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## THE INTERPLAY OF FACILITATION AND COMPETITION IN PLANT COMMUNITIES

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**Abstract.** If plants cannot simultaneously acclimate to shade and drought because of physiological trade-offs, then plants are expected to be less tolerant to shading under drier conditions. One observation that, at first sight, seems incompatible with this idea is the fact that the establishment of new plants in dry areas is often restricted to shady sites under the canopy of other plants, called “nurse plants.” We use a graphical model to resolve this paradox. The model visualizes how facilitative patterns can be understood from the simultaneous effects of plant canopies on microsite light and moisture, and the growth responses of establishing seedlings to those factors. The approach emphasizes the fact that positive and negative effects of plant canopies always occur simultaneously. In the presented light–water model, facilitation only occurs when the improvement of plant water relations under the canopy exceeds the costs caused by lower light levels. This may be true under dry conditions, whereas in less dry situations, competition rather than facilitation is observed. The model shows how changes in water availability may shift interactions from competitive to facilitative and vice versa, as observed in some field patterns. It is argued that other environmental factors explaining facilitative patterns can be understood in the same context.

**Key words:** competition; facilitation; light; model; nurse plants; physiological trade-offs; plant communities; water.

### INTRODUCTION

Facilitation, the positive effect of plants on the establishment or growth of other plants, has long been recognized as an important driving force in primary and secondary succession (Clements et al. 1926, Connell and Slatyer 1977). Nonetheless, competition has received far more attention in ecological research over the last decades (see reviews by Connell and Slatyer 1977, Connell 1983, Schoener 1983, Keddy 1989, and Goldberg and Barton 1992). Recently, however, there has been renewed interest in the topic of facilitation (Hunter and Aarssen 1988, Goldberg 1990, Callaway 1995) and the environmental conditions that make it possible. Bertness and Callaway (1994) hypothesized that competition increases in importance toward the more productive part of the environmental gradient, whereas facilitation is more important under harsh conditions.

Facilitative interactions have been demonstrated in a broad range of ecosystems. Most evidence comes

from ecosystems where plants are exposed to severe stress, for instance, as a result of heat and desiccating conditions. In such situations, the establishment of new plants is often restricted to the shady places under the canopy of other plants, called “nurse plants.” However facilitative interactions have also been described for lush vegetation, such as temperate grasslands and forests, and moist tropical savannas.

Obviously, positive and negative interactions will probably occur simultaneously. Although they improve some environmental conditions, nurse plants will tend to have negative effects on other factors. They can, for instance, enhance air humidity and prevent extreme temperature fluctuations, improve soil properties (accumulation of nutrients and organic matter), and reduce the probabilities of mechanical or herbivory damage. On the other hand, nurse plants can impede seedling emergence by litter accumulation (Barton 1993), and they can limit the potential growth of newly established plants by reducing the availability of light and soil water (Franco and Nobel 1988, 1989, Nobel 1989), or by excreting allelopathic substances (Muller 1953, Muller and Muller 1956, Callaway et al. 1991).

To understand the mechanisms behind the net effect of nurse plants on seedling establishment, it is necessary to know the combined response of the seedlings

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to multiple environmental factors. Multifactorial studies are surprisingly rare in ecophysiology (Chapin et al. 1987, Osmond et al. 1987), but some appealing hypotheses have been formulated about the simultaneous effects of interacting stresses (Bloom et al. 1985, Tilman 1988, Smith and Huston 1989, Chapin 1991, Luxmoore 1991). Smith and Huston (1989), for instance, hypothesized that the response of plants to the combined effects of light and water is characterized by a trade-off between drought tolerance and shade tolerance. The authors based their trade-off hypothesis on expected physiological responses of plants to light and water, and used it to predict the growth and survival of different plant functional types along gradients of light and water availability. Smith and Huston (1989) predicted that plants would be less shade tolerant under drier conditions. Similarly, plants would become less drought tolerant when growing under low light levels. Note that such physiological trade-offs make the occurrence of facilitation less likely. If plants were to become shade intolerant under dry conditions, one would not expect growth and/or survival to be higher in the shade under dry conditions, as is often observed.

In this paper, we seek to resolve this paradox. The first section briefly presents an array of examples of facilitation in which amelioration of water stress is an important mechanism. We then present a graphical model to discuss the interplay of facilitative and competitive effects, in view of the combined response of plants to light and moisture conditions. In the final section, we discuss the applicability of the model to facilitative patterns in general.

#### EXAMPLES OF FACILITATION THROUGH IMPROVEMENT OF WATER CONDITIONS

Evidence for facilitative interactions comes from a variety of ecosystems. Here, we present a selected set of examples found in deserts, dunes, mediterranean shrublands, tropical savannas, salt marshes, tundras, and temperate grasslands and forests. These cases illustrate that: (1) facilitation is a common phenomenon in a wide range of plant communities, and (2) the improvement of plant water relations in the shade is a commonly involved mechanism, although, in many cases, facilitative patterns can result from other mechanisms, such as an increase in nutrients or a reduction in herbivory. This overview is by no means exhaustive. Callaway (1995) presents an extensive review of facilitative patterns and mechanisms involved in both terrestrial and marine ecosystems.

In deserts, seedlings of succulent and nonsucculent plants generally occur under the canopy of larger perennial plants. The establishment of succulent plants seems to be facilitated mainly by reduction of extreme soil temperatures (Turner et al. 1966, Franco and Nobel 1989, Valiente-Banuet and Ezcurra 1991). This is crucial for succulents, because they cannot prevent over-

heating through transpiration. Soil water content might be only slightly higher (Shreve 1931), or even lower, under the shade than in the open (Nobel 1989), but the thermal stress is much lower close to the nurse plant. Establishment of nonsucculent plants is facilitated under the shade, due to a reduction of transpiration demands (Shreve 1931, Abd El Rahman and Batanouny 1965*a, b*). However, seedling growth could also be reduced by the presence of nurse plants. Simulation results predict that this is mainly a consequence of a drastic reduction in photosynthetically active radiation and competition for soil water with the nurse plant (Franco and Nobel 1988, 1989, Nobel 1989). An increase in nitrogen availability under the nurse canopy can also add to the facilitative effects (Franco and Nobel 1989), but this is not always the case (Valiente-Banuet et al. 1991*b*, Arriaga et al. 1993). The establishment of new plants does not leave the nurse plants completely unaffected. Competition, especially for soil water, can have a negative effect on the nurses, leading to a reduction in their growth and fecundity (Flores-Martínez et al. 1994), or to an increased branch mortality among those nurse plants associated with succulents (McAuliffe 1984*a*, Valiente-Banuet et al. 1991*a, b*).

Desiccation and nutrient deficiency are the primary causes of poor seedling establishment in coastal dunes (Maun 1994). Severe water stress results from the combination of very low water-holding capacity of the sand, exposure of the root system by wind action and high soil temperatures. Under these extreme conditions, the shade provided by nurse plants significantly increases seedling survival because of improved plant water relations (Fuller 1914, McLeod and Murphy 1977, De Jong and Klinkhamer 1988). Experimental manipulations have not only shown that seedlings under the nurse shade can survive, but also that artificial watering can increase seedling survival and growth, especially in open areas (De Jong and Klinkhamer 1988).

In mediterranean ecosystems characterized by dry summers and wet winters, the interplay of facilitative and competitive interactions seems to be more variable than in the very dry conditions of the desert. In the oak savannas close to the coast of northern California, United States, the productivity of herbaceous plants growing under the oak canopy is lower than in open grasslands, and removal of trees has a positive effect on herbaceous production (Murphy and Crampton 1964). In contrast, in the drier foothills of the Sierra Nevada in central California, shading increases herbaceous production, especially during dry years (Frost and McDougald 1989). These patterns support the idea that, with increasing dryness, facilitation becomes more important than competition. However, Callaway et al. (1991), also working in central California, showed that apparent facilitative or interfering effects under

oak canopies can be found within several meters of each other. They found that nutrient inputs tend to facilitate grassland productivity, but in some trees, root allelopathic exudates seem to have an interfering effect. In the Chilean matorral, also with a mediterranean climate, natural patterns and experimental manipulations have shown that shrub seedlings establish mainly under shrubs as a result of high mortality (primarily from desiccation, but also from rabbit herbivory) in the open surrounding grassland (Fuentes et al. 1984, 1986). Although recruitment of shrub seedlings occurs under nurse shrubs along the whole matorral range (Fuentes et al. 1986), in moister areas, the establishment of shrub seedlings can occur also in the open areas (M. Holmgren, A. M. Segura, and E. R. Fuentes, *unpublished data*).

The arid Patagonian steppe is a mosaic of shrubs, each tightly surrounded by a dense ring of grasses and scattered tussocks interspaced with bare soil (Soriano et al. 1994). Experimental manipulations suggest that small shrubs that are able to establish on bare soil can initially facilitate the recruitment of grasses by a reduction in evapotranspiration demands under the shrub canopy (Aguiar and Sala 1994). However, once the ring has been formed, strong competition for soil moisture with the established grasses overshadows the positive effect of the shrub canopy (Aguiar and Sala 1994).

In the dry African savannas, herbaceous productivity is often higher under the tree canopy than in open grassland. This increase in productivity seems to be mainly a result of higher nutrient concentration under the trees (Belsky 1994). Interestingly, the magnitude of this increase is highly correlated with water conditions. In the low-rainfall areas, the increase in herbaceous productivity below the trees, relative to the grasslands, is much greater than at the high-rainfall sites (95% vs. 52%, respectively; Belsky et al. 1993). In drier sites, two mechanisms lead to lower water stress under trees: a reduction in evapotranspiration demands and a relative reduction in competition for soil water with the tree roots. Experimental results have shown that trees compete more strongly and reduce productivity of herbaceous plants only in high-rainfall sites because they concentrate their roots close to their own canopy, intensifying competition for water with the understory grasses (Belsky 1994). In savannas, therefore, as in mediterranean systems, the microclimatic changes under nurse plants have stronger effects in the drier areas.

In salt marshes, plants can also be exposed to severe desiccating conditions, due to high radiation, low water availability, and high salinity. Here, winter annual species can either have negative or positive associations with perennial shrubs. In the latter case, the effects of shade in reducing salinity and increasing water availability more than compensate for the effects of reduced photosynthetically active radiation and root interference (Callaway 1994). Experimental manipulations have demonstrated that alleviation of the stress pro-

duced by salinity can shift the nature of the interspecific interactions from facilitative to competitive (Bertness and Shumway 1993, Bertness and Hacker 1994, Bertness and Yeh 1994, Shumway and Bertness 1994).

Tundras are characterized by slight precipitation but also low potential evaporation. Although the climate is considered humid (Walter 1985), it has been shown that shrubs can facilitate the growth of herbs in tundras by reducing the impact of desiccating winds (Carlsson and Callaghan 1991).

Under certain circumstances, even taller grasses can act as the necessary shelter for the establishment of grass seedlings. In a limestone grassland of northern Switzerland, Ryser (1993) found that the roots of the focal plant stabilize the soil, preventing the seedling roots from being uprooted by frost heave and exposed to desiccation during the dry spring days. Seedling survival of those species particularly vulnerable to this environmental impact was significantly lower in gaps than under the shelter of neighboring plants (4% vs. 40%). Positive effects of the presence of other plants on seedling establishment have also been reported for chalk grasslands (Schenkeveld and Verkaar 1984). Again, the effect of already established plants on new seedlings depends on environmental conditions. In the chalk grasslands of England, Hillier (1990) found that, on the drier south-facing slopes, established plants enhanced the survival of some species, whereas on the moister north-facing slopes, seedling establishment was strongly dependent on the availability of open gaps.

Facilitative interactions are also important in explaining the distribution and successional dynamics of forests. In the mountains of the southwestern United States, the lower altitude limits of some pine species seem to be controlled by water stress. With decreasing elevation, pine seedlings increasingly occur in microsites with relatively low light, but lower soil temperature and higher soil moisture. Seedlings of some species are nearly restricted to this type of microsite beneath nurse trees (Barton 1993). In early successional communities of deciduous forest in the eastern United States, Berkowitz et al. (1995) experimentally show that surrounding vegetation can strongly inhibit tree seedling growth in productive sites, but has little effect, or actually improves it, on harsh sites, especially during drought periods. Comparing gaps of different sizes, Sipe and Bazzaz (1995) found that tree seedling survival was substantially reduced in large gaps. This pattern could result from water stress. Large gaps have higher levels of photosynthetically active radiation and temperature, but lower soil moisture in the top soil layers (Kozlowski et al. 1991).

Indications of facilitation have also been found in humid forested regions, originally covered by rain forests and now transformed into pastures, with large, isolated trees still remaining. These isolated trees func-



tion as a nursery for tree seedlings, many of them rain forest species, that are not found in the surrounding open places (Guevara et al. 1992). Trees probably facilitate seedling colonization by providing perching sites for seed-depositing birds and bats and by modifying the microclimatic conditions (Guevara et al. 1992). Light reduction under the tree might also reduce competition with the shade-intolerant grasses, and might facilitate the establishment of the more shade-tolerant tree seedlings (Huston 1982).

In summary, these cases illustrate that an increase in growth or survival under the nurse shade seems to be a rather general phenomenon in harsh conditions. Facilitative effects are stronger in drier sites and drier years. Moreover, several field experiments support the causal link of moisture conditions to seedling establishment in dry environments. Many factors can contribute to lower water stress in the shade: (1) lower transpiration demands (due to lower vapor pressure deficit and thermal stress); (2) increased soil water availability (because of lower evaporation, reduced salinity, or improved water-holding capacity); and (3) improved conditions for root growth (due to enhanced soil stability and structure, increased soil moisture, or reduced soil temperatures). Obviously, the relative importance of these factors will depend on the particular ecosystem.

#### A CONCEPTUAL MODEL

In this section, we derive a graphical model to show that much of the interplay of facilitation and competition can be understood from two components: (1) the growth and survival of plants in relation to water and light availability; and (2) the effect of plant canopies on microsite light and moisture.

##### *Plant growth responses*

A simple way to visualize the growth response of a plant to the levels of two environmental factors is by plotting its zero isocline in the resource plane (Fig. 1). This line indicates the resource levels at which growth is zero, thus demarcating the area in the resource space where growth is possible. The most naive approach to constructing the isocline is to assume that growth simply requires a fixed, minimum critical light level ( $l_0$ ) and moisture level ( $m_0$ ). This results in a rectangular isocline (Fig. 1a).

However, isoclines with more or less rounded shapes are probably more realistic (Smith and Huston 1989). Under low light conditions, plants invest proportionally more biomass in leaves and aboveground parts; this increases the transpiration surface relative to the amount of roots and, consequently, the susceptibility to dry conditions. Thus, under low light levels, plants would require higher levels of water to grow and survive. Therefore, the horizontal part of the isocline is expected to bend upwards to the left (Fig. 1b). In con-

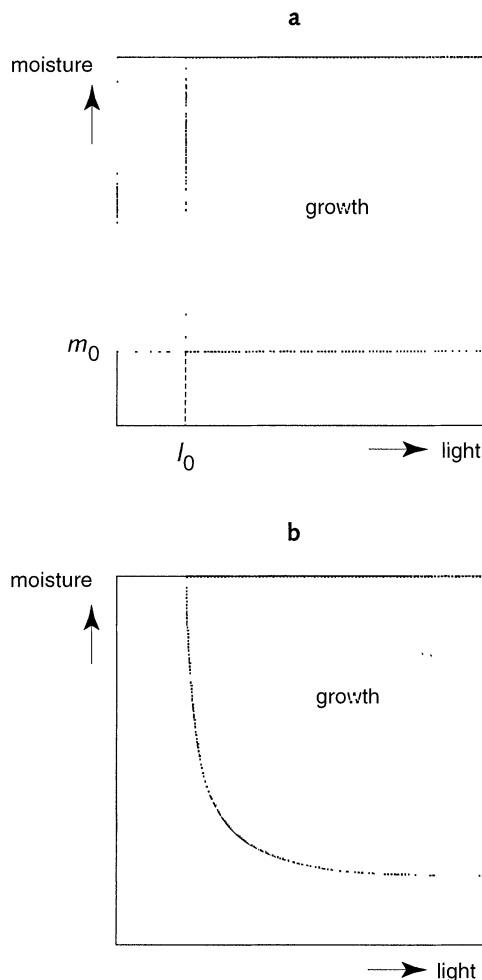


FIG. 1. Plant growth response to light and moisture, showing a positive net plant growth in the shaded region delimited by the zero-growth isoclines. (a) The simplest assumption, with respect to the shape of the isocline, is that plants can grow if both light and moisture exceed a critical minimum level ( $l_0$  and  $m_0$ , respectively). However, a rounded isocline (b) is more realistic for plants facing a physiological trade-off between drought and shade tolerance.

trast, under drier conditions, plants allocate relatively more biomass to roots than to aboveground structures. As a consequence, the ratio of respiring biomass to photosynthetic material would increase and, therefore, the amount of light necessary to keep a positive carbon balance should be higher (whole-plant light compensation point). Also, because plants avoid water loss under low water conditions by closing their stomata, higher light levels could compensate for reductions in photosynthetic activity by enhancing the photosynthetic rate. Based on these assumptions, Smith and Huston (1989) predicted that, under drier conditions, the whole-plant light compensation point (i.e., the amount of light at which photosynthesis equals respiration) would shift to higher values and plants would be less

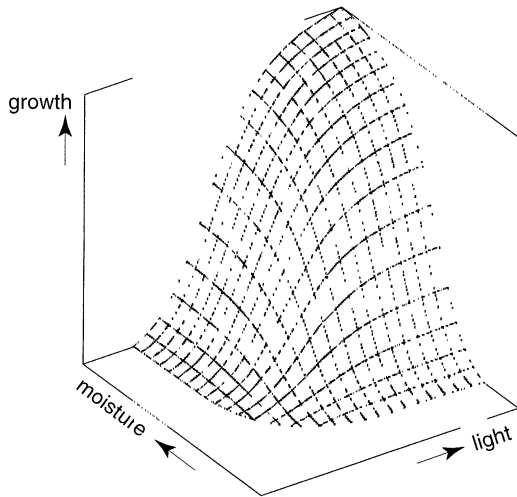


FIG. 2. Plant growth as a function of light and moisture conditions, assuming a physiological trade-off between drought tolerance and shade tolerance. The projection of the shaded area on the horizontal plane is equivalent to the isocline representation of Fig. 1b.

shade tolerant. Consequently, the vertical part of the isocline is expected to bend off to the right at low moisture conditions (Fig. 1b).

When we depict not only the zero isocline but also the growth rate, the picture becomes three dimensional (Fig. 2). If one assumes that the growth response to one factor can be described by a saturation curve, the response to two factors has the shape of a quarter bell.

#### *Canopy effect on light and moisture*

Light is obviously reduced under a plant canopy. The effect of a plant canopy on the moisture environment that a seedling experiences is more complicated. Any large plant that provides a canopy will also take up soil water and, therefore, will reduce the overall soil water available (Joffre and Rambal 1988). However, for at least two reasons, the moisture environment for an establishing seedling is likely to be more influenced by other mechanisms. First, its shallow root system is initially dependent mainly on the soil water of the most superficial soil layers. For many established trees and shrubs, this may not be an important rooting zone. Second, and probably more important, the water status of a seedling is dependent not only on soil water, but also on its transpiration demands and thermal stress. Many studies have shown that, under the canopy, soil and air temperatures are lower, wind velocity is lower, and air humidity is higher than in the open (Geiger 1965, Larcher 1983, Chen et al. 1995). Because of these microclimatic changes, transpiration demands are lower in the shade and evaporation from the superficial soil layer will also be lower (Larcher 1983). In fact, evaporation and transpiration rates tend to follow the same patterns (Abd El Rahman and Batanouny 1965b). This

reduced evaporation generally helps to maintain higher water availability in the shaded top layers of the soil for longer periods of time (Fuller 1914, Shreve 1931, Parker and Muller 1982, Joffre and Rambal 1988, Bradshaw and Goldberg 1989, Vetaas 1992, Barton 1993).

In some cases, upper-horizon water conditions may improve only slightly, or may even decline under the nurse plant (Shreve 1931, Nobel 1989). However, even when soil water conditions do not improve under the shade, the reduction in transpiration demands and thermal stress will tend to improve the seedling water relations. In summary, the microsite for a seedling under a nurse plant has its own microclimate, which is usually characterized by more favorable moisture conditions but less light than in nearby open areas. This implies that, in a given area with otherwise homogeneous topographic, soil, and precipitation conditions, microsite moisture decreases as microsite light increases from the canopy to the open places. It is difficult to infer, *a priori*, the precise form of this relationship in any specific case. Therefore, we simply assume a straight line as a default (Fig. 3). The slope of this line represents the decrease in microsite moisture going from the shade to the open. This slope depends critically on the general climatic conditions. In very wet areas, moisture will be high, irrespective of the radiation exposure, whereas in drier situations, light availability and microsite moisture conditions will be more negatively correlated. Note that zero light does not occur in practice. Therefore, the (dotted) left part of the depicted gradients is not found in nature. The maximum shade that occurs in an area depends on the number of leaf layers shading

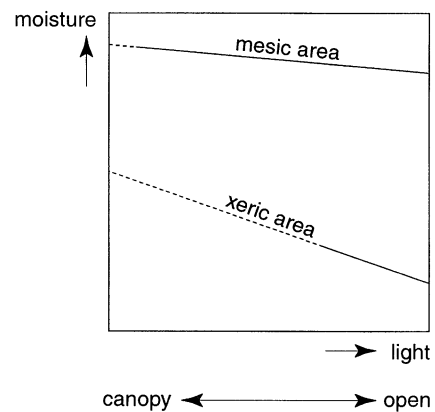


FIG. 3. Hypothesized correlation between microsite light and moisture conditions for establishing seedlings, along a gradient from shade under the canopy to unprotected open places. In mesic areas, moisture conditions will be relatively good even in the open. In drier areas, however, the canopy of the overstory reduces the evapotranspiration demands, resulting in enhanced moisture conditions for establishing plants (higher slope). Under xeric conditions, plants do not produce a dense canopy, and deep shade does not occur. Therefore, the dashed left-hand part of the microclimatic gradient is unlikely to be found in nature.

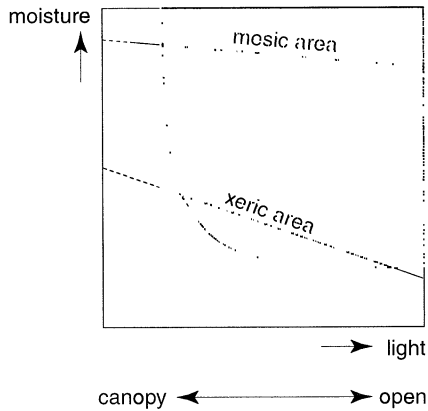


FIG. 4. Overlay of the plant growth response (Fig. 1b) and the microclimatic gradients of light and moisture (Fig. 3). In dry areas, water stress inhibits growth in the open, and seedling establishment will be restricted to shady sites.

the grounded surface (leaf area index). Deep shade is more likely to be found in mesic, productive environments (Whittaker and Likens 1975, Larcher 1983). Therefore, in dry areas where vegetation is sparse, the relevant part of the gradient is further restricted to the right (light) side.

#### *Implications for facilitation and competition*

The consequences of the interplay of microclimatic gradients and physiological trade-offs can be explored by combining the graphical relationships we have introduced. A first impression can be obtained from an overlay of the zero-growth isocline with the microclimatic gradients (Fig. 4). In humid (mesic) areas, growth is possible along the entire gradient, with the exception of the deep shade. In the dry (xeric) areas, however, growth is also impossible at the high-light end of the gradient because of increased water stress in the open, unprotected sites. Here, seedling growth is only possible in the shade of nurse plants. As we have argued, deep shade may be rare in xeric areas. Therefore, this facilitative effect of nurse plants can actually dominate the field patterns of seedling establishment under dry conditions.

Note that facilitation can occur despite the fact that the isocline is not rectangular. Thus, even if plants in the shade are assumed to be more sensitive to drought, seedlings in xeric areas may perform better in the shade, due to the inverse correlation between microsite moisture conditions and light. Facilitation occurs only if the improvement of microsite moisture with shade exceeds the hypothesized increased moisture requirements due to shade acclimation (the trade-off).

Intersection of the microclimatic gradients with the seedling growth response to light and moisture (Fig. 5) gives a more detailed view of the net effect of altered light and moisture conditions under nurse canopies on seedling growth. In very mesic areas, overall growth

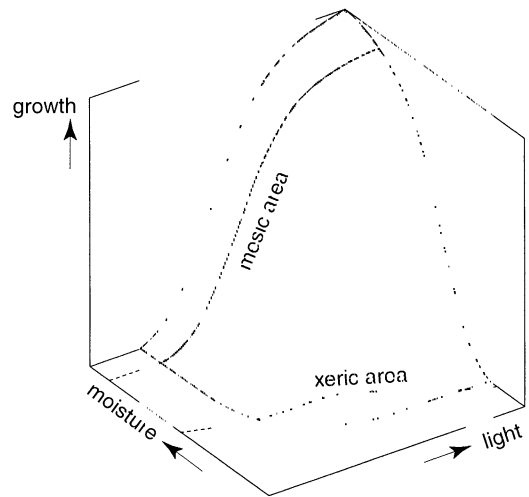


FIG. 5. Intersection of the hypothesized correlation between microsite light and moisture (Fig. 3) with seedling growth (Fig. 2) as a function of those factors. It shows the resulting variation in growth along a gradient from the shade to the open, in both moist and dry areas.

rates are much higher than under xeric conditions. Under such climatic conditions, water stress might never be really important, even in the open, and growth simply declines with shade. In more xeric areas, however, the decrease of microsite moisture toward the open becomes important.

The net effect of the interplay of shading and enhanced water relations along the gradient from the open to the canopy can be seen more clearly if the growth along the gradient is projected in the light-growth plane (Fig. 6). Growth in xeric areas shows an unimodal

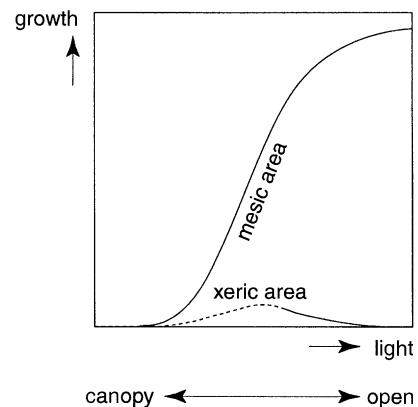


FIG. 6. Growth of establishing plants along a gradient from shady to open places, obtained by projecting the intersections shown in Fig. 5 on the light-growth plane. For xeric areas, the negative slope on the right-hand side of the growth response implies facilitation, because growth decreases with the distance from the canopy of nurse plants. Very shady conditions (dashed) may be absent in dry areas; hence, facilitation may actually be the only obvious pattern with respect to seedling establishment.

response along the gradient from shade to light. On the high-light side of the gradient, seedling growth declines with distance from the established "nurse" vegetation. Obviously, this is what is commonly referred to as facilitation.

#### DISCUSSION

The graphical model presented here focuses on the effects of shade and dry conditions on the growth response of a single, hypothetical species to clarify the balance of facilitative and competitive aspects. In practice, communities consist of many species with different responses to environmental conditions. Drought-tolerant plants will often prevail in the open, whereas shade-tolerant plants are found under the canopy. Also, plant communities in xeric areas will have more drought-tolerant species, whereas lush forests in mesic areas will harbor more shade-tolerant species. From the previously discussed physiological trade-offs, one would expect shade-tolerant species to be relatively sensitive to water stress (Smith and Huston 1989). This implies that, even in mesic areas, facilitation through improvement of microsite moisture conditions may occur. Water stress is less extreme than in xeric areas, yet more species will tend to be intolerant of dry conditions. In terms of growth isoclines (Fig. 4), such shade-tolerant, but drought-intolerant, species will have an isocline that reaches farther to the left (shady) side of the graph, but does not extend as much to low moisture levels as does the depicted isocline. As a result, even a moderate decline in microsite moisture, on a gradient from the canopy to the open in mesic areas, may result in a noticeable reduction of seedling performance. Indeed, as shown in our examples of field patterns, facilitation is often found in xeric areas, but occurs also in mesic environments such as temperate forests and grasslands. A tulip poplar seedling in a forest gap may have drought problems as severe as those of a succulent seedling in the open desert, even though the latter site is drier in absolute terms.

As illustrated by the field studies we have cited, improvement of plant water relations under the shade of a nurse plant is thought to play an important role in many reported cases of facilitation, over a wide array of different plant communities. Nonetheless, factors other than water are often found to explain facilitative patterns. Enhanced nutrient conditions (Muller 1953, Franco and Nobel 1989, Callaway et al. 1991, Belsky 1994, Maun 1994) and protection from herbivores (Ellison and Houston 1958, Turner et al. 1969, Atsatt and O'Dowd 1976, Jaksic and Fuentes 1980, Fuentes et al. 1984, 1986, McAuliffe 1984b, 1986) under the nurse canopy are frequently reported. In principle, the graphical model could also be applied to these mechanisms. Largely, the same graphs could be defended after changing the text on the vertical axis from moisture to nutrients, or (inverting the axis) to herbivory losses.

However, rather than adjusting the model to analyze other specific mechanisms, we extend the basic idea to a more general, mechanistic framework for understanding the balance of facilitation and competition.

In practice, there will always be a complex gradient of various resources and disturbances going from the open to the canopy. Over this gradient, some factors (e.g., nutrients, water) will change for the better, whereas others (e.g., light, allelopathic exudates) will change for the worse. The net effect of these correlated changes will depend on the combined response of plants to all factors involved. If a factor that improves under the canopy happens to be the only "limiting factor," that is, if the effect of the simultaneous change in other factors is nil, the net effect of the canopy will obviously be facilitative. However, in reality, the matter will usually be more complicated. Rarely will the impact of one environmental factor be independent of the value of others. As argued by Smith and Huston (1989), physiological trade-offs may affect the capacity of a plant to simultaneously tolerate shade and drought. Similarly, plants with a better nutrient status are probably more tolerant of moderate water stress, because of changes in their capacity for osmotic adjustment (Morgan 1984, Munns 1988) and their response to abscisic acid (Schulze 1991). Additionally, plants will be less capable of compensating for herbivory losses when their productivity is low due to shading. In summary, the general pattern is probably that the negative effects of one limiting factor often can be compensated for, to a certain extent, by improvement in other environmental conditions.

If the interactive effects of various environmental factors act in such a way that, when one environmental factor becomes unfavorable, then the requirements for other factors increase, this implies that isoclines in the multidimensional environmental-factor space will tend to be curved rather than rectangular. Whether facilitation will occur depends on the way in which the various factors change over a gradient from the canopy to the open. In the model we have presented for light and water, facilitation occurs only if the environmental line declines more steeply than the growth isocline at the right side (Fig. 4). Thus, in order to lead to facilitation, the increase in microsite moisture under the canopy should exceed the increase in moisture demand when plants acclimatize to shade. Phrased in general terms, the condition required for facilitation to occur is that improvement in an environmental factor (e.g., water, nutrients, herbivory) under the canopy must exceed the increased "demand" for that factor caused by deterioration in another factor (e.g., light). Only when factors such as herbivory, water, or nutrient limitation pose a dominant constraint to plant recruitment may the effect of an improvement in these factors under the nurse canopy outweigh the costs of reduced light levels, enabling facilitation to occur. This fits with the view that



facilitation is typical of stressful environments (Bertness and Callaway 1994). However, as argued earlier, even environments that may seem mild at first glance may be stressful for particular species, leading to facilitation.

It is obvious that the net effect of nurse canopies on the understory may easily shift from facilitative to competitive, or vice versa, when conditions change. For example, many studies show that facilitative effects are stronger on drier sites and in drier years (Parker and Muller 1982, Fuentes et al. 1984, Frost and McDougald 1989, Hillier 1990, Belsky et al. 1993, Berkowitz et al. 1995). Experimental addition of water has been shown to enhance seedling survival and growth much more in open areas than under the canopy (De Jong and Klinkhamer 1988, Shumway and Bertness 1992). Also, experimental manipulations in salt marshes have shown that alleviation of the stress can switch the effects of the interaction from facilitative to competitive (Bertness and Shumway 1993, Bertness and Hacker 1994, Bertness and Yeh 1994, Shumway and Bertness 1994). In addition, the net effect of plants on other plants can change dramatically over time, as a result of growth. Newly established plants can eventually shade out the former nurse plant, and their extending root systems allow uptake from limited sources that were previously available only to the nurse plant (Conard and Radosevich 1982, McAuliffe 1984a, Valiente et al. 1991a, b). Moreover, competition with other small plants in the shade can increase because of the common exploitation of limited resources in the top soil layers (Aguilar and Sala 1994).

Clearly, the net effect of one plant on another plant can easily shift from negative to positive and vice versa. The terms facilitation and competition refer to the net effect of changes in the environment of a plant, caused by the presence of other plants. In practice, however, competition and facilitation are often discussed almost as if they were completely exclusive processes acting in plant communities. Addressing explicitly the intertwined positive and negative effects that plants have on the environment of other plants may prove to be a fruitful way to enhance our understanding of the highly variable nature of plant-plant interactions.

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