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In order to examine the role of position in the tidal range on biomass production and nutrient pools in *Spartina alterniflora* in an Argentinian estuary, we estimated productivity, the concentration of C, N and P in tissues and pools (concentration × biomass) of these elements in low (LM) and high (HM) zones. Aboveground biomass of *S. alterniflora* was higher in HM than in LM. Aboveground primary productivity was 106 and 439 g dry wt m^{-2} year^{-1} in LM and HM, respectively. Belowground biomass was similar in LM and HM. Belowground primary productivity was 526 and 744 g dry wt m^{-2} year^{-1} for LM and HM, respectively. Nutrient pools were higher in HM than in LM. Biomass and productivity values were low, which makes nutrient pools low. The lower values of the parameters analysed in LM than in HM indicate that position in the tidal range is an important factor in this system, possibly due to the effect of flooding. Moreover, this pattern is opposite to the general one observed in the northern hemisphere, meaning that studying marshes from different environments is worth doing. Because pools were higher in HM, this zone would be more important for nutrient input to the estuary.

Keywords: *Spartina alterniflora*; biomass; primary productivity; nutrient pools; low marsh; high marsh

1. Introduction

Salt marshes can act as either a source or a sink of nutrients to the surrounding environment, depending on different factors (the element analysed, the time scale, the age of the marsh, the degree of tidal flooding, etc.) [1–3]. Halophytes play an essential role in determining the quantity and quality of these nutrients because they are the link between the inorganic and organic forms of nutrients through the production of biomass [4]. Therefore, productivity in salt marshes has been extensively studied all over the world [1,5–8].

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Productivity may be influenced by tidal flooding, one of the most conspicuous characteristics of salt marshes [6,9–11]. Flooding can also modify tissue composition by inducing the synthesis of particular compounds to tolerate salinity [12], influence decomposition rate [13,14] and, especially, determine whether the plant material is exported to the coastal waters or remains in the marsh substrate [9,15]. Low zones within the tidal range are flooded every day by seawater, whereas higher zones are only flooded by spring tides [16,17]. Hence, material is more likely to be exported from low zones, whereas the high zones in a salt marsh could be important in the input of nutrients and organic matter, through decomposition, to the marsh sediments or in the exchange of carbon with the atmosphere, through photosynthesis [9,15].

The amount of nutrients potentially available for exchange (= nutrient pools) can easily be estimated by multiplying the biomass production and the content of an element, such as carbon (C), nitrogen (N) or phosphorus (P), in plant tissues [18]. Biomass fluctuates throughout the year, as does the concentration of nutrients in the tissues; hence, nutrient pools show seasonal variation [8,11]. Nutrient concentrations in the tissues are also important because they influence the rate of decomposition, which is responsible for the release of nutrients back into the sediments [19,20].

Spartina alterniflora Loisel (Poaceae) is a perennial grass that grows in the intertidal zone and is widespread in salt marshes throughout the world. Numerous studies have reported its biomass production, which varies greatly according to the study area and the method used. Most research has been done in the USA [6–8], although studies have also been carried out in China [21,22]. These studies found high values of productivity, reinforcing the general idea that salt marshes are very productive systems; however, information about the productivity of *S. alterniflora* in South America is scarce, especially considering the belowground biomass [23–26], and should be taken into account in order to establish general patterns [27].

In the Bahía Blanca estuary (approximately 39°S), *S. alterniflora* occupies a considerable area and, because it is found throughout the whole intertidal zone, experiences different degrees of influence and connection with tidal water. Because the natural range of this species in South America is between 10 and 40°S [28], this area constitutes its lower limit of distribution. In addition, the Bahía Blanca estuary is situated in a transition zone between humid subtropical and semi-arid climates, which implies that this system has a unique combination of large interannual climatic variations; this, in turn, may have important implications for the productivity of this species because temperature is a key factor in its growth [27,29]. Therefore, the main aims of this study were to: (1) estimate above- and belowground production of *S. alterniflora* in this particular environment; (2) determine the nutrient pools potentially available (for *in situ* decomposition or exchange) through this species; and (3) examine biomass and nutrient differences between low and high zones in order to evaluate the role of the position in the tidal range in these parameters.

2. Materials and methods

2.1. *Study area*

The Bahía Blanca estuary is located between 38°45′ and 39°25′S and between 61°45′ and 62°25′W. It is a coastal plain, mesotidal estuary with a semidiurnal tidal regime. Tides constitute the most important energy input to the system. The mean tidal amplitude ranges from 2.2 to 3.5 m and the spring tidal amplitude ranges from 3 to 4 m [30]. The estuary is characterised by a temperate climate (mean temperature is 15 °C), with variable annual precipitation, the maximum and minimum mean annual rainfall being 712 and 540 mm, respectively. Strong north-west and north winds dominate the typical weather pattern of the region, with a mean annual velocity of 22.5 km h^{-1} and strong winds, >43 km h^{-1}, blowing over the estuary for 54% of the year [31]. These winds cause the greatest variation from astronomical tides [30].
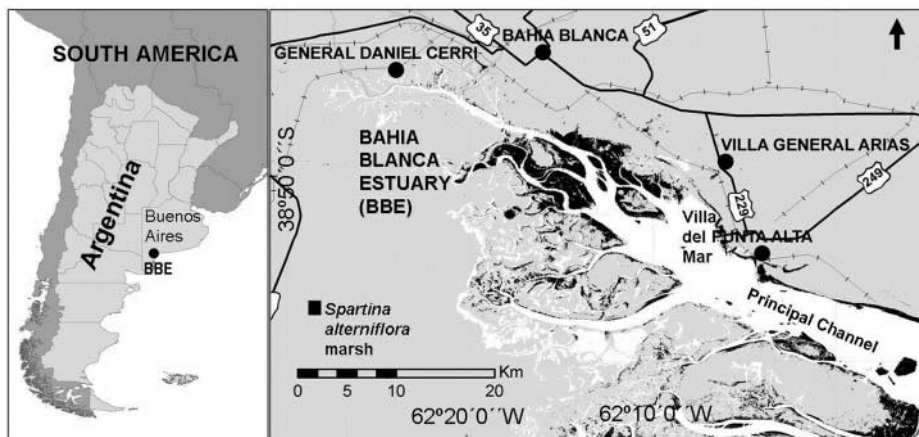
Figure 1.   Location of the study area.

Freshwater input to the estuary is low and comes mainly from two tributaries on the northern shore of the ecosystem: the Sauce Chico river and the Napostá Grande creek (average rate of $1.72\,m^3\,s^{-1}$ and $1.05\,m^3\,s^{-1}$, respectively, for 2006–2007) [32]. This is responsible for the quite high salinity of the waters [33]. Porewater salinity is also high (42.5 in late spring, personal observation) and the sediment is usually neutral (pH varies between 6 and 8.5) and reduced (Eh varies between -200 and $100\,mV$) [34]. Inorganic nutrient and organic matter levels are high in estuarine water [33] and in the sediment porewater [34,35].

The estuary is formed by a series of north-west- to south-east-oriented tidal channels separated by extensive tidal flats, salt marsh patches and islands. The total surface of the system is $\sim 2300\,km^2$, of which $1150\,km^2$ is intertidal, $740\,km^2$ is subtidal and $410\,km^2$ are islands [36]. *S. alterniflora* salt marshes cover $\sim 100\,km^2$ in the estuary [37] and their area has increased in recent years [38]. This modification of the land cover might be related to human influence [39] because several ports, towns and industries are located on the northern boundaries of the estuary, discharging their processing residues into streams or directly into the estuary.

The study was conducted in a natural salt marsh in the proximities of Villa del Mar, a small village in the intermediate reach of the estuary (Figure 1), where the mean tidal amplitude is $\sim 3.2\,m$ and the spring tidal amplitude is $\sim 3.8\,m$ [30]. The flats are partially covered by vegetation, *S. alterniflora* being the main species, which may be as high as $1.50\,m$ [40]. This species is found in two distinct situations: a regularly flooded zone, located lower than the mean high tide (hereafter low marsh – LM), and an irregularly flooded zone, located between the mean high tide and the spring high tide (hereafter high marsh – HM).

2.2.   *Sampling*

Above- and belowground biomass were sampled from October 2006 to April 2008 from monospecific stands of *S. alterniflora* in the two zones: LM and HM. The period between sampling dates varied between 1.5 and 3 months. The aboveground tissues were harvested by clipping vegetation at the sediment surface in randomly established $25 \times 25\,cm$ plots ($n = 5$ on each sampling date). All standing live and dead culms were removed and placed in plastic bags. The belowground biomass of both zones was collected using 15 cm long $\times$ 11 cm diameter PVC corers ($n = 5$ on each sampling date). Sediment cores were taken in the middle of each plot after the aboveground biomass sample had been collected. All samples were transported to the laboratory in a cooler and frozen until processed.

2.3. *Laboratory work*

Samples of aboveground tissues were washed and the dead and senescent shoots and leaves (hereafter dead) were identified by their yellowish or brownish coloration and separated from living material. The live and dead plant material was dried at $60\,^\circ$C for $\sim$72 h, and weighed to the nearest 0.01 g. Annual net aboveground primary productivity was estimated using the Smalley method which considers the production in each sample interval and adds them [41]. The production in each interval takes into account the increases and decreases of live as well as dead biomass. Turnover rates (annual production/peak total biomass) in both zones were also estimated.

The samples of belowground tissues were washed in a 500-μm sieve and plant material was dried and weighed as described for aboveground tissues. Live plant material was not separated from dead material due to the inaccuracy of such a procedure. Therefore, annual net belowground primary productivity was estimated as the difference between the maximum and minimum total biomass, as described by de la Cruz and Hackney [42]. Turnover rates and belowground/aboveground ratios were determined.

Dried aboveground material from all samples of each zone at each sampling date was pooled and ground in a grinder. Belowground biomass was also pooled and ground. C was determined by dry combustion, N using the Kjeldahl method and P using atomic emission spectrometry (ICP-AES). The elemental concentration of C, N and P and biomass of both total aboveground and belowground tissues were multiplied to yield element pools. C/N and C/P ratios were calculated due to their relationship with decomposition rate [19,20] and N/P was estimated to determine whether plant production is likely to be N or P limited [43].

2.4. *Statistical analysis*

One-way analysis of variance (ANOVA) and Tukey's test were used to evaluate differences between dates in each zone for each type of tissue (live aboveground, dead aboveground, total aboveground and total belowground). The differences in biomass and belowground/aboveground ratios between LM and HM on each sampling date were evaluated using Student's *t*-test. Two-way ANOVAs were run to evaluate differences between zones and tissues (aboveground and below-ground) in the percentage of nutrient content, molar ratios and element pools, using data from the whole study period. The acceptable level of statistical significance was 5%. When necessary, data were ln-transformed to meet the parametric assumptions. Statistical analyses were done according to Zar [44]. Data presented in the figures were not transformed.

3.   Results

3.1. *Aboveground biomass*

Live aboveground biomass of *S. alterniflora* was always present in both LM and HM during the study period, but varied seasonally (Figure 2a). In LM, the highest biomass was found in January 2007, April 2007 and December 2007, and values were all significantly different from the minimum biomass recorded in July 2007 (Tukey's test: $p < 0.05$). In HM, the highest biomass was recorded in April 2007, February 2008 and April 2008 and values were all significantly higher than the lowest biomass, recorded in September 2007 (Tukey's test: $p < 0.05$) (Figure 2a).

Dead aboveground biomass was always present, but differed greatly over the study period in both zones (Figure 2b). In LM, it was quite constant throughout the study period (ANOVA: $F = 1.47$; $p > 0.10$), whereas in HM it showed marked seasonality. The highest dead aboveground biomass

was found in October 2006, April 2007 and April 2008 and all values were significantly different from the minimum biomass, recorded in December 2007 (Tukey test: $p < 0.05$) (Figure 2b).

Live and dead biomass was higher in the HM than in LM over the whole study period. Dead biomass in HM was significantly higher than in LM on all dates (Student's t-test: $p < 0.05$ in each case), but for live biomass the differences were significant only in October 2006, April 2007, June 2007, July 2007, February 2008 and April 2008 (Student's t-test: $p < 0.05$ in each case). On average for the whole study period, live aboveground biomass in HM was more than twice that in LM, whereas dead biomass was more than six times more abundant (Figure 2a,b). The total (live + dead) aboveground biomass was significantly higher in the HM than in the LM during the whole period (Student's t-test: $p < 0.05$ in each case), except for December 2007 when no statistical difference was detected (Student's t-test: $p > 0.10$). On average for the whole studied period, the total aboveground biomass was almost four times higher in the HM than in the LM (364.08 ± 27.14 versus 97.06 ± 7.46 g dry wt m^{-2}) (Figure 2c).

The importance of each fraction (live and dead) in the total aboveground biomass was different in both zones. In LM, only approximately a quarter of the total aboveground biomass was represented by dead material, whereas in HM, on average, half of the aboveground biomass was actually dead. In LM and, in the last months also in the HM, the seasonal dynamics of the total aboveground biomass reflected mainly that of the live component.

Aboveground primary productivity was 106 and 439 g dry wt m^{-2} year^{-1} in the LM and the HM, respectively. Turnover rate was 0.69 year^{-1} for LM and 0.80 year^{-1} for HM.

3.2. *Belowground biomass*

Belowground biomass did not show any pronounced seasonal differences in either zone. However, in LM a maximum value was found in February 2008, which was significantly different from the lowest biomass observed in February 2007 (Tukey test: $p < 0.05$). In HM, on the other hand, the seasonal differences were never significant (ANOVA: $F = 1.78$; $p > 0.10$). There were no significant differences in belowground biomass between HM and LM in all sampling dates ($p > 0.05$ in each case), with the exception of December 2007 when it was higher in HM ($p < 0.05$) (Figure 2d).

The relative importance of the belowground fraction in the total biomass differed among both zones. On average, 84% of the total biomass was represented by belowground material in LM, whereas in HM, only a half of the biomass was found below the ground. Belowground/aboveground ratios were significantly higher in the LM than in the HM for the whole period ($p < 0.05$ in each case) except for December 2007 ($p > 0.50$) and July 2007 ($p > 0.05$). In the LM, the ratio varied between 4.24 ± 0.80 (December 2007) and 12.02 ± 3.44 (October 2006) whereas in the HM it ranged from 0.63 ± 0.34 (April 2008) to 5.17 ± 1.15 (December 2007).

Belowground primary productivity was 526 and 744 g dry wt m^{-2} year^{-1} for LM and HM, respectively. Turnover rate was 0.61 year^{-1} and 0.52 year^{-1} for LM and HM, respectively. The total (above + belowground) primary productivity was 632 and 1183 g dry wt m^{-2} year^{-1} for LM and HM, respectively.

3.3. *Tissue nutrient content and nutrient pools*

The concentration (%) of C, N and P in *S. alterniflora* varied mainly between types of tissues and sometimes also between zones (Table 1). The N and P content was similar between zones ($p > 0.05$), but significantly higher in aboveground than in belowground parts ($p < 0.05$). By contrast, the content of C in aboveground tissues was significantly higher in HM than in LM
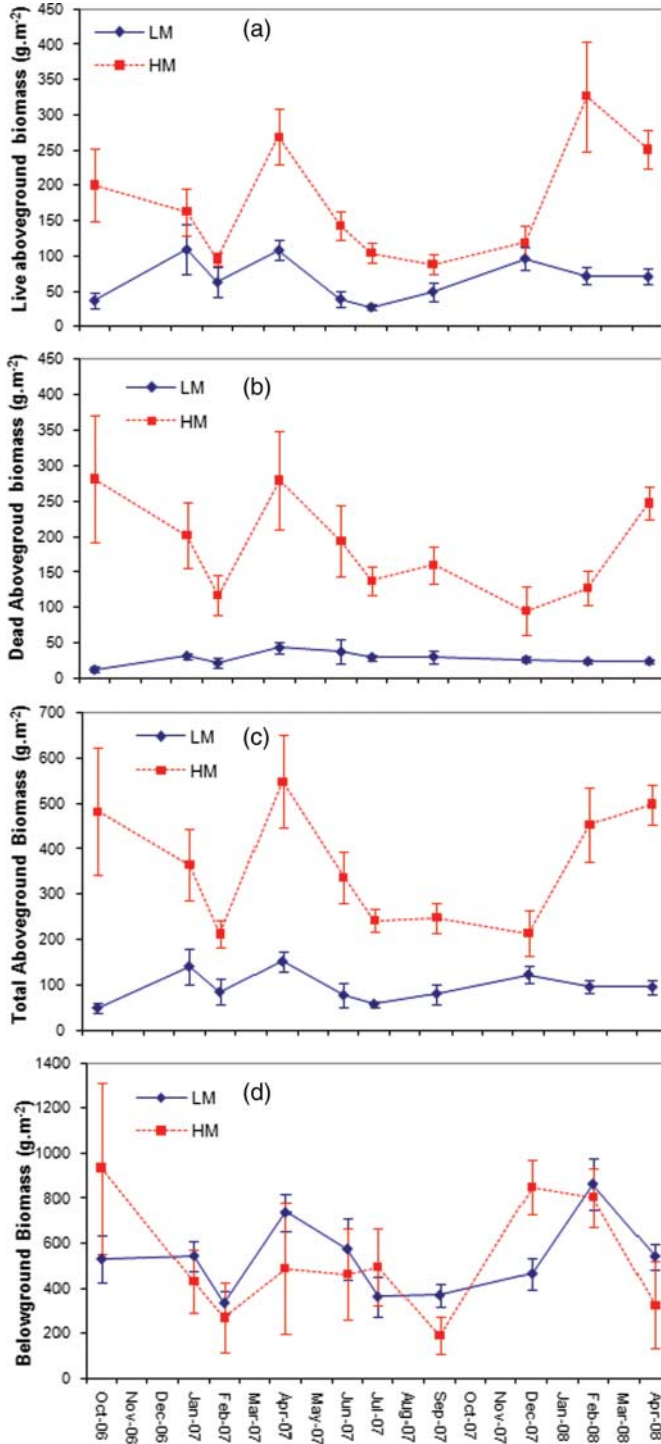
Figure 2. Live aboveground (a), dead aboveground (b), total aboveground (c) and total belowground (d) biomass in low marsh (LM) and high marsh (HM) (mean ± SE; *n* = 5).

plants ($p < 0.01$), while no statistical difference was observed in the belowground ones ($p > 0.05$). Considering types of tissues, the concentration of C was higher in belowground biomass in both zones, but the difference was only significant in the LM ($p < 0.01$).

Table 1. Content of C, N and P (%) in *S. alterniflora* tissues in low marsh (LM) and high marsh (HM).

	LM			HM		
	C	N	P	C	N	P
Aboveground	39.46 ± 0.24	**1.33**$^* \pm 0.09$	**0.11**$^* \pm 0.01$	41.30 ± 0.31	**1.12**$^* \pm 0.10$	**0.10**$^* \pm 0.01$
Belowground	**41.50**$^* \pm 0.33$	1.07 ± 0.09	0.06 ± 0.01	**41.37**$^* \pm 0.27$	0.96 ± 0.10	0.06 ± 0.01

Note: Values are means $\pm$ SE of all sampling dates ($n = 10$). The highest value in each column is shown in bold and is marked with an asterisk if it is significantly higher than the corresponding value in the same column. The difference in C content in aerial tissues between sites was also significant.

Table 2. Molar ratios in *S. alterniflora* tissues in low marsh (LM) and high marsh (HM).

	LM			HM		
	C/N	C/P	N/P	C/N	C/P	N/P
Aboveground	31.26 ± 2.57	396.26 ± 29.03	13.10 ± 1.01	41.02 ± 4.98	463.99 ± 42.27	12.22 ± 1.45
Belowground	41.90 ± 4.10	818.13 ± 103.76	21.77 ± 3.86	48.56 ± 5.44	509.49 ± 123.41	16.80 ± 1.77

Note: Values are means $\pm$ SE of sampling dates ($n = 10$).

Table 3. C, N and P pools ($g \cdot m^{-2}$) of *S. alterniflora* in low marsh (LM) and high marsh (HM).

	LM			HM		
	C	N	P	C	N	P
Aboveground	38.46 ± 4.30	1.23 ± 0.14	0.093 ± 0.007	149.99 ± 7.20	3.74 ± 0.39	**0.328** ± 0.036
Belowground	**222.56**$^* \pm 21.56$	**5.56**$^* \pm 0.50$	**0.299**$^* \pm 0.035$	219.21 ± 4.14	5.18 ± 1.07	0.317 ± 0.054
Total	**260.58** ± 23.83	**6.79** ± 0.56	**0.393** ± 0.033	**369.20** ± 41.82	**8.92** ± 1.26	**0.645** ± 0.082

Note: Values are means $\pm$ SE of all sampling dates ($n = 10$). The highest value in each column (between above- and belowground tissues) is given in bold, and is marked with an asterisk if it is significantly higher than the corresponding value in the same column. The differences between sites in aerial tissues were also significant.

Some differences were also observed in C/N, C/P and N/P (Table 2). All the ratios were higher in belowground tissues than in aboveground tissues ($p < 0.05$). However, no significant differences were found between LM and HM plants ($p > 0.05$).

The element pools analysed varied over the study period. Aboveground pools of N and P showed a general trend to decrease in autumn and winter and increase in spring and summer, whereas in the case of C, minimum values were found in late winter and spring and maximum values were observed in autumn (Figure 3). Belowground pools showed an erratic course over the study period for the three elements analysed; however, a general trend of low values in winter and high values in summer 2008 was observed in all cases (Figure 4). In addition, high values were also found in October 2006, especially for the HM, and there was a decrease in February 2007, mainly for C and N (Figures 3 and 4).

Considering the marsh zones, the pools of C, N and P recorded in aboveground tissues were significantly higher in HM than in LM ($p < 0.05$), whereas no differences were found for the

belowground ones ($p > 0.05$). Regarding both types of tissues, belowground pools were significantly higher than aboveground ones, but only for LM ($p < 0.05$). The pools of C, N and P for the total biomass (above + belowground) were ~1.5 times higher in HM than in LM (Table 3).
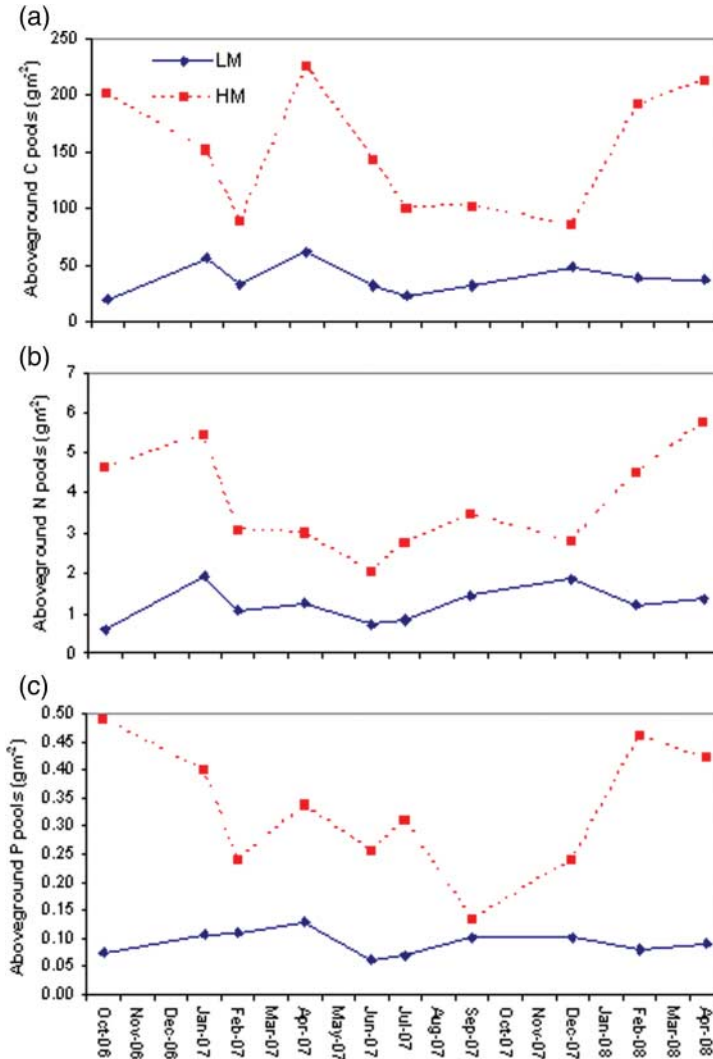
Figure 3.   Aboveground pools of C (a), N (b) and P (c) in low marsh (LM) and high marsh (HM).

4.   Discussion

Live, dead and total aboveground biomass varied over the study period in both zones, spanning two growing seasons. The highest values were reported in April, showing that the material storage was maximum in autumn after active growth in summer. High values of live biomass were also observed in late spring 2007 and summer 2008, for LM and HM respectively, which might suggest that there was an early growth in spring for the second growing season. On the other hand, belowground biomass did not show any important seasonal differences in either zone, although there was a
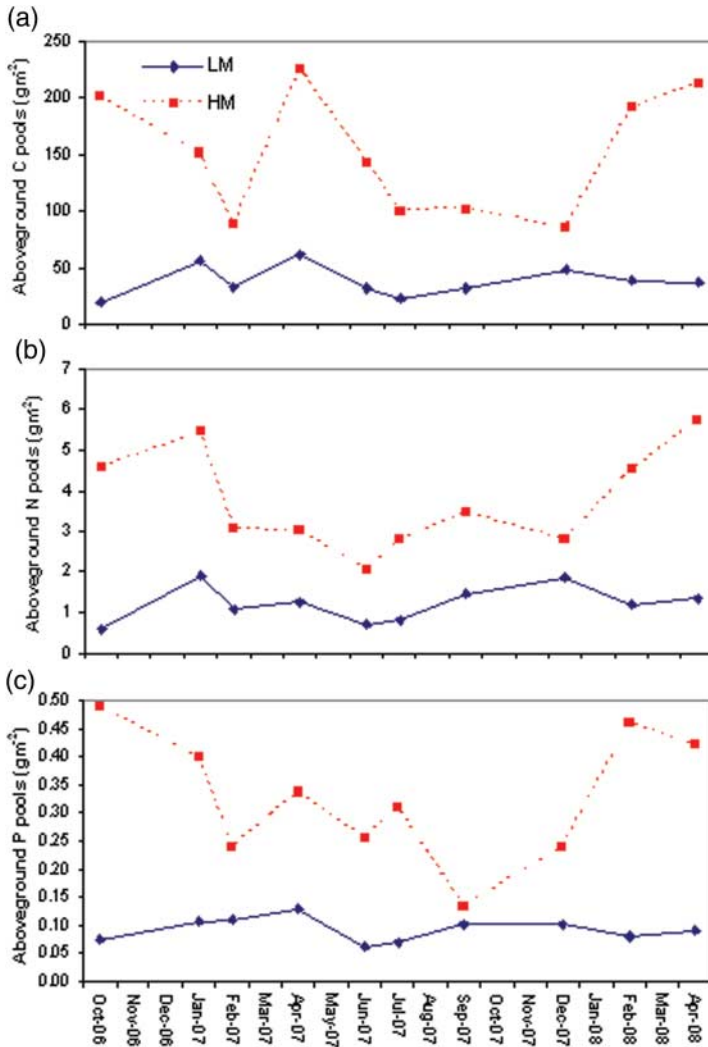
Figure 4. Belowground pools of C (a), N (b) and P (c) in low marsh (LM) and high marsh (HM).

slight trend towards maximum values in spring–summer 2008, similar to that observed in the aboveground biomass. This might indicate the absence of a translocation of resources between aboveground and belowground components. It has been speculated that an extended growing season and mild winter conditions may minimise the degree of translocation [45,46], but other workers have reported the existence of this phenomenon in quite warm climates. Da Cunha Lana et al. [24], who worked in Paranaguá Bay, Brazil ($\sim 25°$S), and Darby and Turner [8], who worked in Louisiana, USA ($\sim 29°$N), observed translocation between above and belowground biomass. The apparent absence of translocation of resources in our study area ($\sim 39°$S) would highlight the importance of studying different environments to achieve a complete understanding of this phenomenon.

Total primary productivity in HM was roughly double that in LM, which highlights the importance of the position of the plants in the tidal range in this parameter. González Trilla et al. [25], working in the same study area, estimated that the productivity in HM in the second year of their study (corresponding approximately to the period analysed here) was $495 \pm 105 \, \mathrm{g m^{-2} \, year^{-1}}$,

similar to the value we reported. However, they found no differences between that value and the one corresponding to LM ($482 \pm 87 \, \mathrm{g m^{-2} \, year^{-1}}$). This apparent disagreement with our work may lie with the large variability in their values, which might mask the differences between zones. In addition, the area defined as LM in this work is more extensive, and the methods used were also different and productivity in salt marshes is very dependant on the estimation technique, especially if one is destructive and the other non-destructive [47]. This emphasises the variability of these systems and hence the importance of studying salt marshes from different environments and different zones within each one.

The lower productivity in LM than in HM may be related to flooding. Even though *S. alterniflora* is adapted to flooding, this condition imposes a great stress on the plants. The more unfavourable conditions in LM are shown in the higher belowground/aboveground ratios, because greater investment in belowground biomass is a sign of stress [45,48,49]. Stress in LM is mainly related to the reduced sediment, because the redox potential is significantly lower there than in the HM, as previously reported in the same study area [34], and these conditions tend to decrease primary production [1,5]. Although *S. alterniflora* is capable of oxygenating the rhizosphere in anoxic soils [50–52], this ability is density–dependent [53], and hence the low density of tillers in the area (729 ± 40 individuals.$\mathrm{m^{-2}}$) [25] would not be enough to oxidise the sediments. In addition, lower biomass in low zones could be associated with a lower photosynthetic rate during submerged conditions [54].

This pattern of lower productivity in LM than in HM is opposite to that generally observed in the well-studied *S. alterniflora* salt marshes in the northern hemisphere ([5] and references therein). The explanation for such disagreement might lie with the physical characteristics of the particular study site. In the northern marshes, the LM is usually dissected by several channels and at the creek bank the sediments are more oxidised (higher redox potential) because there is greater subsurface water movement and hence the conditions for the growth of *S. alterniflora* are better and plants there are taller and more productive. In HM, which is inland, the lower water movement implies an increase in salinity, another important factor decreasing productivity [1,5] and therefore the productivity is lower there. Our study site is characterised by the total absence of tidal creeks, with the exchange of tidal water taking place across the entire marsh surface [55]. This situation would indicate that in this salt marsh the stress imposed by flooding in the LM (generating reduced conditions) would be an important factor determining the differences in production between both zones.

Despite the higher values of productivity in HM than LM, they are still fairly low if we compare them with other salt marshes around the world. Aboveground primary productivity using Smalley method varies between 113 and 2318 g dry wt $\mathrm{m^{-2} \, year^{-1}}$ [7,8,24] and belowground primary productivity, using the max–min (of total belowground biomass) method, range from 1670 to 4850 g dry wt $\mathrm{m^{-2} \, year^-}$ [6,8,10] in other areas in the world. The low values in our study may be the result of the high salinity, which has previously been suggested as a determining factor in the same study area by Gonzalez Trilla et al. [25], especially regarding the high levels of salinity in porewater. Although the salinity in porewater is higher in HM than in LM (46.9 vs 38.2 in late spring; personal observation), the values are high for both zones. The high salinity condition of the study area is associated with its location, which is characterised by low air humidity, low freshwater input, low precipitation and high evaporation resulting from the strong winds.

The content of N and P in *S. alterniflora* tissues in the Bahía Blanca estuary was in the range for this species observed in other salt marshes in other parts of the world [18,23,56]. The differences in the content of both elements between aboveground and belowground tissues might be related to the high enzymatic activity of the photosynthetic structures, as suggested by Biudes and Camargo [23]. High values of C/N and C/P imply low decomposition rates [19]; hence, the values found here are in agreement with decomposition rates estimated in the area which were low for both aboveground and belowground tissues [57]. This also agrees with the low turnover rates found in this marsh.

Although there were differences in N/P between tissues, the ratios were always <33 (Table 2), which indicates N limitation [43,58], as is generally observed in wetlands [59].

The values for both aboveground and belowground nutrient pools reported here are lower than those observed for *S. alterniflora* in other parts of the world [8,21,60], due to the low biomass [18]. The seasonal dynamics of C pools reflects exactly the same changes in aboveground and belowground biomass. The N and P pools, although in a general trend reflect the biomass dynamics, have different high values, which varied according to differences in the concentrations of the nutrients in tissues. The aboveground and belowground pools of all C, N and P tend to decrease in winter, due to the reduced growth rate and/or the loss of biomass through litter production, which is typical in that season. The timing of maximum pools of the different elements, tissues and zones was variable, which implies that the maximum uptake of nutrients varies greatly.

Total (aboveground and belowground) nutrient pools were higher in HM than in LM (Table 3), due to the differences between zones for aboveground pools, which in turn reflect the differences in biomass. In the particular case of C pools, they are even greater in HM than in LM due to differences in the percentages of this element in the tissues (Table 1). This big difference in C pool between zones is in agreement with the higher organic matter concentration in porewater in HM [34] and probably would affect also carbon storage in sediments, although in the long-term due to the low decomposition rates [61]. In addition, we could obtain the amount of these elements that are fixed in plant biomass annually in the whole estuary. For this, we should consider the surface covered by *S. alterniflora* in the system and assume that the productivity levels and C, N and P concentrations in plant tissues in all salt marshes in the estuary are the same as the ones estimated here. Because productivity levels and C content in aboveground tissues varied between zones, we considered them separately. Hence, the amount of C fixed in the estuary would vary between 26012 ± 199 and 49910 ± 337 ton, that of N between 706 ± 57 and 1206 ± 118 ton and that of P between 41 ± 3.5 and 86 ± 6.8 ton.

Once the plant senesces, nutrient pools could have different fates. The material could remain in the marsh sediment and decompose there, as usually occurs in HM due to its scarce connection with seawater [9,15]. However, in the few times the tides reach this zone, the plant material is deposited rather than washed away by the water, because large lines of wrack coming from other marshes of the estuary are found in the study area (personal observation), showing the importance of the tides in the movement of material, as observed in other coastal marshes [62]. In LM the situation is different. We did not see dead shoots there, probably because they are washed away by the tides and/or the wind. This material might be deposited in other areas of the estuary and contribute with nutrients there or remain in the water body.

5. Conclusions

Aboveground and belowground biomass productivity of *S. alterniflora* in the study area is low. In addition, taking into account the zones within the marsh, it is higher in HM than in LM, contrary to the general trend in salt marshes of this species. This highlights the importance of the position of the plants in the tidal range, mainly associated to flooding, in the growth of *S.alterniflora*.

The pools of C, N and P of *S. alterniflora* in the studied salt marsh are low, which is due to the low biomass values. However, they may be important if the area covered by this species in the estuary and its expansion over the last few years are taken into account. Because production is higher in HM than in LM, the former would be more important than the latter for the input of nutrient to the system, especially to the marsh itself. Although biomass is the main factor determining the seasonal dynamics of the pools, the concentration of some elements (N and P) in the tissues should also be taken into account at certain times of the year.

The results presented here highlight the importance of plant zonation in salt marshes, since flooding played a significant role in productivity and nutrient pools values as well as being the tides the main force for material distribution. In addition, this work contributes to a better knowledge of this species in the southern hemisphere. However, more research is needed, especially to evaluate if general concepts originated in well-studied systems can be supported in other regions where the particular conditions may create alternative scenarios. Therefore, although it seems that we know almost everything about this worldwide distributed species, a lot is still ignored and further research is highly desirable.

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