

Grazer facilitation of fungal infection and the control of plant growth in south-western Atlantic salt marshes

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Summary

1. While great effort has been made in documenting the processes that drive plant-induced susceptibility after herbivore attack and it is widely accepted that herbivores can facilitate plant diseases, the relative importance of this interaction in controlling plant growth in natural systems remains largely unexplored.

2. In south-western Atlantic salt marshes, we investigated the importance of disease after herbivory by examining: (i) whether or not a herbivorous crab facilitates disease (i.e. fungus infection) in marsh plants (*Spartina alterniflora* and *S. densiflora*) when clipping off small portions of leaves and (ii) the separate and interactive effects of crab grazing but fungal infection in controlling marsh plant growth.

3. Our results show that crab grazing facilitates fungal infection in *Spartina* leaves. A factorial field experiment shows that both direct crab herbivory and fungal infection strongly suppress plant production (by more than 50%).

4. *Synthesis.* These experimental results demonstrate that fungal infection following herbivory attack can decrease salt marsh plant production and that increased disease susceptibility can be a fundamental factor in controlling plant production in natural ecosystems, even in cases where herbivores do not directly inoculate the pathogen but only damage plant tissue.

Key-words: facilitation, fungal infection, herbivory, plant production, salt marshes, *Spartina*, top-down control

Introduction

Herbivore attack often results in carbon and nutrient removal from plants, indirectly affecting the plant's subsequent interactions with other consumers due to the alteration of the plant's quantity and quality as a food source (Thelen *et al.* 2005). The response of plants to herbivory damage can vary from induced defences (e.g. increased resistance or tolerance to future attack; Karban & Baldwin 1997) to induced susceptibility (e.g. decreased resistance or tolerance to future attack; Nykanen & Korechiva 2004). An extensive literature documents the changes in chemical composition, morphology, phenology, growth and photosynthetic capacity that ultimately drive both induced defences and susceptibility (see Karban & Baldwin 1997; Nykanen & Korechiva 2004). However, far less is known about the relative importance of these kinds of

interactions in controlling plant production in natural plant communities.

Pathogens and small herbivores often share the same plant host and thus, both can affect the food source of the other species (Hatcher & Paul 2000; Kruess *et al.* 2004; Silliman & Newell 2003). This generates the potential for strong interactions that can either dampen or strengthen their individual impacts. For example, pathogens can decrease herbivory by affecting the nutritional quality of plants or by segregating deterrent or toxic compounds (Hatcher 1995). Herbivores, in turn, can activate plant induced-defences that then reduce pathogen infection (Hatcher & Paul 2000; Paul *et al.* 2000; Hatcher *et al.* 2004). Besides dampening the intensity of each other's attack, disease organisms and small grazers can also interact in ways that enhance the other's top-down effects. For example, fungal infections in marsh plant tissues often act as targets that attract and intensify grazing (Silliman & Newell 2003), while herbivores in terrestrial systems can

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facilitate pathogen infection by transporting disease between plants, by inoculating disease propagules (Costa *et al.* 1976; Hohn 2007; Fraedrich *et al.* 2008) and facilitating disease infection in plant tissues by physically damaging plant protective barriers (Friedli & Bacher 2001; García-Guzmán & Dirzo 2001).

When mesograzers facilitate pathogen attacks by exposing plant tissues to infection, there is the potential for these grazers to exert a strong, indirect effect on plant communities which is greatly disproportionate to both their biomass and the mass of the live plant material they consume. Recent evidence from experiments in salt marshes in south-eastern United States investigating the nature of snail–fungal–plant interactions shows that the disease facilitation pathway of small grazers (that were previously thought to be detritivores and unimportant plant growth controllers) can indirectly exert strong top–down control of plant growth (see Silliman & Newell 2003). In these salt marshes, the small gastropod *Littoraria irrorata* grazes the surface of live salt marsh grasses (see Silliman & Zieman 2001; Silliman & Bortolus 2003). However, instead of directly eating the grass, the snails passively farm fungi in grazer-induced wounds on the surface of the live leaves (Silliman & Newell 2003). The marsh snails facilitate fungal infection in green leaves in two ways: (i) by exposing plant tissue to naturally occurring fungal spores through grazing of live leaf surfaces and (ii) by passively depositing faecal pellets containing spores in and around wounds. Their fully factorial experiment crossing snail and fungi presence showed that snails exert strong control on plant growth (commonly reducing it by 20–90%) and that almost 100% of this negative impact is due to the deleterious impacts of facilitated fungal infection and not snail consumption of live plant tissue (Silliman & Newell 2003). In this context, it is widely accepted that herbivores can spread diseases among plants (e.g. Costa 1976; Hohn 2007; Fraedrich *et al.* 2008) and be a key contributor to some catastrophic diseases (e.g. Costa 1976; Mamiya 1983; Paine *et al.* 1997; Rostás *et al.* 2003). This mechanism of disease spread, nevertheless, can be also an important way of controlling plant growth in systems where grazers do not necessarily inoculate the pathogen but only damage plant protective barriers. Thus, the herbivore–disease link can be important every time herbivores damage plant protective tissue.

The salt marshes occurring between southern Brazil (32°S) and northern Argentinean Patagonia (42°S) are dominated by *Spartina densiflora* and *S. alterniflora* (Isacch *et al.* 2006). In these marshes, the burrowing crab *Neohelice granulata* (= *Chasmagnathus granulatus*, family: Varunidae; for recent taxonomic revision see Sakai *et al.* 2006) is the dominant grazer similar to *L. irrorata* in the Northern hemisphere (see Silliman & Bortolus 2003). This crab (approximately 3–4 cm in carapace width) inhabits almost the entire intertidal zone, from the soft non-vegetated bottoms to the upper vegetated zones (Iribarne *et al.* 1997). *Neohelice granulata* is a herbivore–detritivore (e.g. Iribarne *et al.* 1997; Bortolus & Iribarne 1999) and stable-isotope analyses show that *Spartina* is its primary food source (Botto *et al.* 2005). This crab has been shown to

exert strong control over marsh plant production through its grazing activities (Bortolus & Iribarne 1999; Bortolus *et al.* 2004; Costa *et al.* 2003; Alberti *et al.* 2007). In marshes recovering after burning, for example, crabs can decrease aerial biomass of *S. densiflora* (primarily through consumption of young shoots) by up to 87% (Bortolus & Iribarne 1999) and in the boundaries between marsh and tidal creeks, nearly 60% of the leaves show herbivory damage (Alberti *et al.* 2007). During preliminary surveys of grazed plants in this system, we observed that the plant tissue immediately surrounding crab-produced wounds was senescent and distinctively brown and black in coloration, suggesting fungal infection following grazing activities. Thus, in addition to grazer control of marsh plant growth via biomass removal, these initial observations indicated that disease facilitation could also be a regulatory mechanism. In this study, we evaluate the hypothesis that fungal infection of marsh plant leaves depends on the generation of damaged leaves by grazing crabs and that this interaction is an important pathway, albeit indirect, by which crabs control marsh plant primary production.

Methods

To evaluate the relationship between the presence of crab-induced wounds and the extent of fungal infection in live marsh plant leaves, we collected leaves of the dominant plant species *S. alterniflora* and *S. densiflora* from four different salt marshes located along a 1500-km strip on the Argentinean coast: Mar Chiquita Lagoon (Argentina, 37°32'S), Bahía Samborombom (36°22'S), Bahía Blanca (38°41'S) and San Antonio Bay (40°45'S; see Isacch *et al.* 2006 for description) and scored them for both degree of crab damage and fungal infection. During January 2006, we collected green (i.e. live) leaves of both plant species at each site (except in Mar Chiquita where *S. alterniflora* does not occur). Given the difference in tidal amplitude between salt marshes, samples were taken from the middle height zone of each species in each marsh. We collected only one leaf per stem and, to avoid infected patches, stems from which leaves were sampled were separated by at least 3 m. We classified the leaves as either intact or with herbivore damage (i.e. characteristic removal of green tissue, see Alberti *et al.* 2007). We sampled 50 leaves from each class (i.e. leaves with and without crab herbivory damage) for each species and for each salt marsh. We evaluated the presence of infection by carefully inspecting each leaf under a binocular microscope (400×). We used this method of quantifying fungal infection (i.e. simply presence or absence) instead of a more complicated fungal biomass measurement, because preliminary observations indicated that once infected, a leaf eventually dies, so the presence of infection is a robust indicator of the impact of infection on the plant community (see also Silliman & Newell 2003). Leaves of each leaf class (i.e. intact or with crab herbivore damage) were then classified as infected or not infected. Fungal species were determined by one of us (N.P., as part of her Doctoral Dissertation at the National University of Mar del Plata, Argentina) based on their reproductive structures (following Kohlmeyer & Volkman-Kohlmeyer 1991). Given that no infection was found in intact leaves (see Results section), no analysis was necessary to evaluate the hypothesis of no differences in the proportion of infection between intact and crab herbivory-damaged leaves. The null hypothesis of no difference between marshes in the proportion of infected leaves damaged by crab herbivory was analysed with a chi-square test for each plant species (Zar 1999).

To experimentally evaluate the relationship between crab herbivory and fungal infection in green leaves, we conducted two field experiments at San Antonio Bay. This is an 80-km² embayment with 9 m semi-diurnal tides. The intertidal zone is characterized by sandy pebble flats at lower tidal elevations (i.e. 0–3 m above mean low tidal level, hereafter MLTL) and salt marshes dominated by the smooth cord grass *S. alterniflora* occurring higher on the intertidal slope (i.e. 3–10 m above MLTL). Both experiments were performed at approximately 5 m above MLTL (i.e. middle height zone of *S. alterniflora*) in a location near the town of San Antonio Oeste at the Western part of the bay.

To evaluate the relationship between leaf damage and infection, we randomly selected and marked (on 3 February 2006) live leaves: (i) with recent crab herbivory damage (but without senescent tissue surrounding the wound); (ii) without damage (i.e. control) and (iii) without damage, but on which an artificial cut similar to those produced by crabs was made ($n = 50$ per group). The artificial cuts were performed with scissors that were carefully washed with distilled water before and after each cut. Selected leaves were from different stems which were separated by at least 3 m. After 3 months, leaves were harvested and transported to the laboratory where we determined the number of leaves with infection in each group by careful inspection under an optic, binocular microscope (400 \times). The null hypothesis of no differences in the proportion of leaves infected in each group was analysed with a chi-square test (Zar 1999).

To evaluate the effect of the interaction between crab herbivory and fungal infection on *S. alterniflora* production, we performed a fully-factorial field experiment (starting on 3 February 2006). This experiment consisted of 28 plots (0.7 m \times 0.7 m) separated by at least 3 m. In 14 randomly chosen plots, we used a plastic mesh (10 mm opening) to exclude crabs; in the remaining 14 plots crabs were not excluded. In half ($n = 7$) of the plots of each treatment (exclusion and control crabs), plants were sprayed with the systemic fungicide Benomyl (I.Q.A. Chemical Industries, Buenos Aires, Argentina) every 30 days. For the treatment, the fungicide was dissolved in marsh channel water (1.5 g fungicide in 1 L of water, per plot, each month; salinity in the channel water was always around 33 ppt). The fungicide was carefully sprayed during the beginning of the low tide in days with low wind speed, thus minimizing the possibility of contamination of control plots. In the rest of the plots of each treatment ($n = 7$), plants were sprayed with channel water (as a procedural control for water input) every 30 days. Thus, the experiment consisted of a factorial design with two factors: (i) crab presence (two levels: control and crab removal) and (ii) fungi presence (two levels: no fungicide and fungicide application). In addition, cage controls ($n = 7$) that consisted of exclusion cages with two open walls (allowing crabs to move in and out) and without fungicide application were set up to test for caging artefacts. At the beginning of the experiment (i.e. base-line conditions), there were no differences in live stem density and the mean height of stems (estimated by averaging the height of five randomly chosen stems per plot) between different treatments (density: $F_{4,30} = 0.315$, $P = 0.87$; height: $F_{4,30} = 0.096$, $P = 0.98$; see Fig. 1). After 5, 10 and 16 months, we measured the number of live stems and the mean height of stems (estimated by averaging the height of five randomly chosen stems per plot) in a 0.5 \times 0.5 m square centred in each plot. After 16 months (29 May 2007), we harvested the above-ground biomass, dried it for 72 h at 60 °C and then weighed it. The null hypotheses of no effect of crabs and fungi removal on stem height and density along the experiment were evaluated with a repeated-measures ANOVA with crab presence and fungus presence as main factors and time as repeated measurement factor. The null hypotheses of no effect of

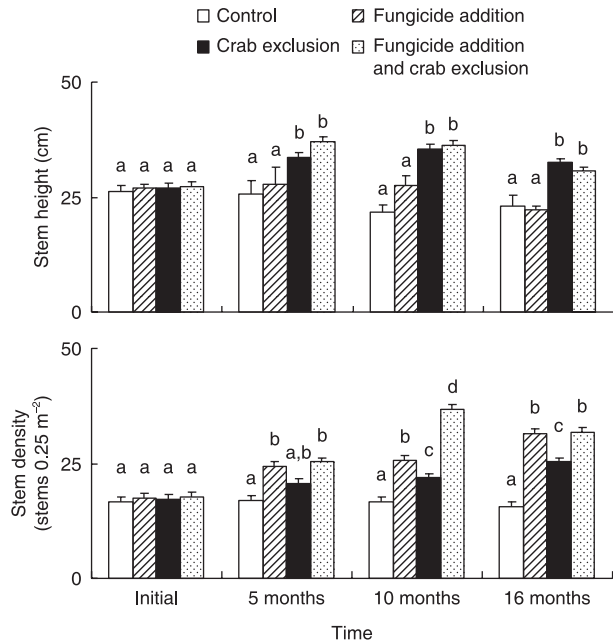


Fig. 1. Effect of crab herbivory and fungal infection on *Spartina alterniflora* stem height and density in a manipulative experiment. Bars represent mean values and standard deviations. Different letters indicate significant differences ($P < 0.05$, $n = 7$) after Tukey test.

crabs and fungi removal on dead, live and total plant biomass between treatments were analysed with a two-way ANOVA (Zar 1999) with crab presence and fungus presence as main factors. The null hypothesis of no cage effect on the measured variables was evaluated by conducting a t -test between control plots (i.e. without crab exclusion and without fungicide application) and cage controls.

To evaluate if fungicide application affected crab herbivory (i.e. if fungicide application affected leaf preference of crabs), differences in the proportion of leaves with herbivory marks between control treatments and fungicide treatments (both without cages) were evaluated with a t -test (Zar 1999). To evaluate the efficiency of the fungicide in suppressing fungal infection, on 3 February 2006, we marked 68 leaves with recent herbivory marks and sprayed them every month as explained above. In addition, as a procedural control, we marked 50 leaves with recent herbivory marks but sprayed them with channel water. After 5 months, we collected the leaves and measured fungal infections as explained above. The null hypothesis of no difference in infection between leaves sprayed with fungicide and with channel water was analyzed with a chi-square test (Zar 1999).

Results

In all sampled salt marshes, fungal infection was associated with herbivory damage. Neither plant species showed infections in live undamaged leaves, while live leaves with damage from crab herbivory showed a high proportion of infection (36% for *S. alterniflora* and 23% for *S. densiflora*); there was no difference between salt marshes (*S. alterniflora*: Bahía Samborombom: 30% (15 of 50); Bahía Blanca: 34% (17 of 50); and San Antonio Bay: 48% (24 of 50); $\chi^2 = 3.57$, d.f. = 2, $P > 0.1$; *S. densiflora*: Bahía Samborombom: 30%

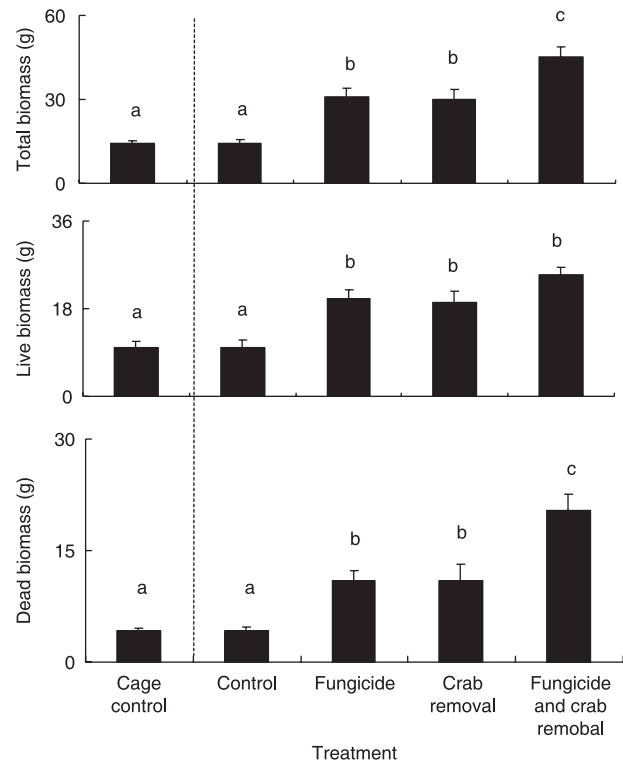
Table 1. Repeated-measures ANOVA of the effect of crab exclusion (Crab effect) and fungi removal (Fungicide effect) on *Spartina alterniflora* stem density and height at three sampling dates (Time)

Source	d.f.	MS	F	P
Stem density				
Crab effect (C)	1	586.71	15.83	< 0.001
Fungicide effect (F)	1	2060.19	55.60	< 0.00001
C × F	1	29.76	0.80	0.38
Error	24	37.06		
Time (T)	2	131.05	3.65	< 0.05
T × C	2	60.14	1.67	0.2
T × F	2	80.19	2.23	0.1
T × C × F	2	116.33	3.24	< 0.05
Error	48	35.90		
Stem height				
Crab effect (C)	1	1914.30	129.50	< 0.00001
Fungicide effect (F)	1	54.51	3.69	0.07
C × F	1	12.45	0.84	0.4
Error	24	14.78		
Time (T)	2	120.76	9.33	< 0.0005
T × C	2	15.94	1.23	0.3
T × F	2	46.51	2.59	0.08
T × C × F	2	16.64	1.28	0.3
Error	48	12.94		

(15 of 50); Bahía Blanca: 16% (8 of 50); San Antonio Bay: 20% (10 of 50); Mar Chiquita: 28% (14 of 50); $\chi^2 = 3.64$, d.f. = 3, $P > 0.05$). The fungus infecting the leaves was the same in all salt marshes and on both plant species, and was identified as the ascomycete *Phaeosphaeria spartinicola* Leuchtman, the same species found in snail-induced wounds on salt marsh grasses in the southern United States (see Silliman & Newell 2003).

Experimental results showed that fungal infection is associated with crab-induced leaf damage. After 3 months, most of the marked leaves that either suffered from natural herbivory or were experimentally damaged were infected (natural herbivory: 43 of 50; experimental damage: 39 of 50, respectively; $\chi^2_{(Yates\ correction)} = 0.6$, d.f. = 1, $P > 0.1$), whereas no intact leaves were infected.

The experiment designed to test for the effect of this interaction on marsh plant production showed that both crab herbivory and fungal infection negatively affected plant growth and that, combined, both factors control plant production. Fungicide application reduced by more than 50% (i.e. from 0.62 to 0.31) the proportion of leaves with fungal infection in grazer-induced wounds (fungicide application: 21 of 68, control: 31 of 50 leaves infected; $\chi^2_{(Yates\ correction)} = 10.09$, d.f. = 1, $P < 0.05$) and did not influence herbivory ($t = 0.43$, d.f. = 13, $P = 0.67$). Crab exclusion increased the height of *S. alterniflora* during the experiment (see Table 1), whereas both crab exclusion and fungicide addition increased stem density (see Table 1). At the end of the experiment, crab exclusion positively affected stem height (approximately 40% increase), but there was no effect of fungicide addition or an interaction between treatments (see Fig. 1). For stem density, however, there was a strong interaction between the two factors, and

**Fig. 2.** Effect of crab herbivory and fungal infection on above-ground biomass of *Spartina alterniflora* after a 16-month factorial experiment in the field. Bars represent mean values and standard deviations. Bars at the right of the dashed line correspond to treatments included in the two-way ANOVA. Different letters indicate significant differences ($P < 0.05$, $n = 7$) after Tukey test.

the effect of crab grazing was dependent on the application of fungicide (Fig. 1); in plots without fungicide, crab exclusion increased stem density by over 95%, but in plots where fungi were removed, crab removal had no additive impact on density of *S. alterniflora* stems (Tukey test; see Fig. 1). Both fungal removal and crab exclusion (separately) increased by nearly 100% total above-ground biomass (Fungicide: $F_{1,24} = 39.72$, $P < 0.0001$; Crab: $F_{1,24} = 35.79$, $P < 0.0001$; Fungicide × Crab: $F_{1,24} = 0.1$, $P > 0.7$), dead standing above-ground biomass (log-transformed data, Fungicide: $F_{1,24} = 23.57$, $P < 0.0001$; Crab: $F_{1,24} = 20.78$, $P < 0.0001$; Fungicide × Crab: $F_{1,24} = 0.71$, $P > 0.4$) and green live biomass (Fungicide: $F_{1,24} = 22.02$, $P < 0.0001$; Crab: $F_{1,24} = 17.14$, $P < 0.0001$; Fungicide × Crab: $F_{1,24} = 1.62$, $P > 0.2$; see Fig. 2). Although no significant interaction was found on biomass, there were trends that followed the significant interaction seen on stem density as crab exclusion increased live biomass by approximately 100% in plots with fungal leaf infections (i.e. crab removal vs. control plots) but only by approximately 30% in plots where fungicide was applied (i.e. crab removal and fungicide application vs. fungicide application; see Fig. 2). There were no differences in any measured variables between unmanipulated controls and cage controls (total biomass: $t = 0.24$, d.f. = 12, $P > 0.8$; live biomass: $t = 0.77$, d.f. = 12, $P > 0.4$; dead biomass: $t = 0.04$, d.f. = 12, $P > 0.9$; see Fig. 2).

Discussion

Our experimental study reveals that crabs can control plant growth both by live biomass consumption and also by facilitating fungal infection in grazer-induced wounds. When grazing marsh plants, crabs sometimes clip the tips of the leaves, but more often they remove biomass from the middle part of a leaf. Thus, direct crab impacts on plant biomass and height is probably due to mechanical reduction of biomass and subsequent growth decrease. In addition, the fungal infection that occurs after crab herbivory and that seems to only depend on plant damage greatly reduces stem density by increasing mortality of individual shoots. Herbivory by crabs may thus directly affect plant biomass by affecting stem size, whereas secondary fungal infection may affect biomass by affecting stem mortality. The overall effect of grazer consumption and fungal infection on this plant is to decrease the above-ground biomass of more than 60%.

Given logistical constraints, we performed these experiments only at the intermediate marsh elevations. However, as the abundance of the fungus, *P. spartnicola*, is not related to tidal elevation (Newell & Wasowski 1995) and crab herbivory is higher at lower tidal elevations (Alberti *et al.* 2007), where an even higher effect may be expected in the low marsh areas. In the high marsh, although crab damage is less common, other sources of plant damage, such as herbivory by small mammals (Kujiper & Bakker 2005; Canepuccia *et al.* 2008) or physical damage by wrack (Brewer *et al.* 1998) are often more frequent and thus plants at these higher elevations may also be infected with the fungus.

The experimental results support the idea that the interaction between herbivores and diseases can affect natural plant communities, an interaction that has long been hypothesized to exist (Friedli & Bacher 2001; García-Guzmán & Dirzo 2001), but which has been experimentally demonstrated in the field only once (i.e. Silliman & Newell 2003). The results indicate that by increasing disease incidence in injured tissue small herbivores can elicit an indirect control over plant production that is greatly disproportionate to the grazers' own biomass (or the amount of plant material they eat). Combined with similar findings in US marshes, these grazer-disease studies reveal that this interaction is a general regulatory mechanism of top-down control in marsh plant communities that transcends both divergent grazer taxa (snails – Silliman & Newell 2003 and crabs – this study), different plant species (*S. densiflora* and *S. alterniflora*) and large geographic distances (North and South America). Our results also show that the herbivore-disease link can be an important control mechanism of plant growth even when grazers do not directly inoculate the pathogens that are responsible for the disease but only damage the plant tissue or, in other words, every time a herbivore attacks a plant.

There is increasing evidence of the dependence of plant pathogen colonization and success on small herbivores that share the same plant host. Insects, for example, can increase fungal, viral, or bacterial infection in a variety of environments, especially when they graze young leaves (see Terhune *et al.*

1991; García-Guzmán & Dirzo 2001). This interaction seems to be so widespread that plants, to avoid pathogen attack and future higher biomass losses, will often abscise young damaged leaves when insect grazing is at moderate to high levels (Blundell & Pearl 2000). In north-western Atlantic saltmarshes, radulation scars generated on live marsh grass by the snail *L. irrorata* combined with spore deposition via faecal pellets, increases fungal infection in live *S. alterniflora* tissue by more than 170% (Silliman & Newell 2003). Similarly, in south-western Atlantic saltmarshes, these experiments show that tissue damaged by crab grazing activities is a common entry point for fungal infections of live leaves. Our results show that there was no interaction between crab exclusion and fungicide application affecting plant biomass (but there was a strong interaction for stem density and a strong trend for biomass), apparently indicating that fungi have another way (other than crab damage) to infect plants. Both field sampling and experiments, however, show that undamaged leaves were not infected, suggesting that the increase in plant biomass when crabs were excluded and fungicide was applied did not occur because fungal infection in live leaves commonly occurs without damage. Exclusion cages are not totally effective in reducing crab herbivory, but they reduce herbivory by at least 60% (see Alberti *et al.* 2008). Thus, small crabs, other herbivores or even other physical causes may have caused some damage in exclusion plots that, combined with initial crab damage on leaves at the beginning of the experiment, may have caused some infection in exclusion plots during the experiment. In this likely case scenario, fungicide application would have benefited plants even in the absence of crabs, but fungal infection would still be reliant on mechanical opening of live plant tissue by some physical or biological agent. Although fungicide application may also have some positive effect on plant growth by affecting other pathogenic fungi that we did not detect, there is clear experimental evidence that crab damage of plant tissue facilitates fungal infection and that this infection drives significant decrease in marsh plant biomass.

Productive plant communities (e.g. tropical forests and grasslands; see Wardle & Bardgett 2004) have long been considered to be weakly controlled by grazers. On average, in terrestrial systems, only 18% of plant biomass is consumed by herbivores (Cyr & Pace 1993). In grasslands, for example, invertebrate herbivory is usually considered to be unimportant (Wardle & Bardgett 2004) because it is hypothesized that, under normal conditions, phytophagous populations are low due to predator control (Hairston *et al.* 1960), or because grasses are a poor quality food (White 1978; Augner 1995). In salt marshes, however, it is now recognized that invertebrate grazers can have large effects on plant biomass, commonly suppressing plant growth by 20–90% (Bortolus & Iribarne 1999; Silliman *et al.* 2005). This study demonstrates that herbivore facilitation of disease can control salt marsh plant production and that small herbivores and diseases may be interacting to exert important, indirect control over natural plant communities even in systems where herbivores do not directly inoculate the disease but only damage plant tissue.

This disease control may be especially important in systems where spores or propagules are very abundant and self-dispersed as is the case with the fungus *P. spartanicola* (see Newell & Wasowski 1995) and where plant damage, generated by herbivory or other causes, is widespread. *Phaeosphaeria spartanicola* is known to be one of the principal detritivores in salt marshes and the major microbial secondary producer (see Newell & Wasowski 1995) and is thus not an obligate pathogen but a decomposer that may infect wound sites and affect plants by the lysis of structural tissues. Its capacity of growth on decaying material may indeed generate the higher abundance of propagules and contribute to the fungus' impact on live plant growth. Moreover, monocultures or single-species stands (as observed in salt marshes) may be especially sensitive to this interaction (as well as to other diseases; see Shipton 1977) because of the higher horizontal transmission. Monocotyledons (as *S. alterniflora* and *S. densiflora*) are commonly physically protected and have a less specific chemical response than dicotyledons (McNaughton 1979); induced susceptibility may therefore be more important in this group than induced defence. Finally, as both grazing rates and fungal growth are expected to increase in some instances with increased temperature and nutrient inputs to coastal waters due to global climate change (Ayres & Lombardero 2000), this interaction could become an even more important forcing factor controlling patterns of plant ecosystems and the key services they provide.

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