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PHYSICAL STRESS AND POSITIVE ASSOCIATIONS AMONG MARSH PLANTS

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Abstract.—The contribution of positive interactions such as facilitations and mutualisms to the structure and organization of natural communities has received little recent attention. Here we show that distribution patterns of New England salt-marsh plants are strongly influenced by facilitative associations among neighboring plants. Positive interactions among marsh plants appear to be the simple by-product of neighbors buffering one another from potentially limiting physical stresses and thus only occur in physically harsh habitats. Positive associations such as these are likely common but unappreciated forces in harsh environments that have been largely overlooked by contemporary ecologists because of their preoccupation with competitive phenomena.

One of the major goals of ecology is to understand the forces that generate patterns in natural communities. In contrast to the roles of environmental factors, competition, predation, disturbance, and recruitment (for reviews, see Tilman 1982; Pickett and White 1985; Menge and Sutherland 1987; Roughgarden et al. 1987; Keddy 1989), relatively little recent attention has been paid to the role of positive interactions in structuring communities. Positive interactions were once hypothesized to be important driving forces in communities (Clements et al. 1926; Allee et al. 1949), but, in spite of continued speculation about the roles they play in natural systems (e.g., hermatypic coral-zooxanthellae associations in coral reefs: Goreau and Goreau 1960; litter, nutrient, and shading effects in forests: Fox 1977; Woods 1979; mycorrhizal associations: Carey et al. 1992), they have received little rigorous experimental attention and are largely ignored in current models of natural community organization (see, e.g., Tilman 1982; Menge and Sutherland 1987).

One of the oldest and most pervasive ideas about the role of positive interactions in nature is that they are prevalent under harsh physical conditions when neighbors buffer one another from potentially limiting physical stresses (Clements et al. 1926). Studies from a range of plant and animal communities have suggested a strong association between physical stress and positive interactions (see, e.g., Muller 1953; Niering et al. 1963; Hay 1981; Wood and Del Moral 1987; Bertness 1989; Bertness and Shumway 1993). Contemporary ecologists, however, have paid little attention to the role of abiotic factors in mediating biotic interactions

(see Dunson and Travis 1991 and Bertness and Shumway 1993 for discussion), and few ecologists have experimentally manipulated communities to determine whether positive interactions are predictable forces in harsh environments.

Salt-marsh plant communities are ideal for examining the forces that structure natural communities. They are simple native vascular plant communities dominated by a handful of plant species usually found in distinct zonation patterns (Chapman 1974). Sharp physical gradients in these intertidal habitats allow close examination of the effects of physical factors on species interactions. The seaward distributions of marsh plant species are set by harsh physical conditions such as waterlogged soils and high soil salinities, whereas the terrestrial distribution borders are generally set by competitive interactions (Bertness 1991a, 1991b, 1992). Marsh plants also have strong ameliorating effects on physical conditions that can potentially limit marsh plant success. Shading by marsh plants limits surface evaporation and the accumulation of soil salts (Bertness et al. 1992b; Callaway 1994), and rhizosphere oxidation by marsh plants can alleviate anoxic substrate conditions (Howes et al. 1981; Shat 1984; Bertness 1991b). The predictable zonation of marsh plant communities and the strong effects that marsh plants have on local edaphic conditions make them particularly valuable for exploring the role of positive forces in natural communities. In this article, we present the results of two field experiments explicitly designed to examine whether positive interactions influence marsh plant distribution patterns and whether positive interactions predictably occur under harsh physical conditions in marsh habitats.

To examine the role of positive interactions on salt-marsh plant zonation, we have focused on the terrestrial border of New England marshes. Terrestrial borders of salt-marsh plant communities are characterized by a sharp transition from halophytic vegetation in soils periodically flooded by salt water to terrestrial vegetation in soils not subjected to frequent flooding (Chapman 1974). In southern New England, terrestrial marsh borders (fig. 1) are dominated by the perennial shrub *Iva frutescens* (marsh elder) mixed with the rhizomatous perennial turf *Juncus gerardi*, which also dominates lower marsh elevations (Miller and Egler 1950; Nixon 1982). The seaward border of this *Iva* zone is often characterized by low densities (1–2 plants/m²) of short (35–50 cm), stunted adult *Iva* plants (>4 yr old), whereas at higher elevations *Iva* are up to 150 cm tall, are markedly more productive, and reach densities of 4–16 plants/m². In contrast to the increased density and stature of marsh elders at higher elevations, *Juncus* density and production markedly decrease (Bertness et al. 1992b).

Our interest in the role of positive forces in determining this zonation pattern was stimulated by data showing *Iva* to be relatively intolerant of high soil salinities and waterlogged soil conditions (Bertness et al. 1992a), coupled with the ameliorating effects of marsh perennials on both high soil salinities (Bertness 1991a; Bertness et al. 1992b) and low soil oxygen levels (Howes et al. 1981). We hypothesized that the seaward distribution of marsh elders could be shifted to lower elevations in the presence of *Juncus*, if *Juncus* lowered soil salinities and/or increased soil oxygen levels sufficiently to override interspecific competition. To examine this hypothesis, we randomly selected 40 adult marsh elders on the

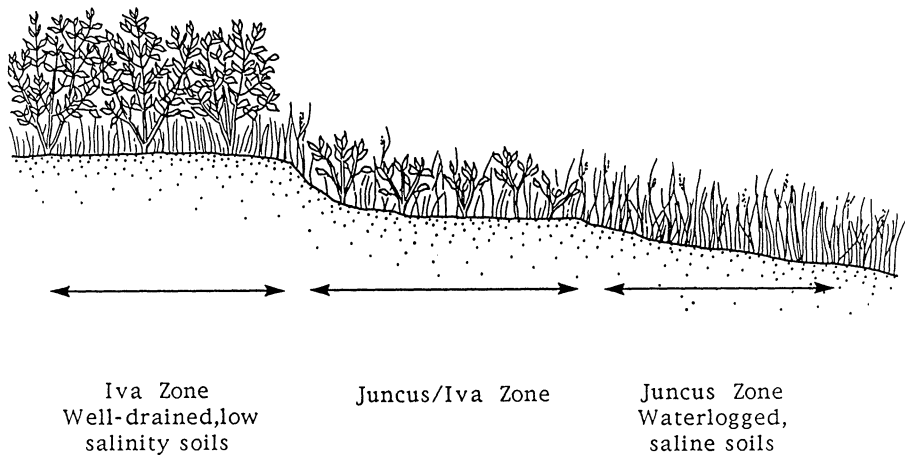


FIG. 1.—Schematic diagram of the terrestrial border of a typical New England salt marsh illustrating the major vegetation zones and physical conditions considered in this study.

seaward border of the marsh elder zone and assigned them to four treatments (in equal number). The four treatments were designed to examine the effect of *Juncus* neighbors on established adult *Iva* and partition the potential effects of *Juncus* on *Iva* due to salt and oxygen stress and thus elucidate the mechanism of any positive association of *Juncus* and *Iva*.

The treatments were *Juncus* removals in which all *Juncus* in a 0.5-m radius around each plant were regularly clipped to ground level; shaded *Juncus* removals in which all *Juncus* in a 0.5-m radius were clipped, and then the soil was covered with a water-permeable fabric made of woven mulch (Weedblock) that mimics the effect of *Juncus* shading on soil salinities without the effects of *Juncus* rhizosphere oxidization, unmanipulated controls, and manipulation controls in which *Juncus* was clipped but allowed to grow back. The 40 adult *Iva* used in the experiment were all initially of similar size (30–50 cm tall with 50–100 leaves), no closer than 2 m from one another, and located along a 200-m stretch of shoreline at Rumstick Cove, Barrington, Rhode Island. The study site is described in detail elsewhere (Bertness 1992). The experiment was set up in May 1991 and monitored until August 1992. Treatments were maintained weekly during the plants' growing season (May–August).

Soil physical conditions and *Iva* performance were monitored in all treatments for 2 yr. Monthly (June–August 1991 and 1992) soil salinity and redox measurements were taken adjacent to each experimental *Iva* plant. Soil salinity was quantified by excising a 2-cm³ piece of soil 15 cm from each plot, squeezing pore water through cotton gauze, and quantifying the salinity of the pore water with a refractometer ($\pm 2\%$). Soil redox, a measure of the oxygen content of soils, was measured (Howes et al. 1981; Shat 1984) monthly (June–August 1991 and 1992) 15 cm from each experimental *Iva* plant at a depth of 2 cm in the soil with a standard redox electrode (Howes et al. 1981). Salinity and redox data were both analyzed with repeated-measurement ANOVA.

We monitored the performance of the experimental *Iva* plants by measuring photosynthetic rates and counting leaves. Photosynthetic rates were measured monthly (May–August 1991) in the first year of the experiment only as an indicator of *Iva* performance. Photosynthetic rates were measured on young leaves of all experimental plants with a portable infrared gas analyzer (Morgan ADC-L2A) at midday on cloudless days. Total leaf counts were made on all experimental plants for two growing seasons (June–August 1991 and 1992). Both the photosynthesis and leaf count data were analyzed with repeated-measurement ANOVA.

Since removing *Juncus* neighbors from the *Iva* zone in the above experiment had strong negative effects on *Iva* (see Results), a second experiment was designed to examine the predictability of this interaction across the marsh habitat. We reasoned that if the buffering of harsh physical conditions leads to the positive association of marsh elders with perennial turfs, this positive association should be found in physically harsh but not physically benign habitats. To test this hypothesis, we transplanted adult marsh elders and *Juncus* across the terrestrial border of the marsh with and without neighbors.

Soil salinity levels decrease and soil oxygen levels increase with increasing elevation across the terrestrial border of the marsh (Bertness et al. 1992a, 1992b). For transplant material, we used 30–50-cm-tall adult *Iva* with 50–75 leaves and *Juncus* turfs randomly collected throughout the study site from the *Juncus/Iva* zone border. Transplants were made by excising 20 × 20 × 20-cm (length × width × depth) root balls that were moved into identically sized holes in desired locations. Fifteen *Iva* and *Juncus* transplants were made with and without neighboring vegetation in three habitats (see fig. 1): the terrestrial border of the *Juncus* zone, which is tidally flooded 10–15 d/mo; the *Juncus/Iva* zone border, which is flooded 7–10 d/mo; and the middle of the *Iva* zone, which is only flooded by monthly, extreme high tides 2–5 d/mo (Bertness et al. 1992b). Three control and vegetation removal plots (25 m²) were established in each zone. For analysis, these plots were pooled by zone and treatment since plot replication did not influence edaphic factors or plant performance (ANOVA, $P > .80$). In the vegetation removal plots, all vegetation was clipped weekly to ground level. Vegetation was left intact in the control plots. Transplants were made in May 1992 and maintained for 3 mo. Soil salinities (measured as described above) were taken adjacent to each transplant monthly. Soil redox was not measured, since our initial experiment (see Results) suggested that redox levels were not responsible for the positive effects of *Juncus* on *Iva*. Treatment effects on plant performance were assessed in August 1992 after 4 mo under treatment. For *Iva* transplants, leaf counts were made on all replicates. For *Juncus*, vegetation in a 10 × 10-cm area in the center of each transplant was harvested, dried, and weighed.

RESULTS

Manipulations of *Iva* neighbors on the seaward border of the *Iva* zone strongly affected local physical conditions (fig. 2). Removing *Juncus* neighbors more than doubled soil salinities in contrast to other treatments (Scheffé test, all cases, $P < .001$), whereas soil salinities in all other treatments were similar (Scheffé test,

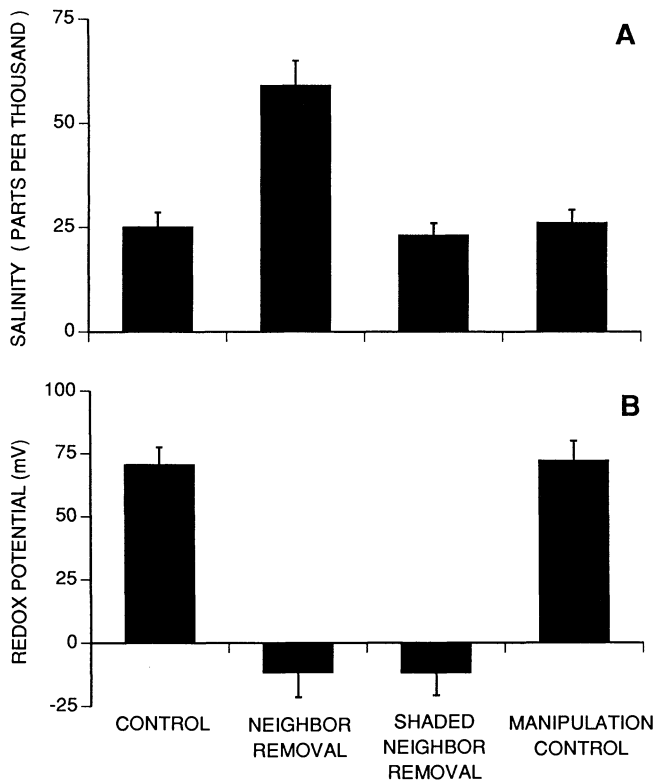


FIG. 2.—A, Surface salinity and, B, redox potential of soil in the *Iva frutescens* neighbor manipulation treatments on the seaward border of the *Iva* zone. The data are means (\pm SE) of pooled monthly (June–September) measurements taken in 1991 and 1992.

all cases, $P > .50$). Removing *Juncus* neighbors also led to more than an order-of-magnitude drop in soil redox (Scheffé test, all cases, $P < .001$), which suggests that the presence of *Juncus* neighbors oxidizes marsh soil. Since shading plots without *Juncus* prevented salinity increases (Bertness et al. 1992b) but did not influence soil redox (Scheffé test, $P > .50$), the shaded and unshaded *Juncus* removal plots nicely separate the effects of *Juncus* on adult *Iva* into total effects caused by both salt buffering and soil oxidization and those caused only by soil oxidization.

Removing *Juncus* neighbors from *Iva* on the seaward borders of the *Iva* zone significantly lowered *Iva* photosynthetic rates (fig. 3A) during the first year of the experiment (ANOVA, $P < .001$). After 4 mo, the photosynthetic rates of *Iva* without neighbors were less than half those of controls or shaded neighbor removals (Scheffé test, each case, $P < .001$). The photosynthetic rates of control, manipulation control, and shaded *Juncus* neighbor removal plants, however, were all similar (Scheffé test, each case, $P > .50$).

The neighbor manipulation treatments also dramatically affected *Iva* leaf pro-

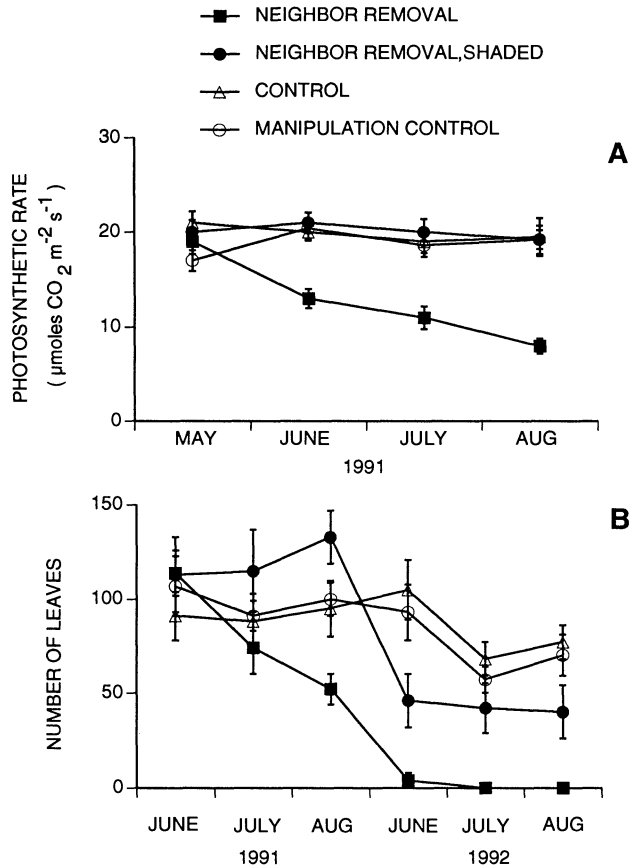


FIG. 3.—A, Photosynthetic rate ($\mu\text{mol CO}_2\text{ m}^{-2}\text{ s}^{-1}$) and, B, total number of leaves of adult *Iva frutescens* on the seaward border of the *Iva* zone under experimentally manipulated conditions with and without neighbors. All data are means of 15 replicates (\pm SE).

duction (fig. 3B; ANOVA, $P < .001$). Fourteen months after the experimental treatments were established, all *Iva* without *Juncus* neighbors or shading were dead (fig. 3B). In contrast, when *Juncus* neighbors were removed, but the substrate was shaded to limit surface evaporation and salt accumulation, *Iva* leaf production was diminished in comparison to controls in the second growing season (Scheffé test, $P < .01$), but all manipulated plants survived (fig. 3B).

Results of the transplant experiment in which both adult *Iva* and *Juncus* were transplanted across a marsh elevation gradient with and without neighbors (fig. 4) revealed that physical conditions and the nature of interactions among neighboring plants shifted with marsh elevation. Surface soil salinity data were pooled across months and analyzed with a two-way (zone-by-treatment) ANOVA. Zone ($P < .001$) and treatment ($P < .001$) both directly affected soil salinities, but treatment effects on salinity changed with marsh zone (zone-by-treatment interaction, $P < .01$). Soil salinities decreased with increasing marsh elevation across

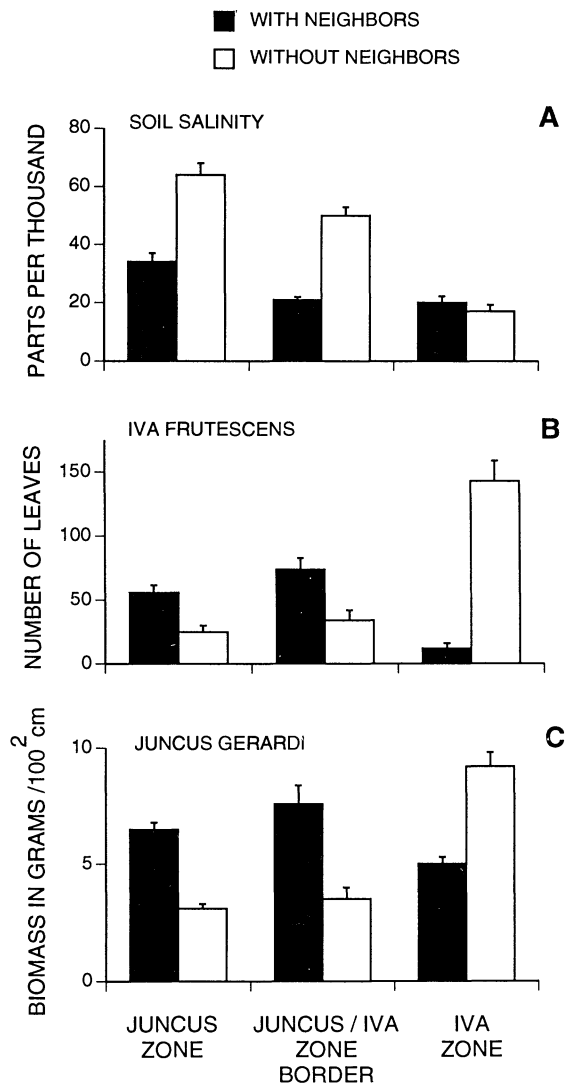


FIG. 4.—Results of transplant experiment in which adult *Iva frutescens* and *Juncus gerardi* were transplanted across the terrestrial border of the marsh with and without neighbors. *A*, Soil surface salinity (pooled monthly, June–August, measurements; $n = 30/\text{case}$, \pm SE) taken adjacent (15 cm away) to each transplant; *B*, total *Iva* leaf counts 4 mo after transplantation; and, *C*, dried aboveground *Juncus* biomass 4 mo after transplantation. For each location and treatment, the data are the mean of 10 transplants (\pm SE).

the terrestrial border of the marsh with and without neighboring vegetation (fig. 4A). Plant cover, however, differentially influenced soil salinities among marsh zones. At lower elevations in the *Juncus* zone and on the *Juncus/Iva* zone border, *Juncus* markedly lowered soil salinities (Scheffé test, $P < .01$), while at higher elevations in the *Iva* zone, soil salinities were relatively low and not affected by plant cover (Scheffé test, $P > .50$).

Paralleling the ameliorating effects of vegetation on soil salinities, performances of *Iva* and *Juncus* (fig. 4B and C) were both enhanced by neighbors at lower elevations but strongly suppressed by neighbors at higher elevations in the *Iva* zone. For both *Iva* leaf counts and *Juncus* biomass (fig. 4B and C), the data were analyzed with a zone-by-treatment ANOVA. For both species, plant performance increased with marsh height ($P < .001$), but the effect of neighbors shifted with marsh elevation (zone-by-treatment interaction, $P < .001$). The nature of the interaction between marsh elders and *Juncus* shifted from positive to negative with marsh elevation. Under harsh physical conditions at low marsh elevations, marsh elders and *Juncus* benefited from neighbors (Scheffé test, each case, $P < .05$), while at higher elevations interactions with neighbors were highly competitive (Scheffé test, both cases, $P < .01$).

DISCUSSION

Our results show that positive associations among species can affect plant distribution patterns and that the nature of species interactions can shift dramatically across environmental gradients.

On the seaward border of the *Iva* zone, removing *Juncus* neighbors led to striking increases in soil salinity and the death of established adult *Iva* (figs. 2, 3). Amelioration of soil salinity is the most parsimonious explanation for the large positive effects of *Juncus* on adult *Iva*. *Iva* is extremely intolerant of soil salinities over 20‰ (Bertness et al. 1992a), and removing *Juncus* while shading the soil surface to prevent soil salt accumulations alleviated most of the adverse effects of *Juncus* removal on *Iva* (fig. 3). Moreover, in experiments currently in progress we have also found that treating *Juncus* removal plots with freshwater alleviates most of the adverse effects of *Juncus* removal on adult *Iva* plants (S. D. Hacker and M. D. Bertness, unpublished data). Therefore, whereas soil oxidation and effects of neighbors on nutrient mobility may also influence this interaction, current evidence strongly suggests that this positive interaction is primarily driven by neighbors' buffering soil salt accumulations (also see Callaway 1994).

Transplanting *Iva* and *Juncus* across the seaward border of the *Iva* zone to test the hypothesis that the nature of interactions among plants shifts with predictable variation in physical stress also yielded dramatic results. At lower marsh elevations, neighbors ameliorated high soil salinities, and both *Juncus* and *Iva* performance were enhanced by neighbors (fig. 4). In contrast, at higher marsh elevations, soil salinities were low with or without plant cover, and all interactions among neighbors were competitive (fig. 4). Thus, interactions among plants on the terrestrial border of marshes shift from positive to negative with increasing elevation and decreasing physical stress.

Since plants and sessile animals often ameliorate harsh and potentially limiting physical conditions (vascular plants: Muller 1953; Niering et al. 1963; Callaway et al. 1991; Bertness and Shumway 1993; algae: Dayton 1975; Hay 1981; sessile invertebrates: Taylor and Littler 1982; Bertness and Grosholz 1985; Bertness 1989), positive associations such as we have shown among sessile organisms are likely common predictable forces in harsh environments. We suggest that contemporary ecologists have underestimated the role of positive interactions in natural communities and that only by giving positive interactions the same attention paid to competitive processes (see Connell 1983 for review) will we come to understand the role of positive forces on the structural dynamics of natural communities.

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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 in acorn barnacle populations in a sheltered habitat. *Ecology* 70:257–268.
- . 1991a. Zonation of *Spartina* spp. in a New England salt marsh. *Ecology* 72:138–148.
- . 1991b. Interspecific interactions among high marsh perennials in a New England salt marsh. *Ecology* 72:125–137.
- . 1992. The ecology of New England salt marsh plant communities. *American Scientist* 80: 260–268.
- Bertness, M. D., and T. Grosholz. 1985. Population dynamics of the ribbed mussel, *Guekensia demissa*: the costs and benefits of a clumped distribution. *Oecologia (Berlin)* 67:192–204.
- Bertness, M. D., and S. W. Shumway. 1993. Competition and facilitation in marsh plants. *American Naturalist* 142:718–724.
- Bertness, M. D., L. Gough, and S. W. Shumway. 1992a. Salt tolerances and the distribution of fugitive salt marsh plants. *Ecology* 72:1832–1851.
- Bertness, M. D., K. Wikler, and T. Chatkupt 1992b. Water table dynamics and the distribution of high marsh plants. *Oecologia (Berlin)* 91:171–178.
- Callaway, R. M. 1994. Facilitative and interfering effects of *Arthrocnemum subterminale* on winter annuals in a California salt marsh. *Ecology* 75:681–686.
- Callaway, R. M., N. M. Nadkarni, and B. E. Mahall. 1991. Facilitation and interference of *Quercus douglasii* on understory productivity in central California. *Ecology* 72:1484–1499.
- Carey, P. D., A. H. Fitter, and A. R. Watkinson. 1992. A field study using the fungicide benomyl to investigate the effect of mycorrhizal fungi on plant fitness. *Oecologia (Berlin)* 90:550–555.
- Chapman, V. J. 1974. Salt marshes and salt deserts of the world. Interscience, New York.
- Clements, F. E., J. Weaver, and H. Hansson. 1926. Plant competition: an analysis of the development of vegetation. Carnegie Institute, Washington, D.C.
- Connell, J. M. 1983. On the prevalence and relative importance of interspecific competition: evidence from field experiments. *American Naturalist* 122:661–696.

- Dayton, P. K. 1975. Experimental evaluation of ecological dominance in a rocky intertidal algal community. *Ecological Monographs* 45:137–159.
- Dunson, W. A., and J. Travis. 1991. The role of abiotic factors in community organization. *American Naturalist* 138:1067–1097.
- Fox, J. F. 1977. Alternation and coexistence of tree species. *American Naturalist* 111:69–89.
- Goreau, T. F., and N. Goreau. 1960. The uptake and distribution of labeled carbon in reef building corals with and without zooxanthellae. *Science (Washington, D.C.)* 131:668–669.
- Hay, M. 1981. The functional morphology of turf-forming seaweeds: persistence in stressful marine habitats. *Ecology* 62:739–750.
- Howes, B. L., R. W. Howarth, J. M. Teal, and I. Valiela. 1981. Oxidation-reduction potentials in salt marshes: spatial patterns and interactions with primary production. *Limnology and Oceanography* 26:350–360.
- Keddy, P. A. 1989. *Competition*. Chapman & Hall, London.
- Menge, B. A., and J. Sutherland. 1987. Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. *American Naturalist* 130:730–757.
- 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.
- Pickett, S., and P. White, eds. 1985. *Natural disturbance: the patch dynamic perspective*. Academic Press, New York.
- Roughgarden, J., S. D. Gaines, and S. W. Pacala. 1987. Supply side ecology: the role of physical transport processes. Pages 491–518 in J. H. R. Gee and P. S. Giller, eds. *Organization of communities: past and present*. Blackwell, London.
- Shat, M. 1984. A comparative ecophysiological study of the effects of waterlogging and submergence on dune slack plants: growth, survival and mineral nutrition in sand culture experiments. *Oecologia (Berlin)* 62:279–286.
- 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.
- Tilman, D. 1982. *Resource competition and community structure*. Princeton University Press, Princeton, N.J.
- Wood, D. M., and R. Del Moral. 1987. Mechanisms of early primary succession in subalpine habitats on Mount St. Helens. *Ecology* 68:780–790.
- Woods, K. D. 1979. Reciprocal replacement and the maintenance of codominance in a beech-maple forest. *Oikos* 33:31–39.

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