

Positive Interactions and Interdependence in Plant Communities

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by

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This book is dedicated to Bruce Mahall

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CHAPTER 1

INTRODUCTION

Over the last 50 years there has been profound growth in the discipline of ecology. To name just a few advances, ecologists have demonstrated, quantified and explained global changes in temperature, developed elegant mathematical models for competitive interactions, constructed wonderfully complicated food webs, integrated soil biota into aboveground processes, and experimentally explored the intricacy of indirect interactions among many species in communities. Some things, however, have not changed very much. This book was written in part to address a surprisingly static idea; the individualistic conceptual paradigm for plant communities. This is the perspective that plant communities are solely the product of population phenomena, and therefore are assemblages of individual species merely because they share adaptations to particular abiotic conditions (Gleason 1926). This leads to the conclusion that plant communities are simply a handy typological construct. In this book I argue that plant communities are not simply suites of species that happen to be dispersed to and adapted to the same biotic conditions at a given place. I argue that many if not most plant communities have fascinating interdependent characteristics, with some species creating conditions that are crucial for the occurrence and abundance of other species.

Most ecologists are not card-carrying members of either individualistic or interdependent guilds, but our perception of plant community organization, and the way we conduct research, is affected by a historical dichotomy with lingering and powerful heuristic impacts; the dichotomy of the individualistic versus organismal nature of plant communities (Clements 1916, Gleason 1926). For example, the legacy of Gleason's triumph lives on in almost all ecology textbooks, neutral theory (Hubbell 2001, Whitfield 2002) and assembly rules (see Lortie et al. 2004). The fundamental thesis of this book is that the current individualistic model is inadequate in the light of the last 20 years of empirical research on facilitation and indirect interactions. This is because these interactions demonstrate that plant communities frequently contain plant species that would not be present at all, or that would be present at much lower abundances, if it were not for the presence of other plant species (Callaway 1995, 1997).

The individualistic view of plant communities has led to very successful research on the importance of the abiotic environment and

competition as factors structuring plant communities. Negative interactions - predation, competition for resources and allelopathy - have been central to the study of ecology and evolution. However, it has become clear that organisms can greatly enhance the performance of their neighbors as well as modify the environment in ways that benefit other species.

Positive interactions among plants, or facilitation, occur when the presence of one plant enhances the growth, survival, or reproduction of a neighbor. Much like the way the term “competition” is used in the literature, the term “facilitation” is also used in a loose manner, and facilitation may occur in concert with negative, positive, or neutral reciprocal responses from neighbors. Facilitation does not have to be mutualism, an interaction where both participants gain (+,+), but some experiments have shown mutualistic bi-directional facilitation. In some cases facilitation may occur as commensalism (+,0) in which one species benefits from another, but does not affect it in return. In a review of interaction types Schoener (1980) noted that “[documented] examples of commensalism are relatively rare”; and commensalism among plants remains relatively unstudied. However, this rarity may be an artifact of scientific disinterest rather than ecological frequency. Futuyma (1979) suggested that commensalism may be so common “that we often do not notice it”. Commensalism may be common, but the empirical research explored in the following chapters indicates that facilitation probably occurs most often as a positive effect of one species on another with a reciprocal competitive effect from the species receiving the benefits on its benefactor (+,-).

It is important to grasp the broad semantic usage of the term facilitation. As one colleague has put it, “I hate the word facilitation because why would a plant make it easier for a competitor to grow next to it”? My colleague’s problem is that of perceived intent, as if plants were trying to befriend their neighbors. The word “facilitation” means nothing like this. The nuances of language are complex and facilitation, like most words, suffers from subtleties in its gestalt. The term facilitation describes a process and not purpose. The fact that seedlings of saguaro cacti occur almost exclusively under shrubs and trees in the Sonoran Desert is almost certainly a by-product of the changes the shrubs and trees create in the environment simply because the shrubs and trees exist, not because they are altruistic. By analogy, in another (+,-) interaction gazelles try hard not to be eaten, but they have a strong positive effect on lions and cheetahs anyway. Like the beneficial effect of gazelles on lions, positive interactions among plants are produced simply by benefactors with characteristic effects on the abiotic and biotic environment that other organisms can utilize.

Just like the suite of different mechanisms we group into the term “competition”, it is not necessary to identify the two-way interaction signs or the precise mechanisms behind a particular facilitative interaction to show that facilitation occurs. Furthermore, casual semantics and unknown mechanisms do

not diminish the fundamental conceptual importance of facilitation for community theory.

For over 50 years most plant ecologists have accepted the notion that the distribution of plant species, and their organization into groups or communities, is determined individually, that is by the adaptation of each species in a “community” to a particular abiotic environment, highly stochastic dispersal events, competition among these similarly adapted species, and the disruption of adaptive and competitive distributions by consumers. Definitions of the “individualistic” paradigm of plant community organization can be controversial (see Nicolson and McIntosh 2002), but have emphasized “the fluctuating and fortuitous immigration of plants and an equally fluctuating and variable environment” (Gleason 1926). Moore (1990, see Nicolson and McIntosh 2002, Chapter 6.9) re-phrased the individualistic concept as “vegetation as an assembly of individual plants belonging to different species distributed according to its own physiological requirements as constrained by competitive interactions.” Even a loose definition of facilitation suggests something fundamentally different than this. If the presence of one species can *increase* another species’ fitness, or the probability that another species will occur in the same place, plant communities cannot be individualistic. In the last 20 years, hundreds of peer-reviewed papers have been published on the positive effects of plants on each other. These papers implicitly challenge the adequacy of a strict definition of the theory of individualistic plant communities (Gleason 1926), one of the most basic and widely accepted conceptual models in ecology, as a foundation for understanding how groups of plant species are organized. The implications of rethinking plant individualism go beyond academic quarreling; if plant communities are even just a little less individualistic than we have thought, the conservation implications are profound (see Byers et al. 2006, Padilla and Pugnaire 2006). Interdependence in plant communities means that the loss of some plant species will have important *negative* effects on others.

Most general conceptual models of community structure are either explicitly or implicitly based on competition, and this perspective has a historical legacy that is intertwined with individualistic theory. After the trouncing given to holistic community concepts in the 1950’s by John Curtis (1959) and Robert Whittaker (1951, 1953, 1956), espousal of ideas with a hint of Clements’ (1916) organismal mysticism was likely to bring disapproval from one’s peers. As a graduate student in the 80’s I was encouraged by some to avoid the word ‘community’ and instead refer to ‘assemblages’. ‘Assemblage’ is a perfectly good word, and stigma for supporting ultra-holistic Clementsian views was certainly warranted. Furthermore, the proscription on holistic theory fostered the successful emphasis on plant competition over the last few decades, an interaction that has no holistic implications (Connell 1983, Schoener 1983,

Fowler, 1986, Aarssen and Epp 1990, Goldberg and Barton 1992). But the reaction against holism created an environment that was not conducive to exploring facilitation.

The emphasis on competitive effects and downplay of facilitative effects has also been exaggerated by the study of plant interactions in the greenhouse. While the isolation of some mechanisms is possible only under controlled conditions and must be conducted in pots and in greenhouses, studies of plants interacting in greenhouses almost always show competition. This may be because cramming several plants into a restricted area reduces their niche options, or because conditions in greenhouses tend to be so benign that neighbors can have no real effects on the harsh conditions that exist in the real world. For example, if there are plenty of nutrients then soil amelioration is inconsequential, if there is no wind the effect of neighborhoods as buffers against wind cannot be important, if there are no herbivores there can be no shared resistance, or if ambient humidity is high then the effects of neighbors on moisture around leaves is minimal. Without the normal stress of real life, studies are far less likely to demonstrate facilitation (see Chapter 4). Much like research on *Paramecium* in aquaria oversimplified theoretical perspectives on interactions among organisms in general; research on plants in greenhouses and pots has overemphasized competition.

To my knowledge, the first experiment on facilitation was published in 1914 by G.A. Pearson. Pearson noticed that conifer species appeared to regenerate better after fires in clones of *Populus tremuloides* (quaking aspen) than in the open and that “herbaceous growth is invariably more luxuriant under the aspen than in the openings.” He then planted seedlings of *Pseudotsuga menziesii* (Douglas-fir) under aspens and in openings and found greater survival under aspens. Recognizing the possibility that site effects may have differed (aspens may simply have been growing in sites with generally superior abiotic characteristics) he measured wind speeds and evaporation rates and hypothesized that amelioration of these effects and those of shade benefited Douglas-fir regeneration independently of site effects.

Until the late 1980's, data such as Pearson's (including a large number of other experimental results) were rarely interpreted as conceptually important in any general way - with the exception of a few ecologists focusing on facilitative interactions driven by herbivores. In 1976, Peter Atsatt and Dennis O'Dowd of the University of California at Irvine published a review in *Science* titled “Plant defense guilds” with the leader titled “Many plants are *functionally interdependent* with respect to their herbivores” (my italics). They went on to argue that the probability that a plant will suffer from herbivory depends on the chemistry, morphology, distribution, and abundance of neighboring plants. Such indirect forms of facilitation, such as described by Atsatt and O'Dowd are treated in detail in Chapter 3 of this book. However, Atsatt and O'Dowd's strikingly

non-individualistic perspective had no impact on plant community theory. Other early papers, such as published by J.D. Ovington as early as 1955 on the species-specific (see Chapter 5) effects of trees on understory composition and productivity also did not stimulate any general interest in the conceptual ramifications of facilitation.

To my knowledge, the first broadly conceptual appreciation of positive interactions emerged in two foundational, but under-cited, publications with strong theoretical stances. The first, “Positive Feedback in Natural Systems” by Don DeAngelis et al. in 1986, explored the general role of positive effects in ecosystems, and the second, “Plants Helping Plants” by Hunter and Aarssen (1988), explicitly argued for facilitation as an important and common process in plant communities. A third under-appreciated paper was published in Europe with the title of “Positive Interaktionen Zwischen Pflanzenarten” by Gignon and Ryser (1986). The most powerful effect on the resurgence of interest on facilitation, however, came from a series of experimental studies conducted by Mark Bertness and colleagues at Brown University (Bertness 1988, 1991, Bertness and Shumway, Bertness and Hacker 1994). Since the late 1980’s, a large number of reviews and commentaries have refined the theoretical role of direct and indirect positive interactions in natural plant communities, and organized the body of evidence that has accrued supporting positive interactions as important and general phenomenon affecting plant distributions, productivity, diversity, and reproduction (Wilson and Agnew 1992, Bertness and Callaway 1994, Callaway 1995, Callaway and Walker 1997, Callaway 1997, Callaway 1998a, Dodds 1997, Brooker and Callaghan 1998, Bertness 1998, Stachowicz 2001, Bruno et al. 2003). These reviews have coincided with an explosion in empirical research on facilitation (Figure 1.1).

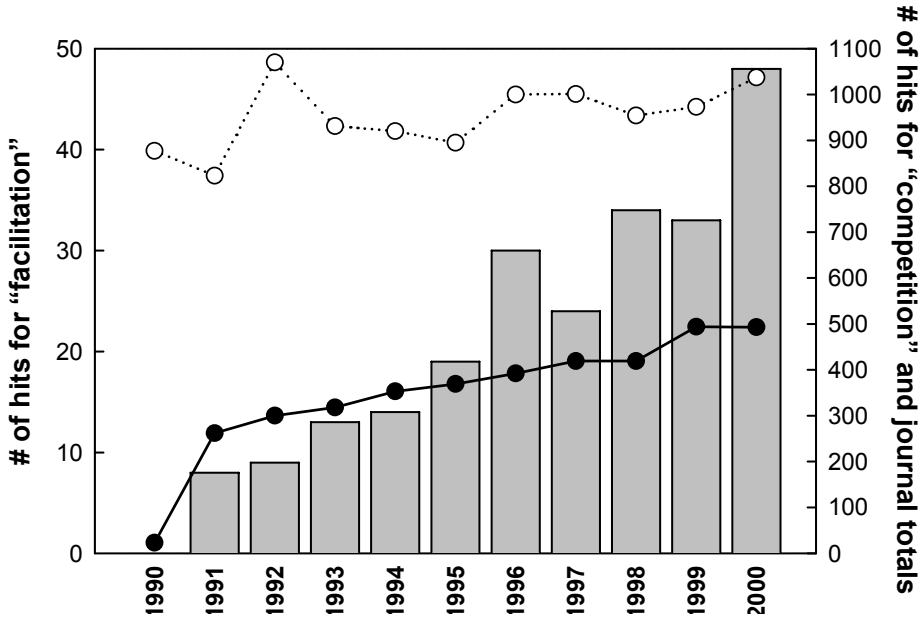


Figure 1.1. Web of science search hits on the terms: [(‘positive interactions’ or facilitation) and plant], shown as bars, [(‘negative interactions’ or competition) and plant] in filled points and total publications of *American Naturalist*, *Ecology*, *Journal of Ecology*, *Oecologia* and *Oikos*, shown as open points, from 1990 to 2000. Reprinted from Dormann and Brooker (2002) with permission from *Acta Oecologia*.

As noted in many of the recent reviews, experimental studies of facilitation and competition rarely provide unbiased neutral estimates of the relative importance of these interactions in communities. This is an important problem for those attempting to understand the fundamental role of interactions in community organization. In an effort to solve this problem, Walter Dodds (1997) constructed a general neutral model based on a number of field studies in which seven or more species were manipulated. As predicted from earlier simulation models (Dodds and Henebry 1996), he found that positive interactions among species were as likely as negative ones in communities as long as relatively large numbers of species and connections were considered. If fewer species were considered in a single interaction matrix, the probability of finding either positive or negative interactions decreased. Dodd’s models are intriguing, and in several other empirical studies involving large numbers of species, generally designed to examine competition, the results have indicated some positive interactions. However, the proportion of positive interactions demonstrated in empirical studies has usually been lower than that predicted by Dodd (Wilson and Tilman 1995, Twolan-Strutt and Keddy 1996, Thomas et al.

1999). A review by Goldberg and Barton (1992) indicated that neighbors promoted the survival or growth of individuals in approximately 10% of experiments. Peter Ryser (1993) found that two of six species studied in a Swiss grassland required shelter by neighboring plants. In a field comparison of spatial patterns and growth correlations Freeman and Emlen (1995) found more competitive than facilitative effects, but for some traits there were large numbers of apparent positive effects of species on each other. Hoffman (1996) found that eight of 12 tree and shrub species in cerrado savanna vegetation of Brazil responded favorably to canopy cover, whereas only one species experienced lower establishment under canopies. Out of a total of 35 species in a Chilean desert community, Gutiérrez et al. (1993) found that five appeared to be facilitated by shrub canopies and five appeared to be inhibited. However, it is unclear how species were chosen for analysis or experimentation in many of these experiments. However, there are many recent studies in which high proportions of species in communities participate in positive interactions (e.g. Choler et al. 2001, Callaway et al. 2002). Furthermore, the distributional positions of particular experimental species on environmental gradients appear to be crucial for predicting the proportions of species involved in facilitation (Choler et al. 2001). The bottom line that we can gain from studies that incorporate multiple species appears to be that competitive interactions are usually more common than facilitative interactions, but facilitative interactions are not rare, and can be common even in communities composed of species with similar morphologies.

Studies of spatial association are not as powerful as experimental evidence, but they also provide important insight into the relative importance of positive interactions versus negative interactions in plant communities. In some cases the consistency of spatial relationships among species can be impressive. Consider the relationship between *Ziziphus lotus* and *Asparagus albus* illustrated by Reyes Tirado and Francisco Pugnaire (2003) in oceanic dunes in southern Spain (Figure 1.2). Not only was the latter species virtually always found inside *Ziziphus* patches, transplanted *Asparagus* seedlings had higher survival rates in patches than in the open and produced more flowers, fruits, and showed a higher mass of seeds in patches than when isolated. This facilitative effect seemed to be due to nutrient enrichment in the patches.

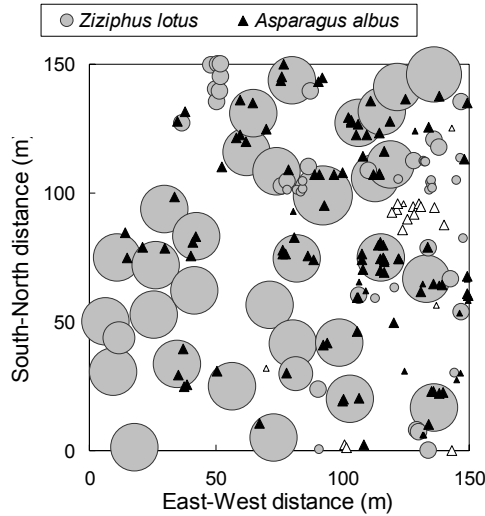


Figure 1.2. Distribution map of *Ziziphus lotus* and *Asparagus albus* in a sand dune-strip on the Almeria coast of Spain. Shrub symbols are represented in three size classes (<1 m, 1–4 m, and >4 m) for *Z. lotus* and two (<0.2 m and >0.2 m) for *A. albus*. Clear triangles represent *Asparagus* plants with other shrub species. Reprinted from Tirado and Pugnaire (2003) with permission from *Oecologia*.

In a correlative study of desert perennials in Namaqualand, South Africa, Eccles et al. (1999) argued that spatial patterns for 23% of species pairs in shrubby ‘short strandveld’ suggested positive interactions, whereas only 6% appeared to be driven by competition. In ‘medium strandveld’ positive interactions appeared to determine spatial associations for 38% of species pairs and negative interactions only 13%. Based on spatial patterns, similar proportions of species also appear to be facilitated or nursed in Sonoran desert systems (McAuliffe 1988). These proportions are only based on correlations, but experiments conducted in alpine plant communities to examine the connection between spatial pattern and the interactions among species found that negative correlative spatial associations between species rarely pointed to competitive interactions (as determined through removal experiments) but positive spatial patterns often signaled facilitation (Choler 2001). Many of the facilitative mechanisms discussed in Chapters 2 and 3 would not be manifest as discrete spatial associations. Therefore empirical comparisons and a clear understanding of mechanism indicate that spatial patterns may be conservative in their estimation of the relative importance of facilitation.

Other evidence for the relative importance of facilitative interactions comes from comparisons of the performance of plants in mixtures to performance in monocultures. Darwin (1858) mused about the potential for species mixtures to be more productive than monocultures, and since then many

studies have been conducted to compare the biomass productivity of mixtures of different field crops to the productivity of the same species grown at the same densities alone (see Chapter 6.2). Legume-grass mixtures commonly “overyield” (produce more than either species grown alone) due to the nitrogen-fixing properties of legumes, but studies of mixtures of nonleguminous species are much less conclusive. In 1974, Trenbath summarized studies on the productivity of 344 different mixtures and found that the means of 60.2% of the mixtures were above the mean yields of the monocultures, a proportion that was highly significantly different ($P < 0.001$). Eighty three of the mixtures were more productive than the most productive monoculture, whereas only 45 mixtures yielded less than the least productive monoculture. Twenty years after Trenbath’s analysis, Peter Jolliffe re-examined comparative studies on the total productivity of species mixtures to monocultures and arrived at similar conclusions (Jolliffe 1997). In 38 of 54 published experiments with two-species mixtures the mixtures were significantly more productive, and significantly lower in 8 studies. On average, mixtures were 12 to 13% more productive than pure stands, depending on the criteria used for inclusion of studies in the analysis. Overyielding is not necessarily produced by facilitation, and can be a by-product of niche partitioning, different temporal patterns of growth and development, and nutritional complementation. However, the more frequent occurrence of overyielding than underyielding in natural and man-made communities suggests profitable mechanistic research directions in community theory.

The relationship of species mixtures to productivity is highly relevant to the current interest in species diversity and ecosystem function (Tilman et al. 1996, Hector et al. 2002, see Chapter 6.2). For example, Symstad et al. (1998) conducted pot experiments in which 4, 8, or 12 species from 4 different functional groups were combined into assemblages with either all species present or assemblages with random deletions of one species. The effect of losing a single species from the assemblage generally reduced the total biomass of the community, but the effects were highly species-specific. Decreasing diversity by one species had either negative, positive, or neutral effects depending on the species – the “idiosyncratic” hypothesis proposed by Naeem et al. (1994). However, Symstad et al.’s results were not completely idiosyncratic as only nitrogen-fixing legumes elicited positive effects on community biomass. The potential importance of facilitation in the diversity-ecosystem function relationship was more clearly demonstrated in a study by Mulder et al. (2001) of bryophyte communities exposed to short-term drought. They found that productivity increased significantly with the species richness of the community. Mulder and her colleagues argued that an increase in positive interactions in drought conditions, and not in more mesic conditions, among plants drove the relationship between diversity and productivity. A similar argument was made by Caldeira et al. (2001) in a semi-arid climate in Spain.

To my knowledge there have been no other studies explicitly investigating the potential for facilitation to account for the effects of species diversity on community function, but understanding positive interactions has great potential to shed light on the biodiversity-community function debate. Also, whether idiosyncratic or not, the positive effects of many species on both ecosystem and community attributes suggest a level of interdependence in plant communities that challenges the individualistic status quo.

Understanding the degree to which plant communities are individualistic or interdependent is not just an academic problem. These concepts have strong implications for conservation theory and application. For example, the view that plant species are fully individualistic and “interchangeable” in communities has been used to advocate active human involvement in “shaping and synthesizing *new* ecosystems, even in the ‘natural’ environment.” (emphasis added, Johnson and Mayeux 1992). If maintaining functional plant communities is simply a matter of finding a suite of species that can form a stable individualistic competitive hierarchy, then Johnson and Mayeux’ ideas may not be so far-fetched. However, if interactions among plants are more complex and interdependent, as suggested by research on facilitation and the indirect effects of herbivores and mycorrhizae (Callaway et al. 1999, Marler et al. 1999), networks of direct and indirect interactions within the plant community (Miller 1994, Pennings and Callaway 1996, Takahashi 1997; Callaway and Pennings 1998, Levine 1999), and novel interactions among exotic invasive plants (Callaway and Aschehoug 2000, Callaway and Ridenour 2004) such shaping and synthesizing will lead to unforeseen and disastrous results.

Interestingly, conservationists often assume a high degree of interdependence in communities when they argue for the preservation of natural systems and biological diversity (Freedman 1989 Erlich 1990, Erlich and Wilson 1991, Miller 1993, Noss 1994). The Ecological Society of America, in an assessment of the use of science in achieving the goals of the Endangered Species Act (Carroll et al. 1996) recommended consideration of the following priorities: “does the species play an especially important role in the ecosystem in which it lives? Do other species depend on it for their survival? Will its loss substantially alter the functioning of the ecosystem?” If applied to plants, these priorities assume interdependence in communities.

Mechanistically, negative and positive interactions can be quite different. Negative direct interactions among plants appear to depend mainly on the effects of plants on common limited resources and the responses of plants to these same resources (Goldberg 1990, Miller and Travis 1996) and the biochemical effects of neighbors on each other (Williams 1990, Mahall and Callaway 1992, Inderjit and Del Moral 1997, Wardle et al. 1998, Bais et al. 2003, Vivanco 2004). Direct positive interactions incorporate a wider

range of different mechanisms than direct negative interactions (see Chapter 2), but like competition facilitation may occur through resource effects, one species increasing nutrient, water, or light availability to another, or through chemical effects.

Facilitation may be also driven by non-resource processes. Most commonly, species that are tolerant to non-resource stress such as cold, heat, wind, salinity, and disturbance buffer these factors on other species. Other non-resource facilitative processes are indirect. In an intraspecific example, Fischer and Matthies (1998) observed that individual *Gentianella germanica* plants, a rare species restricted to central Europe, produced more seeds per plant when they occurred in large populations than in small populations (40 to 5000 flowering individuals), and that population growth rates of large populations were higher than those of small populations. They also conducted a common garden experiment in which seeds from plants from the different populations were germinated in a greenhouse and transplanted into a common garden. They found that seed number and survival rates were significantly correlated with the size of the source population. Other experiments demonstrated that seed bank size and seed production were important to maintaining population size for *G. germanica* (Fischer and Matthies 1998). At the scale of individuals it is no surprise that an outcrossing plant needs another of its own kind nearby, but Fischer and Matthies' results suggest that an interesting positive density-dependent mechanism operates at larger scales. In the field, pollinator limitation appears to decrease individual fitness, and common garden experiments indicate that individuals in larger populations benefit from amelioration of pollinator limitation and maintain higher fitness levels. Others have shown positive correlations between population size and plant fecundity and these correlations have been attributed to pollen limitation (Jennerston 1988, Petanidou et al. 1993, Lamont et al. 1993, Widen 1993) and genetic deterioration (Menges, 1991, Heschel and Paige 1995, Menges and Dolan 1998).

Facilitation affects plant community structure and diversity in very different ways than competition. Inherently, competitive interactions limit coexistence among species, and therefore competition-based theory focuses on how species avoid competitive exclusion (Lotka 1932, Gause 1934, Hardin 1960, Hutchinson 1961). Coexistence in a world dominated by competition has been attributed to 1) "niche partitioning" (Parrish and Bazzaz 1976, Cody 1986), 2) variation in the physical environment and subsequent subtle differences in competitive advantages, 3) disturbance that continuously provides patches of competition-free microhabitat and alters competitive hierarchies (McNaughton 1985), 4) heterogeneity in the *ratios* of limiting resources that alter competitive hierarchies (Tilman 1976, 1985, 1988), 5) the development of local and species-specific resource depletion zones that, under certain conditions, do not strongly affect the resources available to neighbors

(Huston and DeAngelis 1994, Grace 1995), and 6) spatial structures that suggest niche partitioning (Van der Maarel et al. 1995). In contrast to the suite of theories that attempt to explain species coexistence *despite* competition for the few resources that are shared by all plants, positive interactions suggest that some interactions among plants *expand* niches (Chapter 6.1) and directly *promote* coexistence and community diversity.

Positive interactions do not increase community diversity in a haphazard manner. The ways in which plants modify their environments create conditions in which the beneficiaries are likely to be functionally different than their benefactors. Therefore we have legumes facilitating non-nitrogen-fixing grasses, trees facilitating shade tolerant grasses, and woody perennial shrubs and trees facilitating stem-succulent columnar cacti. This fundamentally inherent process of plant-driven environmental modification creates a situation in which something *functionally different* than the benefactor can thrive is a very important aspect of positive interactions in general. An excellent example of this process occurs in savannas of southern Africa. *Acacia nilotica*, a tree with very small drought-deciduous leaves, is the predominant species colonizing open grassland (Smith and Goodman 1987). *Acacia* cannot recruit under conspecifics, but many other broad-leaved evergreen shrubs and trees can. This broad-leaved evergreen functional group apparently would not occur in this environment without the positive effect of *Acacias*. *Acacias* are maintained as a dominant species in the system by large-scale disturbance by elephants. Where elephants have been eliminated many areas once dominated by *Acacia* are now dominated by thickets of the evergreen shrub *Euclea divinorum*. Positive interactions do not only increase species diversity, they also increase functional diversity.

Environmental modification by plants is generally assumed to facilitate the growth or reproduction of other species, or even the replacement of themselves by other species. However, in a review of positive-feedback switches in plant communities, Wilson and Agnew (1992) make a convincing case for processes in which plants, or communities of plants, can also modify their environment in ways that favor themselves. They argue that positive-feedback switches may produce stable mosaics in originally uniform habitat, sharp boundaries between plant communities on environmental gradients, and either accelerate or retard succession. These positive-feedback switches may be particularly important in exotic invasions.

In this book, I focus on several fundamental questions about positive interactions in plant communities: Are positive interactions widespread among different biomes and climates? What kinds of mechanisms drive direct and indirect positive interactions? How do positive and competitive interactions function together? Are positive interactions species-specific? How do positive interactions affect community dynamics? What do positive interactions mean for

community theory? By organizing the literature and concepts around these questions I hope to place positive interactions on solid theoretical footing in plant ecology and support a new conceptual paradigm for the nature of plant communities.

CHAPTER 2

DIRECT MECHANISMS FOR FACILITATION

This chapter and the next are reviews of the empirical research that provides evidence for positive interactions among plants. These chapters are organized by mechanism and I emphasize both experimental and correlative studies. The latter approach is crucial for connecting the processes demonstrated in fine-scale experiments to community-scale organization (see Kikvidze et al. 2005), but correlative studies have a hard time distinguishing between biological effects, shared physical microhabitat requirements, or the tendency of large perennials to act as foci for seed deposition. Positive spatial correlations among plant species that have been explored experimentally are generally supported in terms of facilitation, but not always (Moen 1993, Meiners and Gorchov 1998; Choler et al. 2001). Field experiments are the strongest evidence for the existence and importance of interspecific facilitation in plant communities and the mechanisms behind the phenomenon. The mistaken notion that positive interactions are not well demonstrated with field experiments may be largely responsible for perceptions of facilitation as an interesting, but not fundamental organizing process in plant communities.

Positive interactions can be direct, simply the effect of one species on another, or positive interactions can be indirect, requiring an intermediate species in order to occur (Strauss 1991, Wootton 1994, Callaway and Pennings 2000). Indirect facilitation, mediated by parasitic plants, fungi, animals, microbes, and other plants within the same trophic level is discussed in Chapter 3. Although direct and indirect mechanisms can be difficult to separate operationally, the purpose of this chapter is to focus on the direct mechanisms that drive positive interactions. In following chapters I address how these mechanisms may interact with each other, establish community structure, and affect community productivity, diversity, and composition.

The most common experiment performed to investigate the positive effects of plants on each other is no different than those typically done to test for competition, with the exception that facilitation has been rarely studied in the greenhouse or experimental gardens. Typically, one or more species is removed from a pair or group of species and growth, survival, reproduction, or some metric is acquired for the remaining target plant. Other approaches include manipulating the canopies or root systems of suspected benefactors separately, but without removing the entire plant. Although removal

experiments may not confirm the specific active mechanism (e.g. shade vs. canopy throughfall) they provide a good way to distinguish between biotic and microsite effects – a distinction that is difficult, if not impossible to accomplish without experiments. But experimental approaches are not without problems. If removal is not thorough, the experiment may create conditions in which the remaining “beneficiary” species is subjected to greater stress than would be experienced in habitats without the benefactor at all. For example, if removal eliminates positive effects such as shade, but does not substantially reduce root competition (e.g. if regrowth is abundant) the remaining target plant may do much worse than if were just exposed to the full impact of the abiotic environment alone. Therefore, removal would result in overly poor performance of target plants and the experiment would overestimate the importance of facilitation. Spatial associations and experiments dovetail when trying to understand immediate effects versus net effects of interactions over the lifespans of the interacting species. For example, removal and other manipulative experiments may provide insight into processes that may last several years, but without evidence from the long-term spatial patterns that integrate interactions over long time periods, the fundamental ecological importance of the interactions is hard to determine. An excellent example of the benefit of examining the relationships among patterns and processes plant communities was provided by Zaal Kikvidze and colleagues who found correlative links among temperature, precipitation, productivity, experimentally documented plant interactions, spatial pattern, and community richness in alpine communities around the world (Kikvidze et al. 2005). They suggested that the relationship between positive interspecific spatial patterns and increased community richness was due to niche construction by facilitators, which allows for the coexistence of more species than would be possible if niches were not built by some of the species in the community.

Long-term effects of facilitative mechanisms that do not disappear with the removal of putative benefactors such as higher soil nutrients or decreased soil density also complicate interpretation of removal experiments. Facilitation is indicated if plants perform significantly worse after the removal of a neighbor. However, if residual facilitative effects make plants perform significantly better after the removal of a neighbor, or if they drive a neutral response, interpretations may be inaccurate. Interpreting improved performance after neighbor removal as competition may be even more problematic. The enhanced performance of the target plant may have more to do with the high-quality conditions left behind by the removed plant than by the elimination of its competitive effects. Considering the strong effects that plants have on the soils they grow in, overestimating the importance of competition is probably common. For example, if soil modification by species A (e.g. increased soil nutrients) produces a strong

positive effect on species B, and competition for water produces a weak competitive effect of A on B, removal of A may result in higher performance by species B due to the residual high nutrient conditions, and be misinterpreted as strong competition. Interpretive problems are magnified by the fact that plants often interact with their neighbors via a number of different, but simultaneous, positive and negative mechanisms (Bertness and Callaway 1994, Callaway and Walker 1997, Chapter 4).

Jack Greenlee and I discovered how important spatial associations can be to corroborate experiments in a study of *Lesquerella carinata*, a rare mustard in Montana (Greenlee and Callaway 1996). Spatially, *Lesquerella* was highly associated with bunchgrass tussocks, but experiments conducted in a wet year found no evidence for facilitation by bunchgrasses. Instead we found strong evidence for competition. The spatial associations convinced us to conduct another experiment the following year, which turned out to be exceptionally dry. In this year shade from the bunchgrasses had substantial facilitative effects on *Lesquerella*. The experimental results suggested that immediate effects may be either positive or negative, but the spatial results suggested that net effects are positive. Understanding these important processes would not have been possible without integrated spatial correlations and experiments.

Greenlee's and my results could not have been demonstrated in the greenhouse, and this is probably true for most studies that have demonstrated facilitation. If two plants are grown together in a pot with adequate water, nutrients, and light, they are quite likely to compete with each other. This is because most facilitative effects occur because a benefactor ameliorates some harsh aspect of the environment, often while simultaneously competing with their beneficiary (Chapter 4). If there is nothing to ameliorate, all that is left is competition. There are facilitative mechanisms that may become apparent only in greenhouse studies, some microbially mediated effects for example, but for the most part greenhouses are bad places to study facilitation.

Other experimental approaches include separation of abiotic microsite effects and biotic facilitation with combinations of removal experiments, controls for treatment effects, and nurse plant "mimic" experiments. The latter are experimental manipulations in which nurse plant characteristics are simulated by constructing structural mimics that provide comparable levels of shade or protection from herbivores, but not long-term substrate effects. Comparison of the performance of beneficiary plants with and without benefactor mimics can provide good evidence for the importance of nurse plants and the mechanisms by which they may aid their neighbors.

The understanding gained by documenting the mechanisms that drive facilitation, or any biological interaction for that matter, is not trivial. If mechanisms for facilitation are few and biologically simple, then facilitation is

less likely to be important in a wide variety of ecosystems and climatic conditions and inanimate objects such as rocks, stumps, or shade cloth may elicit the same effects as living plants (see Chapter 5). As we shall see, however, facilitative mechanisms are complex. Furthermore, if the specific facilitative mechanisms described below change substantially in intensity and importance along environmental gradients (see Chapter 4), the potential for highly variable hierarchies of advantages and disadvantages for different species in a community will be even greater. Species diversity and coexistence in plant communities may depend on such variation in competitive and facilitative hierarchies.

2.1. WATER RELATIONS: HYDRAULIC LIFT

One of the first published reports of positive spatial associations among plant species was written by Phillips (1909), who found that seedlings of *Pinus monophylla* (pinyon pine) were found often under *Artemisia tridentata* (Great Basin sagebrush) and rarely in the open. This “nurse plant” spatial pattern was later described by others for *P. monophylla* and the closely related species *P. edulis* (Drivas and Everett 1988, Everett et al. 1986, Welden et al. 1990, Callaway et al. 1996, Sthultz et al. 2006). In woodlands of New Mexico Martens et al. (1997) found that young *Pinus edulis* and young *Juniperus monosperma* were highly associated with adults of different shrub species. Almost 90 years after Phillips’ observations I conducted removal and transplant experiments with colleagues at the University of Illinois and University of Nevada, Reno (Callaway et al. 1996) to study the nature of the relationship between these species. Confirming the claims of others, we found that *A. tridentata* shrubs significantly improved the survival rates of *P. monophylla* seedlings in comparison to open inter-shrub spaces and plots where *A. tridentata* had been removed. Shrubs provided indirect facilitation by reducing herbivory, but also directly reduced mortality due to ameliorating desiccation and heat stress. Shrubs may simply shade *P. monophylla* seedlings during the hottest and driest times of the year, but other, more complex facilitative mechanisms appear to be involved.

Not long after Phillips’ observations, Magistad and Breazeale (1929) hypothesized that deep-rooted plant species might extract water from far below the surface and lose a portion of this water into dry soils at the surface. Five

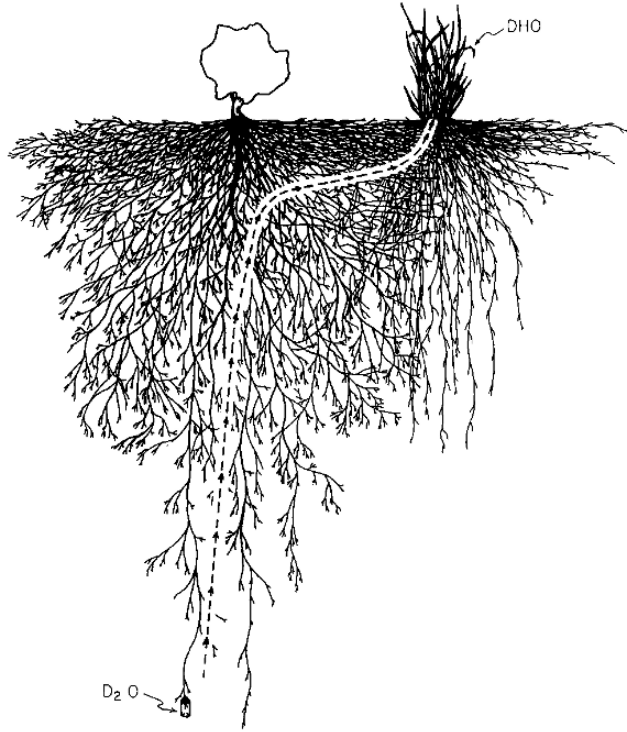


Figure 2.1. Deuterium-labeling experiment designed to show if water absorbed by the deep roots of *Artemisia tridentata* (left) would appear in the stem water of neighboring *Agropyron desertorum* grasses. Intact deep roots of *A. tridentata* were immersed in vials of D_2O , and DHO content of stem water in the grasses was measured. The dashed line shows the presumed pathway of deuterium. Reprinted from Caldwell et al. (1990) with permission from the *Israel Journal of Botany*.

decades later Harold Mooney observed that surface soils under *Prosopis tamarugo* in the Atacama Desert were relatively moist, despite the almost total lack of precipitation, and hypothesized that the moisture might come from the roots of the *Prosopis* itself (Mooney et al. 1980). Since then, the redistribution of soil water through root systems has been shown for a large number of species in a wide variety of conditions (Caldwell et al. 1998) including relatively shallow rooted species (Wan et al. 1993). The phenomenon, christened “hydraulic lift” was first clearly documented for *Artemisia tridentata* when Jim Richards and Martin Caldwell recorded substantial diurnal cycles in shallow soils under *Artemisia tridentata* and hypothesized that the shrub was transporting water from deep, moist soils to dry surface soils during the night (Richards and Caldwell 1987; also see Chapter 5.2). In a later experiment, light provided throughout the

night significantly reduced the diurnal cycles, presumably because open stomata maintained a steep gradient of water potential to the atmosphere (Williams et al. 1993). Hydraulic lift is a passive process, in which nocturnal stomatal closure establishes a water potential gradient running from high-water potential deep soils, along the gradually decreasing gradient within the plant, and then to the low water potential endpoint in the dry surface soils. When stomata open, the low water potential endpoint is re-established in the atmosphere. By caching water in shallow soils during the night *Artemisia* plants can increase their total daily transpiration rates.

Facilitation occurs when cached water at the surface becomes available to other species. Cached water may play a role in the nursing of *Pinus monophylla*, but movement of water through *Artemisia* via hydraulic lift to *P. monophylla* has not been demonstrated. However, Caldwell and Richards (1989) and Caldwell (1990) demonstrated that deuterated water absorbed by the deep roots of *Artemisia* appeared 11 hours after application in stems of neighboring *Agropyron desertorum* tussocks (Figure 2.1). However, the amount of water transferred from *Artemisia* to *Agropyron* was small, suggesting that any positive effects caused by this facilitative mechanism were probably not strong. Thus this form of facilitation may not be important relative to the intense competition that has been shown to occur between these species (Caldwell 1990).

In another effort to understand hydraulic lift as a facilitative mechanism, Todd Dawson (1993, also see Brooks et al. 2002, Chapter 5) used stable isotopes to investigate the magnitude of the water lifted by *Acer saccharum* (sugar maple) in northeastern forests of the United States and the effects of the hydraulically lifted water on understory plants. He quantified hydraulically lifted water in the xylem of all understory plant species examined, and found that the proportional use of hydraulically lifted water by understory species ranged from 3 to 60%. Within a species, individual plants that used large proportions of hydraulically lifted water had more favorable water potentials, conductances and growth than those that did not. For 12 understory species that varied in morphology from herbs to woody perennials, being close to hydraulically-lifting *A. saccharum* (0.5 m versus 5.0 m) resulted in 2-4 times higher rates of conductance and much higher water potentials. Comparison of the amount of hydraulically lifted water in understory plant xylem and the amount calculated for soil water budgets suggest that understory plants may preferentially take up lifted water due to its higher matric potential, or that the roots of understory plants are spatially associated with the roots of *A. saccharum* (Emerman and Dawson 1996). The positive effects of *A. saccharum* on the species that grow underneath them also depended on the size of the *A. saccharum*. Only trees larger than 10-cm dbh used large amounts of ground water, a prerequisite for hydraulic lift (Dawson 1996). Trees that were smaller than 10-cm in diameter

used surface soil water exclusively and did not lift. Mature *A. saccharum* may hydraulically lift 100 L (25% of their entire daily water budget) (Emerman and Dawson 1996), giving them the potential to have large-scale effects on ecosystem processes (Dawson 1996) and function as “ecosystem engineers” (Jones et al. 1994, 1997).

This potential for large-scale ecosystem engineering through hydraulic lift has recently been emphasized in a study of evergreen tropical trees in the Amazon rainforest. In a fascinating scaling up of hydraulic lifting by individual tropical trees (see Oliviera et al. 2005), Lee et al. (2005) used an atmospheric general circulation model to estimate that large numbers of hydraulically lifting trees could have strong effects on climate in the Amazon region.

A widely described positive effect of *Quercus douglasii* canopies on understory grass productivity has been attributed primarily to the way that canopy throughfall and litterfall increase soil nutrients near the trees (Holland and Morton 1980, Holland 1980, Callaway et al. 1991, see Chapter 4). However, Ishikawa and Bledsoe (2000) observed gradual increases in soil water potential at night and rapid decreases during the day in soils under *Q. douglasii* trees. These diurnal fluctuations in water potential are indicative of hydraulic lift. Hydraulic lift is discernable only in relatively dry soils; when soils are wet their high water potential, relative to that in shallow tree roots, does not allow water to passively move into the soil. For example, Dawson’s findings were reported from an unusually dry year, and Ishikawa and Bledsoe found that diurnal hydraulic lift patterns developed a month earlier in a dry year than in a wet year. But it is unlikely that hydraulic lift plays a role in the general facilitative effect of *Q. douglasii* trees because diurnal patterns in soil moisture do not develop until later in the summer, and by this time the annual grasses that are facilitated by trees are dead. Alternatively, water released by *Q. douglasii* roots could delay the rate of soil water depletion and increase the growing season for the annual understory species or affect other soil processes that ultimately benefit understory grasses.

Hydraulic lift has now been reported in the literature for at least 27 species (unofficially over 59, personal communication, T. Dawson) and the process occurs in a diverse number of biomes including shrub steppe, savannas, temperate forests, and tropical forests (Caldwell et al. 1998). The ecosystem effects of hydraulic lift may be large (Horton and Hart 1998, Lee et al. 2005), and clearly hydraulic lift may have broad importance as a facilitative mechanism. Although the facilitative effects of hydraulic lift have been emphasized primarily in the context of perennial trees and shrubs benefiting herbaceous understory beneficiaries, this mechanism may also be important for the survival and growth of seedlings of perennials growing under nurse plants, such as the pinyon pine seedlings that are found so often under the canopies of *Artemisia*.

A form of hydraulic lift, or “water transfer”, has also been described between *Zea mays* (corn) and *Medicago sativa* (alfalfa). Corak et al. (1987) grew these species in an experimental apparatus designed to examine the transfer of water from *Medicago* to *Zea*. A single *Medicago* plant was grown so that its roots connected with a *Zea* plant through two tubes separated by a 5 cm air gap, bridged only by the *Medicago* roots. The *Zea* roots were unable to cross the air gap between the tubes. When both the top tube and the bottom tubes were watered frequently, water potentials of *Zea* remained ≈ -0.20 MPa for the duration of the 50 day experiment. When only the bottom tube was watered, the water potentials of *Zea* in the top tube decreased to ≈ -4.0 MPa after 50 days. However, when *Medicago* was present, and its roots bridged the gap between the tubes, water potentials of *Zea* were above -2.0 MPa. Furthermore, high levels of labeled tritium supplied only to *Medicago* roots were detected in *Zea* tissue. These results indicate that water transferred from moist soil to dry soil by *Medicago* facilitated the survival of *Zea* in otherwise lethal drought conditions.

Although hydraulic lift can have strong facilitative effects in many different systems, it should be noted that the very trees that lift can also have strong competitive effects on understory species for water, to the point that the competition overwhelms facilitation (Ludwig et al 2004, see Chapter 4).

2.2. WATER RELATIONS: CANOPY INTERCEPTION

Many studies have shown that water input or soil moisture is higher around tree canopies or in forest stands where moisture from the air is intercepted and condensed (Vogelmann et al. 1968; Azevedo and Morgan 1974; Ingwersen 1985; Schemenauer et al. 1988; Huntley et al. 1997, Rigg et al. 2002). Furthermore, when canopy trees are removed the water input from fog drip and stream flow declines (Ingwersen 1985). This circumstantial evidence suggests that canopies can intercept and condense water from air may facilitate neighbors and create more mesic habitats. In an elegant study of *Sequoia sempervirens* (coastal redwood), perhaps the world’s greatest fog collector, Todd Dawson combined extensive sampling of fog and rainwater input with isotope analyses to quantify the amount of water collected by *Sequoia* trees and the acquiring of *Sequoia*-collected fog water by its smaller neighbors. Dawson found that forested sites received more total water inputs than nonforested sites and on average 35% of the total forest water inputs was due to fog drip from the *Sequoia* trees. In nonforested sites fog accounted for only 17% of total input. Isotopic analyses indicated that the average *Sequoia* obtained 19% of its annual water input from fog,

with smaller trees receiving almost 40% of their annual budget from fog. Understory plants benefited from the water intercepted by *Sequoia* trees, with shallow rooted herbs acquiring up to 100% of their moisture from fog inputs in dry years. While smaller species appear to collect a little fog themselves, the presence of *Sequoia*, a far better fog collector, provided understory species with much greater water inputs. Dawson noted that “loss of the canopy tree *S. sempervirens* is not only a loss of biomass and the nutrients contained within it, but will lead to a loss of the diverse canopy ‘community’ ... as well as the organic-rich forest soils to post-disturbance erosion. Tree loss will also convert a once moist, cool, closed ecosystem into a more drought prone, warmer, open ecosystem. Plants and animals which depend upon the moisture input from fog drip or other microclimatic benefits caused by the presence of fog will experience more frequent water stress when *S. sempervirens* is removed. In addition, both *S. sempervirens* seedlings and understory plant species which require moist and cool conditions to regenerate could suffer or disappear if inputs of fog decline.”

In New Caledonia, *Araucaria laubenfelsii*, a species that is morphologically similar to *S. sempervirens*, collects large amounts of water from fog, even on days with no recorded rainfall, and deposits this water beneath the tree canopy (Rigg et al. 2002). They found that *A. laubenfelsii* facilitated succession to rainforest by reducing stress experienced by late seral species and acting as “nuclei for forest species invasion of the maquis”. Once mature *A. laubenfelsii* establish nuclei, rain forest develops by expansion from these patches and their coalescence.

2.3. SHADE

The benefits of shade include maintenance of plant tissues below lethal or near-lethal temperatures, decreasing respiration costs, lowering transpirational demands by decreasing the vapor pressure difference between leaves and air, reduction of ultraviolet irradiation, and increased soil moisture due to lower evaporative demand. Most plants suffer substantial physiological damage at temperatures between 50 and 60°C because at these temperatures enzymes, cell membranes and thylakoid membranes begin to degrade (Larcher 1995). However, mitochondrial respiration rates increase exponentially with temperature, so temperatures much lower than 50°C can have negative effects on the carbon balance of plants. Shade can also reduce the vapor pressure difference between plant tissues and the air surrounding them by increasing ambient humidity (Geiger, 1965, Keeley and Johnson 1977, Larcher 1983), and by decreasing the temperature difference between plant tissues and the air.