

# Does low temperature prevent *Spartina alterniflora* from expanding toward the austral-most salt marshes?

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**Abstract** Along the Atlantic coast of South America, the northern salt marshes (lower than 43°S) are dominated by *Spartina* species while the southern salt marshes (greater than 43°S) are dominated by *Sarcocornia perennis*. The most abundant *Spartina* species are *Spartina densiflora* which is present in most coastal marshes, and *Spartina alterniflora* that was never recorded above the ~42°25'S. It is not clear why *S. alterniflora* has not succeeded in the southern marshes, in which the low marsh zone remains as an extensive bare mud flat. We address the hypothesis that the absence of *S. alterniflora* in the south is driven by the cold temperatures inversely related with increasing latitudes along the East coast of Patagonia. To evaluate this hypothesis, we carried out an experiment in which we manipulated the temperature in combination with frost formation and photoperiod. We found that cold temperature produced a negative effect on *S. alterniflora*, and this effect seems

accentuated by the frost but not by the reduction in the photoperiod. Our results support the hypothesis that the absence of *S. alterniflora* in the southernmost salt marshes of Patagonia is a consequence of the frost as an outcome of the co-occurrence of low temperature and high humidity. The importance of our results are discussed in the context of the global warming and how *Spartina* species enlarge their distributional range toward higher latitudes.

**Keywords** Cold · Frost · Geographic expansion · *Spartina alterniflora* · Salt marshes · Patagonia

## Introduction

In salt marsh environments, plants tend to show a conspicuous zonation pattern that seems to be the result of the trade off between physical stress and ecological processes, regardless of the botanical species and the salt marsh location (see reviews in Adam 1993; Mitsch and Gosselink 2000; Weinstein and Kreeger 2000; Pennings and Bertness 2001). Many ecophysiological studies focusing on salt marsh plants were performed to better understand the causal processes of local zonation patterns by examining morphological and physiological adaptations of low marsh plants to high salinities, flooding and soil anoxia (e.g., Cooper 1982; Burdick 1998; Brown et al. 2006; Maricle et al. 2007; Idaszkin et al. 2010).

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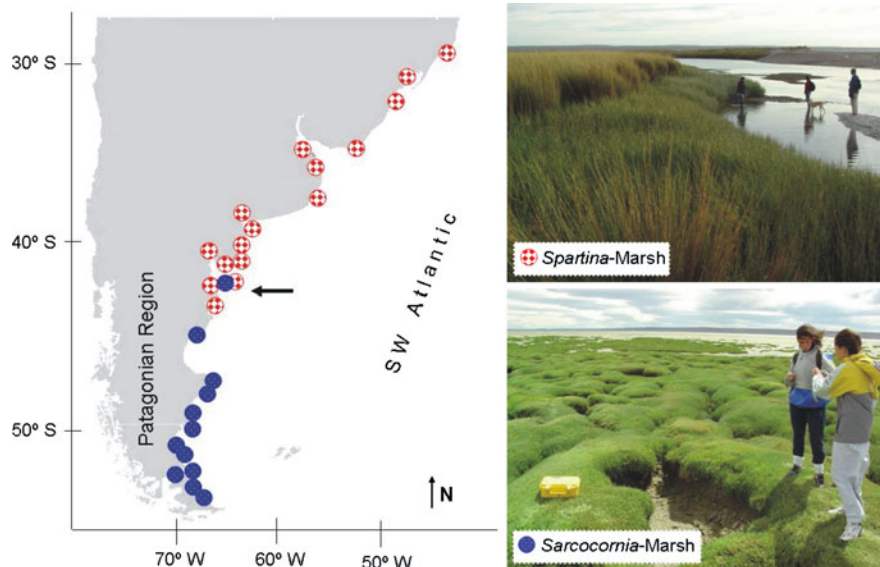
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However, probably because of the intrinsic logistic constraints, relatively less effort was directed to understand the causal processes shaping the distribution of salt marsh plants at larger scales. Some large-scale studies recently produced have focused on, for example, the effect of herbivory on plant production/productivity (Silliman and Bortolus 2003; Silliman et al. 2005; Alberti et al. 2007), the variation in plant palatability along the East coast of North America (Pennings et al. 2001; Salgado and Pennings 2005; Pennings et al. 2009) and Europe (Pennings et al. 2007) among others. Nevertheless, the processes controlling the continental geographic distribution of salt marsh plants and their relative zonation at large scale still need more attention.

Along the Atlantic coast of South America, salt marshes show a clean macrogeographic pattern. The northern salt marshes (i.e. latitudes lower than 43°S) are dominated by *Spartina alterniflora* and *Spartina densiflora* (*Spartina*-marshes), while southern salt marshes (at latitudes greater than 43°S) are dominated by *Sarcocornia perennis* with a rare or nil presence of *Spartina* species across the intertidal frame (*Sarcocornia*-marshes; Fig. 1; Bortolus et al. 2009; Bortolus 2010). These two types of salt marshes overlap their

geographic distribution between 42°S and 43°S, and a feature shared by them is that the *S. alterniflora*, when present, always occupies the lowest marsh level, and *S. perennis* the highest one along with *S. densiflora* (Bortolus et al. 2009). However, while *S. perennis* and *S. densiflora* are present in virtually all the South American salt marshes along the Atlantic coast, *S. alterniflora* was never recorded above the ~42°25'S (Correa 1998; Bortolus et al. 2009). The absence of *S. alterniflora* in the austral salt marshes is relevant and visually conspicuous, since the topographic surveys show that the *S. alterniflora* level remains free of vegetation. Our experiments have recently showed that *S. perennis* is not able to colonize this low marsh zone because it is not able to survive the frequent and prolonged immersion (Idaszkin et al. 2010). With plenty of space to colonize, and apparently free of potential competitors and/or important herbivores, it is not clear why *S. alterniflora* has not succeeded yet in colonizing the austral-most marshes.

The cordgrass *S. alterniflora* is a rhizomatous species that acts as an intertidal pioneer species, stabilizing substrate and trapping sediment (Adam 1993; Pennings and Bertness 2001). It is a widespread halophyte considered native to the Atlantic coast of the



**Fig. 1** *Left*: macrogeographic pattern of distribution of the South American salt marshes (modified from Bortolus 2010) along the south western Atlantic, and the southernmost limit reported for *S. alterniflora* (marked by the arrow). *Up-right* typical *Spartina*-marsh physiognomy (photo: Riacho marsh,

Chubut, Argentina). *Down-right* typical *Sarcocornia*-marsh physiognomy dominated by a monospecific carpet of *S. perennis* in the southernmost Patagonian marshes (photo: Loyola marsh, Río Gallegos, Argentina). Photo credits: A. Bortolus

Americas (Adam 1993) and it has been introduced along the Pacific coast of North America, and in several locations in England, France, The Netherlands, New Zealand, Australia, Tasmania, and China (Ayres et al. 2004; Chung 2006). In its native region this species shows a wide distribution range including very different climatic conditions, from humid subtropical in Texas (USA) to regions in Labrador (Canada) where winter conditions are extremely cold with temperatures for January between  $-10$  and  $-15^{\circ}\text{C}$ , and seriously affected by ice formation (Adam 1993). On the other hand, along the South American coast its range extends between  $10^{\circ}$  and  $\sim 42^{\circ}25'S$  (Mobberley 1956; Bortolus et al. 2009); its northern limit of distribution being in the Brazilian SE coast, where the climate is subtropical humid (mean annual average  $\sim 2,250$  mm), with hot rainy summers and mild winters. There, the mean temperature is  $16^{\circ}\text{C}$  in winter and  $34^{\circ}\text{C}$  in summer (Netto and Lana 1997; Trilla et al. 2009). In spite of the latitudinal range of distribution of this species in the Northern Hemisphere (where it reaches the  $\sim 50^{\circ}\text{N}$ ), its austral limit of distribution in the Southern Hemisphere was recorded in the Valdés Peninsula, Chubut province (Fig. 1; Bortolus et al. 2009), where the climatic conditions are mostly arid, precipitations are scarce (mean annual average 180 mm), annual temperatures range from  $27.5^{\circ}\text{C}$  in summer to  $1^{\circ}\text{C}$  in winter, and snow falls only on rare occasions (Meteorological Station of CENPAT-CONICET).

Climatic factors are known to constrain the development and distribution of plant species (Woodward and Williams 1987). Low temperatures and, in particular, freezing injury have been reported as the major factors limiting plant distribution in many habitats (Burke et al. 1976; Pearce 2001). Although a few  $C_4$  plants (such as *S. alterniflora*) were shown adapted to cool climates, they are mostly in warmer climates because their physiological processes are negatively affected by low temperatures (Naidu et al. 2003). In fact, several studies in different regions worldwide recorded that the species richness of  $C_4$  grasses increases with increasing temperature (Teeri and Stowe 1976; Vogel et al. 1978; Hattersley 1983; Collins and Jones 1985). Along the South American Atlantic coast, air temperature and winter daylength decrease notably as the latitude increases, but air humidity gradually increases toward the south leading to higher frost frequency and duration due to the

combination of the below zero temperatures with high air humidity (Correa 1998). Consequently, in the southern salt marshes of South America, the climate is temperate cold and semi-arid, with mean temperatures ranging from about  $-0.6$  to  $19^{\circ}\text{C}$ . Annual rainfall is about 300 mm, and the snow frequency is 15 days/year (2000–2009, Río Gallegos Aerodrome). Although in the northernmost marshes of North America *S. alterniflora* succeeds under extra cool climatic conditions, it seems possible and parsimonious that the populations spreading to the opposite extreme of the American Continent evolved with genetic structures (Blum et al. 2007) and loose their overwintering ability that enable them to tolerate cold conditions (Bertness 1999) among others. This hypothesis is supported by the fact that in Southern South America, *S. alterniflora* does not even lose the aboveground structures during winter (Correa 1998; Bortolus unpublished). The lack of an overwintering mechanism that reallocates the aboveground biomass into dormant rhizomes during the harshest part of the Patagonian winter is likely to determine the southernmost geographical limit of distribution for *S. alterniflora*. In this study, we address the hypothesis that temperature plays a key role in setting its southern limit of distribution along the South American east coast, which in turns define the regional salt marsh landscape macrogeographic pattern recently described (Bortolus et al. 2009). By performing manipulative experiments under controlled conditions, we addressed the following specific question: Is *S. alterniflora* affected by cold temperatures and/or its combined effect with high air humidity and/or a shorter photoperiod? Although the study does not pursue the physiological description of causal mechanisms, our results supply critical information that will help in developing further eco-physiological research.

## Materials and methods

### Plant material and experimental design

In order to evaluate whether *S. alterniflora* is affected by cold air temperatures and/or air humidity and/or photoperiod, we performed an experiment manipulating these variables in a climatic chamber. Cores with *S. alterniflora* were collected from low marsh zones at the Riacho *Spartina*-marsh ( $42^{\circ}25'S$ ,  $64^{\circ}37'W$ ), at the

Valdés Peninsula Protected Natural Area under the administration of the Organismo Provincial de Turismo of the Chubut Province (Argentina). Each core (15-cm-diameter  $\times$  15-cm-deep) consisted of a block of sediment with tillers, rhizomes and roots of *S. alterniflora* which were potted. The initial average tiller density in all the *S. alterniflora* cores used was 10.60 stems per pot (SE = 16.39; this was not significantly different among treatments with  $P > 0.05$ ). Pots were randomly arranged in five treatments; four of which consisted in keeping the pots outdoors under natural environmental conditions during daytime (10–12 h), and in an adapted climatic chamber during the nighttime (12–14 h). The chamber (thermal range:  $-18$  to  $\sim +5^{\circ}\text{C}$ ) has two horizontal sealed doors to minimize inner thermal disturbance during operation, and has rubber borders that allow the setting of sensors and/or air filtering tubes while preventing the entrance of light and humidity when closed. It was programmed to recreate the temperature of an average winter night on the southernmost continental Argentinean salt marsh (i.e., Loyola marsh; see Bortolus et al. 2009), from  $-3^{\circ}$  up to  $-6^{\circ}\text{C}$  with peaks of  $-10^{\circ}\text{C}$  once a week. The experimental treatments were: (1) “Cold”: ten pots were placed in the chamber from dusk until dawn; (2) “Cold-Photoperiod”: ten pots were placed in the chamber from dusk until 2 h after dawn (14–16 h); (3) “Humidity”: ten pots were placed in the chamber from dusk until dawn and were frequently sprayed with fresh water to induce frost formation on the tillers; and (4) “Humidity-photoperiod”: ten pots were placed in the chamber from dusk until 2 h after dawn (14–16 h) and were frequently sprayed with fresh water to induce frost formation on the tillers. A “Control” treatment was also performed by keeping ten pots outdoors under natural environmental conditions during the daytime and the nighttime to evaluate and quantify any potential chamber effect. Pots of each treatment were placed randomly interspersed *sensu* Hulbert (1984), and at the same level to prevent differences due to elevation within the chamber. Pots located outdoors under natural environmental conditions were also placed at random.

#### Plant measurements

The experiment was coordinated to match the winter season of 2009 to avoid physiological stress due to

the use of plants with the wrong phenological state. After this 3-month period, we determined the proportion of living tillers and their height, the proportion of living leaves and the potentially photosynthetic leaf area for each plot of each treatment as the summation of the green leaf area of all the leaves. Each leaf was scanned individually, on a black background, with 200 DPI resolutions. Scanned leaf images were saved separately as bmp 24-bit files. Each leaf-image files was later processed and analyzed with ImageJ (Version 1.40g) to estimate the area. Then, above-ground biomass was harvested from each plot and oven-dried at  $70^{\circ}\text{C}$  to constant weight.

#### Data analysis

To evaluate differences on plant measurements among treatments, we used one-way ANOVA. For significant results ( $P < 0.05$ ), parametric Student–Newman–Keuls test was applied (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 aboveground biomass and potentially photosynthetic leaf area of *S. alterniflora* variables were  $\ln(X)$ -transformed (Zar 1999).

#### Results

The periodic monitoring of the experiment showed that all the treatments worked as expected throughout the study. At the end of the experiment, we found that cold temperature produced a sharp negative effect in the proportion of living tillers (decreasing up to 70%), the height of tillers (decrease nearly 30%), the proportion of living leaves (decrease more than the 40%), the potentially photosynthetic leaf area (decrease over a 85%) and the aboveground biomass (decrease up to  $\sim 50\%$ ) of *S. alterniflora* (Tables 1, 2; Fig. 2). Excepting the proportion of living leaves, this effect is even more important in treatments with increased air humidity (Table 2; Fig. 2). When the frost was experimentally induced, we found that the proportion of living tillers and their height decreased about 50% by slowing down their grow respect to the control plants. The proportion of living leaves was also reduced in about 45%, and the potentially

**Table 1** Statistic parameter values of each plant measurement of each treatment

Treatment	Mean ( <i>n</i> = 10)	SE	Min	Max
Proportion of living tillers				
Cold	0.75	0.05	0.44	1.00
Cold-photoperiod	0.66	0.05	0.44	0.83
Humidity	0.48	0.06	0.23	0.78
Humidity-photoperiod	0.41	0.03	0.25	0.55
Control	0.90	0.03	0.70	1.00
Proportion of living leaves				
Cold	0.40	0.02	0.31	0.50
Cold-photoperiod	0.39	0.02	0.31	0.46
Humidity	0.44	0.02	0.33	0.55
Humidity-photoperiod	0.45	0.03	0.30	0.63
Control	0.68	0.03	0.56	0.82
Living tiller height (cm <sup>2</sup> )				
Cold	15.64	1.09	11.33	22.75
Cold-photoperiod	15.27	1.44	10.05	23.60
Humidity	11.79	1.23	6.89	20.10
Humidity-photoperiod	10.22	0.69	6.78	15.00
Control	21.27	0.96	15.64	26.35
Potentially photosynthetic leaf area (cm <sup>2</sup> )				
Cold	24.76	4.28	11.16	56.02
Cold-photoperiod	19.58	3.20	8.76	39.08
Humidity	10.66	2.12	1.60	25.70
Humidity-photoperiod	7.49	0.88	3.01	12.13
Control	128.74	17.35	64.98	242.19
Aboveground biomass (g m <sup>-2</sup> )				
Cold	207.38	33.33	85.11	356.03
Cold-photoperiod	176.50	37.97	62.09	401.79
Humidity	67.66	11.89	24.72	144.08
Humidity-photoperiod	54.40	6.65	29.18	86.28
Control	427.13	68.64	164.61	912.13

photosynthetic leaf area decreased more than the 90% showing a surface predominantly yellow and/or brown along the leaves. Since the aboveground biomass decreased nearly 85% in the humidity treatments too, at the end of the experiment the plants in this treatment were dramatically damaged in comparison to the other treatments. We did not detect an effect caused by the reduction in the photoperiod on the other manipulated variables (Table 2; Fig. 2).

## Discussion

Scientific literature often referred to the South Western Atlantic salt marshes as ecosystems dominated and characterized by *Spartina* grasses (e.g., Bortolus and Iribarne 1999; Isacch et al. 2006; Alberti et al. 2007; Canepuccia et al. 2007). However, this is mostly due to a historical lack of appropriate surveys covering the entire SW Atlantic coast, which includes the austral-most end of Patagonia and its distinctive salt marsh physiognomy and flora (Bortolus 2008, 2010; Bortolus et al. 2009). We currently know that along the Atlantic coast of South America, the salt marshes show a clear macrogeographic pattern with two major kinds of landscapes determined either by tall grasslands of the genus *Spartina* or by prairies of the cryptogenic dwarf fleshy bush *S. perennis* (Bortolus et al. 2009). Within this context and considering that *S. densiflora* occurs in most Patagonian salt marshes, we wondered why its sister *S. alterniflora* has not succeeded in marshes southern than ~42°25'S. The experimental results which we show here suggest that the absence of *S. alterniflora* in the southernmost marshes of Patagonia is severely affected by climatic conditions.

Although *S. alterniflora* was recorded in salt marshes at higher latitudes in England and in The Netherlands where it was introduced in the early nineteenth century, this cordgrass species is now extremely rare or virtually extinguished there (Davy et al. 2009; Strong and Ayres 2009). It has been suggested that *S. alterniflora* was out competed by *Spartina anglica*, its fertile hybrid with *Spartina maritima* (Adam 1993; Strong and Ayres 2009). However, this is the opposite of what was recorded in coastal China, where it is *S. alterniflora* which seems to exclude *S. anglica* by competition (Zhi et al. 2007). These variations in space and time suggest that a warmer climate may improve the long-term survival of *S. alterniflora*, as well as its competitive abilities. Despite that, the fact that the low intertidal level in the austral marshes of Patagonia remains as mudflat devoid of vascular plant species, lead us to momentarily reject any competitive exclusion hypothesis.

On the North Western Atlantic coast, *S. alterniflora* is a native species that occupies and dominates the low marsh zone, and it was recorded as far north as Newfoundland (Canada, ~50°N; Baerlocher et al. 2004). There, the cordgrass faces harsh cold climatic

**Table 2** Analyses of variance (ANOVA) for effect of the treatments on the proportion of living tillers, the proportion of living leaves, the living tiller height, the potentially photosynthetic leaf area and aboveground biomass of *S. alterniflora*

Source	df	MS	F	P value
Proportion of living tillers				
Treatment	4	0.39	19.36	<0.0001*
Error	45	0.02		
SNK: Ct > C = CP > H = HP				
Proportion of living leaves				
Treatment	4	0.15	25.90	<0.0001*
Error	45	0.01		
SNK: Ct > C = CP > H = HP				
Living tiller height				
Treatment	4	181.84	14.74	<0.0001*
Error	45	12.33		
SNK: Ct > C = CP > H = HP				
Potentially photosynthetic leaf area				
Treatment	4	12.59	45.22	<0.0001*
Error	45	0.28		
SNK: Ct > C = CP = H = HP				
Aboveground biomass				
Treatment	4	7.01	25.07	<0.0001*
Error	45	0.28		
SNK: Ct > C = CP > H = HP				

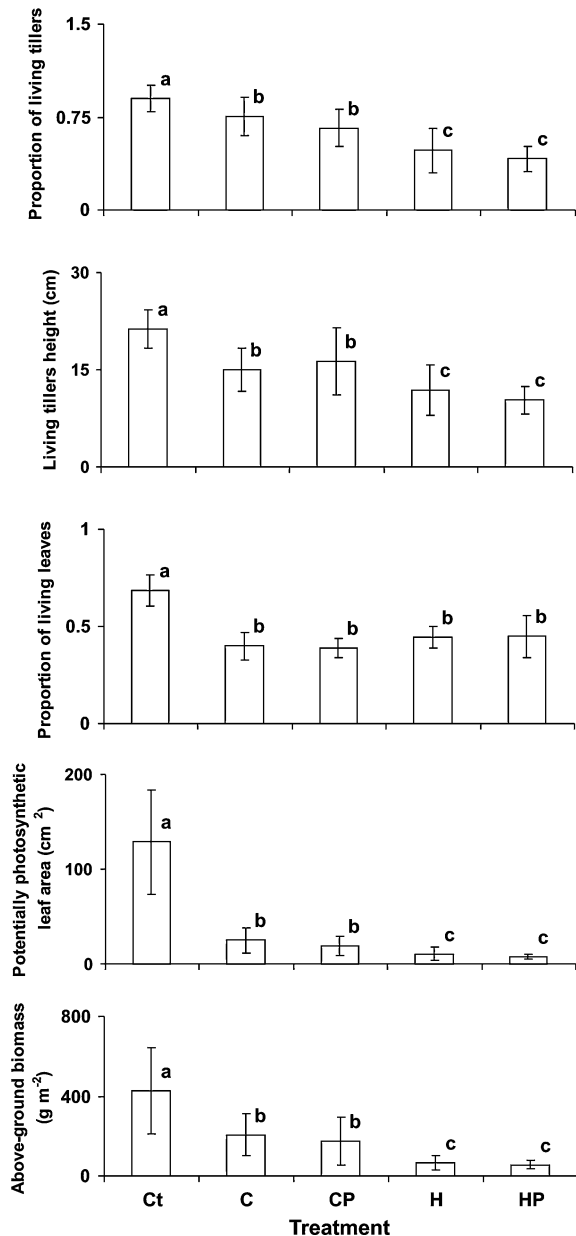
C cold treatment, CP cold-photoperiod treatment, H humidity treatment, HP humidity-photoperiod treatment, Ct control treatment

\*  $P \leq 0.05$ . Student–Newman–Keuls (SNK) tests ( $\alpha = 0.05$ ) were used to test for differences among plant measurements when the factor treatment was significant

conditions, comparable to some of the southernmost Argentinean salt marshes where the species was never recorded (Correa 1998; Bortolus et al. 2009). However, along the Atlantic coast of North America, *S. alterniflora* shows a tendency to decrease its primary productivity with increasing latitude, probably as a consequence of temperature decreases (Hatcher and Mann 1975; Mendelssohn and Morris 2002; Kirwan et al. 2009). In addition to this, in the northernmost marshes the aboveground structures of *S. alterniflora* decay every winter season while it reallocates the aerial biomass into overwintering rhizomes and enters in dormancy until next spring (Bertness 1999). This overwintering mechanism that helps *S. alterniflora* to avoid the physiological stress associated with frost, snow and ice, was never reported for the Argentinean populations, where the cordgrass stands stay green and relatively constant year round in terms of standing crop. These macrogeographic patterns agree with our results showing that the aerial structures of this cordgrass are highly susceptible to cold temperatures. Therefore, for those populations spreading toward high latitudes, cold climatic conditions are likely to work as a selective pressure of higher rank than biotic interactions.

*Spartina alterniflora* was negatively affected in the treatments where we simulated the austral winter of Argentina. Since the plants we used in our experiments came from the species' southernmost limit of distribution, they are expected to show the highest potential to resist and succeed a local cool climate. Therefore, plants from northern populations should be more susceptible and likely to be affected more rapidly. Low temperatures may determine plant distribution and even the composition of local vegetation (Sakai and Wardle 1978). This is what seems to happen in southern Patagonia, where winter temperatures reach more negative values and last longer than in central and northern Patagonia (Correa 1998). In addition, frost frequency increases toward the South, the Loyola *Sarcocornia*-marsh (the largest austral Patagonian salt marsh) being commonly frosted and covered by snow during winter (Correa 1998; Bortolus et al. 2009).

Far away from its geographic center of origin in North America, it seems like the Patagonian populations of *S. alterniflora* have evolved without ecological and physiological traits that help them to overcome harsh winter conditions. In fact, the lack of the overwintering mechanisms previously discussed



**Fig. 2** *Spartina alterniflora* responses to the cold (C), cold-photoperiod (CP), humidity (H), humidity-photoperiod (HP), and control (Ct) experimental treatments ( $n = 10$ ). Data are means  $\pm$  SD. Different letters indicate significant differences ( $P < 0.05$ ) in SNK test

above in this section is not the only problem that this species has to deal with. Our results suggest that also frost may represent an important problem. Cold temperatures are likely to damage thylakoid membranes, break down chlorophyll, and reduce their photosynthetic efficiency in  $C_4$  species (Pearce 2001;

Al-Shoaibi 2008). In addition, ice crystals formation can cause the disruption of cellular structures and even desiccation stress (Ashworth and Pearce 2002; Al-Shoaibi 2008). It was shown that ice crystals enter the plant through the stomata (Pearce 2001), and also that most plants (including trees, shrubs, and annual or perennial grasses with different photosynthetic pathways) open their stomata during nighttime (Snyder et al. 2003). In Patagonian marshes, *S. alterniflora* keeps most of the aboveground structures green and standing throughout the year, and their wide flat leaves do not have the capacity to curl (a common characteristic for the leaves of *S. densiflora*; Bortolus 2006; Maricle et al. 2009). The lack of a dormant period combined with the lack of a mechanism that prevents the entrance of ice through the stomata is likely to make *S. alterniflora* highly susceptible to the physiological stress caused by frost. Our experimental results support this hypothesis.

The impact of climatic change on the distribution of plant species is hard to predict. However, considering our result and that Patagonia shows an increment in the temperature (Rusticucci and Barrucand 2004), it is predictable that *S. alterniflora* will extend its geographic distribution toward higher latitudes over time. On the other hand, warming conditions are accompanied by an increment in atmospheric  $CO_2$  concentration that could benefit species with  $C_3$  photosynthetic pathway, such as *S. perennis*. Currently, the low marsh in the austral salt marshes of Patagonia seems available for *S. alterniflora* and free of competitors, since *S. perennis* does not resist the prolonged flooding that characterizes this intertidal level (Idaszkin and Bortolus 2010). Since both species seem to benefit from the potential effects driven by the global warming change, we expect the physiognomy of the austral salt marshes of Patagonia to converge with the Central Patagonia salt marshes, where *S. alterniflora* dominates the lower marsh and *S. perennis* the higher one, along with *S. densiflora*. Further studies, at local and regional scale, are needed to determine the one or several specific ways by which global warming affects these plants and the salt marshes they dominate.

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