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Osmotic potential and turgor maintenance in *Spartina alterniflora* Loisel.

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Summary. The dependence of leaf water potential (ψ), osmotic potential (π) and turgor pressure (P) on relative water content (RWC) was determined for leaves of tall and short growth forms of *Spartina alterniflora* Loisel. from a site on Canary Creek marsh in Lewes, Delaware. Tall plants (ca. 1.5 m) occured along a drainage ditch where interstitial water salinity was approximately 20‰, and short plants (ca. 0.2 m) were 13 m away near a pan and exposed to 80‰ salinity during the most stressful period. Leaves were collected at dawn and pressure-volume measurements were made as they desiccated in the laboratory. Pressure equilibrium was used to measure ψ, RWC was determined from weight loss and dry weight, π was determined from the pressure volume curve, and P was calculated as the difference between ψ and π. Physical properties of the bulk leaf tissue that have a role in regulating water balance of the two growth forms were estimated: relative water content of apoplastic water (RWC_a) relative water content at zero turgor (RWC_0), the bulk modulus of elasticity (E), and water capacity (C_w). There were no detectable temporal trends in any of the parameters measured from June through September and no significant differences between the two growth forms when compared on the basis of RWC_a, RWC_0, E, and C_w. There was a clear difference between the two growth forms with respect to π; at RWC_0, π was -4.5 ± 0.40 MPa for short form plants and -3.3 ± 0.40 MPa for tall form.

Turgor pressure of plants in the field (P') was lower in leaves from short form than for the tall form plants with average difference of about 0.4 MPa. In July, P' in short form leaves dropped to zero by mid-morning as expected for leaves experiencing water stress.

These results show that *S. alterniflora* is capable of reducing osmotic potential in response to increased salinity and that turgor pressure was lower in short growth form than in tall forms.

Introduction

Spartina alterniflora Loisel. is the dominant higher plant species throughout Atlantic coastal salt marshes (Reimold 1977). Its primary productivity declines with increasing latitude (Turner 1976) and is highly variable within marshes (Gallagher et al. 1980). Throughout its range, reduction of plant height and of biomass production of *S. alterniflora* correlates with gradients in several factors including salinity, drainage, soil anoxia, pH, redox potential, and soil phytotoxins (Howes et al. 1981; Linthurst 1979; Mendelssohn et al. 1982; Nestler 1977). Tall form plants are found along creekbanks where drainage and soil aeration are most favorable and salinity is near that of sea water. Short growth form plants occur away from creekbanks toward the interior of marshes in finely textured soils where drainage is poor, aeration low, and salinity high. Physiological mechanisms that have been proposed to account for the effect of soil anoxia and salinity on height and biomass production in *S. alterniflora* include the following: inhibition of the uptake and metabolism of nitrogen (Morris 1980; Mendelssohn et al. 1982), significant loss of carbon skeletons resulting from anerobiosis (Mendelssohn et al. 1982), direct inhibition of plant growth by phytotoxins, especially hydrogen sulfide (King et al. 1982), and failure of osmoregulation (Cavalieri and Huang 1981).

Daytime water potentials (ψ) of leaves of salt marsh species are low. Ustin et al. (1982) report both midday and dawn values of ψ for three San Francisco Bay salt marsh species declined through the summer and minimum daytime values were less than -4.5 MPa in September. Daytime leaf water potentials in Chesapeake Bay brackish salt marsh species were typically -2.5 to -4.5 MPa and daytime leaf water potentials for *S. alterniflora* in marshes along Delaware Bay were -3.5 to -5.5 MPa with ψ of short form plants less than ψ for tall form plants (B.G.D. unpublished data). Short form *S. alterniflora* in a South Carolina marsh also had lower midday water potentials than tall form plants (Cavalieri and Huang 1981). Low water potential may be an indication of water stress when it results from volume loss because turgor pressure would also be reduced. But low water potential is also an indication of acclimation or adaptation to water stress when accompanied by an equivalent reduction in osmotic potential which can mediate maintenance of leaf water volume and turgor pressure. Thus, the measurement of relatively low leaf water potential in different species or different ecophenes of the same species without the measurement of osmotic potential as well does not permit one to distinguish between water stress and acclimation to water stress.

Spartina alterniflora appears to be capable of excluding salt (Smart and Barko 1980), accumulating it in the leaf tissue in response to increased salinity of root medium (Nestler 1977), and of extruding it onto leaf surfaces through salt glands (Anderson 1974).

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Osmoregulation occurs in some species when tissue osmotic potential declines in response to an increase in soil salinity (Turner and Jones 1980) with the resultant control of water volume and maintenance of turgor pressure (Jeffries 1981). Osmoregulation could therefore be expected to result in reduction of osmotic potential and water potential accompanied by maintenance of turgor pressure in different growth forms of *S. alterniflora* adapted to a range of soil interstitial water salinities. Wyn-Jones et al. (1977) proposed a model for osmoregulation in which Na^+ accumulates in the vacuole and organic osmotica (primarily betaine and proline) accumulate in the cytoplasm of cells in shoot tissue of *Spartina* × *townsendii*, a species developed from the cross of *S. alterniflora* with *S. maritima*. If osmoregulation fails to occur (due either to inhibition of Na^+ uptake or accumulation of organic osmotica or both) when interstitial water salinity increases, bulk leaf turgor pressure would fall with the probable consequence of reduced leaf expansion (Bradford and Hsiao 1982).

Cavalieri and Huang (1981) suggest that the failure of osmoregulation in short form *S. alterniflora* results in reduced growth. Growth depends in part upon maintenance of turgor pressure above some critical level (Bradford and Hsiao 1982), so if this hypothesis applies to the observed differences in height of *S. alterniflora*, then turgor pressure in short form plants ought to be lower than turgor pressure in tall forms. To test this dependence, we have characterised the water relations of both height forms growing a few meters apart in a coastal tidal marsh. In this paper we report measurements of leaf water potential, osmotic potential, turgor pressure, and other aspects of the water relations of the bulk leaf tissue.

Methods

Study site. Leaves were collected from populations of *Spartina alterniflora* on Canary Creek marsh near the mouth of the Broadkill River where it enters Delaware Bay at Lewes. Biomass production and plant height decline along a transect from the edge of drainage ditches to the interior of the marsh (Morgan 1961). Between the ditches there are zones, called pans, where there is no vegetation. Tall plants (1.0–1.5 m) were collected along the ditch and short plants (less than 0.25 m) were found along the margin of a pan approximately 13 m from the ditch bank. These growth forms have been viewed by some as genetically distinct groups and by others as evidence of the environmental control of growth and development of a single genotype. Because we wanted to establish whether the response to soil environment causes the hypothesized effects on the water relations of the plants, we also collected leaves from both growth forms established for four years in a common garden at the Lewes, Delaware campus of the College of Marine Studies. Some measurements were also made on plants one month after being transplanted from the common garden back to the field sites.

Theory. Leaf water potential (ψ) consists of two components, osmotic potential (π) and turgor pressure (P) (Tyree and Jarvis 1982). Turgor pressure of bulk leaf tissue cannot be measured directly and its determination depends on measurements of ψ and π. When leaf water content drops to a volume at which turgor pressure is zero, ψ is functionally identical to π and the volume dependence of π in a leaf can be determined from measurements of ψ and RWC (Tyree and Jarvis 1982). The relationship between π and relative water content (RWC) can be extrapolated to plant water content where $\psi = P + \pi$ and P is determined as $\psi - \pi$.

ψ is equal to the equilibrium pressure required to bring liquid water to the cut surface of a leaf enclosed in a pressure bomb; the application of the pressure bomb to the measurement of the components of the leaf water potential has been discussed (e.g., Tyree and Hammel 1972; Wilson et al. 1979). RWC, the volume of water in the plant at any water content as a fraction of the volume of water at full hydration, is calculated as in Wilson et al. (1979) and Ladiges (1975). Leaf water potential was measured using a pressure bomb (Soil Moisture Corporation, Model 3000) with a binocular microscope attached. Leaf weight was measured on a Mettler balance.

Procedure. Leaves were collected before dawn to insure full hydration, quickly sealed in test tubes with cut surfaces in distilled water, returned to the laboratory, and kept in darkness at constant temperature for two hours. At the beginning of an experiment a leaf was wiped dry, cut to 19 cm length, weighed, and inserted into a length of 1.0 cm wide dialysis tubing, leaving the cut end of the leaf extending beyond the tubing approximately 0.5 cm. The opposite end of the tubing extending beyond the leaf tip was folded to prevent entry of gas from the pressure chamber into the aerenchyma in the leaf. The leaf enclosed in the dialysis tubing was sealed into the pressure bomb, the pressure elevated at a rate of 0.3 to 0.5 MPa min^{-1}, and the cut surface examined through the binocular microscope. When the cut surface darkened as equilibrium pressure was approached, the increase of pressure was slowed. After equilibrium pressure was obtained and recorded, pressure was reduced about 0.2 MPa, and the equilibrium pressure was very slowly approached to verify its determination. Pressure was then slowly reduced, the leaf removed from the bomb, and weighed again. The weight corresponding to each equilibrium pressure was taken to be the average of the weight before and after pressurization.

About 12 min were needed to complete one measurement of leaf weight and ψ, and the total number of measurements obtained per leaf was between 8 and 12 with at least four measurements in the region of $RWC < RWC_0$. Between determinations of ψ, leaves were allowed to dessicate at room temperature on the laboratory bench. Leaf dry weight was obtained by drying at 60 C for 24 h.

Field measurements. Two warm sunny days (30 June and 27 July) were selected for measurements of time course of ψ. A leaf was collected, immediately inserted into the dialysis tubing, and its ψ determined in the pressure bomb. Six to ten leaves were measured to obtain a representative value for ψ for the population of each growth form at each sampling time. Sampling was started near sunrise and continued at intervals of 1–2 h through the day.

Calculation of results. Pressure volume curves were constructed by plotting ψ^{-1} as the dependent variable and RWC as independent variable (see Fig. 2). Relative water content at zero turgor pressure (RWC_0) was determined by inspection of the pressure volume curve. The linear dependence of π on RWC was obtained by regression of ψ^{-1}

on RWC for $0.70 > \mathrm{RWC} > 0.45$ and this linear relationship was extrapolated to $\mathrm{RWC} > \mathrm{RWC}_0$ to obtain the value of π^{-1} at each measured value of ψ in the region of RWC where $\psi = P + \pi$. The value of RWC at the intercept of the linear portion of the curve extrapolated to $\psi^{-1} = 0$ gives an estimate of apoplastic water ($\mathrm{RWC_a}$). A power function was fit to the data for the dependence of P on RWC for $\mathrm{RWC} > \mathrm{RWC}_0$:

$$P = a(\mathrm{RWC} - \mathrm{RWC}_0)^b \quad \text{(MPa)} \tag{1}$$

and the modulus of elasticity (E) was calculated as the first derivative of this function:

$$E = \frac{dP}{d\mathrm{RWC}} = ab(\mathrm{RWC} - \mathrm{RWC}_0)^{b-1} \quad \text{(MPa)} \tag{2}$$

The water capacity (C_w), change in the water volume (V) per unit change in leaf water potential, was determined as the quotient of V by E plus π (Dainty 1976; Molz and Ferrier 1982)

$$C_w = dV/d\psi = V/(E + \pi) \quad (\mathrm{mg\ MPa^{-1}}) \tag{3}$$

For this calculation, values for V, E, and π were selected at $P = 0.4$ MPa.

Results

1. *Plant height, biomass, and soil salinity.* Salinity, plant height, biomass, and spatial relationship of the height forms at the study site are compared in Fig. 1. Plant height and biomass decline sharply as interstitial water salinity increases. Leaves of tall plants were collected from the drainage ditch (first location on left of the figure) and leaves from short plants from the margin of a pan (location at 13 m from the center of the ditch).

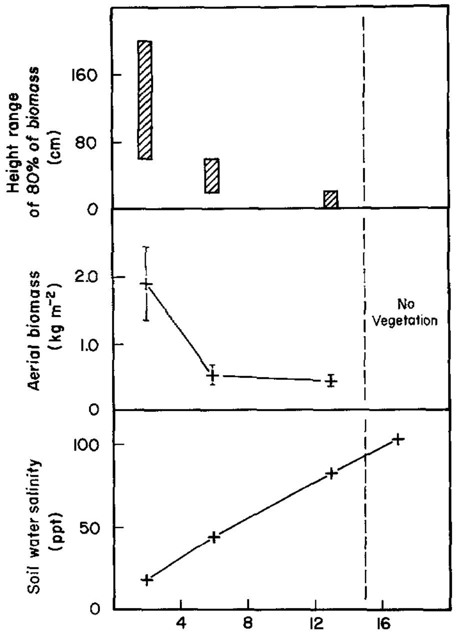

Fig. 1. Relative plant height, biomass, and interstitial water salinity along a transect from a drainage ditch to a pan on Canary Creek Marsh, Delaware

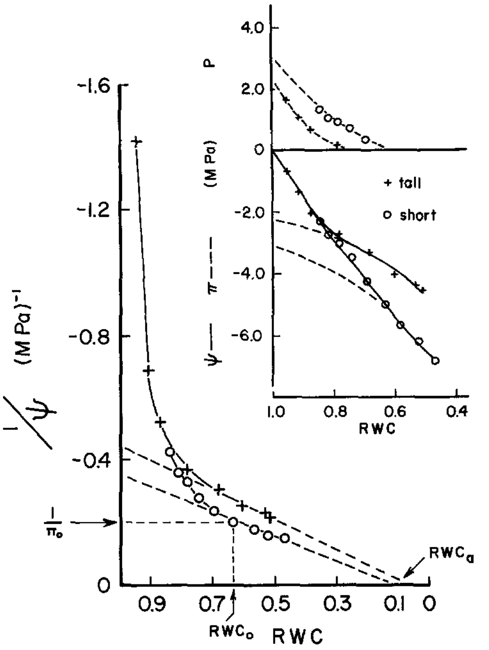

Fig. 2. Pressure volume curves for a leaf from the short (o) and tall (+) populations of *Spartina alterniflora*. The inset shows the relationship between relative water content (RWC), leaf water potential (ψ), osmotic potential (π), and turgor pressure (P)

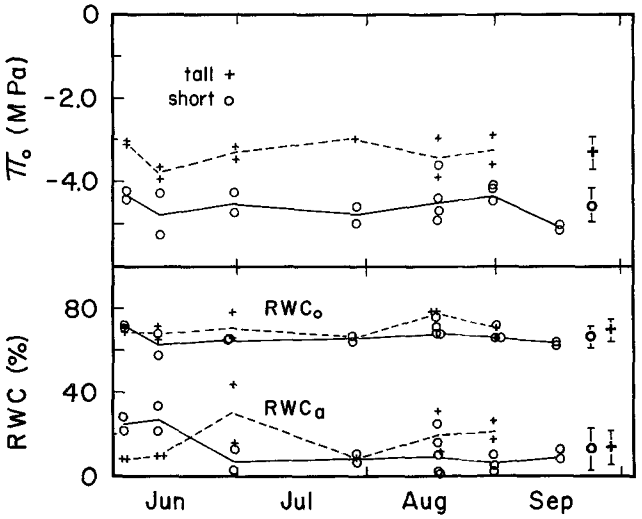

Fig. 3. Seasonal trend in RWC_0, $\mathrm{RWC_a}$, and π_0, for short (o) and tall (+) growth form *Spartina alterniflora*

The data shown in Fig. 1 were collected in October and probably represent the most severe conditions of the year because salinity late in the season tends to be higher than early in the year.

2. *Pressure volume curve.* Data on ψ and RWC were used to construct the pressure volume curve in Fig. 2. The data were obtained from a single leaf from the short population (o) and a single leaf from the tall population (+) both collected on June 29, 1982. The linear regression of ψ^{-1} against RWC was obtained for each leaf individually. Below RWC values of 0.45, ψ^{-1} values tended to depart from the linear relationship. The behavior of π, ψ, and P with

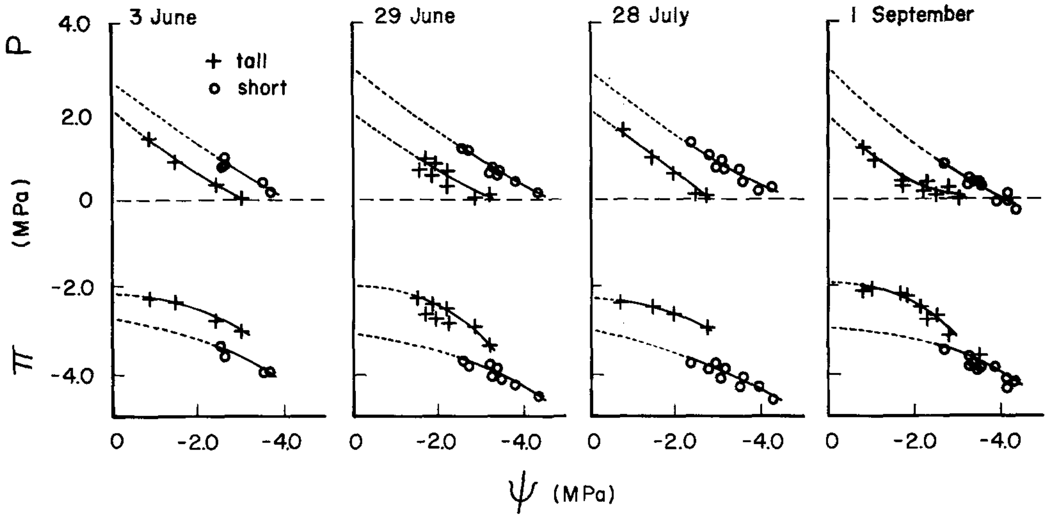

Fig. 4. The dependence of P and π and ψ for short (o) and tall (+) growth form *Spartina alterniflora*

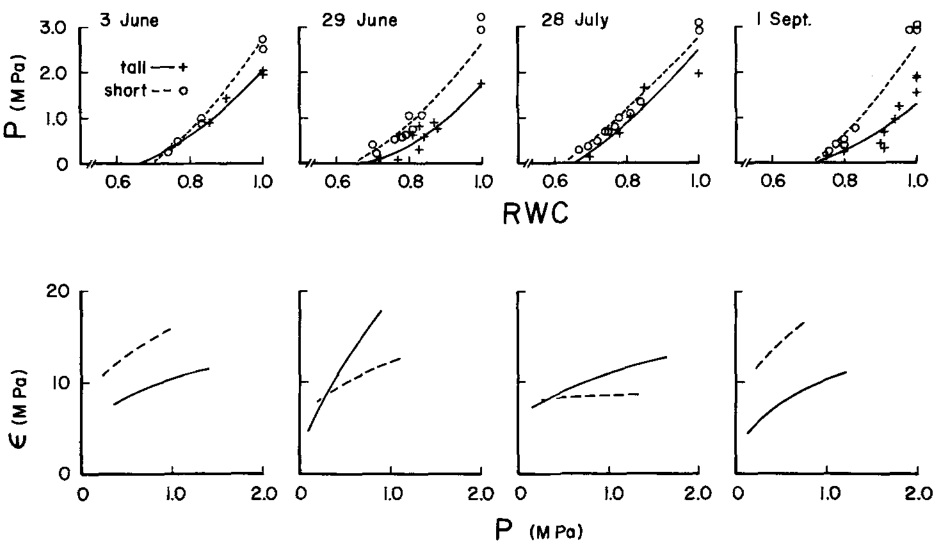

Fig. 5. The dependence of P on RWC and the dependence of E on P for the same data set. E was determined as the first derivative of the power function describing the dependence of P on RWC (Equation 4)

respect to RWC is shown in the inset of Fig. 2. All data on π, RWC, RWC_0, RWC_a, E, and C_w in this paper are derived from such pressure volume curves constructed for each leaf separately.

3. *Seasonal trend in* RWC_0*,* RWC_a*, and* π_0. Values of the relative water content at zero turgor (RWC_0), the relative water content of the apoplastic water fraction (RWC_a), and the osmotic potential at zero turgor (π_0) from experiments between June and September are shown in Fig. 3. There was no detectable seasonal trend in any of these for leaves from short or tall form plants and no statistically significant differences between the two growth forms for either RWC_0 or RWC_a. The seasonal mean value was 0.71 ± 0.062 for RWC_0 and 0.14 ± 0.09 for RWC_a. The value RWC_a was more variable because small changes in the slope of the line ($\Delta\psi^{-1}/\Delta\mathrm{RWC}$) give relatively larger changes in RWC_a than in RWC_0. There was a statistically significant difference ("τ" test; $P < 0.01$) between the mean values of π_0 for the two growth forms. Seasonal mean value of π_0 for leaves from short form plants was -4.5 ± 0.4 MPa and for leaves from tall plants, -3.3 ± 0.4 MPa. The range of osmotic adjustment required to maintain full turgor in different species in response to water stress imposed over periods of days to weeks appears to be 1.0 to 2.0 MPa (Turner and Jones 1980).

4. *Dependence of* π *and* P *on* ψ. Tall and short form plants are compared in Fig. 4 for the dependence of π and P on ψ in four experiments at about equal intervals throughout the season. Second order polynomial regressions were fit to the data. The purpose of this determination was to use the ψ of field plants to estimate P' of leaves in the field at different times of the day from the pressure volume data obtained from leaves collected at dawn.

5. *Relationship between P and RWC.* Mean and standard deviations of coefficients for the power function (Equation 3) for the dependence of P on RWC were $a = 9.97 \pm 4.0$ and $b = 1.19 \pm 0.24$ for the short form; $a = 9.90 \pm 4.8$ and

Table 1. Seasonal means and standard deviations ($N=12$) for water capacity, $C_w = V/(E+\pi)$ (mg MPa^{-1}) estimated for short and tall growth forms of *S. alterniflora* for June through August. *V*, *E* and π were determined at $P=0.4$ MPa

	E	π	C_w
Short	7.14±1.47	3.98±0.32	12.9±3.25
Tall	7.32±1.45	2.92±0.38	9.09±4.4

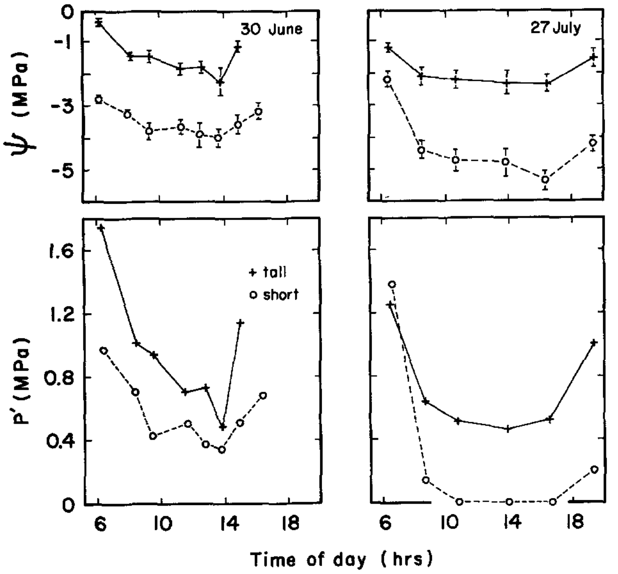

Fig. 6. Daily time courses for leaf water potential (ψ) and turgor pressure (P') in the short (o) and tall (+) growth forms of *Spartina alterniflora*. P' was determined by applying the daytime values for ψ (Fig. 6) to the appropriate function describing the dependence of P on π (Fig. 4). Values are means ($N=5$) and standard deviations

$b=1.24\pm0.23$ for the tall form. The departure of the value for b from 1.0 indicates the non-linear dependence of P on RWC. The dependence of P on RWC shown in Fig. 5 was computed from data shown in Fig. 4. At any value of RWC > RWC$_0$, P was lower in the tall form plants than in the short form plants.

6. *Modulus of elasticity.* In the lower half of Fig. 5 the behavior of the function, $E=dP/d\text{RWC}$ (first derivative of Equation 4) is shown opposite P for the range of P measured for each experiment and excluding the value of P when $\psi=0$. In the range of values of P from 0 to 1.5 MPa, the values of E are approximately 5–18 MPa for tall form plants and 8–17 MPa for short form plants. Dainty (1976) quotes values of E for higher plants in the range 5–20 MPa with shrubs and tree species having highest values.

7. *Water capacity (C_w).* An estimate of C_w (change in leaf water volume per unit change in ψ) is given by Equation 3. Values for π and E were selected at $P=0.4$ MPa, a value which was observed to occur under field conditions. Seasonal mean values of C_w for the two growth forms are 12.85 ± 3.25 mg MPa^{-1} for short and 9.09 ± 4.4 mg MPa^{-1} for tall form plants (Table 1). The difference between the values of C_w for the two growth forms reflects the influence of the different values of π, but differences between the growth forms with respect to C_w are not statistically significant. The values of C_w translate to approximately 7% loss of leaf water for short form and 8.5% for tall form per MPa reduction of leaf water potential.

8. *Daily time course of ψ and P' of plants in the field.* ψ was determined at intervals throughout the day on June 30 and July 27 (Fig. 6). Leaf water potentials compared at the same time of day averaged 2.1 MPa higher in tall plants than short on June 30 and 2.4 MPa higher on July 27. The reduction in ψ from dawn until midday was 1–3 MPa and this represents a loss of from 7–24% of leaf volume as estimated from the values of C_w computed above.

Estimated values of turgor pressure (P') throughout the daytime (Fig. 6) were obtained by applying values of ψ (measured in the field at the time indicated) to the second order polynomial regressions obtained in the laboratory experiments (Fig. 4). Turgor was maintained on both the June and July sampling dates in the tall form plants, but only on the June sampling date in the short forms. The average difference between the turgor pressure of the two growth forms estimated in this manner was approximately 0.40 MPa on June 30 and somewhat greater on July 27.

9. *Plants from a common garden.* Leaves of short and tall form *S. alterniflora* were collected on June 16 from representatives of the two growth forms in a common garden. Plants had been growing at this site for four years and watered with sea water approximately three times weekly. The large difference in height and production of these two growth forms noted in the field (Fig. 1) was reduced in the plants in the common garden but not eliminated, and the origins of the respective transplant groups were still apparent in their height differences in the common garden. Data for the results of the pressure volume analysis on three leaves from each growth form are shown in Table 2. There were no significant statistical differences between values obtained for RWC$_0$, RWC$_a$, E, and C_w of the plants from the common garden and the short and tall growth form plants from their respective native sites in the field. Values of π_0 (-3.44 and -3.64 for a short and tall forms) were within one standard deviation of the mean value of π for short form plants from the field site (Fig. 3).

10. *Transplant experiment.* Plants from the common garden were transplanted to the field site on June 30 and ψ was measured at midday on July 27, shown in Table 3. The differences between ψ for both short and tall form transplants reflect the differences between ψ for the indigenous short and tall plants (Fig. 6).

Table 2. Comparison of π_0 (MPa), RWC$_0$, RWC$_a$, and C_w (mg MPa^{-1}) for short and tall growth forms of *S. alterniflora* from a common garden. E and π were computed at $P=0.4$ MPa. Values are means ($n=3$)

	Short	Tall
π_0	−3.44	−3.64
RWC$_0$	0.70	0.67
RWC$_a$	0.24	0.19
E	6.05	5.64
C_w	14.1	13.2

Table 3. Transplant experiment. ψ (MPa) measured at noon on 27 July on leaves of short and tall form *S. alterniflora* transplanted to each site on 30 June. One leaf on each of three surviving plants for each treatment at each site was collected for ψ. Values are means ($N = 3$)

	Transplanted to	
	Dieback site with short forms	Ditch site with tall forms
Growth forms from common garden	ψ	ψ
Short	-5.3	-2.8
Tall	-5.3	-3.4

Discussion

Osmotic potential (π) of the two growth forms of *Spartina alterniflora* from the natural marsh field sites differs significantly when compared at relative water content (RWC) less than 0.8 (Fig. 2). This difference in π only partially accounts for the difference in ψ between the two growth forms under field conditions (Fig. 6). ψ and turgor pressure (P') of short form plants were lower than ψ and P' of tall form plants (Fig. 6). P' was maintained in tall form plants during June and July, but it was lower in short form than in tall form plants during both sampling periods (Fig. 7) and, during the July sampling date P' of short form plants, was reduced to zero by mid-morning.

Physical properties of the leaf which could affect the modulus of elasticity might be expected to respond to increased intensity of stress in salt marsh soils. Leaf tissue having relatively rigid cell walls would have large values of the modulus of elasticity and this would result in greater reduction in turgor pressure per unit loss of volume than would occur in leaves with small values of the constant (Dainty 1976; Tyree and Jarvis 1982). In both tall and short form plants, E declines with decreasing P. Values for E are typically in the range 5–20 MPa for herbaceous plants (Dainty 1976; Cutler et al. 1980a; Jones and Turner 1980). The factors in the environment of this plant, such as increased salinity, that result in an accumulation in osmotica with accompanying reduction in osmotic potential bring about no apparent change in the modulus of elasticity. Whether or not E changes in response to drought stress in leaves is unclear from the available evidence as Cutler et al. (1980a) found no effect of drought conditioning on E in rice and Jones and Turner (1980) report no effect of water stress treatment on E in sunflower although water stress did produce a reduction of E in sorghum while E measured in shoots of woody plants did respond to water stress (Tyree and Jarvis 1982).

The relative effectiveness of reduction of π and of E in the control of volume changes in the plant can be estimated by the water capacity (C_w). In *S. alterniflora* as in most other species, E is the controlling parameter because at the same turgor pressure, E is approximately twice the value of π (Table 1). Not surprisingly, therefore, the loss in volume per unit reduction in ψ (ca. 9–13 mg MPa^{-1}) is similar for the two growth forms (Table 1). Thus, the reduction of ψ between dawn and midday (1–3 MPa for both growth forms, Fig. 6) was caused by an estimated reduction in RWC of the order of 7 to 24 percent.

The absense of temporal variation in the data on osmotic potential at zero turgor pressure (Fig. 3) raises the question whether the factors in the environment which are hypothesized to affect changes in tissue osmotic potential are also constant with time. Interstitial water salinity in soils of the short form of *Spartina* is not constant with time as shown by data reported by Gallagher and Daiber (1974) for the Canary Creek marsh. Salinity in the field sites where the short form grows was extremely variable with the week to week range being from less than $20^0/_{00}$ to over $50^0/_{00}$, but salinity along the ditches remained at or slightly below sea-water concentration (Gallagher 1971). Plants along the ditch banks may not be exposed to a fluctuating soil water potential sufficient to produce a severe reduction of leaf water potential and to require a reduction in tissue osmotic potential. Plants growing in the sites away from the ditches toward the interior of the marsh may be exposed to fluctuating salinity and may be unable to adjust osmotic potential either because they are unable to assimilate nitrogen needed for production of cytoplasmic osmotica as suggested by others (Cavalieri and Huang 1981; Cavalieri 1983), or because the changes in soil water potential occur too rapidly for the plant to affect the needed changes in concentrations of osmotica.

Measurements on plants from the common garden show that the osmotic potential of both the short and tall forms of *S. alterniflora* can change in response to environmental factors, perhaps salinity (Table 2). Osmotic potentials of plants in the two field sites differed significantly from osmotic potentials of plants in the common garden (Table 2). Plants from the common garden that were returned to the field site had water potentials similar to those of the plants in the sites to which they were transplanted after one month of growth (Table 3). Cavalieri (1983) showed that proline and glycine betaine concentrations in leaves of *S. alterniflora* increased rapidly in plants grown in high salinity (0.5 M) at low light intensity if the leaves were supplied with high nitrogen (i.e., > 14.0 mg l^{-1}).

Osmoregulation in *S.* × *townsendii* (and by extrapolation, this probably applies to *S. alterniflora*) includes accumulation of inorganic osmotica, presumably salt, in the vacuole, and accumulation of proline and glycine betaine in the vacuole and the cytoplasm (Cavalieri and Huang 1981; Storey and Wyn Jones 1978). The organic osmotica, which appear to be non-toxic to cytoplasmic enzymes (Cavalieri 1983; Stewart and Lee 1974), contain about 12% nitrogen and the fraction of total soluble leaf nitrogen associated with these compounds in *S. alterniflora* leaves may reach 20%. Although nitrogen is abundantly available in the soil environment of short form *S. alterniflora* (Chalmers 1979), these plants show nitrogen deficiency symptoms (Mendelssohn 1979; Mendelssohn et al. 1982). Factors common to its environment (including anoxia and redox potential, salinity, and hydrogen sulfide) have been proposed to influence the uptake of nitrogen by *S. alterniflora* (Howes et al. 1981; King et al. 1982; Linthurst 1979; Mendelssohn et al. 1982; Morris 1980). In the sites where production is reduced, the demand of *osmoregulation* for nitrogen may exert a severe drain on the nitrogen reserves of the plant. To the extent that reduction of turgor is accompanied by reduced growth, our data are thus consistent with the hypothesis that nitrogen deficiency is partially expressed through a failure of osmoregulation (Cavalieri and Huang 1981).

Reduction of leaf water potential and turgor pressure may reduce plant height if it results in reduction of expansive growth. Leaf elongation rate in rice was markedly reduced when plants were exposed to either rapid or slow reduction of leaf water potential and this occurred even though turgor was maintained (Cutler et al. 1980b). Leaf elongation in corn, soy bean, and sunflower ceased at water potentials much higher than those required to produce an effect on photosynthesis (Boyer 1970). Leaf elongation rate in corn was inhibited as leaf water potential and turgor pressure declined even though turgor pressure was maintained in the zone of elongation (Michelena and Boyer 1982).

Conclusions

Osmoregulation in *Spartina alterniflora* was sufficient to maintain turgor pressure in short forms compared to the more productive, taller growth forms. The reduction in osmotic potential in either growth forms of plants from field sites or from a common garden was not accompanied by changes in the physical properties of the bulk leaf tissue having an effect on turgor pressure. Although osmotic potential was reduced in short growth form plants, this reduction was not sufficient to maintain turgor pressure equal to that in the tall forms.

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