

•Review•

# Positive Interactions: Crucial Organizers in a Plant Community

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## Abstract

For more than a century, ecologists have concentrated on competition as a crucial process for community organization. However, more recent experimental investigations have uncovered the striking influence of positive interactions on the organization of plant communities. Complex combinations of competition and positive interactions operating simultaneously among plant species seem to be widespread in nature. In the present paper, we reviewed the mechanism and ecological importance of positive interactions in plant communities, emphasizing the certainties and uncertainties that have made it an attractive area of research. Positive interactions, or facilitation, occur when one species enhances the survival, growth, or richness of another. The importance of facilitation in plant organization increases with abiotic stress and the relative importance of competition decreases. Only by combining plant interactions and the many fields of biology can we fully understand how and when the positive interactions occur.

**Key words:** competition; environmental gradient; facilitation; plant community; plant-plant communications; positive interactions.

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Interactions among species are central to community ecology (Connell 1983; Schoener 1983; Bruno et al. 2003). Early studies focused on the importance of competition (or negative interactions) in shaping plant communities (Connell 1983; Schoener 1983; Goldberg and Barton 1992). Among a series of issues, one of the themes debated was how the competition varied along the environmental gradient. According to the C-S-R model proposed by Grime (1979), it was argued that the negative interactions along environmental gradients of community productivity should be greater with the productivity. In contrast, using the Resource Ratio Model, Tilman (1982, 1988) predicted that competition would remain constant with an increase in soil resources (Figure 1). Interest in positive interactions among plant communities has increased over the past decade. Growing quantitative evidence has indicated that positive interactions are likely to be as

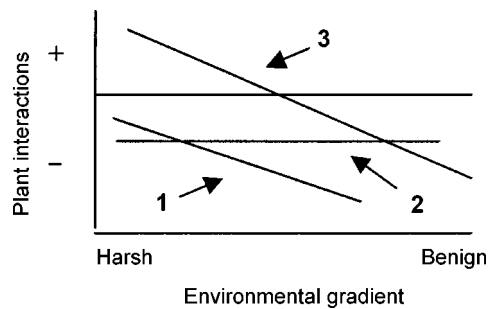
ubiquitous as competitive interactions (Bertness and Callaway 1994; Callaway 1995, 1997, 1998; Callaway and Walker 1997; Hacker and Gaines 1997; Hacker and Bertness 1999; Hector et al. 1999; Levine 2000a; Tewksbury and Lloyd 2001). Based on these studies, recent efforts have been concerned chiefly with the role of positive interactions in structuring plant communities and the way in which positive interactions vary along the environmental gradient. Wang (1993) predicted that the balance between competition and facilitation may vary with differences in species, environmental condition, or life stage; Bertness and Callaway (1994) hypothesized that the importance of facilitation in plant organization increased with abiotic stress and the relative importance of competition decreased (Figure 1). Based on previous studies, a combination of the effects of competition and facilitation, operating simultaneously among plant species, appears to be the rule in nature (Pugnaire and Luque 2001).

In the present paper, we review the positive interactions in plant communities. We begin with a definition of “positive interaction” and its mechanisms, and then discuss how positive interactions are measured. In addition, we introduce some current methods used to investigate positive interactions and discuss their possible limitations. Finally, we discuss several questions related to the roles of positive interactions in community organization and

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**Figure 1.** Predictions about the plant interactions across the environmental gradient (after Suding and Goldberg, 1999).

(1) Grime (1979) predicted that competition intensity would increase as the productivity increases. (2) Tilman (1988) predicted that competition would not change along the environmental gradient. (3) Bertness and Callaway (1994) predicted that plant interactions would possibly alter from harsh to benign environments (i.e. either positive or negative under harsh and benign environments, respectively).

vegetation dynamics with consideration of research implications for the future.

## Plant positive interactions

Positive interactions, or facilitation, occur when one species enhances the performance of another (DeAngelis et al. 1986; Hunter and Aarssen 1988; Wilson and Agnew 1992; Bertness and Callaway 1994; Callaway and Walker 1997). Experimental investigations from a wide variety of habitats have demonstrated the strong effect of facilitation on individual fitness, population distributions and growth rates, species composition and diversity, and even landscape-scale community dynamics (Callaway 1995; Bertness and Leonard 1997; Bruno and Bertness 2001).

Many positive interactions are simple, direct, and apparent: in physically stressful environments, a benefactor plant (Franco and Nobel 1989; Tewksbury and Lloyd 2001) facilitates another by making the harsh conditions more suitable for the beneficiary; that is, by modifying light (Greenlee and Callaway 1996; Weltzin and McPherson 1999), temperature (Franco and Nobel 1989; Valiente-Banuet and Ezcurra 1991), and soil moisture (Joffre and Rambal 1993) or nutrient regimens (Callaway et al. 1991; Belsky 1994). In addition to these direct mechanisms, plant community structure is also highly affected by indirect interactions that modify direct resource competition among species (Kareiva 1994; Wootton 1994). If a third species modifies the direct interactions between a pair of species, indirect interactions will occur (Connell 1990). A number of investigators have explored the consequences of indirect facilitation through modeling (Lawlor 1979; Vandermeer 1990; Stone

and Roberts 1991), and many experimental studies have examined indirect interactions in the field (Pennings and Callaway 1996; Levine 1999; Tielbörger and Kadmon 2000; Callaway et al. 2001; Pages and Michalet 2003). Some particular examples are discussed below. Miller (1994) found that the direct effects of five species were generally competitive and indirect effects were generally positive. The strong competitor annual ragweed (*Ambrosia artemisiifolia* L.) had indirect positive effects on two poor competitor species, namely white clover (*Trifolium repens* L.) and lambsquarters (*Chenopodium album* L.), by suppressing two moderately competitive species, specifically quackgrass (*Agropyron repens* L.) and narrowleaf plantain (*Plantago lanceolata* L.). Penning and Callaway (1996) showed that the competitive dominant species virginia glasswort (*Salicornia virginica* L.), in a Californian salt marsh, was suppressed by the parasitic plant saltmarsh dodder (*Cuscuta salina* Engelm.), which, thus, indirectly facilitated california sealavender (*Limonium californicum* (Boiss.) Heller) and alkali heath (*Frankenia salina* (Molina) I.M. Johnston). It is clear that these studies have demonstrated the importance of explicitly considering indirect interactions in positive interactions.

Both direct and indirect interactions may vary spatially and temporally, which is determined, in part, by the abiotic context. Greenlee and Callaway (1996) found that the effects of bunchgrass species on the rare mustard idaho bladderpod (*Lesquerella carinata* Rollins) were competitive in the wet, cool summer of 1993, but highly facilitative during the hot, dry summer of 1994. Summer drought is a main source of stress in many environments that limits the recruitment of both natural and planted seedlings. Under such conditions, seedlings may benefit from the habitat amelioration afforded by shrubs (Callaway 1995).

## Measurements of positive interactions

In plant communities, it is difficult to distinguish positive interactions from negative interactions owing to the two effects occurring simultaneously (Holmgren et al. 1997; Holzapfel and Mahall 1999; Maestre et al. 2003), which may help explain the phenomenon that investigations into positive interactions have not kept pace with competition studies. The net effect of plant interactions is frequently measured as the ratio of some performance variables, usually biomass between individuals, with and without removing their neighboring plants. Several indices have been used to explore the net effect of plant interactions (Weigelt and Jolliffe 2003). These include: the relative competition index (RCI; Wilson and Keddy 1986), the log response ration (lnRR; Hedges et al. 1999), the relative neighbor effect (RNE), which is the RCI modified to account for facilitative effects (Markham and Chanway 1996), and the relative interaction index (RII; Armas et al. 2004). Equations for the four indices of interactions are given below:

$$RCI = (B_0 - B_w) / B_0$$

$$RNE = (B_0 - B_w) / (\text{MAX}(B_w, B_0))$$

$$\ln RR = \ln (B_0 / B_w)$$

$$RII = (B_w - B_0) / (B_w + B_0)$$

where  $B_w$  is the mass of plants with neighbors and  $B_0$  is the mass of isolated individuals. Armas et al. (2004) compared the statistical properties of the four indices:  $\ln RR$  and  $RCI$  lack upper or lower limits,  $RNE$  has an undesirable mathematical characteristic because its denominator is a MAX function (there are two possible solutions depending on which type of interaction prevails), and  $RII$  is easy to obtain and apply, involving only basic mathematical operators, which makes the index better for measuring multispecific interactions at the community level.

## Balance between positive and negative interactions

### Why do positive interactions vary along abiotic gradients?

Positive mechanisms may act simultaneously with competitive mechanisms and the overall effect of one plant species on another depends on which mechanisms are the most important in a given environment (Callaway and Walker 1997; Holmgren et al. 1997). In physically harsh environments, such as salt marsh, desert, and alpine habitats, where the limited resource is inadequate, benefits provided by a tougher neighbor may be more likely to favor growth than competition with that tough neighbor is likely to reduce growth. The shift from competition to facilitation will occur. Here, the results of selected sets of experiments illustrate the importance of positive interactions to the organization of plant communities.

### Salt marsh plant communities

Salt marshes are considered an excellent environment in which to study positive and negative interactions between plants, with both facilitation and competition having been observed frequently (Gray 1985; Scholten and Rozema 1990; Castellanos et al. 1994; Callaway and Pennings 2000). Plants in salt marshes usually experience physical stresses, owing to lack of oxygen and salinity contained in the soils, and interactions among plants can vary from negative to positive through shading the soil and reducing pore water salinities (Bertness 1991; Bertness and Shumway 1993; Callaway 1994). Under conditions of high salinity, positive plant interactions are likely to be relatively more important if the presence of neighboring plants ameliorates potentially harsh abiotic conditions, resulting in increased growth rather than a reduction in growth owing to competition (Bertness and Hacker 1994; Hacker and Bertness 1995; Pennings and Bertness 2001).

Based on the observation that low-latitude salt marshes have higher soil salinities than do marshes at high latitudes, Pennings and Bertness (1999) predicted that positive interactions would be

increasingly common and important in marshes at lower latitudes. Bertness and Ewanchuk (2002) tested this hypothesis by comparing plant interactions in New England marshes south (Rhode Island) and north (Maine) of Cape Cod.

### Semi-arid and, arid plant communities

The physical stress of desert plant communities is severe and stress gradients arise with variation in water availability or fertility (Tewksbury and Lloyd 2001). Accordingly, positive interactions are thought to be of great importance in arid and semi-arid areas (Whitford 2002). The first clear examples of the role of positive interactions among desert plants was the "nurse plant" effect (Shreve 1931, 1951; Hutto et al. 1986; McAuliffe 1988; Burquez and Quintana 1994; Tewksbury and Petrovich 1994; Suzan et al. 1996), in which larger desert trees, such as palo verde (*Cercidium* spp.), mesquite (*Prosopis* spp.), and ironwood (*Olneya tesota* Gray), have a strong effect on the structure of plant communities, causing large increases in plant species richness and abundance in the most xeric habitats by providing protection from herbivores (McAuliffe 1984; Haase et al. 1997) and by improving soil texture, nutrient content, and water availability (Pugnaire et al. 1996, 2004; Moro et al. 1997) or by reducing evaporative demand and photo-inhibition owing to strong irradiance (Valiente-Banuet and Ezcurra 1991). Moreover, recent studies have demonstrated that the interaction effects of desert plants changed from clearly positive in the water-stressed or infertile environment to negative in the more fertile habitat (Maestre et al. 2001, 2003; Pugnaire and Luque 2001; Tewksbury and Lloyd 2001).

### Alpine plant communities

Some researchers have used removal experiments to test plant interactions shifting from competitive effects to facilitatory effects (Choler et al. 2001). Callaway et al. (2002) designed a large-scale experiment to examine positive interactions among alpine plants. Using 115 species in 11 mountain ranges, Callaway et al. (2002) revealed that, at high elevations where abiotic stress was high, the interactions among plants were predominantly positive, whereas competition prevailed at lower elevations where conditions were less physically stressful. Furthermore, this result was due, in part, to neighboring plants ameliorating the low temperatures at high-elevation sites.

### Relationship between facilitation and environmental severity

The relationship between facilitation and environmental severity is more complex than recognized previously. The effects of plant interactions can vary in relation to the life stage (e.g. seedling, growth) of the species and the ecological context (Bertness and Callaway 1994; Goldberg and Novoplansky 1997; Schenk et al.

2003). For example, Hastwell and Facelli (2003) found that there is no evidence supporting the prediction that the facilitation of growth increases with environmental severity, but the importance of shade-induced facilitation of survival was high under severe conditions, as predicted. Notably, some of the studies have not supported the significant theory that the relative importance of positive interactions to the organization of plant communities increases with abiotic stress. Penning et al. (2003) studied plant interactions over a broader geographic scale. After comparing southern (Georgia and Alabama) coastal salt marshes with northern (Rhode Island and Maine) coastal salt marshes, Penning et al. (2003) indicated that interactions between salt marsh plants in Georgia and Alabama were strongly competitive. Goldberg et al. (1999) analyzed the published results and found no trend in the relationship between competition/facilitation intensity and productivity in plant communities.

### Positive interactions and spatial patterns in arid plant communities

Spatial structuring of plant communities is a consequence of restricted dispersal and the action of mortality factors, such as competition, pollinators, herbivory, and abiotic stress, which often has a local and species-specific impact. Positive interactions are often related to the spatial clumping of individuals, which raises the question as to whether such interactions are important for shaping the structure and function of these communities (Schlesinger et al. 1990; Aguiar and Sala 1999). Thus, analysis to link the spatial patterns and positive interactions has become popular among plant ecologists (e.g. Haase et al. 1997; Kikvidze and Nakhutsrishvili 1998; Eccles et al. 1999; Schenk et al. 2003).

Plants growing below tree or shrub canopies in xeric ecosystems often exhibit higher growth or survival than conspecifics growing in the open. Tirado and Pugnaire (2003) pointed out that interspecies aggregation would significantly increase plant products, such as flowers and fruits, and show a higher mass of seeds as a result of enrichment in patches, and they indicated that the spatial aggregation of species could be indicative of a positive interaction among them, whereas benefactor plants, such as shrubs and semi-shrubs, often have different spatial distribution patterns. Comparing the spatial patterns of the semi-shrub burrobush (*Ambrosia dumosa* (Gray) Payne) on adjacent geological substrates, Schenk et al. (2003) found that *A. dumosa* aggregated under harsh edaphic conditions (alluvium), but segregated under benign conditions (sand), and the degree of segregation on sand increased with the total aboveground biomass. Moreover, Stoll and Prati (2001) pointed out that a relatively superior competitor would perform better in aggregation than segregated at a low density. As mentioned above, we suggest that abiotic conditions affect plant interactions and that positive interactions may result in the aggregation of plant species in arid

areas.

## Positive interactions and the integrated community theory

### Integrated community theory

Numerous studies indicate that positive interactions are common in plant communities. However, the theoretical framework of modern ecology has not kept pace with the advances coming from experimental field research. Bruno et al. (2003) proposed that the inclusion of facilitation into ecological theory "...alters many basic predictions, and argue that this is crucial to our understanding and conservation of natural communities".

Plant communities have traditionally been viewed as either a random collection of individuals (Gleason 1926) or as organismal entities (Clements 1916). Based on the studies of positive interactions, Lortie et al. (2004) synthesized the two theories and introduced a new community concept, the integrated community (IC) which proposes a range from highly individualistic natural plant communities to highly interdependent depending on synergism among: (i) stochastic processes; (ii) the abiotic tolerances of species; (iii) positive and negative interactions among plants; and (iv) indirect interactions within and between trophic levels.

The IC theory is just one of many possible ways to synthesize early communities. As Lortie et al. (2004) pointed out, "...this theory should not be viewed as yet another framework in which all new results must fit, but rather an attempt to break down the old paradigms for community, open new avenues of investigation with greater breadth".

### Relationship between IC and community invasion

Current theory states that competition is a primary force controlling community composition and diverse assemblages should use resources more fully and leave little niche space for potential colonists (Levine and D'Antonio 1999). However, current evidence in support of a negative diversity-invasion relationship comes from relatively small-scale experiments that implicitly or explicitly ignore positive and negative habitat interactions that occur at larger spatial scales and that may be crucial for invasion success (Levine 2000b). For example, Callaway and Aschehoug (2000) compared the competitive effects of white knapweed (*Centaurea diffusa* Lam.), an invasive Eurasian forb, on three bunchgrass species that co-exist with *C. diffusa* in Eurasia to the effects of *C. diffusa* on three bunchgrass species from North America. *C. diffusa* had much stronger negative effects on the North American species than it had on the Eurasian species. Correspondingly, none of the North American grass species had a significant competitive effect on the biomass of *C. diffusa*, but the Eurasian species significantly reduced *C. diffusa* biomass. Hence, at least this study

illustrates that applying the IC theory of plant community can provide novel and extremely productive experiments that test for interdependence to better understand invasion ecology.

## Conclusions

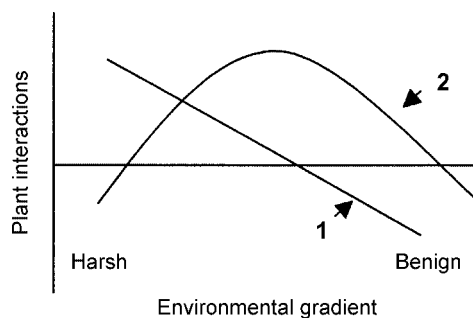
Positive interactions between plant species are widespread in natural communities and have been acknowledged as a major driver of plant community dynamics and ecosystem processes (Bruno et al. 2003). Although much is known about plant interactions in response to abiotic environments (i.e. plant interactions would be positive under a harsh environment but would be negative under benign environment), we are inadequately prepared to predict how strongly positive interactions occur. A full understanding of when and how positive interactions take place and their ecological importance requires input from many fields of biology. Progress would be helped by experiments integrating the resource emphasis of physiological ecology and measurements of positive interactions along environmental gradients.

## Field experiments

Do plant communities maintain positive interactions with each other under an extremely harsh environment? Maestre and Cortina (2004) investigated the net effect of the tussock grass esparto (*Stipa tenacissima* L.) on the shrub mastic tree (*Pistacia lentiscus* L.) in a semi-arid region and found that competitive interactions were prevalent at the extremes of the abiotic gradient. Consequently, they suggested that a shift from facilitation to competition under high abiotic stress conditions is likely to occur when the levels of the most limited resource are so low that the benefits provided by the facilitator cannot overcome its own resource uptake. Furthermore, in studies on the competition and coexistence of three tall clonal perennial plant species, Rebele (2000) pointed out that positive interactions played an important role over a broad range of the productivity scale with a peak at intermediate levels of fertility. Our field data also show similar transitions of positive interactions along environmental stress (Cheng DL et al. 2004, unpublished data). Based on these indications, we may further point out that competitive interactions will be dominant at the extremes of the abiotic gradient (Figure 2). Recent studies (e.g. Penning et al. 2003) do not tally with our prediction, partly because most of the previous studies were performed at only two sites and within two growth seasons, which could not cover a wide range of abiotic environments (Pennings et al. 2003). More importantly, only a few studies have evaluated how changes in abiotic conditions modify the relative importance of facilitation and competition. So, future studies should be conducted at multiple sites, lasting several years, to test the dynamic nature of different positive and negative effects.

## Positive interaction and plant-plant communications

The communication of plants communication with their neighbors is crucial for the comprehension of how plants interact with each other (Callaway 2002). Both plant-plant communications and positive interactions play an important role in structuring plant communities. Recent studies have undertaken considerable work in plant communication. For example, cytosolic calcium oscillation signaling is closely related to phytohormone abscisic acid (ABA), ABA reduces water loss from plants during drought stress via a signal transduction network in guard cells that leads to stomatal closure and triggers an oscillation in the cytosolic  $\text{Ca}^{2+}$  concentration, which is perceived by  $\text{Ca}^{2+}$ -binding proteins, initiating a series of signaling cascades that controls many physiological processes, including adaptation to environmental stress (Allen et al. 2001; Wang et al. 2001; Yang et al. 2004). In addition, volatile organic compounds, such as ethylene, isoprene, mono and sesquiterpenes, alkanes, alcohols, aldehydes, organic acids, and ketones, among others, have been found in some plants in response to an attack or an injury by external agents (Peñuelas and Llusà 2003). Moreover, not only the infested leaves, but also the whole plants and even neighboring uninfested plants have been shown to emit chemical signals in response to phytophagous attack owing to systemic responses in infested plants (Langenheim 1994; Peñuelas et al. 1995; Röse et al. 1996; Peñuelas and Llusà 2003, 2004). Root exudation also plays an active and relatively well-documented role in the regulation of symbiotic and protective interactions with microbes and in maintaining root-soil contact in the rhizosphere by modifying the biochemical and physical properties of the rhizosphere and contributing to root growth and plant survival (Gersani et al. 2001; Inderjit and Weston 2003;



**Figure 2.** Predictions about plant interactions across the environmental gradient.

(1) Bertness and Callaway (1994) predicted that plant interactions would be positive under a harsh environment but would be negative under a benign environment. (2) We predict that competitive interactions will predominate at the extremes of the abiotic gradient and positive interactions will be observed at medium environmental stress.

Bais et al. 2004).

It is clear that a combination of the dual perspectives of plant interactions and plant-plant communications for forming a new plant community and environment feedback signal regulation theory is especially important. New and adequate approaches should be developed to explain the facilitation and competition that have occurred, are occurring and that will occur in plant communities.

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