

CRAB HERBIVORY REGULATES PLANT FACILITATIVE AND COMPETITIVE PROCESSES IN ARGENTINEAN MARSHES

JUAN ALBERTI,^{1,2,6} MAURICIO ESCAPA,^{1,2,3} OSCAR IRIBARNE,^{1,2} BRIAN SILLIMAN,⁴ AND MARK BERTNESS⁵

¹Laboratorio de Ecología, Departamento de Biología (FCEyN), Universidad Nacional de Mar del Plata, CC 573 Correo Central, B7600WAG, Mar del Plata, Argentina

²Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Rivadavia 1917, CP C1033AAJ, Ciudad de Buenos Aires, Argentina

³Instituto Argentino de Oceanografía, Consejo Nacional de Investigaciones Científicas y Técnicas (IADO CONICET), Florida 8000, CP 8000, Bahía Blanca, Argentina

⁴Department of Zoology, University of Florida, Gainesville, Florida 32611 USA

⁵Department of Ecology and Evolutionary Biology, Brown University, Providence, Rhode Island 02912 USA

Abstract. Interactions among plants have been hypothesized to be context dependent, shifting between facilitative and competitive in response to variation in physical and biological stresses. This hypothesis has been supported by studies of the importance of positive and negative interactions along abiotic stress gradients (e.g., salinity, desiccation), but few studies have tested how variation in biotic stresses can mediate the nature and strength of plant interactions. We examined the hypothesis that herbivory regulates the strength of competitive and facilitative interactions during succession in Argentinean marshes dominated by *Spartina densiflora* and *Sarcocornia perennis*. *Spartina densiflora* is preferred by the dominant herbivore in the system, the crab *Chasmagnathus granulatus*. We experimentally manipulated crab herbivory, plant structure, and shade, and we found that, when herbivory was low in the spring and summer, competitive interactions between plants were dominant, but in the fall, when herbivory was highest, facilitative interactions dominated, and *Spartina densiflora* survival was completely dependent upon association with *Sarcocornia perennis*. Moreover, experimental removal of *Sarcocornia perennis* across recently disturbed tidal flats revealed that, while *Sarcocornia perennis* positively affected small *Spartina densiflora* patches by decreasing herbivory, as patch size increases and they can withstand the impact of herbivory, competitive interactions predominated and *Spartina densiflora* ultimately outcompeted *Sarcocornia perennis*. These results show that herbivory can mediate the balance between facilitative and competitive processes in vascular plant communities and that the strength of consumer regulation of interactions can vary seasonally and with patch size.

Key words: *Chasmagnathus granulatus*; competition; facilitation; herbivory threshold; *Sarcocornia perennis*; southwest Atlantic; *Spartina densiflora*.

INTRODUCTION

Facilitation and competition are biotic processes that influence the structure and organization of plant communities (e.g., Callaway and Walker 1997, Pugnaire and Luque 2001). The relative importance of facilitative and competitive processes has been hypothesized to be a function of both physical and biological conditions (e.g., Bertness and Callaway 1994, Callaway and Walker 1997, Holmgren et al. 1997). Facilitation is predicted to be important in physically and biologically stressful environments in which neighbors can ameliorate physical (e.g., reduce salinity or desiccation stress) or biological stresses (e.g., alleviating competition or consumer pressure), while competition is predicted to be more important in less stressful physical and biological situations (e.g., Bertness and Callaway 1994,

Callaway and Walker 1997, Stachowicz 2001, Bruno et al. 2003). These predictions have been confirmed in a wide variety of communities in which neighbors buffer one another from abiotic (e.g., Bertness and Leonard 1997, Callaway et al. 2002) and/or biotic stress (e.g., Hay 1986, Milchunas and Noy-Meir 2002, Callaway et al. 2005) and in which biotic and abiotic stresses are greatly reduced (e.g., Bertness and Shumway 1993, Greenlee and Callaway 1996, Callaway and Walker 1997).

Many studies have found that the balance between competitive and facilitative processes can shift spatially as abiotic stress varies across landscapes (e.g., Bertness and Hacker 1994, Pugnaire and Luque 2001, Tewksbury and Lloyd 2001, Kuijper et al. 2004), while a few others have found that the importance of competition and facilitation can shift temporally among years and seasons as a function of variation in abiotic conditions (interannual, Berkowitz et al. 1995, Greenlee and Callaway 1996; seasonal, Kikvidze et al. 2006) and also with ontogeny (i.e., life stages) of beneficiaries (Callaway and Walker 1997, Holmgren et al. 1997, Miriti 2006) or

Manuscript received 10 January 2007; revised 30 April 2007; accepted 21 May 2007. Corresponding Editor: J. J. Stachowicz.

⁶ E-mail: jalberti@mdp.edu.ar

benefactors (i.e., the ones that facilitate another species; Ervin 2005). Furthermore, there are many studies of associations among plants driven by herbivory (e.g., Harris et al. 1984, Callaway et al. 2000, Gagnon et al. 2003), but studies experimentally testing the manner in which changes in biotic stress intensity (i.e., consumer pressure) can affect the balance between positive and negative associations among plant communities in both early and late stages of development are scarce (but see Hay 1986, Oosterheld and Oyarzábal 2004, Callaway et al. 2005).

Experimental studies from a variety of natural systems have shown that herbivores can impact community development (e.g., marshes, Jefferies et al. 2006; rocky intertidal, Farrell 1991; sand dunes, Bach 1994; grasslands, Chase et al. 2000; reefs, Belliveau and Paul 2002). Connell and Slatyer (1977) identified three models of succession during community development in which early successional species can have either a positive (facilitation), neutral (tolerance), or negative (inhibition) effect on the establishment of later species. Herbivore impacts on community development have been shown to depend on herbivore feeding preferences (Farrell 1991). During inhibitory succession, herbivory on early colonizers accelerates community development (e.g., Lubchenco and Menge 1978, Bryant 1987), whereas during facilitative succession herbivory on early colonizers slows community development (e.g., Bach 1994, Fagan and Bishop 2000). In contrast, herbivory on late successional species retards community development regardless of the model (e.g., Farrell 1991, Belliveau and Paul 2002, Kuijper et al. 2004, Kuijper and Bakker 2005).

Salt marshes are harsh abiotic environments in which amelioration of physical stresses and sharp physical gradients can shift plant interactions from facilitative to competitive in both fully developed communities and those in the early stages of recovery after disturbance (e.g., Bertness and Shumway 1993, Bertness and Hacker 1994). Herbivory, however, can also directly and indirectly (e.g., changing the abiotic environment by increasing light availability, nutrients; e.g., Fagan and Bishop 2000) have strong impacts on marsh plant growth and distribution (e.g., Costa et al. 2003, Kuijper et al. 2004, Silliman et al. 2005, Jefferies et al. 2006) and thus may also be an important driver of marsh plant associations across landscapes and community development stages (e.g., Hay 1986, Milchunas and Noy-Meir 2002).

In this paper, we use northern Argentinean salt marshes to evaluate the hypotheses that herbivory can affect plant facilitative succession and that decreasing biotic stress can shift interactions from facilitative to competitive, seasonally and/or ontogenetically. Southwestern Atlantic marshes are vegetated predominately by monoculture zones of the cordgrass *Spartina densiflora* and in some marshes, additionally *Spartina alterniflora*. In many of these marshes, *Sarcocornia perennis* is the dominant succulent and occurs on

disturbed tidal flats and in interior marsh patches (Costa and Davy 1992, Isacch et al. 2006). The abundant (10–60 burrows/m² throughout all the intermediate and low parts of marshes) herbivore/detritivore burrowing crab *Chasmagnathus granulatus* (e.g., Iribarne et al. 1997, 2005) is the dominant herbivore in this system and feeds mainly on both *Spartina* species (Iribarne et al. 1997, Bortolus and Iribarne 1999, Costa et al. 2003; in extremely rare occasions crabs consume only very young individuals of *Sarcocornia perennis*; J. Alberti, unpublished data). In this study we: (1) evaluate whether *Sarcocornia perennis*, the early successional species, facilitates tidal flat colonization by *Spartina densiflora*, the late successional species, by protecting it from abiotic (desiccation or salinity) and/or biotic factors (crab herbivory); (2) determine the potential role of herbivory in mediating facilitative plant succession; (3) determine the mechanism of this plant–plant facilitation; and (4) examine whether there are ontogenetic or seasonal shifts in facilitative and competitive interactions during succession.

METHODS

Study area

This work was conducted between December 2002 and June 2005 at Mar Chiquita coastal lagoon (37°29'–37°46' S, Argentina) and the Bahía Blanca estuary (38°41'–39°30' S, Argentina) in irregularly flooded (10–15 times per month) marshes characterized by halophytic vegetation, dominated by *Spartina densiflora* and *Sarcocornia perennis* (see Isacch et al. 2006; for clarity we will henceforth refer to these species by the genus names). Both sites are densely populated by the burrowing crab *Chasmagnathus granulatus* (Bortolus and Iribarne 1999, Iribarne et al. 2005). At low elevations, circular patches of *Sarcocornia* colonizing the mud flat (over areas of >600 m) are found at both sites (patch diameter at Bahía Blanca, 2.26 ± 1.02 m, mean ± SE; at Mar Chiquita, 0.99 ± 0.45 m) adjacent to mature *Spartina* marshes. *Spartina* is commonly found inside these *Sarcocornia* patches (see Plate 1; hereafter we will refer to patches containing both *Spartina* and *Sarcocornia* as mixed patches). In some cases these *Spartina* patches may be clones, but they are usually composed of individual plants (of 40 patches sampled, ranging from 6 to 48 stems, none was connected, even those separated by <50 cm, the minimum distance between *Spartina* patches in the field). More than one *Spartina* patch can be found in a single *Sarcocornia* patch, and these are the only two plant species found in the study areas. Even though we know that working on several sites would be the ideal situation, we could work only in two sites due to logistic constraints.

Patterns of plant distribution and herbivory

*Quantifying the co-occurrence of *Spartina* and *Sarcocornia*.*—We investigated how commonly *Spartina* and *Sarcocornia* co-occurred in patches on tidal flats

(recovering from an intense flooding that occurred during fall of 2002) by comparing the number of *Spartina* patches growing inside *Sarcocornia* or on exposed sediments in nine square areas (10-m side) using a paired *t* test (Zar 1999) for Bahía Blanca and a Wilcoxon matched-pairs test (Conover 1980) for the Mar Chiquita lagoon. In the same areas, the percent cover of *Sarcocornia* was also estimated to establish whether it explained the co-occurrence of species by counting the times *Sarcocornia* was present in 100 randomly distributed points per area.

Herbivory.—To evaluate the relationship between patch size and herbivory, 18 random *Spartina* patches at Mar Chiquita (during spring of 2003) were scored for the percentage of live leaves damaged (i.e., lacking tips; leaf tissue removal by crabs approximates 20%; J. Alberti, unpublished data) from 10 stems per replicate, half located on the patch edge and the other half in the patch interior. Mean damage on the patch edge or interior was calculated for each replicate. Differences in percentage of leaves damaged (an estimation of herbivory) between patches of different size classes (based on the number of stems: <50, between 50 and 99, and >99; $n = 6$ per category) and between patch edges or interiors were evaluated using a two-way ANOVA (square-root transformed; Zar 1999). We used Tukey post hoc contrasts to test for differences between treatments when significant results were found using ANOVA (Zar 1999).

Species composition of patches.—To determine whether the proportion of *Sarcocornia* occupied by *Spartina* increased over time, we quantified the area of *Sarcocornia* patches ($n = 10$) occupied by *Spartina* patches for one year (April 2003 to April 2004). We tested the hypothesis of no differences in the proportion of *Sarcocornia* patches occupied by *Spartina* between dates with a paired *t* test (log-transformed; Zar 1999).

Effect of Sarcocornia removal on Spartina within patches of the two species

Since sampling revealed that *Spartina* and *Sarcocornia* commonly occur in patches, we experimentally evaluated (in the same marsh where samplings were performed) whether: (1) the association between *Sarcocornia* and *Spartina* was the product of a facilitation; (2) there was a shift from facilitation to competition with the number of stems per *Spartina* patch and/or season; (3) facilitative interactions were mediated by physical and/or biotic factors; and (4) crab herbivory on *Spartina* was affected by the branch structure of *Sarcocornia*. These experiments were done at Mar Chiquita from December 2002 to May 2005.

Is the co-occurrence of Sarcocornia and Spartina the product of facilitation?—To evaluate whether the occurrence of *Spartina* in *Sarcocornia* patches was affected by *Sarcocornia* removal, 20 *Sarcocornia* patches were identified and randomly assigned to two different treatments: (1) unmanipulated controls (*Spartina* patch-

es growing inside 10 mixed patches) and (2) *Sarcocornia* removal (*Spartina* patches growing inside 10 mixed patches in which *Sarcocornia* was removed). After one year (beginning in December 2002), the number of *Spartina* patches remaining per replicate was compared between treatments using a *t* test for unequal variances (Welch approximation t_c ; Zar 1999) and was considered an estimate of patch survival.

Do facilitative interactions shift to competitive with patch size and/or season?—To test the hypothesis that *Sarcocornia* facilitates *Spartina* and that this interaction varies seasonally and with patch size, we conducted a *Sarcocornia* removal experiment and followed *Spartina* success (proportion of consumed leaves, seasonal patch growth rate, and change in stems number). Sixty-six mixed patches were randomly assigned to two different treatments in December 2002. Half of them ($n = 33$) were left as unmanipulated controls while *Sarcocornia* was removed from the remaining patches (removal treatment).

Field observations showed that *Spartina* patches from the removal treatment grew differently according to their size (with more or fewer than ~ 25 stems), but this did not happen when *Sarcocornia* was left intact. Thus, on the basis of these differences according size, we divided patches from the removal treatment into two classes. To examine patch size effects on the relationship between *Sarcocornia* and *Spartina*, patches of *Spartina* from the removal treatment were separated into small patches with initially fewer than 25 stems ($n = 29$) and large patches with initially 25 or more stems ($n = 4$; this division could not be balanced because different size classes were evident three months after the experiment was initiated). For analyses, response variables included herbivory, patch growth rate, and patch index (cumulative change in number of stems per *Spartina* patch).

We examined the hypothesis that the balance between facilitation and competition shifted with patch size and/or season comparing herbivory and patch growth rates of small and large *Spartina* patches within *Sarcocornia* removals vs. control patches with *Sarcocornia* present. Differences in herbivory between treatments were evaluated seasonally by randomly choosing and scoring percentage of leaves damaged (once in the middle of each season during a year) on five stems per patch (averaged for the analysis). To evaluate seasonality in herbivory, we compared the four seasons using the values from the control treatment ($n = 33$ per season) with ANOVA (square-root transformed; Zar 1999). Patch growth rate was estimated seasonally as the percentage of change in stem number ([number of live stems at the sampling period – number of live stems approximately one month before] \times [number of live stems approximately one month before] $^{-1} \times 100 \times$ [number of days between samplings] $^{-1}$).

When analyzing large patches vs. control (either for herbivory or patch growth rate), we randomly reduced the original sample of control *Spartina* patches ($n = 33$)

to four in order to equalize the replicate number among treatments. For each iteration (10000 total), we estimated the mean value of the sample and calculated pairwise seasonal differences (*Sarcocornia* removal – unmanipulated control) with the group of patches that initially had at least 25 stems. The two patch groups (i.e., control and *Sarcocornia* removal) were considered to be significantly different if zero was outside the 95% confidence interval of the distribution of resampled differences (following Manly 1998). Given that some small *Spartina* patches (from the *Sarcocornia* removal treatment) were totally consumed during this study, the number of replicates per treatment was not the same in all seasons, and hence, samples from the control treatment were randomly reduced (to 19 and 29 in the summer, 16 and 19 in the fall, 14 and 16 in the winter, and 8 and 14 in the spring, for herbivory and patch growth rate, respectively) and then, for each season, compared to the group of small *Spartina* patches (from the *Sarcocornia* removal treatment).

Patch index reflected how much patches had increased or decreased between the sampling date and the beginning of the experiment and was estimated as: (number of live stems at the sampling period) \times (number of live stems when experiment started)⁻¹. Values of 0 mean that the patch disappeared, values between 0 and 1 signify that the number of stems decreased, a value of 1 means that the size remained the same, and larger values mean that patches increased in size. Note that this index is calculated comparing the number of stems at each sampling period to the number of stems at the beginning of experiments.

Is facilitation mediated by abiotic and/or biotic stress?—A second experiment examined whether the association between *Sarcocornia* and *Spartina* was mediated by biotic and/or abiotic stresses and was conducted from November 2003 (early in the growing season) to April 2004 (when desiccation and salinity are expected to be more severe). Fifty mixed patches (with 15–20 *Spartina* stems) were identified and randomly assigned to the following treatments: unmanipulated controls ($n = 10$), *Sarcocornia* removals ($n = 10$), crab and *Sarcocornia* removals ($n = 10$), cage controls on *Sarcocornia* removals ($n = 10$), and shaded *Sarcocornia* removals ($n = 10$).

Crab exclusion and cage control treatments were surrounded with wire mesh cages (30 cm diameter, 25 cm high, 1-cm mesh size; cage control treatments had three entrances at the surface level that permitted movement of crabs of all sizes). All other known invertebrates present in the marsh could pass freely through the mesh, and field observations showed that they produce leaf wounds different than those of crabs (i.e., small circular or semicircular holes in the leaves and circular holes in stems, while crabs, on average, remove 20% of leaf tissue from the tip). Effects of insects on plant performance are expected to be more important during the spring and summer period, when herbivorous

insects are more abundant (A. Canepuccia, *personal communication*). Even though vertebrate herbivores could be potentially excluded, when present in the marsh, they use much higher intertidal levels and produce very distinctive marks, as they eat only stem bases and leave the scraps on the soil surface (wild guinea pig, *Cavia aperea*; A. Canepuccia and J. Alberti, *unpublished data*). During the experiment, there were no signs of grazing by vertebrate grazers in our treatments.

Shaded treatments were used to reduce salinity and desiccation stress and mimic presence of removed aboveground plant material (as in Bertness and Hacker 1994). For this treatment, a black cloth reducing incoming solar radiation by 50% was placed 15 cm above the soil surface surrounding *Spartina* patches (mean *Sarcocornia* height). To quantify edaphic conditions in the treatments, soil samples were taken in each replicate (April 2004) and salinity and soil water content were quantified (Pennings and Callaway 1992). Treatment differences in edaphic conditions (i.e., soil salinity and water content) were contrasted using ANOVAs (Zar 1999). Herbivory, patch growth rate, and patch index were quantified as described in *Patterns of plant distribution and herbivory: Herbivory and Do facilitative interactions shift to competitive...* above, and treatment differences were also compared using ANOVAs (Zar 1999) (herbivory was arcsine square-root and square-root transformed and change in the number of stems was log- and square-root transformed, in summer and fall, respectively).

Does facilitator plant structure prevent herbivory?—A third experiment conducted in the fall of 2005 (March to June), examined whether amelioration of herbivore pressure by *Sarcocornia* was due to its structure. Twenty-four mixed species patches were selected and randomly assigned to three treatments: unmanipulated controls ($n = 8$); *Sarcocornia* removals ($n = 8$); and *Sarcocornia* removals with its structure simulated ($n = 8$). In the simulation treatment, dead stems of *Sarcocornia* were placed inside *Spartina* patches, simulating facilitator structure, while in the *Sarcocornia* removal treatment, dead stems were placed adjacent to but not mixed with *Spartina*. Herbivory (mean of five stems randomly selected per replicate, arcsine square-root transformed), patch growth rate, and patch index were calculated for each replicate three months after the experiment was initiated (most of the replicates were lost during a heavy storm) and compared using ANOVAs.

RESULTS

Patterns of plant distribution and herbivory

Quantifying the co-occurrence of Spartina and Sarcocornia.—More than 95% of *Spartina* patches were growing inside *Sarcocornia* patches (Bahía Blanca, 95.5% \pm 1.6% [mean \pm SE]; Mar Chiquita, 96.6% \pm 1.3%) rather than on exposed sediments (Bahía Blanca, paired $t = 6.01$, $df = 8$, $P < 0.001$; Mar Chiquita, $Z = 2.67$, $n = 9$, $P < 0.01$). However, the area occupied by

Sarcocornia was less than one-third of the tidal flat area sampled (Mar Chiquita, $23.7\% \pm 4.3\%$; Bahía Blanca, $14.7\% \pm 1.4\%$), while the rest was exposed sediment.

Herbivory.—In Mar Chiquita, herbivory was 2.5 times higher on patch edges ($29 \pm 4\%$ of leaves damaged per stem) than in patch interiors ($13\% \pm 2.7\%$ of leaves damaged per stem of *Spartina*; $F_{1,30} = 8.34$, $P < 0.01$). Herbivory was also twice as high in smaller patches ($26\% \pm 3.9\%$ leaves damaged per stem) than in larger ones ($13\% \pm 5.1\%$ leaves damaged per stem; $F_{2,30} = 4.15$, $P < 0.05$).

Species composition of patches.—After one year, the proportion of *Sarcocornia* patches occupied by *Spartina* more than doubled, with *Spartina* covering $4.3\% \pm 1.3\%$ of *Sarcocornia* patches in April 2003 and $9.7\% \pm 4.5\%$ in April 2004 (paired $t = 4.93$, $df = 9$, $P < 0.001$).

Effect of *Sarcocornia* removal on *Spartina* within patches of the two species

Is the association between *Sarcocornia* and *Spartina* the product of facilitation?—When considering the number of *Spartina* patches per *Sarcocornia* patch, the unmanipulated controls (with *Sarcocornia*) had more patches of *Spartina* present (3.5 ± 0.67) than patches with *Sarcocornia* removals (1.1 ± 0.43 ; $t_c = 3.01$, $df = 15.4$, $P < 0.01$). Hence, entire patch survival was reduced to less than one-third when *Sarcocornia* was removed.

Do facilitative interactions shift to competitive with patch size and/or season?—There was clear seasonality in crab herbivory, with highest herbivory in the winter, when leaves were two times more heavily consumed than in the fall and the spring and seven times more than in the summer ($F_{3,128} = 38.24$, $P < 0.001$). Regardless of season, control patches were (between 66% and 38%) less consumed than small *Spartina* patches situated within *Sarcocornia* removal treatments, but they were not significantly different from large *Spartina* patches without *Sarcocornia* (Fig. 1A; see Appendix). During the growing season (i.e., spring and summer), removing *Sarcocornia* increased *Spartina* patch growth rate of large patches by more than twofold in the summer and sixfold in the spring (Fig. 1B; see Appendix). However, during those periods, there were no significant differences between control patches and small patches without *Sarcocornia* (Fig. 1B; see Appendix). In contrast, during the fall and the winter, small *Spartina* patches without *Sarcocornia* exhibited a significant reduction in the patch growth, a pattern that was not observed in the control patches (Fig. 1B; see Appendix). These experimental results generated differences in the number of stems per *Spartina* patch (large vs. control, summer; small vs. control, fall) that were maintained and increased during the rest of the year (Fig. 1C). At the end of the experiment, control patches had grown (in stem number; patch index) by 72%, while large patches with *Sarcocornia* removed had grown by 346%. In contrast, small patches with *Sarcocornia* removed shrank by 55% (Fig.

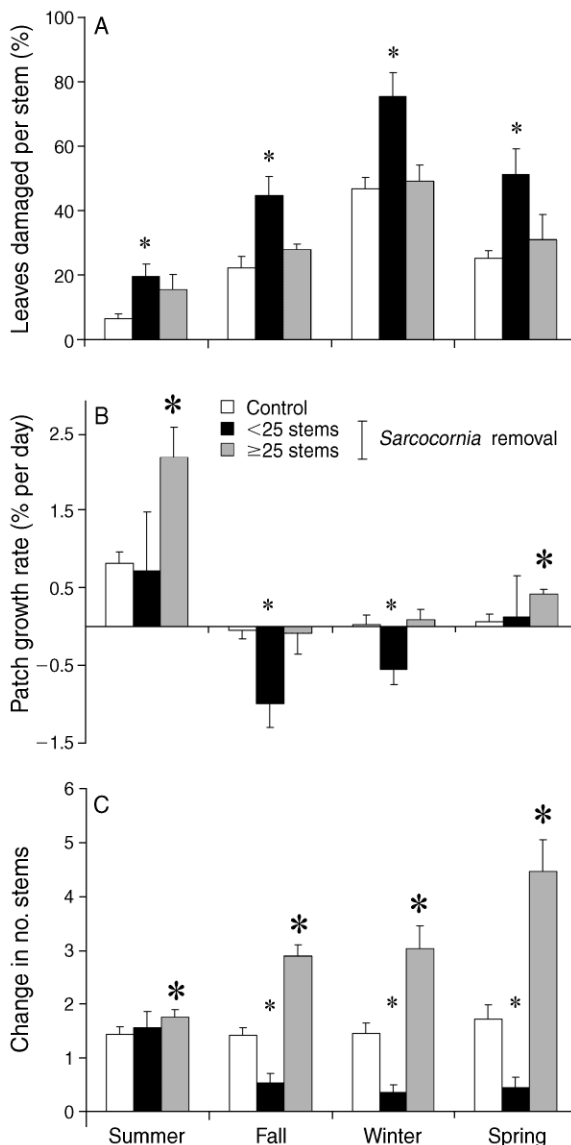


FIG. 1. (A) Percentage of leaves damaged per *Spartina densiflora* stem, (B) *Spartina* patch growth rate, and (C) patch index (number of stems at the sampling period divided by that at the beginning of experiments) as a function of season. Small asterisks denote significant differences ($P < 0.05$) between control and small patches (<25 stems) from the *Sarcocornia perennis* removal treatment. Large asterisks denote significant differences between control and large patches (≥ 25 stems) from the *Sarcocornia* removal treatment. Bars show means \pm SE, and data are presented prior to transformations. The work was conducted in the Mar Chiquita coastal lagoon and the Bahía Blanca estuary, Argentina.

1C). Then, after one year, control *Spartina* patches were found to have, on average, four times more stems than small patches in which *Sarcocornia* was removed, but only half of large *Spartina* patches in which *Sarcocornia* had been removed (Fig. 1C).

Is facilitation mediated by abiotic and/or biotic stress?—No differences were found between treatments

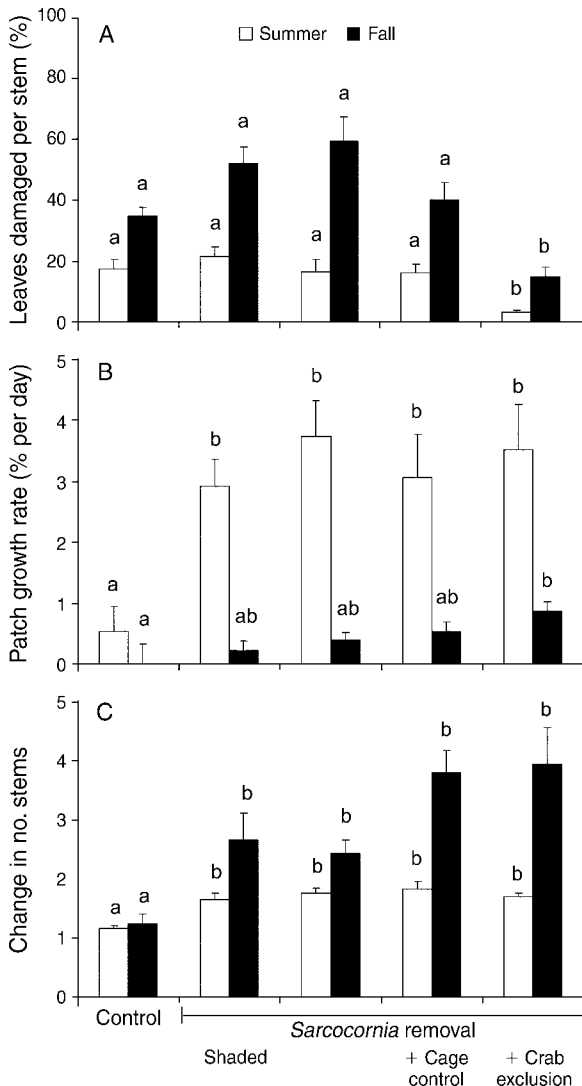


FIG. 2. (A) Percentage of leaves damaged per *Spartina densiflora* stem, (B) patch growth rate, and (C) patch index in relation to controls and the different treatments with *Sarcocornia perennis* removed. The shaded treatment consisted of shade cloth surrounding *Spartina* patches to reduce the effect of abiotic stress; the “+ crab exclusion” treatment consisted of a wire mesh cage surrounding *Spartina* patches to reduce the effect of herbivory; the “+ cage control” treatment consisted of cages similar to those in the “+ crab exclusion” treatment but with three entrances to allow free movement of crabs to detect potential artifacts of the cage; the unlabeled treatment refers to unshaded and uncaged *Spartina* patches. Different lowercase letters denote significant differences between treatments for a given season. Bars show means + SE, and data are presented prior to transformations.

in soil salinity ($F_{4,45} = 0.57, P > 0.68$) or water content ($F_{4,45} = 0.68, P > 0.6$). Regardless of season (i.e., summer or fall), herbivory was greatly reduced (between 60% and 80%) in the crab and *Sarcocornia* removal treatment, but there were no significant differences between the four other treatments (summer, $F_{4,45} =$

8.60, $P < 0.001$; fall, $F_{4,45} = 13.44, P < 0.001$; Fig. 2A). During the summer, *Spartina* patches with *Sarcocornia* removed grew six times faster than the control patches ($F_{4,45} = 4.71, P < 0.01$; Fig. 2B), resulting in a 45% increase in stems per patch ($F_{4,45} = 10.09, P < 0.001$; Fig. 2C). During the fall, differences in growth rate persisted only between crab exclusion + *Sarcocornia* removal and control treatments ($F_{4,45} = 2.80, P < 0.05$; Fig. 2B), and, as in the previous experiment, differences in the patch index generated in the summer remained (and increased) the following seasons ($F_{4,45} = 9.67, P < 0.001$; Fig. 2C).

Does facilitator structure prevent herbivory?—Herbivory on *Spartina* patches was 36% higher in treatments without structure than in treatments with *Sarcocornia* or with dead plant structure ($F_{2,21} = 6.31, P < 0.01$; Fig. 3A). These differences led to different growth rates between treatments, with negative values (i.e., decreasing number of stems per patch) in patches without structure, but positive values (i.e., increasing number of stems per patch) in patches in which *Sarcocornia* or its structure were present ($F_{2,21} = 6.22, P < 0.001$; Fig. 3B).

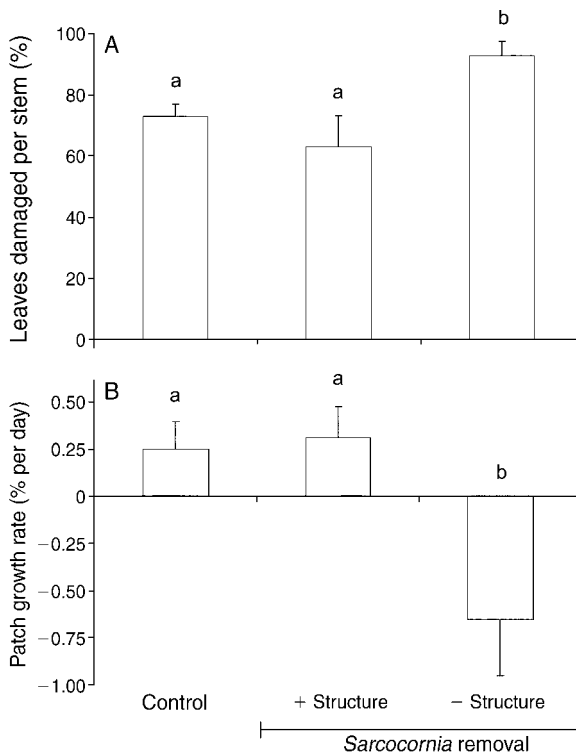


FIG. 3. (A) Percentage of leaves damaged per *Spartina densiflora* stem and (B) patch growth rate in relation to unmanipulated controls and the *Sarcocornia perennis* removal treatments (“+ structure” indicates *Sarcocornia* structure simulated; “- structure” indicates *Sarcocornia* structure not simulated). Different lowercase letters denote significant differences between treatments. Bars show means + SE, and data are presented prior to transformations.

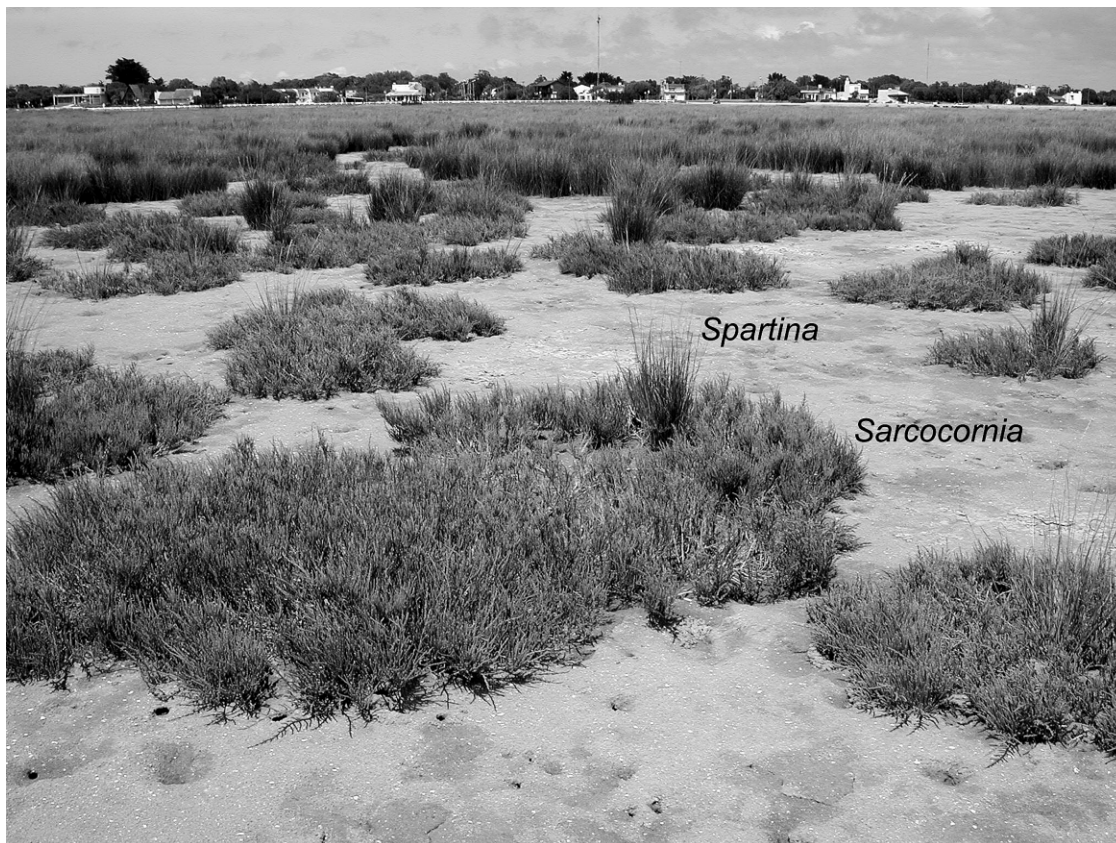


PLATE 1. The study site in the Mar Chiquita coastal lagoon, Argentina. Small *Spartina* patches growing inside *Sarcocornia* patches. Photo credit: J. Alberti.

DISCUSSION

Our results reveal that plant succession in Argentinian salt marshes can be affected by crab herbivory. The succulent pioneer *Sarcocornia* initially invades mudflats and facilitates the recruitment of the cordgrass *Spartina*, which dominates these marshes, potentially competitively displacing *Sarcocornia*. Cordgrass is preferentially consumed by the herbivorous crab *Chasmagnathus granulatus* (Costa et al. 2003), but in association with *Sarcocornia*, cordgrass herbivory is reduced. This consumer-driven associational defense varies seasonally and with patch size, increasing during the fall/winter months when herbivory is most intense and decreasing with patch size, since as colonizing cordgrass patches achieve larger size they are less vulnerable to herbivory. These results illustrate the important role played by crab herbivory in southwestern Atlantic salt marshes, providing one of the first experimental demonstrations of consumer-driven facilitation succession in a vascular plant assemblage and documenting two potentially common features of consumer-mediated facilitation in plant communities: (1) seasonal variation in facilitation intensity modulated by consumer pressure and (2)

variation in the importance of facilitation during community development or patch expansion.

Context dependence of facilitation and competition in natural communities

The balance between competitive and facilitative interactions has been shown to be context dependent, commonly varying with environmental conditions (Stachowicz 2001, Tewksbury and Lloyd 2001, Callaway et al. 2002) and occasionally with biological conditions (Hay 1986, Oosterheld and Oyarzabal 2004). Evidence for the context dependency of facilitative and competitive interactions has come from a variety of communities including North American marshes (Bertness and Hacker 1994, Rand 2004), cobble beaches (Bruno 2000), dunes, (Shumway 2000), semiarid grasslands (Pugnaire and Luque 2001), deserts (Tewksbury and Lloyd 2001), and alpine plant communities (Callaway et al. 2002). In spite of the copious evidence for the importance of physical-stress-driven, context-dependent facilitation in communities, relatively few studies have examined the manner in which biotic factors can influence facilitation-competition shifts in vascular plant communities (but see Oosterheld and Oyarzabal 2004, Callaway et al. 2005). Our study experimentally addressed this little-

studied issue and revealed that temporal and spatial variation in consumer pressure can mediate the relative strength of facilitative and competitive interactions in structuring communities.

Temporal shifts in the importance of facilitation have been associated with interannual differences in the intensity of abiotic stresses (Berkowitz et al. 1995, Greenlee and Callaway 1996) and with age of beneficiaries (Callaway and Walker 1997, Holmgren et al. 1997, Holzapfel and Mahall 1999) or benefactors (Holzapfel and Mahall 1999, Ervin 2005). In general, age-related interaction shifts proceed from facilitative to competitive as beneficiaries grow and become less susceptible to stresses (Bertness 1991, Callaway and Walker 1997, Holmgren et al. 1997). However, there is little information on the role played by seasonal changes in the outcome of these interactions (but see Kikvidze et al. 2006). Here we demonstrate age-related and cyclic shifts between competition and facilitation (for young *Spartina* patches that are too small to escape herbivory) occurring at different temporal scales (at least a couple of years and seasonally within a year, respectively) between perennial plants (for annuals see Holzapfel and Mahall 1999).

Shifts in the balance between competition and facilitation along stress gradients (whether temporal or spatial) occur mainly due to a decrease in the importance of facilitation, while variation in the intensity of competition is less important (Pugnaire and Luque 2001). We found similar results; the positive effect of facilitation decreased as patches of *Spartina* increased in size (being more tolerant to herbivory), while the negative effect of competition was always present, regardless of *Spartina* patch size. This finding is similar to previous results that show shifts from facilitation to competition as beneficiaries grow (Callaway and Walker 1997) and that the relative importance of neighbor competition increases as herbivore pressure is relaxed (Hay 1986, Van der Wal et al. 2000).

Models of succession

The original model of succession proposed by Clements (1916) focused on interactions between plants and the environment. Later, when biotic interactions were considered, three models of succession arose: facilitation, neutral, and inhibition (based on the effects of early successional species on the later successional species; Connell and Slatyer 1977, Farrell 1991). Most studies in North American salt marshes have found plant succession facilitated by pioneer species, which are ultimately replaced by dominant competitors. In these previous studies, however, facilitated succession was entirely driven by the amelioration of physical stresses (Bertness 1991, Huckle et al. 2000). In contrast, our results emphasize the importance of consumer pressure in mediating the balance between competition and facilitation during marsh succession. In our system, colonization of the tidal flat by *Spartina* is limited by

crab herbivory (a biotic stress factor) and positively affected by *Sarcocornia* (through an associational defense). The pioneer species, *Sarcocornia*, can then be replaced by *Spartina*, probably by competitive displacement as in other marshes (see Bertness 1991, Bertness and Shumway 1993). As predicted by models of succession, since herbivory was concentrated on late successional species in our system, it retards facilitative succession (Farrell 1991). Our study, however, presents an interesting new insight since herbivores not only affect the rate of succession but change the succession model, from inhibitory into facilitative.

Consumer control of natural communities

While nutrients often control the primary production of ecosystems (Valiela et al. 1976), herbivores can also exert strong controls on plant production in a wide variety of environments (sand dunes, Bach 1994; rain forests, Green et al. 1997; marshes, Silliman et al. 2005; kelp forests, Halpern et al. 2006). Among the most important effects of herbivory are on plant distributions (Lubchenco 1980), rates of succession (Farrell 1991), primary production (Bortolus and Iribarne 1999), changing plant–plant species interactions (Hay 1986), and ecosystem functioning (Silliman et al. 2005, Jefferies et al. 2006). Plant distribution and production in salt marshes has long been thought to be regulated by bottom-up factors (Valiela et al. 1976), and invertebrate herbivory has been considered to be of negligible importance (Teal 1962). Our work contributes to the growing recognition of the importance of invertebrate consumers controlling salt marsh primary production and community structure (Silliman et al. 2005).

Facilitation, herbivory, and succession in Argentinean salt marshes

Our results suggest that the common association between *Spartina* and *Sarcocornia* in Argentinean marshes is driven by facilitation. Facilitation is critical for the establishment of *Spartina*, since it is highly dependent on *Sarcocornia* to survive when young and susceptible to crab herbivory. When *Spartina* patches are large, however, they reach a threshold size for escaping crab herbivory (see also Green et al. 1997), probably because the impact of herbivores is distributed among more stems. Consequently, while *Spartina* is initially dependent upon association with *Sarcocornia* when young, at larger sizes they become less vulnerable to herbivory and interspecific plant competition becomes more limiting. The mechanism by which *Sarcocornia* facilitates the survival and growth of *Spartina* recruits is decreased herbivory caused directly by its structure (see Harris et al. 1984, Gagnon et al. 2003) and probably not by reducing desiccation or salt stress, since there were no significant differences in these variables among treatments with and without *Sarcocornia*. *Sarcocornia* structure probably limits crab herbivores by increased mechanical constraints (*Sarcocornia*

branches horizontally cross *Spartina* patches), but probably not simply by increasing stem density, given that *Sarcocornia* stem densities are <5% of that of *Spartina* plants. We also found temporal shifts in the balance between these positive and negative interactions. Since the impact of herbivory is highest during the fall and the winter (i.e., even though crabs consume the same or less than in summer, plants are not growing, and hence, they are not recovering the lost tissues; J. Alberti, unpublished data), the intensity of herbivore-driven facilitation is highest in these seasons, while during the rest of the year facilitation is weaker and competition increases in importance.

This study contributes to our general understanding of natural community dynamics by revealing that herbivory can strongly mediate the balance of facilitative and competitive interactions in a plant community historically thought to be entirely controlled by bottom-up forces and demonstrating that herbivory may drive switches between succession models, suggesting a new way in which consumers can be important for community dynamics.

ACKNOWLEDGMENTS

We thank D. Alberti, A. García Coni, M. Merlo, F. Vera, and E. García for field and/or writing help. We also thank two external reviewers for their valuable suggestions and corrections on previous versions of this manuscript. This project was supported by Universidad Nacional de Mar del Plata, Fundación Antorchas (grant number 13900-13), ANPCyT (1-7213), and CONICET (PIP 2851; 165-01, all granted to O. Iribarne) and grants from the Andrew Mellon Foundation (to M. D. Bertness) and the National Science Foundation (to M. D. Bertness and B. R. Siliman). J. Alberti and M. Escapa were supported by doctoral scholarships from CONICET.

LITERATURE CITED

- Bach, C. E. 1994. Effects of a specialist herbivore (*Altica subplicata*) on *Salix cordata* and sand dune succession. *Ecological Monographs* 64:423–445.
- Belliveau, S. A., and V. J. Paul. 2002. Effects of herbivory and nutrients on the early colonization of crustose coralline and fleshy algae. *Marine Ecology Progress Series* 232:105–114.
- Berkowitz, A. R., C. D. Canham, and V. R. Kelly. 1995. Competition vs. facilitation of tree seedling growth and survival in early successional communities. *Ecology* 76:1156–1168.
- Bertness, M. D. 1991. Interspecific interactions among high marsh perennials in a New England salt marsh. *Ecology* 72:125–137.
- Bertness, M., and R. M. Callaway. 1994. Positive interactions in communities. *Trends in Ecology and Evolution* 9:191–193.
- Bertness, M. D., and S. D. Hacker. 1994. Physical stress and positive associations among marsh plants. *American Naturalist* 144:363–372.
- Bertness, M. D., and G. H. Leonard. 1997. The role of positive interactions in communities: lessons from intertidal habitats. *Ecology* 78:1976–1989.
- Bertness, M. D., and S. W. Shumway. 1993. Competition and facilitation in marsh plants. *American Naturalist* 142:718–724.
- Bortolus, A., and O. O. Iribarne. 1999. The effect of the southwestern Atlantic burrowing crab *Chasmagnathus granulata* on a *Spartina* salt-marsh. *Marine Ecology Progress Series* 178:79–88.
- Bruno, J. F. 2000. Facilitation of cobble beach plant communities through habitat modification by *Spartina alterniflora*. *Ecology* 81:1179–1192.
- Bruno, J. F., J. J. Stachowicz, and M. D. Bertness. 2003. Inclusion of facilitation into ecological theory. *Trends in Ecology and Evolution* 18:119–125.
- Bryant, J. P. 1987. Feltleaf willow–snowshoe hare interactions: plant carbon/nutrient balance and floodplain succession. *Ecology* 68:1319–1327.
- Callaway, R. M., D. Kikodze, M. Chiboshvili, and L. Khetsuriani. 2005. Unpalatable plants protect neighbors from grazing and increase plant community diversity. *Ecology* 86:1856–1862.
- Callaway, R. M., Z. Kikvidze, and D. Kikodze. 2000. Facilitation by unpalatable weeds may conserve plant diversity in overgrazed meadows in the Caucasus Mountains. *Oikos* 89:275–282.
- Callaway, R. M., and L. R. Walker. 1997. Competition and facilitation: a synthetic approach to interactions in plant communities. *Ecology* 78:1958–1965.
- Callaway, R. M., et al. 2002. Positive interactions among alpine plants increase with stress. *Nature* 417:844–848.
- Chase, J. M., M. A. Leibold, A. L. Downing, and J. B. Shurin. 2000. The effects of productivity, herbivory, and plant species turnover in grassland food webs. *Ecology* 81:2485–2497.
- Clements, F. E. 1916. Plant succession: an analysis of the development of vegetation. Carnegie Institution of Washington, Washington, D.C., USA.
- Connell, J. H., and R. O. Slatyer. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. *American Naturalist* 111:1119–1144.
- Conover, W. J. 1980. Practical nonparametric statistics. Second edition. Wiley, New York, New York, USA.
- Costa, C. S. B., and A. J. Davy. 1992. Coastal saltmarsh communities of Latin America. Pages 179–199 in U. Seeliger, editor. Coastal plant communities of Latin America. Academic Press, New York, New York, USA.
- Costa, C. S. B., J. C. Marangoni, and A. M. G. Azevedo. 2003. Plant zonation in irregularly flooded salt marshes: relative importance of stress tolerance and biological interactions. *Journal of Ecology* 91:951–965.
- Ervin, G. N. 2005. Spatio-temporally variable effects of a dominant macrophyte on vascular plant neighbors. *Wetlands* 25:317–325.
- Fagan, W. F., and J. G. Bishop. 2000. Trophic interactions during primary succession: herbivores slow a plant reinvansion at Mount St. Helens. *American Naturalist* 155:238–251.
- Farrell, T. M. 1991. Models and mechanisms of succession: an example from a rocky intertidal community. *Ecological Monographs* 61:95–113.
- Gagnon, P., J. H. Himmelman, and L. E. Johnson. 2003. Algal colonization in urchin barrens: defense by association during recruitment of the brown alga *Agarum cribrosum*. *Journal of Experimental Marine Biology and Ecology* 290:179–196.
- Green, P. T., D. J. O'Dowd, and P. S. Lake. 1997. Control of seedling recruitment by land crabs in rain forest on a remote oceanic island. *Ecology* 78:2474–2486.
- Greenlee, J. T., and R. M. Callaway. 1996. Abiotic stress and the relative importance of interference and facilitation in montane bunchgrass communities in western Montana. *American Naturalist* 148:386–396.
- Halpern, B. S., K. Cottenie, and B. R. Broitman. 2006. Strong top-down control in southern California kelp forest ecosystems. *Science* 312:1230–1232.
- Harris, L. G., A. W. Ebeling, D. R. Laur, and R. J. Rowley. 1984. Community recovery after storm damage: a case of facilitation in primary succession. *Science* 224:1336–1338.
- Hay, M. E. 1986. Associational plant defenses and the maintenance of species diversity: turning competitors into accomplices. *American Naturalist* 128:617–641.

- Holmgren, M., M. Scheffer, and M. A. Huston. 1997. The interplay of facilitation and competition in plant communities. *Ecology* 78:1966–1975.
- Holzappel, C., and B. E. Mahall. 1999. Bidirectional facilitation and interference between shrubs and annuals in the Mojave Desert. *Ecology* 80:1747–1761.
- Huckle, J. M., J. A. Potter, and R. H. Marrs. 2000. Influence of environmental factors on the growth and interactions between salt marsh plants: effects of salinity, sediment and waterlogging. *Journal of Ecology* 88:492–505.
- Iribarne, O., A. Bortolus, and F. Botto. 1997. Between-habitat differences in burrow characteristics and trophic modes in the southwestern Atlantic burrowing crab *Chasmagnathus granulata*. *Marine Ecology Progress Series* 155:137–145.
- Iribarne, O., M. Bruschetti, M. Escapa, J. Bava, F. Botto, J. Gutiérrez, G. Palomo, K. Delhey, P. Petracci, and A. Gagliardini. 2005. Small- and large-scale effect of the SW Atlantic burrowing crab *Chasmagnathus granulatus* on habitat use by migratory shorebirds. *Journal of Experimental Marine Biology and Ecology* 315:87–101.
- Isacch, J. P., C. S. B. Costa, L. Rodríguez-Gallego, D. Conde, M. Escapa, D. A. Gagliardini, and O. O. Iribarne. 2006. Distribution of saltmarsh plant communities associated with environmental factors along a latitudinal gradient on the south-west Atlantic coast. *Journal of Biogeography* 33:888–900.
- Jefferies, R. L., A. P. Jano, and K. F. Abraham. 2006. A biotic agent promotes large-scale catastrophic change in the coastal marshes of Hudson Bay. *Journal of Ecology* 94:234–242.
- Kikvidze, Z., L. Khetsuriani, D. Kikodze, and R. M. Callaway. 2006. Seasonal shifts in competition and facilitation in subalpine plant communities of the central Caucasus. *Journal of Vegetation Science* 17:77–82.
- Kuijper, D. P. J., and J. P. Bakker. 2005. Top-down control of small herbivores on salt-marsh vegetation along a productivity gradient. *Ecology* 86:914–923.
- Kuijper, D. P. J., D. J. Nijhoff, and J. P. Bakker. 2004. Herbivory and competition slow down invasion of a tall grass along a productivity gradient. *Oecologia* 141:452–459.
- Lubchenco, J. 1980. Algal zonation in the New England rocky intertidal community: an experimental analysis. *Ecology* 61:333–344.
- Lubchenco, J., and B. A. Menge. 1978. Community development and persistence in a low rocky intertidal zone. *Ecological Monographs* 48:67–94.
- Manly, B. F. J. 1998. Randomization, bootstrap and Monte Carlo methods in biology. Second edition. Chapman and Hall, London, UK.
- Milchunas, D. G., and I. Noy-Meir. 2002. Grazing refuges, external avoidance of herbivory and plant diversity. *Oikos* 99:113–130.
- Miriti, M. N. 2006. Ontogenetic shift from facilitation to competition in a desert shrub. *Journal of Ecology* 94:973–979.
- Oesterheld, M., and M. Oyarzábal. 2004. Grass-to-grass protection from grazing in a semi-arid steppe: facilitation, competition, and mass effect. *Oikos* 107:576–582.
- Pennings, S. C., and R. M. Callaway. 1992. Salt marsh plant zonation: the relative importance of competition and physical factors. *Ecology* 73:681–690.
- Pugnaire, F. I., and M. T. Luque. 2001. Changes in plant interactions along a gradient of environmental stress. *Oikos* 93:42–49.
- Rand, T. A. 2004. Competition, facilitation, and compensation for insect herbivory in an annual salt marsh forb. *Ecology* 85:2046–2052.
- Shumway, S. W. 2000. Facilitative effects of a sand dune shrub on species growing beneath the shrub canopy. *Oecologia* 124:138–148.
- Silliman, B. R., J. van de Koppel, M. D. Bertness, L. E. Stanton, and I. A. Mendelsohn. 2005. Drought, snails, and large-scale die-off of southern U.S. salt marshes. *Science* 310:1803–1806.
- Stachowicz, J. J. 2001. Mutualism, facilitation and the structure of ecological communities. *Bioscience* 51:235–246.
- Teal, J. M. 1962. Energy flow in the salt marsh ecosystem of Georgia. *Ecology* 43:614–624.
- Tewksbury, J. J., and J. D. Lloyd. 2001. Positive interactions under nurse-plants: spatial scale, stress gradients and benefactor size. *Oecologia* 127:425–434.
- Valiela, I., J. M. Teal, and N. Y. Persson. 1976. Production and dynamics of experimentally enriched salt marsh vegetation: belowground biomass. *Limnology and Oceanography* 21:245–252.
- Van der Wal, R., M. Egas, A. Van der Veen, and J. Bakker. 2000. Effects of resource competition and herbivory on plant performance along a natural productivity gradient. *Journal of Ecology* 88:317–330.
- Zar, J. H. 1999. Biostatistical analysis. Fourth edition. Prentice-Hall, Upper Saddle River, New Jersey, USA.

APPENDIX

Statistical results for the effects of *Sarcocornia perennis* removal on herbivory and growth of two *Spartina densiflora* patch size classes (*Ecological Archives* E089-008-A1).