PHOTOSYNTHETICA 36 (3): 397-406, 1999

Gas exchange and chlorophyll fluorescence of C_3 and C_4 saltmarsh species

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Abstract

Spartina maritima (Curtis) Fernald, *Spartina densiflora* Brong, *Arthrocnemum perenne* (Miller) Moss, and *Arthrocnemum fruticosum* (L.) Moq are very frequent halophytes on the coasts of SW Europe. The first two are perennial *Gramineae* with C_4 metabolism; the last two are perennial *Chenopodiaceae* with C_3 metabolism. Controlled garden experiments were carried out with the four species to compare their physiological response, *i.e.*, water potential (Ψ), net photosynthetic rate (P_N), transpiration rate (E), stomatal conductance (g_s), intercellular CO_2 concentration (C_i), and chlorophyll fluorescence of photosystem (PS) 2 under saline and non-saline conditions. *S. maritima* behaves as an osmoconformer species, the other three as osmoregulators. In the four species, P_N, E, and g_s improved following freshwater irrigation. The variations in P_N might be related with biochemical changes (which appear not to affect PS2), but not with significant stomatal fluctuations, which are associated with a lower water use efficiency in the case of *Arthrocnemum*. The species were segregated into two groups (not depending on their C_3 or C_4 photosynthetic pathway), in relation with the topographic level of this species in natural conditions: the relative responses of P_N in *S. maritima* and *A. perenne* were lower than those of *S. densiflora* and *A. fruticosum*. The salt-tolerance index supports such segregation. *S. densiflora* demonstrated the best competitive possibilities against salt-tolerant glycophytes, with its more flexible response in saline or brackish environments, which explains its spreading along the rivers draining into the estuaries of the SW Iberian Peninsula.

Received 9 October 1998, *accepted* 17 March 1999.

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Abbreviations: C_i - intercellular CO_2 concentration; Chl - chlorophyll; E - transpiration rate; F_0, F_m, F_v - initial, maximal, and variable fluorescence; g_s - stomatal conductance; P_N - net photosynthetic rate; P_{Ns} - P_N under saline irrigation; P_{Nf} - P_N under freshwater irrigation; PS - photosystem; $t_{1/2}$ - half-rise time to get maximum fluorescence; Ψ - water potential; $\Psi_{leaf/stem}$ - leaf/stem water potential; Ψ_{soil} - soil water potential.

Acknowledgements: This work was supported by grants from the Spanish DGICYT (grant PB94-1455) and the Junta de Andalucía (Plan Andaluz de Investigación, Research group No. RNM224).

Additional key words: *Arthrocnemum*; C_3 and C_4 plants; halophytes; intercellular CO_2 concentration; leaf gas exchange; net photosynthetic rate; *Spartina;* stomatal conductance; transpiration rate; water potential.

Introduction

Soil salt content is a key factor in the zonation of saltmarsh plants and an important regulator of plant productivity in such ecosystems (Adam 1990). The ionic composition of the rooting environment for saltmarsh plants is dominated by sodium and chloride; in addition, the species have to endure periods of partial or total immersion in saline water, using their thick cuticles to minimize the direct entry of salt *via* the leaves.

Physiological aspects of plant species' response to salt stress and the costs of growth in a saline habitat have been the subject of numerous studies (see reviews of Epstein 1980, Yeo 1983, Shalhevet 1993). The costs of being a halophyte are frequently considered to be disadvantageous. Nevertheless, such costs are essential for the occupation of these habitats, and become a drawback for halophytes only in a non-saline environment (Adam 1990).

The marine influence on the estuaries in the Atlantic coast of SW Europe extends several kilometres upstream, due to the high tidal coefficients. However, certain human activity, such as the recent planning of reservoirs for irrigation of areas under crop very close to the mouths of some of the rivers, or the increase in sea level as a result of the greenhouse effect, could affect the distribution of halophytes and salt-tolerant glycophytes that compete for these spaces, by altering the salt levels of the sediments that they occupy. Forecasting changes in species composition in future environmental scenarios is still in the early stages of development (Schulze and Caldwell 1995).

Neither the response capacity of halophytes in the absence of salinity, nor whether the specialization of these species enables them to grow better outside saline environments, has been analyzed often. The aim of this work is to discover the effect of higher availability of fresh water on different physiological variables, for four taxa having different photosynthetic strategies, and being widely distributed in mid-latitude saltmarshes. It is intended to obtain a better understanding of the levels of salt-tolerance under which these species grow, and to discover their potential competitive qualities in the face of predictable changes in the saltmarsh plant composition, in relation with changes in the soil salinity pattern on medium and height topographic levels in mediterranean marshes, where low salinity periods show up due to the rainfall effect on the sediment and the stream flow (Nieva 1996), promoted by the climatic change and human activities. In summary, the aim of this experiment was to compare the physiological responses of different saltmarsh species in high salinity environments with their responses after a punctual period in absence of salinity, simulating the sudden, critical, and short-lasting conditions coming about with quick changes in this kind of environment.

Materials and methods

Plants: *Spartina maritima* (Curtis) Fernald, *Spartina densiflora* Brong, *Arthrocnemum perenne* (Miller) Moss, and *Arthrocnemum fruticosum* (L.) Moq are frequent halophytes on the coasts of SW Europe. The first two are perennial grasses with C_4 metabolism, while *A. perenne* and *A. fruticosum* are perennial long-lived, shrubby species plants with C_3 metabolism, having succulent, photosynthetic stems and completely atrophied leaves. All these species have a superficial root system, characteristic of saltmarsh plants. *S. maritima* and *A. perenne* are primary colonists, and support many hours of flooding; the former grows well even on strongly reduced (Eh < -300 mV) bare mud, while the latter, on raised levels of low marsh, requires well-drained, oxidizing sediments (Castellanos *et al.* 1994). *A. fruticosum* occupies the higher levels of middle marsh areas and the lower ones of high marsh areas, and is subjected to a lesser tidal effect (Rubio García 1985). Lastly, *S. densiflora*, a naturalized species introduced from South America, grows with notable ecological success on a wide range of topographical levels and of salinity, from euhaline to oligohaline (Nieva 1996), and spreads along the rivers in the south-west of the Iberian Peninsula.

Treatments: In spring 1994, uniformly sized clumps of *S. maritima*, *S. densiflora*, *A. perenne*, and *A. fruticosum* were collected in the Odiel Marshes, SW Spain (37°08'-20'N, 6°45'-7°02'W). The plants were placed in plastic pots keeping the original soil, and remained in the open air under prevailing climatic conditions (31 ± 0.3 °C, 1370 ± 10 μmol m^{-2} s^{-1} PAR, and 41 ± 1 % relative humidity maximum at mid-day; and approximately 12-12 h light/dark cycle).

Half of the pots were watered with 0.59 M NaCl, equivalent to the salinity of the sea-water in the Odiel Marshes. The other half were watered abundantly with fresh water to reduce drastically the soil salt content. In both cases, a standard nutrition solution was added once a week. The treatment was carried out for 30 d, after which soil electrical conductance ranged between 13 and 21 mS cm^{-1} (soil water potential ranged between -0.4 and -0.76 MPa) for the pots irrigated with NaCl, and between 0.2 and 1 mS cm^{-1} (-7.2×10^{-3} and -0.04 MPa) for those with freshwater irrigation.

Leaf water potential was measured simultaneously in selected leaves of *Spartina* and photosynthetic stems of *Arthrocnemum* (5 for each species and treatment), similar in length and maturity to those later monitored for gas exchange and for chlorophyll (Chl) fluorescence. The value of $\Psi_{leaf/stem}$ was obtained according to Scholander *et al.* (1965) using a pressure bomb (*Manofrigido*, Lisbon, Portugal).

Gas exchange measurements were made on intact, well developed leaves of *Spartina* and photosynthetic stems of *Arthrocnemum* attached to the plant, at midday, on a clear, cloudless day. P_N, E, g_s, and C_i were recorded on 8 samples of leaves (*Spartina*) or stems (*Arthrocnemum*) per species and treatment, using a portable open system with infrared CO_2 analyser (model *LCA-3, Analytical Development Co.*, Hoddesdon, UK) equipped with an *ADC Parkinson* leaf chamber (models *PLC-3N* and *PLC-3P*) and operating in differential mode, keeping up the relative humidity in the leaf chamber similar to that prevailing outside the chamber. The water-use efficiency was measured as the ratio between P_N and E [mmol(CO_2 assimilated) mol^{-1}(H_2O transpired)], and the salt-tolerance index P_{Ns}/P_{Nf} (Rozema *et al.* 1988) was calculated.

Chlorophyll fluorescence was measured on 8 leaves or stems, attached to the plants, per species and treatment, using a portable non-modulated fluorimeter (*PSM MarkII, Biomonitor AB*, Umea, Sweden). The leaves/stems were adapted to darkness using leaf-clips (*Biomonitor 1020*) 30 min before measuring the characteristics of fluorescence (F_0, F_m, F_v, F_v/F_m, $t_{1/2}$). An actinic radiation of 400 μmol m^{-2} s^{-1} for 5 s was used for all measurements (Öquist and Wass 1988, Bolhàr-Nordenkampf *et al.* 1989).

Statistical analyses: Values were subjected to analyses of variance. The level of significance of the ANOVA among absolute values is shown in the figures.

Results

Leaf water potential (Fig. 1*A*) showed no significant differences between *Spartina* and *Arthrocnemum*, although it did distinguish well the different irrigation treatments, with values markedly lower at high salinity in all the species (between -5.1 and -7.0 MPa for the treatment with salt water, and from -3.0 to -4.6 MPa for that with fresh water). Only *S. maritima* did not show a significant difference between the two treatments, with Ψ increasing only by some 23 %. *S. densiflora*, in contrast, showed an increase of 47 % compared with the saline irrigation, a value similar to that recorded for both species of the genus *Arthrocnemum*, with an increase in Ψ between 41 and 43 %.

Gas exchange: Under saline irrigation, P_N was markedly higher in *Spartina* species (between 6.2 and 7.6 μmol m^{-2} s^{-1}) than in *Arthrocnemum* (between 1.2 and 1.7 μmol m^{-2} s^{-1}) (Fig. 1*B*). Under freshwater irrigation, P_N increased significantly in all species studied, and the differences between species were kept: *S. densiflora* showed higher P_N (20.2 μmol m^{-2} s^{-1}) than *S. maritima* (14.6 μmol m^{-2} s^{-1}); the two species of *Arthrocnemum* showed similar increased values (3.5 and 4.0 μmol m^{-2} s^{-1}). In absolute terms, the response of *S. densiflora* to the irrigation salinity was significantly broader than those of the other species; in relative terms the increase in P_N at low salinity was similar to that detected in *A. fruticosum* (around 220 % in both cases). The response of *S. maritima* was similar to that of *A. perenne*, with increases in P_N close to 100 %.

Similar differences as for P_N were found for g_s (Fig. 1*C*). In the saline treatment, g_s values were between 51.2 and 71.2 mmol m^{-2} s^{-1} for *Spartina*, and between 10.0 and 17.5 mmol m^{-2} s^{-1} for *Arthrocnemum*. Low salinity significantly increased g_s in all the species studied. *S. densiflora* irrigated with fresh water gave the highest values of g_s, exceeding 200 mmol m^{-2} s^{-1}, while the values for *S. maritima* did not exceed 100 mmol m^{-2} s^{-1}, and 50 mmol m^{-2} s^{-1} for both species of *Arthrocnemum*. The relative response of g_s to decreased salinity was very high (between 200 and 300 %)

in *S. densiflora* and the two species of the genus *Arthrocnemum,* while the increase in *S. maritima* was markedly lower (85 %).

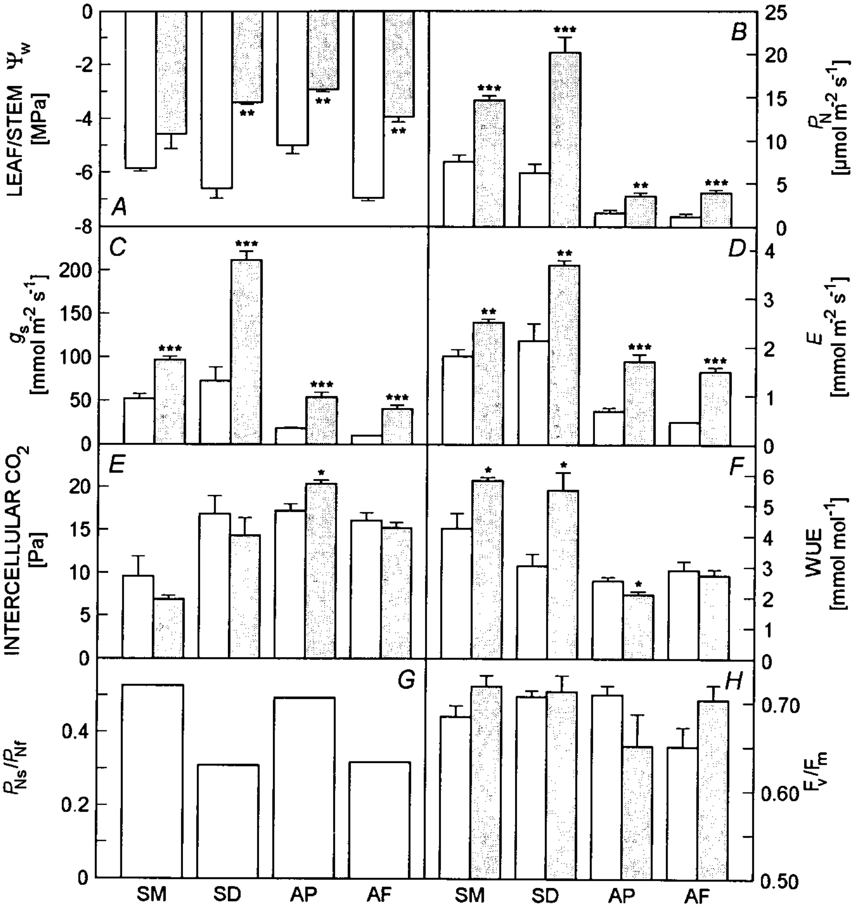

Fig. 1. Means ± SE of (*A*) leaf/stem water potential, (*B*) net photosynthetic rate, (*C*) stomatal conductance, (*D*) transpiration rate, (*E*) intercellular CO_2 concentration, (*F*) water use efficiency, (*G*) P_{Ns}/P_{Nf}, and (*H*) F_v/F_m for *Spartina maritima* (SM), *Spartina densiflora* (SD), *Arthrocnemum perenne* (AP), and *Arthrocnemum fruticosum* (AF). $n = 8$, with the exception of *A* ($n = 5$). *Open columns*: sea water irrigation; *hatched columns*: tap water irrigation. ANOVA between treatments are shown: $^*p < 0.01$; $^{**}p < 0.001$; $^{***}p < 0.0001$.

Similar differences as in g_s were found also for *E*, although the changes induced by freshwater irrigation were less marked (Fig. 1*D*). *S. densiflora* always showed higher *E* than did *S. maritima*, although in saline irrigation the difference between the two was not significant. In contrast, there were no differences between the two *Arthrocnemum* species (between 0.4 and 0.67 mmol m^{-2} s^{-1} in the saline irrigation, and between 1.47 and 1.7 mmol m^{-2} s^{-1} in the freshwater one), with *A. perenne* always presenting slightly higher *E*. In relative terms, the response to freshwater irrigation was markedly higher in *Arthrocnemum*, with increased *E* of 150 and 230 %; the increase observed in *S. maritima* and *S. densiflora* was 40 and 70 %, respectively. The absolute maximum *E* was again recorded for *S. densiflora*, at 3.7 mmol m^{-2} s^{-1}.

S. densiflora showed high C_i values (Fig. 1*E*), similar to those of *Arthrocnemum* (between 14.5 and 20.5 Pa), and significantly higher than those of *S. maritima* (between 6.9 and 9.8 Pa). C_i in the species studied was not very sensitive to the different salinity in irrigation, and no significant differences were detected, except in *A. perenne*; however, while *Spartina* maintained higher C_i in the saline irrigation (14 % decrease for *S. densiflora* and 29 % for *S. maritima*, compared with sea-water irrigation), *A. perenne* showed the opposite behaviour (an increase of 18 %), and *A. fruticosum* was hardly affected (the value decreased by 5 %).

Spartina showed greater efficiency in water use (between 3 and 5.8 mmol mol^{-1}) than *Arthrocnemum* (between 2 and 2.86 mmol mol^{-1} - Fig. 1*F*). However, *Spartina* presented lower WUE in salt water, with a more pronounced pattern in *S. densiflora* (82 % gain in freshwater irrigation) than in *S. maritima* (36 % gain). In contrast, this ratio P_N/E in *Arthrocnemum* was notably insensitive to the saline treatments, with a slight trend in the opposite direction to that described for *Spartina*.

The salt-tolerance index P_{Ns}/P_{Nf} (Rozema *et al.* 1988) resulted in a different segregation, grouping *S. maritima* with *A. perenne* and *S. densiflora* with *A. fruticosum* (Fig. 1*G*).

Table 1. $t_{1/2}$, F_m, F_0, and F_v (means ± SD, $n = 8$) in *Spartina densiflora*, *S. maritima*, *Arthrocnemum perennis*, and *A. fruticosum* irrigated with sea and tap water. $^*p<0.05$.

		S. densiflora	*S. maritima*	*A. perennis*	*A. fruticosum*
$t_{1/2}$ [ms]	Tap water	175.40 ± 10.24*	161.60 ± 5.16	169.20 ± 9.33	197.20 ± 21.79
	Sea water	144.80 ± 3.18	153.20 ± 12.59	172.80 ± 7.12	164.00 ± 11.71
F_m	Tap water	0.50 ± 0.04*	0.47 ± 0.04	0.32 ± 0.04	0.35 ± 0.04
	Sea water	0.38 ± 0.02	0.53 ± 0.05	0.35 ± 0.03	0.28 ± 0.04
F_0	Tap water	0.13 ± 0.00*	0.13 ± 0.01	0.11 ± 0.01	0.10 ± 0.01
	Sea water	0.11 ± 0.00	0.17 ± 0.01	0.10 ± 0.01	0.10 ± 0.01
F_v	Tap water	0.37 ± 0.04	0.34 ± 0.03	0.21 ± 0.03	0.25 ± 0.03
	Sea water	0.27 ± 0.02	0.36 ± 0.04	0.25 ± 0.03	0.18 ± 0.03

Chl fluorescence: The ratio F_v/F_m in the four species was not very sensitive to salinity (Fig. 1*H*), with mean values between 0.65 and 0.71. Other measurements related with PS2 Chl fluorescence ($t_{1/2}$, F_m, F_0, and F_v) also presented no significant differences between the different saline treatments, except in the values of $t_{1/2}$, F_m, and F_0 for *S. densiflora* (Table 1).

Discussion

Under field conditions, the matric and solute potentials are additive, decreasing the free energy of water in the soil; they would also be additive in their effect on plant growth, through a reduction in the availability of water (Shalhevet 1993). Despite the different mechanisms used by the studied genera to regulate their internal salt content (secretion in *Spartina* and succulence in *Arthrocnemum*), the responses of leaf water potential to increasing freshwater in the substrate were similar. Only the increase in Ψ_{leaf} in *S. maritima* was not significant following the increase in Ψ_{soil}, probably indicating a poorer osmoacclimation for this species (Reed 1984), habitually restricted to the lower marsh mud flats, where conditions of low salinity are probably a transitory phenomenon. This is in accord with the deep distribution of its roots and rhizomes (Castellanos *et al.* 1994), as with other osmoconformer halophytes (Jefferies 1980, Wyn Jones 1980), and with the need of a daily tidal bath for the elongation of its stems (Adams and Bates 1995). The other three species, shallow-rooted plants (Castellanos *et al.* 1994, Nieva 1996, Figueroa, unpublished), could be considered osmoregulators (Wyn Jones 1980), which match their Ψ_{leaf} to different salinity.

The sensitivity in the response of P_N is an ideal indicator of salt tolerance (Rozema and van Diggelen 1991), and an increase in the salinity of the medium is associated to a decrease in P_N, E, and g_s (Pearcy and Ustin 1984, Rozema and van Diggelen 1991). However, survival under high salinity means high metabolic costs, which are nevertheless essential for the occupation of these habitats, although most halophytic species grow well under freshwater irrigation, and many show optimal growth in such circumstances. In our experiment, the decrease in salinity led to an increase in P_N, E, and g_s, with significant differences in all cases. This behaviour suggests high productivity during low salinity periods, in relation with rainfall and/or short tides, in the high topographic levels of this saltmarsh.

Although salinity may reduce photosynthesis simply through decreases in g_s, in some species reduction in P_N occurs despite turgor maintenance (Beadle *et al.* 1985), and biochemical changes resulting in an increase in the resistance of the mesophyll to CO_2 uptake seem to be the immediate cause of a drop in P_N. In the four species studied, the lower P_N under greater salinity is not due to a decrease in the contribution of CO_2 by reduction in g_s (Tenhunen *et al.* 1984). The non-stomatal limitation of CO_2 assimilation capacity is seen from the considerable increase in P_N for statistically similar C_i values in freshwater and saline irrigation. These values are usually less affected by partial stomatal closure than by water loss (Nobel 1974), and the variation in P_N could be related with biochemical changes that affect carboxylase activity of the ribulose-1,5-bisphosphate carboxylase/oxygenase and the size of the phosphate triose pool (Ziska *et al.* 1990, Antolín and Sánchez-Díaz 1993). Only in *A. perenne*, the C_i values were significantly lower under sea-water salinity, suggesting a better stomatal control, seen as increased WUE by this species under normal conditions of salinity. No such variation was observed in *A. fruticosum*.

The greatest WUE was detected in *Spartina*, with highest absolute values under both irrigation conditions, in agreement with other comparative studies of C_3 and C_4

species. This behaviour, attributable to the higher P_N and/or lower E of the C_4 species (Pearcy and Ehleringer 1984, Knapp 1993), is in our case due to the high P_N of *Spartina*, even with lower values of E for *Arthrocnemum*. Other species of the genus *Spartina*, such as *S. foliosa*, also present high WUE at low salinity, with decline at higher salinity (Mahall and Park 1976).

The significant increase of E in the four species confirms the evidence of other authors that even after osmotic adjustment, under high salinity, E can remain low (Gorham *et al.* 1984). In absolute values, the high E detected in *Spartina*, even at sea-water salinity irrigation, is sustained by the presence of salt glands, which enable high g_s to be maintained even with the risk of water loss. However, the variation in E and g_s with the change of irrigation was proportional in *Arthrocnemum*, and there was a low dependence between the two in *Spartina*.

The values of F_v/F_m obtained situate our results in the same line as studies of Mishra *et al.* (1991), Havaux (1992), or Jimenez *et al.* (1997), and show that salt stress has no significant effect on Chl fluorescence, and thus the reduction in P_N under salinity is not due to alterations in PS2 (Gamon and Pearcy 1990). Only *S. densiflora* was sensitive to other parameters related with Chl fluorescence, with significantly higher values in freshwater irrigation, probably indicating a greater size of the PS2 electron acceptor pool, which would lead to a decrease in non-photochemical quenching, but also to a greater basal fluorescence of the antenna pigments (Bolhàr-Nordenkampf *et al.* 1989, Krause and Weis 1991, Bolhàr-Nordenkampf and Öquist 1993).

Although the distribution of species on the marsh and the composition of the communities is not well correlated with particular physiological traits (Adam 1990), the succulent C_3 species, with lower photosynthetic capacity than the C_4 species at low salinity, usually lose little of this activity when the salinity increases, in contrast to the C_4 species, which show greater loss at higher salinity (Pearcy and Ustin 1984, Drake 1989). *Arthrocnemum* did not follow this pattern, and the reductions in photosynthetic activity under salinity were equal to, or even higher than, those recorded in *Spartina*. In summary, even with a marked trend towards a behaviour defined by their physiological pathway (C_3 or C_4), the four species studied were segregated in two groups related with their normal distribution in the marsh. *S. maritima* and *A. perenne*, confined to lower levels always having higher environmental salinity, presented a shorter response for P_N against increasing fresh water in the pots than did *S. densiflora* and *A. fruticosum*, the latter with the typical behaviour of brackish marsh species such as *S. patens* (Pezeshki *et al.* 1989) or of those species occupying a broad range of levels in the marsh, such as *Aster tripolium* (Rozema and van Diggelen 1991), which are subjected to considerable seasonal fluctuations in salinity. The ratio P_{Ns}/P_{Nf} as an index of salt tolerance (Rozema *et al.* 1988) supports this segregation. *Spartina* is found at both extremes. *S. maritima* seems to have a certain specialization in saline environments, where it is most successfully distributed. However, the improvement in its values with increasing fresh water means that it cannot be considered an obligate halophyte. *S. densiflora*, with high P_N when subjected to scarcely saline conditions and with a high salt tolerance, would be highly competitive in sites subjected to large seasonal fluctuations in salinity. This would also explain its wide distribution in different levels of the estuaries, from hypersaline spaces to tidal freshwater marsh, including places of medium and high saltmarshes where soil salinity changes widely during the year due to the equilibrium amongst rainfalls, stream flow, and tidal influence, demonstrating its competitive possibilities against salt-tolerant glycophytes in slightly saline environments. *S. densiflora* is considered an invader species from the estuaries, with a high competitive capacity over the Mediterranean salt-tolerant glycophytes of brackish habitats, with its rates and forms of growth being decisive (Nieva 1996).

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