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2

A Neighborhood View of Interactions among Individual Plants

Peter Stoll and Jacob Weiner

2.1 Introduction

In no area of ecology is the role of space more fundamental than in the study of plant communities (Hutchings 1986; Crawley and May 1987). Individual plants are rooted in one place and their ability to move and occupy space is restricted to growth (Eriksson 1986). A plant cannot relocate from an unfavorable location to a more favorable one. Rather, it grows as well as possible where it finds itself or it dies. Basic plant biology suggests that plant–plant interactions are inherently local in nature. For example, individual plants do not experience global population density *per se*, but only interact with neighbors over restricted distances. The mobility of animals makes their spatial behavior potentially far more complex than that of plants, but, ironically, this ability to move can make the modeling of space for animal populations unnecessary in many cases. For example, because animals can "diffuse" in space from areas of higher density to areas of lower density, models based on mean spatial behavior or overall density may often be sufficient. Because a plant's ability to move is quite restricted (except during dispersal), local conditions are of much greater significance to plants than to animals. When feeding fish in a tank, it does not matter where on the water surface one places the food, because the fish will come to it. But when watering or fertilizing the garden one must make sure that the resource comes close to the plant – if one waters only half the garden the other half will not obtain sufficient water. Thus, while it is possible that the spatially averaged behavior of individuals may sometimes provide sufficient information for modeling some processes within populations and communities, this is much less likely to be the case for plants than for animals.

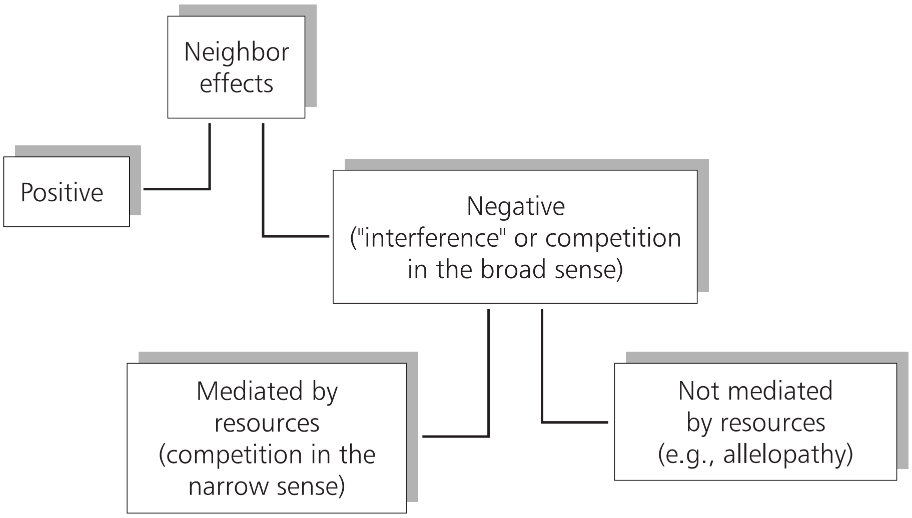

Figure 2.1 Classification of neighbor effects in plants.

In this chapter, we discuss the role of local spatial processes in plant communities, focusing on the concept of an individual's neighborhood. We emphasize competition among plants because it is thought to be one of the primary factors determining plant performance in the field and has therefore been the most studied ecological interaction in plant communities. However, the neighborhood approach taken here could also be applied to other ecological interactions, such as herbivory or pollination. Our goal in the context of the present volume is to foster much-needed communication between theoreticians and empiricists in ecology by providing modelers with an empirical perspective on local plant interactions, which we hope will be of use in building models and developing modeling techniques.

2.2 Competition Mechanisms

The study of interactions among plants in natural communities presents the ecological researcher with daunting complexity. The mechanisms by which plants interact are understood only at a general nonquantitative level (Bazzaz 1990), although we can be encouraged by a few robust patterns at the population level, such as the relationship between density and biomass (Silvertown and Lovett Doust 1993). In discussing interactions among plants, our conceptual framework follows that of Harper (1977). Plants are influenced by neighbors, and we call all such interactions "neighbor effects" (Figure 2.1). While many of these effects are negative ("interference" *sensu* Harper or competition in the broad sense), some are positive. Positive neighbor effects, such as protecting neighbors from excessive solar radiation and resultant water loss and providing mechanical support and

Box 2.1 Positive neighbor effects

Plants can have positive as well as negative effects on their neighbors. The classic example of positive neighbor effects is that of "nurse plants" in arid systems (e.g., Franco Pizana *et al.* 1996). Some desert plants can only establish themselves in close proximity to a larger plant, usually a shrub, because the shade of the larger plant provides protection from the intense solar radiation and resultant heat and transpiration that a seedling otherwise would experience. Plant establishment in deserts is largely determined by the negative effects of a superabundant plant resource – solar radiation – for which plants in other environments compete. There has been increased interest in positive plant–plant interactions. Below are two examples.

During drought periods, sugar maple (*Acer saccharum*) demonstrates "hydraulic lift," nocturnal uptake of water by roots from deep soil layers that is released from shallow roots into upper soil layers (Dawson 1993). Neighboring plants use from 3–60% of the hydraulically lifted water supplied by sugar maple trees. Hydraulic lift may not be limited to arid or semiarid environments where chronic water deficits prevail and might be important in relatively mesic environments when subjected to periodic soil water deficits.

Facilitation by neighbors may be quite common in wetlands. For example, emergent wetland plants often alleviate the effects of anaerobic soils on root respiration by transporting oxygen below-ground through continuous air spaces (aerenchyma) within the plant. Oxygen leaking from the roots into the rhizosphere may oxidize minerals in the soil or become available to other plants. Callaway and King (1996) investigated the ability of cattail (*Typha latifolia*), a widespread wetland plant with aerenchymous tissue, to aerate sediments and affect the growth of two neighbors, a willow (*Salix exigua*) and forget-me-not (*Myosotis laxa*). At lower temperatures, rooted willow cuttings survived only when planted with cattail and forget-me-not transplants grew significantly larger when planted with cattail. At higher soil temperatures, however, there was evidence of competition rather than facilitation.

protection from herbivores, may be more common than previously thought (Box 2.1; Aarssen and Epp 1990). In some ecosystems, particularly those of nutrient-poor or other extreme environments such as salt marshes (e.g., Bertness and Shumway 1993), positive effects may be as important as negative effects. It is important to remember that the net effect of one plant on another is the sum of positive and negative effects (Berkowitz *et al.* 1995). Because the relative importance, timing, and spatial structure of the numerous positive and negative mechanisms may vary, it is not easy to summarize the effects plants have on one another by using simple coefficients. Chapter 3 gives an overview of how plant ecologists have tried to obtain this information and the results accumulated so far.

Negative neighbor effects are usually more important than positive ones, because all plants require basically the same resources. If plants are growing in close proximity, it seems almost inevitable that they will eventually compete for some of these resources. Negative neighbor effects can be divided into those mediated by resources (competition in the narrow sense) and those mediated by other mechanisms or organisms (Figure 2.1). Indirect neighbor effects include changes in environmental conditions such as temperature, humidity, and wind velocity, and attraction or repelling of animals, which thereby affects predation, trampling, etc. (Harper 1977). Most plant ecologists consider competition for resources to be generally more important and more likely to be predictable than other neighbor effects, but there may be communities in which other mechanisms such as allelopathy play a major role (Rice 1984). Quantifying mechanisms such as allelopathy in a field situation is a distant goal, but ecologists have begun to study resource-mediated competition quantitatively (Tilman 1982, 1988; Fitter 1986; Keddy 1991).

It is important to distinguish between the effects an individual plant has on resources and how that plant responds to the preemption of resources by its neighbors (Goldberg 1990; Tremmel and Bazzaz 1993). Thus, the intensity of competition is determined by two processes: (1) the effects of neighbors on resource availability and (2) the ability of individuals to tolerate or compensate for these effects through plasticity and other “behavioral” responses (Box 2.2). Plasticity is the ability of a single genotype to develop into different phenotypes in different environments (Bradshaw 1965). For example, plants can change their growth form in response to neighbors – for instance, by putting more effort into height growth at the expense of lateral growth when they are shaded (Schmitt 1993; Schmitt and Wulff 1993) or can “expect” to be shaded in the near future (Ballaré *et al.* 1990). Resource acquisition depends on the placement of plant parts in relation to resources and the ability to take up these resources when they are encountered. The ways plants obtain resources, use them to obtain more resources, and consequently make these resources unavailable to neighboring plants, and the ways plants respond to reduced resource levels caused by neighbors can be considered the mechanisms of resource competition (Bazzaz 1990). The effects of plants on each other in the field are primarily the result of such mechanisms.

Box 2.2 Plant behavior: Clonal growth, foraging, and division of labor

Higher plants are composed of a repetitive branched system of units (e.g., ramets, modules), each consisting of a segment of stem, leaves, and axillary buds (meristems) with the potential to form a new unit. The whole shoot system is a population of such units that may be united in sharing a common root system. This unity is often lost during clonal growth – lateral spread by "vegetative reproduction" – of plants such as strawberries (Figure 2.2). When connecting horizontal parts of the shoot systems (stolons or rhizomes) die and rot away, rooted, physiologically independent offspring are left (Harper 1977). One consequence of the modular construction of plants is that leaves and root tips are located on branches that project them into habitat space (Bell 1984; Schmid 1990; Hutchings and de Kroon 1994). The architecture of resulting branching patterns can be described by variables such as spacer length, branching frequency, and branching angles. Morphological plasticity refers to changes in these architectural parameters in response to the plant's environment.

In an analogy to foraging in animals, Slade and Hutchings (1987a) defined "foraging" in plants as "the process whereby an organism searches or ramifies within its habitat in the activity of acquiring essential resources." According to this analogy, leaves and root tips (resource-acquiring structures) are "feeding sites," which are located at the ends of "spacers" (i.e., horizontal branches). Shortening spacers and increasing branching in response to high local abundance of resources in order to place more feeding sites into resource-rich microhabitats should increase resource acquisition from the habitat and enhance plant fitness (Hutchings 1988).

Spacers not only place feeding sites within the environment, they also perform bidirectional transport processes, thus providing intraclonal specialization and cooperation analogous to the economic principle of spatial division of labor between shoots in different patches within the environment (Stuefer *et al.* 1994; Stuefer 1995). Water provided through stolons from shoots growing in shaded microhabitats may be delivered to shoots growing in full sunlight, while shoots in full sunlight may provide assimilates to shoots growing in areas with lower light levels (Evans 1991, 1992).

Simply put, resource-mediated competition occurs when individual plants consume resources which are therefore not available to other individuals. If the lack of a resource limits the growth of an individual, then that individual has suffered from competition. One important difference between plants and animals is that animals of different species may have varying degrees of overlap in the resources they need. In some cases, two different animal species may use few, if any, of the same resources. Plants,

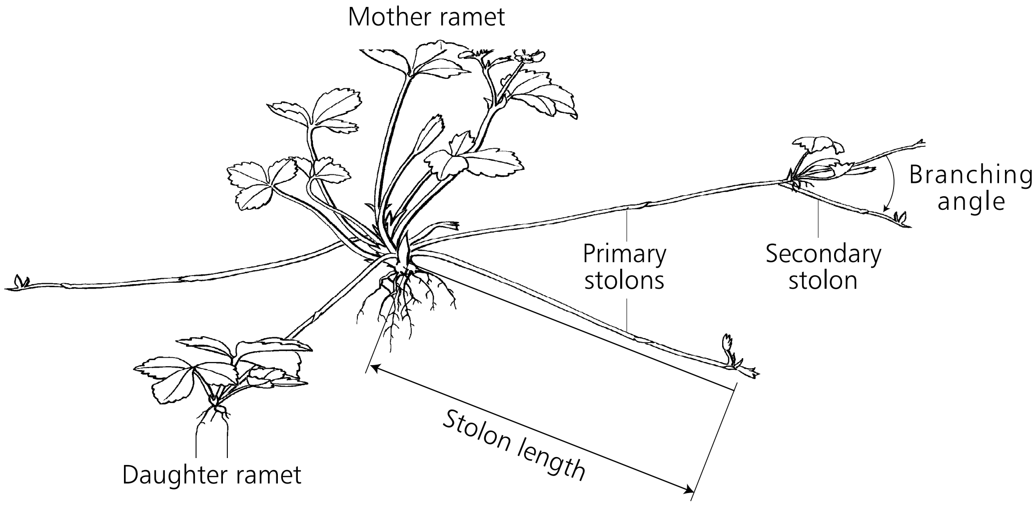

Figure 2.2 A strawberry (*Fragaria* sp.) as an example of clonal growth. The genetic individual ("genet") consists of numerous physiological/morphological individuals ("ramets") that may exchange resources if they remain connected or live independently if connections (stolons, i.e., horizontal shoots) are no longer functional. Clonal growth by plants can be seen as analogous to movement by animals.

on the other hand, all need the same basic resources: physical space, light, carbon dioxide, water, oxygen, and a suite of mineral nutrients. Thus, the ability of plants to avoid competition through niche differentiation is quite limited, although plants can use resources in different proportions (Tilman 1982), at different depths in the soil (Parrish and Bazzaz 1976, 1985), or at different times of the year (Eissenstat and Caldwell 1988).

Ecologists have begun to develop general models for local depletion and renewal of soil resources (Fitter and Stickland 1991; Fitter *et al.* 1991; Huston and DeAngelis 1994; Leadley *et al.* 1997), but it is not clear how far such generalizations can take us. Light, for example, is so fundamentally different from other resources that it is difficult to imagine how it can be treated similarly to soil resources. Light is unidirectional, cannot be stored (although the products of photosynthesis can), and does not diffuse from one point in space to another. In this sense, light as an energy source is inherently local: a plant cannot benefit from light that it does not intercept. Moreover, because plant movements are so limited, a plant's ability to move to areas of greater light availability is very restricted, although one can consider plants to be "foraging" through their growth patterns (Slade and Hutchings 1987b).

Although mineral nutrients are not unidirectional or renewable in the same sense as solar radiation, the diffusion of nutrients through the soil appears to be extremely limited. For example, plant roots can deplete local

Box 2.3 Competition at the microscale: Distribution and dynamics of neighboring plant roots

Although roots are difficult to observe, especially under field conditions, progress is being made. Caldwell and his coworkers (Caldwell *et al.* 1991, 1996) have used various techniques to investigate the deployment of roots in relation to neighboring plants and the availability of soil resources, which may vary both in space and time. For example, they found that root proliferation of the sagebrush (*Artemisia*) was considerably influenced by the presence of different grass species (*Agropyron* or *Pseudoregneria*). Root density of the shrub was generally two to three times higher with *Pseudoregneria* than with *Agropyron*, and there was a greater tendency for the roots of the shrub and *Pseudoregneria* to segregate (i.e., to avoid one another). Caldwell *et al.* (1991) interpreted these patterns as interference at the level of individual roots but only speculated about the possible mechanisms, such as resource pre-emption or allelopathy. In a subsequent experiment, Caldwell *et al.* (1996) found that shrub and grass roots tended to avoid each other at a scale of millimeters to centimeters, although there was no direct evidence of resource competition. While resource competition cannot be entirely dismissed, other mechanisms may have contributed to the species-specific relationships between shrub and grass roots. Growth inhibition of roots following contact with roots of other plants has been shown (Mahall and Callaway 1992; Krannitz and Caldwell 1995; Huber-Sannwald *et al.* 1996), and Caldwell *et al.* (1996) conclude that such species-specific and sometimes even genotype-specific responses strongly suggest a recognition mechanism.

nitrogen, which can diffuse from areas where it has not been depleted, but this occurs over very short distances and at the local level of neighboring fine roots (Box 2.3). Water is perhaps the most diffusible of plant resources, but the distances involved are still quite limited relative to the size of the plant. For example, in an experiment where water was supplied only to the outer root system (more than 10 cm from the center) of branch units of bunchgrass (*Bouteloua gracilis*) in containers, growth was significantly less than when water was applied only to the central root system (Hook and Lauenroth 1994).

Dispersal is one way that plants "move" extensively, and seeds can sometimes move great distances via wind and water, or with the help of animals. One function of dispersal may be to escape local competition. However, most studies show that, by far, most seeds end up very close to the mother plant. Seed dispersal can be modeled as a diffusion process, with fewer and fewer seeds at increasing distances from the plant (e.g., Pacala *et al.* 1996). Although long-distance dispersal is quite rare, it may be extremely important for plant community dynamics. Plant species diversity, for example, may often be limited by dispersal (Ricklefs and Schluter 1993; Tilman 1997). The few seeds that are dispersed far from their mother plant – that is, those that escape from the maternal plant's neighborhood – may be able to escape mortality due to seed predators (Janzen 1970) or diseases (Augspurger 1984) concentrated near the mother plant. We can think of plants interacting at a local scale as they survive and grow, and subsequently experiencing a more mobile phase during propagule dispersal.

2.3 Moving from the Population to the Individual Level

Because of the local nature of plant interactions, analysis and modeling of plant–plant interactions have moved from "mean-field approximations" toward explicit modeling of local interactions. Until the mid-1980s the study of density dependence focused on mean plant behavior (Bleasdale and Nelder 1960; Watkinson 1980; Vandermeer 1984). However, there has been an increase in the study of what one could call local density dependence, that is, the study of the performance of individual plants as a function of their local competitive conditions. As is often the case in ecology, models of local competition have been less successful in accounting for variation in the observed phenomena in the field than in stimulating new ideas and approaches to the study of plant–plant interactions, and more questions have been raised than have been answered. It has been demonstrated that

- plants do interact locally;
- local crowding reduces plant growth, reproductive output, and probability of survival;
- the effect of neighbors attenuates with distance (although the nature of this attenuation is not well understood);
- beyond a certain distance plants have no detectable effect on each other.

For example, Tyler and D'Antonio (1995) showed that, for seedlings of the shrub *Ceanothus impressus*, both survivorship and growth increased with increasing distance from near neighbors. Their study site was a burned area, and disturbances such as fire might preclude competition by releasing a flush of nutrients or by reducing biomass and thereby diminishing the consumption of resources. Thus, even after disturbance, when some resources are apparently abundant on a large scale, competition for resources may be important in determining small-scale patterns of seedling growth and survival. Survival of seedlings was reduced by the presence of neighbors up to a distance of 20 cm. More distant neighbors no longer had an effect on survival but still reduced growth. There are numerous studies that demonstrate negative neighborhood interactions (see Chapter 3). However, information on the relative importance of different mechanisms in different environments and evidence for the importance of the observed effects for population or community processes are rarely available.

2.4 What is a Plant's Neighborhood?

The study of local interactions begins with the question of what "local" means. We define a competitive neighborhood as an area within which a plant can be affected by local factors, such as the abundance of neighboring plants. There are two different approaches to the definition of a neighborhood. In one approach the neighborhood is defined as a patch of space within which plants interact. Interactions do not occur between patches, and all individuals within a patch can potentially interact. This framework comes from the study of environmental heterogeneity and has been further developed in the context of patch dynamics (Pickett and White 1985). Although such an approach has the virtue of simplicity, most plant ecologists find it insufficient to capture the spatial dynamics of plants. In contrast, a "plant-centered" view of neighborhoods does not aggregate all individuals within a patch of space but lets the individual define the neighborhood, usually thought of as a circular area around the individual. The study of local interactions among plants has moved in the direction of plant-centered neighborhoods.

In an ecological perspective that emphasizes plants' local neighborhoods, a major goal would be to describe the performance of a plant (its growth and reproductive output) as a function of the plant's genotype and local environment, broadly defined to include neighboring plants and other organisms. We are far from being able to describe such a function. In many studies, environmental heterogeneity, such as local variation in soil quality (Lechowicz and Bell 1991), seems to be more important than the local abundance of competing plants (Mitchell-Olds 1987). The question for modelers becomes, What would be an adequate description of a plant's neighborhood for a specific ecological purpose or research problem?

In the simplest plant-centered neighborhood approach, a neighborhood is defined by a radius from an individual plant's center, and the number of neighbors of different species within the area defined by the neighborhood radius is a measure of the local density. This approach has been extensively developed by Pacala, Silander, and their coworkers. Starting with populations of a single species of annual plant (Pacala and Silander 1985; Silander and Pacala 1985), they progressed to two-species models (Pacala 1986, 1987; Pacala and Silander 1987) that were fitted to field data (Pacala and Silander 1990). Predictors of individual plant performance, such as survival, growth, and reproduction, are functions of the number of neighbors in the neighborhood – a circular area around a subject plant circumscribing all other individuals that interact with the subject plant. In Pacala and Silander's models, the positions and sizes of neighbors within the neighborhood are not considered. They argue that when the "optimal" neighborhood size (i.e., the neighborhood radius of the circle that explains most of the variability in performance) was determined by statistical fitting, the number of neighbors within the neighborhood alone had almost equal predictive power as more detailed and complicated models. The assumptions of this approach are that the neighborhood can be considered internally homogeneous and that individuals of the same species can be considered equal, independent of their size. If these assumptions hold, then modeling and analyses of plant neighborhoods are quite tractable. In apparent contradiction to the emphasis on spatial dynamics in the recent literature (Durrett and Levin 1994b; Pacala and Deutschman 1995) and in this book, Pacala and Silander's model collapses into a mean-field model (Pacala and Silander 1990). This may be due to the fact that their local neighborhood model differs only in scale (local) and location (plant-centered) from mean-field models of density dependence (S. Thomas, personal communication). Pacala and Silander's local density model is just that: neighborhoods are defined around individuals and the local density (in the simplest sense, the number of individuals) is the independent variable.

Neighborhood competition studies have been criticized recently for several reasons. First, some researchers have questioned the implicit assumption that competition among nearby individuals is the primary determinant of observed dynamics. For example, Ellison *et al.* (1994) cite theoretical and experimental evidence showing that intrinsic variation in plant growth rate alone can give rise to hierarchical distributions of biomass or other metrics of plant size. Second, the statistical analysis of local competition is fraught with problems. For example, in most spatial models of plant population dynamics, plants are represented by mathematical points in space that occupy no area. For rosette-forming plants like *Arabidopsis*, individuals with a large diameter will necessarily have fewer neighbors than those with a small diameter when plants are considered as points and neighborhoods are defined by a fixed radius. A plant with a tight rosette of leaves at its base cannot have a neighbor above ground within the radius of the rosette itself. Thus, it is then unclear whether a particular individual is small because it has many neighbors or has many neighbors because it is small. This can be seen as another example of the general problem that it is usually inappropriate to look at plant performance (e.g., size) at time t as a function of neighborhood conditions at time t because these two quantities are not statistically or inferentially independent. Rather, we should take a dynamic perspective and try to look at performance over the period t to $t + \Delta t$ as a function of neighbor conditions at time t. By including appropriate controls and alternative hypotheses in replicating Silander and Pacala's (1985) experiment with *Arabidopsis*, Ellison *et al.* (1994) concluded that neighborhood competition significantly affects population dynamics in plant monocultures because neighbors impair target plants' biomass, growth, and fecundity (relative to plants grown in the absence of competition). However, in addition to the expected effects on fecundity mediated by biomass, there were also neighbor effects on plant fecundity that were independent of the effects on plant shape and biomass. This suggests that we cannot always infer fecundity from plant size alone, which presents more obstacles to the development of neighborhood models of plant performance.

Because of the indeterminate, modular nature of plant growth and the resultant plasticity in plant size, which means that a neighbor may be a tiny seedling or a huge adult, many researchers consider the number of neighbors alone an insufficient measure of local crowding. Therefore, several researchers have attempted to describe the competitive neighborhoods of plants more fully by looking at the distance and size as well as the number and species of neighbors. Some researchers have adopted a more complete physical *Ansatz* to describing a plant's neighborhood: the effect of a neighbor is proportional to its size and decreases with the square of its distance from the subject plant (Weiner 1984). In such models different species can still have different per-unit-biomass effects through the use of competition coefficients. The amount of variation in individual plant performance that such models can "explain" ranges from nearly 0% to almost 90%, depending on the model, the species, and the environment (Bonan 1993; Hara and Wyszomirski 1994). The amount of variation accounted for is usually quite low, possibly due to other factors such as genetic variation and microsite heterogeneity. For example, from 75 neighborhood analyses in 20 manuscripts Bonan (1993) derived an average of $42\% \pm 28\%$ (mean ± s.d.)

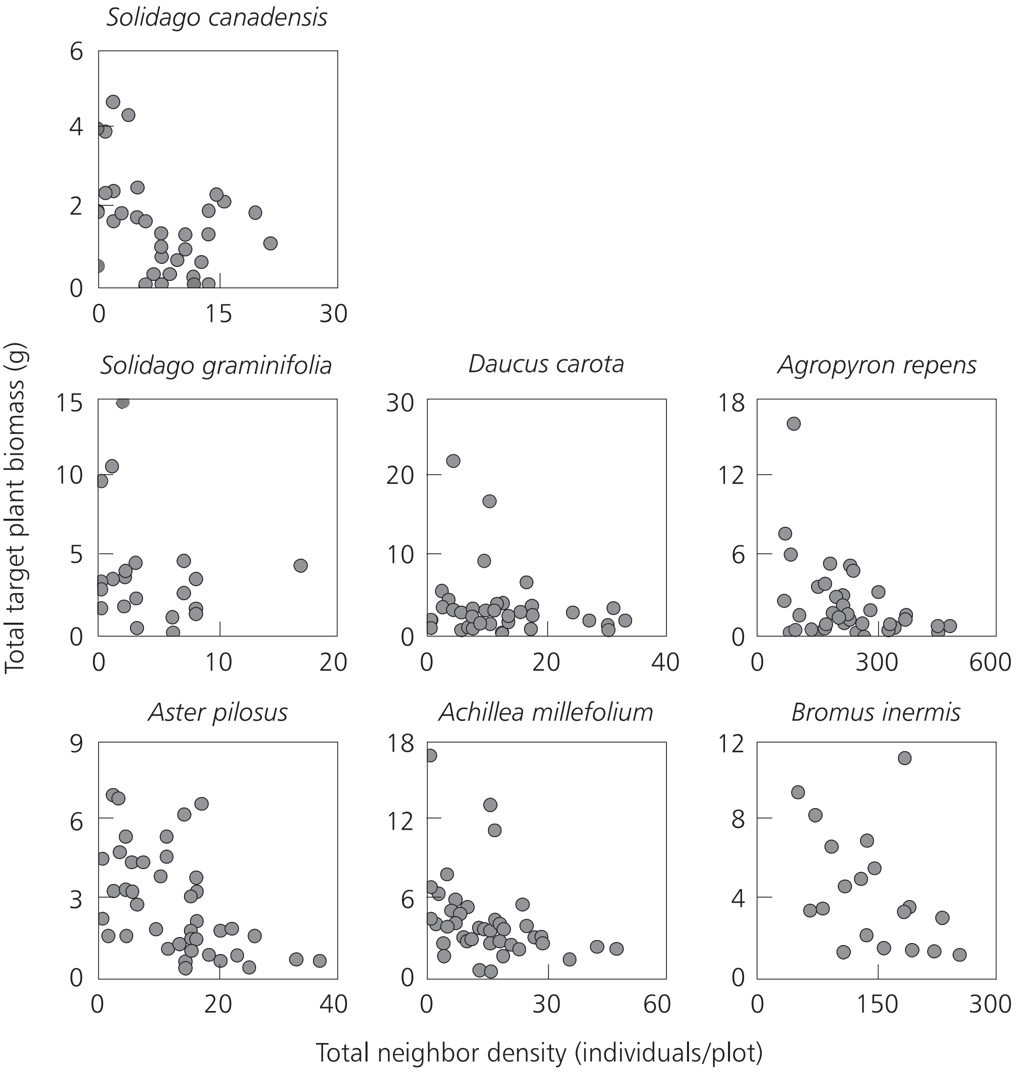

Figure 2.3 Biomass of target *Solidago canadensis* individuals versus local density for several species of neighbors. *Source*: Goldberg (1987).

of accounted-for variation. Sixty percent of these analyses accounted for less than half of the total variation in individual plant performance. These figures roughly correspond to an effect size of competition of 34% ± 5% (mean ± 95% confidence interval) given for producers in a meta-analysis of 73 studies (Gurevitch *et al.* 1992).

The relationship between plant performance (e.g., growth or size) and the abundance of neighbors is often triangular (see Figure 2.3), suggesting that local competition is more a limiting condition than a direct determinant of plant performance. When neighbors are very abundant, plants will be small; but when neighbors are scarce, plants can be either large or small. This type of relationship suggests that either our measures of local competition are inadequate or local competition is just one of many factors determining individual plant performance. When local crowding is severe, it limits plant growth; but when local crowding is not so severe, plant growth is often limited by other factors in the local environment, such as soil quality or water availability.

Because plant growth is indeterminate and modular, leading to huge plasticity in plant size, and because all plants have basically the same requirements, several researchers have proposed that the size or biomass of neighbors is perhaps more important than their number or species. Size is thought to be an important determinant of competitive ability (Keddy and Shipley 1989). If neighbor size is important, equal per-unit-biomass effects of neighbors is the appropriate null model for comparing the effects of different species of neighbors on a target species (Goldberg and Werner 1983). Of course, different species may have different per-unit-size effects, but the size of a neighbor may be the single most important factor determining its effect on another plant. Although some researchers think that an emphasis on the size of neighbors rather than their species may be a useful first approximation for describing and modeling neighborhoods (whereas other researchers think this would be "throwing out the baby with the bathwater"), even modeling size effects alone is not as straightforward as it might seem at first. The relative size of neighbors with respect to a target plant is often as important as their absolute size, because competition among plants is usually "size asymmetric," that is, larger plants have a disproportionate (for their relative size) effect on smaller plants. The inclusion of size asymmetry can result in a marked improvement in the performance of neighborhood models of competition (Thomas and Weiner 1989).

Recent work in forest ecosystems (Pacala *et al.* 1996) demonstrates how useful a neighborhood approach can be when combined with mechanistic models of resource competition, as long as a balance between the level of detail and generality can be found that meets the basic design criteria of simplicity, observability, and biological realism. However, this balance can only be found if field methods, statistical estimators, and model structure are designed simultaneously to ensure that parameters can be estimated from data collected in the field (Pacala *et al.* 1996). Many plant ecologists believe that such mechanistic neighborhood models are much more promising than earlier, purely phenomenological models.

2.5 Challenges for a Neighborhood Perspective of Plant Interactions

Another problem in developing a neighborhood-based view of plant–plant interactions is that the location of an individual, and often the individual itself, usually is not easy to define. In certain cases where plants have an erect main stem, an individual's location can be adequately described as a point in two-dimensional space (Stoll *et al.* 1994). However, many plants do not have such a straightforward location or identity. Plants are often clonal (Figure 2.2; Box 2.2; see Chapters 3 and 4) and it is their open, "modular" architecture (Schmid 1990) that enables them to respond to their local environment by "adjusting" birth, growth, and death of modules (Box 2.4). The modules (also called ramets if they are capable of living on their own) can remain connected through horizontal structures, and the extent and importance of transport processes and possible sharing of resources among modules are much debated in the literature. However, in contrast to modules such as branches of trees, the ramets of clonal plants are also capable of living independently when the connections become severed; indeed, in many clonal plants the loss of connections after ramets have been placed and established seems to be the rule. Thus, clonal plants (and to some degree non-clonal plants) have a hierarchical structure in which the genetic individual (genet) is made up of smaller physiological units (ramets).

In the field it is usually quite difficult, if not impossible, to identify genets: what we see are ramets. In a ramet-based neighborhood view, many of an "individual's" neighbors may be (genetically) the individual itself. Severe competition among genetically identical individuals decreases Darwinian fitness. From a sociobiological viewpoint, one can ask if individuals are able to recognize "themselves," and there is evidence that plant roots react differently to contact with genetically identical roots than to roots of other genets (Huber-Sannwald *et al.* 1996). It could be that such recognition is quite limited, in which case we could build hierarchical neighborhood models with genets growing by iterating and placing ramets that maintain their connections for a given amount of time or under given conditions (Bell 1986). In fact, clonal growth can make the description of growth easier to the extent that we can describe size simply as the number of ramets, either considering all ramets equal or having just a few size classes. The modeling of clonal growth can benefit from a neighborhood perspective (e.g., Cain *et al.* 1995). For example, most models of clonal spread are based on simple rules for internode length, branching frequency, and branching angle, and these parameters are assumed to apply to a whole

Box 2.4 Demography of plant parts and neighborhood interactions below the individual scale

It has been shown that modules of trees, like ramets of herbaceous plants, respond to their local environment (Jones 1985; Franco 1986; Jones and Harper 1987a, 1987b; Franco and Harper 1988). These studies used the demography of modules (see also Maillette 1982a, 1982b) to describe tree growth. The most comprehensive approach is to combine the study of allocation patterns with that of the demography of modules (Küppers 1994). It should be noted that even if modules within branches respond to their immediate local environment, branches within trees may still be integrated (Sprugel *et al.* 1991). For example, within shaded branches of trees that had some branches in full sunlight yearly growth increments were smaller than growth increments of branches of control trees growing completely in the shade (Stoll and Schmid 1998). This difference was interpreted as correlative inhibition, for example, resource allocation to branches in the sun that therefore inhibited the growth of shaded branches. Evidence for such an interpretation was demonstrated in pea plants (*Pisum sativum*) by Novoplansky *et al.* (1989). When they grew two connected shoots in different light conditions, the shaded shoot was inhibited and eventually even withered and died. It elongated and became etiolated only when the shoot in the stronger light was removed.

We know of only one model of plant competition that explicitly includes plasticity at a modular level (Sorrensen-Cothern *et al.* 1993). Including plasticity through modular foliage in their spatially explicit model of competition fundamentally changed the population structure. For example, if trees were equipped with plasticity through modular foliage, the whole stand had a greater leaf area index and individuals grew taller than without plasticity.

genet (Sutherland and Stillman 1988). A more recent view is that the general rules are not completely fixed for an individual, but vary locally in response to local conditions. A parallel can be drawn between the growth of individual plants responding locally to the environment and foraging animals (Hutchings and de Kroon 1994). The point here is simply that even if the individual plants we see above ground are genetically and sometimes physiologically parts of larger organisms, behavior can, to some degree, be explained by local neighborhood conditions. The definition of an individual and of its neighborhood is best determined in the context of the scientific question being asked.

The difficulties of spatially delimiting plant neighborhoods are made much worse because the size of a plant increases by many orders of magnitude during its growth from a seedling to a reproducing adult. Thus, we would expect the area in which a plant experiences and is experienced by neighbors to increase accordingly. Most neighborhood studies investigate plant performance over one time interval with one neighborhood definition. It is difficult for many field ecologists to imagine such an approach yielding sufficient information to enable us to predict the dynamics of the system. In many cases, it may be necessary to model plant growth over several intervals during which the neighborhood grows along with the plant. Therefore, we predict better performance of future models with dynamic neighborhoods as opposed to the *a priori* fixed neighborhoods used in cellular automata.

2.6 Suggestions for Modelers

We have taken an empirical approach in an attempt to communicate to theoreticians some of what we empiricists think are the essential aspects and central questions in the development of a neighborhood approach to interactions among plants. There has been an increasing emphasis on bridging the gap between modeling and empirical work in ecology, although the tendency for the two to go in totally different directions is still very strong (Weiner 1995). In the spirit of building this much-needed bridge, we make the following suggestions to our theory-oriented colleagues.

- Models are more likely to be useful in solving empirical problems if they are directed at observed patterns in nature rather than at very general, abstract questions (Grimm 1994; Weiner 1995).
- Each model should have a clear purpose. The model should not be the object of study, but merely a tool. If the "occupational hazard" of being a field ecologist is thinking that everything is important and therefore must be included, the occupational hazard of theoreticians is building general, abstract models without a clear goal other than exploring the dynamics of the model itself. The question of how to simplify the model (or, in other words, how to determine what can be ignored) is closely linked to the model's goal. If the purpose of a model is to predict community dynamics (i.e., the abundance of different species over time), then what is essential for the model may be very different from what is essential in a model concerning persistence (how many species can coexist, independent of their specific abundances) or the genetic diversity of some species.

Perhaps the most important potential role for modeling in ecology today could be to help direct empirical research. At this point in the development of ecology, models may be most useful not for what they can deliver in the near future in terms of prediction, but for elucidating the sorts of information that are most needed if we are to build models that can do what we want them to do. Models can help make empirical research more strategic and less haphazard. If a formal, systematic theoretical framework can serve as an alternative to trial and error in exploring empirical "parameter space," advances in mathematical theory will have contributed much to what future generations of scientists will (we hope) call the emergence of a mechanistic and predictive ecology.

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