

# Rainfall intensity modulates the interaction between the marsh cordgrass *Spartina densiflora* and the mouse *Akodon azarae*

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**ABSTRACT:** Changes in rainfall patterns caused by anthropogenic global climate change or planetary-scale events, such as the El Niño Southern Oscillation, can significantly affect the abundance and distribution of organisms. Despite the evidence of such effects on marine and terrestrial systems, ecological consequences of rainfall fluctuations in coastal marine ecosystems remain poorly understood. Here we evaluate the effects of rainfall intensity on the interaction between the cordgrass *Spartina densiflora* and Azara's grass mouse *Akodon azarae* in a southwestern Atlantic salt marsh (Mar Chiquita coastal lagoon, Argentina). Field surveys showed that the abundance of *A. azarae* increased during rainy summers (i.e. El Niño 2005 and 2007) and had lowest values during dry summers (i.e. La Niña 2008). Salt content in sediment and plant tissue were negatively related with rainfall. In addition, field experiments showed that increased sediment salinity resulted in increased salt content in plant tissues. Elevated soil salinity also increased the proportion of senescent *S. densiflora* tissues and reduced plant growth. The consumption of *S. densiflora* leaves by *A. azarae* also decreased with increased soil salinity. The proportion of *S. densiflora* in feces collected during the driest summer was very small. Therefore, changes in the abundance of *A. azarae* could be mediated by plant–rodent trophic interaction or by plant cover changes. In conclusion, rainfall fluctuations changed the abiotic environment (i.e. salinity), decreasing primary production and indirectly modifying habitat use by the omnivore *A. azarae* and its trophic interaction with *S. densiflora*. The present study provides evidence that rainfall can modify ecological processes that affect the structure and dynamics of coastal marine ecosystems.

**KEY WORDS:** Climate change · Rainfall changes · *Spartina densiflora* · *Akodon azarae* · Habitat use

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## INTRODUCTION

Among physical factors, rainfall has great importance, directly and indirectly affecting the structure and dynamics of terrestrial (Knapp et al. 2002, Sala et al. 2012) and marine environments (Philippart et al. 2011). Due to global climate change (GCC) and other global-scale events such as the El Niño Southern Oscillation (ENSO), rainfall patterns change worldwide (Bates et al. 2008). For example, rainfall can

directly modify the flow and availability of water in terrestrial systems, generating extreme droughts (Ciais et al. 2005) as well as persistent floods (Camilioni & Barros 2000). In coastal marine ecosystems, rainfall can increase freshwater input through river runoff (Philippart et al. 2011). Biological responses may be behavioral (Parmesan 2006), phenological (Peñuelas et al. 2004), or demographic (Ogutu et al. 2008), and may even entail species distribution shifts (Zhu et al. 2012) and extinctions (Parmesan 2006). In

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addition, new biological interactions or changes in existing ones may arise (Birkett & Stevens-Wood 2005). Thus, extreme rainfall fluctuations can lead to changes in carbon cycling (Ciais et al. 2005), above-ground productivity (Knapp et al. 2002, Fay et al. 2008) and biological diversity (Walther et al. 2002).

On a global scale, physical factors such as temperature and rainfall determine climatic conditions, biome boundaries, species distributions (Whittaker 1975) and belowground productivity (Pandey & Singh 1992). However, at smaller spatial scales, the abundance and distribution of organisms are affected by both physical and biological factors (Bertness & Callaway 1994). Biological interactions are important ecological processes that modify the structure and organization of natural communities (Brown et al. 2001, Bruno et al. 2003) and can even affect their biological diversity (Hillebrand et al. 2007). Trophic interactions may be key factors in natural systems, and can have large-scale ecological effects (Pace et al. 1999, Estes et al. 2011). Nevertheless, biological interactions are context dependent because their effects may change along physical gradients (Menge & Sutherland 1987, Bruno et al. 2003). In summary, extensive evidence shows how rainfall fluctuations and biological interactions affect many terrestrial and marine systems, but ecological consequences under this changing climatic scenario in coastal marine communities remain poorly understood (but see Eslami Andargoli et al. 2009, Canepuccia et al. 2010).

Salt marshes are coastal marine ecosystems subject to variations in the timing and amount of fluxes of freshwater, nutrients, sediment and tides (Scavia et al. 2002, Valiela 2006). Salt marshes are physically harsh environments where periodic tidal floods and high evaporation lead to high sediment salinities, usually generating a physical gradient that varies according to marsh elevation (Bertness 1999). Salt stress has strong impacts on the biomass (Brown et al. 2006), zonation (Bertness et al. 1992, Pennings et al. 2005), and survival (Brown et al. 2006) of salt marsh plants as well as their consumption by invertebrates (Silliman et al. 2005) and vertebrates (Canepuccia et al. 2010). Thus, rainfall fluctuations could directly and indirectly trigger biological responses in salt marshes through changes in sediment salinity.

Rainfall patterns in South America are intensely affected by GCC and ENSO events (Grimm & Tedeschi 2009). The climate of the eastern-central region of Argentina is temperate-subhumid, but rainfall intensity has shown an increasing trend during the last 5 decades (Berbery et al. 2006, Canepuccia et al. 2010), with disruptions by cycles of heavy rainfall (El Niño)

and dry periods (La Niña) (Grim & Tedeschi 2009). This region has many salt marshes, where the halophytic species *Spartina densiflora*, *S. alterniflora* and *Sarcocornia perennis* dominate (Isacch et al. 2006). The structure and dynamics of these marshes can be mediated by plant–consumer interactions (Alberti et al. 2007, Canepuccia et al. 2010); the most abundant marsh herbivores are the wild guinea pig *Cavia aperea* (Canepuccia et al. 2010) and the burrowing crab *Neohelice (Chasmagnathus) granulata* (Alberti et al. 2007). However, these marshes also harbor Azara's grass mouse *Akodon azarae* (Canepuccia et al. 2008), which is one of the most abundant murid rodents inhabiting grassland and agroecosystems of the Pampas region (Bilenca & Kravetz 1998). *A. azarae* can feed on the leaves and seeds of *S. densiflora* (Canepuccia et al. 2008). Previous studies focusing on the interplay between rainy periods and herbivory in southwestern Atlantic salt marshes have shown that crab herbivory on *S. densiflora* is enhanced during rainy periods due to prolonged floods (Alberti et al. 2007), whereas herbivory by wild guinea pigs is reduced during dry periods due to reduced plant quality (Canepuccia et al. 2010). However, it is not clear how rainfall changes affect omnivorous species such as *A. azarae*, which does not exclusively feed on marsh plants.

The aim of this study was to evaluate the effects of rainfall fluctuations on the cordgrass *S. densiflora*, marsh use by *A. azarae* and the trophic interaction between them. Specifically, we studied the relationship between rainfall and (1) sediment salinity, (2) *S. densiflora* salinity, and (3) the abundance of *A. azarae* in the vegetation. Finally, we evaluated if increased sediment salinity modified their trophic interaction.

## MATERIALS AND METHODS

### Study site

The present study was conducted in a marsh located at the Mar Chiquita coastal lagoon (Argentina, 37°45' S, 57°23' W; Fig. 1). The climate in the region is subhumid to humid (76 to 84 % humidity), mesothermal (12.9 to 15°C) and with greater seasonal rains during the warm semester (October–March). Precipitation peaks in December (104 mm) and March (107 mm). The annual mean precipitation oscillates between 578 and 1200 mm (Reta et al. 2001). The lagoon is a 46 km<sup>2</sup> body of brackish water affected by low-amplitude tides (up to 1.38 m at the lagoon entrance; Lanfredi et al. 1987). It is charac-

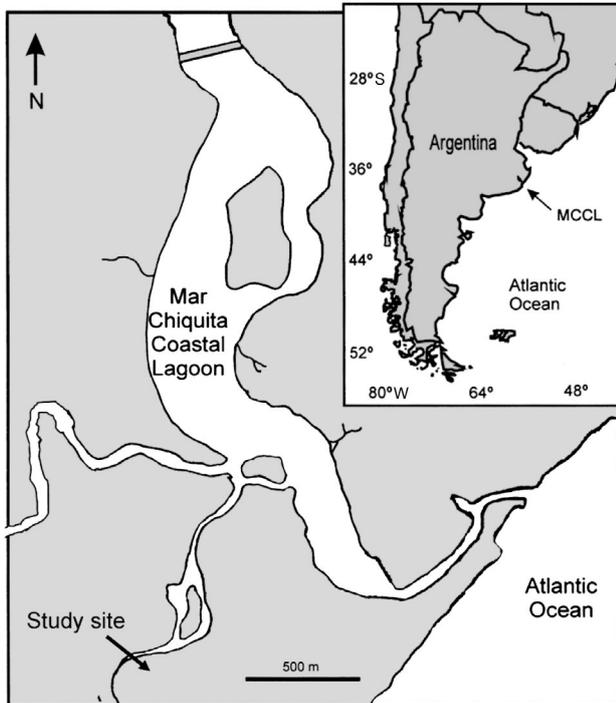


Fig. 1. Location of study site in Mar Chiquita coastal lagoon (MCCL) in Buenos Aires, Argentina

terized by intertidal mudflats and large surrounding marsh areas dominated by *Spartina densiflora* and *Sarcocornia perennis* (Isacch et al. 2006). During the study period (February 2004 to March 2008), 2 El Niño (2005 and 2007) and one La Niña (2008) events occurred (Climate Prediction Center). The Argentinean National Weather Service (Servicio Meteorológico Nacional Argentino, SMN) provided rainfall data from Mar del Plata weather station, located 25 km south of the study site.

#### Relationship between rainfall and sediment salinity

During the summer of 2008, we evaluated whether variations in sediment salinity were related to rainfall fluctuations and marsh elevation. We obtained sediment samples for 8 wk with different cumulative rainfall levels each week (hereinafter weekly rainfall). Sampling was performed on December 21 and 31, January 5, 18, 25 and 31, and February 1 and 28. We divided the marsh into 3 tidal zones with elevations above mean low tides of 0.70, 0.80 and >0.92 m for low, middle and high zones of marsh, respectively. High marsh flooding occurs only during the highest spring or storm-induced tides. The low marsh area is ~9225 m<sup>2</sup>, while the middle and high zones

are ~6750 and 10 125 m<sup>2</sup> respectively. Each week, 7 sediment samples (12 m apart, 2 cm deep and 4 cm diameter) were collected in each marsh zone and in areas with similar vegetation cover. Sediment samples were weighed, oven dried (60°C until constant weight) and dissolved with distilled water (30 ml). After a 48 h period, the salinity of the solution was measured with a conductivity meter (*sensION156* Hach, accuracy of 0.1 psu). We estimated soil salinity as mg salt per g sediment. To evaluate the relationship between sediment salinity and weekly rainfall, we randomly reduced salinity samples to one for each cumulative weekly rainfall (1000 iterations). For each iteration, we calculated a simple linear regression model (Zar 1999) and then obtained the distributions of slope values. The relationship between sediment salinity and weekly rainfall was considered significant when zero was not included within the 95th percentile of the slope values (following Manly 1998). Statistical assumptions of all models and tests were evaluated in all cases. If necessary, transformations were used to meet the assumptions. Square root transformations of the salt content in sediment were performed to satisfy the assumptions of the linear regression models (see Zar 1999).

#### Relationship between rainfall and *Spartina densiflora*

The salt content in *S. densiflora* was quantified during the 8 wk period described above. Each week in each marsh zone, 7 samples (6 plants each) were taken. Plants were dissected to separate stems and leaves, washed and dried to constant weight (60°C). Stems and leaves were crushed and hydrated with distilled water (30 ml) and the salinity of the solution was measured after 48 h as described previously. Water content was estimated as the difference between wet and dry weight. To evaluate the relationships between weekly rainfall and water content and between weekly rainfall and plant salinity, we randomly reduced plant samples and calculated significance as described in the previous section.

Finally, we compared the flower production of *S. densiflora* among years with spring rainfall regimes, since the growing season of *S. densiflora* starts during spring (Alberti et al. 2011) and salinity can affect reproductive output (Minchinton 2002). For this comparison, we counted inflorescences of *S. densiflora* in 10 plots (1 m<sup>2</sup>) in the middle marsh (zone with the greatest abundance of *A. azarae*; Canepuccia et al. 2008) during the summers of 2006, 2007 and 2008

( $n = 3$ ). An ANOVA (Zar 1999) was used to compare the mean number of reproductive structures of *S. densiflora* between years with different rain intensities, followed by a Tukey test to determine which years differed. Square root transformation of the number of spikes was performed to satisfy the assumptions of ANOVA (see Zar 1999).

### Relationship between rainfall and *Akodon azarae*

At a local scale, sediment salinity changes across marsh elevation (Pennings & Bertness 2001) and the performance and nutritional quality of marsh plants is affected by salinity (Canepuccia et al. 2010). Therefore, precipitation could indirectly affect herbivory by rodents through sediment salinity changes. Thus, during the 2004 to 2008 southern hemisphere summers ( $n = 5$ ), we studied the relationship between rainfall and the abundance of *A. azarae*. To estimate rodent abundance ( $\text{ind. ha}^{-1} \text{d}^{-1}$ ), capture samplings were carried out at each marsh zone by placing two  $5 \times 10$  grids of Sherman live traps ( $n = 50$  traps, 10 m apart,  $5000 \text{ m}^2$  per grid). Baited traps (mix of bovine fat and rolled oats) were left for 24 h (following Canepuccia et al. 2008). Captured species were identified and then released at the original location. All procedures for rodent trapping followed the guidelines recommended by the American Society of Mammalogists (ACUC 1998). Linear regression analyses (one per tidal zone; Zar 1999) were used to evaluate the relationship between weekly rainfall and the abundance of *A. azarae*.

### Effects of salt addition on *A. azarae* and *S. densiflora*

To test the relative importance of increased salinity to marsh plants, consumers and their interaction, we conducted a field experiment manipulating sediment salinity. During the summer of 2008, 20 plots ( $3 \times 3 \text{ m}^2$ , 10 m apart) were selected in the middle marsh. Salinity was increased in 10 plots (salt addition plots) by adding salt pellets on the sediment surface, while the other 10 plots remained undisturbed (ambient plots). Salt addition plots and ambient plots were randomly intermixed in areas with similar vegetation cover. The amount of salt added was enough to maintain the sediment salinity at  $\sim 53\text{‰}$ , which was the highest salinity observed during our samplings (see Results). Sediment salinity was monitored weekly as described above. After a month, a  $2 \times 2$  grid using

Sherman traps (1.5 m apart) was placed in each plot. Traps were baited with *S. densiflora* plants from the corresponding plot and were left for 4 nights but checked daily. Captures were identified to species and then released in far locations to prevent recaptures. Finally, salt content in *S. densiflora* was determined by analyzing 6 plants per plot as described above. *t*-tests (Zar 1999) were used to compare the abundance of *A. azarae* and salt content in *S. densiflora* between treatments with and without salt addition.

To evaluate the separate and interactive effects of salinity and *A. azarae* herbivory on *S. densiflora*, a  $2 \times 2$  full-factorial field experiment was conducted. The experiment ran from December 2007 to March 2008. Two factors were manipulated: salt content in the sediment and the presence of *A. azarae*; 50 plots were placed in the middle marsh, in areas with similar vegetation cover ( $n = 10$  per treatment, plus 10 cage controls). Salt content in the sediment was monitored weekly as described above. Plots with salt addition were kept at highest salinity values (as explained before). Ambient plots maintained the natural variation of salt in sediment. Plastic fences ( $50 \times 50 \times 50 \text{ cm}$ , 1 cm mesh) were used to manipulate the presence of *A. azarae* (no fences in grazed plots). Cage controls had 3 fence sides, allowing free movement of rodents (Fig. 2).

To evaluate the effects of salt addition on *S. densiflora*, 5 plants in each plot were tagged using plastic flags. The height and basal diameter of stems were measured both at the beginning and at the end of the experiment. We then quantified both the number of nibbles and the proportion of senescent tissues in leaves at the end of the experiment. For this, we only considered the youngest 4 leaves to exclude the effects of tissue senescence over time. Leaf nibbling by *A. azarae* was easily distinguished from traces of consumption made by other consumers such as *Cavia aperea*, since the latter only consumes the bases of *S. densiflora* stems and discards the rest (Canepuccia et al. 2010). The abundance and activity of the herbivorous burrowing crab *Neohelice granulata* is greatly reduced at this intertidal height (Méndez Casariego et al. 2011). At the end of the experiment, green cover was estimated and the aboveground biomass of *S. densiflora* was harvested and oven dried at  $60^\circ\text{C}$  to constant weight. Two-way ANOVAs were used to evaluate the effects of both factors on *S. densiflora* stem growth and basal diameter, proportion of senescent tissues, green cover, live aboveground biomass and number of nibbled leaves. Finally, to identify possible effects of fences, *t*-tests were used to com-



Fig. 2. Study area (top), exclusion (bottom left) and cage control (bottom right) treatments in the experiment to evaluate the effects of increased salinity and *Akodon azarae* on *Spartina densiflora* performance and their trophic interaction

pare the variables between ambient plots and cage controls. Square root transformation was performed on stem growth to satisfy the assumptions for 2-way ANOVA. To confirm the herbivory of *S. densiflora* by *A. azarae*, composition of 50 fresh feces was analyzed during the summer of 2008. Feces were collected from live traps used during rodent samplings. The percentages of different food items in feces were estimated through microhistological analyses (Holeček et al. 1982). Using an optical microscope (400 $\times$ ), fecal fragments were quantified and classified in 3 categories: *S. densiflora*, other plants, and invertebrates. To confirm that plant fragments were correctly assigned to *S. densiflora*, a collection of *S. densiflora* slides was prepared following the Metcalfe scraping technique (Metcalfe 1960).

## RESULTS

### Relationship between rainfall and sediment salinity

There were negative relationships between weekly rainfall and salt content in sediment in the middle (mean slope =  $-1.29$ , min. =  $-2.22$ , max. =  $-0.01$ , mean  $r^2 = 0.46$ , mean  $p < 0.001$ ) and low marsh (mean slope =  $-1.15$ , min. =  $-2.21$ , max. =  $-0.26$ , mean  $r^2 =$

$0.36$ , mean  $p < 0.05$ ). In both cases, zero was not included within the first 950 iterations of the slope values. No relationship was found in the high marsh (mean slope =  $-0.04$ , min. =  $-0.33$ , max. =  $0.20$ , mean  $r^2 = 0.02$ , mean  $p > 0.05$ ) because zero was included within the first 950 iterations of the slope values.

### Relationship between rainfall and *Spartina densiflora*

Water content in *S. densiflora* was not related to weekly rainfall (in all cases, zero was included within the first 950 iterations of the slope values). There was a negative relationship between rainfall and salt content in stems of *S. densiflora* in the middle marsh (mean slope =  $-1.19$ , min. =  $-2.57$ , max. =  $-0.01$ , mean  $r^2 = 0.19$ , mean  $p < 0.05$ ). Similar relationships were found between rainfall and salt content in leaves of *S. densiflora* in the middle (mean slope =  $-1.23$ , min. =  $-1.91$ , max. =  $-0.35$ , mean  $r^2 = 0.23$ , mean  $p < 0.05$ ) and low marsh (mean slope =  $-1.49$ , min. =  $-2.92$ , max. =  $-0.05$ , mean  $r^2 = 0.22$ , mean  $p < 0.05$ ). No relationships were found in the high marsh. The flower production of *S. densiflora* decreased during years with spring rainfall below the historical mean (200 mm; Table 1).

Table 1. Flower production of *Spartina densiflora* after growing seasons with different rainfall regimes during the 2006–2008 period, and ANOVA results

Year	Spring rainfall (mm)	Flower production (spikes m <sup>-2</sup> )				
		Mean	SD	df	F	p
2006	172.9	10.4	8.59			
2007 El Niño	256.5	12.2	11.72			
2008 La Niña	68.1	1.3	3.86	2.27	8.16	<0.01

### Relationship between rainfall and *Akodon azarae*

There was a positive relationship between the abundances of *A. azarae* and rainfall ( $r^2 = 0.89$ ,  $p < 0.05$ ,  $n = 5$ ; Fig. 3) in the middle marsh. Higher abundances of rodents were observed during rainy summers (El Niño 2005 and 2007), but rodents were not captured in any of the marsh zones during the driest summer (La Niña 2008). No relationships were found at the high and low marsh (in both cases  $p > 0.1$ ).

### Effects of salt addition on *A. azarae* and *S. densiflora*

As expected, the abundance of *A. azarae* in plots with salt addition was 21.5% lower than in ambient plots (Table 2). In turn, the salt content in plants from plots with salt addition was 75% higher in stems and 43% higher in leaves compared with plants from ambient plots (Table 2). However, there were no effects of increased salinity on *S. densiflora* water content ( $p > 0.05$ ).

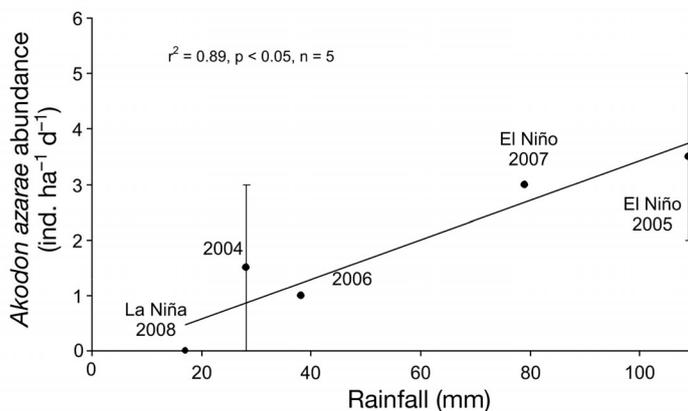


Fig. 3. Relationship between *Akodon azarae* abundance and rainfall in the middle marsh during the summers of 2004–2008. Captures were obtained from two  $5 \times 10$  grids of Sherman live traps ( $n = 50$  traps, 10 m apart, 5000 m<sup>2</sup> per grid). (●) Mean values from total captures in grids ( $n = 2$ )

Table 2. *t*-tests of the effects of salt addition on the abundance of *Akodon azarae* and on *Spartina densiflora* salt content. Significant values in **bold**

	Mean	SD	n	$t_{18}$	p
<b>A. azarae abundance (ind. ha<sup>-1</sup> d<sup>-1</sup>)</b>					
Salt addition	186	5	10	-2.92	<b>&lt;0.05</b>
Control	237	7.48			
<b>Salt content in <i>S. densiflora</i> (mg g<sup>-1</sup>)</b>					
Stem					
Salt addition	128.9	21.2	10	-7.34	<b>&lt;0.05</b>
Control	73.8	10.7			
Leaves					
Salt addition	134.6	25.77	10	-3.27	<b>&lt;0.05</b>
Control	93.9	29.66			

In the second experiment, *A. azarae* presence and salinity did not show interactive effects for any of the dependent variables (Table 3). *S. densiflora* stem growth, live biomass and green cover were reduced by salt additions by 18, 21 and 24% respectively, while the proportion of senescent tissue increased by 32%, but was not affected by herbivory (Table 3). The basal diameter of stems was not affected by salt

Table 3. Two-way ANOVA of the effects of salt addition (S) and herbivory by *Akodon azarae* (H) on the cordgrass *Spartina densiflora*. Significant values in **bold**

	df	MS	F	p
Stem growth				
Herbivory (H)	1	4.45	2.47	0.12
Salt (S)	1	36.04	20.06	<b>0.001</b>
H × S	1	0.09	0.05	0.82
Error	36			
Senescent tissues (leaves)				
H	1	106.25	2.29	0.13
S	1	478.75	10.32	<b>&lt;0.005</b>
H × S	1	0.95	0.02	0.88
Error	36	46.40		
Aboveground live biomass				
H	1	162.7	1.17	0.29
S	1	1507.5	10.85	<b>&lt;0.01</b>
H × S	1	153.2	1.1	0.3
Error	36	138.9		
Damaged leaves				
H	1	0.7	64	<b>&lt;0.001</b>
S	1	0.07	6.58	<b>0.01</b>
H × S	0.03	2.75	0.1	
Error	36	0.01		
Green cover				
H	1	2.5	0.02	0.87
S	1	1428.02	13.94	<b>&lt;0.001</b>
H × S	1	2.5	0.02	0.87
Error	36	102.39		

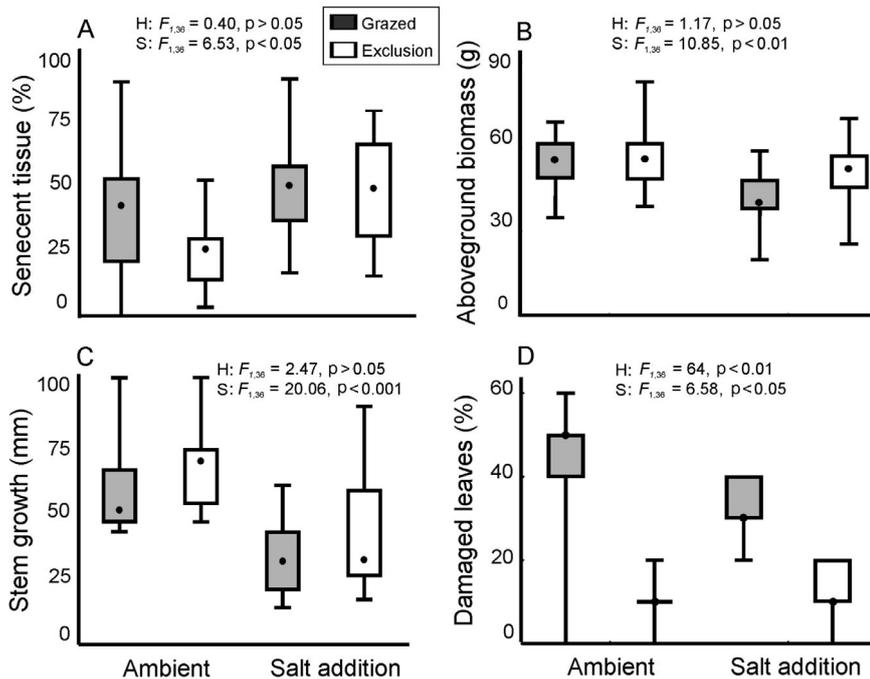


Fig. 4. Effects of salt addition (S) and herbivory by *Akodon azarae* (H) on the proportion of (A) senescent tissues in leaves, (B) live aboveground biomass, (C) stem growth and (D) damaged leaves of *Spartina densiflora*. Boxes: quartiles, vertical lines: 1st and 95th percentiles, dots: medians

addition ( $F = 0.002$ ,  $df = 1$ ,  $p > 0.1$ ). Finally, leaves of *S. densiflora* nibbled by *A. azarae* (damaged leaves) decreased by 40% in salt addition plots (Fig. 4).

Microhistological analyses show that feces of *A. azarae* were mostly composed of invertebrates (mean = 63%, SD = 24), followed by non-*Spartina* plants (mean = 32%, SD = 24) and finally by *S. densiflora* fragments (mean = 5.2%, SD = 2.5).

## DISCUSSION

Salinity stress has pervasive effects in salt marshes, being able to affect species distributions (Bertness 1999) and biological interactions (Bertness & Ewan-chuk 2002, Goranson et al. 2004). Tidal flooding frequency and sun exposure jointly regulate the salinity of marsh sediment (Bertness et al. 1992). In the middle and low marsh, sediment salinity decreased with rainfall, but this was not observed in the high marsh. Previous evidence showed that the highest mean values of sediment salinity are observed in the middle marsh (Fanjul et al. 2008). In our case, sediment salinity in the middle marsh varied widely due to rainfall fluctuations, ranging from being high during the dry periods (~50 psu) to being reduced by 80% during rainy weeks. High salinity in sediment imposes severe diffi-

culties for marsh organisms, particularly for plants, because it reduces water potential (Brown & Pezeshki 2007), nutrient uptake and growth (Brown et al. 2006). *Spartina densiflora* has developed adaptations to reduce both water loss and internal salt concentrations, including salt-secreting glands on leaf surfaces (Maricle et al. 2009). In addition, the genus *Spartina* may store salt in vacuoles, allowing it to tolerate high concentrations of salt (Brown & Pezeshki 2007, Maricle et al. 2009). Our results are consistent with previous knowledge, because salt content in *S. densiflora* was negatively correlated with rainfall. Indeed during dry periods, the salt content in leaves and stems was 2× higher than during rainy periods. In addition, our field experiment supported these observations, showing the same effects following increased salinity (Table 2).

Salinity stress reduces translocation and availability of nutrients (Hu & Schmidhalter 2005). Jointly, the osmoregulatory effort required and the toxicity of  $\text{Cl}^-$  and  $\text{Na}^+$  ions reduce photosynthetic capability, plant growth via translocation of nutrients (Cavaliere & Huang 1981) and plant survival (Brown & Pezeshki 2007). As expected, the performance of *S. densiflora* was impaired by salt addition (see Results), showing reduced growth and biomass and increased proportions of senescent tissue. However, these negative effects can be reduced during rainy periods. For example, reproductive structures of less salt tolerant species are positively affected by increased rainfall during El Niño episodes (Minchinton 2002). In our study, during rainy periods (El Niño 2007), the number of reproductive structures was 3.5× higher than during dry periods (La Niña 2008) when there was almost no spike production. Although *S. densiflora* mainly spreads through clonal growth (Nieva et al. 2005), seed production provides an important resource for seed eaters, such as birds (Cardoni et al. 2007) and rodents (Canepuccia et al. 2008).

Herbivory has been extensively studied in salt marshes (Bos et al. 2005, Silliman et al. 2005) and how this interaction varies along environmental gradients has been of primary interest to ecologists (Crain 2008, Pennings et al. 2009). Plant–consumer interactions may change in different ways depending on the identity of the species involved (Goranson et

al. 2004, Pennings & Silliman 2005). At local scales, high salinities may increase (Silliman et al. 2005, Gedan et al. 2009) or decrease top-down effects (Moon & Stiling 2002, Canepuccia et al. 2010). In addition, salinity conditions can also indirectly affect habitat use by herbivores (Parsons & De la Cruz 1980). For example, during the breeding and post breeding phases, the clumped distribution of the salt marsh harvest mice may be associated with mid-range salinities in plants (Padgett-Flohr & Isakson 2003). Here we show that the abundance of *Akodon azarae* in the marsh decreased under stressful conditions (e.g. during dry years or experimentally increased salinity) and that the consumption of *S. densiflora* by rodents decreased by ~40% following salt addition. Moreover, live *S. densiflora* cover, height and biomass decreased under these experimental conditions. Consistent with studies of stomach content (Bilenca & Kravetz 1998), the fecal analyses of *A. azarae* during the driest summer (La Niña 2008) showed that rodents consumed both invertebrates and plants. The proportion of *S. densiflora* in these feces was very small. Hence, feces should also be analyzed during rainy summers for a better understanding of the relationship between the *S. densiflora* – *A. azarae* trophic interaction and the rodent's habitat use. Changes in the abundance of *A. azarae* could also be mediated by other mechanisms (e.g. plant cover changes; see Table 3) (Bonaventura et al. 1992, Bilenca & Kravetz 1998). Alternatively, the availability of non-vegetal trophic resources (e.g. invertebrates) could also explain the observed changes in *A. azarae* abundance since the abundance and composition of insect assemblages may change with rainfall variations (Polis et al. 1997). Finally, this study provides evidence that rainfall can modify *A. azarae*'s use of suitable habitats other than cropfield edges, roadsides and fencerows affected during postharvest periods (Busch & Kravetz 1992, Bilenca & Kravetz 1998).

The future climate scenario (GCC and ENSO) predicts more frequent and extreme rainfall events (Timmerman et al. 1999, Bates et al. 2008, Re & Barros 2009). Therefore, understanding how rainfall fluctuations can affect natural systems is of considerable importance in managing and preserving biological diversity and ecosystem functioning.

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#### LITERATURE CITED

- Alberti J, Montemayor D, Álvarez F, Méndez Casariego A and others (2007) Changes in rainfall pattern affect crab herbivory rates in a SW Atlantic salt marsh. *J Exp Mar Biol Ecol* 353:126–133
- Alberti J, Cebrian J, Méndez Casariego A, Canepuccia A, Escapa M, Iribarne O (2011) Effects of nutrient enrichment and crab herbivory on a SW Atlantic salt marsh productivity. *J Exp Mar Biol Ecol* 405:99–104
- ACUC (Animal Care and Use Committee) (1998) Guidelines for the capture, handling and care of mammals as approved by the American Society of Mammalogists. *J Mammal* 79:1416–1431
- Bates BC, Kundzewicz ZW, Wu S, Palutikof JP (2008). Climate change and water. Technical paper of the Intergovernmental Panel on Climate Change. IPCC Secretariat, Geneva
- Berbery EH, Doyle M, Barros V (2006) Regional precipitation trends. In: Barros V, Clarke R, Silva Dias P (eds) Climate change in the La Plata Basin. CIMA-CONICET-UBA, Buenos Aires, Argentina, p 61–73
- Bertness MD (1999) The ecology of Atlantic shorelines. Sinauer Associates, Sunderland, MA
- Bertness MD, Callaway R (1994) Positive interactions in communities. *Trends Ecol Evol* 9:191–193
- Bertness MD, Ewanchuk PJ (2002) Latitudinal and climate-driven variation in the strength and nature of biological interactions in New England salt marshes. *Oecologia* 132:392–401
- Bertness MD, Gough L, Shumway SW (1992) Salt tolerances and the distribution of fugitive salt marsh plants. *Ecology* 72:1842–1851
- Bilenca N, Kravetz FO (1998) Seasonal variations in microhabitat use and feeding habits of the pampas mouse *Akodon azarae* in agroecosystems of central Argentina. *Acta Theriol (Warsz)* 43:195–203
- Birkett A, Stevens-Wood B (2005) Effect of low rainfall and browsing by large herbivores on an enclosed savannah habitat in Kenya. *Afr J Ecol* 43:123–130
- Bonaventura SM, Kravetz FO, Suárez OV (1992) The relationship between food availability, space use and territoriality in *Akodon azarae* (Rodentia, Cricetidae). *Mammalia* 56:407–416
- Bos D, Loonen MJ, Stock M, Hofeditz F, van der Graaf A, Bakker JP (2005) Utilization of Wadden Sea salt marshes by geese in relation to livestock grazing. *J Nat Conserv* 13:1–15
- Brown CE, Pezeshki SR (2007) Threshold for recovery in the marsh halophyte *Spartina alterniflora* grown under the combined effects of salinity and soil drying. *J Plant Physiol* 164:274–282
- Brown CE, Pezeshki SR, DeLaune RD (2006) The effects of salinity and soil drying on nutrient uptake and growth of *Spartina alterniflora* in a simulated tidal system. *Environ Exp Bot* 58:140–148
- Brown JH, Whitham TG, Morgan Ernest SK, Gehring CA (2001) Complex species interactions and the dynamics of ecological systems: long-term experiments. *Science* 293: 643–650

- Bruno JF, Stachowicz JJ, Bertness M (2003) Inclusion of facilitation into ecological theory. *Trends Ecol Evol* 18: 119–125
- Busch M, Kravetz FO (1992) Competitive interactions among rodents (*Akodon azarae*, *Calomys laucha*, *Calomys musculinus* and *Oligoryzomys flavescens*) in a two habitat system. Spatial and numerical relationships. *Mammalia* 56:45–56
- Camilloni I, Barros V (2000) The Paraná river response to El Niño 1982–83 and 1997–98 events. *J Hydrometeorol* 1: 412–430
- Canepuccia AD, Fanjul MS, Fanjul E, Botto F, Iribarne OO (2008) The intertidal burrowing crab *Neohelice (=Chasmagnatus) granulata* positively affects foraging of rodents in South Western Atlantic salt marshes. *Estuaries Coasts* 31:920–930
- Canepuccia AD, Cicchino A, Escalante A, Novaro A, Isacch JP (2009) Differential responses of marsh invertebrates to rainfall-induced habitat loss. *Zool Stud* 48:174–183
- Canepuccia AD, Alberti J, Pascual J, Alvarez G, Cebrian J, Iribarne OO (2010) ENSO episodes modify plant/terrestrial herbivore interactions in a southwestern Atlantic salt marsh. *J Exp Mar Biol Ecol* 396:42–47
- Cardoni A, Isacch JP, Iribarne OO (2007) Indirect effects of the intertidal burrowing crab *Chasmagnatus granulatus* in the habitat use of Argentina's South West Atlantic salt marsh birds. *Estuaries Coasts* 30:382–389
- Cavaliere AJ, Huang AH (1981) Accumulation of proline and glycinebetaine in *Spartina alterniflora* Loisel in response to NaCl and nitrogen in the marsh. *Oecologia* 49: 224–228
- Ciais P, Reichstein M, Viovy N, Granier A and others (2005) Europe-wide reduction in primary productivity caused by the heat and drought in 2003. *Nature* 437:529–533
- Climate Prediction Center, NOAA/ National Weather Service. <http://www.cpc.ncep.noaa.gov> (accessed Sep. 2009)
- Crain CM (2008) Interactions between marsh plant species vary in direction and strength depending on environmental and consumer context. *J Ecol* 96:166–173
- Eslami Andargoli L, Dale P, Sipe N, Chaseling J (2009) Mangrove expansion and rainfall patterns in Moreton Bay, southeast Queensland, Australia. *Estuar Coast Shelf Sci* 85:292–298
- Estes JA, Terborgh J, Brashares JS, Power ME and others (2011) Trophic downgrading of planet earth. *Science* 333:301–306
- Fanjul E, Grela MA, Canepuccia A, Iribarne O (2008) The southwest Atlantic intertidal burrowing crab *Neohelice granulata* modifies nutrient loads of phreatic waters entering coastal areas. *Estuar Coast Shelf Sci* 79:300–306
- Fay PA, Kaufman DM, Nippert JB, Carlisle JD, Harper CW (2008) Changes in grassland ecosystem function due to extreme rainfall events: implications for responses to climate change. *Glob Change Biol* 14:1600–1608
- Gedan KB, Silliman BR, Bertness MD (2009) Centuries of human-driven change in salt marsh ecosystems. *Annu Rev Mar Sci* 1:117–141
- Goranson CE, Ho CK, Pennings SC (2004) Environmental gradients and herbivore feeding preferences in coastal salt marshes. *Oecologia* 140:591–600
- Grimm AM, Tedeschi RG (2009) ENSO and extreme rainfall events in South America. *J Clim* 22:1589–1609
- Hillebrand H, Gruner DS, Borer ET, Bracken MES and others (2007) Consumer versus resource control of producer diversity depends on ecosystem type and producer community structure. *Proc Natl Acad Sci USA* 104: 10904–10909
- Hodara K, Busch M, Kittlein M, Kravetz FO (2000) Density-dependent habitat selection between maize cropfields and their borders in two rodent species (*Akodon azarae* and *Calomys laucha*) of Pampean agroecosystems. *Evol Ecol* 14:571–593
- Holechek JL, Vavra M, Pieper RD (1982) Botanical composition determination of range herbivore diets: a review. *J Range Manage* 35:309–315
- Holmgren M, Scheffer M, Ezcurra E, Gutierrez JR, Mohren GMJ (2001) El Niño effects on the dynamics of terrestrial ecosystems. *Trends Ecol Evol* 16:89–94
- Hu Y, Schmidhalter U (2005) Drought and salinity: a comparison of their effects on mineral nutrition of plants. *J Plant Nutr Soil Sci* 168:541–549
- Hutchinson GE (1957) Concluding remarks. *Cold Spring Harb Symp Quant Biol* 22:415–427
- Isacch JP, Costa CSB, Rodríguez-Gallego L, Conde D, Escapa M, Gagliardini DA, Iribarne OO (2006) Distribution of saltmarsh plant communities associated with environmental factors along a latitudinal gradient on the south-west Atlantic coast. *J Biogeogr* 33:888–900
- Knapp AK, Fay PA, Blair JM, Collins SL and others (2002) Rainfall variability, carbon cycling, and plant species diversity in a mesic grassland. *Science* 298:2202–2205
- Lanfredi NW, Balestrini CF, Mazio CA, Schmidt SA (1987) Tidal sandbanks in Mar Chiquita Coastal Lagoon, Argentina. *J Coast Res* 3:515–520
- Manly BFJ (1998) Randomization, bootstrap and Monte Carlo methods in biology, 2<sup>nd</sup> edn. Chapman & Hall, London
- Maricle BR, Koteyeva NK, Voznesenkaya EV, Thomasson JR, Edwards GE (2009) Diversity in leaf anatomy, and stomatal distribution and conductance, between salt marsh and freshwater species in the *C<sub>4</sub>* genus *Spartina*. *New Phytol* 184:216–233
- Méndez Casariego A, Alberti J, Luppi T, Daleo P, Iribarne O (2011) Habitat shifts and spatial distribution of the intertidal crab *Neohelice (Chasmagnathus) granulata* Dana. *J Sea Res* 66:87–94
- Menge BA, Sutherland JP (1987) Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. *Am Nat* 130:730–757
- Metcalfe CR (1960) Anatomy of the monocotyledons, Graminae. Clarendon Press, Oxford
- Minchinton TE (2002) Precipitation during El Niño correlates with increased spread of *Phragmites australis* in New England, USA, coastal marshes. *Mar Ecol Prog Ser* 242:305–309
- Moon DC, Stiling P (2000) Relative importance of abiotically induced direct and indirect effects on a salt-marsh herbivore. *Ecology* 81:470–481
- Nieva FJJ, Eloy M, Castellanos EM, Castillo EM, Figueroa ME (2005) Clonal growth and tiller demography of the invader cordgrass *Spartina densiflora* Brongn at two contrasting habitats in SW European salt marshes. *Wetlands* 25:122–129
- Ogutu JO, Piepho HP, Dublin HT, Bhola N, Reid RS (2008) Rainfall influences on ungulate population abundance in the Mara-Serengeti ecosystem. *J Anim Ecol* 77: 814–829
- Pace ML, Cole JJ, Carpenter SR, Kitchell JF (1999) Trophic cascades revealed in diverse ecosystems. *Trends Ecol Evol* 14:483–488

- Padgett-Flohr GE, Isakson L (2003) A random sampling of salt marsh harvest mice in a muted tidal marsh. *J Wildl Manag* 67:646–653
- Pandey CB, Singh JS (1992) Rainfall and grazing effects on net primary productivity in a tropical savanna, India. *Ecology* 73:2007–2021
- Parmesan C (2006) Ecological and evolutionary responses to recent climate change. *Annu Rev Ecol Evol Syst* 37: 637–669
- Parsons KA, de la Cruz AA (1980) Energy flow and grazing behavior of conocephaline grasshoppers in a *Juncus roemerianus* marsh. *Ecology* 61:1045–1050
- Pennings SC, Bertness MD (2001) Salt marsh communities. In: Bertness MD, Gaines SD, Hay M (eds) *Marine community ecology*. Sinauer Associates, Sunderland, MA, p 289–316
- Pennings SC, Silliman BR (2005) Linking biogeography and community ecology: latitudinal variation in plant–herbivore interaction strength. *Ecology* 86:2310–2319
- Pennings SC, Grant MB, Bertness MD (2005) Plant zonation in low-altitude salt marshes: disentangling the roles of flooding, salinity and competition. *J Ecol* 93:159–167
- Pennings SC, Ho CK, Salgado CS, Wieski K, Dave N, Kunza AE, Wason EL (2009) Latitudinal variation in herbivore pressure in Atlantic Coast salt marshes. *Ecology* 90: 183–195
- Peñuelas J, Filella I, Zhang XY, Llorens L and others (2004) Complex spatiotemporal phenological shifts as a response to rainfall changes. *New Phytol* 161:837–846
- Philippart CJM, Anadón R, Danovaro R, Dippner JW and others (2011) Impact of climate change on European marine ecosystems: observations, expectations and indicators. *J Exp Mar Biol Ecol* 400:52–69
- Polis GA, Hurd SD, Jackson CT, Sanchez Piñero F (1997) El Niño effects on the dynamics and control of an island ecosystem in the Gulf of California. *Ecology* 78: 1884–1897
- Re M, Barros VM (2009) Extreme rainfalls in SE South America. *Clim Change* 96:119–136
- Reta R, Martos P, Perillo G, Piccolo MC, Ferrante A (2001) Características hidrográficas del estuario de la laguna Mar Chiquita. In: Iribarne O (ed) *Reserva de Biosfera Mar Chiquita: características físicas, biológicas y ecológicas*. Editorial Martín, Mar del Plata, p 31–52
- Sala OE, Gherardi LA, Reichmann L, Jobbágy E, Peters D (2012) Legacies of precipitation fluctuations on primary production: theory and data synthesis. *Philos Trans R Soc Lond B* 367:3135–3144
- Scavia D, Field JC, Boesch DF, Buddemeier RW and others (2002) Climate change impacts on US coastal and marine ecosystems. *Estuaries* 25:149–164
- Silliman BR, van de Koppel J, Bertness MD, Stanton LE, Mendelssohn IA (2005) Drought, snails, and large-scale die-off of southern U.S. salt marshes. *Science* 310: 1803–1806
- Timmerman A, Oberhuber J, Bacher A, Esch M, Latif M, Roeckner E (1999) Increased El Niño frequency in a climate model forced by future greenhouse warming. *Nature* 398:694–696
- Valiela I (2006) *Global coastal change*. Blackwell, Oxford
- Walther GR, Post E, Convey P, Menze A and others (2002) Ecological responses to recent climate change. *Nature* 416:389–395
- Whittaker RH (1975) *Communities and ecosystems*, 2<sup>nd</sup> edn. Macmillan, London
- Zar JH (1999) *Biostatistical analysis*, 4<sup>th</sup> edn. Prentice-Hall, Upper Saddle River, NJ
- Zhu K, Woodall CW, Clark JC (2012) Failure to migrate: lack of tree range expansion in response to climate change. *Glob Change Biol* 18:1042–1052

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