Physical stress modifies top-down and bottom-up forcing on plant growth and reproduction in a coastal ecosystem

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Abstract. Bottom-up and top-down effects act together to exert strong control over plant growth and reproduction, but how physical stress modifies those interactive forces remains unclear. Even though empirical evidence is scarce, theory predicts that the importance of both top-down and bottom-up forces may decrease as physical stress increases. Here, we experimentally evaluate in the field the separate and interactive effect of salinity, nutrient availability, and crab herbivory on plant above- and belowground biomass, as well as on sexual and clonal reproduction in the salt marsh plant *Spartina densiflora*. Results show that the outcome of the interaction between nutrient availability and herbivory is highly context dependent, not only varying with the abiotic context (i.e., with or without increased salinity stress), but also with the dependent variable considered. Contrary to theoretical predictions, our results show that, consistently across different measured variables, salinity stress did not cancel bottom-up (i.e., nutrients) or top-down (i.e., consumers) control, but has additive effects. Our results support emerging theory by highlighting that, under many conditions, physical stress can act additively with, or even stimulate, consumer control, especially in cases where the physical stress is only experienced by basal levels of the trophic chain. Abiotic stress, as well as bottom-up and top-down factors, can affect salt marsh structure and function not only by affecting biomass production but also by having other indirect effects, such as changing patterns in plant biomass allocation and reproduction.

Key words: *bottom-up; herbivory; nutrients; physical stress; salinity; salt marshes;* Spartina; *top-down.*

Introduction

After decades of an intense debate about whether top-down (i.e., consumers) or bottom-up (i.e., resources) factors regulate communities, current evidence shows that both factors simultaneously regulate the biomass, structure, and function of primary producers (Burkepile and Hay 2006, Gruner et al. 2008). In general, the joint impact of these two factors seems to be additive rather than truly interactive (Gruner et al. 2008), but the net outcome and the relative importance of these two factors is strongly dependent on ecosystem type, productivity, and latitude (Burkepile and Hay 2006). Recent experimental studies have added complexity to this scenario, showing that the relative importance of top-down and bottom-up factors can be variable within a given site, following temporal changes in the physical environment (Meserve et al. 2003). In this context, and although the empirical evidence is limited, theory provides some predictions on how physical stress can modify the relative importance of bottom-up and top-down processes. The

environmental-stress model (Menge and Sutherland 1987), for instance, clearly predicts that, because higher trophic levels are expected to be more susceptible to physical stress than basal levels, top-down control of basal prey decreases with increasing abiotic stress (Menge and Sutherland 1987). Thus, in environments with high abiotic stress, physical factors will, in theory, become the primary limiting factor for biomass production, shutting down both top-down and bottom-up control as a consequence of both decreased herbivory rates and nutrient demand (Reed et al. 2011). Alternatively, stress could increase consumer pressure in cases where basal levels are more susceptible than consumers, a theory that has received much less attention than the environmental-stress model (Menge and Olson 1990). Recent synthesis work on consumer fronts and their interaction with global change, indeed, indicate that the environmental-stress model may only apply to a subset of situations, and that physical stress can also increase top-down control (either additively or synergistically) over plant ecosystems (Silliman et al. 2013). Based on these findings, Silliman et al. (2013) predict that ecosystem resilience and production will decrease in systems where consumption rates increase (i.e., synergistic effect) or are unaffected (i.e., additive effect) by increasing physical stressors.

Although nutrient availability and consumer pressure are now recognized as important factors that can regulate the structure of shoreline plant communities (Silliman and Bertness 2002, Gruner et al. 2008), one of the main physical factors that has been intensively studied and is known to strongly regulate the structure and function of those coastal communities is salinity stress (e.g., Moon and Stiling 2000, Castillo et al. 2005, Pennings et al. 2005, Jiménez et al. 2012). Salinity has effects on virtually all aspects of plant physiology and metabolism, including disruption of osmotic and ionic homeostasis (Zhu 2001), damage in structural and functional proteins (Munns 2002), as well as interference in root nutrient and water uptake (Hu and Schmidhalter 2005). Thus, spatial and temporal variation of soil salinity can have profound effects on the structure and function of these communities (Pennings and Bertness 2001).

Many two-factor experiments have shown that salinity stress can interact with top-down and bottom-up controls of plant growth. Salinity stress consistently decreases bottom-up control because stressed plants have low growth rates, and resource supply rates exceed demands (Reed et al. 2011). In contrast, the effect of salinity on top-down control seems to depend on plant species and/or herbivore type (Goranson et al. 2004). In some cases, and in accordance with the plant vigor hypothesis (Price 1991), salinity stress decreases plant palatability, increases salt concentration in plant tissue, or even activates induced resistance, thus decreasing pressure by herbivores (e.g., insects [Moon and Stirling 2002, Mopper et al. 2004], small mammals [Canepuccia et al. 2010], and birds [Stahl et al. 2002]). In other cases, in accordance with the plant stress hypothesis (White 1984), salinity generates increased levels of amino acids, and C/N ratios of plant tissue, thus driving increased herbivory (e.g., crabs [Pennings et al. 1998], insects [Jiménez et al. 2012]). Despite this extensive body of work providing keen insight into two-way interactions, no studies have simultaneously tested how salinity, nutrient availability, and grazing can interact to control primary production. Better understanding of how these multiple environmental factors interact to influence the function of plant communities under natural conditions is essential not only to further test emerging theory on predator stress functional responses (Silliman et al. 2013), but also to better anticipate the possible effects of global change (e.g., drought, eutrophication, alteration of consumer populations) on shoreline plant ecosystems that provide important and valuable benefits to humans (Barbier et al. 2011).

Consumers, nutrients, and stress are extensively known as forces that can affect plant biomass production, but they also may impact other aspects of plant ecology, including morphological, physiological, and phenological changes. The sessile nature of plants, for example, favors phenotypic plasticity as a primary mechanism by which plants deal with environmental fluctuation (Dudley 2004). In addition to the presence or absence of significant biomass removal, plants can activate several chemical, physiological, phenological, and morphological strategic defenses in response to herbivory (Karban and Baldwin 2007), including modifications in resource allocation patterns to tissues inaccessible to foraging herbivores (Orians et al. 2011), which can in turn affect community structure and function. Similarly, plants usually modify resource allocation to different organs in relation to nutrient and water availability (Ericsson 1995), which can lead to a rearrangement of biomass distribution rather than a drastic change in total biomass. Several studies have also shown significant variation in allocation to sexual and clonal reproduction in response to changes in environmental variables, including stress, herbivory, and nutrient availability (e.g., Liu et al. 2009). Abiotic stress, and top-down and bottom-up forces, then, can directly affect aboveground plant biomass production, but can also change resource allocation patterns to different plant organs and functions (Ericsson 1995), thus potentially affecting community structure (Brewer et al. 1998) and function (e.g., Mcleod et al. 2011).

Salt marshes are common and well-studied shoreline communities that, although very productive, are characterized by the presence of strong limiting factors for plant growth (Pennings and Bertness 2001), including salinity, anoxia, nitrogen availability, and herbivory (e.g., Silliman et al. 2005, Jefferies et al. 2006, Alberti et al. 2010). The strong top-down and bottom-up control of plant biomass production and the presence of striking physical stressors make salt marsh communities ideal systems for assessing how physical stress affects the relative impact of top-down and bottom-up forces (Moon and Stiling 2002). This is fundamental not only because salt marsh primary production is linked to the function of nearby estuaries, but also because salt marsh production and allocation patterns are strongly related to fundamental ecosystem services, including carbon burial rates (and thus carbon sequestration [Mcleod et al. 2011]) and coastal protection (Deegan et al. 2012, Silliman et al. 2012). In this context, we evaluate the effect of physical stress on the relative impact of top-down and bottom-up control on the growth, reproduction, and biomass allocation patterns of a dominant salt marsh grass. We hypothesized that salinity stress would not cancel top-down control of marsh plant production exerted by an herbivorous crab, but would increase its importance in relation to bottom-up control. We also predicted that the outcome of the interaction between the three forcing factors would change with different plant response variables.

Materials and Methods

Study site

This study was performed in an extensive salt marsh located near a creek at the mouth of the Mar Chiquita coastal lagoon (Argentina, 37°32′ S; 57°19′ W; see Plate 1).

This lagoon is affected by semidiurnal microtides (<1 m) and is characterized by mudflats in the low zone followed by a monoculture of the austral cordgrass *Spartina densiflora* Brongn. (Poaceae), and an extended salt marsh community at high elevations. This species is a perennial salt-tolerant grass native to South America (see Bortolus 2006) that can tolerate a wide range of environmental conditions (Nieva et al. 2001), but is usually associated with strong phenotypic changes (Castillo et al. 2014). The Mar Chiquita salt marsh community is characteristic of the salt marshes occurring between southern Brazil (32° S) and northern Argentinean Patagonia (42° S) that are dominated by the intertidal burrowing crab *Neohelice granulata* Dana (Grapsoidea: Varunidae). This crab inhabits the entire intertidal zone and can occur at densities higher than 60 crabs/m^2 (Iribarne et al. 1997). Through grazing, crabs can exert strong control over marsh plant production by directly removing plant tissue as well as by facilitating fungal infection in crab-generated injuries (Daleo et al. 2009). As in other salt marshes worldwide, nutrient availability and soil salinity can also strongly control primary production (Alberti et al. 2010).

A fully factorial experiment was conducted in the *S. densiflora* monoculture zone. The factorial design includes: salinity (with and without salt addition), nutrients (with and without nutrient addition) and herbivory manipulation (with and without crabs). Given the variability and patchy nature of crab herbivory pressure, herbivory manipulation was implemented in a split-plot design (i.e., salinity and nutrient factors were implemented in a factorial design using 0.7 × 1.5 m plots that were then divided into two 0.7 × 0.7 m subplots (units) with a 0.1-m buffer between them). Each treatment combination was replicated six times (for a total of 24 plots and 48 units). Crab-exclusion subplots were surrounded using a plastic mesh (10-mm opening) fence 0.6 m high and supported by iron stakes. Crab exclosures have been widely used in this system, and the use of cage controls revealed that there were no associated cage artifacts (e.g., Daleo et al. 2007, 2009, Alberti et al. 2010). Salt addition treatments received 40 g (~40 g/m^2) of commercial pelletized salt spread superficially every two weeks (see Canepuccia et al. 2010). Nutrient addition treatments received 120 g (~120 g/m^2) of a slow-release pelletized fertilizer (NPK: 29:5:5) monthly. This fertilization rate is similar to rates previously used in other nutrient addition studies in salt marshes (see Emery et al. 2001, Alberti et al. 2010), including previous work in this system, where nutrient loading rates increased sediment nitrates by more than an order of magnitude (1.37 ± 0.14 μmol/L without nutrient addition vs. 85.24 ± 24.28 μmol/L with nutrient addition, see Daleo et al. [2008]) and duplicate *S. densiflora* leaf N content (Alberti et al. 2011). Fertilizer was spread into 12 artificial holes (5 cm deep, 1 cm diameter) evenly distributed in each plot, that were then filled with mud. In unfertilized plots, holes were

made and then filled without fertilizer application. The experiment started on March 2010 and finished on April 2012, when the number of live and dead stems, the maximum height of stems, and the number of inflorescences were counted in each experimental subunit. Aboveground plant material was harvested and classified as dead or alive. Belowground biomass was harvested, divided in two fractions (0–0.1 and 0.1–0.2 m depth), and washed. After washing, rhizomes were used to measure the length of five randomly chosen internodes. Plant material fractions were dried (60°C, 72 h) and weighed (precision 0.0001 g). Herbivory pressure was estimated before plant harvesting by measuring the proportion of leaves with a characteristic herbivory mark (see Alberti et al. 2008) in five randomly selected stems. Sediment salinity was measured in each plot by collecting sediment samples (5 cm diameter, 8 cm deep) at the end of the experiment (i.e., April, 2012, after two weeks of the last salt application), which were weighed, dried to constant mass, mixed with a known volume of distilled water, measured by refractometry after 48 h, and then corrected by the initial sample water volume, to reflect the original concentration of salt. Those samples show that salt loading increased soil salinity at least up to 35% (i.e., from 0.013 ± 0.001 to 0.017 ± 0.002 g salt/g soil).

Statistical analyses

The effect of salt, nutrients, and herbivory on above- and belowground biomass production, on the relative allocation to clonal and sexual reproduction, as well as on internode length, was modeled using linear mixed-effects models with de lme function from the nlme package (Pinheiro et al. 2013) in R 3.0.1 (R Development Core Team 2013). Nutrients, salinity, and herbivory were treated as fixed factors and plot was treated as a random factor. These analyses reflect the split-plot nature of the design. To improve normality, biomass data were natural log-transformed before analyses.

RESULTS

Biomass production

Total (i.e., aboveground + belowground) biomass production was interactively affected by nutrient availability and the presence of herbivores; herbivores decreased total biomass by nearly 50% without nutrient addition, but had no effect with nutrient addition, which alone increased biomass production by >400% (nutrients (N) × herbivory (H); $F_{1,19} = 8.71$, $P = 0.0082$; Appendix A: Table A1). Total biomass was also affected by salinity; salt addition decreased it by nearly 50% and did not interact with other factors ($F_{1,20} = 29.20$, $P < 0.0001$; Appendix A: Table A1). Aboveground biomass was affected by the interaction between nutrient availability and the presence of herbivores; herbivores reduced aboveground biomass by nearly 50% without nutrient addition but had no effect with nutrient addition, which alone increased aboveground biomass >10 times (N × H;
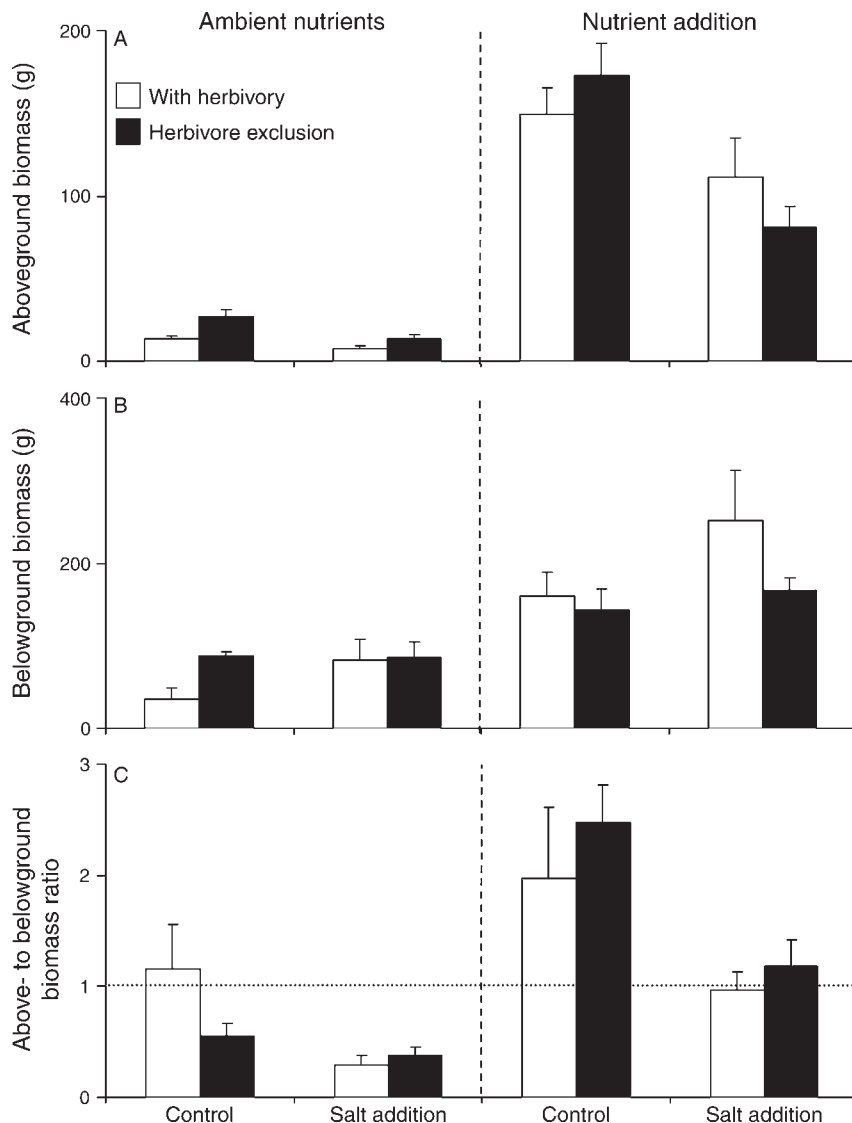
Fig. 1. Effect of nutrient addition, exclusion of herbivores, and salt addition on *Spartina densiflora* (A) aboveground biomass production, (B) belowground biomass production, and (C) above- to belowground biomass ratio. Bars show means and standard errors.

$F_{1,19} = 6.11$, $P = 0.023$, Fig. 1; Appendix A: Table A1). Salt addition decreased aboveground biomass by nearly 50% and did not interact with other factors ($F_{1,20} = 15.09$, $P < 0.0001$; Fig. 1; Appendix A).

Belowground biomass was affected by the interaction between nutrient availability and herbivory; herbivory decreased belowground biomass nearly 50% at ambient nutrient levels, but increased it nearly 20% when nutrients were added, and nutrient addition increased it nearly 400% (N × H; $F_{1,19} = 6.53$, $P = 0.019$; Fig. 1; Appendix A). Salinity (S) increased belowground biomass nearly 35% and did not interact with other factors ($F_{1,20} = 4.86$, $P = 0.039$; Fig. 1; Appendix A, Table A1). When belowground was discriminated by depth, the shallow fraction (i.e., 0–0.1 m depth) was

affected by the interaction between nutrients and herbivory; herbivory decreased it nearly 50% at ambient nutrient levels, but has no effect when nutrients were added, and nutrient addition increased it nearly 400% (N × H; $F_{1,19} = 4.89$, $P = 0.039$). Salinity increased the biomass of the shallow fraction nearly 40% and did not interact with other factors ($F_{1,20} = 5.02$, $P = 0.037$; Appendix B: Fig. B1). For the deeper root fraction (i.e., 0.1–0.2 m), there was a full interaction between the three factors (N × S × H; $F_{1,19} = 5.66$, $P = 0.028$; Appendix B: Fig. B1).

Above- to belowground biomass ratio

Nutrient addition increased above- to belowground biomass ratio by >200% ($F_{1,20} = 34.38$, $P < 0.0001$; Fig.
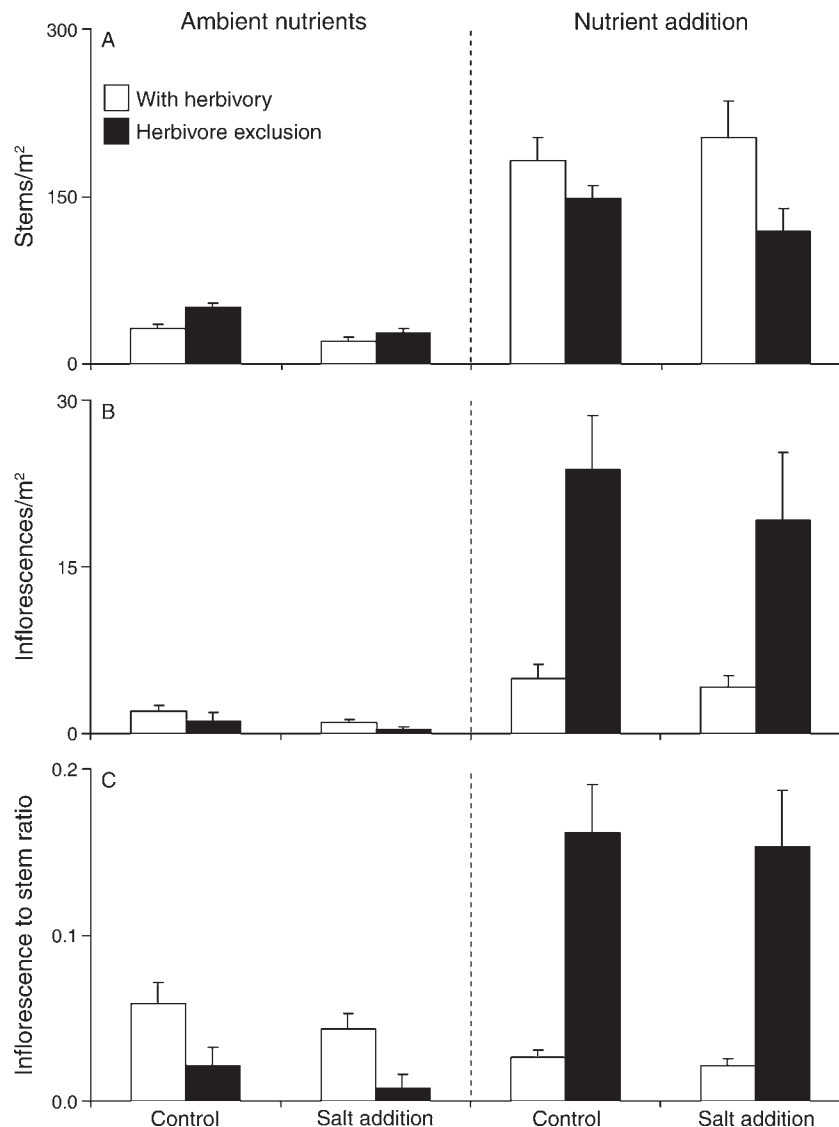
FIG. 2. Effect of nutrient addition, exclusion of herbivores, and salt addition on *Spartina densiflora* (A) stem production, (B) inflorescence production, (C) inflorescence to stem ratio. Bars show means and standard errors.

1; Appendix A: Table A1). Salt addition, in contrast, decreased above- to belowground biomass ratio nearly 50% ($F_{1,20} = 17.02$, $P < 0.0005$; Fig. 1; Appendix A: Table A1).

Clonal and sexual reproduction

Similar to aboveground biomass, the number of stems was determined by the interaction between nutrient availability and herbivory; herbivory decreased the number of live stems at ambient nutrient levels, but increased it when combined with nutrient level addition (N × H; $F_{1,19} = 16.17$, $P = 0.0007$; Fig. 2; Appendix C: Table C1). The number of stems was also determined by the interaction between nutrient availability and sediment salinity; salt addition decreased the number of stems but only without nutrient addition (N × S; $F_{1,20} =$

4.72, $P = 0.042$, Fig. 2; Appendix C: Table C1). The number of spikes, or inflorescences, was only affected by the interaction between nutrient availability and herbivory; nutrients increased the number of spikes nearly 1500% and herbivory increased it nearly 100%, but when combined, both nutrient addition and herbivory increased spikes by only 300% (N × H; $F_{1,19} = 29.88$, $P < 0.0001$; Fig. 2; Appendix C: Table C1). The ratio between sexual and clonal reproduction (i.e., the ratio between spikes and stems) was also only determined by the interaction between nutrient availability and herbivory. Nutrients increased the spike-to-stem ratio nearly 1000% and herbivory increased it nearly 400%, but when combined, both factors increased it by only 50% (N × H; $F_{1,19} = 47.28$, $P < 0.0001$; Fig. 2; Appendix C: Table C1). This pattern of change in the relative biomass
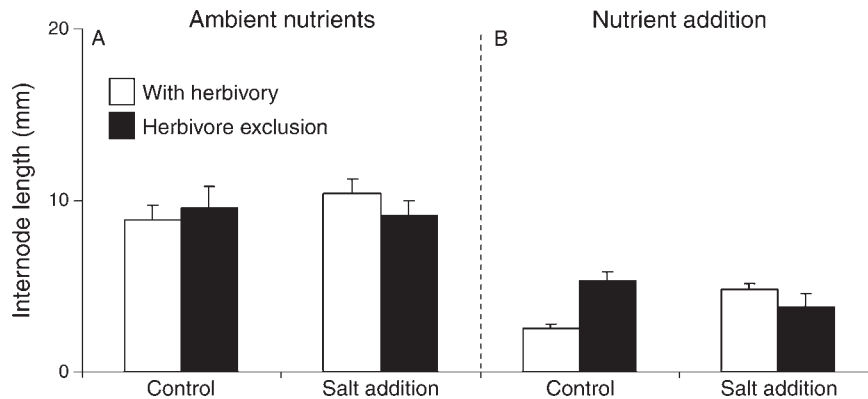
FIG. 3. Effect of nutrient addition, exclusion of herbivores, and salt addition on *Spartina densiflora* internode length. Bars show means and standard errors.

allocation to sexual reproduction was also observed for the ratio between inflorescences and live aboveground biomass (N × H; $F_{1,19} = 36.07$, $P < 0.0001$; Appendix C: Table C1).

Nutrient availability, sediment salinity, and herbivory interacted to determine internode length (N × S × H; $F_{1,19} = 12.82$, $P = 0.002$; Fig. 3; Appendix C). Nutrient addition consistently decreased internode length, but the sign of the effect of both salt addition and herbivory depended on the combination with the other factors (Fig. 3; Appendix C: Table C1).

DISCUSSION

Our results show that top-down and bottom-up forces, as well as abiotic stress, are strong forcing factors that control salt marsh plant biomass production, allocation patterns, and reproduction, but their relative importance and interdependence varies depending on whether aboveground biomass, belowground biomass, sexual, or asexual reproduction is considered. These results reveal that a complete understanding of controls on salt marsh plant production requires more complex understanding of interactions of more than two factors. Herbivory and abiotic stress show a strong additive effect in controlling biomass production, providing evidence in support of the hypothesis that physical stress can often positively impact the influence of top-down control over whole ecosystems (Silliman et al. 2013). Moreover, as abiotic stress dampens the otherwise very strong impact of nutrients, the net effect of abiotic stress is to increase the relative importance of top-down control while suppressing the impacts of bottom-up forcing.

Control of biomass production

After nearly two decades of discussion, it is now widely accepted that top-down and bottom-up control are coupled (e.g., Gruner et al. 2008). Although the combined effect of both factors is commonly additive (Gruner et al. 2008), nutrient addition in salt marshes commonly drives great amplification of top-down effect,

as herbivores are N limited (e.g., Silliman and Zieman 2001, Jiménez et al. 2012). Our results show that southwest Atlantic salt marshes are strongly limited by nutrients; fertilization increased total plant biomass more than 4 times and aboveground biomass more than 10 times. Herbivory, however, was also a strong control agent, decreasing plant biomass by nearly 30%. The combined effect of both factors was interactive, but surprisingly, we found that fertilization canceled top-down control instead of amplifying it, a pattern also seen by Bertness et al. (2008) when examining the interaction between nutrient availability and crab herbivory in New England salt marshes. This may be related to the complex life history of marsh crabs (e.g., with planktonic larvae) that may not necessarily translate to a fast herbivore population increase following nutrient addition. Impact of herbivores, thus, may be distributed among a larger number of stems, and densely packed patches of *S. densiflora* may impede crab penetration (see Alberti et al. 2008). Thus, the combined effect of top-down and bottom-up factors in salt marshes seems to be highly context dependent, as it can range from amplification to cancellation effects depending on the type of herbivore considered.

According to the environmental-stress model (Menge and Sutherland 1987), physical stress per se is expected to become the limiting factor for biomass production in stressful environments, canceling out both top-down and bottom-up control (Reed et al. 2011). Many studies have supported this general pattern, showing that the relative importance of either top-down (e.g., Pennings et al. 2005, Crain et al. 2008, Bromberg Gedan et al. 2009) or bottom-up (Bradley and Morris 1991) factors decreases as environmental stress increases. Contrary to environmental-stress model expectations but in accordance with other stress models (Menge and Olson 1990) and evidence of consumer impacts across terrestrial and aquatic systems (e.g., Pennings et al. 1998, Jiménez et al. 2012, Silliman et al. 2013), our results show that abiotic stress did not change the relative effect of herbivory (as there was no interaction between those

PLATE 1. Mar Chiquita salt marshes (Argentina) are characterized by monocultures of the cordgrass *Spartina densiflora* and dominated by the intertidal burrowing crab *Neohelice granulata*. Photo credit: Paulina Martinetto.

factors). Environmental-stress models (Menge and Sutherland 1987) assume a unique stress factor that similarly affects different trophic levels. Opposing stress gradients, or single-stress gradients that differentially affect different trophic levels, nevertheless, are not uncommon in natural systems (Silliman et al. 2013). For example, in salt pans of many southern Atlantic U.S. salt marshes, salt stress negatively affects *Spartina alterniflora* Loisel. (smooth cordgrass; Poaceae) but has no effect on the herbivorous snail *Littoraria irrorata*, leading to large-scale die-off areas (Silliman et al. 2005). On the rocky shores of Oregon (United States), desiccation stress during the summer strongly affects fast-growing algal species but has no effect on herbivorous limpets; thus, the strongest impact of herbivores on algae abundance are observed during the months with harshest abiotic conditions (Cubit 1984). Moreover, crab consumption of mangrove tree seedlings is higher at low and anoxic tidal levels because crabs avoid desiccation stress related to higher tidal levels (Sousa and Mitchell 1999). When the stress is decoupled among trophic levels, a range of functional response can be expected, including the intensification of consumer pressure that can trigger increased occurrence of consumer fronts and decreased system stability and resilience (Silliman et al. 2013).

Similarly, increased salinity stress did not cancel bottom-up control of biomass production but had an additive effect. Salinity decreased plant biomass, probably as a consequence of sodium ion interference with ammonium uptake as it competes for carriers in the root membrane, lowering the efficiency of ammonium (the primary form of N in anoxic marsh soils) uptake mechanism by the plant roots (Bradley and Morris 1991). Despite the fact that there was no interactive effect, and that the proportional biomass increase, compared to ambient nutrient levels, was the same at both scenarios, nutrient addition resulted in lower plant biomass production at high salinity in comparison to ambient levels; that is, salinity stress decreased plant response to nutrient addition. Thus, in this system, the net effect of abiotic stress was to increase the relative importance of top-down at the cost of decreased bottom-up control.

Beyond biomass production

Although nutrient availability, soil salinity, and herbivory can strongly regulate plant production, results show that these factors can also have a strong effect on other plant traits. Specifically, relative biomass allocation to above- and belowground structures and reproductive allocation (sexual or asexual) were impacted by one or more of these three driving factors. Increased nutrient availability drives a drastic increase in the relative allocation of plant tissue to aboveground relative to belowground structures, while increased sediment salinity drives the opposite pattern. Increased resource allocation to those organs that obtain the limiting resource is a common response to changing environmental conditions (Poorter et al. 2012). For example, increases in the relative biomass allocation to photosynthetic structures are widely reported in re-

sponse to increased nutrient availability (e.g., Ericsson 1995). The opposite effect, produced by salinity, is probably a consequence of a decrease in nutrient uptake efficiency (Hu and Schmidhalter 2005).

Plant sexual and clonal reproductive investment can also be influenced by environmental factors, especially resource availability (van Kleunen et al. 2002). Some models predict that increases in nutrient availability will raise the relative allocation to sexual reproduction because sexual propagules are more nutrient demanding than clonal growth (Aarssen 2008). Other models, based on dispersal strategies, predict the opposite pattern because dispersal capacity of sexual reproduction allows escape from unfavorable patches (van Kleunen et al. 2002), and clonal reproduction allows rapid filling of nutrient-rich patches (Gardner and Mangel 1999). Our results show that, when acting alone, both nutrients and herbivores increased the relative allocation to sexual reproduction, but the proportion of inflorescences in relation to stems (and in relation to biomass) did not change when both factors act together. (That is, fertilization greatly increased biomass allocation to sexual reproduction without herbivory, but decreased it in presence of herbivores.) In addition to the changes in resource allocation to above- and belowground components or to sexual and clonal reproduction, plasticity in some clonal plants allows them to change their growth form in order to become more compact or more widely spaced in response to environmental conditions (van Kleunen and Fischer 2001). According to the foraging hypothesis, shorter spacing between stems (i.e., stolon length) that maximizes biomass allocation to favorable sites are expected in good habitats, while longer spacing allows escape from unfavorable habitats (van Kleunen and Fischer. 2001). In agreement with this theory, our results show that nutrients decrease *S. densiflora* internode length. Internode length was also influenced (although to a lesser extent than nutrients) by herbivory and salinity. The direction of the effect of herbivory and salinity, nevertheless, interact with each other and with nutrient levels; thus, no clear pattern of response to herbivory and salinity stress can be inferred from the results.

Although it can be argued that top-down and bottom-up direct control of biomass production is the main path by which those factors can affect salt marsh ecosystem function, changes in traits such as relative allocation to above- and belowground structures, or to sexual and asexual reproduction, are not peripheral given that they can also have profound effects on ecosystem function (e.g., Moon and Stiling 2002, De Deyn et al. 2008). Salt marshes are highly productive systems that provide fundamental ecosystem services to human societies, and the provision of those services such as shoreline protection from erosion (Gedan et al. 2011) and C sequestration (Mcleod et al. 2011) depend not only on the high productivity but also on other aspects of the integrity of salt marshes. Decreases in root-to-shoot

biomass ratio caused by eutrophication or heavy oiling, for instance, drive decreases in geomorphic stability and increases in the rates of coastal erosion (Deegan et al. 2012, Silliman et al. 2012). Salt marshes are also recognized as extremely valuable systems because of their C sequestration capacity (Mcleod et al. 2011). A great part of the salt marsh C stock is belowground, in the form of living roots or nonliving litter; thus, belowground biomass allocation patterns, along with total primary production, are the main plant traits that regulate soil C sequestration (De Deyn et al. 2008). Seed availability, in addition, can determine salt marsh plant composition at patch size (Rand 2000), which would have important consequences, particularly for bare patch dynamics (e.g., Daleo et al. 2014), and thus, system functioning. Changes in stem density and internode length drive changes in how densely packed stems are, affecting water flow, sediment stabilization and retention, evaporation, and sediment salinity, as well as refuge availability to invertebrate animals (Brusati and Grosholz 2006). Thus, pervasive anthropogenic changes in nutrient cycles, herbivore populations, and levels of abiotic stress may challenge salt marsh function not only by directly regulating plant productivity but also by affecting other plant traits that influence this integrity.

In summary, results show that, in southwest Atlantic salt marshes, changes in nutrient availability related to eutrophication, increases in soil salinity related to climatic change, or changes in crab herbivore populations, can lead to a great alteration, not only in biomass production but also in other plant traits that are related to ecosystem function and services. In combination, our results highlight that physical stress can interact with linked bottom-up and top-down forces and that physical stress can act additively with consumer pressure instead of suppressing it. Our results also emphasize the importance of studying often overlooked biomass allocation patterns in plant assemblages to accurately predict human impacts on natural systems.

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SUPPLEMENTAL MATERIAL

Ecological Archives

Appendices A–C are available online: http://dx.doi.org/10.1890/14-1776.1.sm