Estuaries and Coasts (2014) 37:411–420
DOI 10.1007/s12237-013-9688-y

Aboveground Biomass Patterns of Dominant *Spartina* Species and Their Relationship with Selected Abiotic Variables in Argentinean SW Atlantic Marshes

Diana I. Montemayor · Alejandro D. Canepuccia · Jesus Pascual · Oscar O. Iribarne

Received: 26 June 2012 / Revised: 23 July 2013 / Accepted: 23 July 2013 / Published online: 14 August 2013

Abstract Salt marsh zonation patterns generate different abiotic and biotic conditions that can accentuate species inherent differences in primary production and biomass. In South West Atlantic marshes, there are two *Spartina* species: *Spartina alterniflora* in the low intertidal and *Spartina densiflora* in the high intertidal. These two species are generally found in all marshes but with different dominance: In some marshes, the *S. densiflora* zone occupies higher extents, and in others, the *S. alterniflora* zone is the one that prevails. We found through field sampling that, in six studied marshes, there is greater *S. densiflora* live and total (i.e., dead+live) aboveground biomass (g m^{-2}) in the marshes dominated by *S. densiflora* than in the ones dominated by *S. alterniflora*. *Spartina alterniflora* had similar aboveground biomass in the six marshes, regardless of the dominance of each species. When comparing the two *Spartina* species within each marsh, *S. densiflora* had greater live and total biomass in the marshes it dominates. In the marshes dominated by *S. alterniflora*, both species had similar live and total biomass. In all marshes, there was greater dead *S. densiflora* biomass. A multivariate analysis using selected abiotic factors (i.e., salinity, latitude, and tidal amplitude) showed that *S. alterniflora* aboveground biomass patterns are mainly correlated with salinity, while *S. densiflora* live biomass is mainly correlated with salinity and latitude, dead biomass with salinity and tidal amplitude, and total biomass with salinity alone. We conclude that in *S. densiflora* dominated marshes, the main processes of that species zone (i.e., nutrient accumulation) will be accentuated because of its higher biomass. We also conclude that climatic conditions, in combination with specific *Spartina* biotic and ambient abiotic parameters, can affect marsh ecological functions.

Keywords Abiotic variables · Aboveground biomass · Regional patterns · *Spartina alterniflora* · *Spartina densiflora*

Introduction

Different abiotic variables such as climate, substratum, and topography (e.g., Moffet et al. 2010), nitrogen loadings (e.g., Emery et al. 2001), groundwater and tides (e.g., Moffett et al. 2012), together with their interaction with biotic variables, generate spatial heterogeneity within an ecosystem (e.g., Turner and Chapin 2005). This spatial heterogeneity may generate important differences in the ecological function among nearby areas (e.g., Bouchard and Lefreuve 2000). Salt marsh biomass and net aerial primary production (hereafter NAPP) are good examples of spatial heterogeneity due to the distinct zonation patterns that marsh species have (Adam 1990). The species that live at different intertidal heights are exposed to different abiotic conditions, which can accentuate inherent differences in relation to primary production and biomass. For example, longer flood periods may result in (a) higher decomposition rates, which could accelerate energy transfer from the biomass to estuarine food webs (e.g., Hemminga and Buth 1991; Menendez and Sanmartí 2007; but see McKee and Seneca 1982); (b) higher broken stems due to tidal action, which generates greater detritus and exportation opportunities (Taylor and Allanson 1995); (c) lower salinity concentrations, which generate better sediment conditions for plant growth (Mendelsshon and Morris 2000); (d) increased sediment anoxia, which decreases *Spartina* growth (Castillo et al. 2000); and (e) decreased photoperiod, which also decreases *Spartina* growth (Castillo et al. 2000). Biotic variables can also change with different flood periods, for

Communicated by Bob Christian

D. I. Montemayor · A. D. Canepuccia · J. Pascual · O. O. Iribarne
Instituto de Investigaciones Marinas y Costeras (IIMyC), UNMDP, CONICET, Mar del Plata, Argentina

D. I. Montemayor (✉)
Laboratorio de Ecología, IIMyC, CC 573 Correo Central, B7600WAG Mar del Plata, Argentina
e-mail: montemayor@mdp.edu.ar

example herbivory rates (Alberti et al. 2007; Canepuccia et al. 2011; Silliman and Bertness 2002), and bioturbation rates (Bertness 1985; Daleo and Iribarne 2009) are greater in the lower intertidal. Moreover, given that low marshes have larger tidal influence, they generally have more chances of exporting organic matter (e.g., Taylor and Allanson 1995; Odum 2000). Thus, the combination of all these variables can generate important primary production and biomass differences among the species of the high and low marsh, which can influence the ecological role of each zone as producer/exporter of organic matter.

In particular, plant assemblages in South West Atlantic (hereafter SWA) marshes from southern Brazil to the north of Argentinean Patagonia are generally characterized by the presence of two *Spartina* species that inhabit different zones of the marsh: *Spartina alterniflora* Loesel. inhabits the low daily flooded marsh, and *Spartina densiflora* Brong inhabits the high occasionally flooded marsh (e.g., Bortolus and Iribarne 1999; Isacch et al. 2006). Marshes vary in the extent they are dominated by each species. The distribution of this type of plant assemblage is intimately related with marsh salinity: Marshes with higher freshwater input are dominated by *S. densiflora*, and more saline marshes are dominated by *S. alterniflora* (Isacch et al. 2006). However, there is no information of how the biomass of the two SWA *Spartina* species behaves with salinity. In this sense, under experimental conditions, in the Odiel river (Spain), *S. densiflora* showed high growth within the range of 5–20 salinity, while at 40, there was a significant decrease (Castillo et al. 2005). Similar results were found in California (USA) *S. densiflora*, where growth started to decrease at 18 salinity (Kittelson and Boyd 1997). Likewise, *S. alterniflora* showed higher growth for values of 20 salinity or less under experimental conditions (Haines and Dunn 1976). In fact, there are several studies that show a negative effect of salinity on *S. alterniflora* (e.g., Adams 1963; Mendelssohn and Morris 2000; Li et al. 2010; Xiao et al. 2011). However, in a salt marsh in New England (USA), there is evidence of a poor relationship between salinity and *S. alterniflora* biomass (Howes et al. 1986). In this sense, under natural conditions, abiotic variables work in combination modulating their effects. For example, the interaction between salinity and rainfall under natural conditions, it is not a direct one (De Leeuw et al. 1990). Thus, not only experimental studies where one variable is being measured are useful to understand how that variable works, but also studies of the combination of effects of different abiotic variables are necessary to understand how they covary and collectively contribute to a biotic response.

Together with salinity (e.g., Zedler 1983; Adam 1990; Mendelssohn and Morris 2000), the other abiotic variables found to modulate regional patterns of marsh aboveground biomass and primary productivity are soil properties (Delaune et al. 1979), nutrient loadings (Nixon and Oviatt 1973; Pennings et al. 2002), tidal amplitude (Steever et al. 1976), and latitude (e.g., paralleling solar energy inputs, Turner 1976; paralleling temperature or growing season, Kirwan et al. 2009). In SWA marshes, though no specific study has been done in relation to biomass regional patterns, important abiotic variables that define plant species assemblages at a regional scale are salinity, rainfall, latitude, and tidal amplitude (Isaach et al. 2006). Hence, the hypothesis of this work is that aboveground biomass of each species could also be differently correlated to these abiotic variables. The hypothesis is based on the correlation that these abiotic variables have with the dominance of each SWA *Spartina* species, as well as on the aforementioned evidence of *Spartina* biomass being affected by these abiotic variables. Furthermore, this hypothesis is strengthened by the fact that the two *Spartina* species live at different intertidal heights and are thus exposed to different combinations of abiotic variables.

In this context, the aim of the present work is to (1) compare the live, dead and total aboveground biomass of each *Spartina* species of six SWA salt marshes that have different abiotic characteristics and dominance patterns and (2) evaluate which of the selected abiotic variables (i.e., latitude, tidal amplitude, and salinity) or their combination best correlate with the aboveground biomass pattern of each species.

Materials and Method

Study Site

The study was performed at six of the most important SWA salt marshes (see Isacch et al. 2006), which from the N to the S are mouth of El Salado river (35°58′ S; hereafter SAL), San Clemente (36°19′ S; hereafter SC), Bahía Blanca (38°59′ S; hereafter BB), Bahía Anegada (40°19′ S; hereafter BA), mouth of the Río Negro river (41°01′ S, hereafter RN); and Bahía San Antonio (40°44′ S; hereafter BSA; Fig. 1, Tables 1 and 2). These salt marshes have the two *Spartina* species. SAL, SC, and RN are dominated by *S. densiflora*, while BB, BA, and BSA are dominated by *S. alterniflora* (Table 1; Isaach et al. 2006). The six marshes have different values for abiotic variables (Tables 1 and 2). For further information about variations on abiotic variables among the different salt marshes, see Isacch et al. (2006).

Spartina densiflora and *S. alterniflora* Aboveground Biomass Patterns

The aboveground biomass was harvested from 10 quadrats (25×25) in each salt marsh and in each species zone (i.e., destructive technique) in order to evaluate aboveground biomass (g m^{-2}) of plant species. Sampling plots were located in the middle area of each species zone. Within

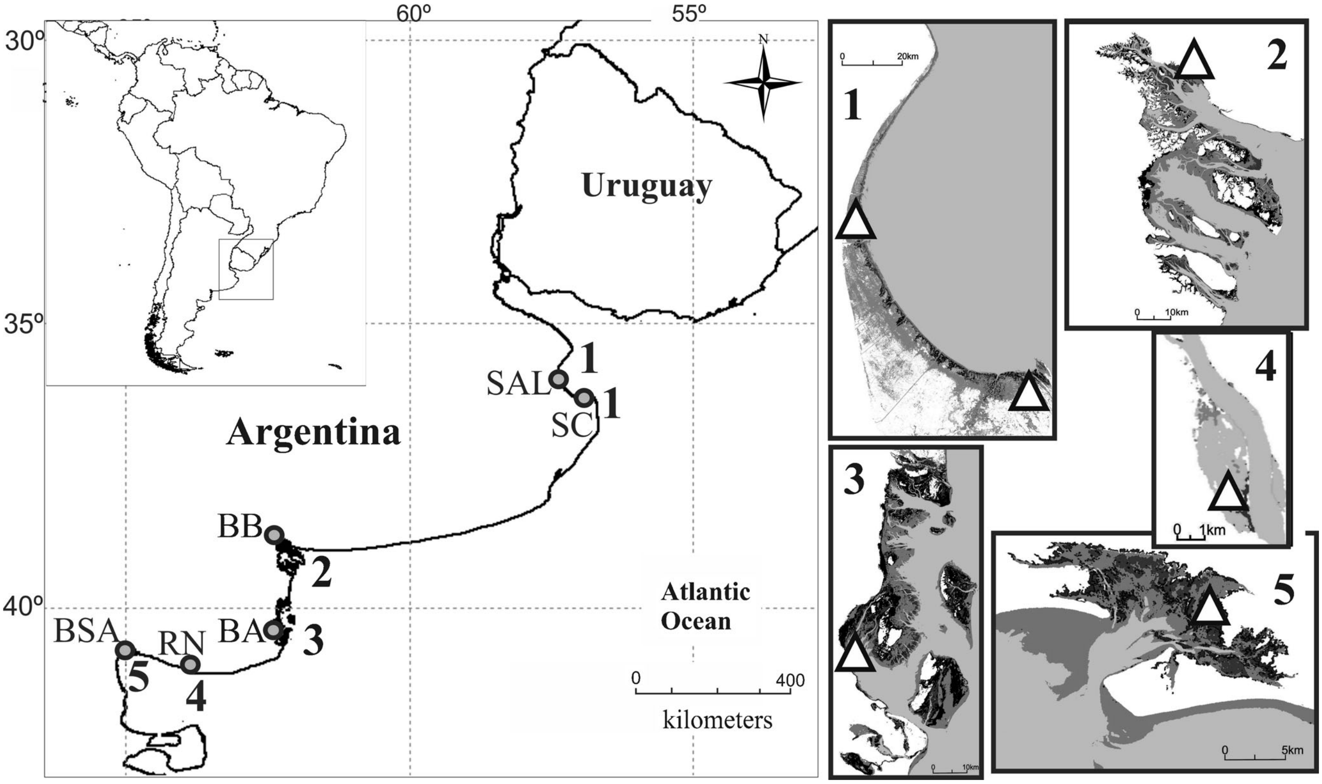


Fig. 1 Geographic location of the six South West Atlantic marshes (*SAL* El salado, *SC* San Clemente, *BB* Bahía Blanca, *BA* San Blas, *BSA* Bahía San Antonio, *RN* Río Negro mouth). *Circles* indicate the estuary zones. *Triangles* within estuary satellite images indicate the sampling zones. Estuaries satellite images were taken from Isacch et al. 2006

each species, zone plots were separated by 10 m. This sampling was seasonally repeated during the period of July 2008 to June 2009 (i.e., four samplings in total for each species zone). In order to assure independence between samples in the different samplings, at least 10 m was left between samples of consecutive seasons. Harvested biomass was separated into live and dead, and dried at 70 °C until constant weight, and weighed (0.1 g precision).

Table 1 Selected abiotic variables for the six salt marshes (hereafter: SAL El salado; SC, San Clemente; BB, Bahía Blanca; BA, Bahía Anegada; BSA, Bahía San Antonio; RN, Río Negro mouth) and total hectares occupied by each species in each salt marsh (i.e., SAL, SC, and RN dominated by *S. densiflora*; BB, BA, and BSA dominated by *S. alterniflora*)

	Latitude	Mean annual salinity (ppt)	Tidal amplitude (m)	Estuary *S. alterniflora* (ha)	Estuary *S. densiflora* (ha)
SAL	35° 58′	9.4	0.73	5,060	26,314
SC	36° 19′	25.6	0.78	5,060	26,314
BB	38° 43′	41.7	3.43	9,193	65
BA	40° 25′	37.9	1.66	20,503	2,908
BSA	40° 44′	39.12	6.46	2,068	+
RN	41° 01′	13.7	2.94	47	656

Latitude, tidal amplitude, and hectares data were taken from Isacch et al. 2006. Salinity values were obtained through field sampling

The null hypothesis of no difference among the aboveground biomass of the six salt marshes was evaluated by means of a three-factor ANOVA model (GMAV 5, 1997, coded by AJ Underwood and MG Chapman, University of Sydney, Australia) with "species of *Spartina*" (fixed, two levels), "salt marshes" (fixed and orthogonal, six levels), and "sampling dates" (random, nested within salt marshes, four levels). The main factor "sampling date" is nested within salt marshes because distances between salt marshes made it very difficult to achieve the same sampling dates and differences of 2 weeks or a month did happen. If there were no differences for the nested factor "sampling dates," then it was pooled. Taking into consideration that ANOVA with balanced data and large samples (i.e., more than five treatments and *n* larger than 6) are robust to departure from its assumptions (Underwood 1997) and that our data satisfied those premises but were not monotonic when transformed to achieve homocedasticity, no transformation was performed. Whenever the assumptions of normality and homoscedasticity could not be met, and in order to reduce the probability of committing type I error, we considered the differences significant if $p<0.005$ (Zar 1999; see Antón et al. 2011 and Alberti et al. 2011 for similar approach). To identify the differences an a posteriori SNK test

Table 2 Additional abiotic variables for the six marshes

	Mean annual air temperature (°C)	Mean annual rainfall (mm)	Grain sediment size	*S. alterniflora* burrows (m^{-2})	*S. densiflora* burrows (m^{-2})	Environmental settings
SAL	20.83	950				River influenced
SC	20.83	950				River influenced
BB	16	645	Fine (sand, silt, clay)	70.4	68	Multichanneled
BA	–	500	Large (cobble, pebble)		100	Multichanneled
BSA	15.4	248	Large (cobble, pebble)	122.6	48.8	Multichanneled
RN	15.2	380		103.3	107.7	River influenced

Temperature and rainfall values (Servicio Meteorológico Nacional), grain sediment size (Daleo et al. 2009), *Spartina* crab burrow densities (Alberti et al. 2007), and environmental settings (Isacch et al. 2006)

was performed for the main factors when no interaction was found and for the interaction of the factors when interaction was found. The ANOVA analysis was performed separately for live biomass, dead biomass, and total biomass (i.e., three ANOVAS).

Correlation Between Abiotic Factors and Biomass Patterns of Each of the Two *Spartina* Species

To evaluate which abiotic variables (i.e., salinity, latitude, or tidal amplitude) or which combination of them were correlated with the aboveground biomass of each plant, two dissimilarity matrixes were calculated. For the aboveground biomass of each *Spartina* species, we used Bray–Curtis dissimilarities from untransformed data and for the abiotic variables, normalized Euclidean distances (Clarke and Warwick 2001). These are the distances that have to be employed for the biotic variables in the first case and for the abiotic variables in the second case because of the different scale of measures in the abiotic variables (Clarke and Warwick 2001). The correlation between these matrices was measured using Bio-Env (PRIMER 6 software) by means of the Spearman correlation rank. The statistical significance of the correlations was evaluated through a permutation test included in the Bio-Env procedure (PRIMER 6 software). This analysis was performed separately for live aboveground biomass, dead biomass, and total biomass (i.e., three independent Bio-Env) of each *Spartina* species. The data used for the biotic matrix were the average aboveground biomass value of each sampled season, calculated from the data obtained in "*Spartina densiflora* and *S. alterniflora* Aboveground Biomass Patterns." The data of tidal amplitude and latitude for each studied site were obtained from Isacch et al. (2006). For the salinity data, five water column samples from each of the six marshes were extracted during high tide and then measured (0.001 precision). The Practical Salinity Scale was used to determine salinity. These samplings were performed in the same places as where the biomass was harvested and repeated in ten different sampling dates along the year.

Results

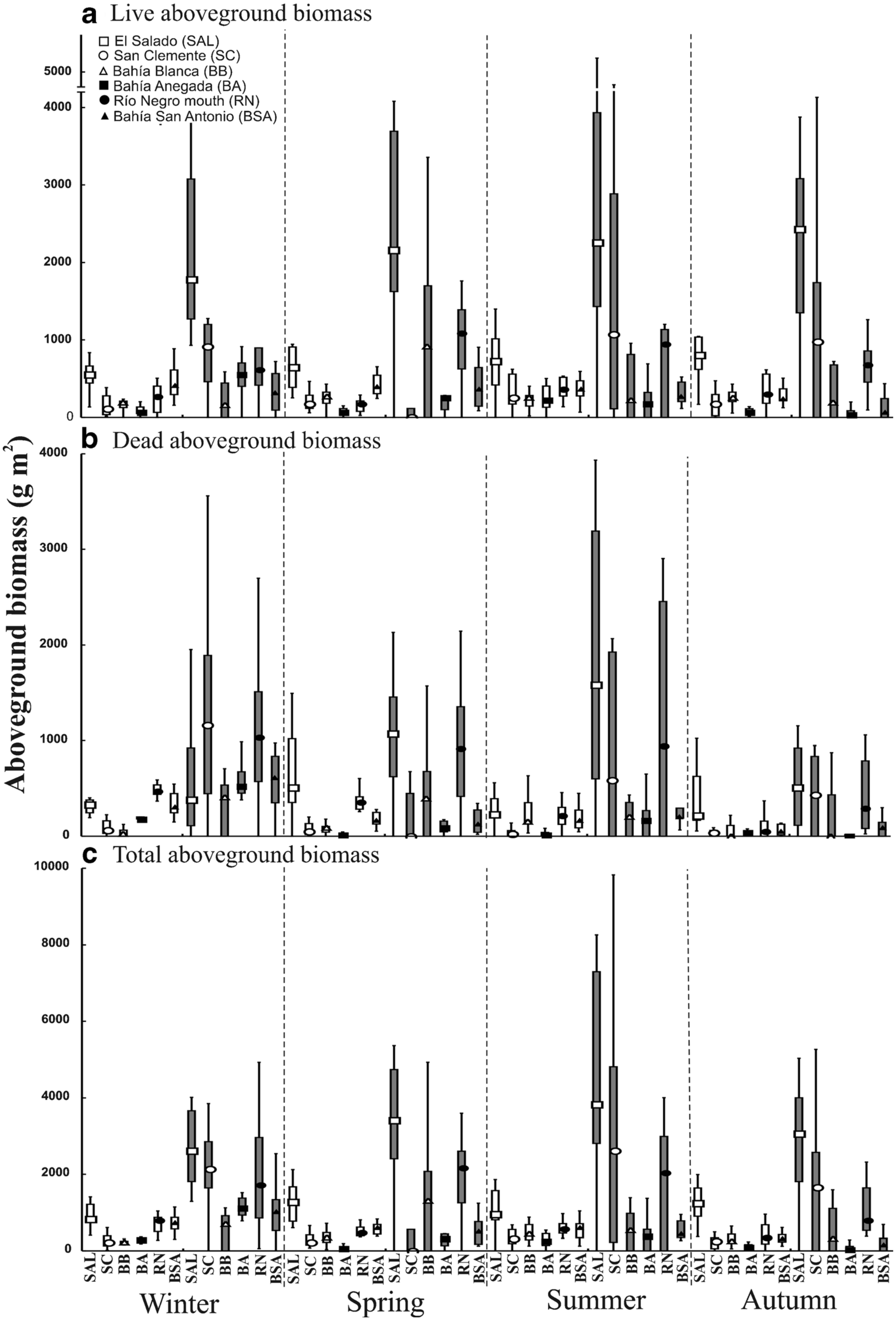
Spartina densiflora and *S. alterniflora* Aboveground Biomass Patterns

There was greater live aboveground biomass of *S. densiflora* than *S. alterniflora* in SAL, SC, and RN, while similar biomass for both plant species was found in BB, BA, and BSA (Fig. 2a; mean and SD values, Table 3; ANOVA results, Table 4; SNK results, Table 5). In relation to the comparison among marshes, *S. densiflora* had greater aboveground biomass in SAL, while there were no differences between the other five salt marshes. *Spartina alterniflora* showed similar aboveground biomass among marshes (Fig. 2a; mean and SD values, Table 3; ANOVA results, Table 4; SNK results, Table 6). No differences were found for the sampling dates.

Aboveground dead biomass of *S. densiflora* was always greater than for *S. alterniflora* (Fig. 2b; mean and SD values, Table 3; ANOVA results, Table 4; SNK results, Table 5). In relation to the comparison among marshes, SAL, RN, and SC have similar amounts of aboveground dead biomass for both plant species. SC has also similar amounts as BB and BSA, and these two have similar amounts as BA. BB, BSA, and BA are different to SAL and RN (Fig. 2b; mean and SD values, Table 3; ANOVA results, Table 4; SNK results, Table 5). In relation to the sampling date, winter, summer, and spring had similar amounts of dead biomass; spring had also similar amounts as autumn, but the latter had lower amounts than winter and summer.

Spartina densiflora had greater aboveground total biomass than *S. alterniflora* in SAL, SC, and RN, while in BB, BA, and BSA both species had similar aboveground total biomass (Fig. 2c; mean and SD values, Table 3; ANOVA results, Table 4; SNK results, Table 5). *Spartina*

Fig. 2 Aboveground biomass of the six salt marshes and the two plant species: **a** live, **b** dead, and **c** total. *Empty box plots* correspond to *S. alterniflora* and *gray box plots* to *S. densiflora. Empty quadrats*, *circles*, and *triangles* are SAL, SC, and BB, respectively, while *full-filled quadrats circles* and *triangles* are BA, BSA, and RN, respectively. *Box plots* constructed with *vertical lines* represent 0.01 and 0.99 percentiles, box limits are the 0.25 and 0.75 percentiles, and *symbols within boxes* are the median



alterniflora had similar biomass for the six salt marshes. *Spartina densiflora* had the largest aboveground biomass in SAL followed by SC and RN with similar amounts and then followed by BB, BA, and BSA with similar amounts (Fig. 2c; mean and SD values, Table 3; ANOVA results, Table 4; SNK results, Table 6). No differences were found for the sampling dates.

Correlation Between Abiotic Factors and Biomass Patterns of Each of the Two *Spartina* Species

Spartina alterniflora live (r=0.22; p=0.045), dead (r=0.21; p=0.031), and total (r=0.32; p=0.005) aboveground biomass were best correlated with salinity alone. *Spartina densiflora* live aboveground biomass was better correlated with the

Table 3 Mean and standard deviations values for the aboveground biomass of the six salt marshes

		Live				Dead				Total			
		Spartina alterniflora		*Spartina densiflora*		*Spartina alterniflora*		*Spartina densiflora*		*Spartina alterniflora*		*Spartina densiflora*	
Marsh	Season	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
SAL	Winter	559	274	2,153	1,078	342	144	576	610	901	341	2,730	990
SAL	Spring	639	248	2,258	1,376	622	451	993	648	1,262	562	3,251	1,852
SAL	Summer	697	420	2,542	1,572	317	325	1,857	1,433	1,015	558	4,400	2,755
SAL	Autumn	841	421	2,434	1,919	383	340	704	759	1,225	510	3,139	2,643
SC	Winter	161	137	903	697	91	79	1,401	1,226	252	186	2,305	1,706
SC	Spring	205	126	266	536	83	77	467	1,109	288	193	733	1,539
SC	Summer	367	355	1,723	1,861	40	46	1,194	1,595	407	390	2,917	3,107
SC	Autumn	179	156	1,203	1,391	36	35	616	832	216	168	1,819	1,957
BB	Winter	164	72	227	236	42	38	315	287	206	84	543	488
BB	Spring	267	152	1,040	1,153	84	56	520	553	352	195	1,561	1,676
BB	Summer	249	143	599	962	234	178	305	469	484	247	905	1,419
BB	Autumn	258	116	580	1,028	54	78	298	460	313	183	879	1,448
BA	Winter	87	62	534	251	211	57	528	252	299	104	1,062	439
BA	Spring	64	53	345	528	15	15	129	150	80	64	475	674
BA	Summer	247	181	214	221	22	27	222	256	270	193	436	463
BA	Autumn	77	36	53	66	50	22	18	34	127	49	71	95
BSA	Winter	241	191	742	604	478	184	1,240	991	720	247	1,983	1,475
BSA	Spring	154	86	967	589	371	104	893	672	525	145	1,860	1,186
BSA	Summer	364	147	648	566	220	144	1,247	1,210	584	187	1,896	1,564
BSA	Autumn	316	212	712	452	106	134	546	645	423	324	1,259	1,045
RN	Winter	443	216	321	248	334	129	708	689	778	328	1,029	744
RN	Spring	415	133	411	278	169	76	154	126	584	142	566	386
RN	Summer	356	153	344	246	196	127	259	150	553	259	603	375
RN	Autumn	283	127	139	160	83	98	100	106	366	206	239	257

combination of salinity and latitude ($r=0.55$; $p=0.001$), while dead biomass with salinity and tidal amplitude ($r=0.32$; $p=0.005$), and total biomass with salinity alone ($r=0.5$; $p=0.005$). All the correlations found were negative.

Discussion

Our results show greater *S. densiflora* aboveground biomass in the marshes it dominates (i.e., SAL, SC, and RN) than in the

Table 4 Three-factor ANOVA results for the live, dead, and total aboveground biomass density ($n=10$)

	df	Live aboveground biomass			Dead aboveground biomass			Total aboveground biomass		
		MS	*F*	*p* value	MS	*F*	*p* value	MS	*F*	*p* value
Spartina species	1	39,250,098.8	91.01	< 0.005	2,388,7781	39.47	<0.005	1,243,78316.5	88.16	<0.005
Salt marsh	5	17,641,840.6	28.39	< 0.005	4,515,618.7	5.49	<0.005	36,487,111.6	18.44	<0.005
Date(Salt marsh)	18	621,453.6	1.38	0.13	821,864.6	2.66	<0.005	19,790,624.8	1.7	0.03
Spartina species x Salt marsh	5	7,437,417.3	17.24	< 0.005	1,973,581.7	3.26	0.02	14,473,789.8	10.26	<0.005
Spartina species x Date(Salt marsh)	18	431,282.7	0.96	0.5	605,288	1.96	0.01	1,410,878.5	1.21	0.24
Error	432	45,0438.4			309,547.6			1,161,498.4		

Table 5 Differences in the *Spartina alterniflora* and *Spartina densiflora* biomass density in the six salt marshes

	Live biomass	Dead biomass	Total biomass
SAL	*S. alterniflora*<*S. densiflora*	*S. alterniflora*<*S. densiflora*	*S. alterniflora*<*S. densiflora*
SC	*S. alterniflora*<*S. densiflora*	*S. alterniflora*<*S.densiflora*	*S. alterniflora*<*S. densiflora*
BB	*S. alterniflora*=*S. densiflora*	*S. alterniflora*<*S. densiflora*	*S. alterniflora*=*S. densiflora*
BA	*S. alterniflora*=*S. densiflora*	*S. alterniflora*<*S. densiflora*	*S. alterniflora*=*S. densiflora*
RN	*S. alterniflora*<*S. densiflora*	*S. alterniflora*<*S.densiflora*	*S. alterniflora*<*S. densiflora*
BSA	*S. alterniflora*=*S. densiflora*	*S. alterniflora*<*S. densiflora*	*S. alterniflora*=*S. densiflora*

marshes dominated by *S. alterniflora* (i.e., BB, BA, and BSA). *Spartina alterniflora* had similar aboveground biomass in the six marshes, regardless of its dominance. When comparing live and total aboveground biomass of the two species within each marsh, *S. densiflora* had more biomass than *S. alterniflora* in the marshes dominated by *S. densiflora* and similar amounts in the marshes dominated by *S. alterniflora*, while for dead aboveground biomass *S. densiflora* always had more. *Spartina alterniflora* biomass patterns are better correlated with salinity, while *S. densiflora* ones correlated better with salinity in combination with other abiotic variables.

The fact that *S. densiflora* had greater biomass in the marshes it dominates, while in *S. alterniflora* dominated marshes biomass was similar for both species, can be the result of a combination of factors. First, this may reflect that *S. densiflora* dominates marshes outcompeting other species, while *S. alterniflora* dominates marshes in a more stressful abiotic environment. This can be accentuated by the fact that *S. densiflora* has more NAPP than *S. alterniflora* (Montemayor 2012). Thus, *S. alterniflora* in the marshes it dominates (i.e., BB, BA, BSA) instead of achieving more biomass only equals the biomass of *S. densiflora*. Moreover, two of the three marshes that are dominated by *S. alterniflora* have well-drained and aerated coarse sediments (i.e., BA, BSA; Daleo and Iribarne 2009). In this type of sediments, the negative effects of herbivory by the *Neohelice granulata* Dana crab on plant biomass are more important than the positive effects of the bioturbation activity of this same crab (Daleo and Iribarne 2009). Hence, there is more suppression of *S. alterniflora* biomass because this species is exposed to higher hervibory rates (Alberti et al. 2007). All these factors suggest that, in SWA marshes, biotic as well as abiotic factors favour higher *S. densiflora* biomass development.

However, dead biomass pattern was different to the live and total biomass. Beyond *Spartina* species dominance, in all of the marshes, *S. densiflora* had greater dead biomass. The latter can also be explained by a combination of biotic and abiotic factors. Firstly, as already mentioned, *S. densiflora* has greater NAPP than *S. alterniflora* (Montemayor 2012). This implies that *S. densiflora* produces more live biomass, which in turn generates a greater accumulation of dead biomass. Secondly, *S. densiflora* accumulated dead biomass is less influenced by tides than *S. alterniflora* (Montemayor et al. 2011). High marshes tend to accumulate dead biomass because tides reach these zones less often and do not remove it as often as in low marshes (Hopkinson et al. 1978). Thirdly, *S. densiflora* tussocks are very compact and with high stem densities, but *S. alterniflora* grows as isolated stems. Thus, *S. densiflora* tussocks are suggested as being more resistant to tidal mechanical action (Nieva et al. 2001) in such a way that dead matter remains for longer time periods. Moreover, in Spanish marshes, dead biomass remains inside the tussock, while live biomass surrounds it from the outside (Nieva et al. 2005). With the latter tussock architecture, live biomass could be protecting dead biomass from tide mechanical action, accentuating presence of dead biomass. Fourthly, tides accelerate the decomposition of dead material. In fact, in the same area, *S. densiflora* had less aerial decomposition than *S. alterniflora* (Montemayor et al. 2011). In this sense, plenty of studies have found larger dead biomass in high versus low marshes (e.g., Schubauer and Hopkinson 1984; Nieva et al. 2001; González Trilla et al. 2009; 2010). The results of our study supports the important effect of tides as we found that tidal amplitude is one of the abiotic factors that best correlates with *S. densiflora* dead biomass pattern, with marshes with less tidal amplitude having greater dead biomass. Finally,

Table 6 Differences in the live, dead, and total biomass density of the six marshes for *Spartina alterniflora* and *Spartina densiflora*

	S. alterniflora	*S. densiflora*
Live biomass	SAL=SC=BB=BA=RN=BSA	SAL>SC=CON=BB=SB=SAO
Dead biomass	SAL=RN=SC	SAL=RN=SC
	SC=BSA=BB	SC=BSA=BB
	SAL=RN>BSA=BB=BA	SAL=RN>BSA=BB=BA
Total biomass	SAL=SC=BB=BA=RN=BSA	SAL>SC=RN>BB=BA=BSA

herbivory by the stem-boring moth larva *Haimbachia* sp. nov. (Canepuccia et al. 2011) and by the burrowing crab *N. granulata* (Alberti et al. 2007) may also be promoting greater dead aboveground biomass. In the marshes with higher herbivory pressure on both *Spartina* species (crab, Alberti et al. 2007; stem borer moth, Canepuccia et al. 2011), there is in fact greater dead aboveground biomass of both *Spartinas*. Thus, it seems that biotic and abiotic factors are working together in the direction of a greater accumulation of *S. densiflora* dead biomass.

In relation to the correlation of aboveground biomass patterns with abiotic variables, while *S. alterniflora* live aboveground biomass is best correlated negatively with salinity, *S. densiflora* is best correlated negatively with salinity and latitude. The latter difference between the two plant species could be related to the different intertidal heights where they live. *Spartina alterniflora* is influenced daily by tides while *S. densiflora* only occasionally (Isacch et al. 2006). Hence, it is likely that *S. alterniflora* is more influenced by marine environment while *S. densiflora* by land environment. In this sense, SWA marshes are distributed in three different land biogeographic provinces that change with latitude due to temperature and rainfall variations (Cabrera and Willink 1973). The northern marshes (SAL and SC) are surrounded by the Pampas grasslands biogeographic province (Cabrera and Willink 1973) and have annual rainfalls of 1,000 mm (Isacch et al. 2006). At the mid-geographic study range (BB), there is an increase in xeric conditions (600 mm annually, Isacch et al. 2006) with thorn bushes characterizing the land (the Espinal biogeographic province, Cabrera and Willink 1973). The southern geographic range (RN, BB, and BSA) has the lowest annual rainfall (around 200 mm, Isacch et al. 2006) and is surrounded by the biogeographic Monte province, characterized by xeric bushes (Cabrera and Willink 1973). Meanwhile, the marine biogeographic province for these marshes is always the same (Spalding et al. 2007). This suggests that differences in *S. densiflora* biomass could be modulated to some extent by abiotic factors variation in the surrounding land environment (i.e., the three biogeographic provinces mentioned above). Meanwhile, differences in *S. alterniflora* could be due to variations in run-off volumes, which affect the amounts of salinity (Isacch et al. 2006).

While *S. alterniflora* dead aboveground biomass is negatively correlated with salinity, *S. densiflora* is negatively correlated with salinity and tidal amplitude. As in the case of live aboveground biomass, the latter difference between the two plant species could be related to their different intertidal heights. Larger tidal amplitude results in larger tidal influence that exports more dead aboveground biomass (Hopkinson et al. 1978). Because *S. alterniflora* is distributed in a lower intertidal level and is frequently flooded by tides, the chances of exporting dead material is approximately the same for the different marshes. However, in the case of *S. densiflora*, differences in tidal amplitude should have a greater effect as it inhabits higher intertidal zones. To sum up, those zones with larger tidal amplitude may have lower aboveground biomass due to the higher chances of being transported by tides.

Total aboveground biomass of *S. alterniflora* and *S. densiflora* is best correlated with salinity. This is probably indirectly related to the effect that salinity has on the aboveground biomass. Low salinity concentrations allow for higher growth of biomass (Mendelssohn and Morris 2000; Xiao et al. 2011), which in turn dies resulting in greater dead and total biomass.

Determining regional patterns in marsh biomass distribution is important for a larger scale understanding of marsh ecological functions. The marked patterns found in our study for the two differently dominated marshes point towards different organic matter recycling processes. Previous studies showed that the main process in the *S. densiflora* zone is detritus biomass accumulation for long time periods, while in the *S. alterniflora* zone, it is nutrient recycling and exportation (Montemayor et al. 2011). Our study emphasizes the results of this previous work, as we have found that particularly in *S. densiflora* dominated marshes, nutrient accumulation will be exacerbated by the fact that aboveground biomass of *S. densiflora* is greater than that of *S. alterniflora*. Moreover, salinity is the abiotic variable that correlated better with the aboveground biomass patterns of both *Spartina* species. While for *S. alterniflora,* salinity was the most important abiotic variable, for *S. densiflora*, there were other abiotic variables influencing it. This difference could be due to the different land-marine influence on the two species because they inhabit different intertidal heights. Thus, climatic conditions, in combination with specific *Spartina* biotic and ambient abiotic parameters, could also affect marsh ecological functions.

Acknowledgments We thank Ann Borsinger for assistance with language edition and two anonymous reviewers for valuable suggestions on the manuscript. We also thank Juan Pablo Isacch for providing us the satellite images of Fig. 1. This project was supported by Universidad Nacional de Mar del Plata, ANPCyT, and CONICET (all granted to O.I.). D.M. and J.P. were supported by a doctoral scholarship from CONICET. This paper is part of the Doctoral thesis of D.M.

References

Adam, P. 1990. *Saltmarsh ecology.* Cambridge: Cambridge University Press.

Adams, D.A. 1963. Factors influencing vascular plant zonation in North Carolina saltmarshes. *Ecology* 44: 445–456.

Alberti, J., J. Cebrian, A. Méndez Casariego, A.D. Canepuccia, M. Escapa, and O. Iribarne. 2011. Effects of nutrient enrichment and crab herbivory on a SW Atlantic saltmarsh productivity. *Journal of Experimental Marine Biology and Ecology* 405: 99–104.

Alberti, J., M. Escapa, P. Daleo, O.O. Iribarne, B. Silliman, and M. Bertness. 2007. Local and geographic variation in grazing intensity by herbivorous crabs in SW Atlantic salt marshes. *Marine Ecology Progress Series* 349: 235–243.

Antón, A., J. Cebrian, K. Heck Jr., C. Duarte, K. Sheehan, M. Miller, and C. Foster. 2011. Decoupled effects (positive to negative) of nutrient enrichment on ecosystem services. *Ecological Applications* 21: 991–1009.

Bertness, M.D. 1985. Fiddler crab regulation of *Spartina alterniflora* production on a New England salt marsh. *Ecology* 66: 1042–1055.

Bortolus, A., and O.O. Iribarne. 1999. The effect of the southwestern Atlantic burrowing crab *Chasmagnathus grannulata* on a Spartina salt-marsh. *Marine Ecology Progress Series* 178: 79–88.

Bouchard, V., and J.C. Lefeuvre. 2000. Primary production and macro-detritus dynamics in a European salt marsh: carbon and nitrogen budgets. *Aquatic Botany* 67: 23–42.

Cabrera, A.L., and A. Willink. 1973. *Biogeografía de América Latina. Serie de biología, monográfica no, 13. Programa regional de Desarrollo Científico y Tecnológico*. Washington: Departamento de Asuntos Científicos, Organización de Estados Americanos.

Canepuccia, A.D., D.I. Montemayor, J. Pascual, J.L. Farina, and O.O. Iribarne. 2011. A stem-boring moth drives detritus production in SW Atlantic marshes. *Marine Ecology Progress Series* 442: 1–9.

Castillo, J.M., L. Fernandez-Baco, E.M. Castellanos, C.J. Luque, M.E. Figueroa, and A.J. Davy. 2000. Lower limits of *Spartina densiflora* and *S. maritima* in a Mediterranean salt marsh determined by different ecophysiological tolerances. *Journal of Ecology* 88: 801–812.

Castillo, J.M., A.E. Rubio-Casal, S. Redondo, A.A. Alvarez-Lopez, T. Luque, C. Luque, F.J. Nieva, E.M. Castellanos, and M.E. Figueroa. 2005. Short-term responses to salinity of an invasive cordgrass. *Biological Invasions* 7: 29–35.

Clarke, K.R., and R.M. Warwick. 2001. *Changes in marine communities: an approach to statistical analysis and interpretation*, 2nd ed. Plymouth: PRIMER-E.

Daleo, P., and O.O. Iribarne. 2009. Beyond competition: the stress-gradient hypothesis tested in plant–herbivore interactions. *Ecology* 90: 2368–2374.

DeLaune, R.D., R.J. Buresh, and W.H. Patrick Jr. 1979. Relationship of soil properties to standing crop biomass of *Spartina alterniflora* in a Louisiana marsh. *Estuarine and Coastal Marine Science* 8: 477–487.

De Leeuw, J., H. Olff, and J.P. Bakker. 1990. Year-to-year variation in peak above ground biomass of six salt-marsh angiosperm communities as related to rainfall deficit and inundation frequency. *Aquatic Botany* 36: 139–151.

Emery, N.C., P.J. Ewanchuk, and M.D. Bertness. 2001. Competition and salt-marsh plant zonation: stress tolerators may be dominant competitors. *Ecology* 82: 2471–2485.

González Trilla, G., P. Kandus, V. Negrin, and J. Marcovecchio. 2009. Tiller dynamic and production on a SW Atlantic *Spartina alterniflora* marsh. *Estuarine, Coastal and Shelf Science* 85: 126–133.

González Trilla, G., S. De Marco, J. Marcovecchio, R. Vicari, and P. Kandus. 2010. Net primary productivity of *Spartina densiflora* Brong in a SW Atlantic coastal salt marsh. *Estuaries and Coasts* 33: 953–962.

Haines, B.L., and E.L. Dunn. 1976. Growth and resource allocation responses of *Spartina alterniflora* Loisel. to three levels of NH_4N, Fe, and NaCl in solution culture. *Botanical Gazette* 137: 224–230.

Hemminga, M.A., and G.J.C. Buth. 1991. Decomposition in salt marsh ecosystems of the S.W. Netherlands: the effects of biotic and abiotic factors. *Vegetatio* 92: 73–83.

Hopkinson, C.H., J.G. Gosselink, and R.T. Parrondo. 1978. Above-ground production of seven marsh plant species in coastal Louisiana. *Ecology* 59: 760–769.

Howes, B.L., J.W.H. Dacey, and D.D. Goehringer. 1986. Factors controlling the growth form of *Spartina alterniflora*: feedbacks between above ground production, sediment oxidation, nitrogen and salinity. *Journal of Ecology* 74: 881–898.

Isacch, J.P., L. Rodríguez, D. Conde, C. Costa, M. Escapa, D. Gagliardini, and O. Iribarne. 2006. Distribution of salt marsh plant communities associated with environmental factors along a latitudinal gradient on SW Atlantic coast. *Journal of Biogeography* 33: 888–900.

Kirwan, M.L., G.R. Guntenspergen, and J.T. Morris. 2009. Latitudinal trends in *Spartina alterniflora* productivity and the response of coastal marshes to global change. *Global Change Biology* 15: 1982–1989.

Kittelson, P.M., and M.J. Boyd. 1997. Mechanisms of expansion for an introduced species of Cordgrass, Spartina densiflora, in Humboldt Bay, California. *Estuaries* 20: 770–778.

Li, R., F. Shi, and K. Fukuda. 2010. Interactive effects of various salt and alkali stresses on growth, organic solutes, and cation accumulation in a halophyte *Spartina alterniflora* (Poaceae). *Environmental and Experimental Botany* 68: 66–74.

McKee, K.L., and E.D. Seneca. 1982. The influence of morphology in determining the decomposition of two salt marsh macrophytes. *Estuaries* 5: 302–309.

Mendelssohn, I.A., and J.T. Morris. 2000. Eco-physiological controls on the productivity of *Spartina alterniflora* Loisel. In *Concepts and controversies in tidal marsh ecology*, ed. M.P. Weinstein and D.A. Kreeger, 59–80. Dordretch: Kluwer Academic.

Menendez, M., and N. Sanmartí. 2007. Geratology and decomposition of *Spartina versicolor* in a brackish Mediterranean marsh. *Estuarine, Coastal and Shelf Science* 74: 320–330.

Montemayor, D.I. 2012. Importancia ecosistémica de las plantas de marisma género Spartina en áreas costeras del Atlántico Sudoccidental. Doctoral thesis, Facultad de Ciencias Exactas y Naturales, Universidad Nacional de Mar del Plata.

Montemayor, D.I., M. Addino, E. Fanjul, M. Escapa, M.F. Alvarez, F. Botto, and O. Iribarne. 2011. Effect of dominant *Spartina* species on salt marsh detritus production in SW Atlantic estuaries. *Journal of Sea Research* 66: 104–110.

Moffet, K.B., D.A. Robinson, and S.M. Gorelick. 2010. Relationship of salt marsh vegetation zonation to spatial patterns in soil moisture, salinity, and topography. *Ecosystems* 13: 1287–1302.

Moffett, K.B., S.M. Gorelick, R.G. McLaren, and E.A. Sudicky. 2012. Salt marsh ecohydrological zonation due to heterogeneous vegetation–groundwater–surface water interactions. *Water Resources Research* 48, W02516. doi:10.1029/2011WR010874.

Nieva, F.J.J., E.M. Castellanos, J.M. Castillo, and M.E. Figueroa. 2005. Clonal growth and tiller demography of the invader cordgrass *Spartina densiflora* Brong. at two contrasting habitats in SW European salt marshes. *Wetlands* 25: 122–129.

Nieva, F.J.J., A. Diaz-Espejo, E.M. Castellanos, and M.E. Figueroa. 2001. Field variability of invading populations of *Spartina densiflora* Brong. in different habitats of the Odiel marshes (SW Spain). Estuarine. *Coastal and Shelf Science* 52: 515–527.

Nixon, S.W., and C.A. Oviatt. 1973. Analysis of local variation in the standing crop of *Spartina alterniflora*. *Botanica Marina* 16: 103–109.

Odum, E.P. 2000. Tidal marshes as outwelling/pulsing systems. In *Concepts and controversies in tidal marsh ecology*, ed. M.P. Weinstein and D.A. Kreeger, 3–7. Dordretch: Kluwer Academic.

Pennings, S.C., L.E. Stanton, and J.S. Brewer. 2002. Nutrient effects on the composition of salt marsh plant communities along the Southern Atlantic and Gulf Coasts of the United States. *Estuaries* 25: 1164–1173.

Schubauer, J.P., and C.S. Hopkinson. 1984. Above- and below-ground emergent macrophyte production and turnover in a coastal marsh ecosystem, Georgia. *Limnology and Oceanography* 29: 1052–1065.

Silliman, B.R., and M.D. Bertness. 2002. A trophic cascade regulates salt marsh primary production. *Proceedings of the National Academy of Sciences USA* 99: 10500–10505.

Spalding, M.D., H. Fox, G.R. Allen, N. Davidson, Z.A. Ferdaña, M. Finlayson, B.S. Halpern, M.A. Jorge, A. Lombana, S.A. Lourie, K.D. Martin, E. McManus, J. Molnar, C.A. Recchia, and J. Robertson. 2007. Marine ecoregions of the world: A bioregionalization of coastal and shelf areas. *Bioscience* 57: 573–583.

Steever, E.Z., R.S. Warren, and W.A. Niering. 1976. Tidal energy subsidy and standing crop production of *Spartina alterniflora*. *Estuarine and Coastal Marine Science* 4: 473–478.

Taylor, D.I., and B.R. Allanson. 1995. Organic carbon fluxes between a high marsh and estuary, and the inapplicability of the outwelling hypothesis. *Marine Ecology Progress Series* 120: 263–270.

Turner, R.E. 1976. Geographic variations in salt marsh macrophyte production: a review. *Contributions in Marine Science* 20: 47–68.

Turner, M.G., and F.S. Chapin. 2005. Causes and consequences of spatial heterogeneity in ecosystem function. In *In Ecosystem function in heterogeneous landscapes*, ed. G.M. Lovett, C.G. Jones, M.G. Turner, and K.C. Weathers, 9–30. New York: Springer.

Underwood, A.J. 1997. *Experiments in ecology: their logical design and interpretation using analysis of variance*. Cambridge: Cambridge University Press.

Xiao, Y., J.B. Tang, and S.Q. An. 2011. Responses of growth and sexual reproduction of *Phragmites australis* and *Spartina alterniflora* to salinity stress. *Chinese Journal of Ecology* 30: 267–272.

Zar, J.H. 1999. *Biostatistical analysis*, 4th ed. Englewood Cliffs: Prentice-Hall.

Zedler, J.B. 1983. Freshwater impacts in normally hipersaline marshes. *Estuaries* 6: 346–355.