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Are positive interactions species-specific?

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Positive interactions among plants, or facilitations, have been demonstrated in a wide variety of communities around the world (see reviews by DeAngelis et al. 1986, Hunter and Aarssen, 1988, Bertness and Callaway 1994, Callaway 1995, Callaway and Walker in press). Neighboring plant species compete with one another for resources, but they may also provide benefits for each other such as shade, higher nutrient levels, more available moisture, soil oxygenation, protection from herbivores, more favorable soil microflora, transfer of resources and fixed carbon via mycorrhizae, and increased pollinator visits (Callaway 1995).

The species-specificity of positive interactions among plants – whether or not benefactor species are highly interchangeable – is central to understanding the general role of positive interactions in plant communities. In other words, are the positive effects of plants simply due to general changes in the biophysical environment; that which can be imitated by inanimate objects like rocks, microtopography, or experimental shade cloth? Or can facilitation depend on the species, with some species eliciting strong positive effects and other morphologically similar species producing neutral or negative effects? The species specificity of positive interactions is pertinent to our general concepts of plant communities (see Gleason 1926, Goodall 1963, Shipley and Keddy 1987, Austin 1990, Collins et al. 1993, Callaway 1997). If positive interactions are often species-specific, then many plant communities may be more interdependent than currently thought.

Here, I have explored the specificity of positive interactions among plants by examining the literature and asking the following questions: 1) Are beneficiary species non-randomly associated with potential benefactors? 2) Are positive mechanisms produced by species-specific plant traits? 3) Can potential benefactors have similar positive effects, but different negative effects?

Are beneficiary species non-randomly associated with potential benefactors?

Clearly, there is specificity to some positive associations as a consequence of differences in plant morphology and size. The positive effects of shade that appear to be required by many cacti cannot be acquired from desert ephemerals. However, there are examples of variation in the effects of potential benefactors that are similar in morphology and would seem to have the same potential to facilitate neighbors.

One of the first, and still most widely publicized, examples of facilitation is that involving *Carnegiea gigantea*, the saguaro cactus in Sonoran Desert communities. Shreve (1931) observed that saguaro seedlings were common under desert shrubs and trees, but not in open spaces. Patterns of positive spatial associations between seedlings of one species and sheltering adults of another species became widely referred to as the “nurse plant syndrome” because of the work of Niering et al. (1963), Turner et al. (1966, 1969), and Steenberg and Lowe (1969, 1977). They found that saguaro seedlings were commonly sheltered by many different species of perennial plants, but predominantly by *Cercidium microphyllum* (paloverde tree). Spatial patterns suggestive of nurse plant relationships have since been reported for many species in arid and semiarid environments around the world (Yeaton 1978, McAuliffe 1986, Franco and Nobel 1989, Yeaton and Elser 1990, Valiente-Banuet et al. 1991, Arriaga et al. 1993, Flores-Martinez et al. 1994, Callaway, 1995, Pugnaire et al. 1996a, b, Suzán et al. 1996).

Hutto et al. (1986) reported that saguaros were distributed non-randomly among potential nurse plants at two locations in Organ Pipe National Monument in the Sonoran Desert. They found that saguaros were proportionally more abundant under many species of shrubs and trees than in the open, but significantly more saguaros were associated with *Prosopis juliflora* (mesquite) and paloverde trees and fewer saguaros were

associated with *Larrea tridentata* (creosote bush) than expected based on the proportional cover of these species. In the northern Sonoran Desert, McAuliffe (1986) found that the common desert nurse plant, *Cercidium*, appeared to be nursed itself by another species. Proportionally more *Cercidium* seedlings were found under *Ambrosia* spp. than other shrub species, but this positive interaction appeared to be due to superior shelter from rabbits provided by the dense, low-lying *Ambrosia* canopies.

McAuliffe (1988) also found strong, species-specific patterns of association in other more complex Sonoran Desert communities and in Mojave Desert plant communities. In both regions, young lifestages of many species were much more frequently under *Ambrosia dumosa* canopies than those of other shrubs. In similar communities in the central mountains of Baja California, young alluvial terraces are codominated by a rich assemblage of shrubs and cacti including the important nurse plant *Viguiera laciniata* (McAuliffe 1991, pers. comm.) and *Larrea*, which is generally a poor nurse plant (see below), is absent. On older, adjacent terraces *Larrea* is dominant, the preferred nurse plant, *Viguiera*, is absent, and there is no regeneration of *Idria columnaris* (boojum) and *Pachycerus pringli* (cardone cactus), which are the species primarily associated with *Viguiera*.

Suzán et al. (1996) identified a large number of aborescent, shrub, and cacti species as highly associated with *Olneya tesota* (ironwood) in the Sonoran Desert and argued that, as a habitat modifier, *Olneya* is a “keystone species” for biodiversity (also see Burquéz and Quintana 1994). They described 30 species as “shade dependent”, with five preferring *Cercidium* species, four preferring *Prosopis* species, and 22 preferring *Olneya tesota*. As many others, Franco and Nobel (1989) found that most saguaro seedlings in their Sonoran Desert study sites were associated with paloverde trees. In contrast, a second cactus species, the exceptionally heat-tolerant *Ferocactus acanthodes*, was preferentially associated with a bunchgrass, *Hilaria rigida*. Valiente-Banuet et al. (1991) found similar disproportional associations among many potential nurse plants and five different species of cacti in central Mexico.

On barren volcanic soils in southern Idaho, two early colonizing species of *Eriogonum* differ strikingly in their positive associations with other species that appear to regenerate underneath them (Day and Wright 1989). Five other species were found to be strongly associated with *Eriogonum ovalifolium*, but no species were consistently associated with *Eriogonum umbellatum*. These differences were attributed to the different aboveground architecture of the two *Eriogonum* species.

In Californian shrubland and woodland, *Quercus agrifolia* and *Q. douglasii* seedlings are disproportionately associated with shrubs versus open grassland, and

experimental manipulations have demonstrated the importance of nurse shrubs for the survival of both species (Callaway and D’Antonio 1991, Callaway 1992). However, not all shrubs had the same positive effects on *Q. agrifolia*. Forty-three percent of germinating seedlings survived under *Ericameria ericoides*, 34% under *Artemisia californica*, 5% under *Mimulus aurantiacus*, and 0% under *Lupinus chamissonis* (Callaway and D’Antonio 1991). In another experimental planting in tropical savannas in Belize, Kellman (1985) found that the survival of *Xylopia frutescens* (a forest tree) was five times higher under *Miconia albicans* than under four other woody trees or shrubs. His data suggested that potassium and phosphorus nutrition may have been more favorable under *Miconia* than the other species.

In other studies, the species of the benefactor plant did not seem to matter. For example, Steenberg and Lowe (1969) reported that 15 different species can apparently act as nurse plants for saguaro and are found associated with saguaro seedlings in proportion to their frequencies, indicating that no specific biotic factor is involved, and that the nurse plant association is only the by-product of general microclimatic changes. Greenlee and Callaway (1996) found that *Lesquerella carinata*, a small perennial herb, was commonly under the canopies of bunchgrasses on xeric sites in western Montana. However, *Lesquerella* was distributed among bunchgrass species in proportion to their abundances.

In some cases, similar beneficiary species cannot utilize the same nurse plant. In many parts of the Great Basin, *Artemisia tridentata* acts as a nurse plant for *Pinus monophylla* (Everett et al. 1986, Callaway et al. 1996). In contrast, experiments showed that *A. tridentata* competitively excluded *Pinus ponderosa* (another pine with high water-use-efficiency) from most soils and restricted it to outcrops of low-P and acidic soils (DeLucia et al. 1988, Callaway et al. 1996).

In summary, beneficiaries are often found associated with particular benefactor species and there is the potential for species-specificity in positive interactions in many plant communities.

Are positive mechanisms produced by species-specific plant traits?

Some facilitative mechanisms are products of unusual plant traits, and thus have a high degree of species-specificity. For example, some of the strongest positive effects are produced by protection from herbivores (Atsatt and O’Dowd 1976, McAuliffe 1984, 1986, Hay 1986). Repelling consumers requires specific morphological traits such as spines, tough tissues, or the possession of chemical defenses. Not all potential benefactors in a community may have these traits.

Strong consumers exist *within* the plant community. Interplant parasitism is a widespread phenomenon with over 3000 species of parasitic plants having been identified worldwide (Kuijt 1969). Most parasitic plants are highly host specific and thus have the potential to indirectly facilitate non-hosts in the community. In California salt marshes, *Cuscuta salina* mediates interactions by preferentially consuming the dominant *Salicornia virginica*, which indirectly facilitates several inferior competitors (Pennings and Callaway 1996). In one of four sites studied, Gibson and Watkinson (1992) found that the hemiparasite, *Rhinanthus minor*, increased grassland plant diversity by suppressing a dominant competitor, and indirectly facilitating non-hosts. Direct effects in these systems are parasitic, but the indirect positive effects are not interchangeable among species.

Soil oxygen often limits plant growth in wetlands (McDrew 1983). To alleviate oxygen limitation in their roots, many wetland emergent plants passively transport oxygen from leaves to roots through aerenchymous tissue (Armstrong 1979). In some cases oxygen may leak out of submerged roots and oxidize toxic substances and nutrients in the rhizosphere and oxygenate marsh sediments (Howes et al. 1981, Armstrong et al. 1992, Howes and Teal 1994). Schat and Van Beckhoven (1991) reported that *Plantago coronopus* and *Samolus valerandi* were clumped around tussocks of the aerenchymous *Juncus maritimus* in dune slacks on the coast of Holland, where higher soil oxygen and oxidation of iron, manganese, and sulfide improved conditions for the beneficiaries. *Spartina maritima* aerates surface sediments in southern Spain, creating conditions favorable for the invasion of *Arthrocnemum perenne* (Castellanos et al. 1994). In greenhouse experiments, pots containing cattails (*Typha latifolia*) had dissolved oxygen contents over four times greater than pots without cattails, and other marsh plants grown with *Typha* survived longer and grew larger than in pots without cattails when pot substrates were kept between 11 and 12°C (Callaway and King 1996). Hacker and Bertness (1995) found that *Iva frutescens* benefited from oxygen lost from the roots of *Juncus gerardi*. For plants to facilitate others via soil aeration, they must possess highly aerenchymous tissues; thus not just any species will do for a benefactor.

Co-flowering species may attract pollinators for their less attractive neighbors. Thomson (1978) found that *Hieracium florentinum* received more pollinator visits when it was mixed with *H. aurantiacum* than when it was alone. Laverty and Plowright (1988) found that fruit and seed set in *Podophyllum peltatum* was enhanced when they were spatially associated with *Pedicularis canadensis*. In later studies, Laverty (1992) found that *Podophyllum*, which produces no nectar, depends on infrequent visits from bumble bees that accidentally encounter them while collecting nectar from *Pedicularis*. Clearly, this type of facilitation is highly species-specific.

Woody perennials may improve the water relations of understory plants through “hydraulic lift”, the movement of water from deep, moist soils to dry, surface soils at night when the stomata are closed and the lowest water potentials are in the upper soil layers (Richards and Caldwell 1987, Dawson 1993). Dawson (1993) showed that all of 12 understory species examined derived some (3–60%) hydraulically lifted water from overstory *Acer saccharum* (sugar maple). The amount of hydraulically lifted water obtained by an understory species decreased markedly with increasing distance from the tree. In this case, as for many others, the positive relationship depends on the specific root architecture that permits a particular overstory species to hydraulically lift water and deposit it near the surface.

Positive effects of one plant species on another may function through fungal intermediaries. Grime et al. (1987) found that labeled ¹⁴C was transferred from *Festuca ovina* to many other plant species (including *Centaurea nigra*) in artificial microcosms that shared a common mycorrhizal network, but not to others that did not share the network. Mutual infection led to decreased biomass of the dominant *Festuca* and increased biomass of otherwise competitively inferior species, and ultimately experimental microcosms that were infected with mycorrhizae were more diverse than those that were not infected. Marler et al. (unpubl.) tested the effects of other *Festuca* and *Centaurea* species, *F. idahoensis* and *C. maculosa*, and found that mycorrhizae mediated strong positive effects of *Festuca* on *Centaurea*. When *Centaurea* was grown with large *Festuca* in the presence of mycorrhizae, they were 66% larger than in the absence of mycorrhizae. Mycorrhizae have also been found to move nutrients among plant species (Walter et al. 1996). Simard et al. (1997) used reciprocal isotope labeling to document bidirectional transfer of carbon among forest trees in the northwest United States. The rate of transfer varied in different shade treatments, but not all species involved in the study were able to participate equally in the interaction. The species-specificity of fungi-mediated positive interactions are not clear; however, considering the broad range of species-specific effects of mycorrhizae on plants it is unlikely that interacting species are highly interchangeable.

Can potential benefactors have similar positive effects, but different negative effects?

Facilitative effects do not occur apart from competition. Therefore, different benefactor species may have the same positive effect, but vary in their negative effects. For example, Suzán et al. (1996) suggested that *Olneya*'s superior facilitative ability may be due to its phreatophytic life history and deeply distributed root

architecture, thus reducing niche overlap (e.g. Cody 1986) relative to other potential benefactors, and accentuating its positive mechanisms. The degree of root overlap between *Quercus douglasii* (blue oaks) and understory annuals has been shown to determine either a negative or positive effect of the overstory oak in savanna and woodlands of central California (Callaway et al. 1991). They found that blue oaks added considerable amounts of nutrients to the soil beneath their canopies and that soil and litter bioassays demonstrated strong facilitative effects of these components on the growth of a dominant understory grass, *Bromus diandrus*. In the field, however, the expression of this facilitative mechanism was determined by the root architecture of individual trees. Trees with low fine root biomass in the upper soil horizons and that appeared to root at the water table elicited strong positive effects on understory biomass. In contrast, trees with high fine root biomass in the upper soil horizons and that did not appear to root at the water table elicited strong negative effects on understory productivity. Experimental exclusion of the roots under trees with high root biomass in shallow soils elicited the expression of positive effects.

The poor performance of *Larrea tridentata* as a nurse plant (Hutto et al. 1986, McAuliffe 1988) may be due to the strong negative effects this species has on perennial neighbors (Fonteyn and Mahall 1981). Mahall and Callaway (1991, 1992) found that *Larrea* substantially inhibited the root elongation rates of *Ambrosia dumosa*, and that these negative effects were reduced by the addition of small amounts of activated carbon, a strong adsorbent to organic molecules (Cheremisinoff and Ellerbusch 1978). Thus *Larrea* canopies may have the potential to facilitate some shade-requiring species (see Yeaton 1978, Casper, 1996), but some prospective beneficiaries appear to be eliminated by root allelopathy and competition. Muller (1953) documented strong positive associations between *Ambrosia dumosa* and many species of desert annuals; however, *Encelia farinosa* shrubs in the same area did not harbor any annual species. He attributed this difference to the inhibitory effects of leachates from *Encelia* leaves.

Species that have similar effects on understory microclimate may vary in their effects on soil nutrients. Turner et al. (1966) found that saguaro seedlings survived better on soil collected from under *Cercidium* trees than on soils from under either *Prosopis* or *Olneya tesota*; however, these differences were confounded by soil albedo and temperature.

Implications for community ecology

Although some facilitative relationships appear to be due to simple, non-species-specific changes in the bio-

physical environment, many others appear to be species-specific. Most positive interactions among plants also appear to be commensal, with only one species benefiting from the presence of the other. However, positive effects may be reciprocal (Pugnaire et al. 1996a) and some facilitative processes such as resource sharing via mycorrhizae and root grafts, and associational defenses have the potential to be mutualistic. If beneficiaries opportunistically take advantage of favorable changes caused by benefactors coevolution is unlikely, but if strong reciprocal species-specific interactions exist, they have the potential to promote coevolution within plant communities. Species-specific positive interactions also have important consequences for community theory. Since the 1950's, plant communities have been widely regarded as largely individualistic, with the distributions of species being determined by their responses to the abiotic environment and modified by competition. Highly species-specific positive interactions within plant communities suggest that plant communities may be less individualistic than currently thought.

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References

- Armstrong, W. 1979. Aeration in higher plants. – *Adv. Bot. Res.* 7: 226–332.
- Armstrong, J., Armstrong, W. and Becket, P. M. 1992. *Phragmites australis*: venturi- and humidity-induced pressure flows enhance rhizome aeration and rhizosphere oxidation. – *New Phytol.* 120: 197–207.
- Arriaga, L., Maya, Y., Diaz, S. and Cancino, J. 1993. Association between cacti and nurse perennials in a heterogeneous dry forest in northwestern Mexico. – *J. Veg. Sci.* 4: 349–356.
- Atsatt, P. R. and O'Dowd, D. J. 1976. Plant defense guilds. – *Science* 193: 24–29.
- Austin, M. P. 1990. Community theory and competition in vegetation. – In: Grace, J. B. and Tilman, D. (eds), *Perspectives on plant competition*. Academic Press, pp. 215–238.
- Bertness, M. D. and Callaway, R. M. 1994. Positive interactions in communities. – *Trends Ecol. Evol.* 9: 191–193.
- Burquez, A. and Quintana, M. A. 1994. Islands of diversity: ironwood ecology and the richness of perennials in a Sonoran Desert Biological Preserve. – In: Nabhan, G. P. and Carr, J. L. (eds), *Ironwood: an ecological and cultural keystone of the Sonoran Desert*. Conservation International, pp. 9–28.
- Callaway, R. M. 1992. Effect of shrubs on recruitment of *Quercus douglasii* and *Quercus lobata* in California. – *Ecology* 73: 2118–2128.
- 1995. Positive interactions among plants. – *Bot. Rev.* 61: 306–349.
- Callaway, R. M. 1997. Positive interactions in plant communities and the individualistic-continuum concept. – *Oecologia* 112: 143–149.
- and D'Antonio, C. M. 1991. Shrub facilitation of coast live oak establishment in central California. – *Madroño* 38: 158–169.

- and King, L. 1996. Oxygenation of the soil rhizosphere by *Typha latifolia* and its facilitative effects on other species. – Ecology 77: 1189–1195.
- and Walker, L. R. 1997. Competition and facilitation: a synthetic approach to interactions in plant communities. – Ecology 78: 1958–1965.
- , Nadkarni, N. M. and Mahall, B. E. 1991. Facilitation and interference of *Quercus douglasii* on understory productivity in central California. – Ecology 72: 1484–1499.
- , DeLucia, E. H., Moore, D., Nowak, R. and Schlesinger, W. H. 1996. Competition and facilitation: contrasting effects of *Artemisia tridentata* on *Pinus ponderosa* and *P. monophylla*. – Ecology 77: 2130–2141.
- Casper, B. 1996. Demographic consequences of drought in the herbaceous perennial *Cryptantha flava*: effects of density, associations with shrubs, and plant size. – Oecologia 106: 144–152.
- Castellanos, E. M., Figueroa, M. E. and Davy, A. J. 1994. Nucleation and facilitation in saltmarsh succession: interactions between *Spartina maritima* and *Arthrocnemum perenne*. – J. Ecol. 82: 239–248.
- Cheremisinoff, P. N. and Ellerbusch, F. 1978. Carbon adsorption handbook. – Ann Arbor Sci. Publ., Ann Arbor, MI.
- Collins, S. L., Glenn, S. M. and Roberts, D. W. 1993. The hierarchical continuum concept. – J. Veg. Sci. 4: 149–156.
- Cody, M. L. 1986. Structural niches in plant communities. – In: Diamond, J. and Case, T. J. (eds), Community ecology. Harper and Row, New York, pp. 381–405.
- Dawson, T. E. 1993. Hydraulic lift and water use by plants: implications for water balance, performance and plant-plant interactions. – Oecologia 95: 565–574.
- Day, T. A. and Wright, R. G. 1989. Positive plant spatial association with *Eriogonum ovalifolium* in primary succession on cinder cones: seed-trapping nurse plants. – Vegetatio 70: 37–45.
- DeAngelis, D. L., Post, W. M. and Travis, C. C. 1986. Positive feedback in natural systems. – Springer-Verlag, New York.
- DeLucia, E. H., Schlesinger, W. H. and Billings, W. D. 1988. Water relations and the maintenance of Sierran conifers on hydrothermally altered rock. – Ecology 69: 303–311.
- Everett, R. L., Koniak, S. and Budy, J. 1986. Pinyon seedling distribution among soil surface microsites. – Res. Pap. INT-363. USDA, Forest Serv. Intermountain Research Station, Ogden, UT.
- Flores-Martinez, A., Ezcurra, E. and Sanchez-Colon, S. 1994. Effect of *Neobuxbaumia tetetzo* on growth and fecundity of its nurse plant *Mimosa luisana*. – J. Ecol. 82: 325–330.
- Fonteyn, P. J. and Mahall, B. E. 1981. An experimental analysis of structure in a desert plant community. – J. Ecol. 69: 883–896.
- Franco, A. C. and Nobel, P. S. 1989. Effect of nurse plants on the microhabitat and growth of cacti. – J. Ecol. 77: 870–886.
- Gibson, C. C. and Watkinson, A. R. 1992. The role of the hemiparasitic annual *Rhinanthus minor* in determining grassland community structure. – Oecologia 89: 62–68.
- Gleason, H. A. 1926. The individualistic concept of the plant association. – Bull. Torrey Bot. Club 53: 7–26.
- Goodall, D. W. 1963. The continuum and the individualistic association. – Vegetatio 11: 297–316.
- Greenlee, J. T. and Callaway, R. M. 1996. Abiotic stress and the importance of interference and facilitation in montane bunchgrass communities in western Montana. – Am. Nat. 148: 386–396.
- Grime, J. P., MacKey, J. M., Hillier, S. H. and Reid, D. J. 1987. Floristic diversity in a model system using experimental microcosms. – Nature 328: 42–422.
- Hacker, S. D. and Bertness, M. D. 1995. Morphological and physiological consequences of a positive plant interaction. – Ecology 76: 2165–2175.
- Hay, M. E. 1986. Associational plant defenses and the maintenance of species diversity: turning competitors into accomplices. – Am. Nat. 128: 617–641.
- Howes, B. L. and Teal, J. M. 1994. Oxygen loss from *Spartina alterniflora* and its relationship to salt marsh oxygen balance. – Oecologia 97: 431–438.
- , Howarth, R. W., Teal, J. M. and Valiela, I. 1981. Oxidation-reduction potentials in a salt marsh: spatial patterns and interactions with primary production. – Limnol. Oceanogr. 26: 350–360.
- Hunter, A. F. and Aarssen, L. W. 1988. Plants helping plants. – Bioscience 38: 34–40.
- Hutto, R. L., McAuliffe, J. R. and Hogan, L. 1986. Distributional associates of the saguaro (*Carnegiea gigantea*). – Southwest. Nat. 31: 469–476.
- Kellman, M. 1985. Forest seedling establishment in Neotropical savannas: transplant experiments with *Xylopia frutescens* and *Calophyllum brasiliense*. – J. Biogeogr. 12: 373–379.
- Kuijt, J. 1969. The biology of parasitic flowering plants. – Univ. of California Press, Berkeley, CA.
- Lavery, T. M. 1992. Plant interactions for pollinator visits: a test of the magnet species effect. – Oecologia 89: 502–508.
- and Plowright, R. C. 1988. Fruit and seed set in Mayapple (*Podophyllum peltatum*): influence of intraspecific factors and local enhancement near *Pedicularis canadensis*. – Can. J. Bot. 66: 173–178.
- Mahall, B. E. and Callaway, R. M. 1991. Root communication among desert shrubs. – Proc. Natl. Acad. Sci. USA, 88: 874–876.
- and Callaway, R. M. 1992. Root communication mechanisms and intracommunity distributions of two Mojave Desert shrubs. – Ecology 73: 2145–2151.
- McAuliffe, J. R. 1984. Sahuaro-nurse tree associations in the Sonoran Desert: competitive effects of sahuaros. – Oecologia 64: 319–321.
- 1986. Herbivore-limited establishment of a Sonoran Desert tree: *Cercidium microphyllum*. – Ecology 67: 276–280.
- 1988. Markovian dynamics of simple and complex desert plant communities. – Am. Nat. 131: 459–490.
- 1991. Demographic shifts and plant succession along a late Holocene soil chronosequence in the Sonoran Desert of Baja California. – J. Arid Environ. 20: 165–178.
- McDrew, M. C. 1983. Plant injury and adaptation to oxygen deficiency in the root environment. – Plant Soil 75: 179–199.
- Muller, C. H. 1953. The association of desert annuals with shrubs. – Am. J. Bot. 40: 53–60.
- Niering, W. A., Whittaker, R. H. and Lowe, C. H. 1963. The saguaro: a population in relation to environment. – Science 142: 15–23.
- Pennings, S. C. and Callaway, R. M. 1996. Impact of a native parasitic plant on salt marsh vegetation structure and dynamics. – Ecology 77: 1410–1419.
- Pugnaire, F. I., Hasse, P. and Puigdefábregas, J. 1996a. Facilitation between higher plant species in a semiarid environment. – Ecology 77: 1420–1426.
- , Haase, P., Puigdefábregas, J., Cueto, M., Incoll, L. D. and Clark, S. C. 1996b. Facilitation and succession under the canopy of the leguminous shrub, *Retama sphaerocarpa*, in a semi-arid environment in south-east Spain. – Oikos 76: 455–464.
- Richards, J. H. and Caldwell, M. M. 1987. Hydraulic lift: substantial nocturnal water transport between soil layers by *Artemisia tridentata* roots. – Oecologia 73: 486–489.
- Schat, H. K. and Van Beckhoven, K. 1991. Water as a stress factor in the coastal dune system. – In: Rozema, J. and Verkleij, J. A. C. (eds), Ecological responses to environmental stresses. Kluwer, Amsterdam, pp. 76–89.
- Shipley, B. and Keddy, P. A. 1987. The individualistic and community unit concepts as falsifiable hypotheses. – Vegetatio 69: 47–55.

- Shreve, F. 1931. Physical conditions in sun and shade. – Ecology 12: 96–104.
- Simard, S. W., Perry, D. A., Jones, M. D., Myrold, D. D., Durall, D. M. and Molina, R. 1997. Net transfer of carbon between ectomycorrhizal tree species in the field. – Nature 388: 579–582.
- Steenberg, W. F. and Lowe, C. H. 1969. Critical factors during the first year of life of the saguaro (*Cereus giganteus*) at Saguaro National Monument. – Ecology 50: 825–834.
- and Lowe, C. H. 1977. Ecology of the saguaro. II. Reproduction, germination, establishment, growth, and survival of the young plant. – Nat. Park Serv. Sci. Monogr. Ser. 8. NPS, Washington.
- Suzán, H., Nablan, G. P. and Patten, D. T. 1996. The importance of *Olneya tesota* as a nurse plants in the Sonoran Desert. – J. Veg. Sci. 7: 635–644.
- Thomson, J. D. 1978. Effects of stand composition on insect visitation in two-species mixtures of *Hieracium*. – Am. Midl. Nat. 100: 431–440.
- Turner, R. M., Alcorn, S. M. and Olin, G. 1969. Mortality of transplanted saguaro seedlings. – Ecology 50: 835–844.
- , Alcorn, S. M., Olin, G. and Booth, J. A. 1966. The influence of shade, soil, and water on saguaro seedling establishment. – Bot. Gaz. 127: 95–102.
- Valiente-Banuet, A., Bolongaro, A., Briones, O., Ezcurra, E., Rosas, M., Nunez, H., Barnhard, G. and Vasquez, E. 1991. Spatial relationships between cacti and nurse shrubs in a semi-arid environment in central Mexico. – J. Veg. Sci. 2: 15–20.
- Walter, L. E. F., Hartnett, D. C., Hetrick, B. A. D. and Schwab, A. P. 1996. Interspecific nutrient transfer in a tallgrass prairie plant community. – Am. J. Bot. 83: 180–184.
- Yeaton, R. I. 1978. A cyclical relationship between *Larrea tridentata* and *Opuntia leptocaulis* in the northern Chihuahuan Desert. – J. Ecol. 66: 651–656.
- and Elser, K. J. 1990. The dynamics of a succulent karoo vegetation. – Vegetatio 88: 103–113.