

COMPETITION AND FACILITATION IN MARSH PLANTS

Historically facilitative interactions were widely believed to be important structuring forces in nature (Clements et al. 1928; Allee et al. 1949; Odum 1969). This point of view, however, has received little recent support (see Connell and Slayter 1977 and Boucher et al. 1982 for reviews of the evidence). In contrast, contemporary ecologists have devoted tremendous effort to documenting the role of competition in nature. Studies of the role of competition in natural communities have found it to be generally stronger and more important in communities under benign than harsh physical conditions (see, e.g., Connell 1972; Keddy 1989). Many ecologists, however, have cautioned that the relationship between interspecific interactions and environmental stress has not been given adequate attention (Connell 1975; Fowler 1986; Goldberg 1990; Dunson and Travis 1991). Moreover, a number of ecologists have suggested that facilitative or positive interactions among species may be more characteristic of harsh physical environments where neighbors can potentially buffer one another from physical stress (Allee et al. 1949; Connell and Slayter 1977; Bertness 1989). The role of physical stress in mediating the relative importance of facilitative interactions in natural communities, however, has received little direct attention.

Here we present the results of a field experiment that examines the relationship between competitive and facilitative interactions in salt marsh habitats. Specifically, we test the hypothesis that facilitation is common in secondary succession under harsh physical conditions but that competition dominates under benign physical conditions. The seaward border of high marsh habitats in New England is dominated by the grass *Spartina patens*, whereas dense stands of the rush *Juncus gerardi* characterize the terrestrial border (Miller and Egler 1950; Nixon 1982). Competition determines this zonation. *Juncus* competitively excludes *Spartina* from the terrestrial border, while both *Juncus* and *Spartina* restrict a third perennial, *Distichlis spicata*, to low densities and disturbed habitats (Bertness 1991).

Natural disturbance in these habitats frequently occurs when tidally transported plant debris smothers underlying plants (Reidenbaugh and Banta 1980; Bertness and Ellison 1987). Secondary succession in the resulting bare patches is very predictable. Bare patches are initially colonized by the succulent annual *Salicornia europaea* (fig. 1), which is competitively displaced by perennial turfs within 2–3 yr (Ellison 1987). *Distichlis* by vegetative growth rapidly invades disturbed patches, but within 3–4 yr it too is competitively displaced by the zonal dominants (Bertness and Ellison 1987).

Because bare patches in marshes become hypersaline (30‰–100‰) without plant

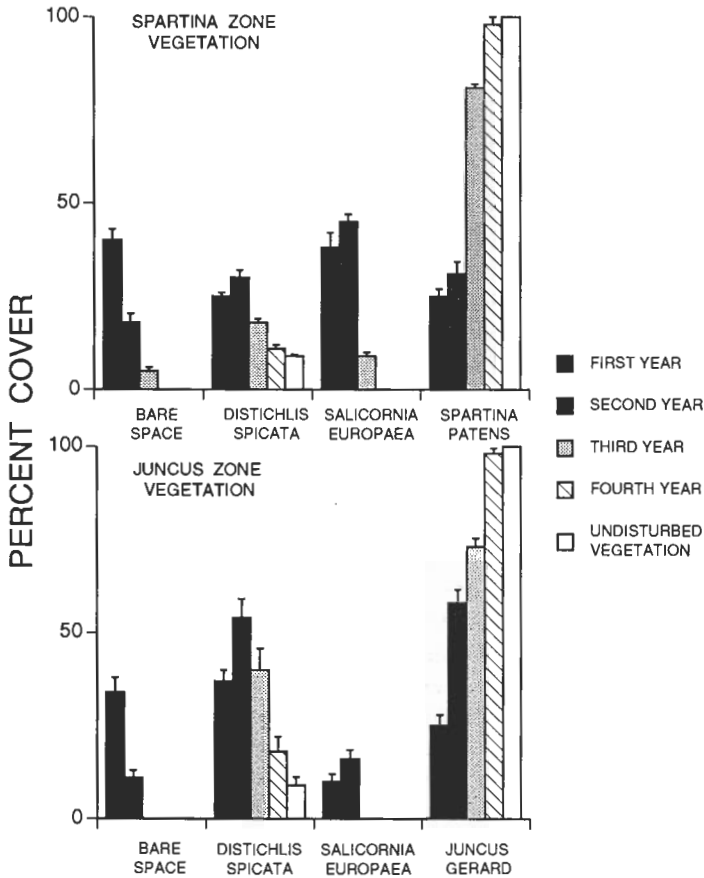


FIG. 1.—Vegetation cover ($\bar{X} \pm SE$) in recovering disturbance-generated bare patches at Rumstick Cove, Barrington, Rhode Island. For each zone the data are from 30 natural bare patches ($0.5\text{--}2\text{ m}^2$) that were annually monitored in September from 1984 to 1989 (see Bertness and Ellison 1987 for methods).

cover (Boston 1983; Bertness et al. 1992) and previous work suggested that initial colonizers shade the substrate, alleviate salt stress, and facilitate further plant colonization (Bertness 1991), we experimentally tested the role of salt stress in mediating species interactions during patch colonization. To quantify species interactions during colonization, 60 1-m^2 experimental patches in each of the *Spartina* and *Juncus* zones and on the border between the *Spartina* and *Juncus* zones were haphazardly located along a 300-m stretch of the marsh shoreline ~ 30 m wide in a typical New England salt marsh (see Bertness and Ellison 1987).

Experimental patches were made by applying a short-lived systemic herbicide (Roundup, Monsanto) to trenched plots and then removing remaining above-ground vegetation. Plots were trenched by cutting around the perimeter of each patch with a knife to 20 cm to sever rhizome connections between plants in the plots and the surrounding vegetation. This procedure assured that the herbicide

was not translocated out of the patch area and left discrete 1-m² plots totally devoid of live vegetation. These bare patches have colonization patterns identical to natural bare patches (Bertness 1991). Patches in each marsh zone were haphazardly divided into an equal number ($N = 20$ each) of spatially interspersed control and species removal plots for each of the common perennial turfs. In the *Spartina* zone *Spartina* removal, *Distichlis* removal, and control plots were followed, whereas in the *Juncus* zone *Juncus* removal, *Distichlis* removal, and control plots were followed. On the *Spartina*/*Juncus* zone border we followed *Spartina* removal, *Juncus* removal, and control plots. *Salicornia*, the only other plant common in the plots, was left at natural densities. To minimize substrate salt accumulation, half the patches in each zone assigned to a particular treatment were regularly flooded with fresh water. Fresh water was delivered to the plots with a watering system driven by a gasoline-powered sprinkler pump fed by a well in the water table adjacent to the marsh. Watered plots were saturated with well water bimonthly during slack tide periods when tides were not covering the plots to limit salt accumulation. This reduced patch salinities by $\sim 10\%$ – 20% , which ameliorated but did not entirely eliminate salt stress (Bertness et al. 1992). Because reducing soil salinities can increase seedling germination (see Shumway and Bertness 1992), we also removed emergent seedlings of all species from half (0.5×1 m) of each patch to examine how salt stress alters the relative importance of sexual versus vegetative colonization.

We maintained all plots by manually weeding out target species in each plot weekly during the growing season (April–September) for 2 yr (April 1990–September 1991). Colonization of the plots was monitored in September 1990 and 1991 by quantifying vegetation cover in the plots (see Bertness 1991 for methods), but since identical patterns were seen in both years only data from 1991 will be presented. For analysis, arcsine-transformed cover data for each species were analyzed for each zone with a three-factorial ANOVA (species removal treatment \times watering treatment \times seedling removal treatment).

In the *Spartina* zone neither watering nor the presence of seedlings affected patch colonization (fig. 2A; table 1). In both watered and unwatered plots *Spartina* competitively dominated *Distichlis*, and virtually all colonization was vegetative rather than sexual. Salt stress does not appear to limit patch colonization in the *Spartina* zone since frequent tidal flooding minimizes salt accumulations at lower marsh elevations (Bertness et al. 1992).

In contrast, lowering patch salinities markedly affected the colonization of bare patches in the *Juncus* zone and on the *Spartina*/*Juncus* zone border (fig. 2B, C; table 1) where hypersaline conditions are common (Bertness et al. 1992). Watering accelerated *Juncus* colonization by both increasing vegetative incursion and enhancing germination from seed banks. Consequently, alleviating salt stress shifted secondary succession from an exclusively vegetative process to a process with a strong sexual component (fig. 2B, C).

Lowering patch salinities also affected the nature of plant interactions in *Juncus* vegetation with and without seedlings present (fig. 2B, C). In unwatered patches, *Spartina* and *Distichlis* invasion facilitated *Juncus* colonization, while in watered patches facilitations were absent and *Juncus* competitively depressed both *Spar-*

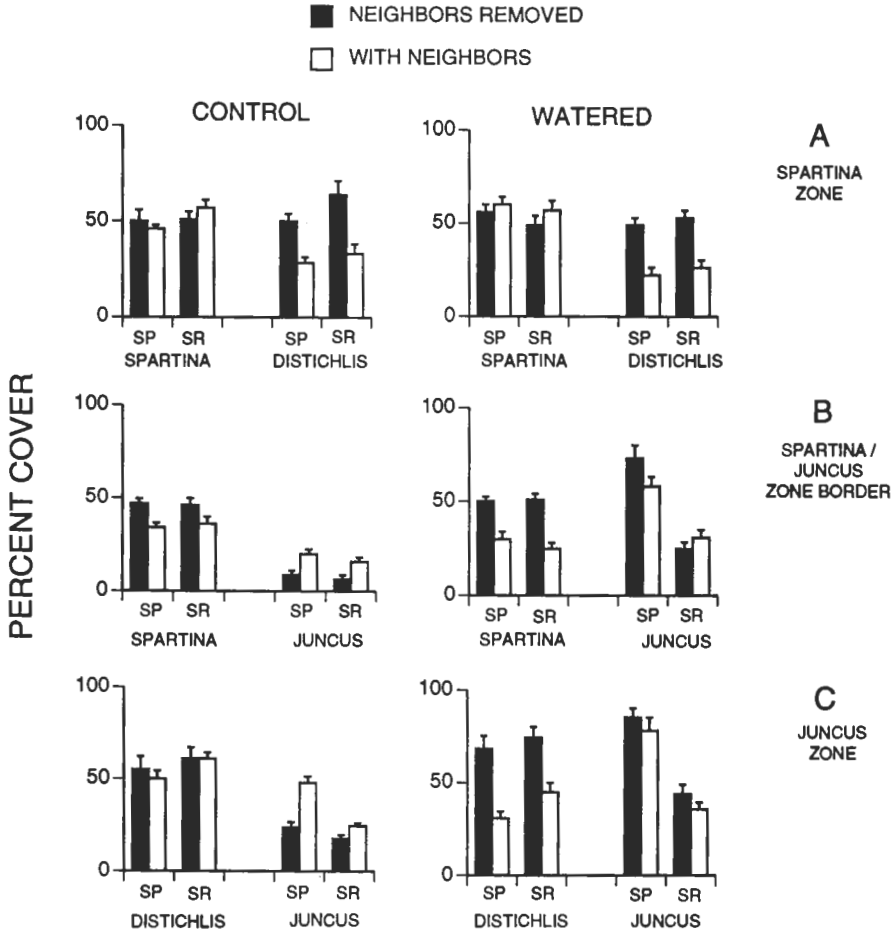


FIG. 2.—Vegetation cover ($\bar{X} \pm SE$ for 8–10 replicates) in experimental bare patches after 2 yr of recovery. For the *Spartina patens* zone (A), the *S. patens*/*Juncus gerardi* zone border (B), and the *J. gerardi* zone (C), data are given for each species invading with and without perennial neighbors under natural patch salinities (= control) and reduced patch salinities (= watered). To illustrate the effect of sexual recruitment on patch colonization, data are presented for areas with and without seedling recruitment (SP = seedlings present, SR = seedling removal). See table 1 for statistics.

tina and *Distichlis*. Alleviating salt stress, therefore, shifted the nature of these interspecific interactions from facilitative to competitive.

These results demonstrate the importance that physical factors can have in dictating the dynamics of natural communities and particularly illustrate how facilitation and competition can characterize the interactions of identical species under different environmental conditions. In saline bare patches in New England salt marshes, initial colonizers shade the substrate, ameliorate stressful conditions, and facilitate further plant colonization (Bertness 1991). In contrast, under less saline conditions competitive processes characterize the interactions of the

TABLE 1
SUMMARY OF THE RESULTS OF THREE-WAY
ANOVA* BY MARSH LOCATION AND SPECIES ON
VEGETATION COVER IN THE EXPERIMENTAL BARE
PATCHES AFTER 2 YR OF RECOVERY

Location, Species, and Source	<i>P</i>
<i>Spartina</i> zone:	
<i>Spartina patens</i> :	
NR	NS
WT	NS
SR	NS
<i>Distichlis spicata</i> :	
NR	<.001
WT	NS
SR	NS
<i>Spartina/Juncus</i> zone border:	
<i>Juncus gerardi</i> :	
NR	NS
WT	<.001
SR	<.001
NR × WT	<.01
WT × SR	<.01
<i>S. patens</i> :	
NR	<.01
WT	NS
SR	NS
<i>Juncus</i> zone:	
<i>J. gerardi</i> :	
NR	NS
WT	<.001
SR	<.001
WR × WT	<.01
<i>D. spicata</i> :	
NR	<.05
WT	NS
SR	NS
NR × WT	<.01

* Neighbor removal (NR) × watering treatment (WT) × seedling removal (SR). All possible interaction terms not shown were not significant (NS indicates $P > .05$).

same species. Since bare patch salinities in salt marshes increase predictably with patch size (Bertness 1991) and are predictably influenced by location and annual variation in rainfall (Bertness et al. 1992), the occurrence of facilitated and competitively driven secondary succession in marsh patches is likely also predictable.

This sort of plasticity in the nature of interspecific interactions may be common in nature. Positive interspecific interactions resulting from neighbors ameliorating physical stresses have been demonstrated in a number of vascular plant communities under harsh physical conditions (deserts: Muller 1953; Niering et al. 1963; alpine primary succession: Woods and Del Moral 1987). Moreover, in intertidal assemblages where the steep tidal gradient is conducive to examining physical

stress mediation of interactions, examples of positive interactions occurring under stressful conditions while competitive interactions dominating identical interactions under less stressful physical conditions have been demonstrated in algal assemblages (Hay 1982), cobble beach associations (Taylor and Littler 1982), and barnacle and mussel interactions on rocky shores (Bertness 1989; Stephens and Bertness 1990). Facilitations may generally be prevalent and overlooked forces in habitats where neighbors can buffer one another from potentially limiting physical stresses. We suggest that positive interactions have been underestimated by ecologists because of their long preoccupation with competitive processes and the habitats in which they are conspicuous and important. We further suggest, as Dunson and Travis (1991) have recently, that only by studying interactions between biotic and abiotic factors under a wide range of field conditions will the processes generating community structure be fully understood.

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LITERATURE CITED

- Allee, W. C., A. E. Emerson, O. Park, and K. P. Schmidt. 1949. Principles of animal ecology. Saunders, Philadelphia.
- Bertness, M. D. 1989. Competitive and facilitative interactions and acorn barnacle populations in a sheltered habitat. *Ecology* 70:257-268.
- . 1991. Interspecific interactions among high marsh perennials in a New England salt marsh. *Ecology* 72:125-137.
- Bertness, M. D., and A. M. Ellison. 1987. Determinants of pattern in a New England salt marsh plant community. *Ecological Monographs* 57:129-147.
- Bertness, M. D., L. Gough, and S. W. Shumway. 1992. Salt tolerances and the distribution of fugitive salt marsh plants. *Ecology* 73:1842-1851.
- Boston, K. G. 1983. The development of salt pans on tidal marshes, with particular reference to southeastern Australia. *Journal of Biogeography* 10:1-10.
- Boucher, D. H., S. James, and K. H. Keeler. 1982. The ecology of mutualisms. *Annual Review of Ecological Systems* 13:315-347.
- Clements, F. E., J. Weaver, and H. Hansson. 1928. Plant competition: an analysis of the development of vegetation. Carnegie Institute, Washington, D.C.
- Connell, J. H. 1972. The ecology of rocky shores. *Annual Review of Ecology and Systematics* 3:169-192.
- . 1975. Some mechanisms producing structure in natural communities: a model and evidence from field experiments. Pages 460-490 in M. L. Cody and J. M. Diamond, eds. *Ecology and evolution of communities*. Belknap, Cambridge, Mass.
- Connell, J. H., and R. O. Slayter. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. *American Naturalist* 111:1119-1144.
- Dunson, W. A., and J. Travis. 1991. The role of abiotic factors in community organization. *American Naturalist* 138:1067-1097.
- Ellison, A. M. 1987. Effects of competition, disturbance, and herbivory in *Salicornia europaea*. *Ecology* 68:576-586.

- Fowler, N. 1986. The role of competition in plant communities in arid and semiarid regions. *Annual Review of Ecology and Systematics* 17:89-110.
- Goldberg, D. E. 1990. Components of resource competition in plant communities. Pages 27-50 in J. B. Grace and D. Tilman, eds. *Perspectives on plant competition*. Academic Press, San Diego.
- Hay, M. 1981. The functional morphology of turf-forming seaweeds: persistence in stressful marine habitats. *Ecology* 62:739-750.
- Keddy, P. A. 1989. *Competition*. Chapman & Hall, London.
- Miller, W. B., and F. E. Egler. 1950. Vegetation of the Wequetequock-Pawcatuck tidal marshes, Connecticut. *Ecological Monographs* 20:143-172.
- Muller, C. H. 1953. The association of desert annuals with shrubs. *American Journal of Botany* 40:53-60.
- Niering, W. A., R. H. Whittaker, and C. W. Lowe. 1963. The saguaro: a population in relation to environment. *Science (Washington, D.C.)* 142:15-23.
- Nixon, S. W. 1982. The ecology of New England high salt marshes: a community profile. U.S. Department of the Interior, Washington, D.C.
- Odum, E. P. 1969. The strategy of ecosystem development. *Science (Washington, D.C.)* 164:262-269.
- Reidenbaugh, T. G., and W. C. Banta. 1980. Origin and effects of tidal wrack in a Virginia salt marsh. *Gulf Research Reports* 6:393-401.
- Shumway, S. W., and M. D. Bertness. 1992. Salt stress limitation of seedling recruitment in a salt marsh plant community. *Oecologia (Berlin)* 92:490-497.
- Stephens, E. G., and M. D. Bertness. 1991. Mussel facilitation of barnacle survival in a sheltered bay habitat. *Journal of Experimental Marine Biology and Ecology* 145:33-48.
- Taylor, P. R., and M. M. Littler. 1982. The roles of compensatory mortality, physical disturbance, and substrate retention in the development and organization of a sand-influenced rocky intertidal community. *Ecology* 63:135-146.
- Wood, D. M., and R. Del Moral. 1987. Mechanisms of early primary succession in subalpine habitats on Mount St. Helens. *Ecology* 68:780-790.

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