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ORIGINAL ARTICLE

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Salicornia ramosissima population dynamics and tolerance of salinity

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Abstract Field and greenhouse studies have been conducted to clarify aspects of population dynamics and NaCl tolerance of *Salicornia ramosissima* J. Woods. Two populations, Varela and Verdemilho, were monitored in the field during two consecutive life cycles and aspects of their morphology and density were recorded monthly. In the laboratory seedlings were exposed to different salinity for 10 weeks and growth and mortality rate were recorded weekly. The growth of the populations differed significantly, possibly because of the different salinities of the two sampling sites and/or genetic adaptations of the two populations to the environmental conditions. The absence of a significant correlation between sediment salinity and stem elongation suggested, however, that salinity, alone was not responsible for the differences observed and was possibly associated with other factors, because of nutritional, edaphic, and microclimatic conditions. *S. ramosissima* did not develop well in conditions of elevated or moderate salinity; its growth was optimum at low salinity. Optimum development of *S. ramosissima* may, nevertheless, depend on the total number of large seeds in a population seed bank, because of their greater success in germination and germinability under stress conditions than small seeds.

Keywords *Salicornia ramosissima* · Density · Stem elongation · Cohort · Mortality

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Introduction

Salt-marsh processes are very dependent on abiotic factors, for example salinity, which in turn depend on a great variety of conditions, for example the extent and frequency of tidal flooding, evapotranspiration, and vegetation (Vernberg 1993). The tidal regime contributes very strongly to the heterogeneity of salt marshes—it affects chemical and physical factors for example salinity, redox potential, and nutrient concentration, and is important in the population biology of halophytes. Environmental stress, i.e. salinity, may induce species to develop resistance mechanisms, thus adapting to the environment during their evolution. Mechanisms of resistance of halophytes to high salt concentrations may be based on salinity-tolerance mechanisms, for example increasing the resistance of cells, promoting increased succulence of stems and leaves, or developing a leafless form (Flowers et al. 1986; Breckle 1990; Vernberg 1993).

The optimum NaCl concentration for the growth of the most halophytes in culture solutions ranges from 20 to 500 mmol L^{-1}, although these optimum values may vary with the age of the plant and environmental conditions, for example moisture and light intensity, which have not often been carefully controlled (Flowers et al. 1977; Ungar 1991). Plants develop plastic responses to a wide variety of ecological conditions including variation of the abiotic environment, one of the major factors affecting the expression of phenotypic plasticity. Individuals within a species may vary by orders of magnitude in size and growth rate (Callaway et al. 2003). Changing environmental conditions correlate with patterns of genetic differentiation in plant populations that carry phenotypic plasticity (Adam 1993). Genetic differentiation between populations of *Salicornia europaea* agg. from the upper and lower salt marsh, which have different tidal regimes, apparent in their growth, phenology, density, and mortality patterns, have been reported. The authors suggest, however, that apparent genetic differentiation may merely be a result of a

physiological "memory" of seedlings transplanted to other environmental conditions and which grow normally when returned to their native environment (Davy and Smith 1985).

Mechanisms of salinity tolerance in *S. europaea* have been studied (Langlois 1971; Keiffer et al. 1994; Momonoki and Kamimura 1994; Momonoki et al. 1994, 1996) by performing greenhouse experiments with seedlings and plants collected in the field during the growth period. According to Langlois (1971) the number of side branches in *S. europaea* is one of the most important features for estimating development associated with growth, because production of many branches is related to increased accumulation of biomass.

The genus *Salicornia* is distributed almost worldwide in saline environments, occupying the most highly saline sites (Chapman 1974). *Salicornia ramosissima* J. Woods, included in the species aggregate *S. europaea* agg. (Stace 1997), is an annual halophyte widely distributed in the salt marsh of Ria de Aveiro (Portugal) and also present in many salt marshes of the Iberian Peninsula (Castroviejo 1990). It preferentially occupies small places not invaded by other halophytes, for example *Halimione portulacoides* and *Sarcocornia perennis* subsp. *perennis*, both Chenopodiaceae. This species can tolerate high salinity and water potentials (Rubio-Casal et al. 2003) and has substantial phenotypic plasticity. Local differentiation of populations has been reported, probably as a result of strong cleistogamy (Jefferies et al. 1981; Adam 1993; Ball and Akeroyd 1996; Davy et al. 2001) which promotes the inbreeding which enables locally differentiated populations (Jefferies et al. 1981). This inbreeding and the substantial phenotypic plasticity are responsible for the great taxonomic complexity of the genus *Salicornia* (Davy et al. 2001). Seed dimorphism occurs in this species. The inflorescence is spike-like with two opposite three-flowered cymules in each segment, each cymule with one large central flower and two smaller lateral flowers. Small seeds (0.8–1.3(1.5)×0.5–0.8 mm) are formed by the two lateral flowers of the cymule and a large seed (1–1.4(1.55)×0.6–1.1 mm) by the flower in the center of the cymule (Ungar 1979; Castroviejo 1990; Silva 2000). Its life cycle is well defined, with discrete generations, and a very small persistent seed bank may be found in the first cm of sediment (Philipupillai and Ungar 1984; Rubio-Casal et al. 2003) almost all corresponding to the small seeds of the lateral flowers (Carter and Ungar 2003). As a saltmarsh pioneer, *S. ramosissima* is frequently the first higher plant to colonize intertidal zones (Davy et al. 2001); it is, therefore, a very important species to include in strategies for management and conservation of the Ria de Aveiro salt marsh, including rehabilitation of some degraded areas of this ecosystem, which is of great economic importance in industry, agriculture, fishery, and tourism (Borrego et al. 1991). The objective of this study was to contribute to a better understanding of *S. ramosissima* population biology in Ria de Aveiro, especially aspects related to salinity, plant growth, and survival.

Methods

Study area

Ria de Aveiro is a shallow coastal lagoon (Fig. 1) located on the Northwest Atlantic coast of Portugal (40°38′N, 8°44′W), connected to the Atlantic Ocean

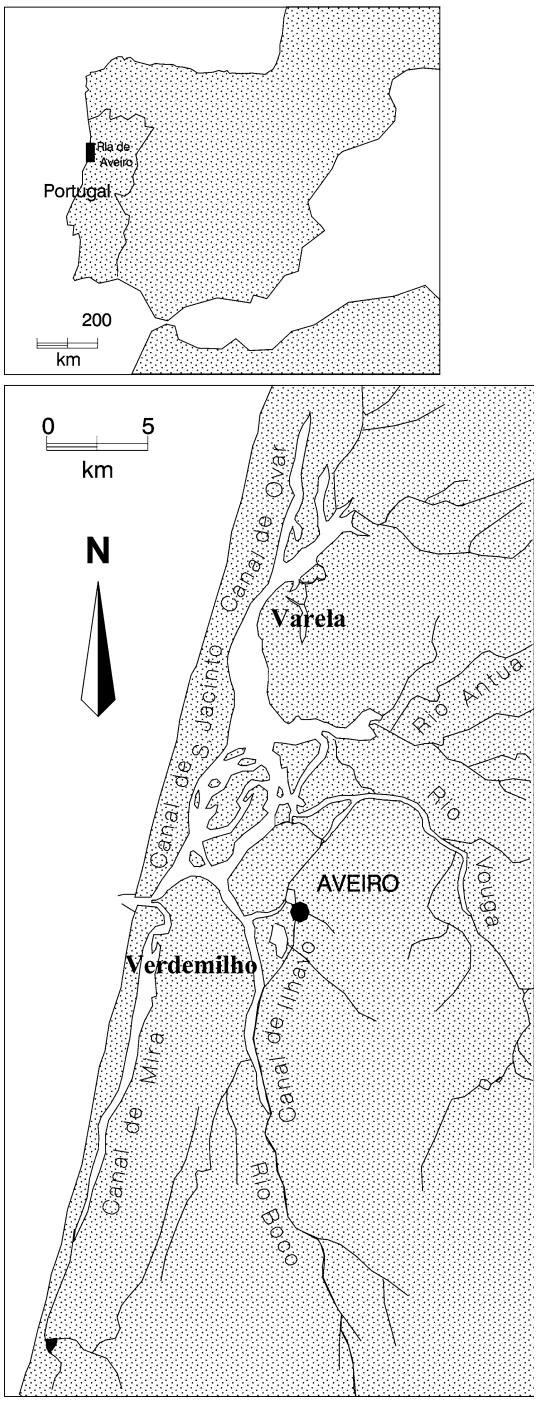

Fig. 1 Aveiro lagoon (Portugal) with location of sampling sites (Varela, Verdemilho)

through an artificial channel on the west side, and separated from the sea by a sand bar. It is formed from a complex pattern of channels characterized by many intertidal zones, for example mud flats and salt marshes, with maximum width and length of 10 and 45 km, respectively, with the highest values during spring tide (83 km^2 at high tide; 66 km^2 at low tide) (Moreira et al. 1993; Dias et al. 2000). This study was performed in the field and complemented with greenhouse experiments.

Field procedures

Two sampling sites of the Ria de Aveiro (Fig. 1) were selected to represent different tidal regimes and different sediment salinity. One site was the Verdemilho salt marsh covering ca. 1.4 vegetated hectares inundated daily by the tide, with maximum salinity mean values of approximately 11‰, and dominated by pure stands of *H. portulacoides*, *S. perennis* subsp. *perennis*, *S. ramosissima* and also well vegetated by *Puccinellia maritima*, *Cotula coronopifolia*, and *Triglochin maritima*. The other was the Varela salt marsh covering ca. 0.8 vegetated hectares, not directly affected by the tide (located 10 m from the margin of the channel), with maximum salinity mean values of approximately 34‰, and dominated by monospecific stands of *H. portulacoides*, *S. perennis* subsp. *perennis*, *S. ramosissima* and the frequent presence of *Parapholis filiformis* and *C. coronopifolia*. Most seedlings of *S. ramosissima* appear from March until May at the Verdemilho site and from April until May at the Varela site. The two populations of *S. ramosissima* were monitored in the field during two consecutive life cycles. The air temperature mean values varied between 13.0°C in November and 20.7°C in July; the daily pluviometric precipitation mean values varied between 0.0 mm in June and 11.8 mm in November, with an annual pluviometric precipitation of 1,181 mm (data supplied by Physics Department of Aveiro University).

Plant growth

Each year, 30 specimens of *S. ramosissima* ca. 4 mm long and with no visible nodes or branches, scattered throughout the whole salt marsh, were randomly chosen and marked ca. 5 cm from the specimen. Aspects of their morphology were recorded monthly to evaluate growth. The number of pairs of side branches produced, nodes on the main stem, and, finally, stem elongation and the diameter of the branched area were recorded. Soil salinity was determined monthly. Ten samples were randomly chosen in the *Salicornia* growth area. A ten-centimeter cube of sediment was collected, dried at room temperature, and homogenized. Salinity was then measured with a conductivity meter (WTW Cond330i with a TetraCon 325) as described by Duchaufour (1970). Sediment (10 g) was added to distilled water (30 mL), the sample was mixed with a magnetic stirrer at 100 rpm for 2.5 h, and the salinity was measured after the sample had been left for 2 h.

Plant density

At the beginning of the growing season, twenty 50 cm^2 patches of *S. ramosissima* were randomly chosen at each site and the number of plants in these permanent patches was recorded monthly.

Greenhouse procedures

Seedlings of *S. ramosissima* were collected, with the surrounding sediment, during April (named "1st cohort") from Verdemilho and Varela salt marshes and the procedure was repeated a month later (named "2nd cohort"). In the laboratory, seedlings with two segments approximately 1.5 cm long were carefully removed from the sediment, washed with distilled water and transplanted into 10 cm diameter×15 cm tall plastic pots containing washed and sterilized sand. The plants were grown in a growth chamber under temperature and luminosity-controlled conditions, at 25°C with a photon flux density of 2,000 μEinstein m^{-2} s^{-1} for 16 h. The pots were watered twice weekly with 500 mL culture solution containing 10 mmol L^{-1} $Ca(NO_3)_2.4H_2O$, KNO_3, $MgSO_4.7H_2O$, and $KH_2PO_4.2H_2O$ and 2 mmol L^{-1} Na-EDTA, 10% $FeCl_3$, H_3BO_3, $ZnSO_4.7H_2O$, $CuSO_4.5H_2O$, $MnSO_4$, $Na_2MoO_4.H_2O$, and $CoCl_2.6H_2O$ (Hoagland and Arnon 1950), pH between 6 and 6.5. Different concentrations of NaCl (0, 200, 400, and 600 mmol L^{-1}) were added to the culture solution and ten pots containing four seedlings each were submitted to one of these four treatments. The range of NaCl concentrations was chosen in accordance with salinity values measured in the field, in previous years, when the maximum was 580 mmol L^{-1} NaCl at Varela in September and the minimum was 20 mmol L^{-1} NaCl at Verdemilho in April (Silva 2000). Stem elongation, number of pair side branches produced, and mortality rate were recorded each week. After 10 weeks the plants were harvested and the dry weight of the aerial portion was determined after careful washing with distilled water and oven drying at 60°C for 48 h.

Data were subjected to statistical analysis according to Zar (1996), to a significance level of $P < 0.05$. The plant density at the sampling sites during the two consecutive years, and the stem elongation of the marked plants at the sampling sites were subjected to analysis of variance (ANOVA) with multiple comparison procedures (Tukey Test). Stem elongation of *Salicornia* in the field, soil salinity, and number of nodes of the main stem were subjected to Pearson correlation analysis, as also was stem elongation of *Salicornia* cultures and the salinity of the soil in the pots.

Results

Field procedures

The results from Varela were obtained a month later than those from Verdemilho owing to the delay in germination of *S. ramosissima* from Varela.

Plant density

The Verdemilho site is usually more dense in spring and summer. The mean plant density observed (Fig. 2) suggests much heterogeneity in the distribution of plants in each site during the year and between the two generations. A coefficient of variation of 57.7% was observed for the 1st generation of Varela. This may be because the plants usually grew in very high-density clumps. Alternation between high and low plant densities was observed in the same sampling site between the two generations. At Varela, in April, mean densities for *S. ramosissima* were 1,672.6 plants m^{-2} in the 1st year and 261.2 plants m^{-2} in the 2nd year. At Verdemilho, however, also in April, mean plant densities were 906.5 plants m^{-2} in the 1st year and 1,750.6 plants m^{-2} in the 2nd year. An abrupt decrease in plant density was observed from July to August (1,164.6 to 40 plants m^{-2}) in the 1st year only at Varela whereas in Verdemilho it was observed from April to August (1,750.6 to 298.3 plants m^{-2}) in the 2nd year only. The decrease in plant density on patches of lowest density was less abrupt (Verdemilho, 1st year, and Varela, 2nd year). Nevertheless, the two-factor ANOVA results only revealed significant differences between plant density in the 2 years at Varela ($F_{1,123} = 18.721$; $P < 0.001$) although differences between plant density in different months was significant at both Verdemilho and Varela (Verdemilho: $F_{8,147} = 39.350$; $P < 0.001$; Varela: $F_{7,123} = 15.466$; $P < 0.001$) especially for months where abrupt decreases in plant density were observed (Tukey Test: July/August from Varela's 1st year $P < 0.001$; April/August from Verdemilho's 2nd year $P = 0.10$).

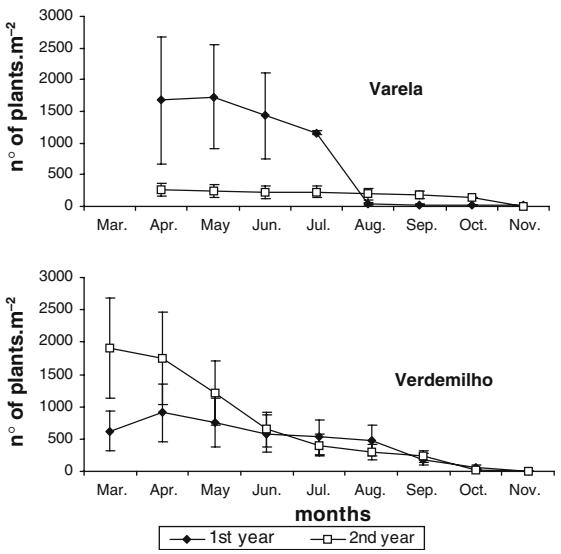

Fig. 2 Mean density (number of plants $m^{-2} \pm$ standard error) of *S. ramosissima* at Varela and Verdemilho during two annual life cycles

Plant growth

The mean increase of morphological data related to growth (stem elongation, number of pairs of side branches produced, nodes on the main stem, and diameter of the branched area) (Fig. 3) did not follow a common pattern, although the mean increases were maximum between April and May and between May and June at Verdemilho, and between May and June and between June and July at Varela. *S. ramosissima* grew more during the first month of field work, April to May at Verdemilho and May to June at Varela, in the two generations. The greatest stem elongation, 46 mm $month^{-1}$, was during April to May in the 1st year at Verdemilho whereas at Varela the greatest stem elongation, 39.91 mm $month^{-1}$, was during May to June in the 2nd year (Fig. 3). Different growth patterns at Varela and Verdemilho were confirmed by two-factor ANOVA—in each year stem elongation was significantly different at the two sampling sites ($F_{1,162} = 28.600$, $P < 0.001$, 1st year; $F_{1,162} = 28{,}835$, $P < 0.001$, 2nd year). There was no significant correlation between plant-stem elongation and sediment salinity at the two sampling sites. No significant differences were observed between the 2 years at the same sampling sites.

The number of nodes on the main stem was in accordance with stem elongation, being greatest when increases in stem elongation were greatest, except in the 2nd year at Verdemilho (Fig. 3). These data are confirmed by the positive significant correlation observed between stem elongation and the number of nodes of the main stem, except in the 2nd year of Verdemilho (Varela 1st year: $r = 0.673$, $P = 0.001$, $n = 82$; Varela 2nd year $r = 0.770$, $P < 0.001$, $n = 86$; Verdemilho 1st year: $r = 0.854$, $P < 0.001$, $n = 84$). The alternation of mean plant densities between the 1st and 2nd years (Fig. 2) was also observed in the pairs of side branches produced by the two generations (Fig. 3), with an increase in the number of branches when plant density decreases, except for August to September at Verdemilho. Alternation of the increase of the mean diameter of the branched area was also observed at Varela with the greatest values in the 2nd year (Fig. 3) corresponding to the smallest densities at the same sampling site (Fig. 2). No alternation of the diameter of the branched area in the 1st and 2nd years was observed at Verdemilho but the greatest values were observed in the 1st year when the density of *S. ramosissima* was smallest .

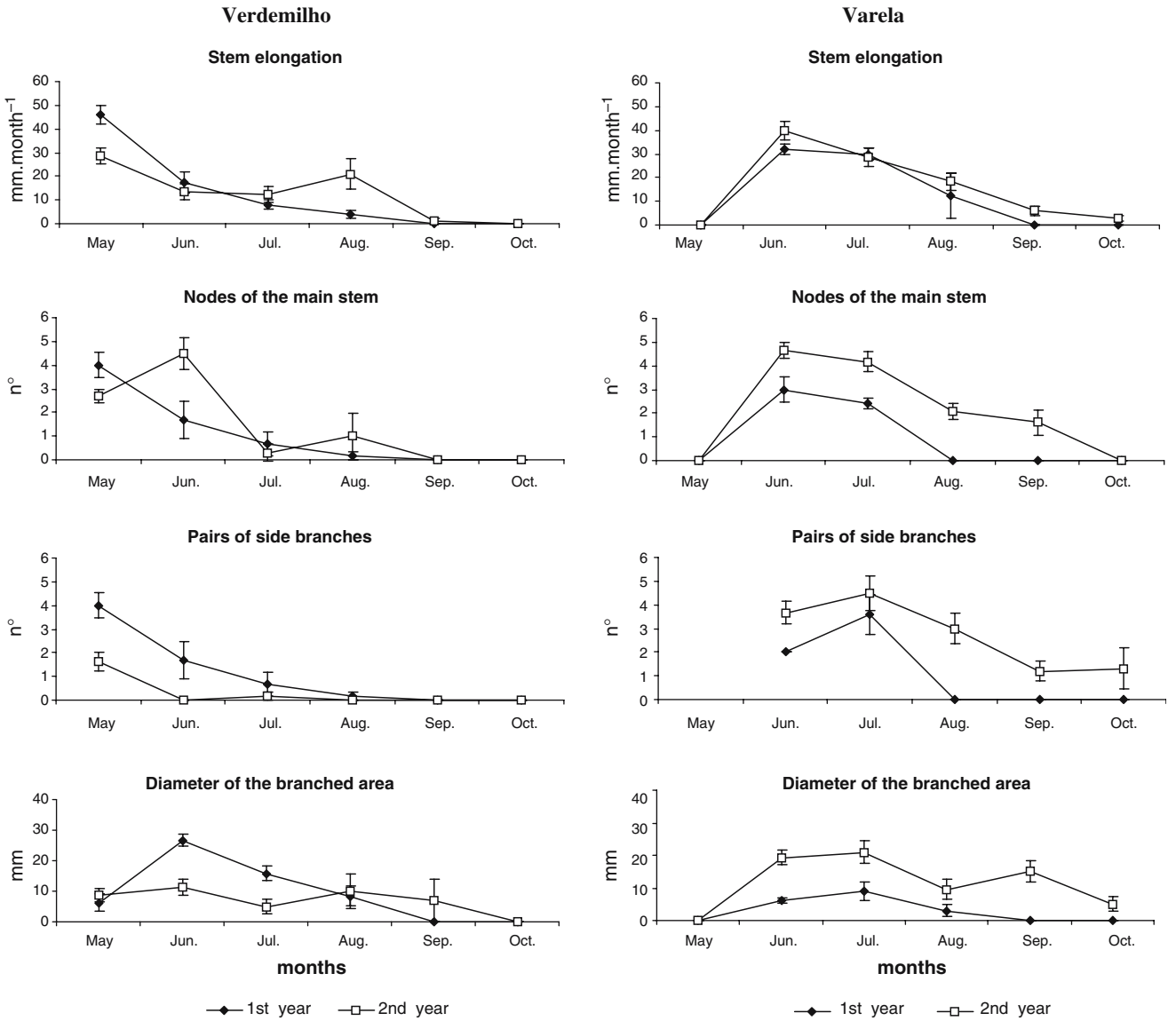

Fig. 3 Mean increment (±standard error) of morphological data related to growth (stem elongation, pairs ofside branches produced, nodes on the main stem, and diameter of the branched area) from two annual life cycles in two populations of *S. ramosissima* from Verdemilho and Varela

Greenhouse procedures

In the greenhouse experiments the mean growth of plants increased continuously during the 10 weeks (Fig. 4). *S. ramosissima* generally grew more when treated with 0 mmol L^{-1} NaCl, with mean stem elongation reaching 70 mm $week^{-1}$ (Verdemilho, 10th week, 1st cohort); mean stem elongation was only 23 mm $week^{-1}$ after treatment with 600 mmol L^{-1} NaCl under the same conditions. Mean stem elongation at the end of the 10 weeks (Fig. 5) was greater for low NaCl concentrations, with the highest values verified after treatment with 0 mmol L^{-1} NaCl, although the highest mean values were recorded for 200 mmol L^{-1} NaCl and the lowest values for 600 mmol L^{-1} NaCl. These results are supported by the significant negative correlation between salinity and plant-stem elongation for Varela's 1st and 2nd cohorts and Verdemilho's 1st cohort (Varela 1st cohort: $r=-0.404$, $P=0.009$, $n=122$; Varela 2nd cohort: $r=-0.561$, $P<0.001$, $n=110$; Verdemilho 1st cohort: $r=-0.588$, $P<0.001$, $n=120$). The dry weight of the shoot at the end of the 10 weeks also usually decreased with increasing NaCl concentration, with maximum mean values for 0 mmol L^{-1} NaCl and minimum mean values for 600 mmol L^{-1} NaCl (Fig. 5). Stem elongation for the 1st cohorts was greater than for the 2nd cohorts, except between the 5th and 10th weeks at Verdemilho after treatment with 400 mmol L^{-1} NaCl (Fig. 4). This is in

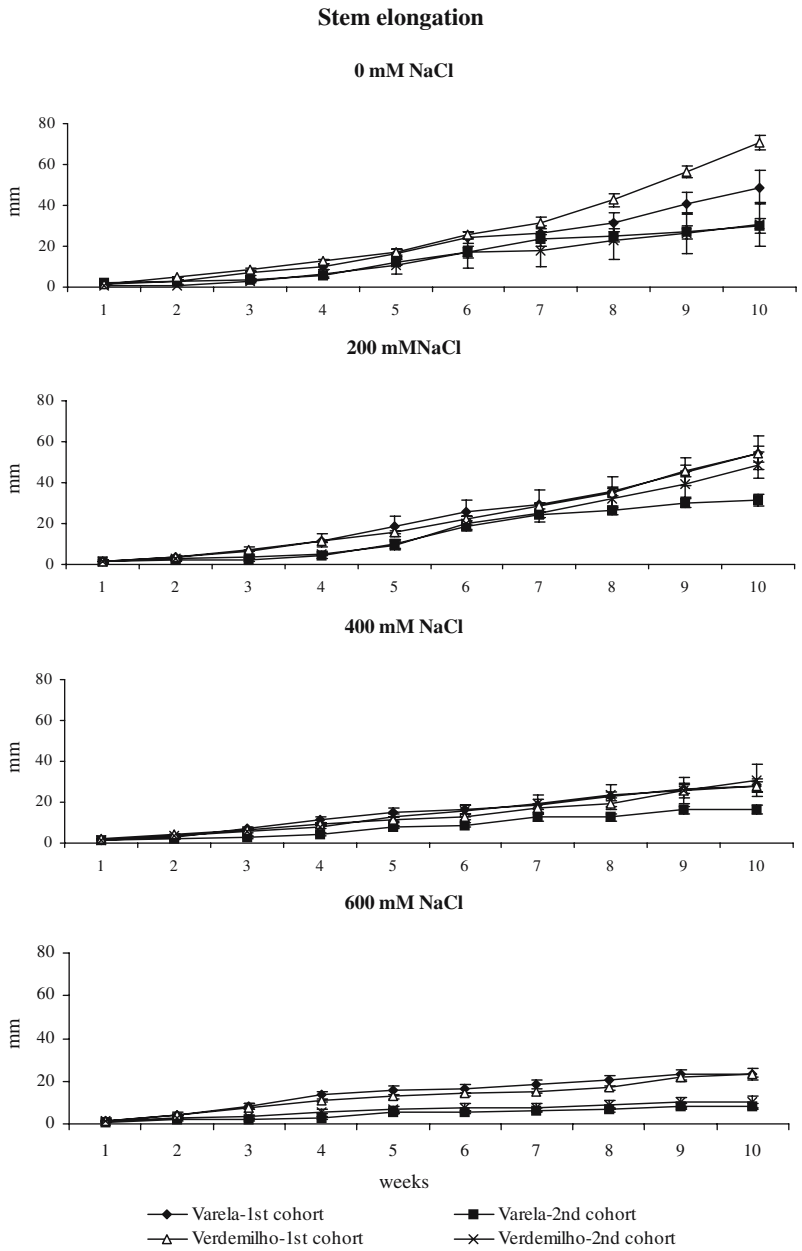

Fig. 4 Weekly mean stem elongation (±standard error) for *S. ramosissima* plants exposed to different concentrations of NaCl

agreement with the highest values of dry weight, after 10 weeks, observed for the 1st cohorts of the two sampling sites (Fig. 5). Although there was no uniform pattern in percentage mortality for different NaCl treatment, the mortality rate was highest for the 2nd cohorts, with a maximum value of 83.3% at Varela, and lowest for the the 1st cohorts, with a maximum value of 41.6%, also at Varela (Fig. 6). The mean number of side branches produced (Fig. 7), which is indicative of growth, was greatest after treatment with 0 mmol L^{-1} NaCl, with a maximum of eight branches for the 1st cohort from Varela, and generally decreased with increasing NaCl concentration for all cohorts. The percentage of plants with branches was also usually higher after treatment with 0 mmol L^{-1} NaCl, the maximum being 100% for the two cohorts from Varela, and was always lower after treatment with 600 mmol L^{-1} NaCl, the minimum being 0% for the 2nd cohorts from both sampling sites. The 2nd cohorts from the two sampling sites did not develop side branches after treatment with 600 mmol L^{-1} NaCl, whereas for the 1st cohorts branches were developed by 44.4 and 10% of cohorts from Varela and Verdemilho, respectively (Fig. 7).

Discussion

The delay in the germination and growth of *S. ramosissima* in Varela may be explained by the higher salinity

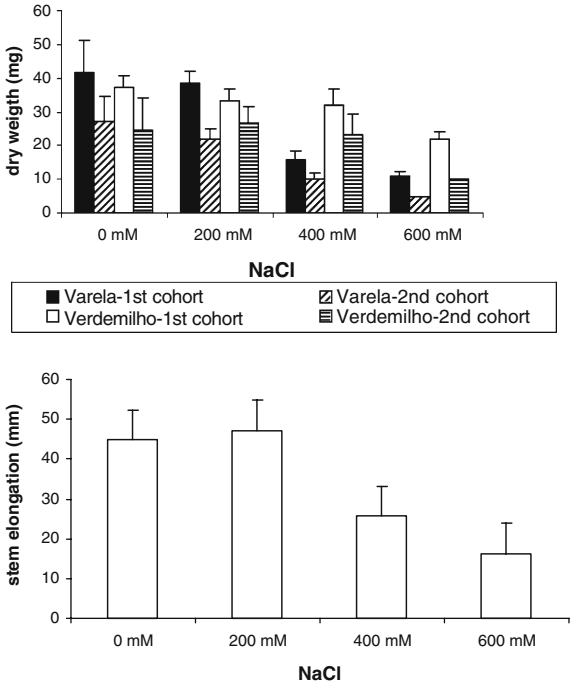

Fig. 5 Mean increment (±standard error) of the fresh weight of the aerial portion and mean stem elongation (±standard error) for *S. ramosissima* after 10 weeks of treatment with different concentrations of NaCl

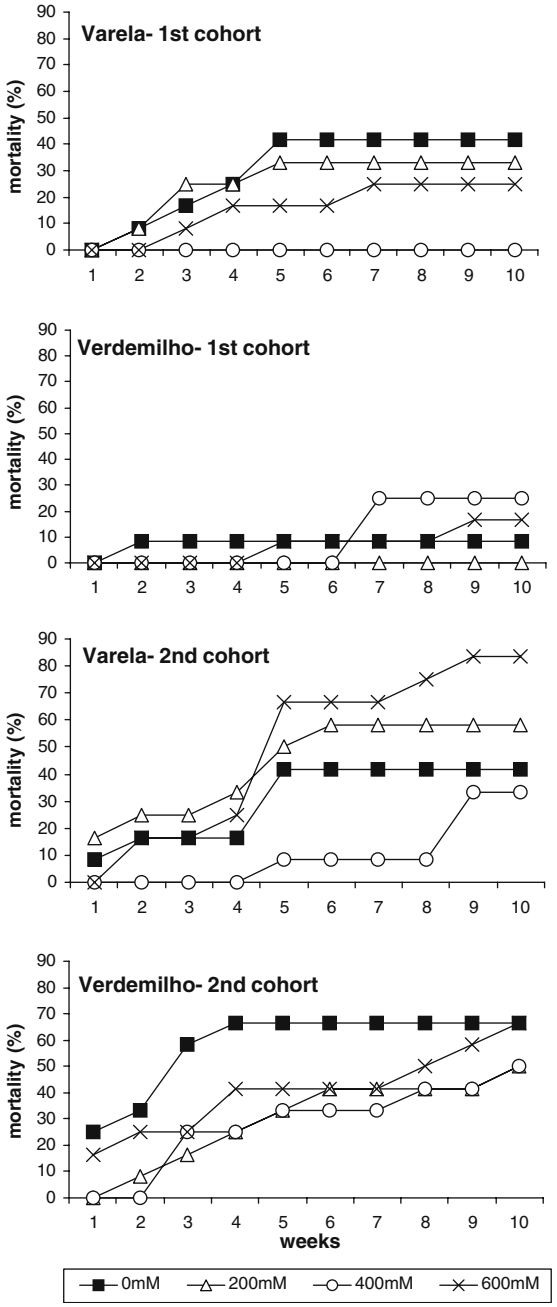

Fig. 6 Percentage mortality of *S. ramosissima* exposed to different concentrations of NaCl

of sediments not directly affected by the tide (Table 1). Many studies suggest that halophyte seeds respond similarly to saline stress, with a delay in the start of germination and the occurrence of germination when soil salinity is reduced (Macke and Ungar 1970; Chapman 1974; Khan and Ungar 1986; Keiffer and Ungar 1997; Katembe et al. 1998; Pujol et al. 2000; Silva 2000). This delay may occur when the salinity causes stress to seeds, for example reduction of germination and dormancy related to the decrease of osmotic potential (Pujol et al. 2000), but do not inhibit germination when the stress conditions are alleviated, i.e. by an increase in the water potential and a decline in salinity (Ungar 1991; Gul and Weber 2001; Tobe et al. 2001; Rubio-Casal et al. 2003). The higher plant density in Verdemilho may also explained by the lower soil salinity than at Varela (Table 1). As reported by Rubio-Casal et al. (2003) for *S. ramosissima* and *Arthrocnemum macrostachyum*, low salinity may increase germination speed and rate, which increases plant density. Biotic factors may also affect survival of *S. ramosissima*, however—according to Khan and Ungar (1986) perennials such as *P. maritima* and *H. portulacoides* may compromise the establishment and development of seedlings of the annual halophyte *Suaeda maritima*. The different cohorts in the same population of *S. ramosissima*, as a result of delayed germination, may be caused by the seed dimorphism reported by Castroviejo (1990) and Silva (2000), with small seeds (lateral flowers) being more dormant and less salt-tolerant than large seeds (central flowers) (Philipupillai and Ungar 1984). This higher dormancy may be related to mechanical resistance to germination as a result of a thicker seed coat in small seeds, as suggested by Osmond et al. (1980) and Khan and Ungar (1985) for species of the related genera *Atriplex*. Jefferies and Gottlieb (1982) suggest that the delay in germination and growth of plants from upper salt marshes may be a consequence of a genetic response of the population to dangerous hypersaline conditions. Many halophytes shoot better when not exposed to saline conditions (Chapman 1974; Ungar 1991), which agrees with our

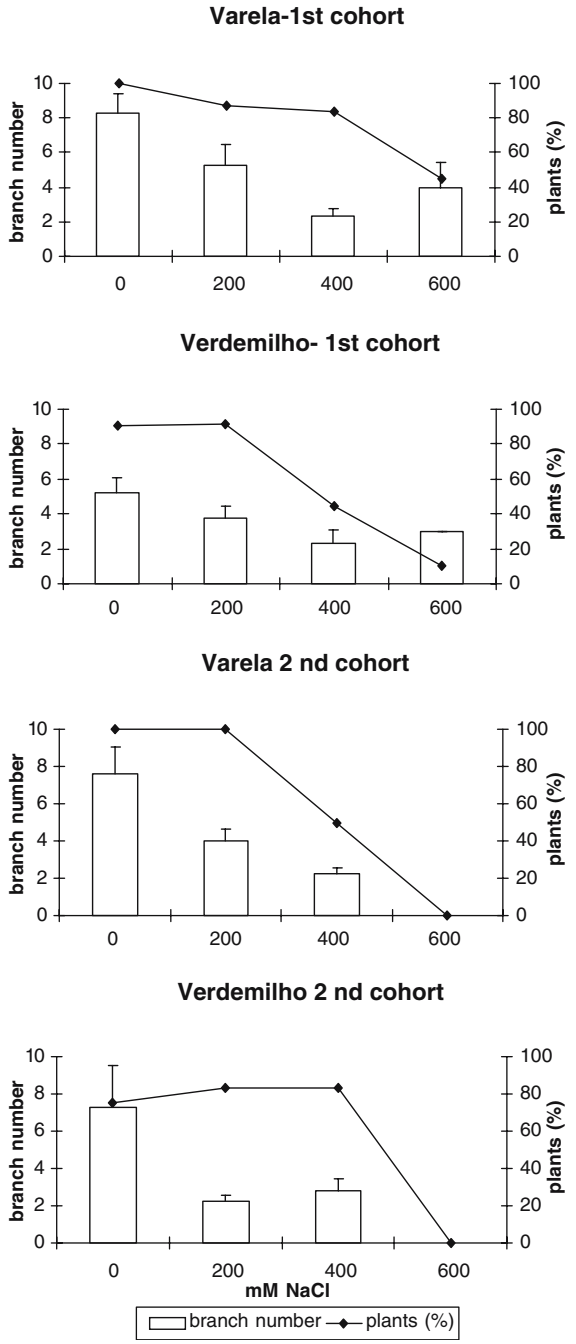

Fig. 7 Number of side branches produced, and respective percentage of branched plants, for *S. ramosissima* exposed to different concentrations of NaCl

observations in greenhouse experiments (Figs. 4, 5) in which growth of plants was usually greater when salinity was low.

The local high-density clumps (Fig. 2) may be the result of germination in situ and the trapping of seeds by algal patches (*Ulva* sp. and *Enteromorpha* sp.) aided by the existence of a seed indumentum of hooked mucilaginous hairs that anchor the seeds to the sediment; this is in agreement with observations by other researchers (Davy et al. 2001). Young seedlings with the root system less firmly established are particularly vulnerable, however, and mortality may be a result of many factors—periods of anoxia as a consequence of temporary immersion, because of precipitation and high tides, periods of desiccation, and seedling burial by sediment during high tides. These observations were similar to those recorded by other investigators for annual halophytes such as *Spergularia marina* (Tortensson 1987), *S. maritima* (Tessier et al. 2000) and *S. europaea* (Jefferies et al. 1981).

The alternation between low and high plant density observed at the same sampling site (Fig. 2) may be because plants growing in high-density areas produce a single terminal spike that can produce only a few seeds, giving rise to a reduced seed bank, and this a low-density population. In contrast, at low density the three-dimensional branching structure can result in large individuals with hundreds of fertile terminal spikes (Jefferies et al. 1981; Watkinson and Davy 1985) which is in accordance with our observations. Thus, the generations with the lowest population densities give rise to generations with the highest population density. The abrupt decrease in plant density observed in the generations for which density was highest during the summer months (Fig. 2) is probably related to competition for nutrients from more developed plants, in accordance with Keiffer et al. (1994). High soil salinity during summer months at Varela may, however, also be responsible for this decrease.

Maximum plant growth (Fig. 3) was observed in the field between April and June, which is in accordance with the low values of soil salinity (Table 1) observed in these months. These observations agree with those of Chapman (1974) and Ungar (1991) that some halophytes develop better under non-saline conditions.

The optimum growth observed when NaCl treatment was between 0 and 200 mmol L^{-1} is in accordance with observations for the annual halophytes *Salicornia rubra* (Khan et al. 2001) and *Salicornia bigelovii* (Ayala and O'Leary 1995). For other succulent and perennials halophytes, however, for example *Allenrolfea occidentalis* (Gul et al. 2000), *Haloxylon recurvum* (Khan et al. 2000) and *Sarcocornia natalensis* (Naidoo and Rughunanan 1990) optimum growth was observed after treatment with 200 to 600 mmol L^{-1} NaCl .

The greater mortality observed for the 2nd cohorts (Fig. 6) may be because seeds with belated germination may furnish less viable plants with much higher mortality and, therefore, few individuals reach the reproductive stage; this is in accordance with Ungar (1991), Adam (1993), and Larcher (1995). This success in germination and growth of seedlings of the first cohorts (large seeds) may be related to chemical constitution and the amount of nutrient reserves (Backer 1972; Harper 1994), in agreement with the observations of Austenfeld (1988) who reported that the total amount of nutrient reserves per seed were slightly higher for large seeds. Thus, the greater success in germination and germina-

Table 1 Mean values of soil salinity at the Verdemilho and Varela sites during two consecutive years

	Verdemilho salinity (‰)		Varela salinity (‰)	
	1st year	2nd year	1st year	2nd year
April	2.73	3.3	10.1	10.2
May	4.2	7.1	10.2	12.6
June	4.6	6.3	21.5	24.6
July	6.13	7.4	31.6	37.2
August	4.2	5.9	29.5	31.3
September	11.1	14.5	34.2	39.2
October	5.9	6.2	11.3	18.4
November	6.1	6.3	9.2	11.4

bility of the large seeds (1st cohorts) may result from total nutrients available per seed and/or, according to Khan and Ungar (1985), from the relative levels of hormones (hormone balance) which may profoundly affect plant growth and development (Naqvi 1995). These statements are in agreement with the lowest weight after 10 weeks and the lowest values of stem elongation for the 2nd cohorts in the greenhouse experiments.

The growth of populations of *S. ramosissima* from Varela and Verdemilho was significantly different, possibly because of the different salinities of the two sampling sites and/or genetic adaptation of the two populations to the environmental conditions (Adam 1993). The absence of a significant correlation between sediment salinity and stem elongation of these plants suggests, however, that salinity, per se, is not responsible for the observed differences but is possibly associated with other factors, for example nutritional, edaphic, and microclimatic conditions.

Analysis of these data leads to the conclusion that *S. ramosissima* does not develop well in areas of elevated or moderate salinity, because its growth is optimum at low salinity. The optimum development of *S. ramosissima* may, nevertheless, depend on the total number of the large seeds in the population seed bank, because of their greater success in germination and germinability under stress conditions than small seeds. This assumption is in accordance with our greenhouse experiments (Silva et al., unpublished data) and with the investigations of Philipupillai and Ungar (1984) and Carter and Ungar (2003). Large seeds are nondormant when produced and have greater germinability than small seeds; small seeds germinate later than large seeds but are more dormant under conditions of high salinity and may need light for germination.

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