

Primary Production and Nutrient Content in Two Salt Marsh Species, *Atriplex portulacoides* L. and *Limoniastrum monopetalum* L., in Southern Portugal

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ABSTRACT: Seasonal variation patterns of aboveground and belowground biomass, net primary production, and nutrient accumulation were assessed in *Atriplex portulacoides* L. and *Limoniastrum monopetalum* (L.) Boiss. in Castro Marim salt marsh, Portugal. Sampling was conducted for five periods during 2001–2002 (autumn, winter, spring, summer, and autumn). This study indicates that both species have a clear seasonal variation pattern for both aboveground and belowground biomass. Mean live biomass was $2516 \text{ g m}^{-2} \text{ yr}^{-1}$ for *L. monopetalum* and $598 \text{ g m}^{-2} \text{ yr}^{-1}$ for *A. portulacoides*. Peak living biomass, in spring for both species, was three times greater in the former, $3502 \text{ g m}^{-2} \text{ yr}^{-1}$, than in the latter, $1077 \text{ g m}^{-2} \text{ yr}^{-1}$. For both the Smalley (Groenendijk 1984) and Weigert and Evans (1964) methods, productivity of *L. monopetalum* (2917 and $3635 \text{ g m}^{-2} \text{ yr}^{-1}$, respectively) was greater than that of *A. portulacoides* (1002 and $1615 \text{ g m}^{-2} \text{ yr}^{-1}$, respectively). Belowground biomass of *L. monopetalum* was 1.7 times greater than that of *A. portulacoides*. In spite of this, the root:shoot ratio for *A. portulacoides* was greater throughout the year. This shows that *A. portulacoides* allocates more biomass to roots and *L. monopetalum* to aerial components. Leaf area index was similar for both species, but specific leaf area of *A. portulacoides* was twice that of *L. monopetalum*. The greatest nutrient contents were found in leaves. Leaf nitrogen content was maximum in summer for both species (14.6 mg g^{-1} for *A. portulacoides* and 15.5 mg g^{-1} for *L. monopetalum*). Leaf phosphorus concentration was minimum in summer (1.1 mg g^{-1} in *A. portulacoides* and 1.2 mg g^{-1} in *L. monopetalum*). Leaf potassium contents in *A. portulacoides* were around three times greater than in *L. monopetalum*. Leaf calcium contents in *L. monopetalum* were three times greater than in *A. portulacoides*. There was a pronounced seasonal variation of calcium content in the former, while in the latter no clear variation was registered. Both species exhibited a decrease in magnesium leaf contents in the summer period. Manganese content in *L. monopetalum* leaves was tenfold that in *A. portulacoides*. Seasonal patterns of nutrient contents in *A. portulacoides* and *L. monopetalum* suggest that availability of these elements was not a limiting factor to biomass production.

Introduction

Salt marshes are generally considered among the most productive ecosystems in the world, despite constant stress conditions such as water deficit and salinity excess (Adam 1990; Hughes and Paramor 2004). Biomass and productivity of coastal wetlands are good indicators of vegetation health, enhancing the importance of such knowledge to the functioning of the overall ecosystem (Pont et al. 2002). Factors such as competition, salinity, degree of waterlogging, and nutrient status play important roles in regulating productivity (De Leeuw et al. 1990; Gross et al. 1990; Pennings and Callaway 1992; Pont et al. 2002).

Several studies assessing aboveground and belowground biomass, as well as annual net primary production of salt marsh species, have already been made. These studies centered mainly on species of *Spartina* (Gallagher et al. 1980; Schubauer and

Hopkinson 1984; Cranford et al. 1989; Gross et al. 1990, 1991), *Juncus* (De Leeuw et al. 1990; Hsieh 1996), or *Arthrocnemum* (Percy and Ulstin 1984; Curcó et al. 2002; Pont et al. 2002), and few concerned *Atriplex* spp. (Groenendijk 1984; Groenendijk and Vink-Lievaart 1987; Bouchard et al. 1998; Khan et al. 2000) or *Limoniastrum* spp. (Daoud et al. 2001), even though they are characteristic of many salt marshes.

Salt marsh halophytic species differ widely in the extent to which they accumulate ions and their overall degree of salt tolerance (Khan et al. 2000; Munns 2002). Generally, potassium (K) is accumulated in response to low soil moisture, while sodium (Na) is accumulated under saline conditions to create and maintain water potential gradients and turgor necessary for water uptake and growth (Flowers et al. 1977; Gorham et al. 1980; Donovan et al. 1997). The uptake and accumulation of Na interacts with the cation macronutrients, K, calcium (Ca), and magnesium (Mg), often leading to relatively small leaf ratios of this cation, resulting in foliar deficiencies (Albert and Popp 1977;

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Gorham et al. 1980; Gul et al. 2000). Different species play different roles in nutrient accumulation, balance, and cycling. Knowledge on species functioning and role is important to increase understanding of the interaction of salt and nutrients in halophytes. Information on chemical compositions of Mediterranean salt marsh species is scarce, and studies dealing with *Atriplex* and *Limoniastrum* species are even more limited.

Climate change predictions for the Mediterranean include increased air temperatures and drought (Miranda et al. 2002). The processes regulating carbon and nutrient budgets are highly influenced by these conditions. This is particularly relevant for salt marsh communities, as they are already subjected to constant physiological water stress. It is desirable to assess salt marsh species adaptability to environmental constraints to improve management techniques to reduce potential damaging effects of climate change.

Atriplex portulacoides L. and *Limoniastrum monopetalum* (L.) Boiss are among the four dominant plant species with an overall distribution in Castro Marim salt marsh, Portugal. They cover extensive areas and are key species to the conservation of marsh wildlife. Detailed information on their functioning and role within the ecosystem is scarce, especially regarding *L. monopetalum*. The assessment of their productivity and biomass allocation patterns, as well as nutrient cycling, will provide novel and needed knowledge, clearly lacking at the present, but crucial to the understanding of their functional ecology and to the development of appropriate management strategies.

The main objectives of this study were to evaluate seasonal variation patterns of aboveground and belowground biomass, to assess and compare net primary production through two evaluation methods, to assess and compare litter decomposition rates, and to determine the seasonal variation of nutrient contents (nitrogen [N], phosphorus [P], K, Ca, Mg, and manganese [Mn]) in *A. portulacoides* and *L. monopetalum*. We expect to find out whether these species differ in adaptiveness to salt and water stress.

Study Site

The study was carried out in Reserva Natural do Sapal de Castro Marim e Vila Real de S^o António, in southeast Portugal (37°13'N, 7°26'W), an area that is protected under the RAMSAR International Convention and the European Directives for HABITATS and CORINE. This reserve covers 2087 ha, 28% of which are salt marshes between the Guadiana River and the Atlantic Ocean. The morphology of the reserve is mostly flat with an

altitude ranging from 0 to 5 m above the mean sea level.

The area has a Mediterranean climate, characterized by a dry period in summer (Rivas-Martínez 1981), with a mean annual precipitation of 492 mm and a mean temperature of 17.2°C. In the sampling year (autumn 2001–autumn 2002) total precipitation was 593 mm, and the monthly maximum precipitation, 100 mm, was registered in September 2002; maximum and minimum absolute temperatures were 35.9°C in July and 5.8°C in December, respectively (Vila Real de Santo António Meteorological Station unpublished data).

The soils, of alluvium origin, are hallomorphic (Lousã 1986) with high lime and organic matter. There are no significant differences in the composition of soils occupied by the two species.

The vegetation shows a clear vertical zonation according to the frequency of inundation and the characteristics of the soil (Lousã 1986). In the low marsh, *Spartina maritima* (Curtis) Fernald and *Spartina densiflora* Brong are the dominant species. In the middle marsh, the vegetation is dominated by *A. portulacoides*, followed by *Arthrocnemum perenne* (Miller) Moss., *Arthrocnemum glaucum* (Delile) Ung-Sternb., and *Arthrocnemum fruticosum* (L.) Moq. The high marsh is dominated by *L. monopetalum*, followed by *Suaeda vera* Forssk. ex Gmelin.

Material and Methods

Two salt marsh species, *A. portulacoides* and *L. monopetalum*, were selected. *A. portulacoides* is an evergreen Chenopodiaceae, ranging 20–50 cm in height, which colonizes the lower and mid marsh, while *L. monopetalum*, an evergreen Plumbaginaceae, ranging 50–120 cm in height, colonizes the upper marsh.

Sampling was conducted for five periods during 2001–2002 (autumn-2001, winter-2001, spring-2002, summer-2002, and autumn-2002). In the beginning of the study, 15 similar individuals (in age and structure) of each species were selected and labelled. At each sampling date, aboveground biomass of three individuals per species was harvested from a square column (50 × 50 cm on a side). Total collected biomass (alive and dead) from each column was separated into live leaves, dead leaves, live stems, dead stems, and reproductive organs. Plant material was oven dried for 48 h at 80°C to a constant mass, and the dry weights of all fractions were obtained. Leaf area was measured in a subsample of each plant leaf fraction using a LI-3000A Portable Area Meter.

At the same sampling dates and beneath the same shrubs used for aboveground biomass estimates, belowground biomass was sampled through the extraction of three soil cores (8 cm diameter) per

plant (nine cores per species), to a depth of 15 cm, with a thin-wall, sharpened stainless steel tube. After separation from the soil material, the roots of each core were dried and weighed similar to above-ground biomass.

Litter was collected and placed in nylon mesh bags at each site, according to the Bock and Gilbert (1957) litterbag method, to assess the decomposition rates.

Samples of each component (aboveground and belowground biomass), collected from autumn-2001 to summer-2002, were pooled and a subsample taken for chemical analysis. Subsamples were ground and analyzed for nutrient (N, P, K, Ca, Mg, and Mn) concentrations. N was determined by the modified Kjeldahl method (Bremner and Mulvaney 1982). Ca, Mg, K, and P were acid-digested before quantification. Ca, Mg, Mn, and K were determined by atomic absorption spectrophotometry. P was estimated by colorimetry followed by UV-V spectrophotometry according to Murphy and Riley (1962) and adapted by Watanabe and Olsen (1965).

Specific leaf area (SLA) was calculated by the ratio of leaf area to leaf dry weight. Leaf area index (LAI) was calculated by the ratio of total plant leaf area to the canopy cover projected on the ground (2500 cm²).

Seasonal aboveground relative growth rate (RGR) was calculated for each sampled individual as:

$$\text{RGR} = (\ln DW_s - \ln DW_{s-1})/t$$

where DW_s is the dry weight of aboveground biomass in a particular season, DW_{s-1} is the dry weight of aboveground biomass in the previous season, and t is the time period in days (90). For each species and growth season, the three individuals sampled were averaged.

Aboveground production was estimated for both species using two methods: Smalley (described in Groenendijk 1984) and Weigert and Evans (1964).

Data of all biomass fractions (aboveground and belowground), SLA, LAI, root:shoot ratio, and relative growth rate were analyzed by analysis of variance/Kruskal-Wallis tests ($\alpha = 0.05$) and Tukey post-hoc tests, to compare species and sampling periods. SigmaStat for Windows version 3.1 was used to perform statistical analyses.

Results

ABOVEGROUND AND BELOWGROUND BIOMASS

Mean annual aboveground biomass was significantly different between species ($p < 0.05$), with *L. monopetalum* having a value (2516 g m⁻² yr⁻¹) approximately four times greater than *A. portulacoides* (598 g m⁻² yr⁻¹), but the amounts determined for

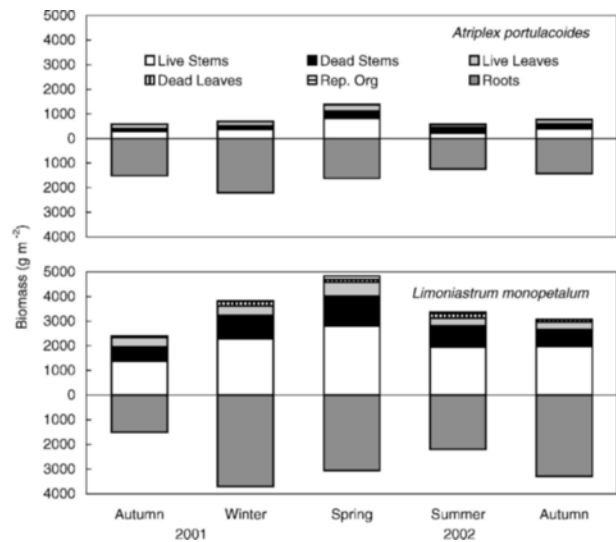


Fig. 1. Seasonal variation of aboveground and belowground biomass in *Atriplex portulacoides* and *Limoniastrum monopetalum*.

each species did not differ significantly ($p > 0.05$) throughout the year (Fig. 1). Aboveground live biomass was maximum in spring for both species (1077 g m⁻² yr⁻¹ for *A. portulacoides* and 3502 g m⁻² yr⁻¹ for *L. monopetalum*; Fig. 1 and Table 1). Biomass of all components decreased thereafter.

Mean annual belowground biomass was also significantly different between the two species, with a value for *L. monopetalum* (2752 g m⁻² yr⁻¹) around twice that of *A. portulacoides* (1601 g m⁻² yr⁻¹; Fig. 1 and Table 1). Significant differences ($p < 0.05$) in root biomass per season were recorded only in summer-2002 and autumn-2002. Differences found for belowground biomass of each species over the sampling dates were not significant ($p > 0.05$).

TABLE 1. Mean aboveground live biomass, peak aboveground live biomass, mean belowground live biomass, annual net primary production (in accordance with Smalley and Weigert-Evans methods), and turnover rates in *Atriplex portulacoides* and *Limoniastrum monopetalum*. Values with different letters in a row are significantly different ($p < 0.05$).

	<i>A.</i> <i>portulacoides</i>	<i>L.</i> <i>monopetalum</i>
Mean aboveground live biomass (g m ⁻²)	598 ^a	2516 ^b
Peak aboveground live biomass (g m ⁻²)	1077 ^a	3502 ^b
Mean belowground live biomass (g m ⁻²)	1601 ^a	2752 ^b
Annual net primary production (g m ⁻² yr ⁻¹)		
Smalley	1002	2917
Weigert-Evans	1615	3635
Turnover rates (yr ⁻¹)	0.96	0.86

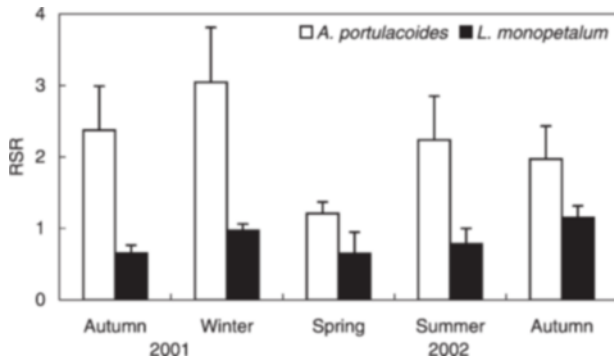


Fig. 2. Seasonal variation of the root:shoot ratio (RSR) in *Atriplex portulacoides* and *Limoniastrum monopetalum* (means \pm SE).

Mean root:shoot ratio (Fig. 2) was significantly different between species ($p < 0.001$), with the values obtained for *L. monopetalum* less than one half of those for *A. portulacoides*. For each species, there were no seasonally significant differences ($p > 0.05$) between this ratio.

Live stems were the main component of total aboveground biomass for both species, with 50% in *A. portulacoides* and 60% in *L. monopetalum*. The proportions of live leaf biomass were 23% and 12% of the total, respectively. Dead stems accounted for 25% of total aboveground biomass in both species. The greatest proportions of live leaves were obtained in autumn-2001 (31% for *A. portulacoides* and 16% for *L. monopetalum*) while the greatest live stem proportions were found in spring-2001 (60%) for the former and autumn-2002 (65%) for the latter (Fig. 1).

LAI values of the two species were not significantly different ($p > 0.05$), except in autumn-2002 (Fig. 3) when the value for *A. portulacoides* (1.31) almost doubled that of *L. monopetalum* (0.75). LAI of both species decreased significantly in summer-2002 (0.60). SLA was much smaller for *L. monopetalum* (less than one half) than for *A. portulacoides*. Minimum values were obtained in the summer period for both species ($54.15 \text{ cm}^2 \text{ g}^{-1}$ for *A. portulacoides* and $19.65 \text{ cm}^2 \text{ g}^{-1}$ for *L. monopetalum*).

Significant differences ($p < 0.05$) between species were obtained in aboveground relative growth rate in the autumn-winter and winter-spring periods (Table 2). Maximum aboveground relative growth rate was obtained in the winter-spring period for *A. portulacoides* ($7.88 \pm 0.98 \text{ g g}^{-1} \text{ d}^{-1}$) and in autumn-winter for *L. monopetalum* ($5.17 \pm 0.30 \text{ g g}^{-1} \text{ d}^{-1}$). Neither of the two species showed significant relative growth in the spring-summer period.

PRIMARY PRODUCTIVITY

Aboveground primary production of *L. monopetalum* was greater than that of *A. portulacoides*, either

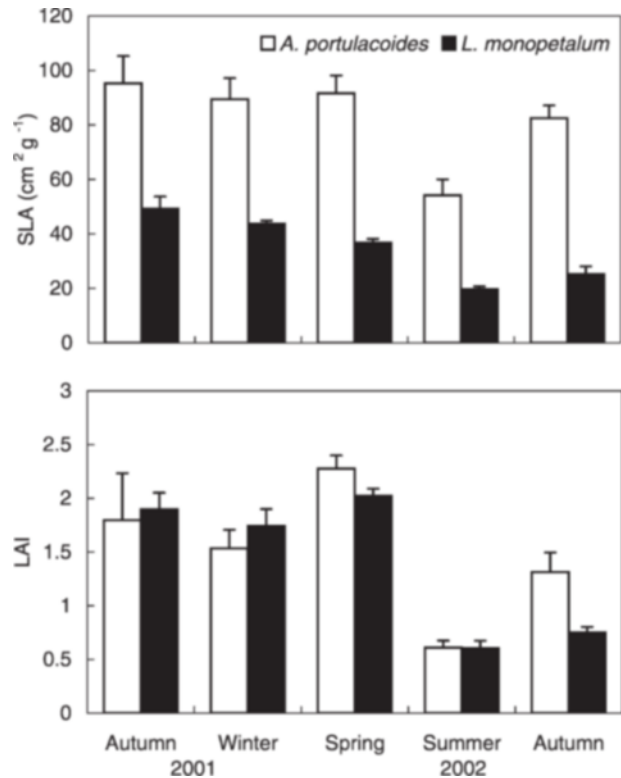


Fig. 3. Seasonal variation of specific leaf area (SLA) and leaf area index (LAI) in *Atriplex portulacoides* and *Limoniastrum monopetalum* (means \pm SE).

through the Smalley (Groenendijk 1984) or Weigert and Evans (1964) methods (Table 1). According to the Smalley method, the value obtained for *L. monopetalum* ($2917 \text{ g m}^{-2} \text{ yr}^{-1}$) was threefold that for *A. portulacoides* ($1002 \text{ g m}^{-2} \text{ yr}^{-1}$); Weigert and Evans method it was only around twice as high (3635 and $1615 \text{ g m}^{-2} \text{ yr}^{-1}$, respectively).

The turnover rate of aboveground live biomass (primary production/peak live biomass) was almost one for both species, although it was greater for *A. portulacoides* (0.96 yr^{-1}) than for *L. monopetalum* (0.86 yr^{-1} ; Table 1).

NUTRIENT CONTENTS

The seasonal dynamics of mineral elements, in the different organs of the plants (leaves, stems, and roots), are expressed in Figs. 4 and 5.

L. monopetalum leaves had greater N content than *A. portulacoides*, except in spring when similar values were obtained due to a marked decrease in *L. monopetalum*. The greatest concentrations were obtained in summer-2002 for both species (15 mg g^{-1} for *A. portulacoides* and 16 mg g^{-1} for *L. monopetalum*). Stem N content was also greater for *L. monopetalum* than for *A. portulacoides*, and the seasonal variation pattern was similar to that of leaves. Concentrations in

TABLE 2. Seasonal variation of aboveground relative growth rate (RGR) in *Atriplex portulacoides* and *Limoniastrum monopetalum* [mean (\pm SE)]. Values with different letters in a column are significantly different ($p < 0.05$).

RGR ($\text{mg g}^{-1} \text{d}^{-1}$)	Autumn-winter	Winter-spring	Spring-summer	Summer-autumn
<i>A. portulacoides</i>	2.00 (0.47) ^a	7.88 (0.98) ^a	0.00 ^a	2.95 (1.28) ^a
<i>L. monopetalum</i>	5.17 (0.30) ^b	2.82 (1.31) ^b	0.00 ^a	0.00 ^a

roots were very similar for both species and did not change greatly over the year.

Leaves of both species had the highest P concentrations, and similar to N, *L. monopetalum* leaves and stems had greater P concentrations than those of *A. portulacoides*. For *L. monopetalum* there was a decrease of leaf and stem concentrations in summer-2002 (1.2 and 1.0 mg g^{-1} , respectively). For *A. portulacoides* leaves, there also was a decrease in this season (1.1 mg g^{-1}). P concentration in the stems of *A. portulacoides* was maximum in summer-2002 (1.0 mg g^{-1}). Root P contents were slightly greater in *A. portulacoides* than in *L. monopetalum*, and there was little variation during the year.

Unlike N and P, concentrations of K in *A. portulacoides* leaves were around three times greater

than those in *L. monopetalum*. The maximum values were observed in autumn-2001 for the former (25 mg g^{-1}) and in summer-2002 for the latter (11 mg g^{-1}). Minimum values (17 and 7 mg g^{-1}) were obtained in summer and winter, respectively. The variation of stem K concentrations was opposite to that of leaves. In *A. portulacoides* the maximum was found in summer-2002 (12 mg g^{-1}), while in *L. monopetalum* it was observed in autumn-2001 (10 mg g^{-1}). Root contents ranged from 3 to 5 mg g^{-1} in both species, with no marked oscillation.

Ca contents in *L. monopetalum* leaves were around three times greater than in *A. portulacoides*. An increase was observed in the former during winter-2001 (26 mg g^{-1}), followed by a pronounced decrease in spring-2002 (16 mg g^{-1}), while there was an insignif-

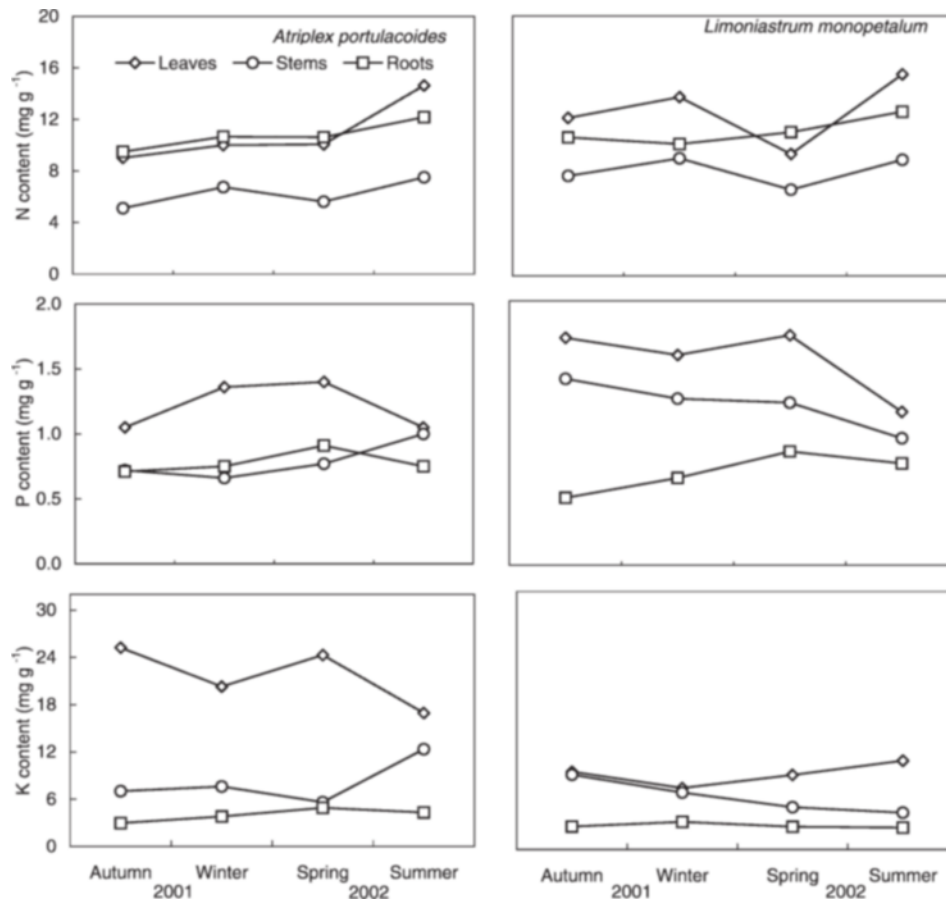


Fig. 4. Seasonal patterns of N, P, and K contents in leaves, stems, and roots of *Atriplex portulacoides* and *Limoniastrum monopetalum*.

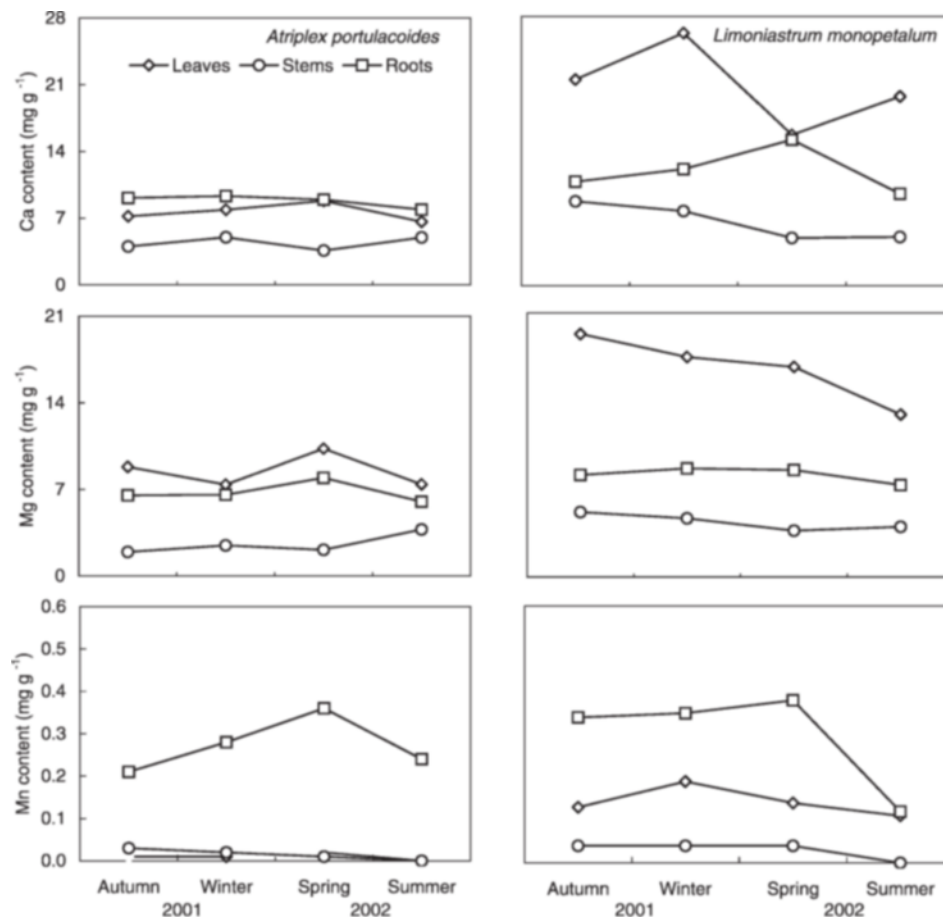


Fig. 5. Seasonal patterns of Ca, Mg, and Mn contents in leaves, stems, and roots of *Atriplex portulacoides* and *Limoniastrum monopetalum*.

icant variation in *A. portulacoides* (between 7 and 9 mg g⁻¹). During the dry period, stem Ca was similar for both species. In the rainy season, concentrations in *L. monopetalum* stems were twice those in *A. portulacoides*. The most pronounced difference between root Ca contents was observed in spring-2002, with *L. monopetalum* showing a value twice that of *A. portulacoides* (15 and 9 mg g⁻¹, respectively).

The greater Mg concentrations were found in leaves, followed by roots and stems for both species. *L. monopetalum* leaf and stem Mg contents were twice those of *A. portulacoides*. In the former, leaf contents ranged from 20 mg g⁻¹ in autumn-2001 to 13 mg g⁻¹ in summer-2002, while there was no marked oscillation in the latter (7-10 mg g⁻¹). Root Mg contents ranged from 7 to 9 mg g⁻¹, for both species.

Concentrations of Mn in roots were greater than in aboveground fractions. Following the general trend, Mn contents were greater for *L. monopetalum* than for *A. portulacoides*, in both leaves (10 times) and stems (twice). Concentrations in roots were similar for both species.

Discussion

ABOVEGROUND AND BELOWGROUND BIOMASS

There are few studies regarding the dynamics of aboveground and belowground biomass of *A. portulacoides* (Groenendijk 1984; Groenendijk and Vink-Lievaart 1987; Bouchard and Lefeuvre 1996, 2000; Bouchard et al. 1998), and to our knowledge, none for *L. monopetalum*. The values obtained for aboveground biomass of both studied species are within the range reported for other salt marsh species (Gallagher et al. 1980; Groenendijk 1984; De Leeuw et al. 1990; Gross et al. 1991; Bouchard et al. 1998). Mean aboveground biomass of *L. monopetalum* (2516 g m⁻² yr⁻¹) was much greater than that of *A. portulacoides* (598 g m⁻² yr⁻¹; Table 1). Biomass and production increased along the vertical gradient of the salt marsh, with the upper marsh species showing the greatest values, followed by the middle or lower marsh species, as found by Lefeuvre (1996).

The present study indicates that both species have a clear seasonal variation pattern for aboveground

and belowground biomass. Growth of both species began in autumn, as soon as the rainy season began, and lasted until summer. *L. monopetalum* reached its maximum growth rate ($5.17 \text{ mg g}^{-1} \text{ d}^{-1}$) in the autumn-winter period and *A. portulacoides* ($7.88 \text{ mg g}^{-1} \text{ d}^{-1}$) in winter-spring (Table 2). These differences are probably related to different soil salinity and flooding conditions of the two species, as the former is less subjected to flooding than the latter. Peak aboveground biomass was observed for both species in spring, despite the marked difference between mean amounts (Table 1). During summer, growth was prevented by increasing temperature, radiation, and water stress (Fig. 1). This pattern is consistent with observations on other salt marsh species: *Spartina alterniflora*, *Juncus roemerianus* (Gallagher et al. 1980), *Juncus maritimus*, *Juncus gerardii*, *Artemisia maritima* (De Leeuw et al. 1990), *Elytrigia aetherica* (Bouchard and Lefeuvre 2000), and *Arthrocnemum macrostachyum* (Curc3 et al. 2002).

The values determined for mean belowground live biomass are within the range obtained for other Mediterranean climate salt marsh species (Curc3 et al. 2002; Scarton et al. 2002). Similar to aboveground biomass, mean belowground biomass was greater for *L. monopetalum* ($2752 \text{ g m}^{-2} \text{ yr}^{-1}$) than for *A. portulacoides* ($1601 \text{ g m}^{-2} \text{ yr}^{-1}$), although the difference was less pronounced. These results indicate that *A. portulacoides* allocates greater resource amounts to roots than *L. monopetalum*, what is also emphasized by the root:shoot ratios (Fig. 2). This strategy is often observed in salt marsh species that suffer periodic waterlogging, like *A. portulacoides*, indicating a greater investment in root system under stressful conditions (Schubauer and Hopkinson 1984; Scarton et al. 1999, 2002; Pont et al. 2002).

Although LAI was similar for both species, SLA was smaller for *L. monopetalum*, improving this species competitiveness to withstand the usually greater salt and water stresses of the upper marsh. The decrease of both LAI and SLA, observed in summer, reflects the decrease of the transpiratory surface (Fig. 1), an adaptive strategy to the particular climatic constraints of this season, such as high temperatures, intense radiation, and depletion of soil water availability (Larcher 1995).

PRIMARY PRODUCTIVITY

Net aerial primary production (NAPP) obtained in this work for *A. portulacoides* through the Smalley method ($1002 \text{ g m}^{-2} \text{ yr}^{-1}$) is slightly smaller than in other studies (Groenendijk 1984; Bouchard and Lefeuvre 1996, 2000; Bouchard et al. 1998), with maximum values of $3600 \text{ g m}^{-2} \text{ yr}^{-1}$. This value is within the range reported to other European mid

marsh species, such as *A. fruticosum*, averaging between 102 and $1260 \text{ g m}^{-2} \text{ yr}^{-1}$ (Ib3ñez et al. 1999; Curc3 et al., 2002; Scarton et al. 2002). The estimate of *L. monopetalum* productivity based on the same method was much greater ($2917 \text{ g m}^{-2} \text{ yr}^{-1}$), making this the maximum value recorded in Mediterranean-type salt marshes. These results are in accordance with the greater photosynthetic capacity and higher water use efficiency of *L. monopetalum* (Neves et al. In press).

The productivity estimates obtained in this work for *L. monopetalum* through the Weigert and Evans method are close to the values reported for *J. roemerianus* (Gallagher et al. 1980), *Spartina anglica* (Groenendijk 1984), and *S. alterniflora* (Hopkinson et al. 1980). By the same method, *A. portulacoides* showed a smaller productivity, similar to *Phragmites australis* (Scarton et al. 2002).

The production estimates through the Smalley method were increased by around 60% for *L. monopetalum* and 25% for *A. portulacoides* using the Weigert and Evans method. These increments may be attributed to the fact that the former method is based solely on biomass changes, while the latter also takes into account the disappearance of dead material. According to several authors (Linthurst and Reimold 1978; Gallagher et al. 1980; Groenendijk 1984), the Weigert and Evans method is expected to be closer to the actual productivity. In spite of this, Linthurst and Reimold (1978) concluded that the Smalley method is the most suitable for salt marshes because of tidal movement of material and also because it allows more intensive biomass sampling.

The aboveground turnover rate obtained for *A. portulacoides* (0.96 yr^{-1}) was higher than reported for the same species in other European salt marshes (0.77 yr^{-1} , Bouchard et al. 1998; 0.69 yr^{-1} , Bouchard and Lefeuvre 2000). The turnover of *L. monopetalum* (0.86 yr^{-1}), although smaller than *A. portulacoides*, was in the range pointed out for other high marsh species, such as *E. aetherica* (0.68 yr^{-1}), *Festuca rubra* (0.78 yr^{-1}), and *Puccinellia maritima* (0.97 yr^{-1} ; Bouchard and Lefeuvre 2000). According to Curc3 et al. (2002), in Mediterranean climate salt marshes, maximum aboveground biomass and net primary production occur in the middle marsh, where the frequent stresses that affect vegetation dynamics (waterlogging and hypersalinity) are more moderate than in the lower and upper marshes. In this study, we obtained a greater aboveground biomass and net primary production in the upper marsh species (*L. monopetalum*), with great NAPP values, similar to those reported for American salt marshes (Linthurst and Reimold 1978; Gallagher et al. 1980). The greater productivity, in accordance with a greater carbon uptake capacity (Neves et al. In

press), smaller root:shoot ratio, and smaller SLA of *L. monopetalum* relative to *A. portulacoides*, suggest that *L. monopetalum* might be at a competitive advantage over *A. portulacoides* in response to varying environmental conditions, including increasing drought stress, which is expected to occur with the ongoing global climatic changes.

NUTRIENT CONTENTS

In salt saturated soils such as salt marshes, Na and Ca concentrations often exceed by one or two orders of magnitude those of most macronutrients and even more in the case of micronutrients, depressing nutrient-ion activities and causing extreme ratios of Na:Ca, Na:K, and Mg:Ca (Qadir and Schubert 2002). As a result, plants become susceptible to high osmotic stress, specific ion toxicity, and nutritional disorders. Plant species vary not only in the rate at which they absorb an available nutrient, but also in the manner by which they distribute that element spatially within their components.

The greatest N concentrations in the living tissue of both species were determined in the dry season in which no growth occurred (Fig. 4 and Table 2). Many halophytes invest a large proportion of N in compatible solutes such as glycinebetaine for cytoplasmic osmoregulation (Gorham and Wyn Jones 1983), and these high N concentrations may be associated with greater salinity tolerance. A general N decrease was observed during the growing season, with the minimum in spring, coinciding with the biomass peak. Similar results were also obtained for other salt marsh species by Gallagher et al. (1980) and Boyer et al. (2001). According to these authors, the minimum N concentration at the end of the growing season suggests a dilution of N as plants accumulate biomass.

The overall P content is closely related to vital growth processes and the efficient functioning and utilization of N. The concentration of this nutrient decreased in the dry season in the leaves of both species (Fig. 4), probably due to translocation during senescence. For *L. monopetalum* leaves, P was translocated to roots, and for *A. portulacoides* the main storage tissue was in the stems.

K is specifically needed for protein synthesis and enzyme activation. High concentrations of this mineral in the stroma are considered essential for the maintenance of optimum photosynthetic capacity, and biomass production, under stress conditions (Grattan and Grieve 1999). The overall K contents in the living tissue decreased, for both species, in summer (Fig. 4), probably due to the presence of Na, which interferes with the function of K as a cofactor in various reactions (Blumwald 2000; Khan et al. 2000). Since K is not bound to organic

compounds in plants but is in ionic form, this mineral is readily leached from plant tissue. Leaching could be responsible for a leaf concentration decrease in winter. While *A. portulacoides* occupies the mid marsh, *L. monopetalum* is found in the upper marsh and is less subjected to waterlogging in summer. This may explain why a summer decrease in leaf K content was observed only for *A. portulacoides*.

One of the main nutritional disorders associated with high salinity soils is impaired uptake of Ca caused by high Na concentration in the soil solution. Ca plays vital nutritional and physiological roles in plant metabolism. It is essential in processes that preserve the structural and functional integrity of plant membranes, stabilizes cell wall structures, regulates ion transport, and controls ion exchange behavior, as well as cell wall enzyme activities (Rengel 1992). As salinity increases during the dry season, high concentrations of Na in the soil reduce the amounts of available Ca and may displace Ca from the cell membrane-bound structure (Cramer et al. 1985). This may explain the greater concentrations of this element in autumn, after the first rains, and the subsequent decrease in spring and summer (Fig. 5).

Mg plays a key role in the photosynthetic process as an important constituent of chlorophyll. *L. monopetalum* exhibited greater leaf Mg contents (Fig. 5), which is in accordance with its higher photosynthetic capacity (Neves et al. In press) and productivity (Table 1).

Similar patterns of Mn contents were obtained for both species (Fig. 5). The greatest concentrations were found in roots, which is related to the low requirement of this nutrient in photosynthesis (water oxidation), respiration, and N metabolism, which occurs mainly in the shoots. Being a relatively immobile element, it accumulates in older components, most likely the roots.

The nutrient contents determined in this study are within the range indicated by Larcher (1995) for terrestrial plants. The results obtained suggest that the availability of these resources is not a limiting factor to biomass production. This may be due to the ability of *A. portulacoides* and *L. monopetalum* to exclude high mineral levels, through their roots and shoots, as the main mechanism of adaptation to high salinity (Greenway and Munns 1980; Cheeseman 1988; Daoud et al. 2001).

ACKNOWLEDGMENTS

This work was supported by grants of the project Estudo das Condições Ambientais do Estuário do Rio Guadiana e Zonas Adjacentes, coordinated by the Instituto da Água/Laboratório Nacional de Engenharia Civil. We also thank A. Bettencourt, coordinator of this project in the Universidade de Évora, and the

Laboratório de Botânica/ Instituto de Ciências Agrárias Mediterrâneas.

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VILA REAL DE SANTO ANTÓNIO METEOROLOGICAL STATION, unpublished data Instituto de Meteorologia/Vila Real de Santo António Meteorological Station, www.meteo.pt

Received, May 17, 2006
Revised, January 3, 2007
Accepted, March 3, 2007