

Positive Interactions among Plants

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I. Abstract	306
II. Introduction	307
III. The Evidence for Facilitation	308
A. Spatial Patterns	308
B. Manipulative Field Experiments	319
IV. Mechanisms of Facilitation	322
A. Resource Modification	322
1. Light and Temperature	322
2. Soil Moisture	323
3. Soil Nutrients	324
4. Soil Oxygenation	325
B. Substrate Modification	326
C. Protection from Herbivores	327
D. Pollination	328
E. Concentration of Propagules	329
F. Root Grafts, Mycorrhizae, and Soil Microbes	329
V. Interactions between Facilitation and Interference	330
VI. Consequences for Community Structure	333
VII. Conclusion	336
VIII. Literature Cited	337

I. Abstract

Experimental evidence for positive interactions, or facilitation, among plants has increased markedly during the last 10 years. Experiments documenting facilitation have been conducted in many diverse ecological systems, which suggests that positive inter-

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actions may be fundamental processes in plant communities. Here, I review the evidence for facilitation, the mechanisms by which facilitation operates, and the effects facilitation has on community structure. Facilitative mechanisms may act simultaneously with resource competition or allelopathy, and the overall effect of one species on another may be the product of multiple, complex interactions. Positive interactions may also determine community spatial patterns, permit coexistence, enhance diversity and productivity, and drive community dynamics. Once viewed as anecdotal and idiosyncratic, facilitation is now contributing to a more complete understanding of community structure and dynamics.

II. Introduction

One of the most vigorous and long-lasting debates in ecology has revolved around the organizational nature of plant communities. The original antagonists, Frederic Clements and Henry Gleason, envisioned diametrically different processes, the former promoting the community as an "organic entity" in which interdependence among plant species created repeatable associations that could be predicted from habitat characteristics (Clements, 1916). In contrast, Gleason (1926) wrote that "it seems that the vegetation of a region is not capable of complete segregation into definite communities, but that there is a considerable development of vegetational mixtures." Ultimately, Gleason's viewpoint triumphed, and Clements has been relegated to playing the "straight man" for Gleason in general ecological texts. The stigma attached to Clementsian synergism within plant ecology may have fostered the intense research emphasis on plant competition and allelopathy over the last few decades, interactions unlikely to be associated with organism-like processes. This focus on interference has proved successful, as during the last 50 years plant ecologists have discovered and quantified profound and complex negative effects of plant species on one another, and have accumulated experimental evidence from many natural systems supporting interference as a major determinant of plant community structure, dynamics, and productivity (Connell, 1983; Schoener, 1983; Fowler, 1986; Aarssen & Epp, 1990; Goldberg & Barton, 1992). Although most general conceptual models of community structure are either explicitly or implicitly based on competition, a large body of empirical evidence and theory has accrued that supports positive interactions, or facilitation, as another important and general phenomenon affecting plant distributions, productivity, diversity, and reproduction (Hunter & Aarssen, 1988; DeAngelis et al., 1986).

In this review I have organized the literature available on facilitation. I have concentrated primarily, but not exclusively, on peer-reviewed publications and addressed the following questions: 1) What evidence exists for the occurrence of facilitation in plant communities? 2) How do plants facilitate other plants? 3) What are the consequences of facilitation for plant communities? and 4) How do facilitative mechanisms interact with interfering mechanisms? I have avoided lengthy discussions of facilitative versus competitive models of succession and analysis of mutualisms involving other trophic levels such as mycorrhizal interactions and nitrogen fixation. (For detailed reviews on these related subjects, see Connell & Slatyer, 1977; Boucher et al., 1982; Rathcke, 1983; Boucher, 1985; DeAngelis et al., 1986; Huston & Smith, 1987; Burrows, 1990; Walker, 1993; Bronstein, 1994.)

III. The Evidence for Facilitation

I have organized the evidence for facilitation among plants into two general categories. First, I review spatial associations among species that suggest facilitative relationships. Although spatial associations provide compelling evidence, they cannot distinguish between biological facilitation, shared physical microhabitat requirements, and the tendency of perennials to act as foci for seed deposition. A second category of evidence is that derived from field perturbations and manipulative experiments. The importance of field experiments and the resulting changes in plant physiology, growth, and survival is emphasized as the strongest evidence for the occurrence, mechanisms, and importance of interspecific facilitation in plant communities. The mistaken notion that positive interactions are not well demonstrated with field experiments may be largely responsible for perceptions of facilitation as an interesting but not compelling process in plant communities.

A. SPATIAL PATTERNS

Spatial patterns that infer negative interactions have been extensively documented in many terrestrial plant systems and have been cited as evidence for the role of interference in community structure and diversity. Numerous studies have also documented spatial patterns that indicate that facilitation is important also as a determinant of community structure and diversity. One of the first published reports of spatial patterns that suggested facilitation among plants was from the shrub steppe vegetation of the Great Basin, where Phillips (1909) found that seedlings of pinyon pine (*Pinus monophylla*) were found predominately under sagebrush (*Artemisia tridentata*) and rarely in the open. In 1929, Compton reported strong positive associations among several species of shrubs in the Karoo Desert and argued that exceptionally stress-tolerant species provided shelter for less tolerant species. In Sonoran Desert communities, Shreve (1931) observed that saguaro (*Carnegie gigantea*) 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 the paloverde tree (*Cercidium microphyllum*). Similar spatial patterns suggestive of nurse-plant relationships have since been reported among many species in deserts around the world (Table I). Most seedlings of the boojum (*Idria columnaris*), a species restricted to Baja California, are found under shrubs (Humphrey, 1974), and seedlings of several other succulent species common in the Sonoran Desert, including *Agave deserti* and *Ferocactus acanthodes*, are associated with nurse plants (Franco & Nobel, 1988, 1989; Jordan & Nobel, 1979, 1981). McAuliffe (1986) found that paloverde, the most common nurse plant for saguaro in other Sonoran Desert ecosystems, was itself highly associated with numerous shrubs. In other species-rich Sonoran plant communities, McAuliffe (1988) measured positive spatial associations between *Ambrosia deltoidea* nurse plants and the young recruits of ~90% of the other perennial species. In the Sonoran Desert of northern Mexico, disproportionate numbers of many species, and columnar cacti in particular, occur under the canopies of ironwood (*Olneya tesota*) (Burquez & Quintana, 1994; Tewksbury & Petrovich, 1994). Many species of cacti are positively associated with tree

(text continues on p. 315)

Table I

Chronological survey of the primary literature on positive interactions among plants including the location species or types of plants involved and the nature of the study.

Authors	Location	Beneficiary species	Benefactor species	Type of study
Phillips, 1909	Great Basin, U.S.A.	<i>Pinus monophylla</i>	<i>Artemisia tridentata</i>	A
Compton, 1929	Karoo Desert, South Africa	Shrubs	Shrubs	A
Shreve, 1931	Sonoran Desert, U.S.A.	<i>Carnegie gigantea</i>	Shrubs, trees	A
Polunin, 1936	Arctic tundra, Norway	Perennial herbs	Perennial herbs	A
Aubrevillé, 1938	Tropical forest, Africa	Trees	Trees	A
Went, 1940	Tropical forests, South America	Epiphyte species	Trees	A
Went, 1942	Mojave Desert, U.S.A.	Annuals	Shrubs	A
Shirley, 1945	Conifer forest, north-central U.S.A.	Conifers	Trees	A, FE, M
Watt, 1947	Beechwood forest, U.K.	Herbs, shrubs	Trees	A
Whitehead, 1951	Alpine tundra, Italy	Perennial herbs	Perennial herbs	A
Muller, 1953	Mojave Desert, U.S.A.	Annuals	Shrubs	A
Bray, 1955	Pastures, midwestern U.S.A.	Herbs	Trees	A
Griggs, 1956	Alpine tundra, U.S.A.	Perennial herbs	Cushion plants	A
Muller & Muller, 1956	Mojave Desert, U.S.A.	Annuals	Shrubs	A
Ellison & Houston, 1958	Montane woodlands, U.S.A.	Herbs	<i>Populus tremuloides</i>	A, FE
Niering et al., 1963	Sonoran Desert, U.S.A.	<i>Carnegie gigantea</i>	Shrubs, trees	A
Borman, 1966	Conifer forest, eastern U.S.A.	<i>Pinus strobus</i>	<i>Pinus strobus</i>	A, FE, M
Turner et al., 1966	Sonoran Desert, U.S.A.	<i>Carnegie gigantea</i>	Shrubs, trees	A, M
Lawrence et al., 1967	Deglaciated substrate, Alaska	<i>Populus trichocarpa</i>	<i>Dryas drummondii</i>	A, M
Bonde, 1968	Alpine tundra, U.S.A.	<i>Trifolium nana</i>	Tussocks of many plants	A
Dancette & Poulain, 1969	Savanna, Senegal	Crop plants	<i>Acacia albida</i>	A, FE, M
Steenberg & Lowe, 1969	Sonoran Desert, U.S.A.	<i>Carnegie gigantea</i>	Shrubs, trees	A, M
Turner et al., 1969	Sonoran Desert, U.S.A.	<i>Carnegie gigantea</i>	<i>Cercidium microphyllum</i>	A, FE, M
Gentry, 1972	Sonoran Desert, Mexico	Succulents	Various perennials	A
Harris & Brock, 1972	Pasture, New Zealand	<i>Trifolium repens</i>	<i>Lolium perenne</i>	M, Lab
Tahvanainen & Root, 1972	Gardens, northeastern U.S.A.	<i>Brassica oleraceae</i>	Herbs	A, FE, M

Table I
(continued)

Authors	Location	Beneficiary species	Benefactor species	Type of study
Doutt & Nakata, 1973	Central California, U.S.A.	<i>Vitis</i> spp.	<i>Rubus</i> spp.	A, M
Kennard & Walker, 1973	Savanna, southern Africa	<i>Panicum maximum</i>	Trees	A
Root, 1973	Gardens, northeastern U.S.A.	<i>Brassica oleracea</i>	Herbs	A, FE, M
Humphrey, 1974	Sonoran Desert, Mexico	<i>Idria columnaris</i>	<i>Ambrosia magdalenae</i>	A
Christie et al., 1974	Grassland, U.K.	<i>Lolium perenne</i>	<i>Plantago lanceolata</i>	M, Lab
Mott & McComb, 1974	Desert, Western Australia	Annuals	Shrubs	A
Pahlsson, 1974	Grassland, southern Sweden	Herbs	<i>Ononis repens</i>	A
Yarranton & Morrison, 1974	Pine-oak forest, Canada	Various species	<i>J. virginiana</i>	A
Halvorson & Patten, 1975	Sonoran Desert, U.S.A.	Winter ephemerals	Shrubs	A
Hazlett & Hoffman, 1975	Shrub steppe, north-central U.S.A.	Herbs	<i>Artemisia</i> spp.	A
Allen & Forman, 1976	Old fields, northeastern U.S.A.	<i>Aster</i> spp.	<i>Daucus carota</i>	FE
Keeley & Johnson, 1977	Matrorral shrubland, Chile	Herbs	Shrubs	A
Sherbrooke, 1977	Mojave Desert, U.S.A.	<i>Simmondsia chinensis</i>	Shrubs	A
Steenberg & Lowe, 1977	Sonoran Desert, U.S.A.	<i>Carnegia gigantea</i>	Shrubs, trees	A, M
Tiedemann & Klemmedson, 1977	Savanna, southwestern U.S.A.	Herbs	<i>Prosopis juliflora</i>	A
Haines et al., 1978	Southeast U.S.A.	<i>Platanus occidentalis</i>	Legumes	A, FE
McNaughton, 1978	Savanna, east Africa	<i>Themeda triandra</i>	Grasses	A, FE, M
Patten, 1978	Sonoran Desert, U.S.A.	Annuals	Shrubs	A
Thomson, 1978	Disturbed roadsides, U.S.A.	<i>Hieracium florentinum</i>	<i>Hieracium auranticum</i>	A, M
Yeaton, 1978	Chihuahuan Desert, U.S.A.	<i>Opuntia leptocaulis</i>	<i>Larrea tridentata</i>	A
Jordan & Nobel, 1979	Mojave Desert, U.S.A.	<i>Agave deserti</i>	Shrubs	A
Palaniappan et al., 1979	Mine tailings	Herbs	<i>Lupinus arboreus</i>	A
Petranka & McPherson, 1979	Prairie-forest ecotone, U.S.A.	Tree species	<i>Rhus copallina</i>	A
Whittaker et al., 1979a	Mesquite savanna, U.S.A.	Herbs	<i>Prosopis juliflora</i>	A
Whittaker et al., 1979b	Mallee scrub, Western Australia	Shrubs	Shrubs	A

Table I
(continued)

Authors	Location	Beneficiary species	Benefactor species	Type of study
Holland, 1980	Savanna, California, U.S.A.	Annual grasses	<i>Quercus douglasii</i>	A
Jaksic & Fuentes, 1980	Matorral shrubland, Chile	Herbs	Shrubs	A, FE, M
Vasek & Lund, 1980	Mojave Desert, U.S.A.	Shrubs	Shrubs	A
Wallace & Romney, 1980	Mojave Desert, U.S.A.	Shrubs, annuals	Shrubs	A, FE
Jordan & Nobel, 1981	Sonoran Desert, U.S.A.	<i>Ferocactus acanthodes</i>	Shrubs	A, M
Schmida & Whittaker, 1981	Mojave Desert, U.S.A.	Herbs	Shrubs	A
Solomon, 1981	Eastern U.S.A.	<i>Solanum carolinse</i>	Herbs	A
Kellman & Miyanishi, 1982	Neotropical savanna, Belize	Tree and shrub species	Tree species	A, FE, M
Parker, 1982	Grassland, southwestern U.S.A.	<i>Gutierrezia</i>	<i>Gutierrezia</i>	A
Parker & Muller, 1982	Savanna, California, U.S.A.	Annuals	<i>Quercus agrifolia</i>	A, M
Rumbaugh et al., 1982	Great Basin, U.S.A.	<i>Agropyron cristatum</i>	Shrubs	A, FE
Silander & Antonovics, 1982	Coastal salt marsh, dunes, U.S.A.	<i>Eragrostis pilosa</i>	<i>Spartina patens</i>	FE
Werner & Harbeck, 1982	Old fields, midwestern U.S.A.	Tree species	<i>Rhus typhina</i>	A
Everett et al., 1983	Great Basin steppe, U.S.A.	Herbs	<i>Pinus monophylla</i>	A
McNaughton, 1983	Serengeti, Africa	Herbs	<i>Acacia tortilis</i>	A
Turner, 1983	Surfgrass beds, west coast, U.S.A.	<i>Phyllospadix scouleri</i>	Algae	A, FE, M
Yavitt & Smith, 1983	Savanna, southwestern U.S.A.	Bunchgrasses	<i>Prosopis juliflora</i>	A
Berendse & Aerts, 1984	Heath bogs, northern Europe	<i>Erica tetralix</i>	<i>Molina caerulea</i>	M, Lab
Fuentes et al., 1984	Mediterranean-climate scrub, Chile	Shrubs	Shrubs	A, FE, M
Harris et al., 1984	Kelp beds, west coast, U.S.A.	Kelp species	Filamentous algae	A, FE, M
Harrison & Werner, 1984	Old fields, midwestern U.S.A.	Oaks	Herbs, shrubs	A
McAuliffe, 1984a	Sonoran Desert, U.S.A.	<i>Carnegia gigantea</i>	Trees, shrubs	A
McAuliffe, 1984b	Sonoran Desert, U.S.A.	Cacti	<i>Opuntia fulgida</i>	A
Schat, 1984	Dune wetlands, Europe	Herbaceous annuals	<i>Juncus maritimus</i>	M, Lab
Sohlberg & Bliss, 1984	Polar desert, Canada	Perennial herbs	Mosses	A, M

Table I
(continued)

Authors	Location	Beneficiary species	Benefactor species	Type of study
Aarssen & Turkington, 1985b	Pasture, British Columbia, Canada	Perennial herbs	Perennial herbs	A
Johnson et al., 1985	River delta, Louisiana, U.S.A.	Various species	<i>Salix exigua</i>	A
Kellman, 1985	Neotropical savanna, Belize	Trees	Trees, shrubs	A, FE, M
Monk & Gabrielson, 1985	Deciduous forest, eastern U.S.A.	Trees	Herbs	A, FE
Turkington et al., 1985	Pasture, U.K.	Perennial herbs	Perennial herbs	A
Everett et al., 1986	Great Basin steppe, U.S.A.	<i>Pinus monophylla</i>	Shrubs	A
Fuentes et al., 1986	Mediterranean-climate scrub, Chile	Shrubs	Shrubs	A, FE, M
Guevara et al., 1986	Tropical rain forest, Mexico	Various species	Trees	A
Hutto et al., 1986	Sonoran Desert, U.S.A.	<i>Carnegia gigantea</i>	Various species	A
McAuliffe, 1986	Sonoran Desert, U.S.A.	<i>Cercidium microphyllum</i>	Shrubs, trees	A, M
Rykiel & Cook, 1986	Oak savanna, Texas, U.S.A.	<i>Juniperus virginiana</i>	<i>Quercus stellata</i>	A
Yeaton & Romero-Manzanares, 1986	Chihuahuan Desert, Mexico	<i>Opuntia streptacantha</i>	<i>Acacia scaffneri</i>	A
Walker & Chapin, 1986	Boreal floodplain, Alaska	<i>Salix, Populus</i>	<i>Alnus tenuifolia</i>	A, Lab
Ovalle & Avendano, 1987a	Shrubland, Chile	Herbs	Shrubs	A
Ovalle & Avendano, 1987b	Shrubland, Chile	Herbs	Shrubs	A
Schuster & Hutnick, 1987	Mine spoils, U.S.A.	Trees	<i>Robinia psuedoacacia</i>	A
Stuart-Hill et al., 1987	Savanna, South Africa	Grasses	<i>Acacia karoo</i>	A
Wood & del Moral, 1987	Subalpine, northwest U.S.A.	Herbs	<i>Lupinus lepidus</i>	A, FE
Allen & Allen, 1988	Shortgrass prairie, U.S.A.	<i>Agropyron</i> spp.	<i>Salsola kali</i>	A, FE
Archer et al., 1988	Arid woodlands, Texas, U.S.A.	Various woody species	<i>Prosopis glandulosa</i>	A
Del Moral & Wood, 1988	Subalpine, northwestern U.S.A.	Herbs	Herbs	A
Fowler, 1988	Shortgrass prairie, U.S.A.	Grasses	Grasses	A
Franco & Nobel, 1988	Sonoran Desert, U.S.A.	Cacti	<i>Hilaria rigida</i>	A, M
Joffre & Rambal, 1988	Savannas, Spain	Herbs	<i>Quercus rotundifolia</i> , <i>Q. suber</i>	A, M

Table I
(continued)

Authors	Location	Beneficiary species	Benefactor species	Type of study
Lavery & Plowright, 1988	Deciduous forest, Canada	<i>Podophyllum peltatum</i>	<i>Pedicularis canadensis</i>	A
Maillette, 1988	Boreal shrubland	<i>Vaccinium</i> spp.	<i>Vaccinium</i> spp.	A
McAuliffe, 1988	Mojave Desert, U.S.A.	<i>Larrea tridentata</i>	<i>Ambrosia dumosa</i>	A
McAuliffe, 1988	Sonoran Desert, U.S.A.	Various species	Various species	A
McPherson et al., 1988	Southwestern savanna, U.S.A.	<i>Juniperus pinchotii</i>	<i>Prosopis glandulosa</i>	A
Pfister & Hay, 1988	Intertidal, southeastern U.S.A.	Red algae	Brown algae	A, FE, M
Belsky et al., 1989	Savanna, Kenya	Herbs	<i>Acacia tortilis</i> , <i>A. digitata</i>	A, M
Day & Wright, 1989	Cinder cones, northwestern U.S.A.	Various species	<i>Eriogonum ovalifolium</i>	A, M
Franco & Nobel, 1989	Sonoran Desert, U.S.A.	Cacti	<i>Hilaria rigida</i> , shrubs	A, M
Frost & McDougald, 1989	California savanna, U.S.A.	Annual grasses	<i>Quercus douglasii</i>	A
Harmon & Franklin, 1989	Conifer forests, northwestern U.S.A.	Tree seedlings	Tree remains	A, FE, M
Holmes & Jepson-Innes, 1989	Grassland, southwestern U.S.A.	<i>Bouteloua gracilis</i>	<i>Aristida</i> spp.	FE, M
Morris & Wood, 1989	Subalpine, northwestern U.S.A.	<i>Anaphalis</i> , <i>Epilobium</i>	<i>Lupinus lepidus</i>	A, FE
Weldon et al., 1990	Great Basin steppe, U.S.A.	<i>Pinus edulis</i>	Shrubs	A
Weltzin & Coughenhour, 1990	Savanna, Kenya	Herbs	Herbs	A, M
Williams, 1990	Subtidal zones, Caribbean	<i>Thalassia testudinum</i>	Rhizophytic algae	A, FE, M
Yeaton & Esler, 1990	Karoo Desert, South Africa	Shrubs	Shrubs	A
Bertness, 1991	New England salt marsh, U.S.A.	Herbaceous perennials	<i>Juncus gerardi</i>	A, FE, M
Callaway et al., 1991	Oak woodlands, California, U.S.A.	Annuals	<i>Quercus douglasii</i>	A, FE, M
Callaway & D'Antonio, 1991	California woodlands, U.S.A.	<i>Quercus agrifolia</i>	Shrubs	A, FE
Carlsson & Callaghan, 1991	Arctic tundra, Swedish Lapland	<i>Carex bigelowii</i>	Evergreen dwarf shrubs	FE, M
Carter & O'Connor, 1991	Savanna, southern Africa	<i>Setaria incrassata</i>	Trees	A
Gill & Marks, 1991	Old fields, northeastern U.S.A.	Trees, shrubs	Herbs	A, FE
Rebertus et al., 1991	Subalpine forests, U.S.A.	<i>Abies lasiocarpa</i>	<i>Pinus flexilis</i>	A

Table I
(continued)

Authors	Location	Beneficiary species	Benefactor species	Type of study
Rostagno et al., 1991	Arid shrublands, Patagonia	Herbs	Shrubs	A, M
Schat & Van Beckhoven, 1991	Dune slacks, Holland	Herbaceous perennials	<i>Juncus maritimus</i>	A
Valiente-Banuet et al., 1991a	Tropical dry forest, Mexico	Cacti	Shrubs	A
Valiente-Banuet et al., 1991b	Tropical dry forest, Mexico	<i>Neobuxbaumia tetetzo</i>	<i>Mimosa luisana</i>	A
Valiente-Banuet & Ezcurra, 1991	Tropical dry forest, Mexico	<i>Neobuxbaumia tetetzo</i>	<i>Mimosa luisana</i>	A, FE, M
Walker & Vitousek, 1991	Tropical forest, Hawai'i	<i>Myrica faya</i>	<i>Metrosideros polymorpha</i>	A, FE, M
Aguiar et al., 1992	Patagonian steppe, Argentina	<i>Bromus pictus</i>	Shrubs	A, FE, M
Callaway, 1992	California woodlands, U.S.A.	<i>Quercus douglasii</i>	Shrubs	A, FE, M
Guevara et al., 1992	Tropical pasture, Mexico	Trees	Trees	A
Kellman & Kading, 1992	Pine-oak forests, Canada	<i>Pinus strobus</i> , <i>P. resinosa</i>	<i>Quercus rubra</i>	A, FE, M
Lavery, 1992	Deciduous forest, Canada	<i>Podophyllum peltatum</i>	<i>Pedicularis canadensis</i>	A, FE, M
Lesica & Shelly, 1992	Intermountain grassland, U.S.A.	<i>Arabis fecunda</i>	Cryptogamic soil crust	A
Arriaga et al., 1993	Tropical dry forest, Mexico	Cacti	Trees and shrubs	A
Bertness & Shumway, 1993	New England salt marsh, U.S.A.	Perennial herbs	<i>Juncus gerardi</i>	A, FE, M
Blundon et al., 1993	Alpine tundra, Canada	Perennial herbs	Perennial herbs	A
Dawson, 1993	Temperate deciduous forest, U.S.A.	Herbs, shrubs, trees	<i>Acer saccharum</i>	M, FE
Del Moral & Bliss, 1993	Subalpine, northwestern U.S.A.	Herbs	<i>Lupinus lepidus</i>	A
Gutierrez et al., 1993	Sclerophyllous scrub, Chile	Annuals	<i>Porlieria chilensis</i>	A, M
Hjalten et al., 1993	Deciduous shrubland, Sweden	<i>Betula pubescens</i>	<i>Alnus incana</i>	A, FE, M
Kikvidze, 1993	Alpine-subnival, Caucasus, Russia	Perennial herbs	Perennial herbs	A
Ko & Reich, 1993	Savanna, midwestern U.S.A.	Herbs	<i>Quercus</i> spp.	A
Magnusson & Magnusson, 1993	Shrublands, Iceland	<i>Betula pubescens</i>	<i>Salix</i> spp.	A
Maranon & Bartolome, 1993	California oak woodlands, U.S.A.	Annual herbs	<i>Quercus agrifolia</i>	A, FE, M
Aguiar & Sala, 1994	Patagonian steppe, Argentina	<i>Bromus pictus</i>	Shrubs	A, FE, M
Belsky, 1994	Savanna, Kenya	Herbs	Trees	A, M

Table I
(continued)

Authors	Location	Beneficiary species	Benefactor species	Type of study
Belsky & Canham, 1994	Savanna, Kenya	Herbs	Trees	A
Bertness & Hacker, 1994	Salt marsh, eastern U.S.A.	<i>Iva frutescens</i>	<i>Juncus gerardi</i>	A, FE, M
Bertness & Yeh, 1994	Salt marsh, eastern U.S.A.	<i>Iva, Juncus</i>	<i>Iva, Juncus</i>	A, FE, M
Bever, 1994	Old fields, eastern U.S.A.	Herbs	Herbs	FE
Burquez & Quintana, 1994	Sonoran Desert, Mexico and U.S.A.	Many species	<i>Olneya tesota</i>	A
Callaway, 1994	California salt marsh, U.S.A.	Annuals	<i>Arthrocnemum</i>	A, FE
Callaway & Bertness, 1994	Subalpine forest, northwestern U.S.A.	<i>Abies lasiocarpa</i>	<i>Pinus albicaulis</i>	A, FE
Castellanos et al., 1994	Salt marsh, Spain	<i>Arthrocnemum perenne</i>	<i>Spartina maritima</i>	A, M
Chapin et al., 1994	Deglaciated substrate, Alaska	<i>Picea sitchensis</i>	<i>Dryas, Alnus</i>	A, FE, M
Flores-Martinez et al., 1994	Desert, Mexico	<i>Neobuxbaumia tetetzo</i>	<i>Mimosa luisana</i>	A
Longpre et al., 1994	Boreal forest, Quebec, Canada	<i>Pinus banksiana</i>	<i>Betula papyrifera</i>	A
Miller, 1994	Old fields, Michigan, U.S.A.	Annuals	Annuals	A, FE
Tewksbury & Petrovich, 1994	Sonoran Desert, Mexico	Many species	<i>Olneya tesota</i>	A
Berkowitz et al., 1995	Deciduous forest, U.S.A.	Trees	Shrubs	A, FE
Evans & Cabin, 1995	Desert, New Mexico, U.S.A.	<i>Lesquerella fendleri</i>	<i>Larrea tridentata</i>	A
Gold & Bliss, 1995	Polar desert, Canada	Perennial herbs	Cryptogams	A
Hacker & Bertness, 1995	Salt marsh, eastern U.S.A.	<i>Iva frutescens</i>	<i>Juncus gerardi</i>	A, FE, M
Callaway et al., in press	Sierran woodlands, U.S.A.	<i>Pinus monophylla</i>	<i>Artemisia tridentata</i>	A, FE, M
Callaway & King, in press	Pothole wetlands, northwestern U.S.A.	<i>Salix, Myosotis laxa</i>	<i>Typha latifolia</i>	M, Lab
Greenlee & Callaway, in review	Montane grassland, U.S.A.	<i>Lesquerella carinata</i>	Bunchgrasses	A, FE

A = correlative spatial association, FE = field experiment, M = evidence for mechanism, Lab = primarily laboratory evidence.

and shrub canopy cover in the dry subtropical scrub of central and northwestern Mexico (Valiente-Banuet et al., 1991a, 1991b; Arriaga et al., 1993). In the Mojave desert, 88–95% of the landscape is open substrate, but only 10–33% of young creosote bushes are found in the open (McAuliffe, 1988). In contrast, 67–85% of young creosote bushes are found under living or dead *Ambrosia* shrubs, which account for only 3–6% of the landscape cover.

Although many of the spatial patterns that infer nurse-plant relationships have been found in deserts, others have measured interspecific associations in many different climates, evidence that facilitation is a widespread ecological phenomenon (Table I). At prairie-deciduous forest ecotones in north-central Oklahoma, Petranka and McPherson (1979) found 1.6 forest species seedlings/m² under shrubby clones of sumac (*Rhus copallina*) that had established in open prairie, but only 0.2 seedlings/m² in the prairie adjacent to the clones. Werner and Harbeck (1982) investigated associations among forest tree seedlings and early successional species in old fields in Michigan and found tree seedlings to be three times as common under another species of sumac (*Rhus typhina*) shrubs than in the open. Kellman and Kading (1992) measured six times as many white pine (*Pinus strobus*) and red pine (*P. resinosa*) seedlings under large oak trees than in open interplant spaces in sand dunes near Lake Huron, Ontario. Also in sand dunes on the shore of Lake Huron, Yarranton and Morrison (1974) found that common juniper (*Juniperus communis*) provided a facilitative "nucleus" enhancing the establishment of many other species including the oak species studied by Kellman and Kading (1992).

In the high plains of western Texas, redberry juniper (*Juniperus pinchotti*) appears to be facilitated by mesquite (*Prosopis glandulosa*) (McPherson et al., 1988). Mesquite also appears to act as a nurse plant in the semi-arid savannas and woodlands near the Rio Grande of southern Texas, where a number of different species including cactus, herbs, and woody perennials do not establish in open spaces beyond the cover of mesquite canopies. These species are not associated with young mesquite trees but become increasingly more abundant under older age classes. Archer et al. (1988) proposed that the more stress-tolerant mesquite is able to establish in open grassland and provide a nucleus for colonization of many other species. In east-central Texas, Rykiel and Cook (1986) found that clusters of red cedars (*Juniperus virginiana*) form only in the understory of post oak (*Quercus macrocarpa*). In the same region, Fowler (1988) studied patterns of spatial association, growth, and survival of *Aristida longiseta* and *Bouteloua rigidiseta* in the short-grass prairie of Texas. She found that seedlings of both species, when associated with other seedlings or juvenile plants of either species, had higher growth rates and survival than did those without neighbors. In some cases, growth was correlated with the proximity of neighboring adults.

In oak woodlands and savannas of central California not grazed by domestic livestock, Callaway and D'Antonio (1991) found that 80% of all coast live oak (*Quercus agrifolia*) seedlings were found under two species of shrubs that occupied only 36% of the sample area. At sites with livestock, 86% of all coast live oak seedlings were found under shrubs. In a similar study, Callaway (1992) found that blue oak (*Quercus douglasii*) seedlings were also strongly associated with shrub canopies.

Patterns that suggest facilitative interactions have also been documented at the upper edges of subalpine forests. Rebertus et al. (1991) found that young Englemann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) were consistently associated with older limber pines (*Pinus flexilis*) in the Colorado Front Range. They hypothesized that the highly stress-tolerant limber pine established and provided safe sites for subsequent establishment of spruce and fir. Similar patterns have been described by Habeck (1969) and Callaway and Bertness (1994) in the Northern Rockies, where whitebark pine (*Pinus albicaulis*) appears to form nuclei around which subalpine fir seedlings establish.

In the boreal forests of Quebec, jack pine (*Pinus banksiana*) growing in mixtures with paper birch (*Betula papyrifera*) grew larger in diameter than those in either pure stands or in stands mixed with quaking aspen (*Populus tremuloides*) (Longpre et al., 1994).

Calcium, magnesium, nitrification rates, and pH were higher in both types of mixed stands.

In arctic and alpine tundra, strong positive spatial associations between plants have been observed by numerous authors (Polunin, 1936, 1955; Whitehead, 1951; Griggs, 1956; Bonde, 1968; Callaghan & Emanuelsson, 1985; Alexandrova, 1988); however, these patterns have been quantified in only a few relatively recent studies. Sohlberg and Bliss (1984) found that 17 of 19 vascular plant species in a polar desert community on King Christian Island, Canada, were significantly more common in moss turfs than on open soil, based on the proportions of these microsites. In a later study on Devon Island, Gold and Bliss (1995) reported that the presence of cryptogams favored the success of vascular plants by increasing nutrient availability and soil temperatures and reducing soil disturbance. In Swedish Lapland, *Carex bigelowii* increased leaf lengths and culm heights when growing within clumps of *Empetrum hermaphroditum* or *Racomitrium lanuginosum*, a response duplicated in plywood shelters (Carlsson & Callaghan, 1991). On alpine glacial moraines in the Canadian Rockies, Blundon et al. (1993) and Dale et al. (1991) found that many different plant species were positively associated with the nitrogen-fixing *Hedysarum boreale*. In alpine-subnival vegetation of the central Caucasus, strong positive spatial associations have also been measured among numerous pairs of vascular plants (Kikvidze, 1993). Maillette (1988) found that three species of *Vaccinium* were distributed differently along gradients of light and temperature and were negatively associated with one another at large spatial scales on the Laurentian Plateau of Quebec. However, individuals of species growing outside of the habitat in which they were dominant were significantly larger when they were in direct contact with individuals of the locally dominant congener. One explanatory hypothesis was that dominants in a given microhabitat facilitate the growth of less tolerant congeneric species. In contrast to these studies, Moen (1993) examined the relative importance of positive and negative interactions in the high-alpine block fields of northern Norway using removal experiments and found no evidence for positive effects.

Positive spatial relationships have also been reported in tropical ecosystems. In tropical pastures, Guevara et al. (1986, 1992) found five times as many seedlings of forest species under isolated adult trees than in the surrounding open grassland and concluded that "isolated trees function as nursery plants for rain-forest species." Kellman and Miyanishi (1982) and Kellman (1985) found similar patterns of associations in tropical savannas in Belize, with preferential establishment of woody seedlings taking place beneath savanna trees.

Although positive spatial associations often appear to reduce the effects of drought or high temperatures in arid or semi-arid ecosystems, some patterns suggest that facilitative processes may ameliorate stress caused by excess soil water. In waterlogged dune depressions in Holland, *Plantago coronopus* and *Samolus valerandi* are strongly clumped around tussocks of *Juncus maritimus* (Schat & Van Beckhoven, 1991). Survival rates around the tussocks appear to be enhanced by soil oxygenation and the concomitant oxidation of iron manganese, or sulphide (see "Mechanisms of Facilitation").

Some spatial patterns suggest that the effectiveness of nurse plants within a general habitat may vary among nurse plant species. Hutto et al. (1986) reported that saguaros were distributed nonrandomly among potential nurse plants at two locations in Organ Pipe National Monument in the Sonoran Desert. They found significantly more saguaros associated with mesquite and paloverde trees and fewer saguaros associated with creosote bush than expected, based on the proportional cover of these species. Low recruitment

under creosote bush may have been due to negative effects of allelopathic root exudates (Mahall & Callaway, 1991, 1992). 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*, and *Larrea* is absent (McAuliffe, 1991, pers. comm.). However, on older, adjacent terraces, *Larrea* is dominant, *Viguiera* is absent, and regeneration of *Idria columnaris* (boojum) and *Pachycerus pringli* (cardone cactus)—the primary beneficiaries of *Viguiera*—are absent.

In the northern Sonoran Desert, McAuliffe (1986) found proportionally more paloverde seedlings under *Ambrosia* spp. than other shrub species, and attributed this to the greater shelter provided by the dense, low-lying *Ambrosia* canopies. McAuliffe (1988) also found strong, species-specific patterns of association in other complex Sonoran Desert communities and in compositionally simple Mojave Desert plant communities. In Californian shrubland and woodland, Callaway and D'Antonio (1991) reported significant differences in coast live oak seedling survival under the canopies of different shrub species. In contrast with these studies, Turner et al. (1966) reported that the 15 different species that can apparently act as nurse plants for saguaro 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 byproduct of microclimatic changes under canopies.

In nurse-plant relationships, the beneficiary species, facilitated as a seedling, may outlive or eliminate its benefactor and persist independently for the majority of its lifespan (see "Interactions between Facilitation and Interference"). On the other hand, many species of understory herbs appear to be dependent throughout their lifespans on facilitative affiliations with overstory perennials (Table I). Went (1942) observed that some species of Mojave Desert annuals occurred only under the canopies of shrubs, an observation quantified by Muller (1953), Muller and Muller (1956), and Schmida and Whittaker (1981). *Larrea tridentata*, which has strong negative effects on many other species, appears to enhance the abundance and reproduction of *Lesquerella fendleri* in central New Mexico (Evans & Cabin, 1995). Similar associations have been reported in many systems including other southwestern deserts of the United States (Halvorson & Patten, 1975; Whittaker et al., 1979a; Yavitt & Smith, 1983), matorral shrubland of Chile (Keeley & Johnson, 1977; Jaksic & Fuentes, 1980), shrub-dominated vegetation in the North Dakota Badlands (Hazlett & Hoffman, 1975), shrubland in Patagonia, Argentina (Rostagno et al., 1991), oak savannas in the midwestern United States (Ko & Reich, 1993), pinyon pine woodlands in the Great Basin (Everett et al., 1983; Weldon et al., 1990), African savannas (McNaughton, 1983; Carter & O'Connor, 1991; Belsky, 1994), arid desert scrub of southern Australia (Whittaker et al., 1979b), and the saline upper zones of coastal salt marshes in California (Callaway, 1994). Canopy facilitation of understory herbs is common in semi-arid savannas throughout the world, where either understory productivity is enhanced or subcanopy microenvironments favor species that are excluded from open grassland habitat (see review by Vetaas, 1992). Belsky et al. (1989) and Belsky (1994) reported a complete change in herbaceous species under acacia (*Acacia tortilis*) and baobab (*Adansonia digitata*) tree canopies in comparison to adjacent open grassland in Kenyan savannas. Others have reported similar strong canopy effects on species distributions in African savannas (Kennard & Walker, 1973; Maranga, 1984). Specific associations between herbs of perennial canopies have also been described in mediterranean-climate oak savannas and woodlands in California (Holland, 1980; Parker & Muller, 1982; Frost & McDougald, 1989; Callaway et al., 1991), Spain (Joffe & Rambal, 1988,

1993), and Chile (Ovalle & Avendano 1987a, 1987b). Similarly, Bray (1955) found distinct differences in species composition between the understory of isolated trees in pastures and in the open in the midwestern United States.

Although spatial correlations are critical for developing meaningful hypotheses, past reliance on correlative data has limited the credibility of arguments for facilitation. Spatial associations are suspect due not only to alternative biological or abiotic causes but also to the dependency of such patterns on scale. Recently, however, a large number of experimental studies have been published which have contributed greatly to understanding positive interactions within plant communities.

B. MANIPULATIVE FIELD EXPERIMENTS

Strong positive spatial associations are important as patterns from which to develop hypotheses for cause, but manipulative field experiments are required to separate biological effects of facilitators from microsite effects. This is done by comparing the performance of beneficiary plants with benefactors present to that with benefactors removed, or with the effects of the benefactors altered by manipulating canopies or roots. Although such experiments may not confirm the specific active mechanism (e.g., shade vs. canopy throughfall), they provide a means to distinguish between biotic and microsite effects. If removal is not thorough, however, the "removal" of the benefactor may create conditions in which the beneficiary is subjected to even greater stress than would be experienced in habitats without the benefactor at all. For example, if removal techniques eliminate positive effects such as shade but do not substantially reduce root competition (e.g., if regrowth is abundant), the importance of facilitation is likely to be overestimated. If the effects of the benefactor were completely eliminated, poor performance of the test beneficiary would then be strong evidence for facilitation.

A further complication is the interpretation of neutral responses of the putative beneficiary after removal of the benefactor. A negative response, after thorough removal of the benefactor, indicates facilitation, and a neutral response may be interpreted as the lack of facilitation. However, the continued effects of facilitative mechanisms such as improved soil nutrients or bulk density may confound this interpretation. Additional confounding factors may be disturbance to the soil caused by the removal of the benefactor or the effects of decaying roots remaining in the soil. A thorough investigation of microsite effects and biotic facilitation may require combinations of perturbation experiments, careful controls for treatment effects, and nurse-plant "mimic" experiments. The latter are experimental manipulations in which nurse-plant characteristics are simulated by constructing nurse-plant mimics, which provide comparable levels of shade or protection from herbivores. Comparison of the performance of beneficiary plants with and without benefactor mimics may provide strong evidence for the importance of nurse plants and the mechanisms by which they may aid their neighbors.

In 1945, Shirley conducted an experiment investigating the interactive effects of hardwood roots and canopies on the survival and growth of conifer seedlings and saplings. He found that under dry conditions, moderate shade improved conifer survival, although the overall effect of hardwoods on conifers under most conditions was negative. These experiments indicated that overstory facilitative effects occurred but that interference was usually more important. In the hotter and drier climate of the Sonoran Desert, Turner et al. (1969) investigated the strong spatial relationships between young saguaros and nurse trees and shrubs by transplanting 5 cm and 15 cm tall saguaros in factorial treatments of

shade and caging for protection from herbivores. They found that predation on seedlings was very high but that the survival of seedlings that were transplanted in the shade of nurse plants was much higher than survival in the open.

Silander and Antonovics (1982) examined interspecific interactions along a salt marsh–dune continuum using multiple combinations of species removals. They found that competitive interactions were more common than facilitation, but the removal of *Spartina patens* greatly decreased the abundance of *Eragrostis pilosa*, a co-occurring species. In similar removal experiments in old fields in the northeastern United States, Allen and Forman (1976) discovered that most species-specific removal responses indicated the occurrence of competition; however, the removal of *Daucus carota* resulted in large decreases in *Aster dumosus* and *A. pilosus*.

In New England salt marshes, Bertness and a number of colleagues have used field experiments to document numerous facilitative processes. By manipulating community composition and measuring target plant responses, they have discovered strong effects of facilitation in the upper, abiotically “stressful” parts of the marsh and weak effects of facilitation in the lower, less stressful parts of the marsh (Bertness, 1991; Bertness & Shumway, 1993). Removal of *Distichlis spicata*, a common first colonizer of saline bare patches, led to a sharp decline in cover of *Juncus gerardi* in the upper marsh, indicating that the survival of the latter was dependent on facilitation by *Distichlis*. In the middle zone of the marsh, removal of *Spartina patens* also resulted in large decreases in *Juncus* cover. In the lower marsh, however, neighbor removal either had no effect on the dominant species or improved their growth, suggesting that competition was more important. In other locations in the marsh where the salt-intolerant shrub *Iva frutescens* (marsh elder) encroaches into zones dominated by *Juncus gerardi*, removal of *Juncus* dramatically reduced photosynthetic rates, leaf production, and survival of *Iva* (Bertness & Hacker, 1994). In a mediterranean-climate salt marsh in central California, Callaway (1994) conducted factorial root exclosure–canopy removal experiments under *Arthrocnemum* shrubs. There, substantial decreases in the survival and productivity of two of three winter ephemeral species occurred when *Arthrocnemum* canopies were removed, whether or not roots were excluded, indicating that facilitative interactions between the shrub and annuals were more important than interference.

Jaksic and Fuentes (1980) experimentally examined the effects of herbivory and shade as mechanisms for the disproportionate abundance of annual plants under shrubs in the Chilean matorral. They removed one-half of the canopies of shrubs and used exclosures to restrict herbivory in one-half of the area exposed by canopy removal and in one-half of the remaining subcanopy area. Their results indicated that protection from herbivores was the most important facilitative factor. Also in the matorral of Chile, Fuentes et al. (1984) found that most species of shrubs, when they were small, were strongly associated with larger shrubs. Experiments indicated that positive associations were due to seed aggregation, protection from herbivores, and reduced desiccation.

Using a combination of field and greenhouse experiments, Callaway et al. (1991) found that the addition of nutrients to the surface soil via the litterfall and throughfall of blue oaks was the primary reason for enhanced productivity of annual grasses in the understory. Manipulative field experiments have also demonstrated other facilitative interactions in California oak woodlands. In experimental plantings of blue oak, a widespread deciduous tree in woodlands and savannas, Callaway (1992) found that 30–55% of seedlings that emerged under shrubs survived for at least one year, but no seedlings that emerged in the open survived. Survival of seedlings that emerged where

the canopy of a shrub had been removed was also zero, paralleling survival in the open grassland. Thus, spatial associations among blue oak seedlings and established shrubs was caused by shrubs and not due to shared microsite requirements of shrubs and blue oak. Similarly, Callaway and D'Antonio (1991) found that 31% of coast live oak seedlings that emerged after being experimentally planted under shrubs survived for more than two years, and no seedlings survived in the open. In many plant communities, shade-tolerant oak species successional replace pines or other shade-intolerant species; however, Kellman and Kading (1992) discovered that seedlings of white pine (*Pinus strobus*) and red pine (*Pinus resinosa*) were six times as common under oak canopies than in treeless areas on sand dunes near Lake Huron, Ontario. Germination and growth of pine seedlings planted under the canopies of medium-sized or large oaks was much greater than that of those planted under small oaks or in the open.

More than 80 years after Phillips (1909) described spatial nurse-plant associations between pinyon pine and Great Basin sage, Callaway et al. (in press) conducted removal and transplant experiments to study the biological nature of the relationship. They found significantly lower survival rates of pinyon pine seedlings in the intershrub spaces and in plots where sagebrush was removed than under shrubs. Shrubs provided indirect facilitation by reducing herbivory, but they also directly reduced mortality due to desiccation and heat stress. Experiments with imitation nurse shrubs suggested that the absence of shrubs on some substrates (excluded by intolerance of the soil chemistry) limited the ability of pinyon pines, which were not affected by the unusual soil chemistry, to occupy those substrates.

Although most studies have focused on *interspecific* facilitation, Parker (1982) observed strong *intraspecific* associations among seedlings of *Gutierrezia microcephala* and conspecific adults. He found that survival of seedlings decreased when adults were removed, due to higher grasshopper herbivory. Such interactions suggest that cycles of self-replacement may be the norm for some plants. In the upper zones of New England saltmarshes, adult *Iva frutescens* shrubs alleviate high soil salinities and enhance conspecific seedling survival (Bertness & Yeh, 1994). Facilitative interactions also occurred among *Iva* seedlings themselves, with many more seedlings surviving in crowded conditions than when growing alone. As found for *Iva* adult nurse plants, dense seedling cover reduced soil salinity.

Facilitative relationships may be the direct result of amelioration of harsh environmental conditions or an indirect effect of such mechanisms as the benefactor species eliminating species that otherwise would outcompete beneficiary species (Miller, 1994). For example, in some California oak woodlands, oak seedlings recruit disproportionately higher under several species of chaparral shrubs (Callaway & D'Antonio, 1991; Callaway, 1992). This may be the result of shade and protection from predators; however, these same shrub species can suppress herbaceous growth (Muller, 1966; Muller & del Moral, 1966; Halligan, 1976), which in turn can suppress oak seedlings (Gordon et al., 1989; Gordon & Rice, 1993). Pennings and Callaway (in press) found that the parasitic plant marsh dodder (*Cuscuta salina*) facilitated two relatively uncommon species, *Limonium californicum* and *Frankenia grandifolia*, in a western coastal marsh by preferentially infecting and suppressing the marsh dominant, *Salicornia virginica*.

In some systems, experimental manipulation may be precluded by the destructive nature of the manipulation or difficult logistics. In subalpine forests in the northern Rockies, Callaway and Bertness (1994) utilized partial diebacks of an apparent benefactor as a natural experiment (see "Spatial Patterns"). They measured growth rates of subalpine

fir trees (*Abies lasiocarpa*) within 50 cm of large, dead and down whitebark pines (*Pinus albicaulis*) that had been killed in the 1920s by pine bark beetles, and compared them to growth rates of firs near living whitebark pines. On ridgeline sites they found that pre-beetle kill growth rates did not differ among the treatments (i.e., before any whitebark pines died); however, growth rates of firs during 1991 and 1992 (long after the beetle kills) were higher when they were next to living pines than when next to dead pines. This suggests that whitebark pine facilitates subalpine fir at the upper end of the latter's elevational range.

Many examples of spatial patterns, laboratory experiments, and field experiments provide strong evidence for the importance of positive interactions among plants from the majority of the world's biomes. These interactions are produced by an equally diverse array of mechanisms.

IV. Mechanisms of Facilitation

Plants may facilitate other plants directly, by ameliorating harsh environmental characteristics, altering substrate characteristics, or increasing the availability of a resource; or may act indirectly, by eliminating potential competitors (e.g., Connell, 1983, 1990; Miller, 1994), introducing other beneficial organisms such as soil microbes, mycorrhizae, or pollinators, or providing protection from herbivores. Since 1927, when Aikman quantified environmental differences between subcanopy and open microhabitats in deciduous forests of eastern Nebraska, ecologists have measured many changes in microhabitat and shifts in multitrophic-level interactions caused by plants that favor the growth and survival of other plant species.

A. RESOURCE MODIFICATION

1. Light and Temperature

Although temperature is not a resource, I have included its consideration with light, because both are a function of total irradiation and both are often incorporated in studies of the effects of shade. Shade provided by the canopies of large plants may protect seedlings and smaller plants from temperature extremes, reduce water loss, and reduce photoinhibition during stomatal closure, but it does so at the cost of reduced energy for photosynthesis. The dependency of many species of cacti and other succulents on nurse-plant benefactors may be due to inefficient heat dissipation of seedlings with low surface:volume ratios and exposure of these seedlings to exceptionally hot temperatures on the desert floor. For example, young barrel cacti (*Ferrocactus acanthodes*) may experience 11°C decreases in maximum stem-surface temperatures in the shade of nurse plants (Nobel, 1984). Turner et al. (1966) tested the combined effects of artificial shade and subcanopy soil types on the survival of saguaro seedlings and found that 100% of unshaded seedlings died, in comparison to 65% of shaded seedlings. Reduced temperatures appeared to be more important than improved water relations, because irrigation of unshaded seedlings did not improve survivorship. Nurse-plant canopies also appear to protect young saguaros from freezing temperatures in the winter (Steenberg & Lowe, 1977; Nobel, 1980).

In the boreal forest of Minnesota, Shirley (1945) used a multifactorial experiment to demonstrate the positive effects of canopy shade on the survival of several species of conifers. He found that as long as light levels did not fall below 20% of irradiance in the

open, benefits of shade from the overstory trees compensated for the negative effects of root interference. Valiente-Banuet and Ezcurra (1991) compared the relative importance of protection from predation and shade in the nurse-plant relationship between *Neobuxbaumia tetetzo*, a columnar cactus, and *Mimosa luisana* in the Viscaino Desert and the Gran Desierto de Altar in Mexico. They found that cages improved survival but that long-term survival was restricted to shade treatments. Callaway (1992) tested the facilitative effects of shade and seedling predation on the survival of blue oak seedlings using unshaded and shaded cages. Unshaded cages reduced mortality rates, but eventually all unshaded seedlings died, whereas 35% of shaded and caged seedlings survived for one year. Muick (1991) also found that artificial shade enhanced the survival of blue oak seedlings. In coast live oak woodlands of California, Parker and Muller (1982) used reciprocal transplant experiments to document higher shade tolerance in *Bromus diandrus* and *Pholistoma auritum*, two species apparently facilitated by oak canopies, than in *Avena fatua*, a species generally excluded from subcanopy habitat. In laboratory experiments, *Bromus diandrus* had comparatively higher relative growth rates when grown in low light (Mahall et al., 1981). In a series of experiments in which whole soil blocks were transplanted between the understory of coast live oak, adjacent open grassland, and artificial shade treatments, Maranon and Bartolome (1993) found that reduced radiation under the evergreen canopies limited the distribution of the open species. Reciprocally, strong interference limited the establishment of the understory species in the open grassland.

Shade may also have secondary facilitative effects. Shade provided by exceptionally salt-tolerant species in salt marshes appears to reduce evaporation from subcanopy soils and consequently maintains lower soil salinities than in soils exposed to direct insolation (Bertness & Hacker, 1994; Callaway, 1994). Bertness (1991) and Bertness and Shumway (1993) experimentally manipulated soil salinity in the upper zones of a New England salt marsh and found that *Distichlis spicata*, a salt-tolerant colonizer of saline bare patches, facilitated the growth of *Juncus gerardi* when soil salinities were high. When soil salinities were artificially reduced by watering, growth of *Juncus* was not improved by *Distichlis*. Similarly, Bertness and Hacker (1994) and Bertness and Yeh (1994) found that shade provided by marsh elder shrubs (*Iva frutescens*) decreased soil salinity and facilitated the growth and survival of *Juncus gerardi*.

In contrast to facilitation via shade, trees often facilitate the growth and survival of other species by providing access to high light for plants that can attach to and survive on their trunks and branches. Epiphytes are salient features of subtropical and tropical forest, with many species appearing to be obligately dependent on facilitation by others for light. Species-specific relationships between hosts and epiphytes may occur as a result of bark texture and chemistry (Went, 1940; Bennett, 1986). Species that are often found on the forest floor may also gain access to light by establishing on the stems of others (Burton & Mueller-Dombois, 1984). Hay (1986) found that epiphytism in seaweed communities may also provide protection from herbivory.

2. Soil Moisture

Generally, species appear to compete for soil water; however, there are examples of facilitative interactions in which water availability for one species is enhanced by the presence of another species. Joffre and Rambal (1988) measured a significant "delay" in soil water loss under *Quercus rotundifolia* and *Q. suber* in Spanish savannas relative to

soils in the open. They argued that increased soil moisture was accountable for large differences in species composition under trees and in the open. In Kenyan savannas, Maranga (1984) found that leaf water potential of grasses under *Acacia tortilis* was significantly higher than in the open. In North American shrub steppe, Great Basin sage (*Artemisia tridentata*) transports water from deep, moist soils to dry surface soils during the night via "hydraulic lift" (Richards & Caldwell, 1987; Caldwell & Richards, 1989; Williams et al., 1993). Additional experiments using stable isotope analysis indicated that water from hydraulic lift was distributed to neighboring plants, although the magnitude of water transferred was small (Caldwell, 1990). Dawson (1993), however, used similar techniques to investigate the magnitude of hydraulic lift conducted by sugar maple (*Acer saccharum*) and the effects of the hydraulically lifted water on understory plants. He found hydraulically lifted water in all understory plants he examined, with proportional use of hydraulically lifted water ranging from 3% to 60%. Plants that used large proportions of hydraulically lifted water had more favorable water relations and growth than those that did not.

Tree islands at forest-alpine ecotones may also create unique soil moisture microhabitat by altering wind flow near the soil surface and snow deposition. Holtmeier and Broll (1992) found that snow accumulated inside and leeward of tree islands in Colorado, increasing soil moisture. Snowdrifts accumulating on the leeward sides of mature trees appear to develop "ribbon forests" in subalpine regions of the Rocky Mountains (Billings, 1969). Snow accumulation inhibits seedling regeneration but enhances the growth of established plants near the drifts. In contrast, Brooke et al. (1970) found that snow next to the stems of trees in subalpine meadows in coastal British Columbia melted faster than snow in the open. Earlier snow melt appeared to facilitate the growth of shrubs and other trees in these "snow craters," eventually creating tree islands.

3. Soil Nutrients

Many researchers have measured higher levels of nutrients in soils directly beneath the canopies of perennials than in the surrounding open spaces without perennial cover. Subcanopy soil enrichment may occur as a result of "nutrient pumping" (sensu Richards & Caldwell, 1987), in which deeply rooted perennials take up nutrients unavailable to shallowly rooted plants and deposit them on the soil surface via litterfall and throughfall. Alternatively, perennial canopies may trap airborne particles which eventually are deposited at the base of the plant. Nutrient enrichment may also occur indirectly via nitrogen fixation.

Subcanopy soil nutrient enrichment (and often a corresponding change in species composition and increased productivity) has been reported in many systems, but these effects are especially common in studies conducted in savannas and similar plant communities with clearly distinguished understory and open microhabitats. Nutrient enrichment has been measured under trees in African savannas (Radevanoki & Wickens, 1967; Dancette & Poulain, 1969; Bernhard-Reversat, 1982; Weltzin & Coughenhour, 1990; Belsky et al., 1989), central American savannas (Kellman, 1979, 1989), Asian savannas (Singh & Lal, 1969), and mediterranean-climate savannas in California (Holland, 1980; Holland & Morton, 1980; Callaway et al., 1991). Similar patterns have been quantified in North American deserts (Went, 1942; Garcia-Moya & McKell, 1970; Charley & West, 1975; Halvorson & Patten, 1975; Patten, 1978; Whittaker et al., 1979a; Schmida & Whittaker, 1981), Australian deserts (Mott & McComb, 1974), and Asian deserts (Aggar-

wal et al., 1976). Perennial trees and shrubs also improve soil nutrient status in North American mixed grasslands (Tiedmann & Klemmedson, 1973, 1977; Barth & Klemmedson, 1978; Yavitt & Smith, 1983), alder shrublands (Goldman, 1961), Patagonian shrublands (Rostagno et al., 1991), and open lodgepole pine (*Pinus contorta*) stands (Zincke, 1962).

Although many researchers have studied distributions of soil nutrients in relation to perennial canopies, fewer have tested for causal relationships between litterfall and soil enrichment, enhanced growth, or species shifts. Turner et al. (1966) found that saguaro seedlings survived better on soil collected from under paloverde trees (*Cercidium microphyllum*) than on soils from under either mesquite (*Prosopis juliflora*) or ironwood (*Olneya tesota*), but the differences were confounded by soil albedo and temperature. Monk and Gabrielson (1985) found that addition of litter from the floor of deciduous forests in South Carolina generally improved the overall productivity in understory plots, but the effects of litter on individual species ranged from facilitation to interference. Surface soils under the canopies of blue oaks are much more nutrient rich than surrounding open grassland (Kay, 1987; Holland & Morton, 1980; Callaway et al., 1991), and in greenhouse tests they improve the growth of *Bromus diandrus*, an understory species, when compared to open grassland soils. Addition of blue oak litter to open grassland soil also improved the growth of *B. diandrus* in the greenhouse, and when blue oak roots were excluded in the field, subcanopy soil facilitated understory growth (Callaway et al., 1991). Walker and Chapin (1986) used greenhouse experiments to demonstrate the facilitative effects of nitrogen-rich soil from under alder (*Alnus tenuifolia*) on willow (*Salix alaxensis*) and poplar (*Populus balsamifera*) seedlings. Facilitative mechanisms were also found in field experiments; however, root interference was generally more important (see "Interactions between Facilitation and Interference"). In a second experiment in Glacier Bay, Alaska, Chapin et al. (1994) found strong facilitative effects of *Alnus sinuata* and *Dryas drummondii*, both nitrogen-fixers, on the growth of sitka spruce (*Picea sitchensis*). In earlier studies, Lawrence et al. (1967) calculated that nitrogen content of soil at Glacier Bay increases from 33 kg/ha to 400 kg/ha as bare soil is invaded by *D. drummondii*.

Others have used laboratory experiments to show the benefits of nutrient additions in litter to the growth of target species. Litter-mediated increases in growth or nutrient uptake have been reported for the litter of savanna and woodland oaks (Monk & Gabrielson, 1985; Callaway et al., 1991), alder (Chapin et al., 1994), and *Metrosideros polymorpha* (Walker & Vitousek, 1991). The effects of litter, however, can be complex. Callaway et al. (1991) found that fresh leaf litter of blue oak strongly suppressed the growth of an understory grass species, whereas old blue oak litter facilitated its growth. Facelli (1994) found that white oak (*Quercus alba*) leaf litter indirectly facilitated the growth of seedlings of *Ailanthus altissima* by suppressing herbs that competed with *Ailanthus*.

4. Soil Oxygenation

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). Schat and Van Beckhoven (1991) reported that *Plantago coronopus* and *Samolus valerandi* were tightly clumped around tussocks of the aerenchymous *Juncus maritimus* in dune

slacks on the coast of Holland, where survival rates appeared to be enhanced by soil oxygenation and oxidation of iron, manganese, and sulfide. When *P. coronopus* and *Centaureum littorale* were grown with *Juncus maritimus* in the greenhouse, growth and nutrient uptake were improved (Schat, 1984). Castellanos et al. (1994) reported that *Spartina maritima* aerates surface sediments in southern Spain, creating conditions favorable for the invasion of *Arthrocnemum perenne*. In eastern salt marshes in North America, Hacker and Bertness (1995) found that the aerenchymous *Juncus maritimus* increased the redox potential in its rhizosphere, which corresponded with increased growth of *Iva frutescens*, a woody-stemmed perennial, and the extension of *Iva*'s distribution to lower elevations in the marsh.

Similar results have been reported for plants from freshwater marshes. In greenhouse experiments, undrained pots containing cattails (*Typha latifolia*) had dissolved oxygen contents more than four times greater than pots without cattails, and other marsh plants grown with *Typha* survived longer and grew larger than those in pots without cattails when pot substrates were kept between 11° and 12°C (Callaway & King, in press). In the field, *Myosotis laxa* (forget-me-not) plants growing next to transplanted cattails were larger and produced more fruit than those isolated from cattails.

Others have reported evidence that the overall contribution of oxygen transported through plants to the total oxygen balance of nutrient cultures or vegetated marshes may be small (Bedford et al., 1991; Howes & Teal, 1994). Berendse and Aerts (1984) reported that *Molina caerulea* did not appear to transport oxygen below ground but transpired rapidly enough to reduce the depth of water in waterlogged containers. Lower water levels permitted aeration of the shallow root system of *Erica tetralix*, which grew better in mixtures of *Molina* than alone.

B. SUBSTRATE MODIFICATION

Perennial canopies can facilitate other species by altering the physical characteristics of substrates. Joffre and Rambal (1988, 1993) studied the effects of two evergreen oaks, *Quercus suber* and *Q. rotundifolia*, on microsite characteristics and found that subcanopy soils had significantly lower dry bulk density and moisture-release curves than did soils from the surrounding open grassland. These differences were associated with much higher subcanopy soil water storage capacities, higher seasonal soil water contents, and shifts in species composition. In California oak woodlands, litter deposition and root penetration develop soils with lower bulk densities under tree canopies, which presumably also increases soil water storage capacity (Kay, 1987; Callaway et al., 1991). In dry lakes of the Mojave Desert, *Kochia californica* establishes in cracks in very fine-textured soil and eventually collects small mounds of coarser-textured soil that *Atriplex torreyi* can colonize (Vasek & Lund, 1980). *Atriplex torreyi* appears to eventually accumulate large mounds of sandy soil that coalesce across the landscape and provide habitat suitable for *A. confertifolia* and *Haplopappus acradenius*. Large shifts in soil chemistry correlated with these soil textural and microtopographic changes. Johnson et al. (1985) argued that *Salix nigra* stabilized alluvial soils deposited in the deltas of southern Louisiana, enhancing the development of many other species.

Incompletely decomposed remains of plants may also facilitate the recruitment of other species by providing favorable substrate (see review by Harmon et al., 1986). In Sitka spruce-western hemlock (*Tsuga heterophylla*) forests of northwest America, 94–98% of tree seedlings are found on "nurse logs" that cover only 6–11% of the forest floor

(Franklin & Dyrness, 1973; Graham & Cromack, 1982; McKee et al., 1982; Harmon, 1985). Logs are also important seedbeds in other Pacific Northwest forests (Christy & Mack, 1984). Griffith (1931) and Smith (1955) found strongly disproportional growth of subalpine fir and Englemann spruce seedlings on nurse logs in subalpine forests in British Columbia. In an extensive series of elegant experiments, Harmon and Franklin (1989) determined that the primary role of these nurse logs during recruitment of Sitka spruce and western hemlock was to provide a substrate free from competition with herbs and mosses on the forest floor.

Comparably, partially decomposed remains of wetland plants and the sediment trapped in their remains provide habitat suitable for colonization for different plant species that are less tolerant of submersion (Barko & Smart, 1986; Bertness, 1988). In the Santee Swamp of South Carolina, Dennis and Bateson (1974) found 11 plant species to be restricted to floating logs and stumps. *Clethra alnifolia*, a widely distributed wetland shrub in eastern North America, regenerates more commonly on logs, tree roots, and stumps than on other, more common microsites (Jordan & Hartman, 1995).

C. PROTECTION FROM HERBIVORES

Some of the most clearly documented instances of interplant facilitation are indirect and mediated through herbivores. Atsatt and O'Dowd (1976) coined the term "plant defence guilds" for groups of plants that interact in ways that reduce herbivory for one or more species. For example, *Themeda triandra*, a highly palatable East African savanna grass, suffers $\approx 80\%$ mortality from ungulate grazers when not associated with other, less palatable grass species; however, as codominance with unpalatable species increases, mortality of *Themeda* rapidly decreases (McNaughton, 1978). Similar examples of associational defenses have been reported by Doult and Nakata (1973), Solomon (1981), Letourneau and Altieri (1983), and Holmes and Jepson-Innes (1989). In English grasslands, *Trifolium fragiferum* is highly grazed by rabbits in the absence of *T. repens* (white clover), but in even mixtures of these species, *T. fragiferum* is ignored (Harper et al., 1961). Harris and Brock (1972) found that herbivory of white clover by larvae of porina caterpillars was much lower when white clover was grown in mixtures of rye grass (*Lolium perenne*) than when grown in pure stands.

In the Sonoran Desert, the positive association between paloverde seedlings and various shrub species documented by McAuliffe (1986; also see "Spatial Patterns") appears to be determined by herbivory. Of 84 naturally occurring paloverde seedlings in the open, 92% were consumed by herbivores; however, only 64% (37/58) of seedlings under shrub canopies suffered the same fate. The protection provided by the shrubs increased with physical contact and proximity as well, with only 14% of the seedlings actually touching shrubs consumed, in comparison to 92% lost when sheltered by the canopy but not touching. McAuliffe hypothesized that the shrubs provided concealment and that the unpalatability of the most common nurse species, *Ambrosia deltoidea* and *A. dumosa*, deterred browsing. McAuliffe (1984b) also found that young barrel-shaped cacti (*Mammillaria microcarpa* and *Echinocereus englemannii*) were much more common under live and dead *Opuntia fulgida*, where they were protected from herbivores by the accumulation of spine-covered stem joints falling from the nurse plant.

In northern Sweden, Hjalten et al. (1993) found that birch (*Betula pubescens*) experienced exceptionally high herbivory when associated with "plants of higher palatability" (*Sorbus aucuparia* or *Populus tremuloides*) but exceptionally low herbivory when

associated with "plants of lower palatability" (*Alnus incana*). Similarly, shrubs in the Chilean matorral appear to facilitate the survival of annual herbs by protecting them from herbivores (Jaksic & Fuentes, 1980). Hay (1986) found that several species of highly palatable seaweeds appeared to avoid local extinction by finding shelter from grazers in safe microsites provided by unpalatable seaweed species.

The facilitative effect of coastal scrub shrubs on blue oak recruitment reported by Callaway (1992; also see "Manipulative Field Experiments") was elicited primarily by shade from the shrub canopies (see "Light and Temperature"). However, analysis of the fates of individual acorns also showed that causes and timing of mortality differed significantly under shrubs and in the open grassland and that herbivory was important. Predation on acorns appeared to be due to rodents and was higher under shrubs than in the grassland only 1 m away. Emergent shoots, however, were eaten by deer and experienced much higher predation in the grassland than under shrubs. Consequently, blue oak acorns that survived early rodent predation under shrubs became seedlings that occupied sites relatively free from deer predation on shoots.

In most cases referred to above, benefactor species appear to physically shelter or hide beneficiary species from herbivores. A similar phenomenon, called "associational resistance" by Root (1972) and "associational plant refuges" by Pfister and Hay (1988), may occur when some species experience less herbivory as a function of the visual or olfactory complexity of the surrounding vegetation. A number of ecologists have found that community complexity serves as an impediment to search efficiency, in contrast to species-specific physical protection from herbivores or association with unpalatable species (Pimentel, 1961; Root 1972). Root (1973) sampled consistently lower "herbivore loads" on collards (*Brassica oleracea*) in pure stands than on collards grown in mixtures with other species (also see Dempster, 1969; Bach, 1980; Risch, 1981). Other experiments by Tahvanainen and Root (1972) showed that chemical stimuli from non-host tomatoes and ragweeds (*Ambrosia artemisiifolia*) interfered with the ability of flea beetles to find and feed on collards. Brown and Ewel (1987) found that rates of herbivory on many species in Costa Rican forests were reduced in diverse species mixtures. The response of herbivorous insects to specific host odors may be influenced by non-host vegetation near the host (Andow, 1986; Kareiva, 1983; May & Ahmad, 1983; Stanton, 1983). Morrow et al. (1989) reported that the goldenrod leaf beetle (*Trirhabda canadensis*) avoided preferred host species when they were grown in high densities of non-host plants.

D. POLLINATION

Plants may compete for pollinators under some conditions; however, co-flowering species have been shown to experience facilitation when the attraction of one species for pollinators is greater than that of a neighbor. Thomson (1978) found that *Hieracium florentinum* received more visits from pollinators when it was mixed with *H. auranticum* than when alone. In the understory of deciduous forests in Ontario, Lavery and Plowright (1988) recorded enhanced fruit and seed set in mayapples (*Podophyllum peltatum*) that were associated with lousewort (*Pedicularis canadensis*) than in those far from lousewort. In later studies, Lavery (1992) found that mayapple, which produces no nectar, depends on infrequent visits from queen bumblebees that accidentally encounter mayapple while collecting nectar from lousewort, the so-called magnet species. Pollinator visits and seed set were also found to be higher in *Trillium ovatum* with magnet neighbors than in those without (T. M. Lavery, pers. comm.). Spatial associations between insect-pollinated

species that produce low amounts of nectar with other high-nectar-producing species suggest similar interactions (Pellmyr, 1986). Brown and Kodric-Brown (1979) and Dafni (1984) found that nectar-seeking pollinators visited plant species with nectarless flowers if they were similar in shape and color to flowers on nectar-producing species.

E. CONCENTRATION OF PROPAGULES

The facilitative "mechanism" considered here, the role of above-ground plant parts in collecting and concentrating propagules of other species, is questionable in its overall positive effect. If propagules are prevented from being lost to the system or destroyed altogether, then propagule filters are clearly facilitative. On the other hand, if the above-ground architecture acts only to alter spatial patterns of distribution without providing sites more favorable for regeneration than open sites, then the process may actually have confounding effects or establish an alternative hypothesis to biological facilitation. Numerous studies have cited the importance of propagule concentration under mature plants by wind and animal vectors, but only a few have quantified seed abundance under canopies and in the open. Hutto et al. (1986) found $5.33 (\pm 2.58 \text{ S.D.})$ saguaro seeds/0.01 m³ of soil under the canopies of paloverde trees, compared to 0.17 ± 0.41 seeds/m³ 1 m from the canopy edge. In the case of the saguaro, propagule concentration and biological facilitation seem to determine spatial patterns (see "Spatial Patterns" and "Manipulative Field Experiments"). Day and Wright (1989) found that seeds of many species were trapped in the canopies of *Eriogonum ovalifolium* on volcanic cinder cones, leading to common preferential establishment under *Eriogonum*. In the mediterranean scrub vegetation of Israel, quantities of bird-deposited seeds vary among shrub species, establishing the potential for species-specific positive spatial relationships (Izhaki et al., 1991). Seed aggregation around plants that exhibit positive spatial patterns with seedlings or adults has also been reported by Fuentes et al. (1984, 1986) and Aguiar and Sala (1994).

F. ROOT GRAFTS, MYCORRHIZAE, AND SOIL MICROBES

The principal interaction between roots of individual mature trees is generally considered to be competition for limited resources. However, there is evidence for intra- and interspecific root grafting in which water, nutrients, and photosynthate are passed between different individuals (Bormann & Graham, 1959; Graham, 1959; Bormann, 1962). Bormann (1966) conducted experiments in which one member of a grafted pair of white pines (*Pinus strobus*) was girdled. He found that bark girdling resulted in a significant drop in the diameter growth of the ungirdled member of the grafted pair, as the intact tree supported root growth in the girdled tree for a period of three years. Bark girdling of nongrafted, suppressed white pines resulted in death within a year, but grafted, suppressed trees remained alive for two or more years after girdling. He argued that the development of naturally occurring white pine stands is shaped by both competition and "a noncompetitive force governed by inter-tree food translocation." An alternative hypothesis for root grafting was proposed by Keeley (1988), who found root grafting in blackgum (*Nyssa sylvatica*) to be more common in swamps than in uplands. He suggested that the greater frequency of root grafting in unstable soils where trees rooted closer to the surface provided greater support and stability to the stand as whole.

Mycorrhizal fungi also appear to form below-ground connections between plants by which nutrients and carbon are exchanged (Chiarello et al., 1982; Whittingham & Read,

1982; Read et al., 1985; Francis et al., 1986; Newman & Ritz, 1986), although whether or not the transfer may occur via root leakage is still debated (Newman & Ritz, 1986; Allen & Allen, 1990). In support of the potential for mycorrhizal connections to mediate facilitative interactions, Grime et al. (1987) found that labeled $^{14}\text{CO}_2$ was transferred from *Festuca ovina* to many other plant species 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 species and increased biomass of otherwise competitively inferior species, and experimental microcosms that were infected with mycorrhizae ultimately were more diverse than those that were not infected. Molina and Trappe (1982) found that mycorrhizae commonly found on Pinaceae also infect two associated ericaceous plants, madrone (*Arbutus menziesii*) and manzanita (*Arctostaphylos* spp.). Soil collected from under madrone and manzanita enhances mycorrhizal development and the growth of trees in comparison to soils collected in the open (Amaranthus & Perry, 1989; Borchers & Perry, 1990); and survival of Douglas fir (*Pseudotsuga menziesii*) seedlings is five times greater in the vicinity of madrone than near shrubs with other mycorrhizal symbionts or herbs (Amaranthus et al., 1990). Magnusson and Magnusson (1993) reported that *Betula pubescens* seedlings were larger and more consistently infected with mycorrhizae when experimentally planted near naturally occurring *Salix* spp. in southern Iceland.

Plants may also alter soil microflora in ways that enhance the growth of other plant species. In laboratory experiments, Christie et al. (1974) found that shoot mass of *Lolium perenne* was higher when grown with *Plantago lanceolata* than when grown alone. In this case, the positive effect also appeared to be indirect, as they attributed the positive growth response to greater microbe abundances in the mixture than in monocultures and the potential positive effects of the microbes on root uptake. Bever (1994) reported that some old-field species grew better in soil microbial communities from the rhizospheres of other plant species than in microbe communities from the rhizospheres of conspecifics. Cryptogamic soil crusts, formed primarily from cyanobacteria and cyanolichens, have been shown to enhance the growth and mineral uptake of associated vascular plants (St. Clair et al., 1984; Lesica & Shelly, 1992; Harper & Pendleton, 1993).

V. Interactions between Facilitation and Interference

Facilitative mechanisms may act simultaneously with resource competition or allelopathy, and thus the overall effect of one species on another may be the cumulative effect of multiple, complex interactions (see Weldon & Slauson, 1986). The earliest interactive effects of competition and facilitation were described from experiments conducted by Shirley (1945; also see "Light and Temperature") and Ellison and Houston (1958). The latter reported that the growth of some herbaceous species in the understory of quaking aspen (*Populus tremuloides*) were stunted unless aspen roots were excluded by trenching; but after trenching, the growth of these species exceeded that of the surrounding open areas. Apparently the facilitative mechanisms of shade or nutrient inputs were present but were outweighed by root interference. Walker and Chapin (1986) demonstrated the existence of facilitative mechanisms for alder (*Alnus tenuifolia*) on willow (*Salix alaxensis*) and poplar (*Populus balsamifera*) in greenhouse experiments and in the field. However, under natural conditions, willow, poplar, and white spruce (*Picea glauca*) grew more poorly in alder stands than in other vegetation. In other experiments, they found that root interference and shading in alder stands was much more

influential on the other species than nutrient addition, and overrode the effects of facilitation. In a similar study in Glacier Bay, Chapin et al. (1994) found that early to mid-successional species, such as *Alnus sinuata*, affected the late-successional *Picea sitchensis* in positive ways (nutrient uptake and growth) and negative ways (germination and survivorship). Sitka spruce seedlings that were planted in alders accumulated more than twice the biomass and acquired significantly higher leaf concentrations of nitrogen and phosphorus than seedlings planted in spruce forests. However, root trenching in alder stands further increased growth and nutrient acquisition, demonstrating that competitive and facilitative mechanisms were operating simultaneously. In contrast to the interior floodplain, however, the facilitative effects of alder on spruce overrode root interference in natural conditions. In the Patagonian steppe, Aguiar et al. (1992) found that various shrub species protected grasses from wind and desiccation, but strong facilitative effects were expressed only when root competition was experimentally reduced. In the same system, Aguiar and Sala (1994) found that young shrubs had stronger facilitative effects on grasses, but the positive effects declined as grass densities increased near the shrubs. During primary succession on volcanic substrates, Morris and Wood (1989) measured both interfering and facilitating mechanisms by which *Lupinus lepidus* interacted with secondary invaders, but they concluded that the net effect of lupine was facilitative.

In blue oak woodlands of central California, Callaway et al. (1991) 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* (see "Soil Nutrients"). 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 had 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 had strong negative effects on understory productivity. Thus, in this ecosystem, as in the Alaskan floodplain studied by Walker and Chapin (1986), root interference, when present, outweighed facilitative effects of nutrient enhancement that were evident in the absence of intense root interference. In intertidal seaweed communities, Hay (1986) found that highly palatable, but competitively inferior, seaweed species grew 14–19% less when in mixtures with superior competitors than when alone, when herbivores were excluded. However, in the presence of herbivores, palatable species survived only when mixed with competitively superior but unpalatable species. In this system, the effects of competition were outweighed by protection from herbivores.

Myrica faya, a tree native to the Azores and Canary Islands, is a very successful invader on volcanic soils on the island of Hawai'i, where it is replacing the native tree *Metrosideros polymorpha* (Whiteaker & Gardener, 1985). Walker and Vitousek (1991) found that direct effects of the invading *Myrica* on the native *Metrosideros* were both positive and negative. *Myrica* enriched the nitrogen content of soils, improving *Metrosideros* growth in greenhouse experiments, and shade from *Myrica* improved *Metrosideros* seedling germination and survival. However, litter from *Myrica* reduced *Metrosideros* germination, and the growth of young *Metrosideros* did not improve in the shade of *Myrica* in the field. They concluded that the net result was negative, as it resulted in the lack of regeneration of *Metrosideros* under the canopies of *Myrica*. As for the other studies described in this section, these results emphasize the importance of presuming

complex, interacting causes of plant community structure including facilitation, interference, and abiotic factors.

The balance of facilitation and interference may be affected by the lifestages of the interacting plants. Patterns of nurse-plant mortality observed in several systems indicate that species that begin their lives as the beneficiaries of nurse plants often become significant competitors with their former benefactors as they mature. McAuliffe (1988) found that young *Larrea tridentata* plants were disproportionately associated with dead *Ambrosia dumosa*, a species critical to the initial establishment of *Larrea*. Similarly, mature saguaros were associated disproportionately with dead paloverde trees, which commonly function as nurse plants to seedling saguaros (McAuliffe, 1986). In the Tehuacan Valley of Mexico, *Neobuxbaumia tetetzo* which is nursed by *Mimosa luisana* (Valiente-Banuet et al., 1991b), eventually suppresses the growth and reproduction of its benefactor (Flores-Martinez et al., 1994). Archer et al. (1988) found that mesquite trees had disappeared from 17% of the large clusters of other species that owed their existence to favorable microhabitat originally provided by the mesquite (see "Spatial Patterns"). Another 24% of the clusters possessed only dead mesquite, indicating that once mesquite established habitat suitable for colonization, colonizers were able either to outcompete the original mesquite nurse plant or to prevent it from reproducing in the clusters. Similar patterns have been reported in Texan post oak (*Quercus stellata*) savanna where red cedars (*Juniperus virginiana*) are initially facilitated by post oak but eventually overtop the oak and kill it (Archer & Rykiel, 1994).

In some cases, a particular benefactor species has been found to have facilitative effects on some species but competitive effects on other, apparently similar species. In the upper zones of southern California salt marshes, the perennial subshrub *Arthrocnemum subterminale* has strong facilitative effects on codominant winter annual species and strong competitive effects on others (Callaway, 1994). Experimental manipulation of root and canopy effects indicated that competitive and facilitative mechanisms operate simultaneously. At the ecotones of Sierran forests and shrub steppe in the Great Basin, *Artemisia tridentata* outcompetes ponderosa pine (*Pinus ponderosa*) for water but acts a nurse plant for pinyon pine, a species that has leaf-level physiological characteristics and nutrient requirements similar to those of ponderosa pine (Callaway et al., in press).

The balance between facilitation and interference often appears to be affected by the harshness of physical conditions. Bertness and Callaway (1994) hypothesized that the importance of facilitation in plant communities increases with increasing abiotic stress or increasing consumer pressure. Alternatively, they hypothesized that the importance of competition in communities would increase when physical stress and consumer pressure were relatively low, because neighbors buffer one another from extremes of the abiotic environment (e.g., temperature or salinity) and herbivory.

In a New England salt marsh, Bertness and Yeh (1994) found that the effects of adult and seedling *Iva frutescens* plants on conspecific seedlings were positive in unshaded bare patches where salinity was moderated by shade from the plants (see "Light and Temperature"). When patches were watered, however, strong competitive interactions developed between adults and seedlings and among seedlings. The interactions between adults and seedlings were clearly dependent on environmental conditions. Bertness and Shumway (1993) also eliminated the facilitative effects of *Distichlis spicata* and *Spartina patens* on *Juncus gerardi* by watering experimental plots and reducing soil salinity. Other facilitative interactions in the marsh differed among zones that varied in salinity stress. In the same marsh, the fitness of *Iva* shrubs associated with *Juncus gerardi* was enhanced

at lower elevations but reduced at higher elevations, where soil salinity was lower (Bertness & Hacker, 1994). Pennings and Callaway (1992) documented intense interspecific interference where abiotic stress was relatively benign in a salt marsh in California, but no detectable interspecific interference occurred in zones where physical factors were extreme. They did not detect facilitation in their experiments, but strong facilitative interactions existed at even higher, more saline, elevations in the marsh (Callaway, 1994). In subalpine forests of the northern Rockies, whitebark pine varies in its effect on subalpine fir along a gradient of stress (Callaway & Bertness, 1994; also see "Manipulative Field Experiments"). They found that firs were randomly distributed with respect to whitebark pines in "low-stress" habitats characterized by high tree biomass and sheltered topography but were highly clumped around whitebark pines in "high-stress" sites characterized by low tree biomass and exposed topography. Furthermore, they found that growth rates of mature firs near pines decreased with the death of pines in high-stress sites but increased after death of nearby pines in low-stress sites. They contended that facilitation was more important to community structure in these subalpine forests in high-stress environments but that interference was more important in low-stress environments. In another experiment involving variation in physical stress, Greenlee and Callaway (in review) used removal experiments to document shifts in interference and facilitation. They found that bunchgrasses interfered with *Lesquerella carinata*, a rare perennial mustard, in a wet and cool (low-stress) year but facilitated *Lesquerella* in a dry and hot year. Overall, *Lesquerella* was positively associated spatially with bunchgrasses. Similarly, Belsky (1994) reported stronger competitive effects of savanna trees on understory grasses in wet sites, versus stronger facilitative effects of trees on grasses on dry sites.

Shifts in interspecific interactions also appear to occur at different temperatures in anaerobic substrates. *Myosotis laxa* appeared to benefit from soil oxygenation when grown with *Typha latifolia* at low soil temperatures (Callaway & King, in press; also see "Soil Oxygenation"); but at higher soil temperatures, significant effects of *Typha* on soil oxygen disappeared (presumably because of increased microbial and root respiration) and the interaction between *Typha* and *Myosotis* became competitive.

Complex combinations of negative and positive interactions operating simultaneously between species appear to be widespread in nature. Such concomitant interactions suggest that current conceptual models of interplant interactions based on resource competition alone are limited in their potential for accurately depicting processes in natural plant communities.

VI. Consequences for Community Structure

Positive interactions may determine community spatial patterns, permit coexistence (see Aarssen & Turkington, 1985a; DeAngelis et al., 1986), enhance diversity and productivity, and drive community dynamics. Facilitation is also an essential, albeit controversial, component of the traditional concept of plant succession. Facilitative processes often provide regeneration niches (sensu Grubb, 1977), and the establishment and maturation of beneficiary plants in the same space as the benefactor suggests that the beneficiary may ultimately replace the benefactor, or at least that intense competition may eventually develop. Such shifts in dominance originating with facilitative interactions have been proposed within many community types.

McAuliffe (1984a) found that the proximity of mature saguaros was correlated with greater mortality of the paloverde trees that had nursed them when they were young. This apparent competition between maturing saguaros and their former nurse plants suggests a dynamic pattern of change in these communities operating at the scale of the individual plants (Vandermeer, 1980). Similar patterns of spatial association among different age groups and mortality rates for *Larrea tridentata* and *Ambrosia dumosa* were documented in simple communities in the Mojave Desert (McAuliffe, 1988; also see "Interactions between Facilitation and Interference"). There, *Larrea* recruited primarily under mature *Ambrosia*, and accelerated the mortality of the *Ambrosia* nurse plant. McAuliffe proposed that the ability of *Ambrosia* to colonize open space, and the subsequent nurse-plant relationship and early death of *Ambrosia* nurse plants due to interference from maturing *Larrea*, establishes a cyclical dynamic process in Mojave Desert communities. Similar facilitative relationships were inferred from nurse-plant patterns among many species in complex Sonoran Desert communities with recruitment of many species being limited to areas beneath the canopies of other plants (McAuliffe, 1988). The dynamics of these species-rich communities appeared to be qualitatively similar to those in the species-poor Mojave Desert. Other spatial patterns suggestive of nurse-plant facilitation have prompted claims of dynamics at the scale of individual plants for west African forests (Aubreville, 1938), heathlands and beech forests of Britain (Watt, 1947), the Chihuahuan Desert (Yeaton, 1978), the Karoo Desert (Yeaton & Elser, 1990), forests in eastern North America (Forcier, 1975; Woods & Whittaker, 1981), and forests in western and central Europe (Remmert, 1991).

Other studies of vegetation dynamics emphasize the importance of facilitation for large-scale changes over landscapes. Archer et al. (1988) found that individual mesquite trees invaded grasslands on the Rio Grande Plains in the southwestern United States and provided "nuclei" for the organization of small clusters of many other species under the canopies of mesquite. By comparing aerial photographs, they measured gradual shifts over time in community type from grassland to savanna to woodland and emphasized the importance of mesquite as a facilitator of dynamic processes in the region (Archer, 1989). Mesquite, a nitrogen fixer, also provides microhabitat higher in nutrients, favorable for herbaceous species that are uncommon in the open grassland, and higher in total herbage productivity (Tiedemann & Klemmedson, 1973, 1977; Yavitt & Smith, 1983).

At the ecotone of tallgrass prairie and eastern deciduous forest in North America, trees encroach rapidly into habitat otherwise dominated by grassland if fire is suppressed (Weaver, 1968). In some regions this process appears to be facilitated by sumac clones (*Rhus copallina*), which are more tolerant of conditions in grassland and invade first (Petranka & McPherson, 1979). After the establishment of sumac, forest trees establish in its canopy. Sumac appears to facilitate trees indirectly by eliminating prairie species via allelopathy and shade and directly by enhancing soil moisture and nutrient content.

Facilitation-induced vegetation dynamics may also occur in community types in central California. The consequences of proportionally high recruitment and survival of oak species under nurse shrubs in coast live oak woodlands (Callaway & D'Antonio, 1991) and blue oak woodlands (Callaway, 1992; also see "Manipulative Field Experiments") were studied by Callaway and Davis (1993) using aerial photographs. They found that the cover of coast live oak canopies visible on aerial photographs increased much more in shrublands than in grassland between 1947 and 1989, and they documented conversion of shrubland to coast live oak woodland on some substrates in a complex

mosaic of community types. The transition of shrubland to oak woodland occurred more rapidly in the absence of fire.

The studies presented thus far in this section indicate that facilitative processes may drive dynamic change in the absence of large-scale disturbances; other studies have built a large body of evidence for the importance of facilitation during primary and secondary succession. Here I will not consider general studies of species replacement during succession which have been thoroughly reviewed elsewhere (Connell & Slatyer, 1977; Huston & Smith, 1987; Burrows, 1990); instead, I focus on those studies that support facilitative interaction during succession by pattern analysis or experimentation.

Because of the exceptionally harsh initial physical conditions common during primary succession, facilitation may be of greater importance there than in secondary succession (Connell & Slatyer, 1977). Nurse-plant relationships also appear to be more common during the early stages of primary succession than during later stages (Chapin et al., 1994). Wood and del Moral (1987) reported nurse-plant relationships among several species colonizing volcanic substrate on Mount St. Helens. In other field experiments on Mount St. Helens, Morris and Wood (1989) found that *Lupinus lepidus*, the initial pioneer on the barren pyroclastic flows, reduced the survival of two invading species, *Anaphalis margaritacea* and fireweed (*Epilobium angustifolium*) in the first year. However, for both invading species, seedlings surviving within lupine patches grew larger than in control treatments in both years, and the survival of both species was higher in lupine patches in the second year. They concluded that a balance of facilitative and inhibitory effects determined successional establishment. The balance between facilitation and competition was emphasized in later studies when del Moral and Bliss (1993) found that *Anaphalis*, *Epilobium*, and *Hypochaeris* seedlings were *less* associated with living *Lupinus lepidus* than expected by chance, but that rapid invasion of nutrient-rich patches occurred soon after the death of *Lupinus* plants. Day and Wright (1989), examined spatial plant associations during primary succession on cinder cones in Craters of the Moon National Park and found that all late colonizers were positively associated with the inner canopy of *Eriogonum ovalifolium*, one of two initial colonizers. Possible mechanisms for these positive interactions included higher soil moisture, total nitrogen and phosphorus, and seed accumulation. On Mount Fuji, Japan, *Polygonum cuspidatum* creates conditions that may favor other plants on recently formed volcanic substrate (Hirose & Taten, 1984).

Facilitation may also play a significant role in post-glacial primary succession. A widely cited study of post-glacial succession (Crocker & Major, 1955) reported that changes in soil characteristics caused by nitrogen-fixing alders (*Alnus sinuata*) were correlated with successful invasions of other species in Glacier Bay, Alaska. Subsequently, Chapin et al. (1994) demonstrated that *Alnus sinuata* and *Dryas drummondii* facilitated the growth of natural and experimentally transplanted *Picea sitchensis* (see "Interactions between Facilitation and Interference" and "Soil Nutrients"). Growth enhancement was associated with increased uptake of phosphorus and nitrogen. In other experiments on post-glacial succession at Glacier Bay, Lawrence et al. (1967) demonstrated that *Dryas drummondii* improved the growth of cottonwood (*Populus trichocarpa*). On recessional moraines in British Columbia and Alberta, Blundon et al. (1993) found that densities of many late successional species were significantly greater in clumps of the pioneering nitrogen fixers *Dryas drummondii* and *Hedysarum boreale* than outside the clumps.

Facilitative processes have also been described during secondary succession in a number of ecosystems. On disturbed sites in short-grass prairie in North America,

densities of *Salsola kali*, a salt-tolerant annual, are positively affected by a late-successional species, *Agropyron smithii*, suggesting a facilitative relationship (Allen & Allen, 1988). Kellman and Kading (1992) documented facilitative mechanisms in dune systems on the Great Lakes in North America which appear to drive some successional patterns, including the establishment of white pine and red pine in locations dominated by mature red oaks (*Quercus rubra*). Harrison and Werner (1984) found that early establishment of red oak in old fields in Michigan was suppressed by other vegetation, but longer-term growth and survival was enhanced as other vegetation developed near oak seedlings. Bertness (1991) demonstrated the importance of facilitation in secondary succession in a New England salt marsh using field experiments. Colonization of bare, highly saline, disturbed patches by zonal dominants was strikingly improved by the prior occupation of the plots by salt-tolerant "competitive subordinates," including *Distichlis spicata*. Gill and Marks (1991) found evidence for facilitation during tree and shrub colonization in New York old fields as seedling survivorship was enhanced by herb cover during periods of stress; however, other experiments emphasized the importance of inhibition.

In most experiments that provide evidence for facilitation in succession, facilitation does not appear to be obligate; species may establish more quickly in the presence of earlier species, but they can also colonize substrate in the absence of other species. In contrast, Turner (1983) reports experimental evidence for facilitative interactions between intermediate successional species of algae and the late colonizing surfgrass (*Phyllospadix scouleri*) in which the relationship appears to be obligate. Experiments with another seagrass species, *Thalassia testudinum*, also showed that early colonization by rhizophytic algae increased densities and biomass of the late-colonizing *Thalassia* in Caribbean subtidal zones (Williams, 1990). In kelp beds off of the central California coast, Harris et al. (1984) conducted experiments in which the densities of late-successional kelp species were measured in plots where early-colonizing algae had been removed from bare rock and in controls with no removals. They found that early-arriving, fast-growing algae facilitated the survival of young kelp by sheltering them from herbivorous fish.

Total ecosystem productivity may also be enhanced by facilitative interactions. In blue oak woodlands in central California, annual grassland productivity may be more than two times higher under oak canopies where soil nutrients are higher than in the surrounding open grassland (Holland, 1980; Frost & McDougald, 1989; Callaway et al., 1991). Belsky et al. (1989) and Weltzin and Coughenhour (1990) reported a two- to threefold increase of herbaceous biomass under acacia (*Acacia tortilis*) and baobab (*Adansonia digitata*) tree canopies in comparison to that of the open grassland in Kenyan savannas, also in part a result of nutrient enhancement (Belsky, 1994; see also "Soil Nutrients"). In South African savannas, *Acacia karoo* also improves the productivity of understory grasses (Stuart-Hill et al., 1987).

Plant communities are profoundly affected by positive interactions. Facilitation increases diversity and productivity in many different systems and plays an important role during recovery from disturbance and dynamics in undisturbed communities.

VII. Conclusion

Renewed interest in positive interactions among species has led to a proliferation of descriptive and experimental studies during the last 10 years in which facilitation has been

assigned an important role. We have greatly expanded our knowledge of the significance of facilitation in plant communities in general and the mechanisms by which facilitation operates. However, we still know little about the relative importance of facilitation and competition in natural field settings, and positive interactions are largely absent from conceptual models of community organization. Competition, by definition, involves a struggle to preempt resources such as light, water, or nutrients that in turn control carbon acquisition. Under physical conditions that permit rapid resource acquisition, competition should be intense. However, severe physical conditions (extreme cold, heat, etc.) may restrict the ability of plants to acquire basic resources; thus, any neighbor amelioration of severe stress may be more likely to favor growth than competition with that neighbor is to restrict growth. Whether a plant competes with or facilitates a neighbor appears to depend on exceptionally subtle differences in palatability to predators, ecophysiology, and tolerance to abiotic stress. The complexity of these interactions clearly indicate that processes that determine the structure of plant communities are not simply functions of resource use. Incorporation of facilitation into community theory that is currently based on competition and abiotic stress will lead to a clearer understanding of community structure and dynamics.

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