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Flooding Effect on the Distribution of Native Austral Cordgrass *Spartina densiflora* in Patagonian Salt Marshes

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ABSTRACT

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Plant zonation is one of the most conspicuous ecological features of salt marshes worldwide. In Patagonian salt marshes the cordgrass *Spartina alterniflora* forms dense monospecific stands along the lowest marsh level, while the higher levels are dominated by *Spartina densiflora* or *Sarcocornia perennis*. In this study, we coupled field transplants combined with neighbor exclusion treatments and greenhouse experiments to evaluate the effect of submersion and waterlogged anoxic soil in the determination of the lower distribution limit of *S. densiflora* in Central Patagonian salt marshes within its native range. In the field experiment, no *S. densiflora* survived the frequent tidal submersion by approximately 2 m of seawater in the low marsh, independent of the *S. alterniflora* neighbor's presence, while in the greenhouse experiment, all plants were able to tolerate strongly reducing soil conditions. Our results suggest that the absence of *S. densiflora* in the low marsh level is a consequence of the effect of the submersion, independent of the presence of *S. alterniflora* neighbors and of the strong soil anoxia. Our results contribute to optimize the efforts addressed to control or eradicate this exotic species in salt marshes where it is invading.

ADDITIONAL INDEX WORDS: Neighbor exclusion, submersion, zonation, invasive species, soil anoxia, Patagonia.



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INTRODUCTION

Studies carried out in salt marshes at different latitudes have shown that the plant zonation pattern is due to the trade-off between physical stress and ecological processes (Adam, 1990; Pennings and Bertness, 2001; and references therein). Flooding is one of the most important physical factors that affect both the faunal and floral assemblages, besides the soil conditions (*e.g.*, waterlogged, salinity, and nutrients; Bockelmann *et al.*, 2002; Pennings and Callaway, 1992; Vince and Snow, 1984). Prolonged immersion causes soil saturation or waterlogging, and in consequence anoxic conditions, because when the soil is flooded, O₂ is consumed by the plant roots and other organisms present in the soil (Pezeshki, 2001). As a result, under these anoxic soil conditions, some compounds concentrate in the rizosphere in their reduced forms, which turn out to be harmful for plants (Pezeshki, 2001). Furthermore, some plant species have different mechanisms to avoid waterlogged anoxic soil stress, such as the development of aerenchyma or the ability to respire anaerobically (Maricle and Lee, 2002; Maricle *et al.*, 2006). Likewise, in addition to the waterlogged soil conditions, which affect belowground plant structures, plants are exposed to tidal submersion stress when

the aboveground structures are completely covered by seawater once or twice a day, potentially interfering with a variety of physiological pathways (Mateos-Naranjo *et al.*, 2007; Mommer and Visser, 2005).

The austral cordgrass *Spartina densiflora* Brongn. is a halophyte species native to South America coastal marshes, and it is successfully invading salt marshes of North America, Spain, Portugal, and North Africa (Bortolus, 2006). Its distribution range, either where is native or introduced, includes very different climate conditions, from subtropical to austral (Bortolus, 2006; Fortuné *et al.*, 2008; Moberley, 1956). In addition, along its wide distribution range, it is exposed to many environmental scenarios, from intertidal to strictly terrestrial, and from brackish to hypersaline (Castillo *et al.*, 2005; Nieva *et al.*, 2003). In addition, it inhabits all salt marsh levels, although in invaded salt marshes of the United States and Spain, *S. densiflora* seems to be restricted to the middle and high marshes, being rare in the low marsh (Bortolus, 2006; Castillo *et al.*, 2000; Clifford, 2002; Nieva *et al.*, 2001). These habitat differences suggest that it may tolerate different hydrological and edaphic conditions (*e.g.*, tidal submergence periods, salinity, or anoxia). Most ecophysiological studies focusing on *S. densiflora* physiological adaptations to flooding have been performed in the salt marshes where it was introduced (Castillo and Figueroa, 2009; Castillo *et al.*, 2000; Mateos-Naranjo *et al.*, 2007; Nieva *et al.*, 2001). Nevertheless,

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the processes controlling its distribution in salt marshes of its native range still need more attention. In this study, we address the hypothesis that stress tolerance plays a key role in setting the lower limit of distribution of *S. densiflora* in salt marshes of its native area in Central Patagonian salt marshes, where it inhabits exclusively the high level of the marsh (*Spartina alterniflora* being the only species inhabiting the low marsh level; Bortolus *et al.*, 2009). In these salt marshes, plants that inhabit the lower marsh are completely submerged twice daily in each tidal cycle, and the soil is permanently waterlogged. In contrast, immersion in the high marsh is shorter, which allows the sediment drain. By performing field and greenhouse manipulative experiments, we addressed the following specific question: Is waterlogged anoxic soil and/or submersion intolerance preventing the presence of *S. densiflora* in the low marsh within its native region?

MATERIALS AND METHODS

Study Area

We worked in the Riacho *Spartina* marsh (42°25' S, 64°37' W; Figure 1), at the Península Valdés, which constitutes a protected area that has been declared a World Heritage site by the United Nations Education, Scientific and Cultural Organization (UNESCO) since 1999. In this marsh, the lowest marsh level, which is only inhabited by the cordgrass *S. alterniflora*, extends between +3.92 m and +4.99 m relative to the Argentinean hydrographic zero (AHZ) and is completely submerged up to ~2 m deep for about 2.5 hours during each tidal cycle. In contrast, the high level, dominated by *S. densiflora*, accompanied by *Limonium brasiliense*, *Sarcocornia perennis*, and *Atriplex* sp., extends between +4.99 m and +6.98 m and is submerged only for ~40 min and to a depth of ~10 cm. The soil redox potential in the root zone (0–10 cm) is highly reducing in the low marsh (Eh: -269.20 ± 12.20 mV; mean \pm SE) and strongly oxidizing in the high marsh (Eh: 150.25 ± 5.14 mV; means of 20 readings using a portable meter and electrode system Termo/pHmetro Altronix TPA-IV, following tidal submersion throughout the year during the period 2007–09; Idaszkin, Bortolus and Bouza, 2011).

Experimental Design

In order to assess the combined effect of waterlogged anoxic soil and submersion during high tide on *S. densiflora* in the low marsh, we performed a transplant experiment in the Riacho marsh, with the following treatments. (1) “Immersion with neighbors” 10 plots (20 cm diameter \times 20 cm deep) with *S. densiflora* transplants from the high marsh level (elevation +5.77 m AHZ) were randomly transplanted into the monospecific *S. alterniflora*-dominated low marsh level (elevation +4.42 m AHZ). (2) “Immersion without neighbors”: 10 *S. densiflora* transplants were randomly transplanted in the same low marsh level as in the previous treatment, but all *S. alterniflora* neighbor plants were removed every 2 wk by clipping a 50-cm-radius border around the plant at the soil surface. To avoid the invasion of roots by surrounding plants, the transplants were potted in 200 μ m black nylon pots with holes in the bottom to ensure soil drainage. Additionally, we trenched around the pots by cutting with a knife (blade: 25 cm long) to cut all root connections between the plots and the surrounding vegetation.

(3) “Manipulation control”: 10 *S. densiflora* transplants were collected as in the previous treatment but replanted into the same high marsh where they were collected. (4) “Total control”: 10 *S. densiflora* plots (20 cm diameter) were randomly chosen and tagged in the high marsh and kept unaltered until the end of the experiment. The experiment started in the early spring of 2007 and finished in autumn of 2008. At the end of the experiment, the number of living stems of *S. densiflora* per plot were counted to determine its density (live stems m^{-2}). From the beginning of the experiment, on a weekly basis, we recorded the percentage of plant survival in each transplant.

In order to evaluate the effect of the waterlogged anoxic soil on *S. densiflora*, we conducted a greenhouse experiment with the following treatments: (1) “Waterlog”: 10 plots with *S. densiflora* from the Riacho marsh (same size as in the previous experiment) were placed in plastic pots with no holes and then saturated with water to generate and maintain natural reducing soil conditions. All pots were watered with fresh water at least twice a week in order to keep the water level 5 cm above the soil surface. (2) “Drainage”: 10 plots with *S. densiflora* were taken and placed in plastic pots perforated to let the soil drain. All pots were watered with fresh water twice a week to keep soil wet but never flooded. The soil redox potential of each pot was periodically surveyed and kept below -100 mV for the waterlog treatment and above $+100$ mV for the drainage treatment. The experiment started in the early spring of 2008 and finished in autumn of 2010. At the end of the experiment, live stem density of *S. densiflora* was determined for each treatment.

Data Analysis

To evaluate differences in *S. densiflora* density among treatments, we used one-way analysis of variance (ANOVA). Before the analyses, data were tested for normality using the Shapiro-Wilk test and for homogeneity of variance using the Levene test (Zar, 1999).

RESULTS

We found an extremely contrasting results, since no *S. densiflora* plant survived the immersion treatments in the first month, but 100% of the control plots did at the end of the experiment. The evaluation of control treatments showed that the experimental manipulation did not affect either the survival or the density of *S. densiflora* ($F_{1,18} = 0.26$, $p = 0.61$; Figure 2). The removal of the *S. alterniflora* neighbors did not lead to the survival of *S. densiflora* in any plot. 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 mV).

Regarding the greenhouse experiment, the soil redox potential was -287.5 ± 33.55 mV in the waterlog treatment and 203.5 ± 4.76 mV in the drainage treatment. All *S. densiflora* plants survived (100% survival) in both treatments, and the density was not significantly different between treatments ($F_{1,18} = 0.06$, $p = 0.81$; Figure 2).

DISCUSSION

Combining field experiments and greenhouse experiments allowed us to evaluate the effects of submersion on *S. densiflora*

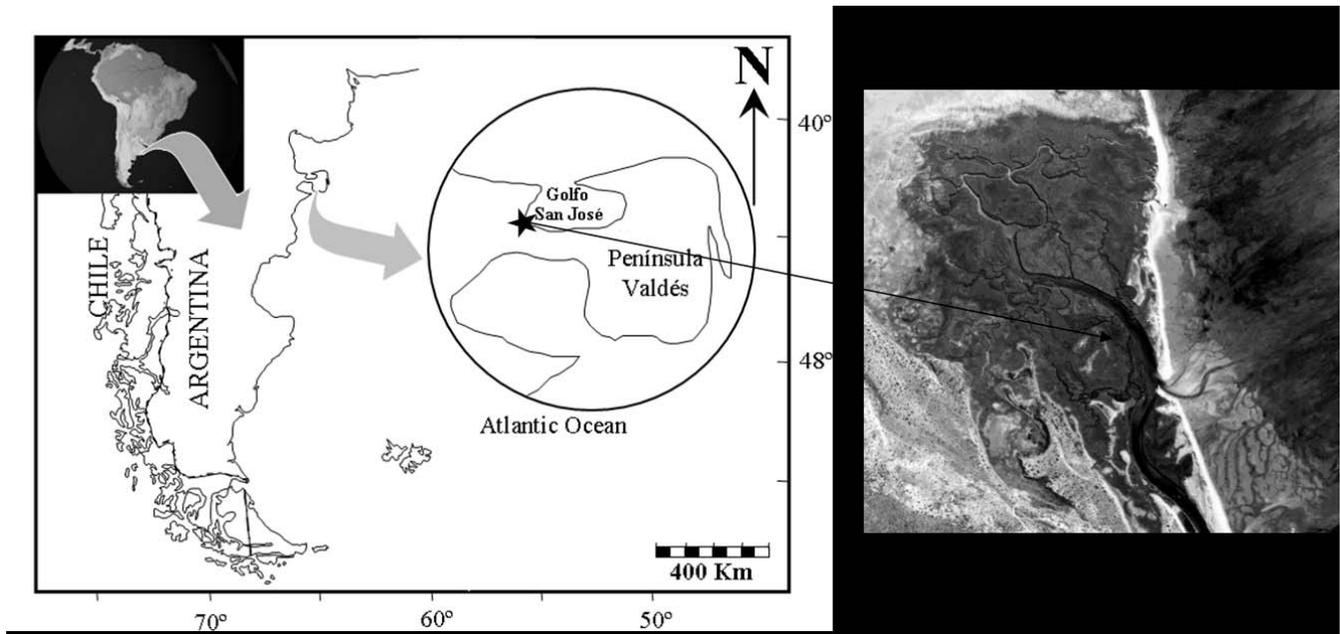


Figure 1. Map showing the location of the Riacho marsh on the isthmus of Península Valdés.

and the effect of soil anoxia separately. In our field experiment, no *S. densiflora* stems survived when transplanted to the low marsh, while in the greenhouse experiment, all plants were able to tolerate strongly reducing soil conditions. These results suggest that, as reported for *Sa. perennis* (Idaszkin, Bortolus and Bouza, 2011), *S. densiflora* is more susceptible to submersion in local tidal water than to waterlogged anoxic soil conditions.

Our results suggest that *S. densiflora* has the ability to tolerate waterlogged and strongly reduced soil conditions. Plants may tolerate anoxic soil conditions through different mechanisms, which can imply structural, morphological, or physiological modifications (Kozłowski, 1997). Several cord-

grasses of the *Spartina* genus (e.g., *S. alterniflora*, *Spartina maritima*, and *Spartina anglica*) are able to survive in the waterlogged salt marsh soils due to the ability to develop aerenchymas in their roots and shoots and to respire anaerobically (Adams and Bate, 1995; Burdick, 1998; Gleason and Zieman, 1981; Li *et al.*, 2011; Maricle and Lee, 2002; Maricle *et al.*, 2006). Likewise, these mechanisms could be responsible for *S. densiflora* survival in anoxic soil conditions (Castillo *et al.*, 2000).

In addition, our results suggest that *S. densiflora* does not tolerate exposure to the typical submersion cycle of the low level of the salt marshes where it is native, possibly due to the lack of a mechanism to acquire O₂ when being submerged. Studies carried out with *S. alterniflora* and *Spartina patens* show that these species can offset the depressive effects of internal O₂ by continuing the photosynthesis process when they are underwater (Gleason and Zieman, 1981). The salt marsh where the experiments were carried out is semidiurnal macrotidal, and the low marsh flooding periods are long, staying totally submerged to ~2 m of depth for 2.5 hours in each tidal cycle. Thus, the photosynthetic period is shorter than in the high marsh, which is submerged only to 10 cm and 40 min in each tidal cycle (Idaszkin, 2011). Mateos-Naranjo *et al.* (2007) found that *S. densiflora* can survive 2 mo in continuous flooding conditions, although this situation resulted in reduced growth and photosynthetic efficiency. Probably, in our field experimental situation, this reduction in the photosynthetic efficiency could be further reduced by the water turbidity combined with the great depth to which it was exposed, resulting in the inability of *S. densiflora* to survive in the low marsh.

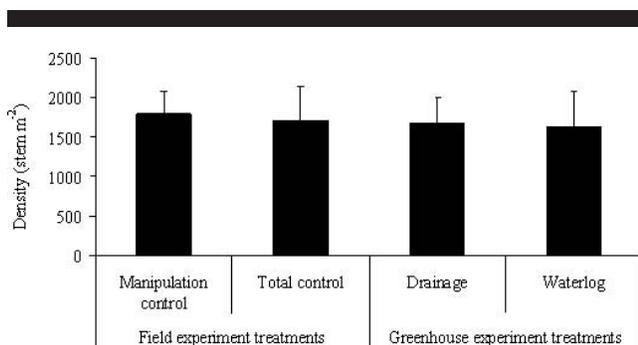


Figure 2. *Spartina* density in manipulation control and total control treatments in the field experiment to evaluate the combined effect of waterlogged anoxic soil and tidal submersion on *Spartina* and in waterlog and drainage treatments in the greenhouse experiment to evaluate the effect of waterlogged anoxic soil on *Spartina*. Data are means + standard deviation.

CONCLUSION

Our study strongly suggests that the distribution of *S. densiflora* in Central Patagonian salt marshes where it is native results from its intolerance to physiological factors, mainly to the seawater tidal immersion. *Spartina densiflora* is an emblematic example of a species capable of dramatically altering the invaded ecosystems; the achieved information about the stress tolerance of a population in its center of origin (Bortolus, 2006) could contribute to optimize the efforts directed at controlling or eradicating this exotic species in an early stage of invasion in salt marshes worldwide.

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