Net Primary Productivity of *Spartina densiflora* Brong in an SW Atlantic Coastal Salt Marsh

Gabriela González Trilla · Silvia De Marco ·
Jorge Marcovecchio · Ricardo Vicari · Patricia Kandus

Abstract Coastal marshes are known as organic matter producers. The goal of this work is to study tiller demography, standing biomass, and net aerial primary productivity (NAPP) in a S*partina densiflora* coastal wetland, using a method applied to permanent sample plots located at two sites differing in topographic location, a regularly flooded zone [relative low marsh (LM)] and an irregularly flooded one [relative high marsh (HM)]. Measurements were made every 2 months during the 2005–2007 period. The annual NAPP was estimated to be $2{,}599\pm705$ gDW $m^{-2}year^{-1}$ for the HM and $2{,}181\pm605$ gDW $m^{-2}year^{-1}$ and 602 ± 154 gDW $m^{-2}year^{-1}$ for the first and second period of the LM populations, respectively, showing a seasonal pattern reaching maximum values in summer. The reduced NAPP values of the LM sites in the second year was associated with an extremely high precipitation period related to the 2007–2008 El Niño event.

G. González Trilla (✉) · R. Vicari · P. Kandus
Grupo de Investigaciones sobre Ecología de Humedales–
Laboratorio de Ecología Regional, Facultad de Ciencias Exactas y
Naturales, Universidad de Buenos Aires,
Pabellón II, 4to piso, Laboratorio N° 56. Ciudad Universitaria.
Intendente Güiraldes 2620 C1428EHA,
Buenos Aires, Argentina
e-mail: gabrielatrilla@ege.fcen.uba.ar

S. De Marco
Departamento de Biología, Facultad de Ciencias Exactas y
Naturales, Universidad Nacional de Mar del Plata,
Buenos Aires, Argentina

J. Marcovecchio
Área de Oceanografía Química, Instituto Argentino de
Oceanografía (IADO-CONICET),
Bahía Blanca, Argentina

Introduction

Spartina densiflora Brong (Dense-flowered cordgrass) is a matted perennial Gramineae with "phalanx" clonal growth (Lovett-Doust, 1982). Populations develop in salt marshes along the southern coasts of South America where it is indigenous (Cabrera 1970; Mobberley 1956; Bortolus 2006) and has invaded salt marshes in SW Iberian Peninsula (Nieva et al. 2002), NW Africa (Fennane and Mathez 1988), and SW North America (Kittelson and Boyd 1997). In Argentina, *S. densiflora* is one of the most important species that dominates coastal tidal marshes with centers of concentration in Samborombon Bay, Mar Chiquita Coastal Lagoon, and Bahia Blanca estuary (Cagnoni and Faggi 1993; Bortolus 2006). This species is also much less widespread in a few continental riverine marshes with salty soils but without actual marine influence (Vicari et al. 2002). As in the USA (Kittelson and Boyd, 1997) and Spain (Castillo et al. 2000), *S. densiflora* communities seem to be restricted to the middle and high elevations of the coastal marshes, and it is rarely found in the low intertidal zone, even when it is the only species present (Nieva et al. 2002; Clifford 2002; Bortolus 2001, 2005). The location of this species is equivalent to that of *Spartina patens* (Aiton) Muhl. in the North Hemisphere (Mitsch et al., 1993) while *Spartina alterniflora* occupies lower intertidal zones in both hemispheres.

Many authors suggest this pattern is probably driven by the physiological constraints produced under anoxic and hypersaline environment in flooded areas (Kittelson and Boyd 1997; Castillo et al. 2000, 2005; Clifford 2002; Nieva

et al. 2003; Bortolus 2006) or even by the disturbance promoted by mechanical action of the waves. As a consequence, *S. densiflora* populations located on the lower part of the intertidal zone are expected to have the lowest net photosynthesis rate owing to high salinity, anoxic sediment, and the reduction of the photosynthetic period by consecutive tides (Nieva et al. 2003; Bortolus 2006).

Spartina species are generally highly productive, exporting a large amount of detritus to the estuarine system where the organic matter fuels food chains in adjacent sea waters (Teal 1962; Odum 1968; Nixon 1980; Landin 1991; Lefeuvre and Dame 1994). Of the many studies estimating net aerial primary productivity (NAPP) of coastal salt marsh species, most are on *S. alterniflora* (Kirby and Gosselink 1976; Linthurst and Reimold 1978; Gallagher et al. 1980; Hopkinson et al. 1980; Shew et al. 1981; Reidenbaugh 1983; Houghton 1985; Dame and Kenny 1986; Cranford et al. 1989; Kaswadji et al. 1990; Morris and Haskin 1990; Dai and Weigert, 1996; Edwards and Mills 2005) but few on *S. densiflora*.

The NAPP of *S. alterniflora* has been traditionally estimated by various destructive harvest methods (see description by Shew et al. 1981); however, these methods are affected by the spatial variation between sampling sites and may yield considerably different results for the same marsh (Kirby and Gosselink 1976; Hopkinson et al. 1980; Shew et al. 1981; Kaswadji et al. 1990; Dai and Weigert, 1996).

In contrast to harvest methods, non-destructive ones have many advantages, though they have been used in only few marshes (Dai and Weigert, 1996; Hardisky 1980; Hopkinson et al. 1980; Cranford et al. 1989; Morris and Haskin 1990; Vicari et al. 2002; Thursby et al. 2002). These methods require only small sampling sites, are sensitive to temporal change, allow long-term continuous monitoring, and give detailed data about individuals, thus permitting estimates of variation within a stand (Dai and Weigert, 1996).

The objective of this work is to estimate the NAPP and aerial biomass of *S. densiflora* in Mar Chiquita Coastal marsh (Argentina), as well as to quantify temporal variation using a non-destructive method based on tiller demography for 2 years (2005–2007). The first year did not differ from historically climate conditions while the other year corresponded to an El Niño Southern Oscillation (ENSO) event that, in this region, increases summer-time precipitation (Saluso 2007). Two different topographic locations were compared, a regularly flooded zone [relative low marsh (LM)] and an irregularly flooded one [relative high marsh (HM)].

Study Site

Mar Chiquita Coastal Lagoon is a man and biosphere reserve located in Buenos Aires coast 26 km north of the largest coastal tourist resort of Argentina, the city of Mar del Plata (Argentina, 37°32 to 37°45 S, and 57°19 to 57°26 W; Fig. 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 1931–1990).

The site is a body of brackish water of approximately 60 km^2 and a drainage basin of ~10,000 km^2, affected by tides of approximately 1 m amplitude (Marcovecchio et al. 2006). The intertidal which is characterized by the presence of mudflats are surrounded by large tidal marsh communities where the cordgrass *S. densiflora* dominates (Cagnoni and Faggi 1993; Cagnoni 1999; Fasano et al. 1982; Bortolus and Iribarne 1999). This plant grows in very dense tussocks—of about 60 tillers dm^{-2}—which are distributed in the marsh showing bare soil between them. The major area of *S. densiflora* vegetation in the study site occurs between the mean high tide (MHW) and the mean higher high water (MHHW), or 40–97 cm above msl (Fig. 2, Table 1). At higher elevations, this community is replaced by a mixed *Juncus acutus–S. densiflora* community (Cagnoni 1999). The study was carried out from June 2005 to October 2007, with the August 2005–August 2006 (winter to winter to the south hemisphere) period referred to as the first year and August 2006–August 2007 as the second one.

Materials and Methods

S. densiflora populations develop mainly through vegetative growth, via the underground interconnected tillers. Due to the difficulty in differentiating true individuals (genets), this species can be treated as a population of leaves and stems (modules) or ramets and the productivity of the population is given by total births, growth, and deaths of individual tillers (Begon et al. 1996; Dai and Weigert, 1996). Therefore, we applied a tiller demography approach through a non-destructive method, following Dai and Weigert (1996) and Vicari et al. (2002), to estimate NAPP and aerial biomass of *S. densiflora* for 2 years (2005–2007). Two situations were compared relative to each other, a regularly flooded site (designated as LM) where the sediment is flooded an average of 22.3% of the time and an irregularly flooded one (designated as HM) where the sediment is flooded an average of 9.4% of the time (Fig. 3).

Tiller Demography

Ten 10×10-cm permanent sample plots were placed inside the *S. densiflora* tussocks along two transects parallel with the shoreline. Five sample plots were located on a transect at LM and the other five on a transect at HM within the
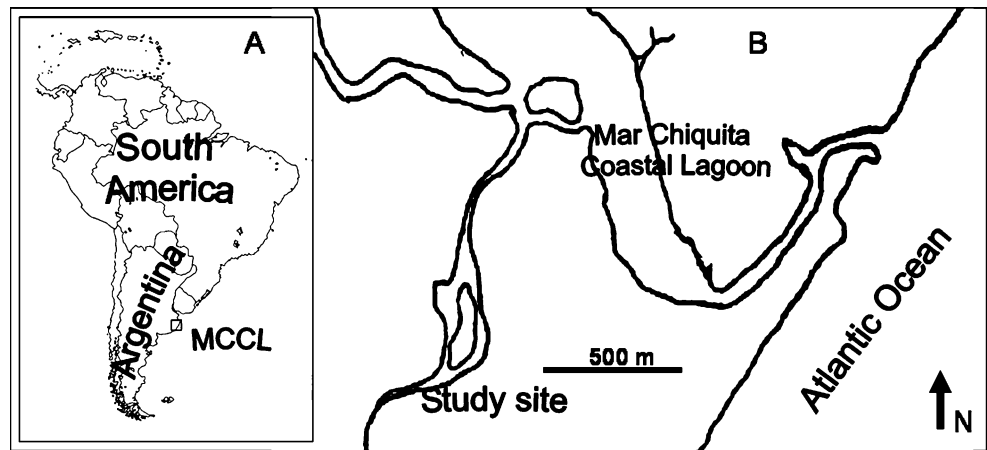
marsh ecosystem. All tillers were tagged at their bases with permanent plastic-aluminum numbered tags at the beginning of the study. Newly emergent tillers were tagged on each subsequent sampling date. Tillers that were not recorded on four consecutive dates were considered as dead individuals. The demographic analysis was conducted by counting all the tillers present in the plots and was conducted every 60 days during the sample period.

In each permanent sample plot, tillers were measured from the base to the tip of the longest leaf and classified following Vicari et al. (2002) according to its phenological condition into green-live (100% of biomass alive), standing dead (100% of biomass dead), and partially standing dead (at least some portion of biomass alive). In addition, tillers were classified as reproductive or non-reproductive based on the presence of sexual structures.

Biomass Dynamic and Production

Height–weight regressions were made from tillers harvested and collected randomly near the permanent sample plots on
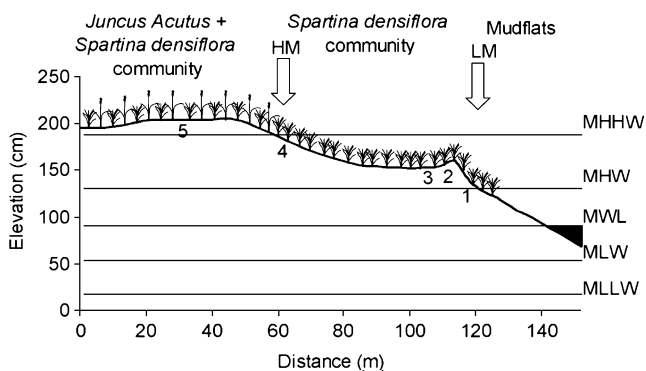

Fig. 2 Topographic profile of the study site showing location of the low marsh (LM) and high marsh (HM) sites. Local data was referred to the Mar del Plata tide gauge. *MHHW* mean higher high water, *MHW* mean high water, *MWL* mean water level, *MLW* mean low water, *MLLW* mean lower low water

each sampling date. These tillers were representative of different phenological conditions and were collected at LM and HM sites. Individual regressions were estimated for HM and LM and for each sample date and also for a general equation considering all the data together (González Trilla et al. 2006). The last one was used for estimating biomass from tiller height data since its predictive power was similar to that of individual models according to the coefficient of determination for prediction, $R_{\text{prediction}}^2$ (Montgomery et al. 2002; $R_{\text{prediction}}^2 = 0.8882$ for the individual models and 0.8844 for the general equation).

The minimum least squares general regression equation used was:

$$ITDW(g) = 1.533 \times H(cm) - 2.585 \tag{1}$$

$$\left(R^2 = 0.898, \ p = p < 0.0000, \ F = 5529, \ N = 641 \right)$$

where ITDW is the individual tiller dry weight and H, the tiller height. ITDW and H were Log-transformed. The biomass of the individual tillers for each permanent plot was calculated from height data using the Eq. 1. The difference in tiller biomass between two sample periods ($ITDW_{\text{dif}}$) was calculated as:

$$ITDW_{\text{dif}} = ITDW_{t+1} - ITDW_t \tag{2}$$

Where t and $t+1$ represents two consecutive sampling periods. This difference could be either positive ($ITDW_{\text{dif}}^{+}$), zero, or negative ($ITDW_{\text{dif}}^{-}$). Positive values were seen as increases in living biomass (production), while negative values were considered as biomass losses (dead biomass output from the plot). Standing dead tillers were not removed from the quadrant, and their height was measured because it was found that the tillers decrease in height progressively when dead, exporting dry biomass in successive steps (author's personal observations).

The total NAPP of each quadrant measured in a 2-month period represents the biomass produced in that period and

Table 1 Characteristics of the sites along a transect across zones in the study site

Site	1	2	3	4	5
Community	S. densiflora	S. densiflora	S. densiflora	S. densiflora	S. densiflora + J. acutus
Sediment textural group	Mud	Mud	Mud	Sandy mud very fine	Mud
Sediment name	Medium silt	Coarse silt	Medium silt	Sandy coarse silt	Coarse silt
Mean tiller height	29	36	31	34	46
Maximum tiller height	52	54	49	64	100
Tiller density (individuals m^{-1})	1,132	1,245	905	2,377	3,565
Biomass (gDW m^{-1})	568	833	474	1,485	3,574
Standing dead biomass (gDW m^{-1})	26	191	198	882	2,617
Percentage of dead biomass	5	23	42	59	73

was calculated by summing the positive growth of each individual tiller present in each quadrant.

$$NAPP = \sum_{t}^{t+1} ITDW_{dif}^{+} \qquad (3)$$

$$DBO = \sum_{t}^{t+1} ITDW_{dif}^{-} \qquad (4)$$

The sum of the negative increments is an estimation of the dead biomass output (DBO) representing the total amount of dead material available to be exported from the quadrant during each sampling interval. Data were scaled into daily NAPP and DBO by square meter dividing by the number of days between two consecutive dates and by mean tiller density of the marsh. Mean tiller density was estimated as the average of the number of tillers present in ten 1×1-m plots randomly distributed in the marsh.

Annual NAPP and DBO was the sum of six consecutive NAPP and DBO values, respectively.

For biomass calculations, the class of tiller defined as partially standing dead was arbitrary computed as 50%

green–50% dead. Thus, according to the previous classification, green biomass was estimated as the sum of green-live biomass plus 50% of the partially standing dead biomass, and dead biomass was the sum of standing dead plus 50% of partially standing dead.

Biomass data was expressed as gDW m^{-2} of dry matter after transforming by plant density.

Data were analyzed according to Sokal and Rohlf (1995). Unless otherwise indicated, error values represent ±1 SE and an acceptable level of statistical significance was established at 5%.

Results

The results show that the HM S. densiflora individuals are taller than those of the LM population, with a difference of 7.48±1.1 cm (ANCOVA $F = 46$, $p < 0.001$, $N = 144$); mean height was 24.46±1.14 cm in the LM and 31.99±1.15 cm in the HM. The mean tiller height decreased gradually over the study period in both HM and LM populations ($p < 0.05$; Fig. 4).
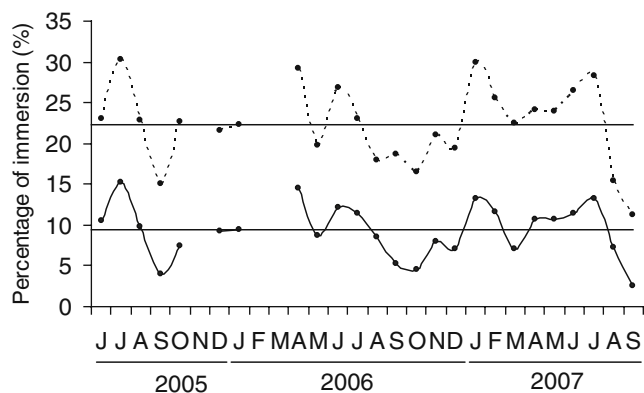

Fig. 3 Percent of immersion of the low marsh (*dotted line*) and high marsh sites (*solid line*) along the study period. Tide gauge records of water level at the Mar del Plata port (38° 05′S, 57° 30′) was provided by the Servicio de Hidrografia Naval. November 2005 and February and March 2006 were not available
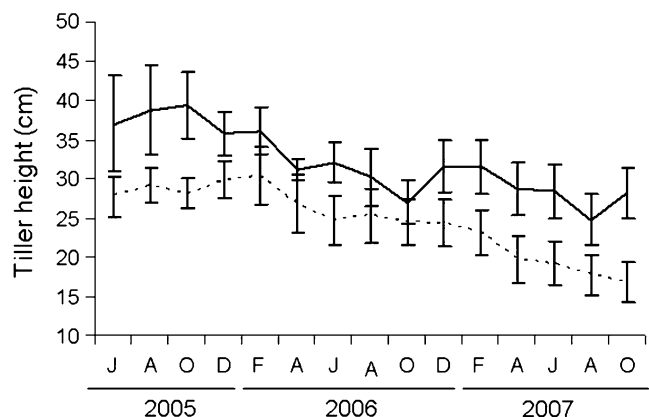

Fig. 4 Mean tiller height in *S. densiflora* low marsh (*dotted line*) and high marsh (*solid line*)

Both HM and LM show a diminishing in tiller height from the beginning to the end of the study period, but it was stronger in LM. HM ranged from 36.9±6.01 cm at the beginning to 28.22±3.22 cm at the end, and LM ranged from 27.69±2.47 cm to 16.71±2.51 cm. In addition, Fig. 5 shows that cohorts of tillers born during the study period in both sites had different behaviors. HM cohorts had quite similar growing rates during the whole period of study and decelerated only during winter (Fig. 5a). In contrast, LM cohorts growing rates decreased during the second year and initial cohort growing rates also decreased into the second year (Fig. 5b).

Similarly, tiller density remained constant in the LM during the first year, but suffered a reduction toward the end of the studied period from 3,300±183 to 2,604±498 tillers m^{-2}. In contrast, the HM showed a sustained increase in the tiller density reaching double its value from 1,830±171 to 3,816±835 tillers m^{-2} (Fig. 6). The HM showed peaks of emergence of new tillers and mortality in both years (Fig. 7a); but, in the LM, there was a net decrease in the emergence of new tillers during the second year (Fig. 7b).
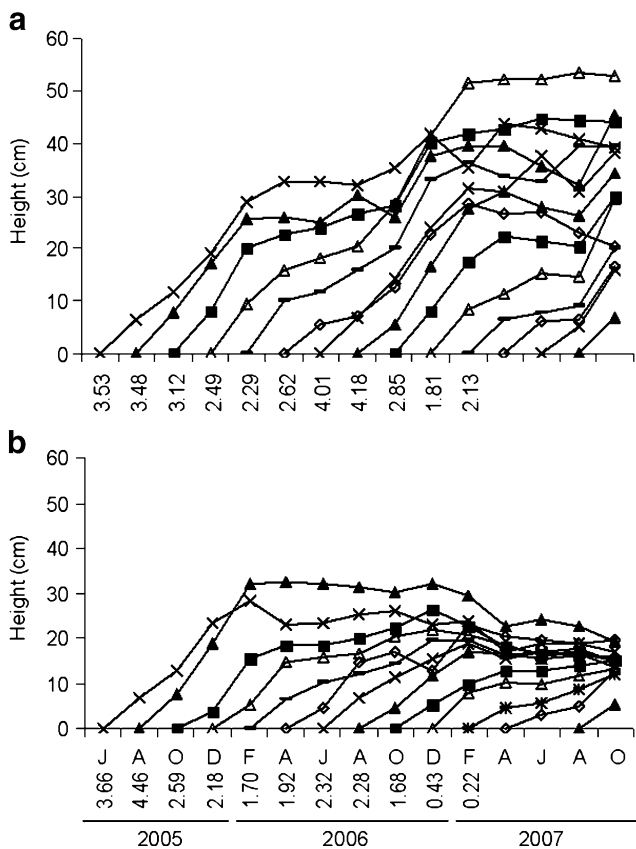

Fig. 6 *S. densiflora* tiller density across the study period for the low marsh (*dotted line*) and high marsh (*solid line*) sites

Green standing biomass estimated from the regression equation (Eq. 1) showed peaks in February in HM populations of similar magnitude in both years (1,716± 540 and 1,866±797 gDW m^{-2}, respectively) and fell to minimal values in winter (589±93 in June 05, 1,036±386 in August 06, and 1,143±556 gDW m^{-2} in August 07). For the LM, the peak of green biomass occurred in February of the first year (1,640±403 gDW m^{-2}) showing similar values to those in the HM, while, in the second year, biomass dropped steadily (Fig. 8a). The total standing biomass

Fig. 5 a Mean tiller height for the different cohorts born during the study period from the high marsh (HM) and **b** low marsh (LM). Data below the curves represent the mean growth rate of each cohort (expressed in centimeters per month) calculated with the first four dates
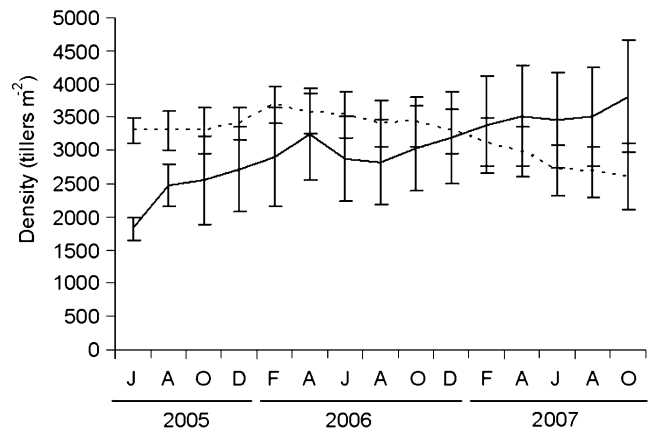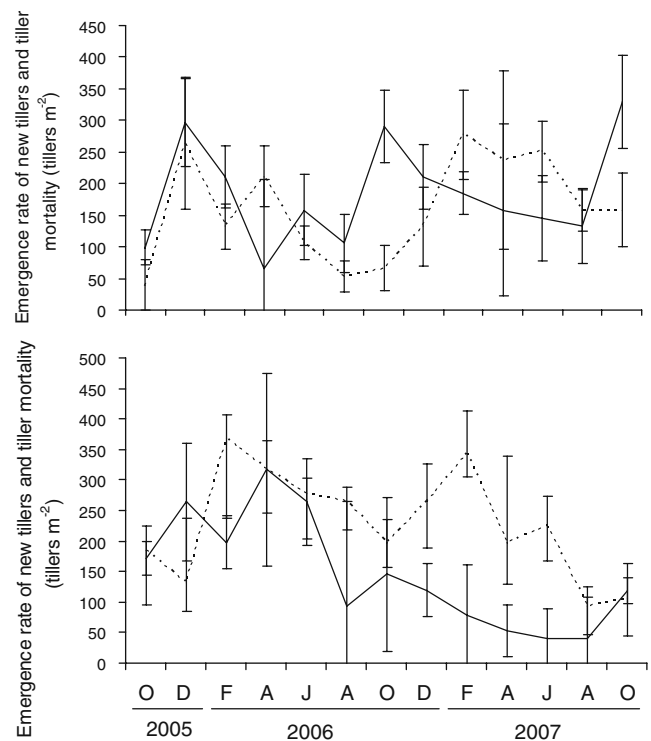

Fig. 7 Emergence rate of new tillers (*solid line*) and tiller mortality (*dotted line*) in population of *S. densiflora*. **a** High marsh. **b** Low marsh
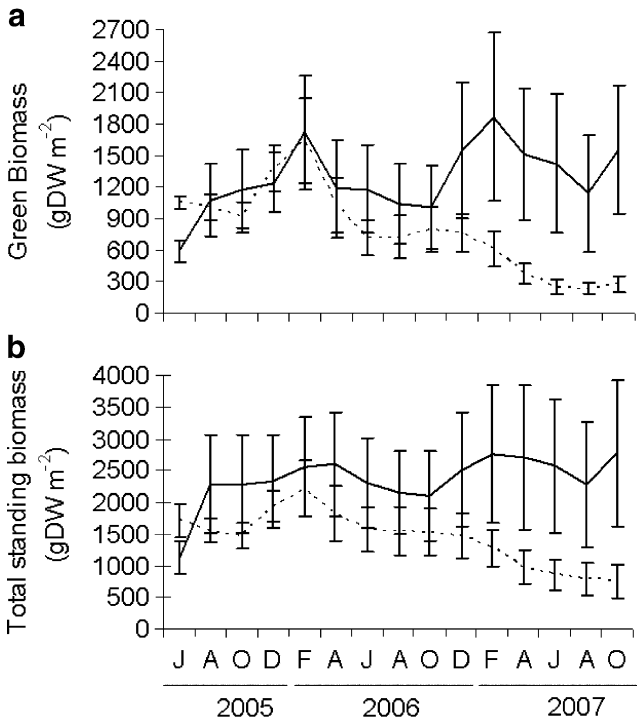
Fig. 8 Green biomass (**a**) and total standing biomass (**b**) in population of *S. densiflora* high marsh (*solid line*) and low marsh (*dotted line*)

264 in June 05, 2,147±664 in august 06, and 2,277± 988 gDW m^{-2} in August 07). For the LM, the highest peak was in February of the first year (2,214±436 gDW m^{-2}) followed by a steady decline.

In the HM, the NAPP reached minimum values in August 05 (250±38 gDW m^{-2} year^{-1}), June 06 (265±72 gDW m^{-2} year^{-1}), and August 07 (296±169 gDW m^{-2} year^{-1}), and maximum values in April 06 (442±198 gDW m^{-2} year^{-1}) and February 07 (684±314 gDW m^{-2} year^{-1}) (Fig. 9a). The peak of productivity of the second year was greater than that of the first. In the LM, the NAPP values were minimal in August 05 (188±21 gDW m^{-2}year^{-1}), June 06 (140± 33 gDW m^{-2}year^{-1}), and June 07 (35±6 gDW m^{-2}year^{-1}), and maximal in December 05 (711±312 gDW m^{-2}year^{-1}). For the second year, a gradual decrease was observed (Fig. 9b).

In the HM, the DBO showed maximum values in June 06 (541±192 gDW m^{-2}year^{-1}) and August 07 (589± 235 gDW m^{-2}year^{-1}, Fig. 9c), and coincided with the minimum NAPP and minimum values on February 06 (214 ±97 gDW m^{-2}year^{-1}) and December 06 (204± 56 gDW m^{-2}year^{-1}). In the LM, the DBO showed maximums occurred in April 06 (587±112 gDW m^{-2} year^{-1}) and February 07 (381±87 gDW m^{-2}year^{-1}) and minima in Aug 05 (115±60 gDW m^{-2}year^{-1}) and Aug 07 (134±24 gDW m^{-2}year^{-1}; Fig. 9d).

In the HM, the differences in the values of the NAPP and the DBO are positive in summer and negative in winter, peaking in February of both years, and minimum in June

followed a similar pattern (Fig. 8b). The HM reached a peak in February–April, of similar magnitude in both years (2,603±820 in April 06 and 2,747±1,088 gDW m^{-2} in February 07) and fell to minimal values in winter (1,123±
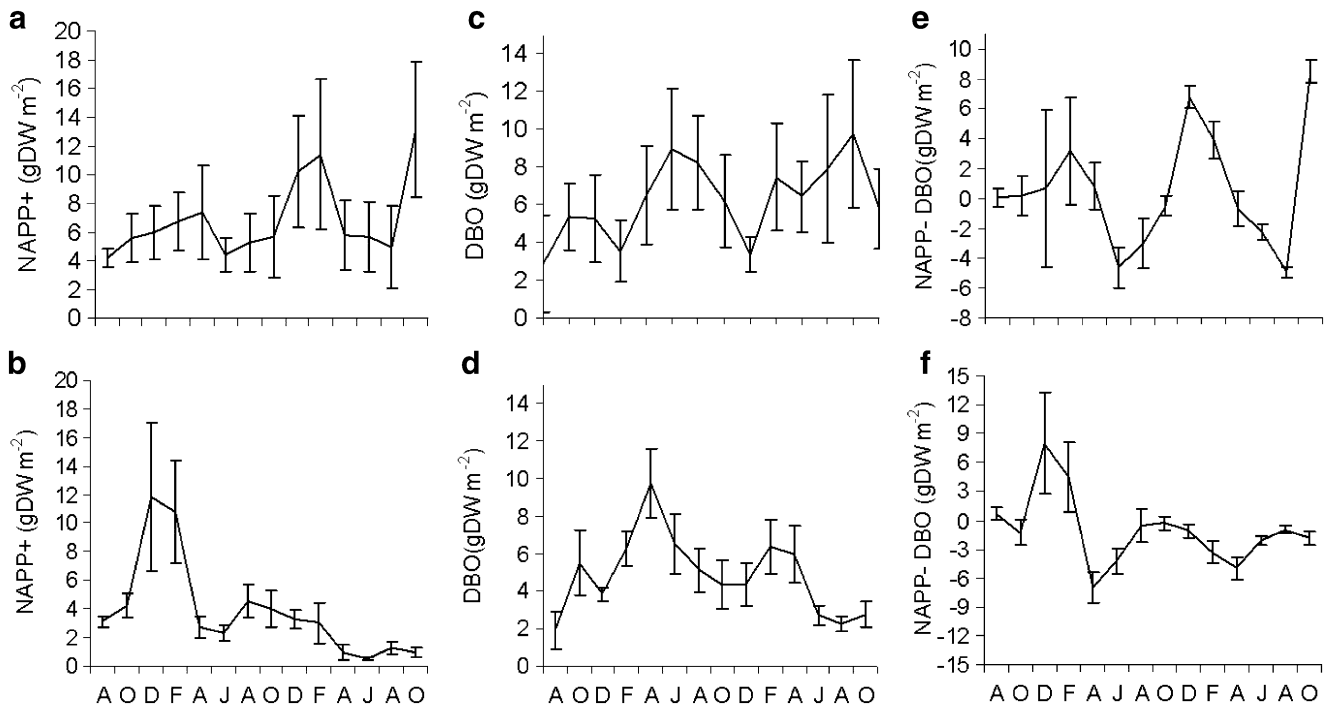

Fig. 9 Net aerial primary productivity (NAPP), dead biomass output (DBO), and its difference (NAPP-DBO) for high (HM) and low (LM) marsh populations of *S. densiflora*

and August (Fig. 9e). In the LM the first year, values were positive in summer, negative in winterpeaked in February, and fell again to a minimum in June. In the second year, in spite of a minimum in winter and a maximum in summer, values were always below zero (Fig. 9f).

When the NAPP annual values of the LM and HM are compared, no significant differences ($\alpha > 0.05$) were found for any year, nor were there differences in NAPP values of the HM in the two periods studied. In the case of the LM, NAPP values significantly differ between years (Table 2).

The annual values of DBO did not differ significantly between sites or years. When the annual NAPP values are compared with the corresponding DBO values, no statistical differences were found ($p > 0.05$).

Discussion

The importance of assessing NAPP of coastal marshes has long been recognized for the central role that it plays in the carbon and energy input to neighboring estuarine and marine ecosystems. Although NAPP has been extensively studied in *S. alterniflora* salt marshes, only few works have been done in *S. densiflora* stands such as in the Laguna de Los Patos (Brasil) (Silva et al. 1993).

The results reported in this study on *S. densiflora* are the first for the South American temperate coast and indicate that the mean annual net primary productivity is approximately $2,599 \pm 705$ gDW m^{-2}year^{-1} for the high marsh and $2,181 \pm 605$ gDW m^{-2}year^{-1} and 602 ± 154 gDW m^{-2}year^{-1} for the LM. These NAPP values are comparable to those founded for the same species in other places (Vicari et al 2002; Peixoto and Costa 2004; Nieva and Figueroa 1997). Vicari et al. (2002), using the same method in a continental riverine marsh (Otamendi Natural Reserve) in Argentina, found lower NAPP values ($1,450 \pm 566$ gDW m^{-2}year^{-1}) than we report. The Otamendi site has salty sediments in a freshwater environment since it used to be an estuarine coast during the mid-Holocene marine transgression (Iriondo and Scotta 1978; Cavallotto et al. 2004; Isla 1989; Pratolongo et

al. 2009). Peixoto and Costa (2004) found higher production rates (>10 gDW m^{-2}day^{-1}) in *S. densiflora* marshes in Brazil where waterlogging occurred more than 50% of the time period analyzed. At the Dos Patos Lagoon coastal marsh, Silva et al. (1993) suggest that waterlogging has a positive effect on the NAPP of *S. densiflora*.

In marshes of Rio Grande, Brazil, *S. densiflora* NAPP was estimated to be 2,391 gm^{-2}year^{-1} (Peixoto and Costa 2004) using the Smalley (1959) harvesting method. The real value is probably higher than that reported, since, as many authors have pointed out, the Smalley method underestimates NAPP (Dai and Weigert, 1996; Daoust and Childers 1998). Nieva (1996), using a destructive method, found higher NAPP values in Huelva, Spain, where *S. densiflora* is an invasive species, following a fire that occurred at that site. The high values found in this case were likely due to the elimination of one of the main limiting factors for the primary production of *S. densiflora*, the self-shading caused by old stems and leaves and intraspecific competition for aerial space (Nieva, personal communication, 2008).

In contrast to North Hemisphere studies, in temperate coasts of South America, there is not a marked temperature seasonality, and winter is not necessarily a dormancy period. In this study, *S. densiflora* produces new biomass during the whole year showing only a short period of decline during winter. The patterns of NAPP throughout the year, as expected, showed maximum productivity in summer and minimal in winter (Fig. 9a, b); productivity correlated well with temperature ($r = 0.63$). Peixoto and Costa (2004) also found a positive correlation between the productivity values and the air temperature in marshes from Brazil dominated by this species. The positive effect of the mean temperature over the productivity was also reported for other species of the genus *Spartina* with C4 metabolism of carbon fixation (Turner 1976; Long and Mason 1983; Cunha 1994).

When the NAPP was compared with the corresponding dead biomass output, no statistical differences were found ($p > 0.05$). Since DBO values were equivalent to the correspondent NAPP, it would suggest that biomass is at steady state, i.e., the system is in balance: there is no expansion or reduction of the marsh. The new biomass each plot produces is exported every year from the plot and no litter remains on the soil, but the ultimate fate of this organic matter is not known.

The 2 years analyzed were different in terms of climate. The first year showed monthly rainfall amount similar to the historical data (1931–1990) while the second year presented extreme precipitation values (Fig. 10a) related to the ENSO phenomenon of 2006–2007 experienced also as an increase in the precipitation in the Pampa region during the spring–summer period (Saluso 2007). In the first year,

Table 2 Annual NAPP and DBO values of low marsh (LM) and high marsh (HM) zones in Mar Chiquita coastal lagoon

Site/year	NAPP (gDWm^{-2}yr^{-1})	DBO (gDWm^{-2}yr^{-1})
LM/1	2181±605 (1584)	2155±316 (2175)
LM/2	602±154 (619)	1465±307 (1492)
HM/1	2128±710 (2010)	2332±800 (2065)
HM/2	3071±1270 (1752)	2386±849 (1711)

The numbers 1 and 2 correspond to the first and second year, respectively. Values are given as means ± SE with median shown in parentheses
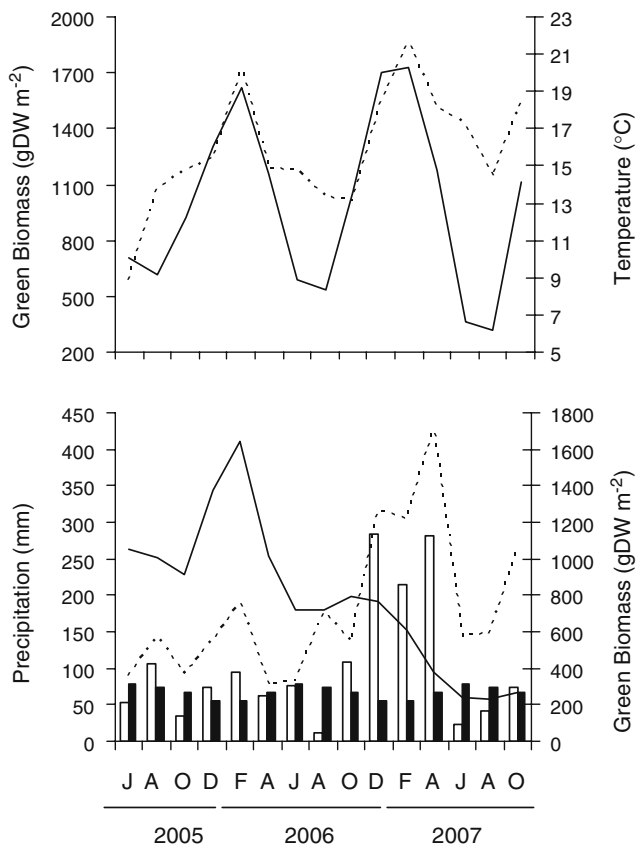
Fig. 10 **a** Green biomass for the high marsh (*solid line*) and mean monthly temperature for the study period (*dotted line*). **b** Mean monthly precipitation for the 1931–1990 period (*black bars*), 1995–2007 (*white bars*), precipitation accumulated in 2 months (*dotted line*) and green biomass of the low marsh (*solid line*)

the NAPP patterns showed greater productivity in the LM than in the HM. However, the total standing biomass, tiller height, and the percentage of dry biomass in the HM was higher than in the LM. Differences in production could possibly be explained by tidal exposure and tide action. According to Nieva et al. (2001), in the *S. densiflora* populations of the lowest levels of the marshes, the tide removes dead biomass, generating high live/dead biomass ratios together with the high rates of production of stems and leaves throughout the year. The significance of this in Europe where the species is exotic is that the accumulation of dead biomass decreases the physical space and light in a synergic action, preventing the introduction of other species into the clones of *S. densiflora* (Figueroa and Castellanos 1988; Nieva et al. 2001; Peixoto and Costa 2004).

In the second year of study, some of these patterns reversed. In the LM, the emergence rate and the density of tillers decreased, as well as the total and green biomass in absolute values and percentage of the total. This is reflected on the patterns of monthly productivity, which decreased

steadily during the second year showing lower levels of monthly productivity in the LM than in the HM (Fig. 9). In addition, exposed rhizomes were observed in the LM in the second year, whereas no such interannual differences were seen in the HM. This marked difference in productivity may be related to the interannual variation in climatic conditions; the second year showed extreme precipitation during the summer period, twice the rainfall for the same months of the previous year. The exceptionally high precipitation rate, coupled with the fact that maximum wind speeds typically occur during summer months, likely produced erosive conditions. This concept is consistent with the results of Castellanos et al. (1998) who found that periods of increased erosion in Mediterranean marshes coincided with maximum monthly rainfall and suggested that periods of intense wind-driven waves would contribute to this process. In addition, Chalmers et al. (1985) found that most of the carbon deposited in the marsh is subsequently eroded as a result of rain falling on the exposed surface. Mwamba and Torres (2002) found that more than 67 t/km^2 of marsh sediment can be mobilized within 5 min of a single low-tide storm event. The chief mechanisms for sediment transport is the detachment by raindrop impact and transfer by sheetflow (see also Pilditch et al. 2008; Torres et al. 2003).

The difference in the response of the two areas of the marsh to the same climatic event may be explained by different exposure to wave action and tides. The HM zone would not be as affected by erosive phenomena because it is more protected from the impact of water turbulence. In this sense, Nieva et al. (2005) distinguish different processes that dominate the *S. densiflora* marshes of the Mediterranean coast. They propose that, at the high marsh zone in Spain, *S. densiflora* ramet demography is driven by phenological phenomena, while catastrophic events (including those caused by storms) shape the characteristics of the low marsh zone; and in their study, these events promoted *S. densiflora* tussock deaths and frequent oscillations in tiller population. We found that the patterns of green biomass of the HM correlate with the air temperature (*r*=0.68; Fig. 10a) and show no interannual differences.

Although presenting seasonal variations, the patterns of green standing biomass in the LM, show an abrupt decrease in the second period, and productivity fell steadily. We believe this decrease in production is associated with an extreme increase in monthly rainfall which occurred during the second summer period, doubling the amount of summer-time precipitation that historically falls in this region.

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