Biomass, decomposition and nutrient cycling in a SW Atlantic *Sarcocornia perennis* marsh

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ABSTRACT

Biomass dynamics, decomposition and nutrient cycling were studied in a *Sarcocornia perennis* salt marsh in the Bahia Blanca estuary (Argentina) to achieve a better understanding of these processes and provide information about a species and a region underrepresented in the literature. Above and belowground biomass stocks and carbon (C), nitrogen (N) and phosphorus (P) concentration in plant tissues were monitored every 2 months during a year. The decomposition rate and the concentration of C, N and P during the process were also estimated in above and belowground tissues. Biomass values were low (mean of 363 ± 43 and 242 ± 27 g m^{-2} for aboveground and belowground tissues, respectively), presumably associated with the high salinity of this estuary. The general trend of higher values for aboveground biomass is in agreement with other reports for this species and has an effect on nutrients pools, which are higher for aboveground tissues for C and N. Above and belowground decomposition rates were high (64 and 70% after a year, respectively), meaning this process plays a significant role in the cycling of organic matter. C/N and C/P ratios changed during decomposition, but final ratios were usually higher, suggesting a net release of nutrients. Our results indicate that significant amounts of C, N and P are recycled by *S. perennis*, highlighting the role of this species and suggesting important consequences of its lost in the study area.

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1. Introduction

Due to their transitional position and commonly high net primary production, salt marshes play a key role in the cycling and exchange of nutrients (Adam, 2002; Mitsch and Gosselink, 2007). These functions are highly dependent on environmental conditions like tidal flooding, climate, freshwater discharge, geomorphology, etc. (e.g., Hyndes et al., 2014; Lewis et al., 2014), but also on biological processes like biomass and detritus production, nutrient content and decomposition of vegetation (e.g., Negrin et al., 2012a, b; Quan et al., 2007; Sousa et al., 2010). Numerous studies concerning biomass, decomposition and nutrient content in salt marsh plants have been reported, but only a few of them considered all these aspects together providing a holistic approach of biogeochemical cycling in these environments (Bouchard

and Lefeuvre, 2000; Elsey-Quirk et al., 2011; Palomo and Niell, 2009; Tong et al., 2011). Thus, it is necessary to develop more integrative studies to achieve a better understanding of the complex dynamics of nutrients in salt marshes.

Sarcocornia perennis (Chenopodeaceae) is a globally distributed halophyte, occurring in Europe, Africa and the Americas (Davy et al., 2006). In the SW Atlantic, it is the common dominant species in salt marshes from the Bahía Blanca estuary to Tierra del Fuego where it forms extensive monospecific stands subjected to mesotidal and macrotidal conditions (Bortolus et al., 2009; Isacch et al., 2006). Despite its wide distribution, *S. perennis* has been scarcely studied, with only a few works about biomass, nutrient cycling or decomposition (Boraso et al., 2009, 2012; Caçador et al., 2009; Curado et al., 2014; Peláez et al., 2009; Sousa et al., 2010). A comprehensive study on this species was published by Palomo and Niell (2009), performed in a salt marsh of the Palmones River estuary (Spain), under a microtidal regime. Since tidal flooding is a significant factor in nutrient cycling in salt marshes (e.g., Bouchard and Lefeuvre, 2000; Curcó et al., 2002; Negrin et al., 2012a), information from systems with different tidal regimes are desirable, especially from scarcely known regions as South America.

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S. perennis is the dominant species in salt marshes at the Bahía Blanca estuary (Argentina), a mesotidal system, covering an area of 203.8 km² (Isacch et al., 2006). A previous work in the study area has already stated the role of *S. perennis* in the distribution of nutrients and organic matter in porewater (Negrin et al., 2013), but for a better approach of the whole picture, information about biomass, nutrient content and decomposition is highly desirable. In this work, we estimated biomass stocks, carbon, nitrogen and phosphorus concentrations and decomposition rate of *S. perennis* in order to evaluate nutrient cycling in a salt marsh in the SW Atlantic, both a species and a region largely underrepresented in the international literature.

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 (Fig. 1a). It is a coastal plain, mesotidal estuary with a semidiurnal tidal regime (Piccolo et al., 2008). Tides and wind waves are the major energy sources to the system (Perillo and Piccolo, 1991). The freshwater input is low and comes mainly from two tributaries: the Sauce Chico river and the Naposta Grande creek (average rate of 1.72 m³ s⁻¹ and 1.05 m³ s⁻¹ for the period 2006–2007, respectively) (Carbone et al., 2008). The low freshwater input is associated with the usually high salinity, which can reach values of 41.3 near the study area in summer (Freije et al., 2008). In addition, this estuary is located in region subjected to large interannual rainfall variations due to El Niño influence (Pratolongo et al., 2013), which

might have implications on salinity values as well as in ecological variables.

The estuary is formed by a series of tidal channels separated by extensive tidal flats and salt marsh patches. The total surface of the system is approximately 2300 km², including 1150 km² of intertidal areas, 740 km² of subtidal ones and 410 km² of islands (Piccolo et al., 2008). The study was conducted in a salt marsh close to Puerto Cuatreros, a small harbor in the inner zone of the estuary (Fig. 1a). Tidal flats are dominant in this area, dissected by tidal courses of different characteristics. The high marsh, between mean high water and the highest astronomical tide, is mainly vegetated by *S. perennis*, which is usually found in association with burrows made by the crab *Neohelice granulata* (Perillo and Iribarne, 2003) (Fig. 1b).

2.2. Biomass dynamics

Biomass was sampled every 2 months from November 2007 to November 2008 from monospecific stands of *S. perennis*. Due to the patchy distribution of this species, with isolated mounds of vegetation within a matrix of bare soil, we established clip plots (n = 6 on each sampling date) within randomly selected plants. Plant cover was visually estimated and percent cover (60%) was used to correct biomass values per unit area. Aboveground biomass was harvested by clipping vegetation at the sediment surface; all standing live and dead tissues were removed and placed in plastic bags. Belowground biomass was collected using 15-cm long × 11-cm diameter PVC corers taken within the same clip plots harvested for aboveground biomass. All samples were transported to the laboratory in a cooler and frozen until processing.
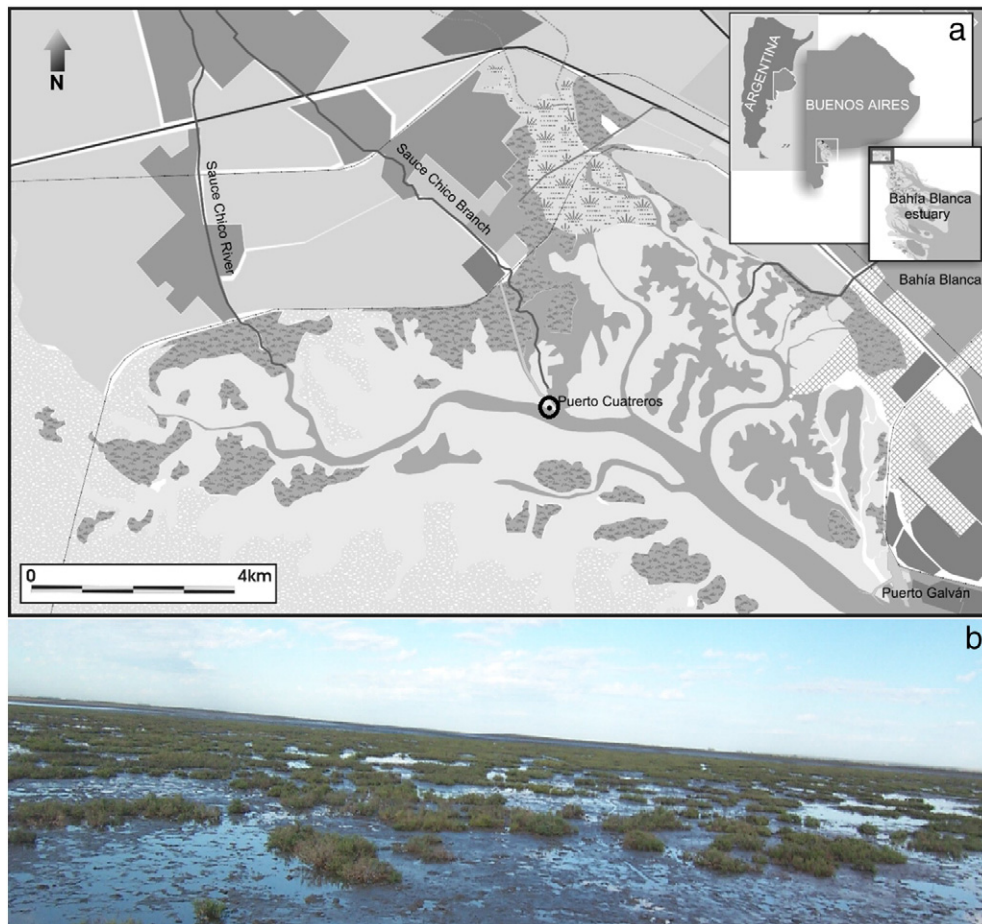

Fig. 1. a) Location of the study area and b) View of the studied salt marsh.

Aboveground samples were washed and the dead shoots were identified by their yellowish or brownish colouration and separated from living material. Belowground samples were washed in a 500 μm sieve to prevent the loss of fine roots; live plant material was not separated from dead one due to the inaccuracy of such a procedure. All samples were dried at 60 °C for approximately 72 h and weighed to the nearest 0.01 g. Biomass values were later multiplied by 0.6 according to the estimated plant cover. Belowground/aboveground ratios in each sampling date were calculated.

2.3. Tissue nutrient content and pools

Dried aboveground biomass from all samples at each sampling date was pooled in one monthly sample representative of the aboveground material that was then ground for nutrient determinations. Belowground biomass was treated in a similar way, which resulted in two monthly values, representative of aboveground and belowground biomass nutrient contents. Carbon (C) was determined by dry combustion, nitrogen (N) with the Kjeldahl technique and phosphorus (P) by the Watanabe and Olsen (1965) method. N/P was estimated in order to determine whether plant production is likely to be N or P limited (Güsewell and Koerselman, 2002; Koerselman and Meuleman, 1996). Nutrient pools were calculated by multiplying the element concentration per the biomass mean at each sampling date; this was done for both above and belowground tissues (Quan et al., 2007; Sousa et al., 2010).

2.4. Decomposition

Decomposition of aboveground and belowground biomass was determined from the disappearance of material from litter bags (Bocock and Gilbert, 1957), a method widely used in salt marshes (e.g., Menendez and Sanmartí, 2007; Simões et al., 2011). Plastic bags (20 × 20 cm, 2 mm of mesh size) were filled with plant tissues collected from the study site, which were previously rinsed and dried at 60 °C for 72 h. Bags were labeled and their content was individually weighed (approximately 20 g of aboveground and 10 g of belowground biomass). At the beginning of the sampling period, the bags containing aboveground tissues (N = 21) were placed on the sediment surface, while those with belowground biomass (N = 12) were buried at a depth of 10 cm. Every 2 months, during a year, between two and four bags were removed and taken to the laboratory. The content of each bag was washed, dried and weighed. Two bags from each sampling date were analyzed for the C, N and P contents (%) using the methods mentioned above. C/N and C/P ratios were calculated.

2.5. Statistical analysis

The differences between above and belowground biomass and between sampling dates were evaluated together by a two-way ANOVA, being the factors "type of tissue" and "date". After that, multiple comparisons with the Tukey test were performed. The differences between live and dead aboveground biomass and between sampling dates were also evaluated by a two-way ANOVA followed by Tukey test. In addition, Student t tests were run to evaluate differences between types of tissues in nutrient concentration, N/P ratio and pools, using the monthly values as replicates.

Statistical analysis followed Zar (1996). When necessary, data was ln-transformed to meet the parametric assumptions. The acceptable level of statistical significance was minor than 5%. Data presented in the figures were not transformed. Error values, either in figures, tables or in the text, represent standard errors.

3. Results

3.1. Biomass dynamics

There was a significant interaction between type of tissue (above or belowground) and sampling date (p<0.01). There was a general trend through the year of higher values of aboveground than belowground biomass (mean values of 363 ± 43 and 242 ± 27 g m^{-2}, respectively), but their difference was only significant in March (p<0.01; Fig. 2a). Belowground/aboveground biomass ratio was always below 1, except in November 2007, when it reached 1.5. Both types of tissues varied along the year, although only belowground biomass showed significant differences. Belowground biomass was significantly lower in March than in November 2007, July and September (p<0.01, p<0.01 and p<0.05, respectively; Fig. 2a).

Regarding aboveground biomass, there was a significant interaction between type of tissue (live or dead) and sampling date (p<0.01). Live aboveground biomass was usually higher than dead aboveground biomass (mean of 259 ± 39 and 105 ± 19 g m^{-2}, respectively), and differences were significant in January (p<0.01) and March (p<0.01) (Fig. 2b). Both types of tissues showed seasonal trends, but only dead aboveground biomass showed significant differences, with values in July higher than values in November 2007 and March (p<0.01 for both pairwise comparisons; Fig. 2b).

3.2. Tissue nutrient content and pools

No significant differences were found in the concentration (%) of C, N and P when comparing aboveground and belowground tissues, but N/P ratio was significantly higher in aboveground tissues (Table 1). C and N pools were significantly higher for aboveground tissues, but P pools did not show significant differences (Table 2). C and N showed a similar seasonal dynamics, with maximum values in January and July for aboveground tissues and in July for belowground ones (Fig. 3a and b). Regarding P, the seasonal pattern was different, with a maximum in January for the aboveground pool and a belowground maximum reported in September (Fig. 3c).
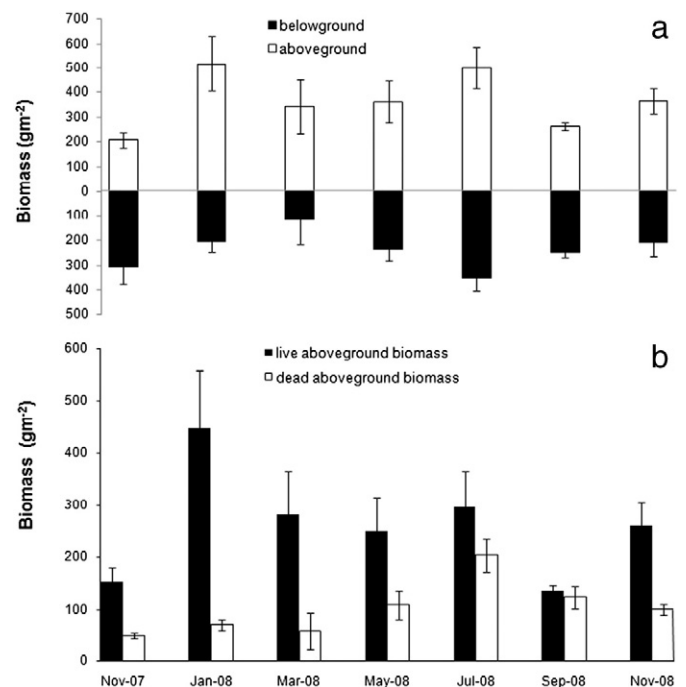

Fig. 2. *S. perennis* biomass (n = 7; mean ± SE): a) total aboveground and belowground and b) live and dead aboveground.

Table 1
C, N and P content (%) and N/P ratio in *S. perennis* tissues (n = 7; mean ± SE). The highest value in each column is in bold and marked with an asterisk if it is significantly higher.

	C	N	P	N/P
Aboveground tissues	**42.87 ± 0.7070**	**1.076 ± 0.06354**	0.06491 ± 0.01107	**19.96* ± 4.185**
Belowground tissues	42.11 ± 0.859	1.016 ± 0.0708	**0.0903 ± 0.013**	12.00 ± 1.029

3.3. Decomposition

The annual decomposition rates for aboveground and belowground tissues were similar (63.93 ± 17.02 and 70.63 ± 4.40% of material lost after a year, respectively). The changes of biomass along the study period fluctuated for both types of tissues, especially for aboveground ones. In both cases the larger losses were observed in the first 2 months, when more than the 40% of the initial biomass disappeared. After that, belowground biomass values were quite constant whereas aboveground biomass continued decreasing even after 100 days from the beginning of the experiment (Fig. 4).

The content (%) of C, N and P in aboveground and belowground tissues of *S. perennis* fluctuated during decomposition (data not shown). Molar ratios (C/N and C/P) also varied during the experiment, but the final values were usually higher than initial ones, except for C/N for belowground tissues (Fig. 5).

4. Discussion

The aboveground biomass estimated here was much lower than values reported for *S. perennis* in the Palmones River estuary, Spain (more than 3000 g m^{-2}; Palomo and Niell, 2009) and in Patagonian salt marshes (up to 5000 g m^{-2}; Boraso et al., 2009; 2012) but similar to that found in the Tagus estuary, Portugal (mean biomass ~ 230 g m^{-2}; Caçador et al., 2009). The belowground biomass was about 10 times lower than that found for the same species in other marshes. In the Tagus and the Palmones River estuaries maximum values were 4860 ± 94 g m^{-2} and 3110 ± 434 g m^{-2}, respectively (Caçador et al., 2009; Palomo and Niell, 2009). The general low values of biomass in our study area could be related to the high salinity, as observed in other salt marshes, either in the same estuary (Negrin et al., 2012a) or in other estuaries in the world (Curcó et al., 2002; Scarton et al., 2002).

Belowground biomass was generally lower than aboveground biomass, in agreement with Palomo and Niell (2009) for the same species but opposite to the general pattern in salt marsh plants (e.g. Curcó et al., 2002; Darby and Turner, 2008; Negrin et al., 2012a; Scarton et al., 2002). This is also reflected in belowground/aboveground ratios lower than 1. A greater inversion in belowground components is associated with stressful sediment conditions (Scarton et al., 2002; Schubauer and Hopkinson, 1984); hence, our results could indicate that the sediment conditions in our area are appropriate for plant growth. This is in agreement with the values of redox potential found in the area, which are mostly oxidized (Negrin et al., 2013). Live tissues were in most cases the major component of the aboveground biomass, as found for the same or other salt marsh species previously (e.g., Curcó et al., 2002; Darby and Turner, 2008; Palomo and Niell, 2009; Scarton et al., 2002).
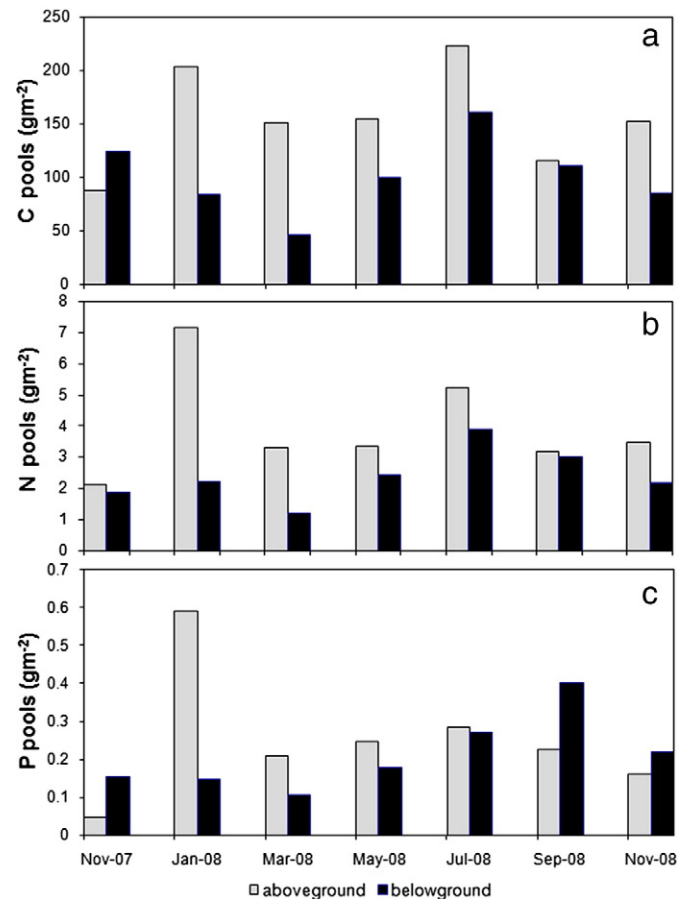
Contents of N and P in *S. perennis* tissues were similar to those reported for the same species in Spain (Palomo and Niell, 2009). Nitrogen concentration did not differ significantly between aboveground and belowground tissues. Differences in P content were also nonsignificant, but the slightly higher concentration in belowground tissues was sufficient to affect P pools as well as N/P ratios. Whereas C and N aboveground pools were higher than belowground ones, reflecting biomass patterns, P pools were similar between both tissues, suggesting that the higher concentration of P in belowground tissues compensated the lower biomass. Regarding N/P ratio, we found a significant difference between above and belowground tissues (~20 versus 12, respectively), which would indicate different nutrient limitations. Usually, N/P ratios > 16 suggest P limitation while N/P ratios < 14 are indicative of N limitation (Güsewell and Koerselman, 2002; Koerselman and Meuleman, 1996). Hence, *S. perennis* belowground tissues are limited by N but aboveground ones by P, suggesting resource allocation in terms of biomass or metabolic pathway, as proposed by Darby and Turner (2008) who found an opposite pattern in *Spartina alterniflora* in Louisiana.

Decomposition rates were high for both types of tissues meaning this process play a significant role in the cycling of organic matter in the study area. The annual decomposition rate for aboveground material (more than the 65% of the initial biomass) is an intermediate

Table 2
C, N and P pools (g m^{-2}) of *S. perennis* (n = 7; mean ± SE). The highest value in each column (between above- and belowground tissues) is in bold and marked with an asterisk if it is significantly higher.

	C	N	P
Aboveground tissues	**155.5* ± 17.66**	**3.974* ± 0.6330**	**0.2521 ± 0.0635**
Belowground tissues	102.87 ± 13.00	2.425 ± 0.3216	0.2133 ± 0.0366
Total	257.8 ± 23.71	6.3897 ± 0.7899	0.4648 ± 0.0700

Fig. 3. Seasonal dynamics of aboveground and belowground pools of a) carbon, b) nitrogen and c) phosphorus.

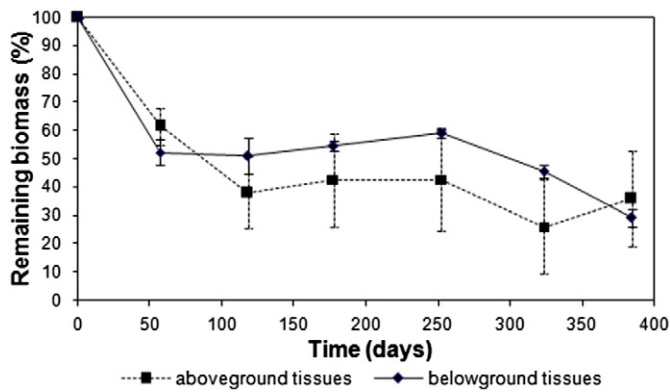**Fig. 4.** Remaining biomass in the litterbag experiment for aboveground and belowground tissues (2 ≤ n ≤ 4; mean ± SE).

value compared to those reported for woody (~30%) and non-woody (~90%) stems of the closely related species *Sarcocornia fruticosa* (Curcó et al., 2002; Scarton et al., 2002). Taking into account that in this study we took all the aboveground tissues together, the values are comparable. On the other hand, belowground tissues showed a higher decomposition rate (~70%) than the estimated for roots of *S. fruticosa* (~30%) (Curcó et al., 2002; Scarton et al., 2002). The differences may be associated with environmental conditions as climate, flooding, marsh elevation, etc. (e.g., Conteaûx et al., 1995; Menendez and Sanmartí, 2007). Decomposition rates for *S. alterniflora* (Negrin et al., 2012b) were lower than the reported here, meaning that, within this estuary, this process has different significance according to the dominant species.

The concentration of C, N and P and the C/N and C/P ratios in both tissues varied during decomposition, as has been observed in other studies (e.g., Menendez and Sanmartí, 2007; Negrin et al., 2012b; Simões et al., 2011; Tong et al., 2011). This could be related to the alternate activity of different groups of decomposers at different moments and the
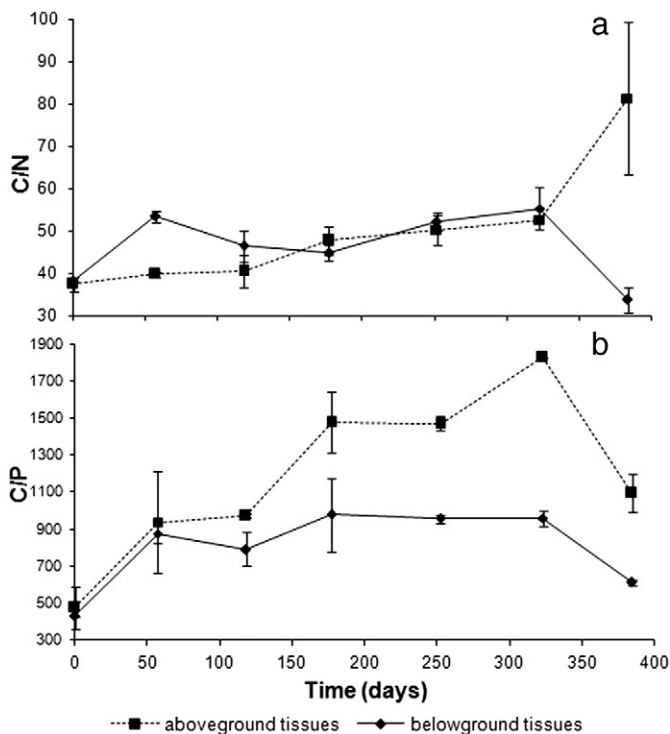
consequent effect on the rate of mineralization of nutrients (Anesio et al., 2003). However, the final ratios were higher than the initial ones, except for C/N in belowground tissues. This means that there is a net release of P by both tissues and of N by aboveground ones, showing the importance of decomposition in the recycling of nutrients. N in belowground tissues is being immobilized, probably because of the bounding of exogenous N, mediated by microbial activity, to plant constituents (Pozo and Colino, 1992; Simões et al., 2011). The differences in N behavior between above and belowground tissues might be associated with differences in C/N ratios and nutrient limitation. Belowground tissues were N limited and thus N was immobilized, whereas in aboveground tissues, where the most limiting nutrient was P, N retention was not necessary (Simões et al., 2011). The different patterns of N and P release could be due to the fact that N remineralization is strictly microbially mediated whereas phosphorus may be remineralized autolytically (Pozo and Colino, 1992).

Our results showed the importance of *S. perennis* in the cycling of C, N and P in Bahía Blanca salt marshes through the incorporation of these elements in plant biomass and their later release after decomposition. This reinforces the role of this species in the biogeochemical dynamics of salt marshes, as previously stated from a different point of view (Negrin et al., 2013). Considering the total area covered by *S. perennis* in the Bahía Blanca estuary (203.8 km², Isacch et al., 2006), and assuming that the same values for mean biomass and C, N and P concentrations apply to the whole estuary, 31,709 ton of C, 796 ton of N and 48 ton of P would be temporarily stored in plant aboveground biomass. These nutrients might reenter the system upon plant death and decomposition and may have an impact on detrital food webs. On the other hand, 20,764 tons of C, 501 tons of N and 44 tons of P would be accumulated in belowground tissues and part of them, upon plant death and decomposition, might get stored as soil organic matter, locked away from the estuarine dynamics in the short term. The storage in the soil organic compartment, however, is vulnerable to erosive processes, and *S. perennis* marshes in the Bahia Blanca estuary are being lost to erosion at a rate of about 0.87% per year, equivalent to 267 ha y⁻¹ (Pratolongo et al., 2013). The consequences of these losses on the estuarine nutrient dynamics are still to be estimated.

Fig. 5. C/N (a) and C/P (b) fluctuations in the litterbag experiment for aboveground and belowground tissues (2 ≤ n ≤ 4; mean ± SE).

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