant level (Bazzaz and Harper 1977; Harper 1982). Because response to increased resources may occur at any time during plant growth, modules can be added rapidly and an individual plant can experience new environments by simply growing into them. Therefore, the three-dimensional space occupied by an individual can become much larger as the plant adds more and more modules.

An alternative view of the coupling between a plant and its choice habitat is that the choice is made by the habitat rather than by the plant. The characteristics of the habitat determine which species or individuals from those that disperse into the habitat actually occupy that particular habitat. For plants it is likely that choice is proximally made by the habitat but ultimately made by the plants through natural selection.

Given the attributes of plants mentioned above, habitats can be chosen in several ways. Here I identify these ways, present examples from the literature, and briefly discuss their implications for plant life. Specifically, I discuss spatial and temporal habitat choice, plant responses that lessen the need for precise habitat choice, and the implication of habitat choice for coexistence and diversity in plant communities.

## SPATIAL HABITAT CHOICE

*Wide Dispersal of Many Propagules*

In most habitats, patchiness of resource availability, competitors, and enemies means that only a subset of these patches are suitable for a given species or genotype. Many plants produce a large number of highly dispersible propagules (an  $r$  strategy; MacArthur and Wilson 1967). These propagules, when dispersed, cover large areas and are likely to arrive in a wide range of habitats, which vary in suitability. Species with these traits are able to replace themselves through the success of those that fall in the most suitable habitats. These individuals, in turn, produce a very large number of offspring of their own and therefore are capable of maintaining the lineage. Many examples of this kind of behavior are found in species that occupy ephemeral habitats (see, e.g., Salisbury 1942; Harper 1977; Grime 1979).

*Targeted Dispersal to Favorable Habitats or away from Unfavorable Ones*

Morphological and phenological characteristics of propagules, or certain kinds of rewards to dispersers, may result in propagules' arriving selectively in habitats that are particularly suitable for their growth and reproduction. Birds (see, e.g., Herrera and Jordano 1981; Tomback 1982) and ants have been shown to be important for targeted dispersal of seed (see discussion in Hanzawa et al. 1988). This dispersal may result in increased survival and growth of seedlings largely because ant heaps can be nutrient-rich habitats. Furthermore, handling by the ants seems to be important for germination (Hanzawa et al. 1988).

Many plant species of temperate and tropical forests require gaps for establishment (see Pickett and White 1985; Whitmore 1985). When these individuals mature and bear seed, they usually find themselves in intact forest canopy as a result of their own growth and that of their neighbors. Dispersal of their propagules into gaps is therefore advantageous and may be accomplished by increased dispersal distance from a parent. One possible mechanism would be specific rewards for animal dispersers that spend a significant amount of their time in gaps and therefore drop seeds in them. Whether or not this happens remains to be demonstrated.

A related form of habitat selection is dispersal away from a decidedly unfavorable habitat. For example, there is much evidence that predation and pathogenic infection of seeds and seedlings are higher near the parent than some distance from it (see Janzen 1971; Harper 1977). Seedlings of *Platypodium elegans* experience higher rates of mortality closer to their parent because of a preponderance of pathogens and because of lower mortality in light gaps than in the understory. Furthermore, light conditions in gaps are particularly suitable for germination and growth. The seeds have special morphological adaptations that facilitate their dispersal from parents and thus increase their probability of landing in gaps (Augspurger 1983*a*, 1983*b*).

Although targeted dispersal has not been thoroughly documented, there is little question that seed dispersal, dormancy, and size interact in complex ways to reduce the risks to seedlings inherent in variable environments. These interac-

tions have been modeled by Templeton and Levin (1979) and Venable and Brown (1988).

*Dispersal with a Supply of Some Required Resource(s)*

Dispersal via animal ingestion may lead to seedling success in three ways. First is the arrival at a distant site, which is more favorable for germination than a site near the parent, as described above. Second is the breaking of dormancy (see Fenner 1985). Third is the supply of some resource required for growth, such as nitrogen and phosphorus in animal dung. For example, a large mammalian grazer may consume thousands of seeds a day. A few of these will germinate in the dung, a resource-rich environment. Dinerstein and Wemmer (1988) reported that seeds of the riverine tree *Trewia nudiflora* are eaten in large numbers by the one-horned rhinoceros and may remain in their guts for several days. Gut passage had no effect on germination, but germinating seeds in dung significantly increased seedling growth. Elephants disperse seeds of many plant species, which readily germinate in their dung (Alexandr e 1982) and perhaps use it as a resource for early growth and establishment.

*Location of Foraging Organs in Habitat Patches Where Resources Are Less Contested by Neighbors*

The modular construction of plants allows much flexibility in their growth patterns and architectures. Normally, growth is most active in areas of high resources and low interference. Branch extension in adjacent forest gaps where light is available is a result of this flexibility of growth and may be an important determinant of individual architecture.

Some plant population biologists have made the analogy that buds on a tree or on a clonal herb are a bank (Maillette 1982) that could be deployed differently by the plant, a form of habitat choice. Jones and Harper (1987) showed that, in *Betula pendula*, buds and branches growing in the zone of high interference, where neighboring canopies are close to each other, have a lower probability of survival and production of daughters than buds in the low-interference zones at the center of the tree crown. The "crown shyness" observed in tropical forests (Ng 1983) may result from such interference among neighboring individuals. There is much evidence that growth of modules within individuals in stands can be highly influenced by interference from neighbors. In trees, the shape of an individual in a stand has been shown to be highly influenced by its neighbors (review in Franco 1986). Although many perennial plants may have specific architectural plans (e.g., the tree models of Hall e et al. 1978), reiteration, which is the environmentally caused modification of the trees' architecture by the activity of meristems and the repetition of development (Oldeman 1974), is common in natural vegetation.

Architectural form and the degree of reiteration may allow trees to occupy certain habitats such as the understory of forest. For example, Tomlinson (1983) suggested that the sympodial trunk form may allow cocoa to grow in the forest understory and to take advantage of small canopy openings above. The crown

form of *Terminalia catalpa* maximizes the interception of light within branch tiers and minimizes shading between successive tiers because they are located at certain distances from each other on the trunk. Terborgh (1985) suggested that the location of the understory canopy of *Cornus florida*, relative to the overstory, maximizes its light interception.

Habitat choice among species under field conditions is shown in other ways as well. Differential root distribution among prairie plants (Weaver 1919) and differential location of both above- and below-ground parts of desert plants have been well documented and may contribute to coexistence (Whittaker 1975; Cody 1986). Adjacent individuals of *Polygonum pensylvanicum*, *Abutilon theophrasti*, and *Setaria faberii* (Wieland and Bazzaz 1975) and other species (Parrish and Bazzaz 1976) differ in the location of their roots in the soil and therefore have different access to water and nutrients. They also differ in the timing of root growth. Location of roots in different portions of the soil profile influences the pattern of leaf-water potential. For example, during sunny days in summer, leaf-water potentials in *Setaria*, which is shallow-rooted, are much more negative than those of *Polygonum*, which is deep rooted. *Abutilon* is intermediate in both rooting depth and leaf-water potential. However, the photosynthetic response to leaf-water status differs in these species in such a way that all gain carbon at a relatively high rate throughout the day despite large differences among them in leaf-water potential (see Bazzaz 1990).

In many plant species, roots also proliferate in resource-rich patches underground (Grime et al. 1986). Roots can be extended into deeper layers of the soil as the soil moisture is progressively depleted. Proliferation in resource-rich patches, changes in frequency of branching, increased branch elongation in favorable patches, and their decrease in unfavorable ones have been proposed as a sort of "foraging behavior" in clonal plants (see, e.g., Harper 1986; Slade and Hutchings 1987). Recent experimental evidence (see, e.g., Ballaré et al. 1987; Novoplansky et al. 1990) suggests that some species avoid areas where there would be interference with neighbors even before they are in physical contact or in common locations where they can contest resources. The plants seem to remotely sense the presence of potential competitors, and the response seems to be mediated by the quality of the reflected light from the neighbors.

#### *Wider Habitat Choice by Integration of Several Patch Types*

In clonal plants, physiological integration may play a major role in their response to habitat factors. Several authors have shown such integration in perennial species (e.g., Hartnett and Bazzaz 1983; Pitelka and Ashmum 1985; Salzman and Parker 1985; Schmid and Bazzaz 1987). Some authors (e.g., Bazzaz 1984; Hartnett and Bazzaz 1985) have speculated about the consequences of this integration for the perception of environmental heterogeneity and the maintenance of diversity in populations. Most studies on physiological integration have shown that translocation of photosynthate occurs largely from the older established parts of the genet to the new developing ramets (see, e.g., Marshall and Sagar 1968; Noble and Marshall 1983). In goldenrods, which have relatively short rhizomes

and therefore compact genets, severing rhizomatous connections early in the growing season resulted in high mortality of daughter ramets, but mortality declined as the severing was delayed during the season (Hartnett and Bazzaz 1983). Field experiments (Hartnett and Bazzaz 1985) have shown that connection of ramets leads to sharing of resources and equability in response among connected ramets, irrespective of the quality of the patches each may occupy. Such clonal integration may thus effectively enlarge the choice habitats available. Physiological integration in *Solidago* also reduces the impact of experimental defoliation on ramets (Schmid et al. 1988). In contrast, in *Trifolium repens*, a species with long rhizomes and spreading genet architecture, responses to neighbors are localized, growth is controlled by local conditions, and shoots appear not to be strongly interdependent (Solangaarachchi and Harper 1989). Experimental evidence shows a range of response between compact and strongly spreading behaviors within a genus (e.g., *Solidago*) (Schmid and Bazzaz 1987) as well as within a species (Solangaarachchi and Harper 1989). Physiological integration permits ramets of *Ambrosia psilostachya* to grow in saline patches (Salzman 1985). Furthermore, Salzman (1985) concluded that genotypes of this species differ in the degree of discrimination between patches of different salinity levels, suggesting the potential for the evolution of habitat selection.

Foraging behavior in clonal plants, which involves both clonal integration and proliferation in resource-rich patches, can best be illustrated in dune plants. In very nutrient-poor sand dune habitats on the Carolina coast, J. Evans (personal communication) has shown that *Hydrocotyle* usually produces spreading genets that locate their leaves at considerable distances from each other. However, in microsites with higher nutrients, the genets produce leaves in close proximity to each other. Translocation of assimilates, which can occur both acropetally and basipetally among ramets via rhizomes, enables these genets to spread widely and to reach other nutrient-containing microsites. This spread can cover remarkably large areas and allows this species to thrive in the sand dune ecosystem despite the restriction of germination sites to the moist depressions behind the foredune.

In the face of competition from neighboring individuals, a successful strategy in species with compact genets may be to have shorter rhizomes and to remain strongly integrated (see, e.g., Schmid and Harper 1985), a response that may reduce habitat choice. In contrast, a species with spreading genets may expand its growth by producing longer rhizomes, thereby reaching new habitats (Harper 1982; Pavlik 1983). Schmid (1986) has shown that pure stands of *Bellis perennis*, with spreading genets, and *Prunella vulgaris*, with compact genets, did not differ significantly in the distance between modules within genets. However, when the species were grown in competition with the grass *Lolium perenne*, *Bellis* increased its aggregation by producing shorter rhizomes, whereas *Prunella* responded by increased rhizome elongation. Furthermore, genets of *Bellis* showed an integrated response to density stress expanding little but equally in all directions, whereas those of *Prunella* expanded more toward the low-density part of the gradient.



*Actual Movement to Choice Habitats by Clonal Spread and Fragmentation*

Clones of some perennials increase the number of modules and remain connected for a long time. However, in many species, although a genetic individual may occupy a large area, the connections among ramets can break up. The production of new modules and the death of old ones may literally allow a genetic individual to move from one location to another, perhaps more favorable, one (Turkington and Harper 1979; Cook 1983; Noble and Marshall 1983). If, as is usual, proliferation occurs largely in resource-rich patches, this behavior will be a kind of habitat choice in plants and may influence the evolution of the species' life history.

Preferences for specific neighbors are known to occur among plants in nature (see Harper 1977; Aarssen and Turkington 1985; Silvertown 1987). For example, certain genotypes of *Trifolium* are associated with and perform best with certain grass species in mixed pastures (Turkington and Harper 1979) and with certain genotypes of *Lolium* (Aarssen and Turkington 1985). In the Mojave Desert, certain species occur more often with some species and less often with others than expected by chance. Apparently, in this system, species with complementary root morphologies appear often as neighbors (see discussion in Cody 1986). However, it is not known whether there are mechanisms that enhance dispersal to a location supporting species with such complementary architecture, or whether these associations result from common requirements for germination and establishment. Synchronous flowering of different species to attract pollinators collectively has been proposed but has not been convincingly documented. Other life-history events may also be timed to minimize exposure to predators, parasites, pathogens, or competitors.

Although these findings suggest that habitat choice in plants may be based on neighbor identity, negative and positive associations among plants may simply reflect underlying similarity or dissimilarity in response along resource gradients or response to correlated aspects of the habitat. Thus, species may be found together in a place simply because they have similar habitat requirements.

## TEMPORAL HABITAT CHOICE

Habitat choice in plants occur temporally as well as spatially. Life-history events are timed to coincide with the availability of necessary resources for plant growth. Seasonal as well as daily flowering phenology in synchrony with their pollinator population peaks and activity may represent a form of temporal habitat choice. The evolution of differential flowering phenology among species that compete for the services of the same pollinators may result in some sort of habitat choice (see, e.g., Parrish and Bazzaz 1978, 1979). Controls on seed dormancy and germination that maximize the probability of plant success are well studied (see Fenner 1985). The availability of enough moisture in some desert soils for the plants to complete their life cycle triggers the germination of some desert annuals (Went 1949). Great seed longevity in many colonizing species is well

known (see, e.g., Baker 1965; Bazzaz 1986). The seed-germination behavior of *Ambrosia artemisiifolia* exemplifies this response. In this species, which grows best with ample light, nutrients, and water, seeds survive in the soil for a long time but germinate in large numbers only after the site has been disturbed, the vegetation removed, and the surface soil churned (Bazzaz 1979). Disturbance generates the appropriate triggers for germination, for example, light, fluctuating temperatures, and near-ambient levels of carbon dioxide. It also signals that there is little competition at the site from winter annuals, to which *Ambrosia* is quite inferior (Raynal and Bazzaz 1975).

The evolution of secondary seed dormancy in some plants of unpredictable habitats may be another form of temporal habitat choice. Secondary dormancy prevents germination of *A. artemisiifolia* if soil disturbance occurs late in the growing season. This response may prevent individuals from experiencing a growing season too short for reproduction or death because of soil-moisture depletion. The timing of fruit ripening in some species may be synchronous with the arrival of the fruits' dispersers (see, e.g., Willson and Thompson 1982). There are undoubtedly several other mechanisms to promote the initiation of life cycles when the environment is more likely suitable for growth and reproduction.

#### PLANT ATTRIBUTES THAT LESSEN THE NEED FOR PRECISE HABITAT CHOICE

Plasticity and acclimation are important features that lessen the need for precise habitat choice in plants and may compensate for their relative immobility. Being sessile and long-lived, plants may experience a wide range of environments during their lives. Immobility may have been a force in the evolution of the observed high phenotypic plasticity permitted by the genotypes of many plants (Bradshaw 1965, 1972; Jain 1979). Acclimation, a change in phenotype with a change in the environment, may also be promoted by modular construction (see, e.g., Sultan 1987). Modules of a given individual that develop at various times during its life may differ morphologically and physiologically, depending on the prevailing environmental conditions. In essence, with these attributes, a sessile individual plant can perform in a changing local environment without having to move into a more hospitable location. Bradshaw (1965) and others have therefore described plasticity as counterpart to behavior in animals. One reaction to predictable environmental change consists of shifts in the plants' response pattern. Shifts in response to temperature have been shown to occur in many plants in relation to changing the temperatures in the field (see, e.g., Mooney and West 1964). Several colonizing winter annuals (in the Cruciferae and Compositae) form rosettes in late summer and early fall, endure cold winters, and bolt in the following summer. These individuals show clear shifts in their photosynthetic response to temperature, having much lower optimum temperatures in winter than in the summer (Regehr and Bazzaz 1979). These shifts result in high carbon gain, growth, and survivorship during the entire life of the plant. The summer annuals in this system show shifts in response to environmental factors with ontogeny. For example, seed germination, seedling growth, and the growth of mature individuals differ

predictably in their responses to changing moisture and temperature gradients during the growing season (Parrish and Bazzaz 1985).

At the population level, habitat choice may vary among genetically different individuals. The response breadth of populations made up of a large number of specialized genotypes should be greater than that of populations with smaller numbers of specialized genotypes (Van Valen 1965). But, a population with a few general-purpose genotypes (in the sense of Baker 1965) may also have an equally broad habitat choice (Lewontin 1957). If so, there is no reason to expect a positive correlation between genetic diversity and ecological response breadth. The limited experimental evidence (e.g., Garbutt and Bazzaz 1987) suggests that both types may be encountered in the progeny of a single individual.

#### HABITAT SELECTION AND COEXISTENCE IN PLANT COMMUNITIES

One consequence of differential habitat choice by species of a community may be their coexistence (the classical niche separation). Species' spatial and temporal patterns of response to environmental resources and controllers dictate the degree of sharing or competition among individuals for the resource pools of the habitat. Differential habitat selection may be a result of consistent interactions between plants leading to differentiation among genetically related individuals and closely related species. Therefore, habitat selection, in evolutionary terms, follows inexorably from differentiation and speciation.

Several mechanisms have been proposed that lead to coexistence in plant communities. Despite much debate and confusion, the issue remains open, and different mechanisms of coexistence may predominate in different communities. One view is that, during evolutionary time, populations of species have acted as reciprocal selective agents, causing a reduction in response of one or more species in the area of overlap and a narrowing of that response to produce niche differentiation and higher species diversity (Whittaker 1972, 1975, based on theoretical studies of, e.g., MacArthur and Levins 1967; May 1973). This outcome is expected in communities at or near equilibrium (late succession) in which encounters between species are consistent and occur over a long time. Several plant species are able to exist because of habitat specialization (see, e.g., Grubb 1977; Braakhekke 1980).

Another view is that of random coexistence, in which species co-occur because of chance and because of a similar response to some critical environmental resource(s)—a Gleasonian view! Other mechanisms believed to explain diversity include spatial and temporal environmental heterogeneity, unpredictable gap formation, the balance between inter- and intraspecific competition, and the resource ratios of Tilman (1982). Aarssen (1983) argued that reciprocal selection for balanced competitive ability may lead to coexistence. Although the notion of coexistence by niche differentiation (differences in habitat selection) is appealing and follows logically from selection theory (selection by biotic factors, selection by physical factors, respectively), evidence for it in plants has not been forthcoming (discussion in Connell 1980). It is also important to remember that competition

among plants is almost always of the diffuse type (Whittaker 1975 sensu MacArthur 1972), and that similarity in response on one resource gradient may be offset by differences along other resource gradients. Our experimental work over the last decade has revealed complex relationships but some discernible patterns (summary in Bazzaz 1987). In general, annual species of early successional and frequently disturbed habitats have similar, broad responses along several environmental gradients. In contrast, late successional species are less similar and narrower in response. The results also suggest that evolutionary interactions among species in the late successional community may have been important in their relatively lower overlap on certain resources axes. However, there is little doubt that in late successional communities, differences in response among species contribute to their coexistence, irrespective of whether these differences are the result of reciprocal selection (niche differentiation) or preadaptation (see Bazzaz 1987).

Plant species of the same community may show large differences in response to some aspects of their environment. For example, *Polygonum pensylvanicum*, like other members of the annual community, grows and reproduces well under a wide range of soil-moisture conditions. But, when competitors are present, the species can grow well only on wet portions of the moisture gradient. Moreover, it is usually more prevalent in wet sites in the field (see Pickett and Bazzaz 1976). This species therefore has a wide range of habitats in the absence of competitors and a refugium from them in wet habitats where the competitors do poorly or do not survive. Because of the high similarities in resource requirements among plants in a community and strong competition among neighbors, selection for use of common resources is likely to operate to increase similarity (Pickett and Bazzaz 1978), and simultaneously, selection for reduced competition for those shared resources may operate to decrease similarity among neighbors. In terms of habitat breadth, the former would increase and the latter would decrease or shift in breadth. This apparent paradox between convergent adaptation to a common environment and divergent adaptation to other members of the community has been discussed by Antonovics (1978). The maintenance of genetic diversity and a wide habitat preference for plants may be aided by high environmental variability and seed longevity in the soil (discussion in Bazzaz and Sultan 1987).

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