Aquatic Botany 120 (2014) 201–204

Contents lists available at ScienceDirect

Aquatic Botany

journal homepage: www.elsevier.com/locate/aquabot

Biomass dynamics of the two dominant SW Atlantic *Spartina* species and its implications on the saltmarsh organic matter accumulation/exportation

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ARTICLE INFO

Article history:
Received 18 September 2013
Received in revised form 20 May 2014
Accepted 27 May 2014
Available online 4 June 2014

Keywords:
Aboveground biomass
Primary production
Mortality
Spartina alterniflora
Spartina densiflora

ABSTRACT

We present a comparative analysis of the biomass dynamics of the two dominant *Spartina* plant species in South West Atlantic saltmarshes: *Spartina densiflora* Brong. (high intertidal zone) and *Spartina alterniflora* Loesel. (mid-low intertidal zone). We assessed aboveground biomass, live: dead ratios, net production, mortality and turnover rates, and then used this information to understand if saltmarshes dominated by one or the other *Spartina* species have different ecosystemic roles in the recycling of organic matter. Through field sampling we found that *S. densiflora* had larger live, dead and total biomass than *S. alterniflora*. When comparing within each species, *S. alterniflora* had larger live than dead biomass for most of the year, while *S. densiflora* had more dead than live biomass. Through the Weigert and Evans (1964) net aerial primary production (NAPP) estimating method we found *that S. densiflora* had larger annual NAPP, annual mortality and live turnover rates than *S. alterniflora*. In both species the amount of NAPP was similar to the amount of annual mortality. These results suggest that *S. densiflora* aboveground biomass is a carbon accumulation zone, while *S. alterniflora* is a carbon recycling one.

1. Introduction

Saltmarsh biomass, primary production, organic matter recycling and exportation, can change within short distances and in an abrupt way. There are examples worldwide showing differences of more than double *Spartina* aboveground biomass between high and low intertidal saltmarsh zones (e.g. Kirby and Gosselink, 1976 for Barataria Bay, USA; Linthurst and Reimold, 1978 for Maine, USA; Liao et al., 2007 for Yangtze Estuary, China). There are similar differences for other saltmarsh species in high and low intertidal zones (e.g. Bouchard and Lefeuvre, 2000 for Mont Saint Michel Bay, France; Cattrijsse and Hampel, 2006 for most of North Sea and European Atlantic saltmarshes). Moreover, these differences in biomass between intertidal zones are accompanied by differences in organic matter recycling and exportation (Bouchard and Lefeuvre, 2000; see Elsey-Quirk et al., 2011). Thus, the need for independent studies of high- versus low-saltmarsh intertidal zones. Furthermore, saltmarshes in each world region have characteristic plant species assemblages (Adam, 1990), and understanding how these plant assemblages behave provide insights on regional saltmarsh ecological functions in organic matter recycling.

South West Atlantic saltmarshes have two *Spartina* species: the dense-flowered cordgrass *Spartina densiflora* Brong. (high intertidal zone) and the smooth cordgrass *Spartina alterniflora* Loesel. (mid-low intertidal zone; Isacch et al., 2006). Both species coexist with either one or the other being dominant (i.e. in the sense of extension of area occupied depending upon the site). In *S. densiflora* dominated saltmarshes, this species has larger aboveground biomass and detritus production, while in *S. alterniflora* dominated saltmarshes both species have similar amounts (Montemayor, 2012; Montemayor et al., 2013). Moreover, *S. densiflora* shows lower decomposition rates and smaller amount of detritus exportation

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http://dx.doi.org/10.1016/j.aquabot.2014.05.017
0304-3770/

(Montemayor et al., 2011). All these results suggest that *S. densiflora* dominated saltmarshes have larger aboveground biomass accumulation and *S. alterniflora* ones larger aboveground biomass recycling (Montemayor et al., 2013). These patterns should be the result of different net aerial primary production (hereafter NAPP), mortality, turnover rate and interaction with the environment. Knowing how these processes differ will give us a better understanding of the organic matter role of each type of saltmarsh. The NAPP studies that exist to date have focused on either one or the other species and have taken place at different South West Atlantic latitudes (*S. alterniflora*: 25°16′ S, Da Cunha Lana et al., 1991; 38°51′ S, González Trilla et al., 2009; 38°51′ S, Negrin et al., 2012; *S. densiflora*: 37°45′ S, Vera et al., 2009; 32°07′ S, Peixoto and Costa, 2004; 34°10′ S, Vicari et al., 2002; 37°45′ S, González Trilla et al., 2010). Thus, differences between the two species can be due to latitudinal changes of abiotic factors, and not to differences between the two species. In this context, our purpose is to compare within the same saltmarsh NAPP, mortality, turnover rates and aboveground biomass of both *Spartina* species.

2. Materials and methods

2.1. Study site

The study was conducted in a saltmarsh located at the Bahia Blanca estuary (38°47′ S, 62°20′ W, Argentina). It is one of the largest South West Atlantic saltmarshes (Isacch et al., 2006) and has both *Spartina* species, *S. alterniflora* (low intertidal zone) and *S. densiflora* (high intertidal zone; Bortolus, 2006; Isacch et al., 2006). This large shallow estuarine embayment shows tidal amplitudes of up to 4 m with hypersaline conditions (salinity range of 17.3–41.9; Freije and Marcovecchio, 2004).

2.2. Aboveground biomass

To estimate aboveground biomass, ten permanent sampling sites (5 m × 5 m each) were randomly chosen in *S. alterniflora* and another ten in *S. densiflora* saltmarsh zones. In each sampling site, in November of the year 2007, and in January, February, March, April, June, July, August, September, October and November of the year 2008, ten random quadrats of 0.3 m × 0.3 m of aerial biomass were harvested (i.e. 10 replicates). To minimize differences due to plant cover and because *S. densiflora* has a patchy distribution, the sampling was performed where there was 100% plant cover. The harvested biomass was separated into live and dead biomass, and then dried at 70 °C to a constant weight, and then weighed (0.1 g precision). Live to dead ratio was estimated for both species in each sampled month. The null hypothesis of no difference on aboveground biomass and on live: dead ratios were evaluated independently by a Repeated measures ANOVA with the between factor “Plant Species” (fixed), the within factor “Months” (fixed) and the subject factor “Sampling sites” (random). The analyses for aboveground biomass were performed separately for live, dead and total biomass (i.e. three ANOVAs). Hereafter when normality and homoscedasticity assumptions were not met data were transformed. For dead aboveground biomass, even when transformations were applied, the homoscedasticity assumption was not met. Thus, in order to reduce the probability of committing type I error in the ANOVA, the differences were considered significant if $p < 0.005$ (Zar, 1999; see Antón et al., 2011; Alberti et al., 2011 for similar approaches). To identify further differences an a posteriori Tukey test was performed for the main factors when no interaction was found and for the interaction of the factors when interaction was found (Underwood, 1997).

2.3. Mortality, NAPP and turnover rates

S. alterniflora and *S. densiflora* mortality and NAPP estimations were done using the Weigert and Evans (1964) method. This method takes into account the disappearance of dead material by means of the contiguous pair plot method (Weigert and Evans, 1964), which consists of a second quadrat next to the first quadrat used for aboveground biomass estimation (see Section 2.2). This second quadrat of 0.3 m × 0.3 m (10 replicates) was selected at the same time as the first, but only its live biomass was harvested. After about two months (between 44 and 64 days given logistical constraints) the remaining dead standing biomass in the second quadrat (i.e. dead biomass) was harvested. In this second quadrat, dead biomass for the beginning of the interval was assumed to be the same as in the first. With this method the instantaneous daily rate of disappearance of dead material during an interval (r_i) (i.e. in our case about two months) was calculated and then used to estimate NAPP and mortality (Weigert and Evans, 1964). Furthermore, to estimate mortality of each species independently of its biomass, we standardized those values by calculating the ratio of annual mortality to the biomass of each species. Next, the null hypothesis of no difference between *S. alterniflora* and *S. densiflora* annual NAPP, annual mortality and the ratio of annual mortality to biomass were evaluated with a corrected t-test for unequal variances (Welch approximation t_c; Zar, 1999). The same statistical test was used to evaluate the null hypothesis of no difference between NAPP and mortality within each species (i.e. *S. alterniflora* and *S. densiflora* separately).

The live turnover rate was estimated as the ratio between NAPP and the peak living standing biomass (10 replicates, one for each sampling site; Linthurst and Reimold, 1978; Bouchard and Lefeuvre, 2000). The null hypothesis of no difference between *S. alterniflora* and *S. densiflora* live turnover rate was evaluated with a t_c test (Zar, 1999).

3. Results

3.1. Aboveground biomass

Live aboveground biomass was larger for *S. densiflora* than *S. alterniflora* ($F_{1,18} = 27.25$, $p < 0.05$; log transformed data; Fig. 1a). Both species had the largest biomass in April and the smallest biomass in July ($F_{10,180} = 4.58$, $p < 0.05$; Fig. 1a; post hoc Tukey tests results in Table 1)

Dead aboveground biomass showed interaction between factors (Plant Species × Months; interaction: $F_{10,180} = 15.31$, $p < 0.005$; log transformed data; Fig. 1b). *S. densiflora* had larger dead biomass than *S. alterniflora* except for September and November 2008 when both plants had similar biomass. *S. alterniflora* had the largest dead biomass in September, October and November 2008 and the smallest in March. *S. densiflora* had the largest aboveground biomass in April and the smallest in November 2008 (post hoc Tukey tests results in Table 1).

Total aboveground biomass had interaction between factors (Plant Species × Months; interaction: $F_{10,180} = 3.91$, $p < 0.05$; log transformed data; Fig. 1c). For all the months *S. densiflora* had larger total biomass than *S. alterniflora*, except in September and November 2008, when both species had similar amounts. No differences were found for *S. alterniflora* total biomass throughout the different months, while for *S. densiflora* April was the month with the largest biomass and November 2008 with the smallest (post hoc Tukey tests result in Table 1).

Live: dead biomass ratios showed interaction between factors (Plant Species × Months; interaction: $F_{10,180} = 18.21$, $p < 0.05$; log transformed data; Fig. 1d). In all the months *S. alterniflora* had a

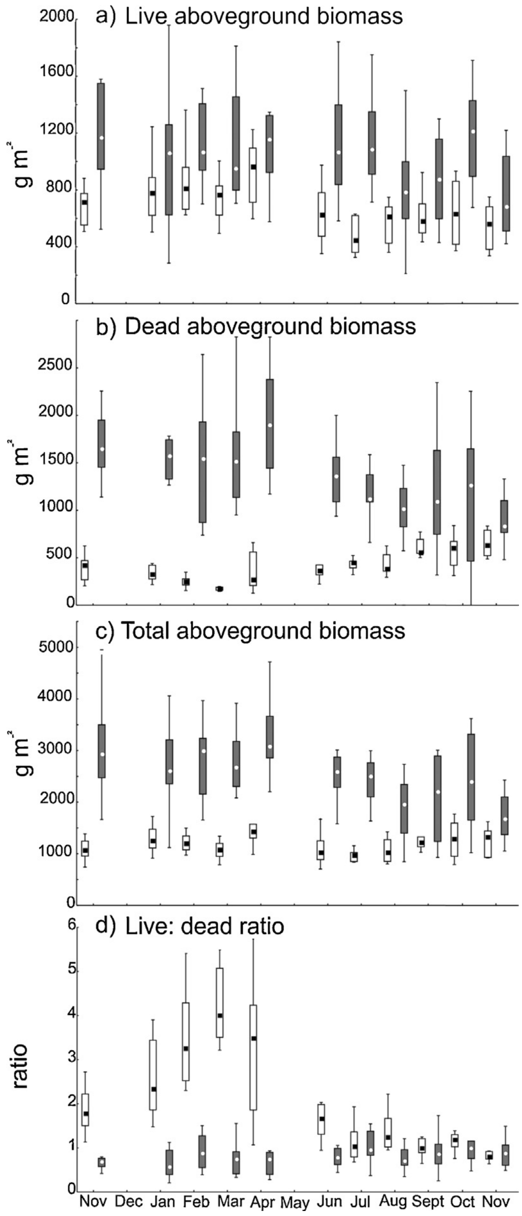

Fig. 1. (a) Live, (b) dead, and (c) total aboveground biomass (g m^{-2}) and (d) live: dead ratio of *S. alterniflora* (white boxes) and *S. densiflora* (grey boxes) from November 2007 to November 2008. Box plots were constructed with vertical lines that represent 0.01 and 0.99 percentiles, box limits were the 0.25 and 0.75 percentiles, and symbols within boxes were the median. All data are presented prior to transformations.

larger live: dead ratio than *S. densiflora*, except for July when both species had similar ratios. *S. densiflora* always had more dead than live biomass (ratios under 1) except for July and October when amounts of live and dead biomass were similar (ratios near 1). *S. alterniflora* had larger live than dead biomass (ratio over 1) for the months of November 2007 through June, while for the other half of 2008 both types of biomass where similar (ratio near 1).

3.2. Mortality, NAPP and turnover rates

S. densiflora had larger NAPP (*S. densiflora* mean = 3674.7 g m^{-2} $year^{-1}$, SD = 1331.3; *S. alterniflora* mean = 1792 g m^{-2} $year^{-1}$, SD = 572.3; $t_c = 4.1$, df = 12.2, $p < 0.05$) and mortality than *S. alterniflora* (*S. densiflora* mean = 4179 g m^{-2} $year^{-1}$, SD = 1563.9; *S. alterniflora* mean = 1481.7 g m^{-2} $year^{-1}$, SD = 523.1; $t_c = -5.2$, df = 11.0, $p < 0.05$).

Within *S. densiflora*, NAPP amounts were similar to those of mortality ($t_c = -0.8$, df = 18.0, $p > 0.05$). The same was found within *S. alterniflora* ($t_c = 1.3$, df = 18.0, $p > 0.05$).

When dividing mortality by the biomass of each species, we found that *S. densiflora* had larger standardized mortality than *S. alterniflora* (*S. densiflora* mean = 0.5 $year^{-1}$, SD = 0.0; *S. alterniflora* mean = 0.4 $year^{-1}$, SD = 0.05; $t_c = -3.8$, df = 16.5, $p < 0.05$).

Live turnover rates were lower for *S. alterniflora* than for *S. densiflora* (*S. alterniflora* mean = 1.9 $year^{-1}$, SD = 0.6; *S. densiflora* mean = 3.3 $year^{-1}$, SD = 1.2; $t_c = 3.2$, df = 12.7, $p < 0.05$).

4. Discussion

S. densiflora showed larger dead aboveground biomass when compared with *S. alterniflora* and when compared with its own live biomass. Similar results were found in an aboveground biomass study performed along six South West Atlantic saltmarshes (Montemayor et al., 2013). The larger *S. densiflora* NAPP, together with its similar mortality and production rates, could facilitate the accumulation of dead aboveground biomass. Moreover, larger *S. densiflora* aboveground biomass accumulation is accentuated by the fact that it is less exposed to tides (Montemayor et al., 2011), which results in lower exportation rates and larger dead biomass accumulation (see for a similar system Tang et al., 2012). In fact, in Cadiz (Spain) *S. densiflora* live: dead ratios were estimated for different saltmarsh types showing a trend towards higher ratio values for lower saltmarsh heights (Nieva et al., 2001). In addition, South West Atlantic *S. densiflora* dead aboveground biomass has been shown to be negatively correlated with tidal amplitude (Montemayor et al., 2013). Thus, its large production and mortality together with low tidal influence seem to be responsible for the dead aboveground biomass accumulation.

When comparing within *S. alterniflora*, this species has similar rates of production and mortality, thus similar amounts of live and dead biomass would be expected. However, for more than half of the year this species showed larger amounts of live than dead

Table 1
Tukey test results for live, dead and total biomass of *Spartina alterniflora* and *Spartina densiflora* in South West Atlantic saltmarshes: differences for the months of maximum and minimum biomass.

Spartina alterniflora	*Spartina densiflora*
Live biomass	
April **>** June–July–Aug–Sept–Oct–Nov’08	April > June–July–Aug–Sept–Oct–Nov’08
July **<** Jan–Feb–March	July< Jan–Feb–March
Dead biomass	
Sept–Oct–Nov’08 > Jan–Feb–March–Apr	April > Aug–Sept–Nov’08
March **<** Nov’07–Jan–Jun–Jul–Aug–Sep–Oct–Nov’08	Nov’08 < Nov’07–Apr
Total biomass	
No differences	April > Aug–Sept–Nov’08 Nov’08 < Nov’07–Apr–March–Feb–Nov’08

biomass. Tides could be responsible for this aboveground pattern (Tang et al., 2012). *S. alterniflora* is flooded by all high tides (Isacch et al., 2006) and in South West Atlantic saltmarshes detritus exportation is larger than for *S. densiflora* (Montemayor et al., 2011). In the USA saltmarshes, *S. alterniflora* live: dead ratio increases with increasing tidal amplitude (Turner, 1976), illustrating the effect that tides can have on dead aboveground biomass patterns. Thus, a large proportion of what *S. alterniflora* produces becomes dead biomass rapidly exported as macrodetritus or decomposed in the saltmarsh.

S. densiflora has larger live turnover rates, production and mortality than *S. alterniflora*, which suggests a larger nutrient recycling. However, it has lower live: dead ratios and larger aboveground biomass indicating as a final result C accumulation in the form of dead aboveground biomass. *S. alterniflora*, on the other hand, has less capacity to produce aboveground biomass. However, a large proportion goes through other paths such as exportation or decomposition (Montemayor et al., 2011). In Maine (USA) and Mont Saint Michel Bay (France) high saltmarsh species were found to have larger NAPP but inferior decomposition rates than low saltmarsh species, which led to larger aboveground biomass and C accumulation in high intertidal zones (USA: Linthurst and Reimold, 1978; Valiela et al., 1985; Elsey-Quirk et al., 2011; France: Bouchard and Lefeuvre, 2000). The Maine (USA) saltmarsh is similar to this Bahia Blanca study saltmarsh in its *Spartina* species assemblage (high saltmarsh *Spartina patens* and low saltmarsh *S. alterniflora*) and in the fact that low *S. alterniflora* aboveground biomass generates more of a nutrient recycling zone. On the other hand in a Yangtze Estuary saltmarsh (China) invasive *S. alterniflora* is mainly a C accumulation zone as it has larger NAPP and less decomposition rates than the native species *Scirpus mariqueter* and *Phragmites australis* (Liao et al., 2007). It is thus common to have different organic matter processes in a same saltmarsh, but depending on the assemblage of each saltmarsh the role of the species can vary.

In salmarshes along the South West Atlantic coast plant assemblage is consistently the same (*S. alterniflora* and *S. densiflora*), but the areas occupied by each species change from saltmarsh to saltmarsh (Isacch et al., 2006). This, together with our results and their agreement with the aboveground biomass patterns of South West Atlantic saltmarshes (Montemayor et al., 2013) suggest that the ecosystemic role of each saltmarsh changes depending on species dominance: *S. densiflora* dominance leads to aboveground biomass C accumulation processes, while *S. alterniflora* dominance leads to aboveground biomass C recycling.

Acknowledgements

We thank Maria Cielo Bazterrica, Agustina Mendez Casariego, Mauricio Escapa and Paulina Martinetto for field assistance. We also thank Juan Alberti for his valuable suggestions on the statistical analysis and Ann Borsinger for language assistance. This project was supported by grants from the Universidad Nacional de Mar del Plata, CONICET, and ANPCyT (all to O.I.). D.M., M.A., F.A. by a scholarship from CONICET (Argentina). This is part of the Doctoral thesis of D.M.

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