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Effect of salinity on water relations of two growth forms of *Suaeda calceoliformis*

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Summary

1. *Suaeda calceoliformis*, a succulent annual halophyte which occurs at Big Salt Marsh (Stafford Co., Kansas, USA), has erect and prostrate growth forms.
2. The two growth forms have similar leaf osmotic potentials over a wide range of salinities (0–5% NaCl), while leaf water (ψ) and pressure (ψ_p) potentials are higher for prostrate individuals.
3. To determine the basis for differences in ψ and ψ_p between the two growth forms, pressure–volume (PV) curves were constructed for individuals of each growth form at 3 and 5% NaCl. Analysis of the PV curves indicated that the prostrate growth form has significantly higher values for tissue bulk modulus of elasticity (ϵ) at both salinities and exhibits greater increases in ϵ with increasing salinity. Lower tissue elasticity, along with greater hydraulic conductance, enables prostrate individuals to maintain higher ψ_p and tissue water content.
4. These results are consistent with observed differences in survival and distribution of the two growth forms at Big Salt Marsh, the prostrate form occurring in more-saline areas of the marsh, and suggest that the ability to decrease tissue elasticity in response to increasing salinity may be of adaptive importance.

Key-words: Bulk modulus of elasticity, pressure potential, pressure–volume curve, water potential
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Introduction

Only a small percentage of the reported 2×10^6 km^2 of world saltmarshes are inland. The range of salinities encountered by plants in inland marshes is considerably greater than that encountered in the more-typical coastal marshes. Halophytes endemic to inland saltmarshes are likely to be uniquely adapted to this greater range of salinities. We believe the inland saltmarsh halophyte *Suaeda calceoliformis* (Hook.) Moq. (Chenopodiaceae), also referred to as *Suaeda depressa* (Pursh) S. Wats. (McNeill, Bassett & Crompton 1977), may provide an excellent opportunity to examine such adaptations.

This annual leafy succulent occurs throughout the western half of North America (Ungar & Capilupo 1968; McNeill *et al.* 1977) and is included in the flora of Big Salt Marsh in Stafford County, Kansas (Ungar 1965). In his description of the vegetation of Big Salt Marsh, Ungar (1965) noted the presence of erect and prostrate growth forms of *S. calceoliformis* (Fig. 1). The erect form has an aerial stem, the lower 15–20 cm of which is unbranched. Above the unbranched portion of the stem, two or more branches extend vertically-to-horizontally 30–40 cm. The prostrate form branches at the soil surface with each of three or more branches extending horizontally for up to 30 cm. Based on our observations and those of Ungar (1965) and Ungar & Capilupo (1968), the two growth forms are distributed differently at Big Salt Marsh. The erect form is widespread throughout the marsh, but is less common on the more-saline depressions or 'flats' to which the prostrate form is restricted.

Ungar (1965, 1974), Williams & Ungar (1972), and Maples (1968) suggest that the morphological differences between the two growth forms are phenotypic in nature and argue that environmental factors such as salinity, available nitrogen and photoperiod play leading roles in creating these morphological types. In contrast, throughout our studies seed collected from prostrate individuals produced only prostrate progeny and seed from erect individuals yielded only erect progeny, despite widely varying growth conditions, suggesting that the differences are genotypic. Culturing these progeny at a variety of salinities causes modification of growth rates, degree of succulence, leaf size and physiological responses (A. L. Youngman & S. A. Heckathorn, unpublished observation). However, we found no indication that salinity is involved in determining whether the growth form of a particular individual is to be erect or

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Fig. 1. *Suaeda calceoliformis* seedlings in sub-irrigated sand culture at 2·0% NaCl salinity. Plants were grown from seed collected from erect (left) and prostrate plants (right) at Big Salt Marsh (Stafford County, KS).

prostrate. These observations suggest that the two growth forms are genetically differentiated to the ecotypic level at the very least, the degree of reproductive isolation between the growth forms having not as yet been established.

Differences in distribution of erect and prostrate growth forms of *S. calceoliformis* at Big Salt Marsh with respect to soil salinity suggest that the two growth forms possibly differ in their tolerance to salinity through differences in water relations. The purpose of this paper is to report results of a comparison of leaf and shoot water relations of the two growth forms as a possible explanation of these distribution patterns.

Materials and methods

PLANT MATERIALS AND CULTURE

Seeds of both growth forms were collected from mature plants at Big Salt Marsh, surface sterilized with Clorox bleach, scarified and placed in petri dishes on moistened filter paper. The seeds were germinated in a growth chamber under 14 h, 25°C days and 10 h, 15°C nights. Photosynthetic photon flux density (PPFD) during germination was 400–500 μmol m^{-2} s^{-1}.

After 10 days, the seedlings were transferred to 9 cm plastic pots containing fine silica sand that had been leached with distilled water. Potted plants were grown in plastic trays containing full-strength Hoagland and Arnon no. 2 nutrient solution (Arditti & Dunn 1969), adjusted to pH 7·5 with 1 N KOH, and to which was eventually added 0·0, 0·25, 0·5, 0·75, 1·0, 2·0, 3·0, 4·0, or 5·0% NaCl. Salinity treatments were chosen primarily on the basis of the range of salinities reported for *S. calceoliformis* sites at Big Salt Marsh (Ungar 1965). We were able to maintain plants under culture conditions up to 5·0% NaCl, thus setting the upper limit of salinity for this study.

The newly potted seedlings were grown at 0·0% NaCl for 1 month. Salinities were then increased to final concentrations in 1·0% increments at 5-day intervals. To increase survival at 4·0 and 5·0%, seedlings destined for these salinities were held at 3·0% NaCl for 20 days before acclimating plants to higher salinities. Plants were grown under light and temperature conditions similar to those under which germination had occurred, except that photon flux density at mean plant height was slightly higher (500–600 μmol m^{-2} s^{-1}). Water was added to each tray, as needed, to maintain salt concentrations. Salinity and pH were adjusted when necessary and nutrient solutions were changed once a week. Plants were allowed to acclimate to final salinities for 3 weeks prior to measurements.

DETERMINATION OF LEAF WATER POTENTIAL AND ITS COMPONENTS

Leaf water and osmotic potentials (ψ and ψ_π) were determined by dewpoint hygrometry for three plants of each growth form at each salinity approximately 90 days after germination using a dewpoint microvoltmeter (HR-33, Wescor, Utah, USA) and a sample-chamber psychrometer (C-52, Wescor). Because we observed diurnal changes in ψ, leaves were sampled only during the middle hours of the photoperiod (11.00 to 15.00 h). One whole, undamaged midstem leaf was used in determining ψ. A second similarly selected leaf, frozen with freon and then thawed, was used in determining ψ_π. Pressure potentials (ψ_p) were calculated from mean ψ and ψ_π. No correction in ψ or ψ_π was made for dilution by apoplastic water; however, the large saturated-to-dry weight ratios (W_s/W_d) observed for both growth forms (Table 1) and absence of negative ψ_p during PV analysis indicate a low fraction of apoplastic water (Campbell *et al.* 1979; Wenkert 1980; Jensen & Henson 1990). Furthermore, equilibrium times for both ψ and ψ_π were generally less than 2 h (indicating high epidermal conductance), thus minimizing potential dilution. *Suaeda calceoliformis* is not a salt excreter, so errors associated with accumulation of salt on the leaf surface during measurement were not of concern.

PV CURVES FOR SHOOTS

PV curves were obtained (Tyree & Hammel 1972) using a technique similar to that of Davis & Mooney (1986). To compare growth forms at intermediate and high salinities where large differences in growth form were anticipated, PV curves were constructed for erect and prostrate individuals acclimated to 3 and 5% NaCl (n=3). PV data were collected on whole branches harvested at 19.00h, 12h prior to use. Each branch was cut under distilled water, transferred to a beaker of distilled water so that the cut end was submerged 1–2cm, and placed in a closed plexiglass chamber containing moistened paper towelling. The branches were then allowed to hydrate overnight at room temperature. The following morning the branches were removed from the beakers, blotted to remove excess water, and weighed (to nearest 0·1mg), giving saturated weight (W_s). Using a pressure chamber (1000, PMS Instrument Co., Oregon, USA), shoot ψ was determined at approximately 10 intervals during tissue water loss to the atmosphere. Fresh weight (W_f) for each branch was determined each time ψ was measured, and dry weight (W_d) was determined for each branch after oven drying at 60°C for 48h. Per cent relative water content (%R) for each branch was calculated at each ψ from W_s, W_f, and W_d [$\%R=(W_f-W_d)/(W_s-W_d)\times100$].

Inverse ψ was plotted against %R. The point at which each curve became linear (zero turgor) was visually estimated, giving %R at zero turgor (%R^0) and osmotic potential at zero turgor (ψ_π^0). Linear regression analysis was performed on the linear portion of the curve, with and without an additional data point beyond the estimated %R^0 (i.e. $\%R>\%R^0$). Comparison of r^2 values was used to confirm our estimate of the turgor loss point. This method for estimating zero turgor is somewhat subjective and subject to error; however, the small standard deviations observed for %R^0 and ψ_π^0 (Table 1) suggest that our estimates were sufficiently accurate. Osmotic potential at full turgor (ψ_π^{100}) was determined by extrapolation of the regression equation to the y-axis. Pressure potentials derived from the PV curves were plotted against %R and values for bulk modulus of elasticity (ϵ) were calculated from this relationship (i.e. $\epsilon=d\psi_p/dV\times V$ where V (volume)$\sim$%R if the apoplastic water fraction is low) following Hellkvist, Richards & Jarvis (1974). The slope of $\psi_p-\%R$ curves of both growth forms increased with increasing %R, becoming linear (or nearly so, and thus treated as such) at high %R. Values of ϵ reported here are values calculated for leaves close to full turgor ($R\sim100\%$) and are therefore maximum or near-maximum values of ϵ.

DATA ANALYSIS

Leaf ψ and ψ_π data were subjected to two-way analysis of variance (ANOVA; Sokal & Rohlf 1981). A probability level of 5% or less was chosen as indicative of a significant test result.

Results

LEAF WATER POTENTIAL (ψ)

Water potentials in both growth forms (Fig. 2a) decreased with increasing salinity; however, the erect form had much lower ψ than the prostrate at salinities>0·25%. Plants raised in the growth chamber and wild plants had previously shown similar trends in shoot ψ, determined using a pressure chamber (A. L. Youngman & S. A. Heckathorn, unpublished results). Water potentials for both forms decreased sharply between 0·0 and 1·0% salinity, but to a lesser extent between 1·0 and 5·0%. Leaf ψ was consistently lower than ψ of the solution (Fig. 2a) to which plants were acclimated. A two-way ANOVA indicated that both salinity (F=541·1, df=8,36) and form (F=1054·97, df=1,36) had significant effects on ψ, and that there was a significant salinity–form interaction (F=30·82, df=8,36).

LEAF OSMOTIC POTENTIAL (ψ_π)

As with ψ, ψ_π of both growth forms (Fig. 2b) decreased sharply between 0·0 and 1·0% salinities, with a more gradual decrease between 1·0 and 5·0%. In contrast to ψ, differences in ψ_π between growth forms were small. The increase in ψ and ψ_π in both growth forms at 0·75% NaCl is consistent with results observed by Maples (1968) and Karimi (1979) for shoot weight *vs* salinity, suggesting that an optimal salinity for growth may exist for *S. calceoliformis* between 0·5 and 1·0% NaCl. Results of a two-way ANOVA for ψ_π were similar to results for ψ, indicating

Table 1. Comparison of tissue water relations derived from PV curves of erect and prostrate growth forms of *Suaeda calceoliformis* at 3 and 5% NaCl

	3% NaCl		5% NaCl	
	Erect	Prostrate	Erect	Prostrate
W_s/W_d	8·17±0·80	8·56±0·22	7·48±0·40	9·04±1·01*
ψ_π^{100} (MPa)	−1·36±0·07	−1·57±0·10*	−1·56±0·12	−1·90±0·22*
ψ_π^{0} (MPa)	−1·98±0·11	−1·88±0·08	−2·11±0·16	−2·17±0·15
R^0 (%)	86·60±1·01	88·61±0·22*	83·83±2·93	87·19±1·87
ϵ (MPa)†	7·85±0·51	12·40±0·95*	8·38±0·78	18·92±1·15*

Mean values between growth forms were compared by Student's t-test. Means±SD, n=4, †n=3.
*$P<0.05$. Other symbols are defined in text.

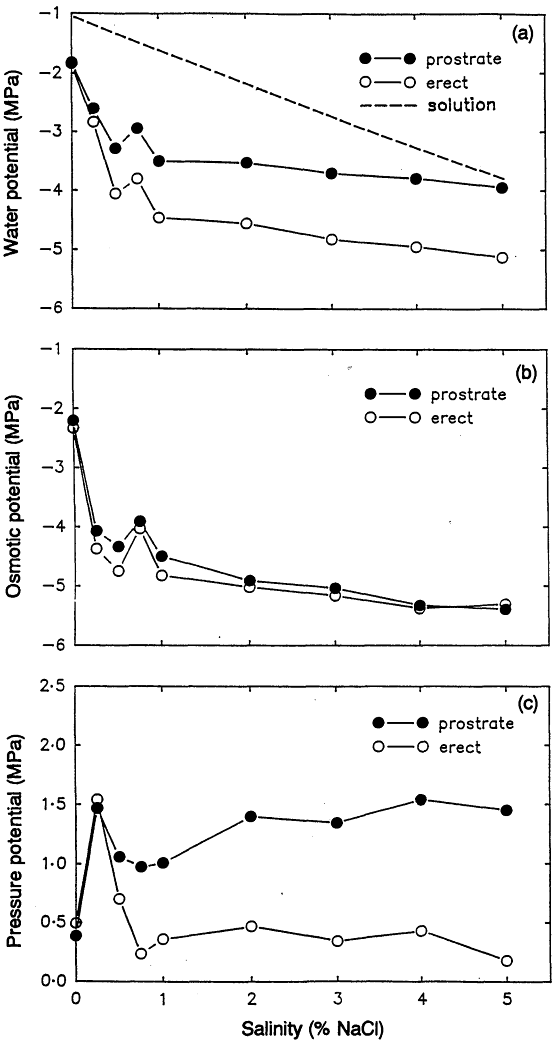

Fig. 2. Leaf water potential (a), osmotic potential (b) and pressure potential (c) of prostrate and erect growth forms of *Suaeda calceoliformis* at 0–5% NaCl salinities. Values are means based on determinations for one leaf from each of three plants. Standard deviations for water potential (ψ) ranged from 0·03 to 0·08 MPa for prostrate forms and from 0·015 to 0·18 MPa for erect forms. Standard deviations for osmotic potential (ψ_π) ranged from 0·03 to 0·16 MPa for prostrate forms and from 0·031 to 0·14 MPa for erect forms. Pressure potential was calculated from ψ and ψ_π means.

that both salinity (F=713·39, df=8,36) and form (F=47·41, df=1,36) had significant effects on ψ_π, and that there was a significant salinity–form interaction (F=4·60, df=8,36).

LEAF PRESSURE POTENTIAL (ψ_p)

The prostrate growth form exhibited markedly higher ψ_p than the erect form at salinities >0·25% (Fig. 2c).

PV CURVES OF SHOOTS

At high %R, shoot ψ decreased more rapidly in the prostrate growth form than in the erect form (Fig. 3). Differences between growth forms were more pronounced at 5% (Fig. 3b), than at 3% NaCl (Fig. 3a). Similar trends were seen for ψ_p; i.e. ψ_p decreased more rapidly at high %R in the prostrate form (Fig. 4) and differences between growth forms were greater at 5% (Fig. 4b), than at 3% NaCl (Fig. 4a). Each curve shown in Fig. 4 and its respective curve in Fig. 3 are from the same plant and are those curves for which ϵ is closest to the mean for that growth form at that salinity.

Because the slopes of the initial portions of the $\psi_p-\%R$ curves were used to calculate ϵ and are proportional to ϵ, it is evident from Fig. 4 that the prostrate growth form has higher values of ϵ, and thus more rigid cell walls than the erect form. Calculated values for ϵ confirm this (Table 1). At each salinity, ϵ was significantly higher for the prostrate growth form. In addition, the prostrate growth form exhibited a larger response of ϵ to increasing salinity than the erect form. There was little difference between growth forms in $\psi_\pi{}^0$, which is in agreement with the hygrometric data (Fig. 2b). Therefore, the differences in $\psi_\pi{}^{100}$ (3 and 5%) between growth forms are most likely attributable to differences in cell wall elasticity. Significant differences between growth forms also were seen in W_s/W_d at 5% and %R^0 at 3% NaCl.

Discussion

Although erect and prostrate growth forms of *S. calceoliformis* exhibit similar ψ_π over a range of

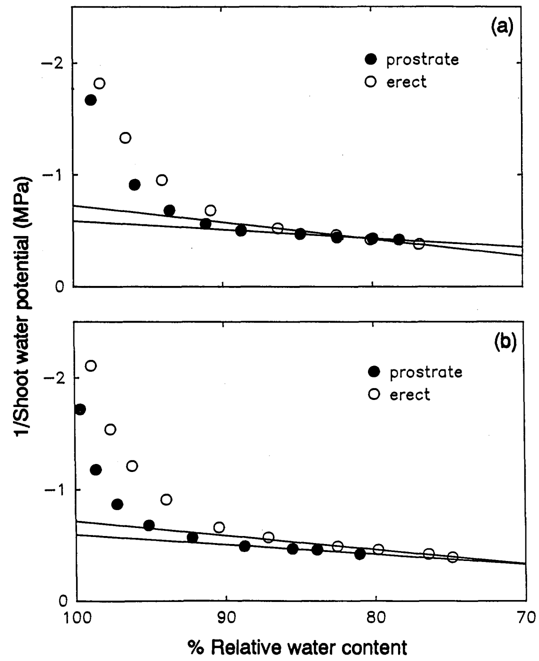

Fig. 3. PV curves for prostrate and erect growth forms of *Suaeda calceoliformis* grown at (a) 3% NaCl and (b) 5% NaCl. Each curve is derived from a single plant and is representative of that growth form at that salinity (see Results).

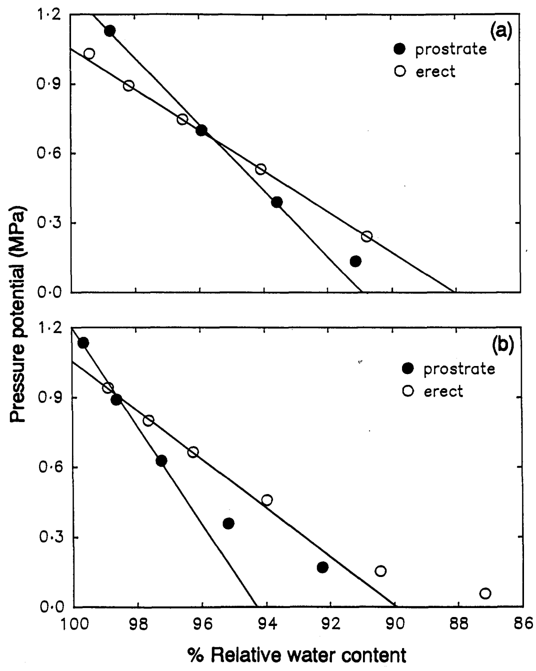

Fig. 4. Relationship of pressure potential derived from PV curves to per cent relative water content for prostrate and erect forms of *Suaeda calceoliformis* grown at (a) 3% NaCl and (b) 5% NaCl. Each curve in this figure and its respective curve in Fig. 3 are from the same plant.

salinities, prostrate plants have higher ψ and ψ_p (Fig. 2). A number of morphological or physiological mechanisms might account for higher ψ, and thus ψ_p, in prostrate individuals including mechanisms that: (1) increase water uptake; (2) decrease transpiration; or (3) alter tissue elasticity.

A more extensive root system (i.e. increased root–shoot ratio) or increased density or depth of roots might allow prostrate individuals to acquire more water per unit leaf area than erect individuals, enabling these plants to maintain higher ψ and ψ_p (Turner 1986). In many habitats this is a possibility, but is less likely for a saltmarsh species such as *S. calceoliformis* growing in saturated soil for much of the growing season. Based on preliminary (unpublished) data, prostrate plants do not have significantly higher root–shoot dry weight ratios than erect plants.

Lower transpiration rates (E) in prostrate plants resulting from either smaller leaf-to-air vapour pressure deficit (LAVPD) or lower stomatal conductance to water vapour (g^{st}) could account for higher ψ and ψ_p. Although differences in LAVPD may exist between growth forms in naturally occurring plants due to leaf microhabitat differences, prostrate individuals exhibit higher ψ and ψ_p under growth chamber conditions where LAVPD is very similar for both growth forms. Under such conditions we found that g^{st} was in fact slightly lower in prostrate plants; however, no differences were observed in E in field-grown plants (Student's t-test, $P>0·05$), despite higher ψ and ψ_p in the prostrate growth form (A. L. Youngman & S. A. Heckathorn, unpublished results).

These results (similar E but different soil-to-leaf ψ gradients) suggest that whole-plant hydraulic conductance (L_p) differs between growth forms, the prostrate form having greater L_p. This is not surprising, since the prostrate form lacks the extended aerial stem that the erect form possesses. Greater L_p would increase the ability of the plant to supply water to transpiring leaf tissue, improving leaf water status (i.e. $\%R$ and ψ).

Leaf ψ, and hence ψ_p, is also influenced by tissue elasticity; ψ at a particular $\%R$ being a function of tissue elasticity and ψ_π (Turner & Jones 1980; Tyree & Jarvis 1982). The fact that ψ_π is similar for erect and prostrate individuals at a given $\%R$, while ψ is different (Fig. 3), indicates involvement of tissue elasticity in ψ differences of erect and prostrate plants. Because $\%R$ varies between growth forms (Fig. 5), differences in ψ and ψ_p between erect and prostrate plants are likely to result from both hydraulic conductance and elasticity differences.

Tissue elasticity can be described quantitatively by determination of the tissue bulk modulus of elasticity (ϵ), rigid tissues having larger values of ϵ (Tyree & Jarvis 1982). Rigid tissues would exhibit larger decreases in ψ for a given decrease in tissue water content, allowing plants with rigid tissues to maintain steep soil-to-plant ψ gradients with little loss of water. The ability to respond to increasing salinity by decreasing tissue elasticity (i.e. increasing ϵ) might therefore be a mechanism to maintain high tissue water content which could result in higher ψ_p (Bolaños & Longstreth 1984). This could be especially important for an inland halophyte such as *S. calceoliformis* which experiences large fluctuations in soil salinity during the growing season.

Results of this study indicate that there are differences in tissue elasticity between erect and prostrate

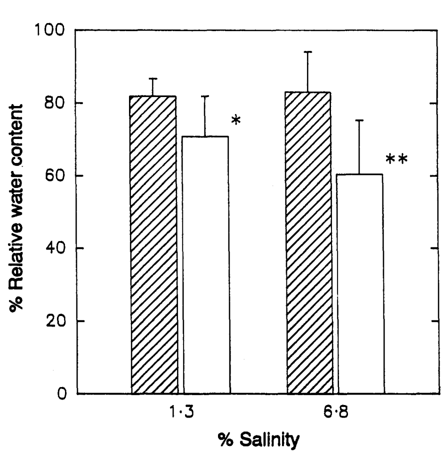

Fig. 5. Shoot relative water content of naturally occurring prostrate ▨ and erect □ growth forms of *Suaeda calceoliformis* at moderate and high salinities. Error bars are 1 SD, $n=5$, $^{*}P<0·07$, $^{**}P<0·05$.

growth forms of *S. calceoliformis* and that tissue elasticity responses to increasing salinity are also different (Table 1). Prostrate individuals had higher ϵ-values than erect individuals at both 3 and 5% NaCl and had larger increases in ϵ with increasing salinity. Increases in ϵ in response to increasing salinity were also observed by Bolaños & Longstreth (1984) in the halophyte *Alternanthera philoxeroides*.

The differences in L_p and ϵ between growth forms do in fact result in differences in tissue water content. Prostrate plants maintained higher shoot %R than erect plants at moderate and high salinities (Fig. 5). These are values for naturally occurring, non-rehydrated plants from an unrelated study. Similar results were seen for plants raised in growth chambers at salinities from 0 to 4%.

Maintenance of high %R and ψ_p, as a result of greater L_p and ϵ, is beneficial to metabolism and growth. Many metabolic processes in plants are thought to be responsive to cell water content, rather than ψ *per se* (Hanson & Hitz 1982), including photosynthesis (Kaiser 1987). Turgor pressure is necessary for cell expansion, structural integrity, stomatal opening and may also regulate certain metabolic events (Hanson & Hitz 1982). Additional benefits of greater L_p and ϵ might include increased drought tolerance due to improved tissue water storage capabilities.

In a leafy succulent such as *S. calceoliformis*, water storage within leaf tissue is adaptive to surviving periods of decreased water availablity. Although individuals of the two growth forms of *S. calceoliformis* normally grow in different areas of Big Salt Marsh, seedlings of both forms typically become established in late March to early May when water levels in the marsh are high and salinities are low, and both are subjected to decreasing water availability and increasing salinity as the growing season progresses. Greater L_p and ϵ could thereby, through maintenance of high tissue water content, facilitate water storage in succulent tissue and provide prostrate individuals with increased ability to tolerate periods of low water availability. Thus, greater L_p and ϵ in prostrate individuals provides an explanation for the difference in leaf succulence between prostrate and erect individuals at high salinities (e.g. >1·0% NaCl), prostrate individuals having noticeably more-succulent leaves at a given salinity than erect individuals (A. L. Youngman & S. A. Heckathorn, unpublished observation; Fig. 1).

Decreases in tissue elasticity can result from increases in cell wall thickness, lignification, or cell size (Steudle, Zimmermann & Luttge 1977; Zimmermann & Steudle 1978; Tyree & Jarvis 1982). Salinity is known to induce such responses in halophytes (Poljakoff-Mayber 1975; Jennings 1976). The mechanism by which tissue elasticity is decreased in *S. calceoliformis* is unknown. Regardless of the mechanism, it would appear that decreases in tissue elasticity, along with greater hydraulic conductance, result in maintenance of higher %R and ψ_p in the prostrate growth form of *S. calceoliformis* and may play a role in increased tolerance to salinity relative to the erect form.

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