Ecological processes shaping Central Patagonian salt marsh landscapes

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Abstract   Plant zonation is one of the most conspicuous ecological features of salt marshes worldwide. In this work we used a combination of field transplant and greenhouse experiments to evaluate the importance of interspecific interactions and physical stress in the determination of the major plant zonation patterns in Central Patagonian salt marshes. There, *Spartina alterniflora* dominates the low marsh, and *Sarcocornia perennis* the high marsh. We addressed two questions: (i) What prevents *Spartina alterniflora* from colonizing the *Sarcocornia perennis*-dominated high marsh zone? and (ii) What prevents *Sarcocornia perennis* from colonizing the *Spartina alterniflora*-dominated low marsh zone? Our experimental transplants combined with neighbour exclusion treatments showed that the presence of *Sarcocornia perennis* negatively affects *Spartina alterniflora*, preventing it from surviving and/or spreading. Complementary field transplant and greenhouse experiments showed that *Sarcocornia perennis* did not survive the frequent tidal submersion by approximately 1.5 m of turbid seawater in the *Spartina alterniflora* zone, but its survival was independent of the presence of *Spartina* neighbours, and of the strong soil anoxia as well. Our results suggest that *Spartina alterniflora* is excluded by *Sarcocornia perennis* towards the low marsh, where frequent and prolonged submersion limit the survival of the latter. We provide and discuss key baseline information to facilitate the future design of ecophysiological experiments designed to accurately identify the exact mechanisms acting in every situation.

Key words: neighbour exclusion, salt marsh, *Sarcocornia*, soil anoxia, *Spartina*, submersion, zonation.

INTRODUCTION

Plant zonation is probably the most conspicuous feature characterizing salt marshes at the landscape scale (Adam 1993). For decades, salt marsh ecologists have produced large numbers of studies describing plant zonation patterns (e.g. USA: Mahall & Park 1976a,b,c; Bertness 1999; Pennings & Bertness 2001; Brazil: Costa *et al.* 2003; Argentina: Isacch *et al.* 2006; Bortolus *et al.* 2009; worldwide: Adam 1993). Most salt marsh plants are found in zones parallel to the coastline with specific species compositions that usually change with relative elevation and distance from the seashore. However, these patterns may differ between regions worldwide (Adam 1993). For example, while the low marsh in New England (USA) is dominated by *Spartina alterniflora*, this same marsh level is dominated by *Puccinellia maritima* in northwestern Europe (Tessier *et al.* 2002), by *Sarcocornia perennis* ssp. *perennis* in Southern Spain (Redondo-gómez *et al.* 2007) and by different species of *Salicornia*, *Suaeda* and *Puccinellia* among others in the Arctic

and some continental European salt marshes (e.g. Vince & Snow 1984; Vevle 1985; Stone 1993; Funk *et al.* 2004). The variation in these patterns is not easy to fully understand, as it may derive from regional differences in the flora, in local environmental conditions (such as tidal amplitude, coastal geomorphology and local currents) and/or in ecological processes (such as biotic interactions; see reviews in Chapman 1960; Adam 1993; Weinstein & Kreeger 2000; Pennings & Bertness 2001).

Few vascular plant species are able to survive in the lowest intertidal level, where tidal amplitudes and inundation frequency are largest, especially in macrotidal systems where the vertical distance between low and high tides can reach values close to 14 m. Nevertheless, as substrate elevation increases, and inundation becomes less frequent, the higher salt marsh levels are commonly characterized by more complex communities with a large variety of ecological interactions going on (Adam 1993). It has been hypothesized that the lower limit of the salt marsh is set by physical stress, such as waterlogged soils with reducing redox potential, soil salinity and/or tidal submersion, whereas the upper limit is set by ecological processes, such as competition, and/or facilitation (Bertness

1999; Pennings & Bertness 2001; Pennings *et al.* 2005). Although these hypotheses are supported by local and regional evidence, most of these data were collected in salt marshes of the Northern Hemisphere (e.g. Pennings & Callaway 1992; Bertness *et al.* 2002; Minchinton & Bertness 2003). More research is needed to evaluate if these hypotheses can be supported in other regions where salt marshes have been less studied, and where the environmental conditions and biotic interactions may create alternative ecological scenarios.

Studies on flooding stress importance have historically concentrated mostly on the tolerance of marsh plant species to waterlogged soil conditions (Cooper 1982; Justin & Armstrong 1987; Pezeshki 2001; Hessini *et al.* 2009). However, in addition to the factors affecting below-ground plant structures, the above-ground structures are completely covered by seawater once or twice a day, potentially interfering with a variety of physiological pathways (Mommer & Visser 2005; Mateos-Naranjo *et al.* 2007). Furthermore, negative interactions like herbivory (Costa *et al.* 2003; Silliman & Bortolus 2003; Bortolus 2006) and predation (Kneib 1984) as well as a variety of positive interactions (Bertness & Callaway 1994; Canepuccia *et al.* 2007) were also shown to affect plant and animal zonation in marshes worldwide. However, the amount of information produced worldwide is not regionally homogeneous. In the temperate northern coast of Argentina, for example, virtually all experimental field studies evaluating the role of ecological interactions shaping the structure of salt marsh communities have been focused on plant–animal interactions (e.g. Bortolus & Iribarne 1999; Bortolus *et al.* 2002; Canepuccia *et al.* 2007; Alberti *et al.* 2008; Daleo & Iribarne 2009), while relatively little is known about plant–plant interactions and tolerance to abiotic stress in this part of the Southern Hemisphere (e.g. Alberti *et al.* 2007; Daleo *et al.* 2008). The salt marshes along the Patagonian coast in Southern Argentina and Chile (Isacch *et al.* 2006; Bortolus *et al.* 2009), are among the least studied worldwide, and only recently have researchers begun to examine the processes that shape the structure of the communities living there (Isacch *et al.* 2006; Alberti *et al.* 2007; Bortolus *et al.* 2009; Fariña *et al.* 2009).

In this work, we evaluate the hypotheses that interspecific interactions and stress tolerance can shape the pattern of distribution of the dominant plant species, *Sarcocornia perennis* and *Spartina alterniflora,* in two Central Patagonian salt marshes where they dominate the high and low marsh, respectively (Bortolus *et al.* 2009). In these marshes, a major difference between the zones dominated by *Spartina* and *Sarcocornia* is that the latter usually forms dense carpets covering more than 80% of the substratum

and may be accompanied by the austral cordgrass *Spartina densiflora*, the marsh shrub *Limonium brasiliense*, and a few other halophytes such as *Suaeda* spp. and *Atriplex* spp., but never *Spartina alterniflora* (Bortolus *et al.* 2009). The cordgrass *Spartina alterniflora*, on the other hand, forms dense monospecific stands along the lowest marsh level (Bortolus *et al.* 2009). While the salt marshes located at 42°S or lower, along the Atlantic coast of South America, are dominated by *Spartina* species, these species become less important with increasing latitude. At latitudes greater than 43°S all salt marshes are exclusively dominated by *Sarcocornia perennis*, and *Spartina* species are rare or absent (Bortolus *et al.* 2009). However, these two types of salt marshes overlap between 42°S and 43°S, in Central Patagonia. By performing field and greenhouse manipulative experiments, we addressed the following questions: (i) Is *Spartina alterniflora* excluded from the high marsh by a negative effect caused or mediated by the presence of *Sarcocornia perennis*? and (ii) Is *Sarcocornia perennis* excluded from the low marsh by *Spartina alterniflora* and/or waterlogged soil and/or submersion intolerance?

METHODS

Study area

We worked in the Riacho *Spartina* marsh (42°25′S, 64°37′W), and the Fracasso *Sarcocornia* marsh (42°25′S, 64°07′W) at the Península Valdés Natural Reserve (Chubut, Argentina; Fig. 1). The marsh levels relative to the Argentinean hydrographic zero in Riacho marsh (slope: 4%) were +4.42 m (low marsh) and +5.77 m (high marsh), and in Fracasso marsh (slope: 0.4%) were +5.67 m (low marsh) and +6.32 m (high marsh). Both salt marshes are semidiurnal macro-tidal systems (tidal amplitude: 7–8 m), with soil redox potential in the root zone (0–10 cm) highly reducing in the low marsh (Riacho: Eh: −269.20 ± 12.20 mV; Fracasso: Eh: −269.88 ± 11.72 mV; mean ± SE) and strongly oxidizing in the high marsh (Riacho: Eh: 150.25 ± 5.14 mV; Fracasso: Eh: 172.82 ± 8.67 mV; means of 20 readings using a portable metre and electrode system Termo/pHmetro Altronix TPA-IV, following tidal submersion throughout the year during the period 2007–2009; P. Bouza and I. Rios, unpubl. data, 2009). Taxonomic identifications were made following the Flora Patagónica identification guide (Correa 1998), updating the taxonomic status of the glasswort *Salicornia ambigua* Michx. to *Sarcocornia perennis* (Mill.) A.J. Scott (following Zuloaga & Morrone 1999, but see Alonso & Crespo 2008).

Neighbour exclusion experiment

In order to evaluate if the absence of *Spartina alterniflora* (henceforth *Spartina*) in the high marsh is due to a negative
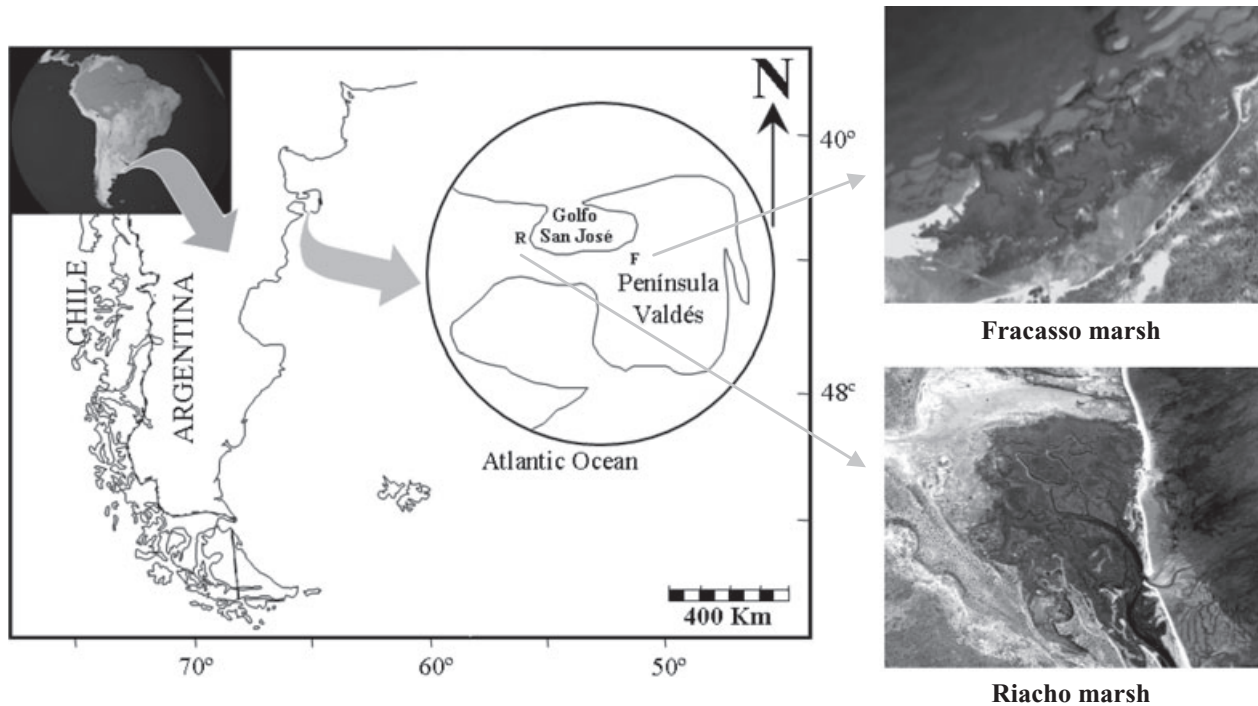
Fig. 1. Map showing the study sites along the isthmus of Península Valdés. F, Fracasso marsh; R, Riacho marsh.

effect caused or mediated by the presence of *Sarcocornia perennis* (henceforth *Sarcocornia*) we performed a field transplant experiment. We replicated this experiment in two sites with similar geomorphology and vegetation characteristics within Fracasso marsh. Cores (20-cm-diameter × 20-cm-deep) with *Spartina* (hereafter called '*Spartina* transplants') transplanted in each site from the low marsh to the high marsh and randomly arranged in the following four treatments: (i) with neighbours: 10 of these *Spartina* transplants were placed in the high marsh. The transplant process was conducted with special care in order to avoid soil trampling and to minimize damages on the surrounding *Sarcocornia* neighbours within an area of 1 m; (ii) without neighbours: 10 *Spartina* transplants were randomly placed in the same high marsh as the previous treatment but all neighbours were removed by clipping a 50-cm-radius border around the plant at the soil surface every 2 weeks until plants stopped regrowing (see Bertness 1991). To avoid the invasion of roots by surrounding plants, the transplants were potted in hard nylon pots (i.e. 200 μm) with holes in the bottom to ensure soil drainage. In addition, we trenched around the transplants by cutting with a knife (25-cm-long blade) any new root intrusion from the surrounding vegetation during the entire experiment; (iii) manipulation control: 10 *Spartina* transplants were collected and then placed back in the soil within the low marsh; and (iv) total control: six unmanipulated areas of salt marsh (20-cm-diameter) with *Spartina* were chosen at random and tagged, within the same low marsh where the *Spartina* transplants were collected for the other treatments but avoiding the areas disturbed by previous collections. The initial average stem density of *Spartina* in all the experimental units was 511 stems per square metre (SE = 16.39), and it was not significantly different among

treatments or between sites (site: $F_{1,64} = 0.069$, $P = 0.42$; treatments: $F_{3,3} = 0.69$, $P = 0.61$; interaction: $F_{3,64} = 1.89$, $P = 0.14$). The experiment lasted 11 months from August 2006 to June 2007, when the density and cover of *Spartina* were estimated for each treatment and site. In addition, the interspecific interactions were evaluated by using the improved relative neighbour effect (RNE) index (following Markham & Chanway 1996): RNE = $(P_{-N} - P_{+N})/x$ where P is density of *Spartina* in the presence (+N) and absence (–N) of *Sarcocornia* neighbours, and x is the highest value of (P_{-N}; P_{+N}). An RNE value of 0 indicates absence of interaction, but negative and positive values indicate positive and negative interactions, respectively. For each site, we estimated the RNE of 10 pairs of *Spartina* transplants, each made up at random of one transplant from the treatment with neighbours and one from the without neighbours treatment.

Waterlogging and submersion experiments

In order to assess the combined effect of waterlogged anoxic soil and submersion during high tide on *Sarcocornia perennis* in the low marsh we performed a transplant experiment in two sites within Riacho marsh, with the following treatments: (i) submersion: 10 cores (20-cm-diameter × 20-cm-deep) with *Sarcocornia* (hereafter called '*Sarcocornia* transplants') from the *Sarcocornia*-dominated high marsh level were transplanted into the monospecific *Spartina alterniflora*-dominated low marsh level; (ii) manipulation control: 10 *Sarcocornia* transplants were replanted into the same high marsh and site from where they were collected; and (iii) total control: 10 unmanipulated areas of salt marsh with *Sarcocor-*

nia (20-cm-diameter) were chosen at random and tagged within the same high marsh level where the *Sarcocornia* transplants were collected for the other treatments but avoiding the areas disturbed by previous collections. (iv) A fourth treatment was added to evaluate possible interaction with the neighbouring *Spartina* in the low marsh. This treatment was similar to the 'submersion treatment' but we then proceeded with the same protocol explained in the previous section for the 'without neighbours' treatment. All treatments were replicated 10 times within each site in the salt marsh. The initial average plant cover of *Sarcocornia* used in the experiment was 95% (SE = 0.50) and this was not significantly different among treatments or between sites (site: $F_{1,54} = 0.41$, $P = 0.52$; treatments: $F_{2,56} = 0.08$, $P = 0.91$; interaction: $F_{2,54} = 0.10$, $P = 0.90$). The experiment started in the early spring of 2006, and finished in autumn of 2008. At the end of the experiment above-ground biomass was harvested and oven-dried at 70°C to constant weight. From the beginning of the experiment, on a weekly basis, we recorded the percentage of plant survival in each core, and measured soil redox potentials in the root zone (0–10 cm) of each core with a portable metre and electrode system (Termo/pHmetro Altronix TPA-IV).

In order to evaluate the effect of the waterlogged soil on *Sarcocornia*, independently of the tidal submersion (i.e. approx 1.5-m deep twice a day), we conducted a greenhouse experiment with the following treatments: (i) waterlog: 10 cores with *Sarcocornia* from the high marsh (same size as in the previous experiment) were placed in plastic pots with no holes and watered with fresh water at least twice a week in order to keep the water level 5 cm above the soil surface; and (ii) drainage: 10 cores with *Sarcocornia* were taken and placed in plastic pots perforated to let the soil drain. These pots were watered with fresh water twice a week to keep soil wet but never flooded. The soil redox potential in the root zone of each pot was periodically measured and found below −100 mV for the waterlog treatment and above 100 mV for the drainage treatment. The initial average plant cover in all *Sarcocornia* pots used in the experiment was 90% (SE = 1.50), and this was not significantly different between treatments ($F_{1,18} = 0.16$, $P = 0.69$). The experiments started in the early spring of 2007 and ended in autumn of 2008, after which above-ground biomass was harvested from each pot and oven-dried at 70°C to constant weight.

We also performed a complementary field experiment in order to assess the effect of tidal water submersion on *Sarcocornia* independently of edaphic factors such as the soil anoxia typical of waterlogged soils. The treatments were: (i) above-ground submersion: 10 cores (20-cm-diameter × 20-cm-deep), each one with a single-stemmed *Sarcocornia* plant, were transplanted from the high marsh to the low marsh; (ii) manipulation control: another 10 single-stemmed *Sarcocornia* plants were collected with a metal core (also 20-cm-diameter × 20-cm-deep), and replanted into the same place from which they were collected. The soil material of every core (in both treatments) was tightly wrapped with a 2-μm-thick, black, nylon bag and hermetically sealed around the base of the stem with Teflon tape in order to prevent water penetration and maintain similar edaphic conditions to those in the high marsh. We found this method highly successful in keeping the soil material dry and isolated from water penetration by conducting preliminary tests in the laboratory (Y.

Idaszkin, unpubl. data, 2006). In addition, we confirmed weekly that the soil redox potential inside each bag of treatments i and ii was constant throughout the experiment (i.e. ≥100 mV); (iii) total control: 10 unmanipulated areas of salt marsh (20-cm-diameter) with single-stemmed plants were chosen at random and tagged within the same high marsh level where the other transplants were collected, but avoiding the areas disturbed by previous collections. The initial average plant cover of *Sarcocornia* used in the experiment was 31% (SE = 1.50) and at the beginning of the experiment this was not significantly different among treatments or between sites (site: $F_{1,54} = 0.49$, $P = 0.48$; treatments: $F_{2,2} = 0.01$, $P = 0.98$; interaction: $F_{2,54} = 1.61$, $P = 0.20$). The experiments started in the early spring of 2007 and ended in autumn of 2008, after which above-ground biomass was harvested from each core and oven-dried at 70°C to constant weight.

Data analysis

To evaluate differences among treatments we used one-way ANOVA. In each case where we replicated the experiment in two sites in the salt marsh, we used two-way ANOVA with interactions to test the effect of treatments and sites on plant measurements. To compare the RNE between sites we used one-way ANOVA. Also, we contrasted the RNE sample mean with the expected mean of zero (i.e. no interaction) using one-sample *t*-test (Zar 1999). Before the analyses, data were tested for normality with the Shapiro–Wilk test and for homogeneity of variance with the Levene test. To correct for non-normality and heterogeneity of variance, the density of *Spartina* variable was ln(X+1)-transformed and *Spartina* cover was arcsine-transformed (Zar 1999).

RESULTS

Neighbour exclusion experiment

The density of *Spartina* was significantly higher in the treatment without neighbours than in the treatment with neighbours (ln(X+1)-transformed, site: $F_{1,36} = 1.09$, $P = 0.30$; treatments: $F_{1,37} = 25.27$, $P < 0.0001$; interaction: $F_{1,36} = 0.87$, $P = 0.35$; Fig. 2a). Also the cover of *Spartina* was significantly higher in the treatment without neighbours than in the treatment with neighbours (arcsine-transformed, site: $F_{1,36} = 1.29$, $P = 0.26$; treatments: $F_{1,37} = 100.90$, $P < 0.0001$; interaction: $F_{1,36} = 0.81$, $P = 0.37$; Fig. 2b). Analysis of controls showed that there was no effect of manipulation (site: $F_{1,28} = 1.62$, $P = 0.21$; treatments: $F_{1,29} = 0.56$, $P = 0.45$; interaction: $F_{1,28} = 0.13$, $P = 0.71$). We did not find signs of herbivory in any of the experimental plots or in the surrounding areas throughout the study in any study site.

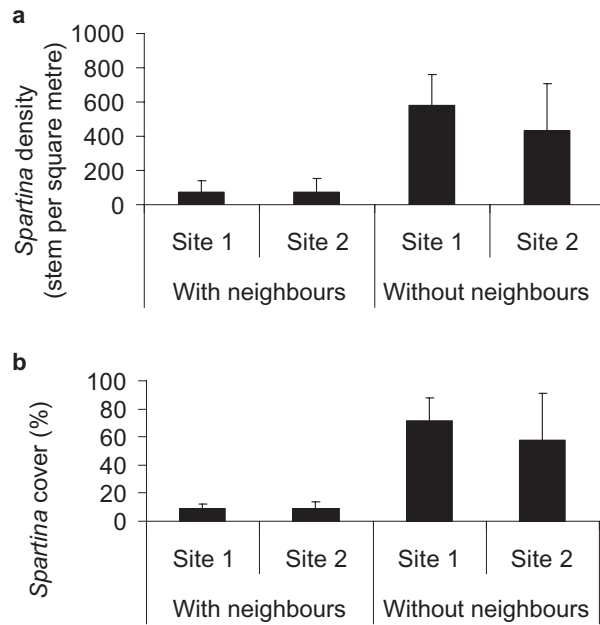The relative neighbour effect index (RNE; mean ± SE; $n = 10$) in site 1 was 0.87 ± 0.04 and in

Fig. 2. *Spartina alterniflora* (a) density and (b) cover in the field experimental treatments with and without neighbours. Data are means + standard deviation (SD).

site 2 was 0.78 ± 0.08. There were no significant differences between the sites in the RNE ($F_{1,18} = 1.08$; $P = 0.31$). Positive values of this index showed a negative effect of *Sarcocornia* neighbours upon *Spartina* (site 1: $t_9 = 22.8$, $P < 0.0001$; site 2: $t_9 = 9.45$, $P < 0.0001$).

Waterlogging and submersion experiments

Sarcocornia transplants did not survive in the submersion treatment, but 100% of the control transplants did. The evaluation of control treatments showed that the experimental manipulation did not affect either the survival or the above-ground biomass of *Sarcocornia* (site: $F_{1,36} = 0.39$, $P = 0.53$; treatments: $F_{1,37} = 0.006$, $P = 0.93$; interaction: $F_{1,36} = 0.25$, $P = 0.61$; Fig. 3a). In the submersion treatment the soil redox potential (mean $\pm$ SE, $n = 10$) declined from strongly oxidizing values (156.20 ± 3.74 mV) to reducing values (-118 ± 17.78). The removal of the *Spartina* neighbours did not have any effect on the survival of the *Sarcocornia* transplants (0% survival). The soil redox potential was -268.5 ± 30.06 mV in the waterlog treatment and 209.8 ± 6.96 mV in the drainage treatment. All *Sarcocornia* survived (100% survival) in both treatments, and there were no significant differences in above-ground biomass between treatments ($F_{1,18} = 0.13$, $P = 0.72$; Fig. 3b). In the above-ground submersion treatment no *Sarcocornia* transplants survived, but all transplants survived in the manipulation
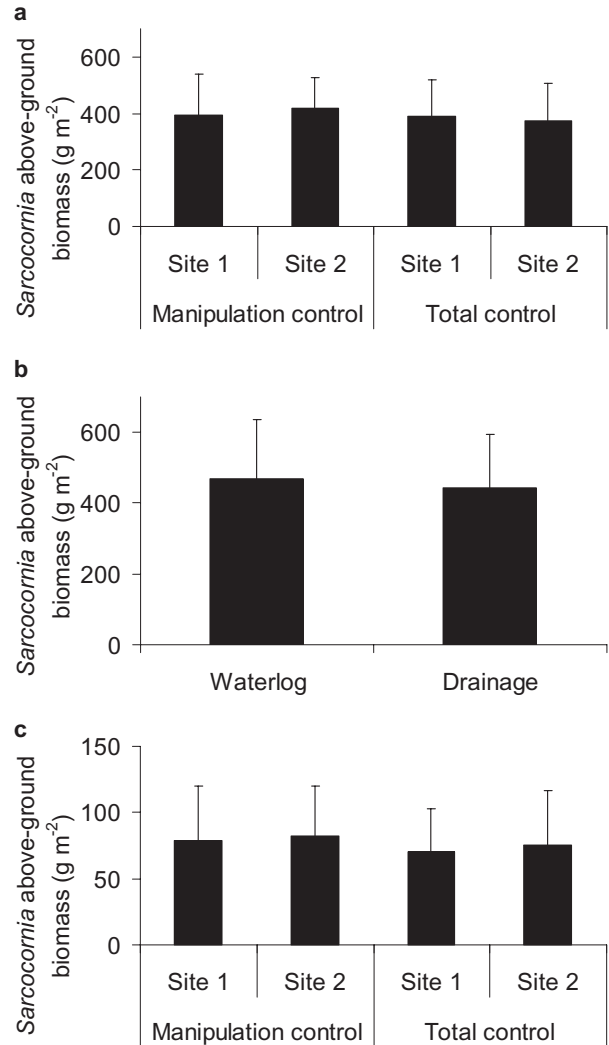

Fig. 3. *Sarcocornia perennis* above-ground biomass in (a) manipulation control and total control treatments in the experiment to evaluate the effect of tidal submersion on *Sarcocornia perennis*; (b) waterlog and drainage treatments in the greenhouse experiment to evaluate the effect of waterlogging on *Sarcocornia perennis*; and (c) manipulation control and total control treatments in the experiment to evaluate the effect of tidal water on *Sarcocornia perennis* independently of the soil anoxia. Data are means + standard deviation (SD).

controls. As in the rest of the experiments, there was no manipulation effect in any case (site: $F_{1,36} = 0.04$, $P = 0.86$; treatments: $F_{1,37} = 0.23$, $P = 0.63$; interaction: $F_{1,36} = 0.58$, $P = 0.45$; Fig. 3c).

DISCUSSION

The Patagonian salt marshes present two major physiognomies based on their dominant botanic composition: *Spartina*-marshes and *Sarcocornia*-marshes (Bortolus *et al.* 2009). The *Spartina*- and the

Sarcocornia-marshes are increasingly common and larger at latitudes lower and higher than 42°S, respectively. A feature common to these two kinds of salt marsh is that *Spartina alterniflora*, when present, occupies the lowest marsh level, and *Sarcocornia perennis* the highest (Bortolus *et al.* 2009). The herbivorous burrowing crab *Neohelice granulata* was reported regulating *Spartina* production and distribution in northern salt marshes of South America (e.g. Bortolus & Iribarne 1999; Costa *et al.* 2003; Alberti *et al.* 2007). However, our study sites are in the southern border of the geographic distribution of this crab and its abundance was virtually nil while we conducted our study, and herbivory signs were not found in any transplant or in the surrounding areas. This is consistent with the fact that *N. granulata* is rare or absent in the rest of the Patagonian marshes at the same or higher latitudes, respectively. Our results support two main conclusions in relation to the marshes where the species of these two genera coexist in Central Patagonia: (i) the higher intertidal limit of distribution of *Spartina alterniflora* is conditioned by a negative effect caused or mediated by the presence of *Sarcocornia perennis*; and (ii) the leading influence shaping the lower intertidal limit of distribution of *Sarcocornia perennis* is the lack of resistance in its above-ground structures to prolonged submersion, probably followed by a toxic effect of the negative soil redox potential (Bouza *et al.* 2008; Bortolus *et al.* 2009). Below we provide and discuss baseline information to facilitate the future design of ecophysiological experiments directed to accurately identify the exact mechanisms acting in every situation.

What prevents *Spartina alterniflora* from colonizing the *Sarcocornia perennis*-dominated high marsh zone?

The *Spartina alterniflora* transplanted into the high marsh grew consistently better when the neighbours were removed than when they were present (Fig. 2). This result is particularly important because it shows not only that *Spartina alterniflora* is able to survive in the high marsh, but also that the presence of *Sarcocornia perennis* exerts a negative effect on *Spartina alterniflora*. In New England salt marshes (USA), a plant zonation pattern occurs with *Spartina alterniflora* dominating the low marsh and *Spartina patens* dominating the seaward border of the high marsh. A manipulative field experimental study showed that the performance of *Spartina alterniflora* improved in the high marsh when *Spartina patens* is removed, and this response was attributed to interspecific competition (Bertness 1991; Levine *et al.* 1998; Emery *et al.* 2001). A similar experimental approach was conducted in a Southern Californian salt marsh, and

concluded that the high marsh dominant *Arthrocnemun subterminale* prevented the low marsh dominant *Sarcocornia pacifica* (formerly *Salicornia virginica*) from succeeding in the higher marsh through competitive interactions (Pennings & Callaway 1992). The study, however, suggested that physical stress as a result of edaphic and climatic conditions likely modulates the strength of the proposed interactions (Pennings & Callaway 1992). Also, in Georgia salt marshes (USA), the upper limit of *Spartina alterniflora* (the middle and low marsh dominant) was suggested to be set by competition, given that this species succeeds better when *Juncus roemerianus* (the high marsh dominant) was experimentally removed (Pennings *et al.* 2005). A recent experimental study on the west coast of South America, in a central Chilean salt marsh, also suggested that interspecific plant competition determines or mediates the segregation of most dominant plant species (Fariña *et al.* 2009). On the east coast of South America, another experimental study conducted in Mar Chiquita coastal lagoon (northern Argentinean coast between 37°29′S and 39°46′S), suggests that *Sarcocornia perennis* facilitates the establishment of *Spartina densiflora* (a middle-high marsh species), which, after reaching a threshold size, seems to start outcompeting the surrounding *Sarcocornia* plants (Alberti *et al.* 2008). Unfortunately, the salt marshes in Mar Chiquita lagoon are devoid of *Spartina alterniflora*, which dominates the low marsh zone in most other salt marshes below 42°S. It is unknown if *Spartina alterniflora* ever existed in these marshes or whether it became locally extinct as a result of negative interactions with the species currently dominating the landscape. Nevertheless, at latitudes higher than 42° along the east coast of Patagonia *Spartina densiflora*, if present, is not a strong competitor and typically forms small patches within the dense carpet of *Sarcocornia perennis* that dominates the landscape throughout the year (Roig & Faggi 1985; Bortolus *et al.* 2009). The species composition of local plants and animal assemblages commonly varies along large latitudinal ranges (Chapman 1960; Adam 1993), as do the major ecological interactions shaping them (for salt marsh examples see Pennings *et al.* 2007, 2009). This is what seems to occur along the east coast of South America, where salt marshes have different dominant plant and animal species, the clime goes from tropical to sub-Antarctic, and the tidal regime varies from micro- to macro-tidal (Isacch *et al.* 2006; Bortolus *et al.* 2009). Our results suggest that *Sarcocornia perennis* sets the upper limit of *Spartina alterniflora* within the intertidal frame in the southern marshes where the two species dominate the high and low marsh, respectively. However, more research is needed to evaluate whether *Spartina densiflora* affects this interaction where the three species coexist.

What prevents *Sarcocornia perennis* from colonizing the *Spartina alterniflora*-dominated low marsh zone?

In our field experiment, no *Sarcocornia perennis* survived when transplanted to the low marsh, independent of the presence of *Spartina alterniflora* neighbours. However, in the greenhouse experiment, all plants tolerated strongly reducing soil conditions. These results suggest that *Sarcocornia perennis* is more susceptible to submersion than to waterlogged anoxic soil conditions. This conclusion agrees with the result of the experiment in which we separated the submersion from the soil anoxia effects, by bagging and sealing the below-ground structures to avoid soil redox changes while the transplants were inundated by the tides. In fact, although edaphic conditions were long considered as the chief factor regulating this kind of plant zonation (Adam 1993; Mendelssohn & Morris 2000; Mitsch & Gosselink 2000; Pennings & Bertness 2001), the experimental separation between complete submersion and soil anoxia effects was overlooked. In the low marsh, submersion is more prolonged and more frequent than in the high marsh therefore the ability to obtain oxygen from the atmosphere and bring it to the submerged tissue is crucial for plants to survive (Maricle & Lee 2002). Adams and Bate (1994) conducted an experimental study showing that *Sarcocornia perennis* survived prolonged submersion by developing a rapid stem elongation when submerged at 5 cm below the surface. This mechanism allows submerged plants to contact the aerial environment in order to get oxygen and supply it to the tissues underwater (Lessmann *et al.* 1997; Jackson & Colmer 2005; Mommer & Visser 2005). Some plant species have different mechanisms to avoid submersion stress, such as the development of aerenchyma or the ability to respire anaerobically (Maricle & Lee 2002; Maricle *et al.* 2006). It is possible that *Sarcocornia perennis* is unable to survive in the low marsh because of a lack of a physiological mechanism that allows it to uptake oxygen underwater during high tides. This may be particularly important in the Patagonian marshes, where the combination of steep slopes and macrotidal amplitudes means that plants living in the low marsh are commonly submerged under several metres of seawater twice a day (Bortolus *et al.* 2009). Moreover, considering that tidal seawater is likely to alter the concentration of electrolytes, which may produce an alteration in the succulence of the shoot tissue and also may alter the plant nutrient intake (Flowers *et al.* 1977; Flowers & Colmer 2008, but see Adams & Bate 1994), more research is needed to understand the physiological stresses preventing *Sarcocornia perennis* from being successful across the low marsh level.

Further salt marsh plant zonation studies

Our work supports the hypothesis that the pattern of distribution of dominant plants in Central Patagonian salt marshes is the result of the trade-offs between ecological and physiological factors. The transplant experiments showed that each of the two dominant species is prevented from occupying the marsh zone dominated by the other. However, more specific physiological studies are necessary to identify the specific mechanism regulating these interactions. The upper border of the marsh plant zonation appears to be shaped by a combination of negative and positive interspecific interactions, and our results are consistent. On the other hand, although there is solid evidence supporting that soil salinity and anoxia, caused by tidal submersion and waterlogging, are the principal factors in determining the absence of high marsh plant species in the low marsh; our results highlight the importance of increasing our effort to address each one of these variables separately. In macro-tidal systems, such as those in Patagonia, another important variable to address is the turbid seawater column of several metres height that covers plants during high tides, and how this water may affect plant architecture and physiology. Only by disentangling these highly related variables, and their separate effects, can we make a qualitative advance in our understanding of this ecological problem.

REFERENCES

Adam P. (1993) *Saltmarsh Ecology*. Cambridge University Press, New York.

Adams J. B. & Bate G. C. (1994) The effect of salinity and inundation on the estuarine macrophyte *Sarcocornia perennis* (Mill.) A.J. Scott. *Aquat. Bot.* **47,** 341–8.

Alberti J., Escapa M., Daleo P., Iribarne O., Silliman B. & Bertness M. (2007) Local and geographic variation in grazing intensity by herbivorous crabs in SW Atlantic salt marshes. *Mar. Ecol. Prog. Ser.* **349,** 235–43.

Alberti J., Escapa M., Iribarne O., Silliman B. & Bertness M. D. (2008) Crab herbivory regulates plant facilitative and competitive processes in Argentinian marshes. *Ecology* **89,** 155–64.

Alonso M. A. & Crespo M. B. (2008) Taxonomic and nomenclatural notes on South American taxa of *Sarcocornia* (Chenopodiaceae). *Ann. Bot. Fennici* **45,** 241–54.

Bertness M. D. (1991) Zonation of *Spartina patens* and *Spartina alterniflora* in New England salt marsh. *Ecology* **72,** 138–48.

Bertness M. D. (1999) *The Ecology of Atlantic Shorelines.* Sinauer Associates, Inc, Sunderland.

Bertness M. D. & Callaway R. (1994) Positive interactions in communities. *Trends Ecol. Evol.* **9,** 191–3.

Bertness M. D., Ewanchuk P. J. & Silliman B. R. (2002) Anthropogenic modification of New England salt marsh landscapes. *Proc. Natl. Acad. Sci. U.S.A.* **5,** 1395–8.

Bortolus A. (2006) The austral cordgrass *Spartina densiflora* Brong.: its taxonomy, biogeography and natural history. *J. Biogeogr.* **33,** 158–68.

Bortolus A. & Iribarne O. (1999) Effects of the SW Atlantic burrowing crab *Chasmagnathus granulata* on a *Spartina* salt marsh. *Mar. Ecol. Prog. Ser.* **178,** 79–88.

Bortolus A., Schwindt E. & Iribarne O. (2002) Positive plant-animal interactions in the high marsh of an Argentinean Coastal Lagoon. *Ecology* **83,** 733–42.

Bortolus A., Schwindt E., Bouza P. J. & Idaszkin Y. L. (2009) A characterization of Patagonian salt marshes. *Wetlands* **29,** 772–80.

Bouza P., Sain C., Bortolus A. *et al.* (2008) *Geomorfología y características morfológicas y fisicoquímicas de suelos hidromórficos de marismas patagónicas.* Abstracts of the XXI Congreso Argentino de la Ciencia del Suelo. San Luis.

Canepuccia A. D., Escapa M., Daleo P., Alberti J., Botto F. & Iribarne O. (2007) Positive interactions of the smooth cordgrass *Spartina alterniflora* on the mud snail *Heleobia australis*, in South Western Atlantic salt marshes. *J. Exp. Mar. Biol. Ecol.* **353,** 180–90.

Chapman V. J. (1960) *Salt Marshes and Salt Deserts of the World.* Interscience Pub. Inc., New York.

Cooper A. (1982) The effects of salinity and waterlogging on the growth and cation uptake of salt marsh plants. *New Phytol.* **90,** 263–75.

Correa M. N. (1998) *Flora Patagónica. Tomo VIII.* INTA, Buenos Aires.

Costa C. S. B., Marangini J. C. & Azevedo A. M. G. (2003) Plant zonation in irregularly flooded salt marshes: relative importance of stress tolerance and biological interactions. *J. Ecol.* **91,** 951–65.

Daleo P. & Iribarne O. (2009) Beyond competition: the stress-gradient hypothesis tested in plant–herbivore interactions. *Ecology* **90,** 2368–74.

Daleo P., Alberti J., Canepuccia A., Escapa M., Fanjul E., Silliman B. R., Bertness M. D. & Iribarne O. (2008) Mycorrhizal fungi determine salt-marsh plant zonation depending on nutrient supply. *J. Ecol.* **96,** 431–7.

Emery N. C., Ewanchuk P. J. & Bertness M. D. (2001) Competition and salt-marsh plant zonation: stress tolerators may be dominant competitors. *Ecology* **82,** 2471–85.

Fariña J. M., Silliman B. & Bertness M. D. (2009) Can conservation biologists rely on established community structure rules to manage novel systems? Not in salt marshes. *Ecol. Appl.* **19,** 413–22.

Flowers T. J. & Colmer T. D. (2008) Salinity tolerance in halophytes. *New Phytol.* **179,** 945–63.

Flowers T. J., Troke P. F. & Yeo A. R. (1977) The mechanism of salt tolerance in halophytes. *Annu. Rev. Plant Physiol.* **28,** 89–121.

Funk D. W., Noel L. E. & Freedman A. H. (2004) Environmental gradients, plants distribution, and species richness in arctic salt marsh near Prudhoe Bay, Alaska. *Wetl. Ecol. Manag.* **12,** 215–33.

Hessini K., Martinez J. P., Gandour M., Albouchi A., Soltani A. & Abdelly C. (2009) Effect of water stress on growth, osmotic adjustment, cell wall elasticity and water-use efficiency in *Spartina alterniflora*. *Environ. Exp. Bot.* **67,** 312–19.

Isacch J. P., Costa C. S. B., Rodríguez-Gallego L. *et al.* (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.

Jackson M. B. & Colmer T. D. (2005) Response and adaptation by plants to flooding stress. *Ann. Bot.* **96,** 501–5.

Justin S. H. F. W. & Armstrong W. (1987) The anatomical characteristics of roots and plant response to soil waterlogging. *New Phytol.* **106,** 465–95.

Kneib R. T. (1984) Patterns of invertebrate distribution and abundance in the intertidal salt marsh: causes and questions. *Estuaries* **7,** 392–412.

Lessmann J. M., Mendelssohn I. A., Hester M. W. & McKee K. L. (1997) Population variation in growth response to flooding of three marsh grasses. *Ecol. Eng.* **8,** 31–47.

Levine J. M., Brewer J. S. & Bertness M. D. (1998) Nutrients, competition and plant zonation in a New England salt marsh. *J. Ecol.* **86,** 285–92.

Mahall B. E. & Park R. B. (1976a) The ecotone between *Spartina foliosa* Trin. and *Salicornia virginica* L. in salt marshes of northern San Francisco Bay. I. Biomass and production. *J. Ecol.* **64,** 421–33.

Mahall B. E. & Park R. B. (1976b) The ecotone between *Spartina foliosa* Trin. and S*alicornia virginica* L. in salt marshes of northern San Francisco Bay. II. Soil water and salinity. *J. Ecol.* **64,** 793–809.

Mahall B. E. & Park R. B. (1976c) The ecotone between *Spartina foliosa* Trin. and *Salicornia virginica* L. in salt marshes of northern San Francisco Bay. III. Soil aeration and tidal immersion. *J. Ecol.* **64,** 811–19.

Maricle B. R. & Lee R. W. (2002) Aerenchyma development and oxygen transport in the estuarine cordgrasses *Spartina alterniflora* and *S. anglica*. *Aquat. Bot.* **74,** 109–20.

Maricle B. R., Crosier J. J., Bussiere B. C. & Lee R. W. (2006) Respiratory enzyme activities correlate with anoxia tolerance in salt marsh grasses. *J. Exp. Mar. Biol. Ecol.* **337,** 30–7.

Markham H. J. & Chanway C. P. (1996) Measuring plant neighbour effects. *Funct. Ecol.* **10,** 548–9.

Mateos-Naranjo E., Redondo-Gomez S., Silva J., Santos R. & Figueroa M. (2007) Effect of prolonged flooding on the invader *Spartina densiflora* Brong. *J. Aquat. Plant Manag.* **45,** 121–3.

Mendelssohn I. & Morris J. (2000) Eco-physiological controls on the productivity of *Spartina alterniflora* Loisel. In: *Concepts and Controversies in Tidal Marsh Ecology* (eds M. P.

Weinstein & D. Kreeger) pp. 59–80. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Minchinton T. E. & Bertness M. D. (2003) Disturbance-mediated competition and the spread of *Phragmites australis* in a coastal marshes. *Ecol. Appl.* **13,** 1400–16.

Mitsch W. J. & Gosselink J. G. (2000) *Wetlands*. John Wiley & Sons, Inc., New York.

Mommer L. & Visser E. J. W. (2005) Underwater photosynthesis in flooded terrestrial A matter of leaf plasticity. *Ann. Bot.* **96,** 581–9.

Pennings S. C. & Bertness M. D. (2001) Salt marsh communities. In: *Marine Community Ecology* (eds M. D. Bertness, S. D. Gaines & M. E. Hay) pp. 289–316. Sinauer Associates, Inc., Sunderland.

Pennings S. C. & Callaway R. M. (1992) Salt marsh plant zonation: the relative importance of competition and physical factors. *Ecology* **73,** 681–90.

Pennings S. C., Grant M. B. & Bertness M. D. (2005) Plant zonation in low-latitude salt marshes: disentangling the roles of flooding, salinity and competition. *J. Ecol.* **93,** 159–67.

Pennings S. C., Zimmer M., Dias N. *et al.* (2007) Latitudinal variation in plant–herbivore interactions in European salt marshes. *Oikos* **116,** 543–9.

Pennings S. C., Ho C., Salgado C. S. *et al.* (2009) Latitudinal variation in herbivore pressure in Atlantic Coast salt marshes. *Ecology* **90,** 183–95.

Pezeshki S. R. (2001) Wetland plant responses to soil flooding. *Environ. Exp. Bot.* **46,** 299–312.

Redondo-Gómez S., Castillo J. M., Luque C. J. *et al.* (2007) Fundamental niche differentiation in subspecies of *Sarcocor-*

nia perennis on a salt marsh elevational gradient. *Mar. Ecol. Prog. Ser.* **347,** 15–20.

Roig F. A. & Faggi A. M. (1985) Analisis geobotanico de la vegetacion. In: *Transecta botanica de la Patagonia austral* (eds O. Boelcke, D. M. Moore & F. A. Roig) pp. 1–189. Cooperativa Grafica General Belgrano, Buenos Aires.

Silliman B. R. & Bortolus A. (2003) Underestimation of *Spartina* productivity in western Atlantic marshes: marsh invertebrates eat more than just detritus. *Oikos* **101,** 549–54.

Stone C. S. (1993) Vegetation of Coastal Marshes near Juneau, Alaska. *Northwest Sci.* **67,** 215–30.

Tessier M., Gloaguen J. C. & Bouchard V. (2002) The role of spatio-temporal heterogeneity in the establishment and maintenance of *Suaeda maritima* in salt marshes. *J. Veg. Sci.* **13,** 115–22.

Vevle O. (1985) The salt marsh vegetation at Vinjekilen, Bamble, SE Norway, with special reference to the *Puccinellietum maritimae*. *Vegetatio* **61,** 55–63.

Vince S. W. & Snow A. A. (1984) Plant zonation in an Alaskan salt marsh: I. Distribution, abundance and environmental factors. *J. Ecol.* **72,** 651–67.

Weinstein M. P. & Kreeger D. A., eds (2000) *Concepts and Controversies in Tidal Marsh Ecology*. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Zar J. H. (1999) *Biostatistical Analysis*, 4th edn. Prentice-Hall, Upper Saddle River.

Zuloaga F. & Morrone O. (1999) *Catálogo de las Plantas Vasculares de la República Argentina. II. Dicotyledoneae (Acanthaceae-Euphorbiaceae) y (Fabaceae-Zygophyllaceae)*. Missouri Botanical Garden, St. Louis.