Allometric Scaling of Dry Weight and Leaf Area for *Spartina densiflora* and *Spartina alterniflora* in Two Southwest Atlantic Saltmarshes

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ABSTRACT

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Southwest Atlantic saltmarshes are characterized by the presence of *Spartina alterniflora* in the lower intertidal zones and *Spartina densiflora* in the middle to high tidal elevations. Because of its dominance and productivity and its central role in carbon and energy fluxes, *Spartina* spp. biomass and primary production have been extensively studied by different techniques. Since nondestructive techniques require relationships between tiller biomass and morphometric parameters, in this work we established allometric relations among biomass, leaf area, and size, in populations of *S. densiflora* and *S. alterniflora* from Mar Chiquita and Bahía Blanca, Argentina. We collected 743 standing tillers of *S. densiflora* and 663 of *S. alterniflora* from different dates, conditions (green, flowered, and dead), and sources (high and low marsh). We obtained strong correlations between all the morphometric parameters. Leaf area and leaf length were strongly related ($R^2 = 0.84$ for *S. densiflora* and 0.91 for *S. alterniflora*). Leaf area *per* tiller and tiller biomass strongly regressed on tiller height ($R^2 = 0.97$ and 0.91 for *S. densiflora* and 0.88 and 0.90 for *S. alterniflora*, respectively) thereby facilitating estimations of these parameters. The predictive power of the biomass *vs.* tiller height equations was satisfactory when applied for different data types (date, condition, and source), suggesting that the models can be widely used for estimating the biomass of a tiller from its length. Moreover, the predictive power of the equations was high even for standing dead tillers, allowing us to use the same equation along the tiller's span life and facilitating detritus production estimations. The allometric relations established in this study may be used to estimate *Spartina* biomass and leaf area at the study sites, with strong implications in the monitoring and assessment of saltmarshes.

ADDITIONAL INDEX WORDS: *Allometry, biomass estimation,* Spartina *spp. marsh, Mar Chiquita, Bahía Blanca, Argentina, tiller length*.

INTRODUCTION

Low-energy intertidal environments of the SW Atlantic show a clear latitudinal pattern at landscape scale. Mangroves dominate tropics, and are replaced by *Spartina* spp. marshes at temperate latitudes, up to approximately 43°S, while southern saltmarshes are dominated by *Sarcocornia* (Bortolus, 2010; Idaszkin and Bortolus 2011).

According to Isacch *et al*. (2006), SW Atlantic saltmarshes constitute a class of temperate type (*sensu* Adam, 1990) with transitional characteristics between Australasian–South African saltmarshes (due to the presence of *Sarcocornia* spp.; Congdon, 1981; Haacks and Thannheiser, 2003) and marshes of the Atlantic coast of North America (due to the dominance of *Spartina alterniflora*; Adam, 2002; Wiegert, Christian, and

Wetzel, 1981). They also have, as a unique characteristic, the presence of extensive areas dominated by *Spartina densiflora*, which is native to South America (Bortolus, 2006).

Smooth cordgrass (*Spartina alterniflora* Loisel) is a widespread marsh macrophyte native to the temperate Atlantic Coast marshes of the American continent (Adam, 1990). It has been introduced worldwide for erosion control efforts in countries such as Great Britain, France, the Netherlands, New Zealand, and China (Spicher and Josselyn, 1985). Although *S. alterniflora* is a perennial grass in the Northern Hemisphere, in southern South America, *S. alterniflora* does not lose aboveground structures during winter (Correa, 1998; Idaszkin, Bortolus, and Bouza, 2010). In South America, the natural range of the species extends between 10° and 40°S (Mobberley, 1956), with the greatest expression along the humid temperate northern coasts of Argentina. *Spartina alterniflora* stands are primarily maintained by vegetative reproduction (Metcalfe, Ellison, and Bertness, 1986), with ramets usually interconnected by belowground rhizomes.

Dense-flowered cordgrass (*Spartina densiflora* Brong.) is a matted perennial gramineae. Its populations develop in saltmarshes along the southern coasts of South America, and it has invaded saltmarshes in SW Iberian Peninsula (Nieva *et al.*, 2001, 2005), NW Africa (Fennane and Mathez, 1988), and SW North America (Ayres *et al.*, 2004; Faber, 2000). In Argentina, *S. densiflora* is one of the most important species that dominates extensive coastal tidal marshes in Buenos Aires Province at Samborombón Bay, Mar Chiquita Coastal Lagoon, and Bahía Blanca estuary (Bortolus, 2006; Cagnoni and Faggi, 1993). This perennial species is characterized by a caespitose growth form. It expands vegetatively by short tillers[1] or sexually by high seed production (Kittelson and Boyd, 1997; Nieva *et al.*, 2005). *Spartina densiflora* is an "ecosystem-engineer" (*sensu* Jones, Lawton, and Shachak, 1994) that mediates and modifies the physical environment and the community structure in both native and invaded marshes (Bortolus, 2006). *Spartina densiflora* populations are found from middle to high tidal elevations, including ecotones with adjacent terrestrial ecosystems (Castillo *et al.,* 2000; Costa 1997; Nieva, Castellanos, and Figueroa, 2002; Nieva *et al.*, 2005), and they are rarely found in the low intertidal zone, even when *S. densiflora* is the only species present (Bortolus, 2001; Clifford, 2002). The location of this species is equivalent to that of *Spartina patens* (Aiton) Muhl. in the Northern Hemisphere (Mitsch and Gosselink, 1993), while *S. alterniflora* occupies lower intertidal zones in both hemispheres.

Because of its dominance, productivity, and central role in the carbon and energy fluxes to the estuarine and marine neighborhood, *Spartina* biomass and primary production had been extensively studied. The monitoring of these parameters is of primary importance to understand the functioning and potential value of saltmarshes. Both biomass and primary production are usually measured by harvesting. However, the use of destructive sampling comprises disadvantages like high variability of the estimates (Hopkinson, Gosselink, and Parrondo, 1978) or underestimation of the production (Milner and Hughes, 1968; Odum and Smalley, 1959). In addition, harvests are not always compatible with long-term monitoring. As an alternative method, nondestructive techniques have been developed (de Leeuw *et al.*, 1996; Giroux and Bédard, 1988; Hardisky, 1980). The technique is based on strong relationships between tiller biomass and morphometric parameters like leaf length, tiller height, and stem diameter. Calculation of regression equations based on tiller height greatly simplifies field measurements (Boyer, Callaway, and Zedler, 2000; Hopkinson, Gosselink and Parrondo, 1980; Morris and Haskin, 1990). Hence, the present work aims to investigate allometric relations among morphologic characteristics, such as biomass and size, in populations of *S. densiflora* and *S. alterniflora*. It also evaluates the possibility of determining an equation that relates tiller height to leaf area and biomass.

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[1] A tiller is a stem produced by grass plants and refers to all shoots that grow after the initial parent shoot grows from a seed (Bell, 1991).

MATERIALS AND METHODS

Study Sites

Bahía Blanca (38°S) is a mesotidal coastal plain estuary located in the SW of Buenos Aires Province, close to the northern limit of the Patagonian desert, Argentina (Figure 1). The estuary is characterized by low depth, the presence of various channels, and fine sand and silt–clay sediments. It comprises a total surface of 2,300 km^2 that include about 410 km^2 of marshes and more than 1,150 km^2 of mudflats (Isacch *et al.*, 2006; Perillo *et al.*, 2000). It is located at a temperate zone with a mean annual rainfall of 559.6 mm and a mean annual temperature of 15.1°C. The principal energy inputs into the Bahía Blanca system are semidiurnal tidal waves. Tidal oscillations of 4 m and predominant winds create strong tidal currents with maximum speeds measured at the surface of about 1.3 m s^{-1}. There are only two small freshwater sources, which provide an annual mean runoff of 1.9 and 0.8 m^3 s^{-1} (Piccolo and Perillo, 1990). Freshwater inflows from other creeks into the estuary are intermittent and only significant during periods of local precipitation. In the middle portion of the estuary salinity is similar to the adjacent sea values. Pure stands of *S. alterniflora* marshes characterize the low intertidal zone of the middle and exterior estuary. This species do not form tussocks, and single tillers expose bare soil between them.

Mar Chiquita Coastal Lagoon (37°40′ S) is a Biosphere Reserve (Man and Biosphere [MAB] program, United Nations Educational, Scientific, and Cultural Organization [UNESCO]) located on the Buenos Aires coast 26 km north of the largest coastal tourist resort of Argentina, the Mar del Plata city (Figure 1). It is located in a temperate zone with mean annual rainfall of 807.7 mm and mean annual temperature of 13.8°C (period 1931–2010, data provided by Servicio Meteorológico Nacional). The lagoon is separated from the sea by an eastern dune barrier (Fasano *et al.*, 1982; Frenguelli, 1935; Violante, Parker and Cavaliotto, 2001), and it is connected to the sea by an ebb channel (Merlotto and Bértol, 2009). The site is a body of brackish water of approximately 60 km^2 and a tributary basin of about 10,000 km^2, affected by low amplitude tides ranging less than 1 m (*i.e.,* Marcovecchio *et al.,* 2006). It is characterized by the presence of mudflats surrounded by large *S. densiflora* marshes (Bortolus and Iribarne, 1999; Cagnoni and Faggi, 1993). Since *S. alterniflora* is not present in this area (González Trilla *et al.,* 2010), *S. densiflora* marsh is the most influenced by the tidal regime. *Spartina densiflora* grows in very dense tussocks, of about 60 tillers dm^{-2}, which are distributed in the marsh exposing bare soil between them. The major area of *S. densiflora* vegetation in the study site occurs between the mean high tide and the mean higher high water, or 40–97 cm above mean sea level (González Trilla, 2010).

Sampling and Data Recording

Spartina densiflora and *S. alterniflora* populations develop mainly through vegetative growth, *via* underground interconnected tillers. Owing to the difficulty in differentiating true individuals (genets), these species were treated as a population of tillers (Dai and Weigert, 1996). *Spartina alterniflora* tillers were harvested in August and December 2005 and February and June 2006 in Bahía Blanca, and *S. densiflora* tillers were harvested in June, August, October, and December 2005 and
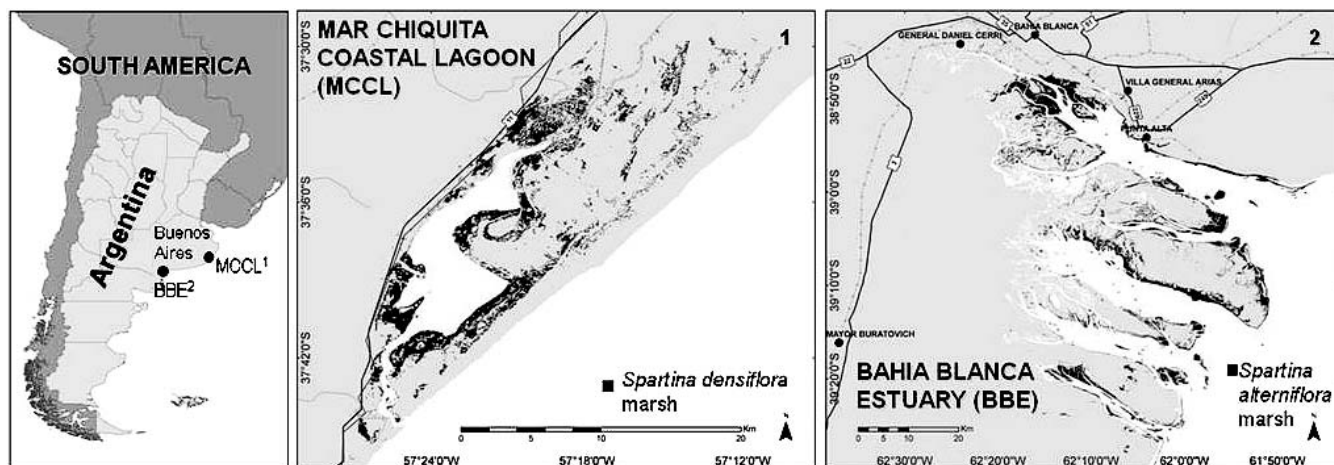
Figure 1. Location of Mar Chiquita Coastal Lagoon (MCCL) and Bahía Blanca Estuary (BBE) *Spartina* spp. marshes in the study site.

February and April 2006 in Mar Chiquita, in both high and low marsh zones. The terms high marsh (HM) and low marsh (LM) were used in relative terms for each species: *S. alterniflora* grows in the lower areas of the marsh, and *S. densiflora* in the upper zone of the marsh, but an upper and a lower zone within each population was defined, which corresponded to the lowest and highest limits of *S. alterniflora* zone and *S. desniflora* zone. The tillers were randomly chosen, regardless of the abundance of each tiller type, and removed by cutting them from the base at the sediment level. We collected a total of 677 standing tillers of *S. densiflora* in Mar Chiquita and 663 tillers of *S. alterniflora* in Bahía Blanca.

Data Processing and Analysis

The tillers were taken to the laboratory where they were washed and the presence/absence of inflorescence (this category includes stems from the beginning of flowering to fruiting and seed release) and plant condition (green or dead) were registered. All tillers were considered, including the standing dead in different stages of decomposition. For each tiller, we measured tiller height (H_t)—from the base to the longest leaf, with a ruler, to the nearest millimeter—and the length of all leaves. Leaves were separated from stems and weighed after being first washed and then dried at 70°C during 48 hours.

A subset of 385 tillers of *S. densiflora* and 367 tillers of *S. alterniflora* were randomly selected and separated. All leaves were separated from the shoot and measured in length and width at the base. Then, the leaf area, A_l, was approximated to a triangular shape (Bortolus Laterra, and Iribarne, 2004; Echavarría-Heras, Solana-Arellano, and Diaz-Castañeda, 2007) as follows:

$$A_l = b_l l_l / 2 \qquad (1)$$

where b_l and l_l stand for the width and the length of the leaf, respectively (Figure 2).

For leaves whose tips were cut off, we also measured the width at the end of the leaf, and leaf area was approximated to

that of an isosceles trapezoid:

$$A_l = (b_{l1} + b_{l2}) l_l / 2 \qquad (2)$$

b_{l1} and b_{l2} being the minor and major bases of the trapezoid, respectively.

Assuming that a given tiller contains a number of leaves, *n*, and designating A_i as the area of the *i*th leaf in the tiller, the
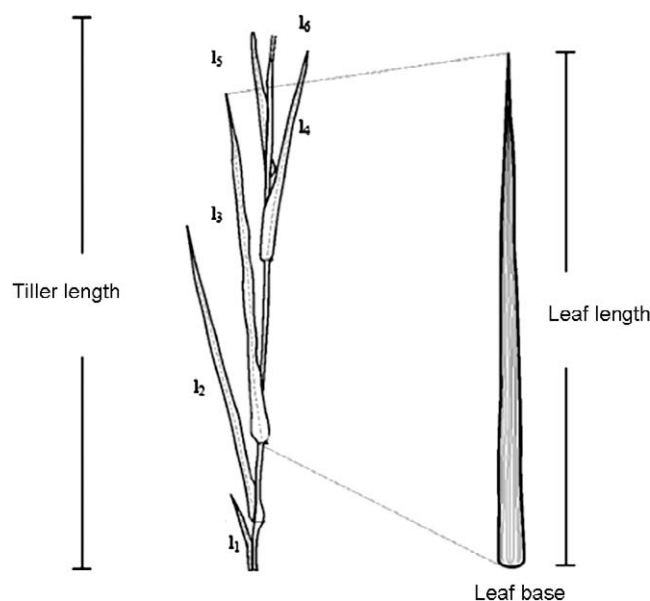

Figure 2. Architecture of a typical *Spartina* tiller showing the shoot and associated leaves ($l_{1...6}$ in this case). Tiller height (H_t) was measured from the base to the longest leaf. Leaves display a triangular shape and their areas were approximated to a triangular shape. Total aboveground biomass was obtained by summing leaves biomass and shoot biomass. Modified from Echavarría-Heras, Solana-Arellano, and Diaz-Castañeda (2007).

area of all the leaves (leaf area *per* tiller, A_t) in the considered tiller is given by

$$A_t = \sum_{i=1}^{n} A_i \qquad (3)$$

Shoots and leaves were also individually weighed to the nearest milligram after being dried. B_l represents biomass of an individual leaf. Assuming that a given tiller contains a number of leaves, *n*, and designating B_i as the biomass of the *i*th leaf in the tiller, the biomass of all the leaves in the considered tiller (B_L) is given by

$$B_L = \sum_{i=1}^{n} B_i \qquad (4)$$

Finally, the total biomass *per* tiller (B_T) is given by the sum of the biomass of the leaves and the biomass of the shoots (B_s):

$$B_T = B_L + B_S \qquad (5)$$

The morphometric parameters described above were integrated into regression models to establish allometric equations. Biomass allometric relations were log transformed (base 10) to attain normality (Sokal and Rohlf, 1995). Model fittings and statistics were performed using the Statistica software package version 8.0 (StatSoft, 2007). Afterward we validated the estimated biomass by calculating the coefficient of determination for the prediction, $R^2_{\text{prediction}}$ (Montgomery, Peck, and Vining, 2002). This coefficient provides a measure of how well observed values are likely to be predicted by the model and was calculated for the high and low marsh, at different times and for different plant conditions (green, standing dead, in flower).

$$R^2_{\text{prediction}} = 1 - \left(\frac{\sum (Yi - \bar{Y})^2}{\sum (Yi - \hat{Y})^2} \right) \qquad (6)$$

Where Yi is the observed (measured) biomass, $\hat{Y}$ is the estimated biomass according to the regression model, and $\bar{Y}$ is the mean observed biomass (average).

Biomass values are expressed as grams of dry weight. Unless otherwise indicated, error values represent ±1 standard error, and an acceptable level of statistical significance was established at 5%.

RESULTS

The results show that *S. densiflora* mean tiller height was 34.79 ± 0.78 cm with maximum tiller length of 98 cm, whereas *S. alterniflora* mean tiller height was 25.73 ± 0.81 cm with maximum tiller length of 99 cm. Leaf bases averaged 0.9 ± 0.3 cm for *S. alterniflora* and 0.36 ± 0.10 cm for *S. densiflora*, reaching maximum values of 1.7 cm (*S. alterniflora*) and 0.6 cm (*S. densiflora*). Mean leaf lengths were of 25.5 ± 12.2 cm (*S. alterniflora*) and 15.17 ± 8.94 cm (*S. densiflora*) and maximum lengths of 53 cm (*S. alterniflora*) and 49.7 cm (*S. densiflora*).

Spartina alterniflora showed an exponential and significant regression between A_l and l_l, whereas *S. densiflora* showed a linear adjustment. The equations explained a high fraction of the variation (91% and 84%, respectively; Figure 3). For both species, B_l is linear and significantly correlated with l_l, explaining 78% and 73% of the variability, respectively
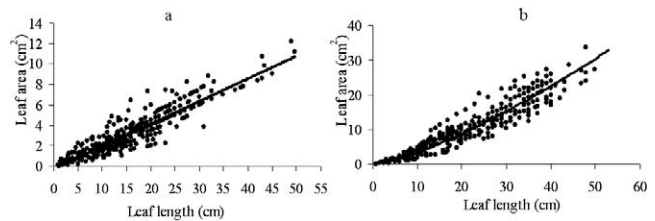

Figure 3.   Leaf area (A_l) *vs.* leaf length (l_l) regression for *Spartina densiflora* (a) and *Spartina alterniflora* (b) individual leaves.

The number of leaves linearly increased with H_t in both species. The average length of leaves, the maximum leaf length, and the sum of all leaf lengths also increased with H_t, and the corresponding equations explained more than 79% of the variation (Table 1; Figure 4). Finally, A_t increases with H_t showing an exponential model that explained a high fraction of the variability (*S. alterniflora*, 97%, and *S. densiflora*, 88%, respectively; Table 1; Figure 5).

For both species, B_s increases linearly with increasing both B_L and B_T. The equations explained, respectively, 97% and 85% of the variance for *S. alterniflora* and 73% and 66% for *S. densiflora* (Table 1). For both species, B_s linearly increased with B_t ($R^2 = 0.9713, N = 267, p < 0.0001$ for *S. alterniflora* and $R^2 = 0.731, N = 234, p < 0.05$ for *S. densiflora*) and B_L ($R^2 = 0.852, N = 267, p < 0.001$ for *S. alterniflora* and $R^2 = 0.658, N = 234, p < 0.01$ for *S. densiflora*).

The rate B_s/B_T showed a mean value of $0.53 \pm 0.006 (N = 273)$ for *S. alterniflora*, whereas the ratio B_L/B_s showed a mean value of 0.964 ± 0.37 for *S. alterniflora* and 1.025 ± 0.28 for *S. densiflora*. There was not a significant regression ($p > 0.05$) between both B_s/B_T and B_L/B_s rates against H_t.

The biomass of the leaves present in a tiller (B_L) and B_s significantly increased with H_t. There was also a significant regression between B_T and H_t. The regression equation model for estimating B_T from H_t (Table 1) explained around 90% of the variability for both species and had, in general terms, a good predictive power (analyzed through the $R^2_{\text{prediction}}$) for the high and low marsh, at different times and for different plant conditions (green, standing dead, in flower, *etc.;* Table 2). In particular, there was a good fit of the regression equation for standing dead tillers ($R^2_{\text{prediction}} = 0.804$ for *S. alterniflora* and 0.940 for *S. densiflora*), which was made with tillers of different aged dead materials (Table 2). The lower predictive power was found in the set of flowering tillers ($R^2_{\text{prediction}} = 0.477$), in the case of *S. densiflora* and in low marsh in December 2005 for *S. alterniflora* ($R^2_{\text{prediction}} = 0.68$).

DISCUSSION

The monitoring of biomass and productivity in saltmarshes is intrinsic to understanding the functioning and potential value of these ecosystems. Traditional biomass and productivity estimation methods are often invasive and destructive and depend on time-consuming laboratory procedures. Conservation efforts and the need for simplification have stimulated the

Table 1. *Allometric relations for* Spartina densiflora *and* S. alterniflora.

Allometric Comparison	N	Equation	R^2	
Spartina alterniflora				
A_l vs. l_l	367	$y = 0.1543x^{1.351}$	0.909	**** Eq. 7
B_l vs. l_l	367	$y = 96.921x - 843.48$	0.783	**
Number of leaves vs. H_t	160	$y = 0.0579x + 2.5881$	0.702	**
Mean leaf length vs. H_t	160	$y = 0.3772x + 1.9847$	0.923	****
Maximum leaf length vs. H_t	160	$y = 0.4779x + 3.563$	0.926	****
Sum of all leaf lengths vs. H_t	160	$y = 0.7017x^{1.3136}$	0.955	****
A_t vs. H_t	63	$y = 0,1263x^{1,5899}$	0.970	**** Eq. 8
B_T vs. H_t	318	$y = 2.0774x - 3.0899$	0.909	**** Eq. 9
Spartina densiflora				
A_l vs. l_l	385	$y = 0.2213x - 0.2761$	0.843	*** Eq. 10
B_l vs. l_l	48	$y = 0.2213x - 0.2761$	0.732	**
Number of leaves vs. H_t	93	$y = 0.0797x + 2.3822$	0.382	*
Mean leaf length vs. H_t	93	$y = 0.3413x + 1.5463$	0.817	**
Maximum leaf length vs. H_t	93	$y = 0.6338x - 0.3818$	0.893	***
Sum of all leaf lengths vs. H_t	93	$y = 2.8753x - 25.485$	0.794	**
A_t vs. H_t	88	$y = 0.0301x1.6965$	0.882	*** Eq. 11
B_T vs. H_t	641	$y = 1.5331x - 2.5847$	0.898	*** Eq. 12

A_l = leaf area of an individual leaf, l_l = leaf length, B_l = biomass of an individual leaf, B_s = shoot biomass, A_t = leaf area *per* tiller (leaf area of all leaves present in a tiller), B_L = leaves biomass (biomass of all the leaves in the considered tiller), B_T = tiller biomass (total biomass *per* tiller, $B_T = B_L + B_s$), H_t = tiller height. The level of significance is indicated beside each allometric comparison: * $p < 0.05$, ** $p < 0.001$, *** $p < 0.0001$, **** $p < 0.00001$.

development of alternative methods of plant biomass assessment. Plant height measurements and regression procedures have been proposed as a way to determine aboveground biomass (Boyer, Callaway, and Zedler, 2000; Echavarría-

Figure 4. Count of leaves, mean leaf length, maximum leaf length, and the sum of all leaf lengths against tiller height (H_t) for *S. densiflora* and *S. alterniflora* tillers.

Heras, Solana-Arellano, and Diaz-Castañeda, 2007; Hopkinson, Gosselink, and Parrondo, 1980; Morris and Haskin, 1990). Various equations have been used to correlate nondestructive measurements of *Spartina* species with dry weight of tillers. The biomass of single tillers of *S. alterniflora* has been estimated from multiple regressions that used tiller height and total length of living green leaves *per* tiller (Hemminga *et al.*, 1996). In order to follow the growth of individual plants, regressions for height *vs.* dry weight have been used on *S. alterniflora* data from Nova Scotia (Hatcher and Mann, 1975). Valiela, Teal, and Persson (1976) used linear regressions to relate the height of the 10 tallest tillers of *S. alterniflora* to the
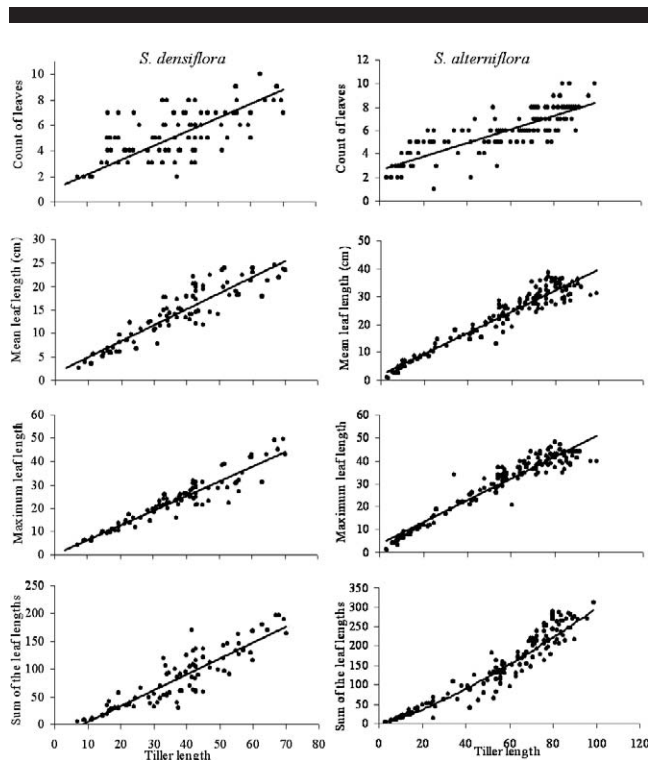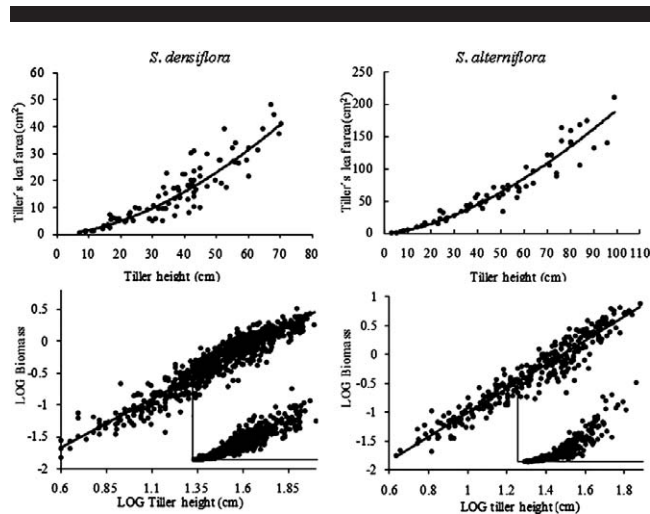

Figure 5. Leaf area *per* tiller (A_t) and biomass (B_T) against tiller height (H_t) for individual tillers of *Spartina densiflora* and *Spartina alterniflora*. Biomass data was log transformed, and untransformed data are shown in the small graph.

Table 2.   *Predictive power of the allometric equation for estimating biomass from tiller height (H$_t$) for* S. alterniflora *(Eq. 9) and* S. densiflora *(Eq. 12).*

Spartina alterniflora			Spartina densiflora		
Tiller type	N	$R^2_{\text{prediction}}$	Tiller type	N	$R^2_{\text{prediction}}$
LM December 2005	154	0.72	HM June 2005	49	0.96
HM December 2005	88	0.68	LM June 2005	97	0.73
HM August 2005	92	0.76	HM August 2005	59	0.90
HM February 2006	106	0.74	LM August 2005	104	0.94
LM June 2006	123	0.99	HM October 2005	54	0.88
HM June 2006	100	0.86	LM October 2005	53	0.94
LM	305	0.69	HM December 2005	93	0.62
HM	358	0.84	HM February 2006	55	0.84
			LM February 2006	56	0.95
			HM April 2006	57	0.93
			HM	367	0.82
			LM	310	0.84
Flowering tillers	121	0.70	Flowering tillers	33	0.48
Dead tillers	129	0.81	Dead tillers	62	0.94
Green tillers	413	0.91	Green tillers	582	0.82
Global	663	0.74	Global	677	0.83

The values correspond to the $R^2_{\text{prediction}}$ using the measured tiller biomass and the biomass calculated using the corresponding allometric equation. All *regression were significant at α = 0.05. LM = low marsh, HM = high marsh.*

standing crop but showed neither data nor correlation coefficients. Reidenbaugh (1983) estimated biomass from tiller height in a *S. alterniflora* Virginia saltmarsh using quadratic regression curves ($R^2 = 0.85$). Teal and Howes (1996) presented a linear regression ($R^2 = 0.83$) between the average height of the 10 tallest nonflowering plants to the maximum biomass (g m^{-2}) for a single marsh in Massachusetts. Data for *S. alterniflora* in several saltmarshes in Rhode Island yielded lower linear relationships between average height and biomass: R^2 of 0.21 (calculated from data of Oviatt, Nixon, and Garber, 1977) and 0.67 (from data of Nixon and Oviatt, 1973). Data for various saltmarshes from Georgia to Nova Scotia (Gross *et al.*, 1991) showed a good relationship between average plant height and peak biomass ($R^2 = 0.93$) (Hardisky, 1980; Morris and Haskin, 1990). More recently several studies estimated aboveground biomass of cordgrasses by allometric relationships relating biomass with tiller density and tiller height. Vicari *et al.* (2002) found good fits ($R^2 = 0.77$) for *S. densiflora* linear, log transformed, regression between tiller dry weight and height in Otamendi, Argentina. Echavarría-Heras, Solana-Arellano, and Diaz-Castañeda (2007) derived a polynomial equation ($R^2 = 0.91$) for estimating *Spartina foliosa* dry weight in Baja California, Mexico. Tyrrell, Dionne, and Edgerly (2008) found a good relationship between stem height and dry stem biomass for *S. alterniflora* in New England marshes ($R^2 = 0.92$), whereas Castillo *et al.* (2008) estimated aboveground biomass using shoot density ($R = 0.77$) in created and natural marshes dominated by *Spartina maritima* in Spain.

In our work, we constructed allometric models based on regression between biomass and height for different dates. Models showed good fits for both species. The predictive power of the equations was determined on the data set as a whole without discriminating according to either their phenological condition or its source (high and low marsh), but also made in groups (Table 2). In all cases the results were satisfactory, suggesting that the models can be used to estimate the standing biomass of a tiller from its length, using the same equation for different dates, locations, and phenological condition. In particular, it was observed that the predictive power of the equation is high even in the case of standing dead tillers ($R^2_{\text{prediction}} = 0.94$ for *S. densiflora* and 0.81 for *S. alterniflora*). This result is important because, once dead, the tillers remain standing for long periods (González Trilla *et al.*, 2009, 2010). During this time, tillers are progressively shortened because of the joint action of the *in situ* decomposition and the mechanical movement mainly caused by wind and tide forces. The fact that the predictive power of the equation is high for all groups suggests that the biomass of a tiller can be accurately estimated at different times from its emergence, as it grows in height, and this monitoring can continue when the tiller dies and is shortened until it finally breaks free and/or decomposes allowing debris production estimations (González Trilla, 2010). The predictive power of the equation for flowering tillers was lower than for the other groups. This fact can be explained because the flowering tillers elongate their terminal internodes compared with nonflowering tillers, having, thus, greater height for the same biomass (Dai and Wiegert, 1996; Reidenbaugh, 1983). It can also be a consequence of the translocation of resources during the maturation of the reproductive organs or biomass losses associated with the release of seeds.

Both *S. densiflora* and *S. alterniflora* had similar architectures. Although values were different, as expected in the case of two different plant species, the trend was the same. Shoot biomass increases linearly with increasing H_t and B_L. The percentage of B_s in relation to the B_T remained constant regardless of the height of the tiller and ranged 50% or, stated in other terms, the relationship between B_L and B_s is close to 1 (values did not differ significantly from 1) regardless of H_t. This shows an equal investment in the biomass of the aerial parts of the plant: when the biomass of the leaves increases by 1 g, the biomass of the shoot also increases by 1 g. This result differs from that of Niklas and Enquist (2002), who predict standing leaf biomass will scale as the 3/4-power of stem biomass in

vascular plants (relationship between the biomass of the leaves and the biomass of the shoot equal to 0.75).

The lanceolate leaves of *S. densiflora* and *S. alterniflora* were approximated to a triangle, as has been previously proposed by other authors for other species of the genus *Spartina* (Bortolus, Laterra, and Iribarne, 2004; Echavarría-Heras, Solana-Arellano, and Diaz-Castañeda, 2007). In our case, the A_l can be estimated with a high degree of accuracy from its length. Also, the biomass of leaves can be estimated from its length. Since A_l is proportional to l_l and B_l is proportional to l_l too, presumably A_l and B_l are proportional to each other. This fact was observed by Solana-Arellano, Echavarría-Heras, and Gallegos-Martinez (2003) for *Zostera marina* and after applied to *S. foliosa* (Echavarría-Heras, Solana-Arellano, and Diaz-Castañeda, 2007) and is related to a leaf thickness more or less constant. Based on the constant leaf thickness, Esteves, Enrich-Prast, and Suzuki (2008) defined the specific leaf weight (g cm^{-2}) for leaves, which was calculated dividing dry weight by leaf area.

In our results B_L increased as B_T and H_t increased. The number of leaves also increased with increasing H_t. The average leaf length, maximum leaf length, and the sum of all lengths of the leaves also increased with H_t. The latter value is a proxy of leaf area *per* tiller: as A_l is proportional to its length, the sum of all lengths of the leaves is proportional to A_L. Finally, as B_L and B_s increases with H_t, it is expected that B_T increases with H_t.

CONCLUSIONS

As a general conclusion we would say that in this paper we obtained strong correlations between several morphometric parameters that characterize *S. densiflora* marshes from Mar Chiquita and *S. alterniflora* marshes from Bahía Blanca. Equation models of leaf area and biomass of a single tiller strongly regressed on tiller height, thereby facilitating field estimations of these parameters. The use of a single general equation *per* species relating biomass to tiller height equations was satisfactory when applied on different data types, suggesting that the models can be used for estimating the biomass of a tiller from its length, using the same equation for different dates, locations, and phenological condition, which is important for simplification purposes. Moreover, the predictive power of the equations was high even for standing dead tillers, allowing use of the same equation *per* species along the tiller's span life and facilitating detritus production estimations. The allometric relations established in this study may be used to estimate *S. densiflora* and *S. alterniflora* biomass and leaf area at the study sites, with strong implications in saltmarshes' monitoring and assessment.

ACKNOWLEDGMENTS

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□ RESUMEN □

Las marismas de *Spartina* spp. del Atlántico Sur-occidental se caracterizan por la presencia de *Spartina alterniflora* en la zona intermareal baja y *Spartina densiflora*, en las zonas medio a altas. Debido a su dominancia, productividad y su papel central en los flujos de carbono y energía, la biomasa y producción primaria de *Spartina* ha sido ampliamente estudiada por diferentes técnicas. Entre ellas, las mediciones destructivas requieren de relaciones entre la biomasa del vástago y parámetros morfométricos, como la longitud de la hoja, la altura de la planta, el diámetro del vástago. En este trabajo se establecieron relaciones alométricas entre biomasa, área y tamaño, en poblaciones de *S. densiflora* y *S. alterniflora* de Mar Chiquita y Bahía Blanca, Argentina. Se recogieron 743 vástagos en pie de *S. densiflora* y 663 de *S. alterniflora* de diferentes fechas, condición (verde, florecidos y muertos en pie) y origen (marisma alta y baja). Se obtuvieron fuertes relaciones entre todos los parámetros morfométricos. El área foliar y la longitud de la hoja estuvieron fuertemente relacionados ($R^2 = 0.84$ para *S. alterniflora* y 0.91 para *S. densiflora*, respectivamente). El área foliar y la biomasa del vástago mostraron una fuerte regresión con la altura del vástago ($R^2 = 0.97$ y 0.91 para *S. densiflora* y 0.88 y 0.90 para *S. alterniflora*, respectivamente), lo que facilita la estimación de estos parámetros. El poder predictivo de las ecuaciones de biomasa en función de la altura del vástago fue satisfactorio cuando se aplicó a diferentes tipos de datos (fecha, condición y origen), en particular, se observó que el poder predictivo de la ecuación fue alto, incluso en el caso de los vástagos muertos de pie, lo que sugiere que los modelos pueden ser utilizados para estimar la biomasa del vástago a partir de su longitud, con la misma ecuación desde su emergencia, a medida que crece en altura. Asimismo, este seguimiento se puede continuar cuando el vástago muere y se acorta hasta que finalmente se libera o descompone permitiendo estimar la producción de detritos. Las relaciones alométricas establecidas en este trabajo pueden ser usadas para estimar biomasa y área foliar de *Spartina* de los sitios de estudio analizados para aplicaciones de monitoreo y evaluación.