Competitive and facilitative interactions within and between two species of coastal dune perennials

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Abstract: While there is substantial evidence for facilitation, the effects of such factors as stress and species identity on positive interactions remain controversial. At two coastal dune sites, I tested the hypotheses that facilitative interactions increase with increasing stress and disturbance along an environmental gradient and that facilitative interactions are stronger among heterospecific than among conspecific individuals. I transplanted Uniola paniculata and Iva imbricata plants into plots along with four conspecific neighbors, four heterospecific neighbors, or no neighbors across an environmental gradient. Neighbors increased target plant survival, suggesting facilitation, but biomass of targets was reduced by the presence of neighbors, suggesting competition. Unexpectedly, competition was greatest in the purportedly most stressful and disturbed zone. In this study, the outcome of neighbor interactions differed for biomass and survival and depended on position along the environmental gradient, but was independent of neighbor identity.

Key words: competition, disturbance, facilitation, Iva imbricata, stress, Uniola paniculata.

Introduction

Competition has long been regarded as one of the most important factors determining population dynamics and community structure. However, ecologists now recognize that interactions range along a spectrum from negative (competitive) to positive (facilitative) and that the net effects of neighbors may be facilitative in many natural systems (Hunter and Aarssen 1988; Bertness and Callaway 1994; Bruno and Bertness 2001). While evidence for facilitative interactions is substantial and rapidly increasing (Callaway 1995), we still lack a general understanding of the conditions under which positive neighbor effects should exceed negative effects, resulting in a net outcome of facilitation. To understand the conditions favoring facilitation, it is necessary to elucidate how neighbor interactions are affected by such environmental factors as stress (defined here as prolonged conditions that reduce fitness) and disturbance (punctuated events that reduce fitness) and how interactions vary within and among species. With this information, we can begin to predict when facilitative interactions may occur.

Several hypotheses suggest that facilitation may increase with increasing stress (Bertness and Callaway 1994; Callaway and Walker 1997; Holmgren et al. 1997) and disturbance (Brooker and Callaghan 1998). These hypotheses are supported by the fact that many examples of facilitation (reviewed in Callaway 1995) come from what are generally thought to be stressful or disturbed habitats, such as the classic studies of nurse plant interactions in deserts (e.g., Niering et al. 1963). The hypothesis of increasing facilitation...
with increasing stress has also been supported by some studies in which stress is experimentally reduced. For example, Bertness and Yeh (1994) found that in New England salt marshes, adult *Iva frutescens* plants facilitated seedling recruitment under naturally harsh conditions but when stress was reduced by watering or shading, interactions were competitive. There are relatively few studies, however, that have examined interactions among species along environmental gradients to test the hypothesis that the strength of facilitative interactions increases with increasing stress or disturbance. Moreover, studies using this approach have produced mixed results. The hypothesis of increasing facilitation with increasing stress and disturbance across a gradient has been supported in some studies (Greenlee and Callaway 1996; Callaway 1998b; Pugnaire and Luque 2001; Tewksbury and Lloyd 2001) and not supported in others (Donovan and Richards 2000; Tielborger and Kadmon 1997, 2000).

In addition to the effects of environmental conditions on neighbor interactions, the strength and direction of these interactions can vary depending on the species involved and whether the interactions are intraspecific or interspecific. Many studies of facilitation have examined particular species such as nurse plants (Niering et al. 1963; Tewksbury and Lloyd 2001) or species with nitrogen-fixing associates (Franco-Pizana et al. 1996; Shumway 2000) in which there is an obvious benefit of one species on others. It is still unknown whether positive interactions are species-specific or general across species or functional groups (Callaway 1998a) and whether interspecific facilitation should exceed intraspecific facilitation. Some recent studies have found reciprocal facilitation among two or more species (Pugnaire et al. 1996; Holzapfel and Mahall 1999), but comparisons of intraspecific versus interspecific facilitative interactions remain virtually nonexistent (Callaway 1995).

Facilitation is predicted to be stronger (effects of neighbors more positive) among individuals of different species than among individuals of the same species if the following assumptions are made: (i) the net outcome of interactions results from both positive and negative neighbor effects, (ii) positive neighbor effects are greatest when negative neighbor effects are minimized, and (iii) negative neighbor effects are minimized for interactions among individuals of different species compared with individuals of the same species. The third assumption is equivalent to the statement that intraspecific competition is stronger than interspecific competition. Stronger intraspecific competition than interspecific competition is, based on classical competition theory (Volterra 1926; Lotka 1932; MacArthur and Levins 1967), a prerequisite for the coexistence of competing species (Beagon et al. 1990, pp. 247–251). However, empirical work has not always supported the hypothesis that intraspecific competition is greater than interspecific competition (Goldberg and Barton 1992; Aguiar et al. 2001).

In this study, I examined intraspecific and interspecific interactions among plants of two coastal dune species, *Uniola paniculata* L., and *Iva imbricata* Walt., across an environmental gradient at two field sites. Previous work showed that facilitative interactions occurred among dune plants in this system and that *Uniola* and *Iva* are often positively associated in the field (Franks 2003). Work at these field sites also demonstrated a gradient of soil stability, with disturbance from burial and erosion greatest closest to the shore (Franks 2003). A previous study in which a burial treatment was experimentally applied showed that burial caused interactions among dune plants to switch from neutral to facilitative, but that there was no effect of diversity on the interactions (Franks and Peterson 2003). The study reported here builds on this previous work, using a field experiment to test the hypotheses that (i) facilitative interactions increase with increasing stress and disturbance along a natural environmental gradient and (ii) facilitative interactions are stronger among heterospecific than among conspecific individuals. Juveniles were transplanted in the field into neighbor interaction arrays replicated across the dune gradient, and plant performance was followed for two field seasons.

### Materials and methods

#### Study sites and species

The experiments were conducted on the southern, accreting ends of two barrier islands: Keywadin Island, Florida (26°08′N, 81°47′W), and Sapelo Island, Georgia (31°28′N, 81°14′W). The climate on Keywadin Island is subtropical, with rainfall abundant in the summer and fall. The soils are composed of coarse sand of limestone and shell fragments. Sapelo is a warm–temperate barrier island with a cooler climate than Keywadin (though rarely at or below freezing), rainfall more evenly distributed throughout the year, and finer sands without large shell fragments as a major component of the soil (for more site information, see Franks 2003).

In coastal dunes, plants experience stresses such as low nutrients and salt spray and disturbances such as sand burial and erosion (Barbour et al. 1985; Ehrenfeld 1990; Ishikawa et al. 1995; Maun 1998). Stress and disturbance on dunes tend to decrease with distance from the shoreline (Oosting and Billings 1942; Barbour 1978; Ranwell 1972; Ehrenfeld 1990). Franks (2003) found that soil stability at the sites used in this study increased with increasing landward distance from the shoreline.

Species used (referred to hereafter by genus) were *Uniola paniculata* (Poaceae) and *Iva imbricata* (Asteraceae). Nomenclature follows Wunderlin (1982). *Uniola* is a rhizomatous perennial C₄ grass that dominates primary coastal dunes in much of the southeastern United States, and *Iva* is a low-growing perennial C₃ shrub common in primary coastal dunes. These species were chosen because they are often found in close association in the field (Franks 2003) and because they differ in life form and other morphological and physiological characteristics, making detection of differences between intraspecific and interspecific interactions more likely than comparisons between more similar species.

#### Transplant experiment

In January 1999, experimental plots were established in the field by removing any existing vegetation in the plots by hand. Juvenile *Uniola* and *Iva* individuals were then transplanted into the plots along with four conspecific neighbors, four neighbors of the other species, or no neighbors in a randomized complete block design. All plants, including targets
(focal plants) and neighbors (individuals planted around the targets) were transplanted from the local site into the experimental arrays. Transplanted individuals were an average of 14 cm (Iva) and 20 cm (Uniola) tall. For targets with neighbors, the four neighbors were placed one in each cardinal direction and were approximately 5 cm from the target. The number of neighbors and distances between neighbors and targets was chosen based on densities observed in the field (Franks and Peterson 2003). Groups of plants (targets plus neighbors) within blocks were separated by at least 50 cm. At each site (Keywadin and Sapelo Islands), there were four replicates of each block in each of three zones: foredune, mid-dune, and rear dune. These zones correspond to, respectively, the shoreward edge of the vegetation, the midpoint between the foredune and rear dune zone, and the landward edge of the primary dune vegetation (approximately 0, 50, and 100 m from the high tide mark). The rear dune refers to the area shoreward of the occurrence of large shrubs (such as Myrica cerifera) or trees. Both Uniola and Iva naturally occur in each of the zones. There were 144 target individuals (N = 2 sites × 3 zones × 2 target species × 3 neighbor treatments × 4 replicates = 144 targets).

To aid establishment and reduce transplant shock at the beginning of the experiment, the plots were fertilized once per week with 15:30:15 (N:P:K) Peters fertilizer (Petersen Chemical Company, Hawthorne, N.J.) diluted to 1/8 strength and watered with fresh water three times per week for the first 3 weeks only. After the first 3 weeks of the experiment, the plants were not supplemented with water or nutrients. Individuals that died during the first 3 weeks were replaced. Throughout the experiment, I clipped or removed by hand any plants other than the experimental individuals that occurred within the plots, taking care not to disturb the experimental plants. Height, total number of leaves, and survival of all target and neighbor plants were measured at the beginning and end of the experiment. Aboveground parts of all surviving plants were harvested in October 2000 (20 months after planting), dried at 60°C to constant weight, and weighed. The root/shoot ratio of these species was shown to be relatively invariant under different densities and different environmental conditions (Franks and Peterson 2003), so aboveground biomass was used as an indicator of total biomass.

**Analysis**

Data were analyzed using SAS (version 8.02, SAS Institute Inc. 2000). Target survival was analyzed with logistic regression, with target identity, neighbor treatment, site, zone, and initial target size as main effects. Final size (biomass and leaf number, both natural logarithm transformed) of targets was analyzed with an analysis of covariance (ANCOVA), with neighbor treatment, site, and zone as main effects and initial target size and final neighbor biomass as covariates. When Iva and Uniola targets did not differ in their response (P > 0.05), the results were pooled, with the species term removed from the analysis. Results were also pooled across sites when the sites were not different or when there were no significant site by species interactions. For analyses of biomass and leaf number, pooling across sites or species was often necessary because of the low number of surviving target individuals. While this may limit comparisions between sites or between target species, this analysis allowed for maximum statistical power to examine the factors of primary interest, which were neighbor presence or absence and neighbor species identity. Pooling did not qualitatively change the results of any analyses. Preplanned orthogonal contrasts (Sokal and Rohlf 1995) were used to compare means within the neighbor treatments and zones. Because others have suggested that competitive effects depend on neighbor size rather than only density (Goldberg and Werner 1983; Gaudet and Keddy 1988; Weiner et al. 2001), I performed a regression of neighbor biomass on target biomass to test for per-gram effects of neighbors. While neighbors were all initially similar in size, mortality and differential growth caused final neighbor biomass to range from 0 to 63.7 g, making a test for the effect of neighbor size warranted.

**Results**

**Survival and growth**

The presence of neighbors significantly increased survival of target plants regardless of the species of neighbor and target (logistic regression df = 1, Wald $\chi^2 = 8.6, \ P = 0.003$; Table 1). The odds ratio indicated that targets were 11% more likely to survive if neighbors were present. There was not a significant difference in survival probability between Uniola and Iva targets (Table 1). While survival was greater on Sapelo than Keywadin, the effects of neighbors was consistent across sites (no significant site × neighbor interaction; Table 1).

The results for biomass contrasted with the results for survival. On Sapelo Island, the presence of neighbors significantly reduced final biomass of Uniola targets (planned contrast $F_{1,8} = 16.6, \ P = 0.015$; Table 2). Uniola targets without neighbors had 4.0 times the biomass of targets with neighbors (Fig. 1a). Biomass of Iva was not reduced by neighbors on Sapelo (planned contrast $F_{1,15} = 0.74, \ P = 0.40$; Table 2). However leaf number may be a better indicator of fitness for this shrub, since much of the total biomass of many of the plants was composed of leafless and apparently dead stems that would not seem to contribute to growth or reproduction (S.J. Franks, pers. obs.). Leaf number was reduced by neighbors on Sapelo (planned contrast $F_{1,3} = 6.1, \ P = 0.019$; Fig. 1b). On Keywadin Island, there was not a significant effect of neighbors on biomass of Uniola (planned contrast $F_{1,3} = 0.1, \ P = 0.737$; Table 2) or Iva (planned contrast $F_{1,5} = 0.03, \ P = 0.878$; Table 2). Neighbor size did not significantly affect size of target plants for either species at either site. Despite a range in neighbor biomass of 0–63.7 g by the end of the experiment, a linear regression for both species at both sites showed no per-gram effects of neighbors ($n = 18$, $MS = 0.56, F_{1,17} = 1.46, \ P = 0.25, r^2 = 0.08$).

**Interactions across the gradient**

To determine the effect of the position along the environmental gradient on plant performance, I examined the main effect of zone in a logistic regression for survival and in an ANCOVA for biomass. Overall survival (with and without neighbors) was significantly greater closer to the shore (df = 2, $\chi^2 = 6.7, \ P = 0.035$; Table 1), but zone did not signifi-
Fig. 1. The effect of neighbor treatment on (a) biomass of *Uniola* targets with *Uniola* neighbors (N = 2), *Iva* neighbors (N = 2), and no neighbors (N = 4); and on (b) number of leaves of *Iva* targets with *Uniola* neighbors (N = 8), *Iva* neighbors (N = 6), and no neighbors (N = 6) on Sapelo Island. The effect of neighbor treatment on (c) biomass of *Uniola* targets with *Uniola* neighbors (N = 3), *Iva* neighbors (N = 2), and no neighbors (N = 2); and on (d) number of leaves of *Iva* targets with *Uniola* neighbors (N = 5), *Iva* neighbors (N = 5), and no neighbors (N = 2) on Keywadin Island. Low sample sizes reflect the high mortality over the course of the study. Error bars are 1 SE. Different letters indicate significant (α < 0.05) differences in means based on planned orthogonal contrasts.

Table 1. Logistic regression table for survival of both target species pooled (N = 144).

<table>
<thead>
<tr>
<th>Effect</th>
<th>df</th>
<th>Wald χ²</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Main effects</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Site</td>
<td>1</td>
<td>4.0</td>
<td>0.046*</td>
</tr>
<tr>
<td>Zone</td>
<td>2</td>
<td>6.7</td>
<td>0.035*</td>
</tr>
<tr>
<td>Neighbors</td>
<td>1</td>
<td>8.6</td>
<td>0.003*</td>
</tr>
<tr>
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<td>0.0</td>
<td>0.997</td>
</tr>
<tr>
<td>Neighbor species</td>
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<td>3.7</td>
<td>0.156</td>
</tr>
<tr>
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<td></td>
<td></td>
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<tr>
<td>Initial height</td>
<td>1</td>
<td>4.2</td>
<td>0.040*</td>
</tr>
<tr>
<td>Interactions</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Site × neighbors</td>
<td>1</td>
<td>0.1</td>
<td>0.741</td>
</tr>
<tr>
<td>Neighbors × zone</td>
<td>1</td>
<td>0.2</td>
<td>0.916</td>
</tr>
<tr>
<td>Target species × neighbor species</td>
<td>2</td>
<td>3.5</td>
<td>0.173</td>
</tr>
<tr>
<td>Contrasts</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Foredune vs. other</td>
<td>4.4</td>
<td>0.036*</td>
<td></td>
</tr>
<tr>
<td>Mid-dune vs. rear dune</td>
<td>0.3</td>
<td>0.581</td>
<td></td>
</tr>
</tbody>
</table>

Note: Neighbors refers to the presence or absence of neighbors. *P < 0.05.

To test the hypothesis that plant interactions changed along the environmental gradient, the zone × neighbor treatment interaction term was examined. There was not a significant zone × neighbor treatment interaction for survival (df = 1, χ² = 0.2, P = 0.916; Table 1), indicating that interactions did not change along the gradient (Fig. 2a). There was a significant zone × neighbor treatment interaction for biomass (F₂,36 = 3.4, P = 0.047), with competition greatest at the foredune zone and no significant competition or facilitation at the mid-dune or rear dune zones (df = 1, χ² = 0.3, P = 0.581).

Intraspecific versus interspecific interactions

Neighbor species did not influence target performance. For *Iva* and *Uniola* targets with neighbors at both sites, the species of the neighbor did not significantly affect target survival (Table 1) or biomass (Table 2). Thus there was no difference between intraspecific and interspecific interactions.
Discussion

Responses to neighbors

The results of this study indicate that interactions among *Uniola* and *Iva* in dunes can vary from competitive to neutral to facilitative. The presence of neighbors reduced target plant biomass at one site, suggesting competition, but increased the probability of target survival at both sites, suggesting facilitation. Interactions were in some cases neutral (or too weak to be detected), with no significant effects of neighbors on target biomass on Keywadin Island and in both the mid-dune and rear dune zones on Sapelo Island.

A key finding of this study is that interactions were facilitative for survival but competitive or neutral for biomass. A possible reason for this pattern is that neighbors could have protected targets from erosion, desiccation, or other environmental extremes that were a source of mortality, but competed with targets for soil resources, reducing biomass. A similar result was reported by Levine (2000), who showed that in a riparian community in California, *Carex* competed with associated species by reducing biomass but facilitated neighbors by protecting them from mortality during winter disturbances. This result of survival facilitation and biomass competition is also supported by the theoretical work of Goldberg and Novoplansky (1997) on competition in temporally heterogeneous environments. Schupp (1995) also points out that conditions favoring survival may not favor growth, and that the effects of these conditions may vary through the life cycle. It may be generally true that neighbors are more likely to have positive effects on survival and negative effects on growth, but more interaction studies examining both growth and survival are necessary to test this idea.

Previous studies of dune plants have reported an entire spectrum of interaction type, including facilitation, competition, and a lack of interactions. In a classic study demonstrating the importance of positive interactions in succession, Yarranton and Morrison (1974) reported that facilitative interactions occurred among dune plants and gave rise to a unique pattern of vegetation establishment, which they termed “nucleation”. More recently, Shumway (2000) found that in New England coastal dunes, nitrogen-fixing *Myrica* shrubs facilitated seedling growth. In another classic study of plant interactions, Silander and Antonovics (1982) conducted neighbor removals and found both positive and negative responses of dune plants to the removal of neighbors, though they focused on competitive interactions. Lichter (2000) also found competitive interactions among dune plants, and reported that the intensity of competition increased during succession on Lake Michigan sand dunes. In contrast, Houle (1997) found neither competition nor facilitation in subarctic dunes. It appears from these and the present study that interactions among dune plants cannot be classified as always competitive or always facilitative, but rather the direction and magnitude of interactions on dunes may depend on a variety of factors, including environmental...

Table 2. ANCOVA table for biomass of *Uniola* on Keywadin (N = 7) and Sapelo Islands (N = 8) and biomass of *Iva* on Keywadin (N = 9) and Sapelo Islands (N = 19) (numbers of individuals per treatment group were reduced from the original numbers because of mortality).

<table>
<thead>
<tr>
<th></th>
<th>Keywadin Island</th>
<th>Sapelo Island</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>df  MS    F  P</td>
<td>df  MS    F  P</td>
</tr>
<tr>
<td><strong>Uniola</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Treatment</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Neighbor</td>
<td>2  59.3  1.9  0.300</td>
<td>2  0.35 8.3  0.037*</td>
</tr>
<tr>
<td>Covariate</td>
<td></td>
<td></td>
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<tr>
<td>Initial target</td>
<td>1  36.2  1.2  0.363</td>
<td>1  0.17 4.1  0.113</td>
</tr>
<tr>
<td>target height</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Contrasts</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Neighbors vs.</td>
<td>1  4.3  0.1  0.737</td>
<td>1  0.69 16.6  0.015*</td>
</tr>
<tr>
<td>alone</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Uniola</em> vs. <em>Iva</em> neighbors</td>
<td></td>
<td>1  0.04 0.9  0.403</td>
</tr>
<tr>
<td>Error</td>
<td>3  31.6</td>
<td>4  0.04</td>
</tr>
<tr>
<td><strong>Iva</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Treatment</td>
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<tr>
<td>Neighbor</td>
<td>2  0.01  0.03 0.971</td>
<td>2  1.33 1.57 0.240</td>
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<tr>
<td>Covariate</td>
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<td></td>
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<td>Initial target</td>
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<td>1  0.45 0.53 0.482</td>
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<td>target height</td>
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<tr>
<td>Contrasts</td>
<td></td>
<td></td>
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<tr>
<td>Neighbors vs.</td>
<td>1  0.01  0.03 0.878</td>
<td>1  0.62 0.74 0.405</td>
</tr>
<tr>
<td>alone</td>
<td></td>
<td></td>
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<tr>
<td><em>Uniola</em> vs. <em>Iva</em> neighbors</td>
<td></td>
<td>1  2.29 2.71 0.121</td>
</tr>
<tr>
<td>Error</td>
<td>5  0.28 15 15.53</td>
<td></td>
</tr>
</tbody>
</table>

Note: The table shows the effects of the three neighbor treatments (*Uniola* neighbors, *Iva* neighbors, and no neighbors), the covariate of initial target height, and planned orthogonal contrasts used to test the effects of neighbor presence or absence and neighbor species. The neighbors versus alone planned orthogonal contrast tests for significant competition or facilitation, and the *Uniola* versus *Iva* neighbors contrast compares intraspecific versus interspecific interactions.

*P < 0.05.
conditions and neighbor identity. Some of the potential effects of environmental conditions and neighbor identity were addressed in this study, and are discussed below.

Interactions and gradients

In a previous study, Franks and Peterson (2003) experimentally applied a burial treatment to coastal dune plants and found that burial caused the interactions to shift from neutral to facilitative. The study reported here compliments this previous work by examining interactions along a natural gradient in the field. Coastal dunes are known to be characterized by environmental gradients, with nutrient, drought, and salt spray stresses as well as disturbances because of burial, erosion, and storm overwash generally decreasing with distance from the shore (Oosting and Billings 1942; Barbour 1978; Ehrenfeld 1990; Ishikawa et al. 1995; Maun and Perumal 1999). Previous work at the field sites where this research was conducted also demonstrated a gradient of soil stability, with stability highest furthest landward from the shoreline (Franks 2003). Based on this previous work, stress and disturbance were thought to decrease with distance from the shore, and the experiment was designed to examine interactions along a gradient based on this assumption. However, the plant performance results, for plants with and without neighbors, do not support a gradient of decreasing stress and disturbance with distance from the shore. Survival was greatest in the foredunes (Fig. 2a), and biomass did not differ significantly among zones (Fig. 2b). This finding indicates that despite previous measurements at these sites, plant performance did not reveal a gradient of decreasing stress and disturbance with increasing landward distance from the shore. Instead there was evidence that with increasing distance from the shore, stress or disturbance moderately increased.

The results of interactions in different zones thus must be examined in light of the fact that the expected gradient was not detected. I had predicted that facilitative interactions, measured by the difference in biomass and survival with and without neighbors present, would be greatest closest to the shore, where stress and disturbance was expected to be greatest. In contrast, I found that competition, measured by biomass, was greatest near the shore and was lower (and not significantly different from neutral) in the mid-dune and rear dune zones (Fig. 2b). In addition, there was not a significant effect of zone on plant interactions as measured by survival (neighbor × zone interaction, Table 1). There was thus not a strong effect of zone on plant interactions. This finding cannot be taken as evidence either for or against the hypothesis of increasing facilitation with increasing stress and disturbance, since zone did not appear to correspond to a strong stress gradient in this study. These results suggest that coastal dune gradients may be more complex and temporally as well as spatially variable than expected, and that additional research on heterogeneity in dune habitats would contribute to our understanding of these systems.

Intraspecific versus interspecific interactions

In this study, there were no differences between intraspecific versus interspecific interactions as measured by survival (neighbor identity factor in Table 1) or biomass (Uniola versus Iva neighbors contrasts in Table 2) at both sites. The hypothesis that facilitation would be greater among heterospecifics than among conspecifics was not supported. This result was somewhat surprising in light of the fact that these two species (one rhizomatous C₄ grass and one woody C₃ shrub) differ in such morphological and physiological characteristics as growth form, rooting patterns, and photosynthetic system (Brown and Gracen 1972; Duncan and Duncan 1987).

It appears that for these two coastal dune species, the presence or absence of neighbors may be more important than their identity. This result would be expected if amelioration of stress or protection from disturbance caused by neighbors is a function of physical presence rather than effects that are species-specific. In dunes, any physical structure can stabilize the soil. If facilitation occurs by a mechanism such as soil stabilization, species of neighbor might not be expected to affect the outcome of interactions. In systems where facilitation is caused by such mechanisms as nitrogen
fixation by a particular species, neighbor identity would be expected to influence the outcome in the interactions. Thus, understanding the mechanism of facilitation is critical for predicting under what conditions facilitation is expected.

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