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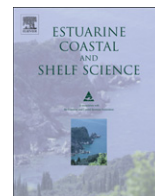
Tiller dynamic and production on a SW Atlantic *Spartina alterniflora* marsh

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ABSTRACT

We used non-destructive methods to study the bi-monthly changes in standing stock, turnover, and net aerial primary productivity (NAPP) of *Spartina alterniflora* in the Bahía Blanca Estuary, Argentina, from 2005 to 2007. Tillers were tagged and counted bimonthly and a weight:height relationship developed for the live and dead stems in a regularly flooded zone (low marsh, LM) and an irregularly flooded one (high marsh, HM). The annual tiller natality in year one compared to year two decreased from 440 ± 68 to 220 ± 58 new individuals m^{-2} yr^{-1} in the HM and from 500 ± 103 to 280 ± 97 new individuals m^{-2} yr^{-1} in the LM ($\mu \pm 1$ SE). Tiller mortality averaged 670 ± 70 individuals m^{-2} yr^{-1}.

Living biomass was present throughout the year in both the sites, but flowering occurred only at the HM where it began in December. The live biomass in the LM was significantly greater than in the HM in the first year, but decreased in the second year from 455 ± 66 to 266 ± 31 g m^{-2} in the HM and from 572 ± 76 to 277 ± 78 g m^{-2} in the LM ($\mu \pm 1$ SE). The highest levels of standing dead material were in the HM (55%) and the lowest in the LM (24%). The average total (live + dead) aboveground biomass in the HM was significantly greater than in the LM in the first year, but decreased in the second year from 1033 ± 120 to 556 ± 33 g m^{-2}, and in the LM from 679 ± 57 to 355 ± 61 g m^{-2} ($\mu \pm 1$ SE). The annual NAPP, calculated as the sum of positive growth in individual tillers between intervals, showed no significant differences between years and sites, and averaged 628 ± 94 g m^{-2} yr^{-1} ($\mu \pm 1$ SE). The dead biomass output (DBO), calculated as the sum of negative increments in NAPP between sampling intervals, was 956 ± 121 g^{-2} yr^{-1}, and was not statistically different between sites. The productivity at this site is not different from that estimated for other marshes, when similar methods are used. The production at this site, however, may be limited by high salinity levels, and the differences observed between years related to climate changes between years, e.g., the 2006–2007 was an ENSO period.

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1. Introduction

Smooth cordgrass *Spartina alterniflora* is a widespread marsh macrophyte native to the temperate Atlantic Coast marshes of the American continent (Adam, 1990). It was introduced to control erosion along the North America's Pacific Coast and in Great Britain, France, The Netherlands, New Zealand, and China (Spicher and Josselyn, 1985; Partridge, 1987). In South America, the natural range of this species extends between 10° and 40°S (Mobberley, 1956),

with the greatest expression along the humid temperate northern coasts of Argentina (Cagnoni, 1999).

Spartina alterniflora stands are primarily maintained by vegetative reproduction (Metcalfe et al., 1986), with ramets usually interconnected by belowground rhizomes. This species usually develops two main growth forms, tall (reaching heights ≥ 2 m) and short (typically < 0.5 m). Bertness (1985), among others, also mentions a medium-size phenotype.

Because of its dominance and productivity, *S. alterniflora* net aboveground primary productivity (NAPP) has been extensively studied in North America (e.g., Keefe, 1972; Turner, 1976; Pomeroy et al., 1981; Marinucci, 1982; Dardeau et al., 1992). Nevertheless, up to now there are no NAPP *S. alterniflora* estimations for South Atlantic Argentinian coast.

The primary production and biomass of macrophytes are usually measured by harvesting. Non-destructive techniques have been developed as an alternative method to study production and biomass in marshes (Hopkinson et al., 1978; Hardisky, 1980;

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Lieffers, 1983; Giroux and Bédard, 1988; de Leeuw et al., 1996). This technique is based on strong relationships between shoot biomass and morphometric parameters like height or diameter. Although non-destructive sampling is labour-intensive and sometimes unsuitable (Dickerman et al., 1986), there are numerous advantages associated with the employment of these techniques. Spatial heterogeneity problems, for example, are mitigated, mortality estimates can be derived, it gives detailed data about individuals, temporal sensitivity is increased, and long-term continuous monitoring is possible (Dai and Weigert, 1996; Nixon and Oviatt, 1973; Gross et al., 1991; Teal and Howes, 1996, Vicari et al., 2002).

The objective of this work was to measure aboveground net primary production of *S. alterniflora* and to estimate the amount of dead biomass output in the Bahía Blanca Estuary, Argentina. The study employed a non-destructive technique based on demographic methods to compare a regularly flooded zone (low marsh, LM) and an irregularly flooded one (high marsh, HM) for two years. The first year did not differ from historical climate conditions, while the second year corresponded to an El Niño Southern Oscillation (ENSO) event that in this region increases summer-time precipitation (Saluso, 2007).

2. Materials and methods

2.1. Study site

The Bahía Blanca Estuary is a mesotidal coastal plain estuary located in the southwest of Buenos Aires Province, close to the northern limit of the Patagonian desert, Argentina. It comprises a total surface of 2300 km^2, which includes about 410 km^2 of marshes and more than 1150 km^2 of mudflats (Perillo et al., 2000; Isacch et al., 2006). It is located in a temperate zone with mean annual rainfall of 559.6 mm and mean annual temperature of 15.1 $^{\circ}$C (1860–1990; Servicio Meteorológico Nacional). Mid-latitude westerlies and the influence of the Subtropical South Atlantic High dominate the typical weather pattern of the region. The resulting circulation induces strong northwesterly and northern winds with a mean annual velocity of 24 km h^{-1}.

The estuary is characterized by low depth (between 3 and 22 m from head to mouth) and the presence of various channels and fine sand and silt-clay sediments. The principal energy into the Bahía Blanca system is produced by standing and semidiurnal tides. Tidal oscillations of 4 m and prevailing winds create strong tidal currents (Piccolo and Perillo, 1990) with maximum velocities measured at the surface of about 1.3 m s^{-1}. Two small fresh-water sources provide an annual mean runoff of 1.9 and 0.8 m^3 s^{-1}, respectively, (Perillo et al., 1987). The freshwater inflow from other creeks into the estuary is intermittent and only significant during periods of local precipitation. The salinity of seawater in the middle portion of the estuary is about 33.79 (annual mean, personal observation), while the inner zone becomes hypersaline during dry summers because of the high rate of evaporation.

The study site is located in the north coast of the Bahía Blanca Estuary, near Villa del Mar (Fig. 1) and presents pure stands of *S. alterniflora* short form.

The vegetation in the intertidal zone of the Bahía Blanca Estuary is scarce and, unlike the better known counterparts of Eastern North America, *S. alterniflora* marshes only occur in discontinuous patches at the mouth of the estuary (Molina et al., 2009). Under the seasonally hypersaline conditions in the inner estuary, vegetation is virtually absent in the intertidal zone except for the circular mounds of *Sarcocornia perennis*, colonizing the upper marshes (Perillo and Iribarne, 2003).

2.2. Allometric relationships

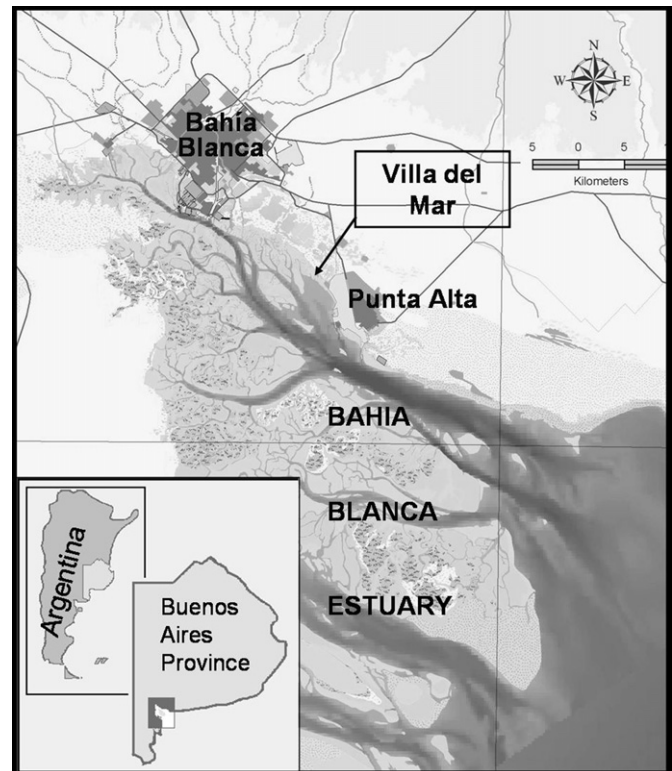We established the relationship between the height of the shoots and their biomass. A grand total of 315 shoots were

Fig. 1. Location of the study area in the Bahia Blanca Estuary, Argentina. The main cities are also shown.

randomly harvested at ground level in the Villa del Mar marsh in August and December 2005 and February and June 2006 in both high and low marsh zones. For each stem, we measured height with a ruler (± 1 mm) and noted the presence/absence of inflorescence and plant condition (green: 100% green; standing dead: 100% dry; and standing partially dead: 50% green and 50% dry). All tillers were considered, including the standing dead in different stages of decomposition. Stems were then washed, dried at 70 $^{\circ}$C during 48 h, and weighed. Morphometric parameters were integrated into a regression model to establish the best allometric equation for each sample. We used covariance analyses to examine the influence of year and marsh type on the allometric equations. Logarithmic relationships were used because height and mass represent growth parameters (Sokal and Rohlf, 1995).

Afterwards we validated the estimated biomass by calculating the coefficient of determination for the prediction, $R^2_{\text{prediction}}$ (Montgomery et al., 2002).

$$R^2_{\text{prediction}} = 1 - \left(\frac{\sum (Yi - \overline{Y})^2}{\sum (Yi - \widehat{Y})^2} \right)$$

2.3. Tiller demography

Tiller demography was determined using ten 10×10 cm permanent sample plots along two transects parallel to the coastal line. Five were located at the low marsh (LM) and five at the high marsh (HM). All tillers present in the plot were tagged at their bases with permanent plastic–aluminum numbered tags at the beginning of the study period. Newly emergent tillers were tagged on each subsequent sampling date. The demographic analysis was conducted by counting all the tillers present in the plots. Counts were conducted every 60 days from October 2005 to October 2007.

The tillers present in each of the permanent plot were measured from their bases to the tip of their longest leaf and classified according to its phenological condition into green, standing dead, standing partially dead or reproductive. Standing dead tillers were not removed from the quadrant, and their height was measured even when they were dead, because the authors observed that tillers show a progressive shortening after death. Because there is a homogeneous coverage of S. alterniflora in the study site, no correction for the percentage coverage was done.

Tiller natality and the emergence of new tillers during the study period were expressed as tillers m^{-2}. Bimonthly values were expressed per day and per year. Mortality was determined as the number of dead tillers that were alive in the previous sampling period. It includes all the tillers in the plots, even those born in the period preceding the study period. Data were expressed as in tiller natality.

2.4. Biomass and NAPP estimations

The biomass of each individual tiller in the permanent plots was calculated from its height using the regression equation.

The green-standing biomass of each plot was estimated as the summed mass of all standing green ramets and the 50% of the mass of tillers classified as partially standing dead in the plot. In the same way, the dead-standing biomass was estimated as the summed mass of all standing dead ramets and the 50% of the mass of tillers classified as partially standing dead in the plot.

The difference of tiller biomass between two consecutive sampling periods was calculated. This difference could be either positive, zero, or negative. Positive values for living tillers were interpreted to as increases in biomass (production), while negative values for either dead or living tillers were considered as a net biomass loss.

The total net above ground primary productivity of the plot (NAPP) represents the biomass produced and was calculated by summing the positive growth of each individual tiller. The sum of the negative increments between sampling (two months) represents the dead biomass output (DBO) that is the total amount of macrodetritus removed from the plot since there is no litter and decomposition, and burial was assumed to be negligible. The NAPP or DBO was estimated for the first (October 2005–October 2006) and second year (October 2006–October 2007) as the sum of the NAPP or DBO values of six consecutive dates.

In this study, all biomass values were transformed in g m^{-2} of dry matter. Data were analyzed according to Sokal and Rohlf (1995). A priori comparisons were computed between years and sites. Homogeneity of variance was tested with the Levene test, and normality was tested with Lilliefors' test. Unless otherwise indicated, error values represent ±1 SE, and the acceptable level of statistical significance was 5%.

3. Results

3.1. Allometric model

The regression equation obtained between tiller dry weight (DW in g) and height (H in cm) was

$$Log(DW) = 2.0774 \times Log(H) - 3.089 \qquad (1)$$

The equation explained over 90% of the variability ($R^2 = 0.909$, $p < 0.000001$, $F = 3$ 156, $N = 315$).

The model had a good predictive power (analyzed through the $R^2_{prediction}$) for the high and low marsh, at different times and for different plant conditions (green, standing dead, in flower, etc.) (Table 1).

3.2. Tiller demography

The mean tiller density was 1250 ± 45 individuals m^{-2} in the HM, showing no statistical differences between years, whereas the mean tiller density in the LM differed between years showing 1150 ± 44 and 729 ± 40 individuals m^{-2} in the first and second year, respectively.

We observed that S. alterniflora produces new tillers during the entire year (Fig. 2) and showed no statistical differences between sites in natality. The total tiller natality decreased in the second year from 440 ± 68 to 220 ± 58 new individuals m^{-2} yr^{-1} in the HM and from 500 ± 103 to 280 ± 97 new individuals m^{-2} yr^{-1} in the LM.

The death rate averaged 670 ± 70 individuals m^{-2} yr^{-1}, and no differences were found between sites and years. The daily mortality calculated for the two-months period did not show a clear pattern (Fig. 3).

The flowering period occurred from December to February in the first year and extended to April in the second year. Only tillers in the HM flowered. Only 20 flowered tillers m^{-2} (1.4%) were registered in the first year and 50 ± 6 (3.4%) in the second year (Fig. 4).

3.3. Aboveground biomass

The living biomass of S. alterniflora was present throughout the year in all of the sites, with a maximum in the warm season (Fig. 5a). The living biomass of the LM was significantly higher than that of the HM in the first year, but decreased in both the sites in the second year from 455 ± 65 to 266 ± 31 g DW m^{-2} in the HM, and from 572 ± 76 to 277 ± 78 g DW m^{-2} in the LM.

There were statistical differences in the amount of dead biomass found in the HM and the LM. High levels of standing dead material were found throughout most of the year in the HM (55%), whereas lower values (24%) were found in the LM shown (Fig. 5b). In addition, during the second year in the LM there was a significant greater percentage of standing dead biomass compared to the first year (17% and 31%, respectively), which agrees with the observed decrease in green biomass. The dead biomass in HM had no statistical differences between the years.

The differences in the mean total (live + dead) aboveground biomass of S. alterniflora in the HM and LM sites and between years were significant. In the HM, the total aboveground biomass in the first was 1033 ± 120 g DW m^{-2}, while in the second year this value decreased to 556 ± 33 g DW m^{-2}. The total aboveground biomass in the LM was 679 ± 57 and 355 ± 61 g DW m^{-2} in first and the second year, respectively. On an average, the total aboveground biomass was higher in the HM than in the LM.

Table 1
Predictive power of the allometric equation used in this work.

Tiller type	$R^2_{prediction}$
LM Dec. 05	0.72
HM Dec. 05	0.68
HM Aug. 05	0.76
HM Feb. 06	0.74
LM Jun. 06	0.99
HM Jun. 06	0.86
LM	0.69
HM	0.84
Dead tillers	0.81
Flowering tillers	0.70
Green tillers	0.91
Global	0.74

The values correspond to the $R^2_{prediction}$ using the measured tiller biomass and the biomass calculated using the allometric equation.
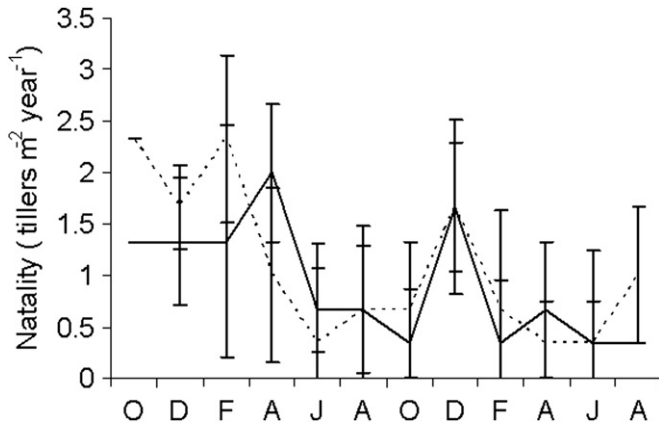
Fig. 2. Tiller natality in a *Spartina alterniflora* marsh from the Bahia Blanca Estuary from October 2005 to October 2007. High marsh (filled line) and low marsh (dotted line) sites are shown.

Fig. 4. Flowering in a *Spartina alterniflora* marsh from the Bahia Blanca Estuary from October 2005 to October 2007. High marsh (filled line) site is shown. No tiller flowered in the low marsh.

The maximum biomass (peak) was 1450 ± 276 g DW m^{-2} in the first year in the HM, being significantly higher than the corresponding value in the second year (677 ± 98 g DW m^{-2}). The maximum biomass in the LM was also higher in the first year than in the second one (906 ± 226 and 553 ± 131 g DW m^{-2}, respectively). The peak biomass was higher in the HM than in the LM.

3.4. NAPP and DBO

The daily NAPP averaged 1.52 ± 0.17 g m^{-2} day^{-1} in the HM and was not statistically different between the years, while it was 2.60 ± 0.36 and 1.34 ± 0.22 g m^{-2} day^{-1} in the LM for first and second year, respectively. The pattern of daily productivity throughout the year was similar for the two sites, reaching peaks in February of 3.55 ± 0.61 and 2.92 ± 0.94 g m^{-2} day^{-1} in the HM, and 6.24 ± 2.10 and 3.65 ± 0.90 g m^{-2} day^{-1} in the LM, for the first and second year, respectively (Fig. 6).

The annual NAPP showed no significant differences between years and sites. In the HM, the NAPP was estimated 599 ± 83 g m^{-2} yr^{-1} for the first year and 495 ± 105 g m^{-2} yr^{-1} for the second year. The NAPP was 936 ± 327 and 482 ± 87 g m^{-2} yr^{-1} for the first and second period of the LM populations, respectively.

The DBO values did not differ statistically when sites were compared between them. The DBO was calculated as 1369 ± 296
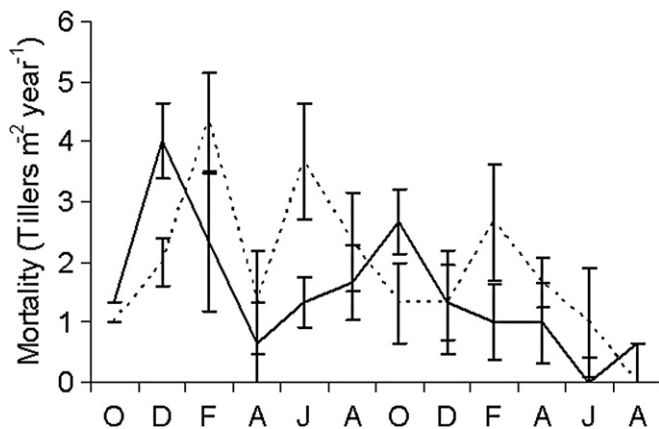

Fig. 3. Tiller mortality in a *Spartina alterniflora* marsh from the Bahia Blanca Estuary from October 2005 to August 2007. High marsh (filled line) and low marsh (dotted line) sites are shown.

and 703 ± 46 g m^{-2} yr^{-1} for the first and the second period of the HM populations, respectively. No significant differences between the years were observed. The DBO for the first and the second year of the LM was estimated to be 931 ± 232 and 822 ± 601 g m^{-2} yr^{-1}, respectively, with no statistical differences between them. When DBO values are compared with the corresponding NAPP, no differences are found in LM, while the HM showed higher DBO values.

4. Discussion

The importance of assessing net aboveground primary productivity of coastal marshes has long been recognized for the central role the emergent biomass plays in the carbon and energy input to the surrounding waters. Although the NAPP has been extensively studied in *S. alterniflora* salt marshes worldwide, there are no previous published works on NAPP *S. alterniflora* estimations in Argentina.

We used a tiller length–biomass regression for estimating biomass and NAPP. This method has been previously used in *Spartina* marshes (Vicari et al., 2002; González Trilla et al., 2008). The calculation of regression equations based on tiller length greatly simplifies field measurements. A limitation of this method, however, is that it does not take into account leaf turnover. However, the estimates of tiller biomass from height explain, in all cases, more than 70% of the variability (Table 1). It also assumes that once dead, tiller biomass decreases as the length of the tiller diminishes, and those biomass losses are exported from the plot, constituting the DBO. This assumption seems to be supported by the good fit of the regression equation for standing dead tillers ($R^2_{prediction} = 0.8044$), which was made with tillers of different aged dead materials (Table 1).

The NAPP values in other natural salt marshes are variable. The aboveground production of short or intermediate height *Spartina* marshes is known to be 2–3 times less than that of the tall grass (Gallagher et al., 1980). The values of productivity shown in Table 2 support this statement. However, part of this variability can be attributed to the method used. Many authors have compared NAPP values in the some marsh using different methods. For example, Linthurst and Reimold (1978) found that NAPP values ranged from 246 to 1611 g m^{-2}·yr^{-1} using different destructive methods in Maine (USA), while data reported by Gallagher et al. (1980) for Georgia (USA) ranged between 700 and 1600 g m^{-2}·yr^{-1} using different non-destructive methods (Table 2). The NAPP of *S. alterniflora* at our study
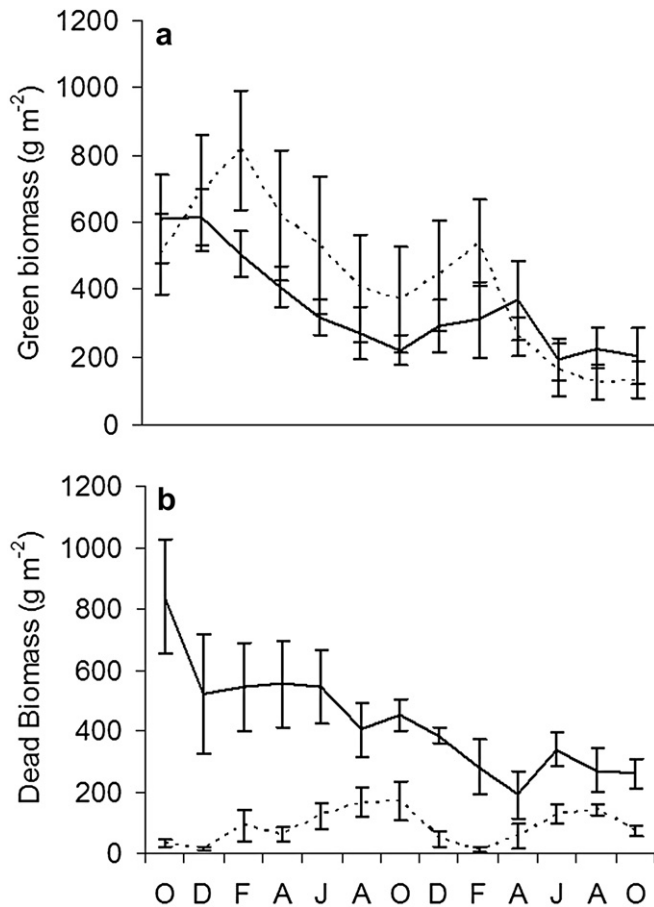
Fig. 5. *Spartina alterniflora* green biomass (a) and dead-standing biomass (b) from high (filled line) and low marsh (dotted line) sites in the Bahia Blanca Estuary from October 2005 to October 2007.

sites was similar to that found at other natural short phenotype salt marshes when a non-destructive method was used. Morris and Haskin (1990), using a non-destructive method, estimated that the NAPP in a natural South Carolina short form marsh ranged between 402 and 1042 over 5 years. Dai and Weigert (1996) estimated that the NAPP was 1118 in a short form Georgia salt marsh, whereas Reidenbaugh (1983) found that NAPP was 399 in a low-density medium marsh in Virginia (Table 2).
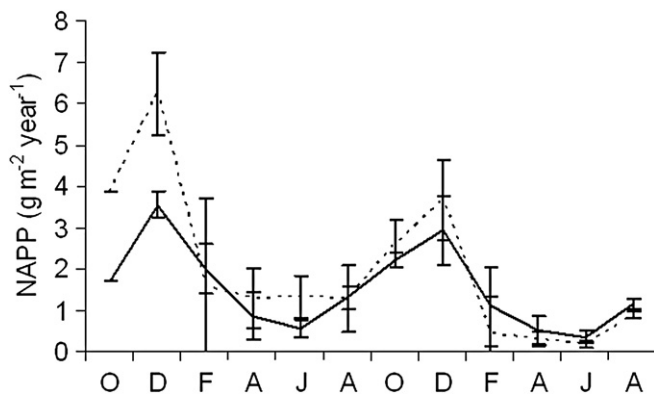

Fig. 6. Net aboveground primary productivity (NAPP) in a *Spartina alterniflora* marsh from the Bahia Blanca Estuary from October 2005 to August 2007. High marsh (filled line) and low marsh (dotted line) sites are shown.

In South America, the NAPP ranged between 101 and 179 using different destructive methods (Da Cunha Lana et al., 1991). In that case, *S. alterniflora* marshes are in the northern limit of their distribution and are pioneer formations along the Brazilian SE coast, colonizing mud flat or tidal creeks as narrow and discontinuous belts in front of mangrove woodland. *Spartina alterniflora* marshes tend to be replaced ultimately by mangroves. Da Cunha Lana et al. (1991) believe that productivity there may be limited by interspecific competition. In our study site, productivity may be limited by abiotic factors such as the high salinity levels, which reach its maximum during hot summers; the salinity in porewater in Villa del Mar reaches values of 46.9 ppt in the HM and 38.2 ppt in the LM in late spring (personal observation). The low input of fresh water from permanent sources (annual mean runoff of $2.7 \, m^3 \, s^{-1}$, Perillo et al., 1987) and rain (mean annual rainfall = 560 mm) and the high evaporation resulting from strong winds (mean velocity of $24 \, km \, h^{-1}$) and solar radiation during summer may contribute to this condition. In addition, these strong winds and the semidiurnal tidal oscillations of 4 m create strong tidal currents (Piccolo and Perillo, 1990) with maximum velocities of about $1.3 \, m \, s^{-1}$.

The NAPP and biomass pattern throughout the year showed peaks in summer and minimums in winter coincident with temperature. This effect of the mean temperature on the productivity of *Spartina densiflora* was reported for other species of the genus *Spartina* with C4 metabolism of carbon fixation (Turner, 1976; Long and Mason, 1983; Cunha, 1994; Peixoto and Costa, 2004).

Although the LM had more green biomass, the total standing biomass was greater in the HM due to the higher values of dead-standing biomass. In the lowest levels of the marsh, the tide removes dead biomass, generating lower percentages of dead biomass. The accumulation of dead material in the HM is a consequence of the lower exposition to waves.

When the differences between the two years were analyzed, a decrease in the total and the green-standing biomass and new tillers emergence was observed for both high and low marsh sites from the first year to the following year. Moreover, the density of tillers and daily productivity in the peak decreased in the LM. These differences would be attributed to the changes in climate conditions. The first year showed monthly rainfall amount similar to the historical data (1931–1990 period), while the second year presented extreme precipitation values that are related to the El Niño Southern Oscillation (*ENSO*) phenomenon produced in the 2006–2007 period that is associated to an increase in the precipitations in the Buenos Aires province region during spring and summer (Saluso, 2007). This change in rainfall was associated with a change in NAPP, DBO, and biomass values in a microtidal marsh dominated by *S. densiflora* in Mar Chiquita, Buenos Aires Province, Argentina (González Trilla et al., 2008). In that case, higher rainfall values were related with higher erosion in the most exposed low marsh sites decreasing, in this way, the biomass and NAPP values. Childers et al. (1990) postulated that El Niño-Southern Oscillation events cause increased flooding of coastal marshes in Louisiana by increasing the rate of precipitation both locally and in the Mississippi River basin, whereas La Niña events generate dry conditions, which lower water levels and decrease marsh flooding in Louisiana (Rozas, 1995).

Since there is no litter on the soil, it is presumed that most of the new biomass each plot produces are exported out of the plot, due to the action of currents and waves. But the ultimate fate of this organic matter is not known. Many salt marshes export a significant fraction of the detritus they produce to adjacent waters via tidal flushing (e.g., Valiela et al., 1975). However, other marshes accumulate in drift lines inside the ecosystem, the majority of the macro-detritus moved by tides from the production site (Bouchard and Lefeuvre, 2000; Reidenbaugh and Banta, 1980; Dankers et al., 1984).

Table 2
Spartina alterniflora net aboveground primary productivity (NAPP) using various calculation methods (units are $g\,m^{-2}\,yr^{-1}$).

Location	NAPP	Method used	Authors
Nova Scotia, Canada	398	Peak-standing crop	Cranford et al. (1989)
Nova Scotia, Canada	434	Smalley (1959)	Cranford et al. (1989)
Nova Scotia, Canada	507	Allen curve	Cranford et al. (1989)
Maine, USA, HM	246	Peak-standing crop	Linthurst and Reimold (1978)
Maine, USA, HM	246	Milner and Hughes (1968)	Linthurst and Reimold (1978)
Maine, USA, HM	763	Smalley (1959)	Linthurst and Reimold (1978)
Maine, USA, HM	662	Valiela et al. (1975)	Linthurst and Reimold (1978)
New York, USA, SF	780	Peak-standing crop	Houghton (1985)
New York, USA, SF	770	Milner and Hughes (1968)	Houghton (1985)
New York, USA, SF	750	Valiela et al. (1975)	Houghton (1985)
New York, USA, SF	825	Smalley (1959)	Houghton (1985)
New York, USA, TF	1220	Peak-standing crop	Houghton (1985)
New York, USA, TF	1310	Milner and Hughes (1968)	Houghton (1985)
Alameda, USA, TF	2318	Smalley (1959)	Callaway and Josselyn (1992)
N. Wallops Island, Virginia, USA, EM, TF	1169	Non-destructive	Reidenbaugh (1983)
N. Wallops Island, Virginia, USA, MM, MF	1020	Non-destructive	Reidenbaugh (1983)
N. Wallops Island, Virginia, USA, CB, MF	587	Non-destructive	Reidenbaugh (1983)
N. Wallops Island, Virginia, USA, MM	399	Non-destructive	Reidenbaugh (1983)
N. Carolina, USA	242	Peak-standing crop	Shew et al. (1981)
N. Carolina, USA	214	Milner and Hughes (1968)	Shew et al. (1981)
N. Carolina, USA	225	Smalley (1959)	Shew et al. (1981)
N. Carolina, USA	1029	Wiegert and Evans (1964)	Shew et al. (1981)
N. Carolina, USA	1028	Lomnicki et al. (1968)	Shew et al. (1981)
North Inlet, S. Carolina, USA, CB, TF	2069	Shew et al. (1981)	Dame and Kenny (1986)
North Inlet, S. Carolina, USA, HM, SF	1113	Shew et al. (1981)	Dame and Kenny (1986)
North Inlet, S. Carolina, USA, MM, MF	649	Shew et al. (1981)	Dame and Kenny (1986)
Oyster Landing, S. Carolina, USA, MM, SF	281–418[a]	Peak-standing crop	Morris and Haskin (1990)
Oyster Landing, S. Carolina, USA. MM, SF	447–701[a]	Non-destructive (similar to Dickerman et al. 1986)	Morris and Haskin (1990)
Goat Island, S. Carolina, USA. MM, SF	402–1042[b]	Non-destructive (similar to Dickerman et al. 1986)	Morris and Haskin (1990)
Goat Island, S. Carolina, USA, MM, SF	209–694[b]	Peak-standing crop	Morris and Haskin (1990)
N. Carolina, USA	931	Smalley (1959)	Hardisky (1980)
Georgia, USA, HM	700	Smalley (1959)	Gallagher et al. (1980)
Georgia, USA, CB	2300	Smalley (1959)	Gallagher et al. (1980)
Georgia, USA, HM	1200	Wiegert and Evans (1964)	Gallagher et al. (1980)
Georgia, USA, CB	3000–4400[a]	Wiegert and Evans (1964)	Gallagher et al. (1980)
Georgia, USA, HM	1600	Wiegert and McGinnis (1975)	Gallagher et al. (1980)
Georgia, USA, CB	2700	Wiegert and McGinnis (1975)	Gallagher et al. (1980)
Georgia, Sapelo Island, USA, MM, SF	404	Peak-standing crop	Dai and Weigert (1996)
Georgia, Sapelo Island, USA, MM, SF	1105	Milner and Hughes (1968)	Dai and Weigert (1996)
Georgia, Sapelo Island, USA, SF	993	Valiela et al. (1975)	Dai and Weigert (1996)
Georgia, Sapelo Island, USA, SF	1118	Non-destructive	Dai and Weigert (1996)
Georgia, Sapelo Island, USA, TF	892	Peak-standing crop	Dai and Weigert (1996)
Georgia, Sapelo Island, USA, TF	1520	Milner and Hughes (1968)	Dai and Weigert (1996)
Georgia, Sapelo Island, USA, TF	1315	Valiela et al. (1975)	Dai and Weigert (1996)
Georgia, Sapelo Island, USA, TF	1557	Non-destructive	Dai and Weigert (1996)
Louisiana, USA, SF	788	Peak-standing crop	Kirby and Gosselink (1976)
Louisiana, USA, SF	748	Milner and Hughes (1968)	Kirby and Gosselink (1976)
Louisiana, USA, SF	1006	Smalley (1959)	Kirby and Gosselink (1976)
Louisiana, USA, SF	1323	Wiegert and Evans (1964)	Kirby and Gosselink (1976)
Louisiana, USA, TF	1018	Peak-standing crop	Kirby and Gosselink (1976)
Louisiana, USA, TF	874	Milner and Hughes (1968)	Kirby and Gosselink (1976)
Louisiana, USA, TF	1410	Smalley (1959)	Kirby and Gosselink (1976)
Louisiana, USA, TF	2645	Wiegert and Evans (1964)	Kirby and Gosselink (1976)
Louisiana, USA, SF	700	Peak-standing crop	Hopkinson et al. (1980)
Louisiana, USA, SF	1500	Valiela et al. (1975)	Hopkinson et al. (1980)
Louisiana, USA, SF	1000	Smalley (1959)	Hopkinson et al. (1980)
Louisiana, USA, SF	831	Peak-standing crop	Kaswadji et al. (1990)
Louisiana, USA, SF	831	Milner and Hughes (1968)	Kaswadji et al. (1990)
Louisiana, USA, SF	1231	Smalley (1959)	Kaswadji et al. (1990)
Louisiana, USA, SF	1873	Wiegert and Evans (1964)	Kaswadji et al. (1990)
Louisiana, USA, SF	1437	Lomnicki et al. (1968)	Kaswadji et al. (1990)
Hog Island, Louisiana, site 1, USA	1642	Lomnicki et al. (1968)	Edwards and Mills (2005)
Hog Island, Louisiana, site 1, USA	561	Peak-standing crop	Edwards and Mills (2005)
Hog Island, Louisiana, site 2, USA	2399	Lomnicki et al. (1968)	Edwards and Mills (2005)
Hog Island, Louisiana, site 2, USA	607	Peak-standing crop	Edwards and Mills (2005)
Paragaguá Bay, Brazil, SF	101	Milner and Hughes (1968)	Da Cunha Lana et al. (1991)
Paragaguá Bay, Brazil, SF	113	Smalley (1959)	Da Cunha Lana et al. (1991)
Paragaguá Bay, Brazil, SF	179	Valiela et al. (1975)	Da Cunha Lana et al. (1991)
Paragaguá Bay, Brazil, SF	110	Wiegert and Evans (1964)	Da Cunha Lana et al. (1991)

Table 2 (*continued*)

Location	NAPP	Method used	Authors
Paraguá Bay, Brazil, SF	116	Peak-standing crop	Da Cunha Lana et al. (1991)
Bahia Blanca, Argentina, HM, SF	599–495[a]	Non-destructive	This study
Bahia Blanca, Argentina, LM, SF	936–482[a]	Non-destructive	This study
Bahia Blanca, Argentina, HM, SF	1450–677[a]	Peak-standing crop	This study
Bahia Blanca, Argentina, LM, SF	903–553[a]	Peak-standing crop	This study

Growth form: tall (TF), medium (MF), and short (SF) and location inside the marsh: high marsh (HM), low marsh (LM), mid marsh (MM), creek bank (CB), and edge marsh (EM) was noted, if available.
[a] NAPP values of a 2-year study.
[b] NAPP values of a 5-year study. Minimum and maximum are shown.

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