



The dynamics of bottom–up and top–down control in a New England salt marsh

N. M. Sala, M. D. Bertness and B. R. Silliman

N. M. Sala (sala.nicolas@gmail.com) and M. D. Bertness, Dept of Ecology and Evolutionary Biology, Brown Univ., Providence, RI 02912, USA. – B. R. Silliman, Dept of Zoology, Univ. of Florida, Gainesville, FL 32611, USA.

Traditionally, salt marsh ecosystems were thought to be controlled exclusively by bottom–up processes. Recently, this paradigm has shifted to include top–down control as an additional primary factor regulating salt-marsh community structure. The most recent research on consumer impacts in southern US marshes has shown that top–down forces often interact with biotic and abiotic factors, such as secondary fungal infection in grazer-induced wounds, soil nutrients and climatic variation, to influence ecosystem structure. In a more northern salt marsh, located in New England, we examined the separate and interactive effects of nutrient availability, insect herbivory and secondary fungal infection, on growth of the foundation species, *Spartina alterniflora*. We used a factorial design with two levels of nutrients (control and addition) insects (control and removal) and fungi (control and removal). Nutrient addition increased plant biomass by 131% in the absence of herbivores. When insect consumers were allowed access to fertilized plots, biomass was reduced by nearly 45% when compared with treatments with nutrients and insecticide. In contrast, insect herbivores did not affect plant biomass in unfertilized control treatments. These differences suggest that consumer effects are triggered under high nutrient levels only. We also found that secondary fungal infections in grazer-induced wounds, in contrast to lower latitude marshes, did not significantly impact primary production. Our results suggest that while New England salt marshes may typically be under bottom–up control, eutrophication can trigger dual control with inclusion of top–down regulation. However, unlike lower latitude marshes, consumer control of plant growth in northern US salt marshes is not dependent on herbivores facilitating fungal infections that then control grass growth, suggesting that the intensity of disease mediated top–down control by small grazers may be regulated by climate and/or grazer identity that co-vary with latitude.

Ecologists have long debated the role that trophic interactions have in determining the distribution and abundance of organisms (Hairston et al. 1960, Power 1992). Some ecologists believe that ecosystems are solely controlled by bottom–up processes (nutrients and productivity), which in turn, regulate ecosystem trophic structure. In contrast, others believe that consumers have a more important role in structuring ecosystems. Hairston et al. (1960) pioneered this idea by stating that because plants are abundant and largely intact, it is usually not the case that herbivores are food limited. The argument follows that the world is green because of the action of predation controlling herbivore abundance. Critics argue that the world is not always green and that, when it is green, it does not mean that herbivores do not play an important role in structuring plant communities (Ehrlich and Birch 1967). Others correctly point out that what is green is not necessarily edible or is of sufficiently high quality to allow increases in herbivore populations (Dixon 1966, Murdoch 1966). This debate has led to a plethora of field experiments designed to test these hypotheses in most major habitats (Sih et al. 1985), with salt marshes being no exception.

Historically, the prevailing view of salt marsh ecosystems was that consumers played an insignificant role in shaping trophic structure (Odum and Smalley 1959, Smalley 1960, Teal 1962, Marples 1966). More recent work, however, has challenged this view and emphasized the importance of consumers and interactions with other biotic and abiotic factors. Jefferies (1997) showed how populations of snow geese, fueled by agriculture subsidies, have led to tens of thousands of hectares of sub-arctic marshes being stripped of vegetation. Similarly, Silliman and colleagues showed that native snails graze live salt marsh plants (Silliman and Zieman 2001), that drought stress triggers intensified grazing by snails (*Littoraria irrorata*, Silliman et al. 2005) and that both factors were culprits in the dieback of over 250 000 acres of southeastern US marshes. Interestingly, the process by which snails exert control over marsh grass is not primarily through herbivory but via secondary fungal infections in grazer-generated scars in leaf tissue (Silliman and Newell 2003).

Fungi and insects are the most abundant and diverse groups of consumers of plants (Hatcher et al. 1997). Insects have been shown to affect almost every aspect of plant

performance including, plant growth, form, seed production, survivorship and development rate (Crawley 1989). In salt marshes, insects have the potential to exert strong control on *Spartina alterniflora* reproduction and productivity (Bertness 1987, Bertness and Shumway 1992, Daehler and Strong 1995). In the cases where insects have been shown to suppress primary productivity, it is not clear whether the mechanism of control is directly through insect consumption of live plant tissue or indirectly through facilitation of fungal infection in grazer-induced wounds. In addition, it is not clear how important eutrophication is to increasing the vulnerability of cordgrass to consumer suppression by insects. Understanding the magnitude and mechanism of top-down control by insects on *Spartina* growth and how the intensity of insect control varies with other biotic and abiotic drivers affecting the functioning of salt marshes was the primary objective of this research.

Elucidating the processes that control the structure of salt marsh ecosystems is critical given the important services that they provide to coastal systems. Currently in North America, the bottom-up paradigm has been shown not to be the sole mechanism through which salt marshes are controlled in the Gulf Coast and southeastern US marshes as well as northern Canada (Jefferies 1997, Silliman and Zieman 2001, Silliman and Bertness 2002, Silliman and Newell 2003, Silliman and Bortolus 2003, Silliman et al. 2005). To examine the relative effects that top-down, bottom-up and grazer-facilitation of fungal infections have in regulating the structure of New England salt marshes, we designed a multi-factorial field experiment in which we controlled for insects, nutrients and fungal infection with the differential application of insecticide, fungicide and fertilizer.

Material and methods

Study site

The experiment was carried out from June to September 2006, on Prudence Island, Narragansett Bay, Rhode Island, USA, part of the Narragansett Bay National Estuarine Research Reserve. The study site was a relatively low impacted marsh (Silliman and Bertness 2004), ditched in the early 20th century. The experiment was done in the low zone of the marsh dominated by monospecific stands of the cordgrass *Spartina alterniflora*, ~50–70 cm tall.

Experimental design

We used a multi-factorial design in the experiment with two levels of nutrient availability (nutrient addition 'N' and control), two levels of fungal infection (fungicide application 'F' and control), and two levels of insect herbivory (insecticide application 'I' and control). All combinations of these factors yielded eight treatments: C (control), N, F, I, N+F, N+I, F+I, N+I+F. Each treatment was replicated eight times, resulting in a total of 64 plots. All plots were 0.5 × 0.5 m and initially had similar vegetation density and height as determined by preliminary data collection.

We maintained fertilization treatments by adding 40 g m⁻² of turf builder (N-P-K: 29-3-4) fertilizer every two weeks starting on 3 June. Fungicide treatments were maintained by applying a broad-spectrum fungicide (active ingredient: chlorothalonil 54%) every 10–12 days (at a dosage of 1.43 and 2.86 cm³ m⁻²) under clear and low wind conditions. This fungicide is effective in suppressing fungal growth in marsh grass, but does not show deleterious effects on grazing by mesograzers or *Spartina* growth (Silliman and Newell 2003). Insect herbivory was controlled using a nursery insecticide (active ingredient: cyfluthrin 0.7% and imidacloprid 2.94%), a broad-spectrum foliar systemic insecticide. Insecticide was applied monthly (at 1.45 cm³ m⁻²) on clear days during low neap tides to prevent contact with water. The applied insecticide showed no significant deleterious effects on plant growth as evidenced when comparing control + insecticide treatments with insect excluding cages ($p > 0.26$, t-test). The cages, built out of metallic mesh, were 1 × 1 m and replicated three times. They were in the field for the duration of the experiment.

Response variables

We chose three response variables to assess treatment effects: insect damage, aboveground plant biomass, and insect densities.

Insect damage

Insect damage surveys were done at three-week intervals (25 June, 16 July, 8 August and 4 September). For each survey, three random stems were selected from each plot. Given the large number of leaves to be analyzed, we developed a similar method to Robertson and Duke (1987), in which we rapidly and visually estimated damage, i.e. on a scale from 0–10 (10 as complete damage – i.e. leaf clipped or completely shredded). We estimated area mottled, linked with damage from the leafhopper *Prokelisia marginata*. We also estimated area shredded, linked with damage from the grasshopper *Conocephalus spartinae*. Finally, we estimated area affected by fungal infections.

Aboveground biomass

Aboveground biomass was sampled monthly (1 July, 2 August, 4 September) using a 10 × 10 cm quadrant. Plants were clipped with scissors 1 cm from the ground. In the lab, plants were dried at 60°C for 48 h and weighed.

Insect surveys

Insect surveys were done in insecticide and fertilizer treated plots on 16 July and 8 August. Plots were sampled by using a method similar to that used by Vince et al. (1981). We swept an insect net (38 cm Ø) three times in the plot and then counted the number of insects captured, mainly grasshoppers and leafhoppers. Results from the two survey results were averaged for analysis.

Statistical analysis

The normality assumption was tested using a Q–Q normal plot followed by a Shapiro–Wilks test modified by Mahibbur and Govindarajulu (1997). The homogeneity of variance assumption was tested using a dispersion graph of the residuals as a function of the predicted values followed by a Levene test. In the case that any of the assumptions failed, data were transformed to their natural log and the assumptions were tested on the transformed data. After all needed transformations were done, all data exhibited homogeneity of variance and normality. Factors and their interactions in time were tested using a three-way repeated measures ANOVA (From now on RMANOVA). The sphericity assumption was tested in this analysis.

Results

Insect and fungal damage Surveys of the direct effects of insects on plants (mottled and shredding damage, Fig. 1 and 2, respectively) revealed that time ($p < 0.001$ mottled, $p = 0.014$ shredding, RMANOVA), nutrients ($p = 0.004$ mottled, $p < 0.001$ shredding, RMANOVA) and insecticide ($p = 0.004$ mottled, $p = 0.037$ shredding, RMANOVA) were significant factors throughout the experiment, and that damage was dependent on the interaction between nutrients and insecticide ($p < 0.001$ mottled, $p = 0.01$ shredding, RMANOVA). Further interpretation of the results from the RMANOVA revealed that nutrients enhanced insect damage, insecticide reduced it, and that there is an interaction between nutrients and insecticide, so that when the level of nutrients was high and there was insecticide applied, damage was low. In addition, the RMANOVA indicated that there was no effect

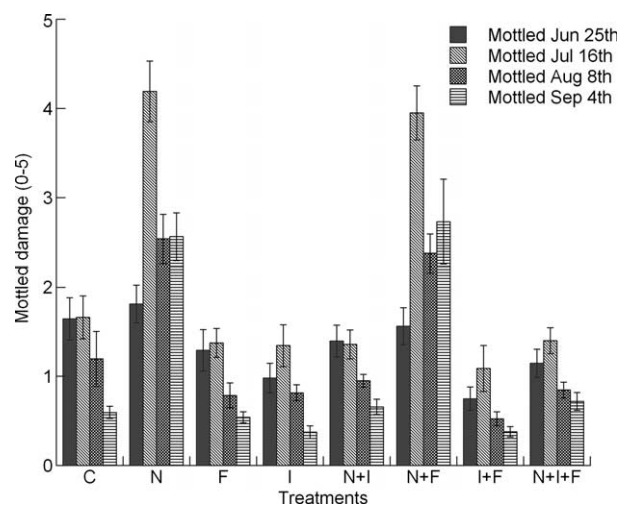


Figure 1. Effect of N fertilization, insecticide and fungicide additions on leaf area mottled of *Spartina alterniflora*, at four sampling dates (25 June, 16 July, 8 August, 4 September). 0 indicates no damage, and 5 indicates 50% of leaf area affected. Nutrients ($p = 0.004$, RMANOVA), insecticide ($p = 0.004$, RMANOVA), and the interaction between nutrients and insecticide ($p < 0.001$, RMANOVA) were significant factors throughout the experiment. Vertical bars represent ± 1 SE.

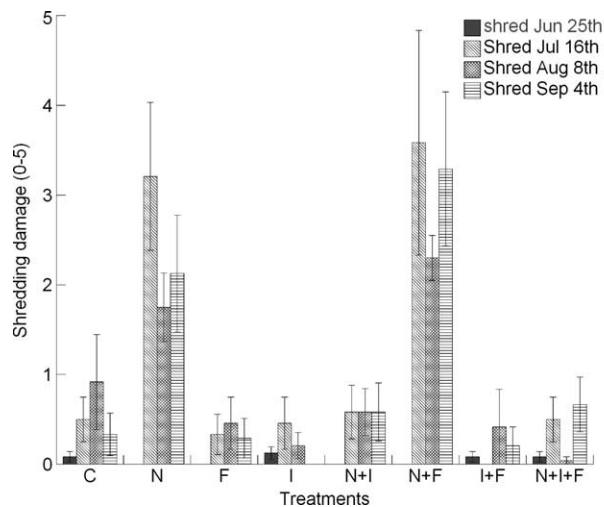


Figure 2. Effect of N fertilization, insecticide and fungicide additions on leaf area shredded of *Spartina alterniflora*, at four sampling dates (25 June, 16 July, 8 August, 4 September). 0 indicates no damage, and 5 indicates 50% of leaf area affected. Nutrients ($p < 0.001$, RMANOVA), insecticide ($p = 0.037$, RMANOVA), and the interaction between nutrients and insecticide ($p = 0.01$, RMANOVA) were significant factors all through out the experiment. Vertical bars represent ± 1 SE.

of fungicide on fungal damage (Fig. 3), as this factor ($p = 0.09$, RMANOVA) and its interactions were not significant ($p > 0.05$ for all interactions, RMANOVA). The patterns previously mentioned were pronounced the most when comparing the means of the different treatments at the last sampling date (4 September). For example, mottled scars (Fig. 1) in nutrient addition treatments were 430% higher than in control treatments, and 680% higher than in insecticide addition treatments. Shredding damage (Fig. 2) followed the same pattern as mottling

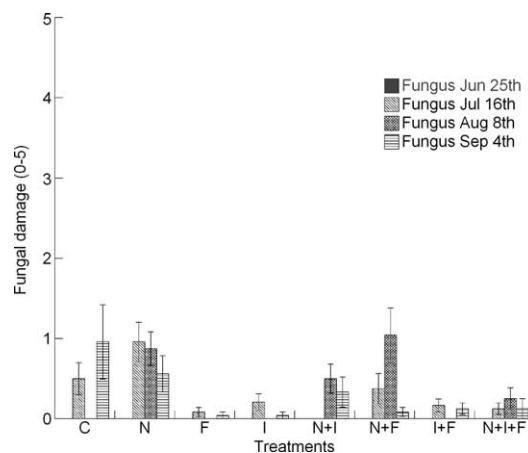


Figure 3. Effect of N fertilization, insecticide and fungicide additions on leaf area affected by fungal infections of *Spartina alterniflora*, at four sampling dates (25 June, 16 July, 8 August, 4 September). 0 indicates no damage, and 5 indicates 50% of leaf area affected by fungal infections. There were no significant factors or significant interactions between factors ($p > 0.05$, RMANOVA) throughout the experiment. Vertical bars represent ± 1 SE.

damage; in the last sampling date, scars in nutrient addition treatments were 640% higher than in control treatments.

Aboveground biomass

Biomass decreased coincident with high insect damage on *Spartina alterniflora* (Fig. 4). The magnitude of this top-down effect on aboveground biomass was again dependent on the significant interaction between nutrients and insecticide ($p = 0.002$, RMANOVA). In addition, the repeated measures ANOVA showed that time and nutrients were significant ($p < 0.001$ for both cases, RMANOVA) factors affecting *Spartina* biomass throughout the season. Further interpretation of the data reveals that nutrients significantly promoted growth, and that the interaction between nutrients and insecticide enhanced growth to an even greater degree when both were added together. In addition, we can interpret that fungal infections played no appreciable role in determining plant biomass, as the factor was not significant for biomass ($p = 0.25$, RMANOVA). Treatment effects were stronger as the season progressed as revealed when comparing different sampling dates. For example, differences between treatments with nutrients and treatments with nutrients and insecticide went from 51% in the first harvest, to 65% in the second harvest, to 81% in the final harvest. The differences were even greater when comparing nutrient and insecticide addition treatments with control treatments; differences were 98%, 125% and 137%, from the first sampling date to the last.

Insect surveys

Surveys of insect assemblages revealed two feeding-strategy types: chewers and sapsuckers. Each feeding type was overwhelmingly represented by a single species. The

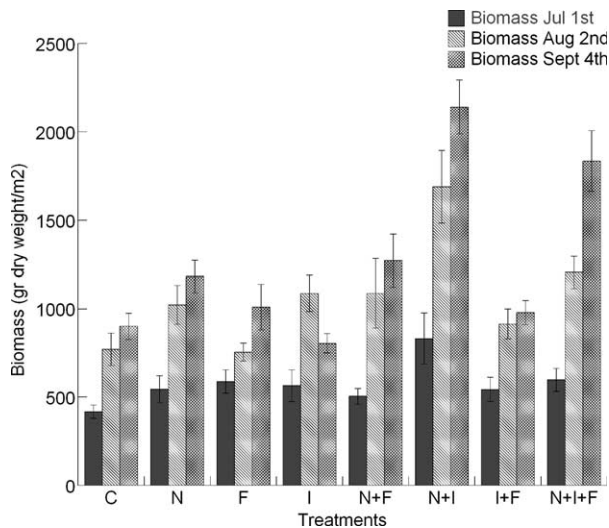


Figure 4. Effect of N fertilization, insecticide and fungicide additions on the aboveground biomass (g m^{-2}) of *Spartina alterniflora*, at three different harvests (1 July, 2 August, 4 September). Nutrients ($p < 0.001$ RMANOVA) and the interaction between nutrients and insecticide ($p = 0.002$ RMANOVA) were significant factors throughout the experiment. Vertical bars represent ± 1 SE.

chewers, whose feeding type is associated with shredding damage, were grasshoppers and grasshopper nymphs of the species *Conocephalus spartinae*; these insects were significantly ($p < 0.001$, ANOVA) more abundant in N treatments (Fig. 5). Their densities decreased from an average of 19.5 per plot/three sweeps in N treatment to only 5 per plot/three sweeps in control treatments. Sapsuckers, whose feeding damage is associated with mottling damage, were mainly represented by leafhoppers of the species *Prokelisia marginata*. Individuals of this species were significantly ($p < 0.001$, ANOVA) most abundant in control treatments, with an average density of 20.2 per plot/three sweeps compared to 8.8 per plot/three sweeps in N treatments.

Discussion

Our experimental results showed that New England salt marshes shifted from being controlled by bottom-up processes alone under low nutrient levels, to being controlled by both bottom-up and top-down processes, under high nutrient levels. Evidence for bottom-up dominance under pristine, low nutrient levels, is suggested by the result showing little or no impact of removing insects under ambient nutrient conditions. However, under high nutrient levels, the community was controlled by nutrients as well as consumers, as there was a 45% decrease in biomass, at the final harvest, between treatments with nutrient enrichment and insecticide and treatments with nutrient enrichment only. The conclusion of dual control under high nutrient conditions is also supported by insect damage data that showed higher damage in treatments that had nutrients and no insecticide. This experimentally demonstrated relationship between the strength of insect grazing impacts and high nutrient content of plants results in a strong, positive interaction between the level of

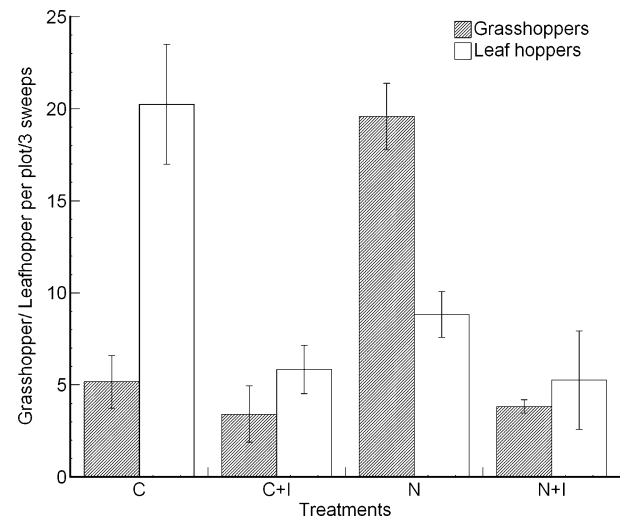


Figure 5. Effect of N fertilization and insecticide addition on the number of insects per plot/three sweeps. Grasshoppers were significantly ($p < 0.001$, ANOVA) more abundant in treatments with nutrients, whereas leafhoppers were significantly ($p < 0.001$, ANOVA) more abundant in control treatments. Results from the two surveys were pooled. Vertical bars represent ± 1 SE.

nutrients and consumer control in the system. Thus, the intensity and location of consumer control by insects across New England salt marshes are likely to be strongly regulated by marsh plant nitrogen content rather than quantity. Interestingly, our investigation into the mechanisms of insect control of marsh plant growth revealed that secondary fungal infections did not play a measurable role in mediating consumer impacts in New England salt marshes. This finding is in stark contrast to the major role they have recently been shown to play in lower latitude marshes in Georgia.

Considerable work has been done on nutrients and insect population dynamics in salt marshes, but rarely has this work focused on the interactive effects of nutrient availability and herbivory on plant growth. Valiela et al. (1975) focused on the effects of N additions on *Spartina* growth and considered that consumption by insects was "less than the errors of measurements". However, it is likely that potential production was underestimated because in that experiment insects were not experimentally excluded. Evidence from southeastern US marshes (Virginia, Georgia, North Carolina) and those in Argentina (Silliman and Bortolus 2003) shows that mesograzers (e.g. insects, crabs and snail) play a large role in controlling primary production. Valiela et al. (1975), while working in a New England salt marsh reported no significant response of biomass after the first year of N additions. These results are similar to our findings in N addition treatments. However, in our nutrient+insecticide treatment, we observed more than a 100% increase in plant biomass. That is, insects suppressed first year fertilization gains by directly consuming biomass to levels similar to those in unfertilized treatments. Other studies which have excluded mesograzers to test their impacts in marshes have also shown strong but previously ignored impacts; snail grazer exclusions from unfertilized treatments, in southeastern US marshes, increased biomass by 49%, whereas in N addition treatments biomass increased by 86% (Silliman and Zieman 2001). In Argentina, grazer exclusions yielded even more striking results, as *Spartina* standing crop increased by nearly 350% when the grazing crab *Chasmagnathus granulata* was excluded (Bortolus and Iribarne 1999). Another study by Gustafson et al. (2006) found that snail exclusion significantly increased *Spartina* biomass, whereas leafhopper exclusion did not play a significant role. Overall, there is clear evidence that crabs and snails exert strong control on salt marsh aboveground production over large spatial scales (Silliman and Bortolus 2003). This study shows that insect herbivores, as well as crabs and snails in other studies, can control production, but potentially only when interacting with nutrients.

Those studies that have focused on the interactive effect of fertilizer additions and insects have generally focused on insect population dynamics, ignoring the possible effects that insects might have on primary producers (Vince et al. 1981, Bowdish and Stiling 1998, Denno et al. 2001, 2002). Vince et al. (1981), while working in a New England salt marsh, showed how nutrient additions resulted in an intense insect density response. Insects more than quadrupled their population density in only one growing season. Nevertheless, when measuring biomass, insects were not excluded, and the possible reciprocal effect of insects on

plants remained unexplored and downplayed. Our experiment, on the other hand, did exclude insects and found a very strong effect of insects on marsh productivity under high nutrient conditions. It is likely that the reported pattern, of increased consumption under high nutrient levels, has been happening cryptically in many other experiments where fertilizer was added and insects were not excluded, and consequently potential primary production is likely to have been underestimated at many sites along the Atlantic coast (Silliman and Bortolus 2003).

The interaction between nutrients and consumers is likely to be related to the quality of the food source as Coley et al. (1985) and Hangrove (1984) suggest. *Spartina alterniflora* is a C_4 plant that under background levels of nitrogen has a high C/N ratio that makes it more resistant to consumption due to its low quality (Caswell et al. 1973). However, when nutrients are added, the nitrogen content (% of dry mass) increases, hence improving the quality of the food source (Valiela and Teal 1974, Vince et al. 1981, Stiling et al. 1982, Osgood and Zieman 1993, Silliman and Zieman 2001, Gratton and Denno 2003). This makes *Spartina alterniflora* more susceptible to consumption (Valiela and Teal 1979, Silliman and Zieman 2001). Vince et al. (1981), found that the amount of N in non-flowering shoots increased from 1.3 to 2.2% when adding N. According to these authors, increased N-content translated into higher palatability of the food source, resulting in rapid responses in herbivore populations. In accordance with Vince et al. (1981), Slansky and Feeny (1977) showed that insect fecundity, survivorship and growth rate varied directly with the nitrogen level of host plants. Similarly, Oedekoven and Joern (2000) showed how mortality of grasshoppers decreased by 50% when feeding on fertilized plants. It follows that the decreased mortality and increased fecundity are likely to result in increased populations that will increase consumption, hence likely increasing top-down control. Taken together, these results indicate that in New England marshes nutrient addition makes *Spartina alterniflora* plants more palatable to insects and shifts ecosystem control from bottom-up only to both bottom-up and top-down.

In contrast with southeastern US marshes, we found no effect of fungicide on biomass or differential fungal damage in our treatments. Silliman and Newell (2003) presented very different results. They found that top-down control in southeastern US marshes did not operate directly through grazer consumption, but indirectly through the wounds that grazing snails made, that then facilitated secondary fungal infections. We propose two hypotheses that may account for the differential incidence of fungal infections in grazer induced wounds at low latitude (fungal effect) and high latitude (no-fungal effect) sites. The first hypothesis is related to the absence of a fungal farming grazing snail. In the south, the snail *Littoraria irrorata*, that commonly reaches densities of 100–400 individuals m^{-2} , opens up wounds that facilitate fungal infection. However, the high latitude equivalent, the snail *Melampus bidentatus*, is present in very low densities in New England salt marshes and does not have the mechanical advantage to rasp open wounds on live plant tissue (Pennings and Silliman 2005). Our second hypothesis is that there is a latitudinal gradient in the standing crop of growth-controlling fungi, with biomass peaking in the south and decreasing significantly in the

north (Newell 1993). This was supported by observations made by Newell (1993) of higher ascomata (fungal sexual structures) densities in the south. A possible explanation that supports this pattern is that higher year round temperatures in the south might promote increased fungal productivity, whereas in the north, lower temperatures with strong seasonality might suppress the role of fungal infection in regulating *Spartina* biomass. In addition, it is possible as Silliman et al. (2005) showed for salt stress and consumer control, that higher physical stress in southeastern US marshes might make plants more susceptible to fungal infections. However, work by Newell et al. (2000) did not find empirical support for this hypothesis. He showed that there was no correlation between latitudinal differences along eastern US marshes (from 29° to 43° N latitude) and living fungal standing crop or rates of fungal growth. However, this work examined fungal biomass on only dead and not in live *Spartina*. This is because before Silliman and Newell (2003) fungi was not believed to infect live *Spartina* plants. As a result, our hypotheses remain of interest and open for further research.

These results contribute to the general understanding of the functioning and management of salt marshes. Unlike previous work, our results show that New England salt marshes can respond to nutrient addition by shifting from bottom-up only, to a bottom-up and top-down controlled ecosystem. Increased N availability is likely to have increased tissue quality, resulting in increased herbivory. Our results show that insects are more likely controlled by plant tissue quality rather than quantity, potentially resulting in outbreaks of herbivorous insect correlated with increased bottom-up forcing in marshes (Port and Thompson 1980). Finally, our results are currently particularly relevant given the large area of marshes under eutrophication. New England salt marshes receive large amounts of reactive N run-off mainly from suburban areas (Silliman and Bertness 2004). The reactive N arrives to marshes dissolved in the water of tributary rivers that in turn discharge into broad watersheds (Howarth et al. 1996). Our results suggest that the resultant increased herbivory may eventually counteract increases in productivity of salt marshes or, alternatively, at even higher insect densities, that these marshes could be overgrazed and denuded (Silliman unpubl., in Georgia salt marshes). Thus, the expected increase in carbon sequestration due to increase N availability may be significantly reduced in this ecosystem.

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References

- Bertness, M. D. 1987. Consumer pressure and seed set in a salt marsh perennial plant community. – *Oecologia* 71: 190–200.
- Bertness, M. D. and Shumway, S. W. 1992. Consumer driven pollen limitation of seed production in marsh grasses. – *Am. J. Bot.* 79: 288–293.
- Bortolus, A. and Iribarne, O. 1999. The effect of the southern Atlantic burrowing crab *Chasmagnathus granulata* on a *Spartina* salt marsh. – *Mar. Ecol. Prog. Ser.* 178: 79–88.
- Bowditch, T. I. and Stiling, P. 1998. The influence of salt and nitrogen on herbivore abundance direct and indirect effects. – *Oecologia* 113: 400–405.
- Caswell, H. et al. 1973. Photosynthetic pathways and selective herbivory: a hypothesis. – *Am. Nat.* 107: 465–480.
- Coley, P. D. et al. 1985. Resource availability and plant antiherbivore defense. – *Science* 230: 895–899.
- Crawley, M. J. 1989. Insect herbivores and plant population dynamics. – *Annu. Rev. Entomol.* 34: 531–564.
- Daehler, C. C. and Strong, D. R. 1995. Impact of high herbivore densities on introduced cordgrass, *Spartina alterniflora*, invading San Francisco Bay. – *Estuaries* 18: 409–417.
- Denno, R. F. et al. 2001. Bottom-up forces mediate natural-enemy impact in a phytophagous insect community. – *Ecology* 83: 1443–1458.
- Denno, R. F. et al. 2002. Predation risk affects relative strength of top-down and bottom-up impacts on insect herbivores. – *Ecology* 84: 1032–1044.
- Dixon, A. F. G. 1966. The effect of population density and nutritive status of the host on the summer reproductive activity of the sycamore aphid, *Drepanosiphum platanoides*. – *J. Anim. Ecol.* 35: 105–112.
- Ehrlich, P. R. and Birch, L. C. 1967. The “balance of nature” and “population control”. – *Am. Nat.* 101: 97–107.
- Gratton, C. D. and Denno, R. F. 2003. Inter-year carryover effects of a nutrient pulse on *Spartina* plants, herbivores and natural enemies. – *Ecology* 84: 2692–2707.
- Gustafson, D. J. et al. 2006. Relative effects of *Littoraria irrorata* and *Prokelisia marginata* on *Spartina alterniflora*. – *Estuaries Coasts* 29: 639–644.
- Hairston, N. G. et al. 1960. Community structure, population control, and competition. – *Am. Nat.* 94: 421–424.
- Hangrove, W. W. 1984. Shifts in insect herbivory in the canopy of black locust, *Robinia pseudoacacia*, after fertilization. – *Oikos* 43: 322–328.
- Hatcher, P. E. et al. 1997. Added soil nitrogen does not allow *Rumex obtusifolius* to escape the effects of insect–fungus interactions. – *J. Appl. Ecol.* 34: 88–100.
- Howarth, R. W. et al. 1996. Regional nitrogen budgets and riverine N & P fluxes for the drainages to the North Atlantic Ocean: natural and human influences. – *Biogeochemistry* 35: 75–139.
- Jefferies, R. L. 1997. Long term damage of sub-arctic ecosystems by geese: ecological indicators and measures of ecosystem dysfunction. – In: Crawford, R. M. M. (ed.), *Disturbance and recovery in arctic lands: an ecological perspective*. Kluwer, pp. 151–166.
- Mahibbur, R. M. and Gobindarajulu, Z. 1997. A modification of the test of Shapiro and Wilks for normality. – *J. Appl. Stat.* 24: 219–235.
- Marples, T. G. 1966. A radionuclide tracer study of arthropod food chains in a *Spartina* salt marsh ecosystem. – *Ecology* 47: 270–277.
- Murdoch, W. W. 1966. Community structure, population control, and competition – a critique. – *Am. Nat.* 100: 219–226.
- Newell, S. Y. 1993. Decomposition of shoots of a salt marsh grass; methodology and dynamics of microbial assemblages. – *Adv. Microbial Ecol.* 13: 301–326.
- Newell, S. Y. et al. 2000. Autumnal biomass and potential productivity of salt marsh fungi from 29 to 43 north latitude

- along the United States Atlantic coast. – *Appl. Environ. Microbiol.* 66: 180–185.
- Odum, E. P. and Smalley, A. E. 1959. Comparison of population energy flow of a herbivorous and a deposit feeding invertebrate in a salt marsh ecosystem. – *Proc. Natl Acad. Sci.* 45: 617–622.
- Oedekoven, M. A. and Joern, A. 2000. Plant quality and spider predation affects grasshoppers (acrididae): food-quality-dependant compensatory mortality. – *Ecology* 81: 66–77.
- Osgood, D. T. and Zieman, J. C. 1993. Factors controlling aboveground *Spartina alterniflora* (smooth cordgrass) tissue element composition and production in different-age barrier island marshes. – *Estuaries* 16: 815–826.
- Pennings, S. C. and Silliman, B. R. 2005. Linking biogeography and community ecology: latitudinal variation in plant–herbivore interaction strength. – *Ecology* 86: 2310–2319.
- Port, G. R. and Thompson, J. R. 1980. Outbreaks of insect herbivores on plants along motorways on the United Kingdom. – *J. Appl. Ecol.* 17: 649–656.
- Power, M. R. 1992. Top–down and bottom–up forces in food webs: do plants have primacy. – *Ecology* 73: 733–746.
- Robertson, A. I. and Duke, N. C. 1987. Insect herbivory on mangrove leaves on north Queensland. – *Aust. J. Ecol.* 12: 1–7.
- Sih, A. et al. 1985. Predation, competition, and prey communities: a review of field experiments. – *Annu. Rev. Ecol. Syst.* 16: 269–311.
- Silliman, B. R. and Zieman, J. C. 2001. Top–down control of *Spartina alterniflora* production by periwinkle grazing in a Virginia salt marsh. – *Ecology* 82: 2830–2845.
- Silliman, B. R. and Bertness, M. D. 2002. A trophic cascade regulates salt marsh primary production. – *Proc. Natl Acad. Sci.* 99: 10500–10505.
- Silliman, B. R. and Bortolus, A. 2003. Underestimation of *Spartina* productivity in western Atlantic marshes: marsh invertebrates eat more than just detritus. – *Oikos* 101: 549–554.
- Silliman, B. R. and Newell, S. Y. 2003. Fungal farming in a snail. – *Proc. Natl Acad. Sci.* 100: 15643–15648.
- Silliman, B. R. and Bertness, M. D. 2004. Shoreline development drives the invasion of *Phragmites australis* and the loss of plant diversity on New England salt marshes. – *Conserv. Biol.* 18: 1424–1434.
- Silliman, B. R. et al. 2005. Drought, snails, and large-scale die-off of southern salt marshes. – *Science* 310: 1803–1806.
- Slansky, F. and Feeny, P. 1977. Stabilization of the rate of nitrogen accumulation by larvae of the cabbage butterfly on wild and cultivated food plants. – *Ecol. Monogr.* 47: 209–228.
- Smalley, A. E. 1960. Energy flow of a salt marsh grasshopper population. – *Ecology* 41: 672–677.
- Stiling, P. D. et al. 1982. Foliar nitrogen and larval parasitism as determinants of leafminer distribution patterns on *Spartina alterniflora*. – *Ecol. Entomol.* 7: 447–452.
- Teal, J. M. 1962. Energy flow in a salt marsh ecosystem of Georgia. – *Ecology* 43: 614–624.
- Valiela, I. and Teal, J. M. 1974. Nutrient limitation in salt marsh vegetation. – In: Reimold, R. J. and Queen, W. H. (eds), *Ecology of halophytes*. Academic Press, pp. 547–563.
- Valiela, I. and Teal, J. M. 1979. The nitrogen budget of a salt marsh ecosystem. – *Nature* 280: 652–656.
- Valiela, I. et al. 1975. Production and dynamics of salt marsh vegetation and the effects of experimental treatment with sewage sludge. Biomass, production and species composition. – *J. Appl. Biol.* 12: 973–981.
- Vince, S. W. et al. 1981. An experimental study of the structure of herbivorous insect communities in a salt marsh. – *Ecology* 62: 662–678.