Osmotic and Turgor Relations of
Three Mangrove Ecosystem Species

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Abstract

The water relations of three mangrove ecosystem species, *Rhizophora mangle, Conocarpus erectus* and *Coccoloba uvifera* were investigated in an intertidal zone of the Venezuelan coast. The influence of a salinity gradient (from seashore to inland) and seasonal fluctuations in salinity were studied. Daily courses of leaf water and osmotic potentials and other water relations characteristics were estimated from pressure-volume curves. All species exhibited a decrease in osmotic potential of leaf tissues during the dry season when salinity levels increased in ground water. This osmotic adjustment was due to changes in either the symplasmic water fraction, the osmotically active solutes in leaf cells, or both. Changes in cell wall elasticity were also observed. The cell walls were more rigid during the dry season in all three species. *Rhizophora mangle*, the species that grows closest to the sea, had much more rigid cell walls than the other two species. The adaptive significance of these mechanisms for turgor maintenance and water uptake in mangrove habitats is discussed.

Introduction

Mangroves are woody species that grow successfully in the interface between land and sea. Subjected to regular flooding by sea water, these plants have to maintain positive leaf turgor pressures in the presence of high salt levels in ground water. Plants can respond to the low soil water potentials produced by salinity by accumulating osmotically active solutes in leaf cells (Tyree and Hammel 1972; Turner and Jones 1980; Popp 1984a, 1984b), or by decreasing the symplasmic water fraction of the leaf tissue resulting in an increase in cellular solute concentration (Wilson *et al.* 1980; Tyree and Jarvis 1982; Pavlik 1984). Changes in elasticity of cell walls may be also responsible for turgor maintenance (Zimmermann 1978). As cell wall elasticity translates changes in relative water content to changes in turgor potential, either a decrease or an increase may lead to turgor maintenance (Meinzer *et al.* 1986). For example, cells which increase their elasticity are able to maintain higher turgor pressures at lower water contents. On the other hand, a decrease in elasticity would induce turgor loss at relatively high water content but would produce a greater water potential difference between leaf and soil and thus increase rates of water uptake and transport.

We have chosen in this study three mangrove ecosystem species that grow along a salinity gradient in Venezuelan Caribbean coastal environments, from flooded soils at the seaward end to inland, less saline, soils. In these environments studied, mangrove trees are also subjected to seasonal fluctuations in substrate salinity due to the diluting effect of precipitation during the wet months. Ground water salinity in the rooting zone is thus dependent on location and season.

The purpose of this study was to investigate the mechanisms exhibited by three mangrove ecosystem species in order to adapt to differing levels of salinity and water stress.

Materials and Methods

Field Site and Plant Material

The study site was located in Morrocoy National Park in northern Venezuela ($10°50'$N, $68°14'$W), which receives an annual average precipitation of 1053 mm distributed bimodally with peaks in October and April and a dry season from May to August. The mean annual temperature is approximately $26·5°C$ with little seasonal variation between the warmest and coolest month. The vegetation is dominated by *Coccoloba uvifera* (L.) Jacq., a conspicuous constituent of the intertidal communities in the study area and four mangroves: *Rhizophora mangle* L., *Conocarpus erectus* L., *Avicennia germinans* L. and *Laguncularia racemosa* (L.) Gaertn.

Rhizophora mangle grows at the seaward edge where salinity is high and tidal fluctuations are relatively great. This species experiences regular flooding and the most exposed plants grow with their roots completely submerged in sea water. *Conocarpus erectus* occupies sites on the coast line where soils are not permanently flooded, while *C. uvifera* grows further inland where salinity is lower and tidal amplitudes are smaller.

Field Water Relations

Diurnal changes in leaf water potentials (Ψ_l) were measured several times over the period July 1985 to July 1986. Leaf water potential was estimated from pressure chamber measurements approximately every 2 h for 48 h. Soil water samples were obtained from tubes buried to a depth of $1·5$ m in the soil at each sampling site along the salinity gradient. These water samples, which were always taken from the water table, were pipetted with a Teflon tube, placed in plastic vials, and kept on ice until brought to the laboratory for measurements described below. We have estimated ground water potential (Ψ_{soil}) from measurements of Na^+ concentration in ground water. These estimates of soil water potential correspond with the predawn leaf water potential values that we assume are reliable estimates of soil osmotic potential. NaCl concentrations obtained in ppm or molarity were transformed to values of osmotic potential using conversion tables (Slavik 1974). Air and leaf temperatures were measured with copper–constantan thermocouples and relative humidity was measured with an Assman aspirated psychrometer.

Pressure-Volume Curves Analysis

Leaf water potential components of small branches were determined from pressure–volume curves (Tyree and Hammel 1972). As Meinzer *et al.* (1986) reported differences on the order of $2·0$ MPa in the osmotic potential of the desert shrub *Larrea tridentata* depending on whether or not the cut shoots had been previously hydrated, two methods were used. In the first, small branches of the three species were cut under water in the field and left hydrating for 24 h covered with polyethylene bags. In the second, the cut branches were not hydrated but immediately enclosed in polyethylene bags.

The following day all branches were quickly weighed and the initial balancing pressure was determined with the pressure chamber. The small branches were allowed to transpire freely on the bench top, then reweighed, and a new balancing pressure was measured. This cycle was repeated until several points on the linear portion of the pressure–volume curve had been obtained. The data of individual curves from different branches were plotted as $1/\Psi_l$ v. the relative water content (RWC). From these pressure–volume curves average values of osmotic potential at full turgor (Ψ_π^{100}) and at turgor loss (Ψ_π^0) were obtained (Tyree and Richter 1981). Turgor potentials for each branch were estimated from field Ψ_l minus Ψ_π determined from the pressure–volume curves at that Ψ_l. The values of symplasmic water content (SWC) are given by:

$$SWC = (W_0 - W_e)/W_0,$$

where W_0 is the weight of symplasmic water at full hydration and W_e is the weight of water lost (turgid leaf weight – leaf weight) at the different pressures (Tyree and Jarvis 1982; Bolaños and Longstreth 1984). The symplasmic water fraction (SWF) was also calculated from the pressure–volume curves by:

$$SWF = W_0/W_t,$$

where W_t is the weight of total leaf water (turgid weight – dry weight) (Tyree 1981; Pavlik 1984). And finally, the bulk modulus of elasticity (ϵ) was calculated from:

$$\epsilon = \Delta P/\Delta((W_0 - W_e)/W_0),$$

where ΔP is the change in turgor and $\Delta((W_0 - W_e)/W_0)$ is the change in SWC (Tyree 1981; Pavlik 1984). The bulk modulus of elasticity was calculated as the mean of the slopes of all the pressure potential values from full hydration to turgor loss in the exponential portion of the pressure–volume curves.

Table 1. Osmotic potential at saturation, Ψ_π^{100} and turgor loss point, Ψ_π^0, obtained from pressure–volume curves for hydrated and non-hydrated leaves for the three species studied

Mean values $\pm$ standard errors, $n = 9$ for hydrated and $n = 7$ for non-hydrated samples

Species	Hydrated	Non-hydrated
Coccoloba uvifera		
Ψ_π^{100} (MPa)	$-2\cdot27 \pm 0\cdot21$	$-2\cdot03 \pm 0\cdot15$
Ψ_π^0 (MPa)	$-2\cdot54 \pm 0\cdot32$	$-2\cdot62 \pm 0\cdot23$
Conocarpus erectus		
Ψ_π^{100} (MPa)	$-2\cdot22 \pm 0\cdot13$	$-1\cdot81 \pm 0\cdot19$
Ψ_π^0 (MPa)	$-2\cdot51 \pm 0\cdot33$	$-2\cdot31 \pm 0\cdot22$
Rhizophora mangle		
Ψ_π^{100} (MPa)	$-3\cdot75 \pm 0\cdot33$	$-3\cdot40 \pm 0\cdot40$
Ψ_π^0 (MPa)	$-4\cdot23 \pm 0\cdot33$	$-3\cdot90 \pm 0\cdot14$
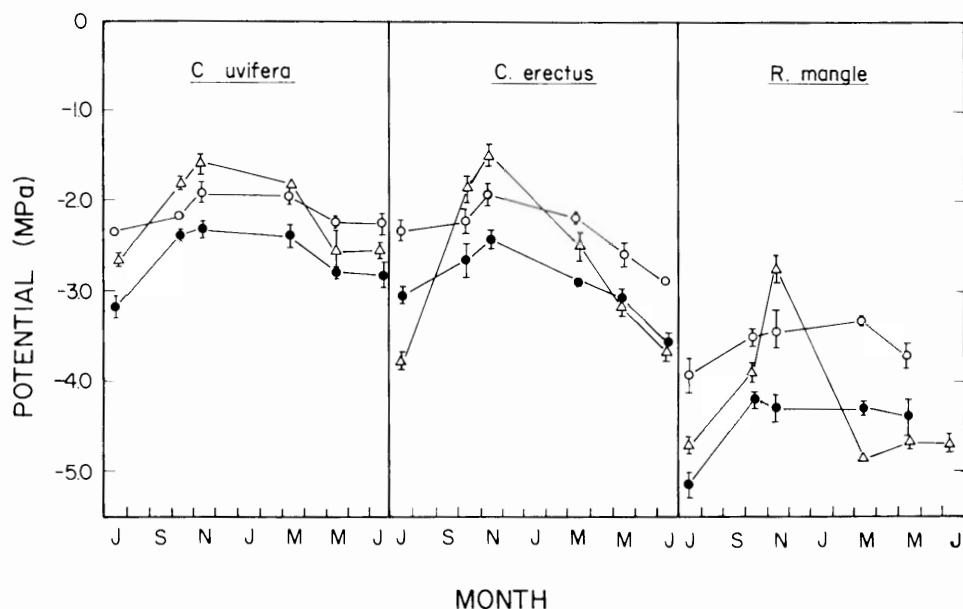
Fig. 1. Minimum leaf water potential ($\Psi_{l,min}$) (Δ), osmotic potential at saturation (Ψ_π^{100}) ($\bigcirc$) and at turgor loss point (Ψ_π^0) ($\bullet$) for the three species studied from July 1985 to July 1986 (May to July represent the dry season months). Vertical bars are standing errors ($n = 4$) for each of the three parameters. Absence of bars indicates that s.e. was smaller than the symbol.

Results

Osmotic potential at full turgor and at the turgor loss point were slightly higher in non-hydrated branches of the three species (Table 1). However, the degree of hydration of the branch samples did not significantly affect these water relation parameters.

Differences between fully hydrated and non-hydrated branches were less than $0 \cdot 3$ MPa for osmotic potential at full turgor and at turgor loss. The results in Table 1 are estimates of Ψ_π^{100} and Ψ_π^0 obtained with branches collected in October 1986. Similar results were obtained with branches collected in November 1986 (data not shown). Below we will consider only results obtained from hydrated branches because they furnish more points along the non-linear portion of the pressure–volume curve, facilitating the calculations of the modulus of elasticity.

Osmotic potential at saturation and osmotic potential at turgor loss and minimum daily leaf water potentials ($\Psi_{l,min}$) varied seasonally (Fig. 1). All three species exhibited a similar seasonal pattern with decreasing Ψ_π^{100} and Ψ_π^0 during the dry months. The difference in osmotic potential at turgor loss between the dry and wet seasons was approximately $1 \cdot 0$ MPa for all species. There was an approximately 20% decline in the levels of NaCl between November and July due to dilution of ground water by rain during the wet season. *Rhizophora mangle* exhibited the lowest $\Psi_{l,min}$ values throughout the year and *C. uvifera* the highest (Fig. 1). These two species grow at opposite extremes of the salinity gradient examined in this study.
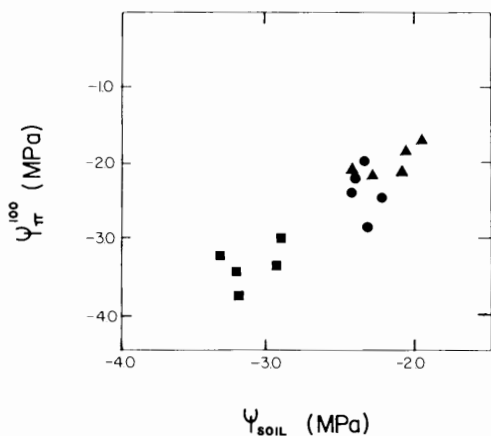

Fig. 2. Osmotic potential at saturation (Ψ_π^{100}) *v.* soil water potential (Ψ_{soil}) for *Rhizophora mangle* (■), *Conocarpus erectus* (●) and *Coccoloba uvifera* (▲).

The osmotic potential at full turgor and at the turgor loss point were similar for *C. uvifera* and *C. erectus* during the wet season, but became more negative in the latter species during the dry season. *Rhizophora mangle* maintained the most negative values throughout the year. Sampling dates for which $\Psi_{l,min}$ was below Ψ_π^0 indicate days in which turgor potential was zero at midday.

There was a linear relationship ($R^2 = 0 \cdot 81$) between ground water potential (Ψ_{soil}) and Ψ_π^{100} (Fig. 2). *Rhizophora mangle* exhibited the lowest Ψ_π^{100} and grows in soils with more negative Ψ_{soil}. *Coccoloba uvifera*, on the other hand, with more positive Ψ_π^{100} grows in soils with relatively high proportion of fresh water.

Seasonal changes of the turgor loss point and of the symplasmic water fraction occurred in all three species. Leaves with a lower SWF showed a more negative osmotic potential at the turgor loss point (Fig. 3). These species can be divided into two groups with respect to these variables: (i) *R. mangle* which has lower SWF and Ψ_π^0 values, and (ii) *C. erectus* and *C. uvifera* which have higher SWF and Ψ_π^0. There was more seasonal variation in SWF in *R. mangle* than in the other two species. The contribution both of variation in the level of osmotically active solutes and of the symplasmic water fraction to seasonal changes in leaf osmotic potential is presented in Table 2. The osmotic potential at full turgor decreased approximately $0 \cdot 35$ MPa between October and May
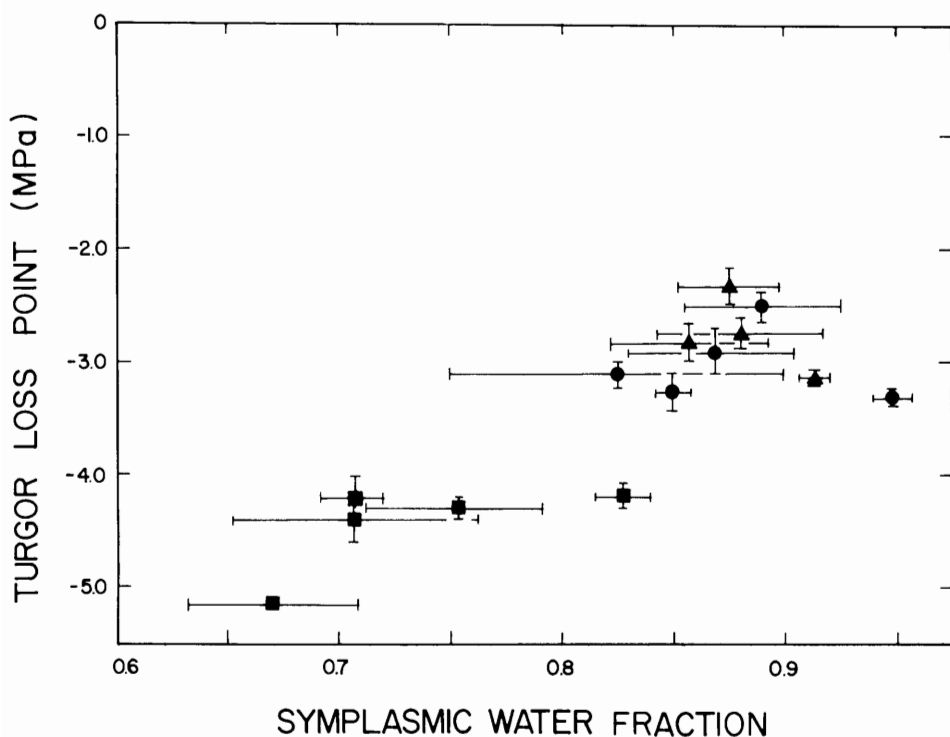
Fig. 3. Turgor loss point (Ψ_π^0) v. symplasmic water fraction (SWF) for *Rhizophora mangle* (■), *Conocarpus erectus* (●) and *Coccoloba uvifera* (▲). Vertical bars indicate the standard error for Ψ_π^0; horizontal bars indicate the standard error for the SWF ($n = 4$).

Table 2. Estimated relative contribution of the osmotic adjustment and changes in the symplasmic water fraction (SWF) to changes in the osmotic potential at saturation (Ψ_π^{100}) for the three mangrove ecosystem species

N_s/V_t is the number of osmomoles per total water volume and V_0 represents the symplasmic water volume (see Pavlik (1984) for details on calculations). Means ± standard errors for $n = 4$

Species	Ψ_π^{100} (MPa)	N_s/V_t	V_0/V_t	$\Delta\pi$ due to ΔV_0	$\Delta\pi$ observed	$\Delta\pi(\%)$ due to: SWF	Osmotic adjust-ment
Coccoloba uvifera							
Wet season	$-1\cdot91\pm\cdot05$	$0\cdot675\pm\cdot016$	$0\cdot877\pm\cdot014$	$0\cdot107$	$3\cdot30$	$3\cdot2$	$96\cdot8$
Dry season	$-2\cdot24\pm\cdot06$	$0\cdot794\pm\cdot019$	$0\cdot881\pm\cdot016$				
Conocarpus erectus							
Wet season	$-2\cdot15\pm\cdot04$	$0\cdot772\pm\cdot015$	$0\cdot891\pm\cdot011$	$1\cdot697$	$3\cdot80$	$44\cdot7$	$55\cdot3$
Dry season	$-2\cdot54\pm\cdot09$	$0\cdot845\pm\cdot024$	$0\cdot825\pm\cdot018$				
Rhizophora mangle							
Wet season	$-3\cdot47\pm\cdot05$	$1\cdot106\pm\cdot018$	$0\cdot828\pm\cdot007$	$2\cdot405$	$2\cdot70$	$89\cdot1$	$10\cdot9$
Dry season	$-3\cdot74\pm\cdot07$	$1\cdot170\pm\cdot020$	$0\cdot775\pm\cdot012$				

in all three species. Whereas seasonal variation in Ψ_π^{100} was similar for all three species, seasonal patterns in leaf SWF differed markedly between species. Using this information and the Boyle Van't Hoff equation it was possible to calculate the contribution of decreases in the symplasmic water content to the observed changes in osmotic potential (Pavlik 1984). *Rhizophora mangle* adjusted its Ψ_π^{100} almost entirely by a decrease of the symplasmic water fraction without a net increase in solute content (accounting for $89 \cdot 1\%$ of the change in Ψ_π^{100}), *C. uvifera* accumulated osmotically active solutes
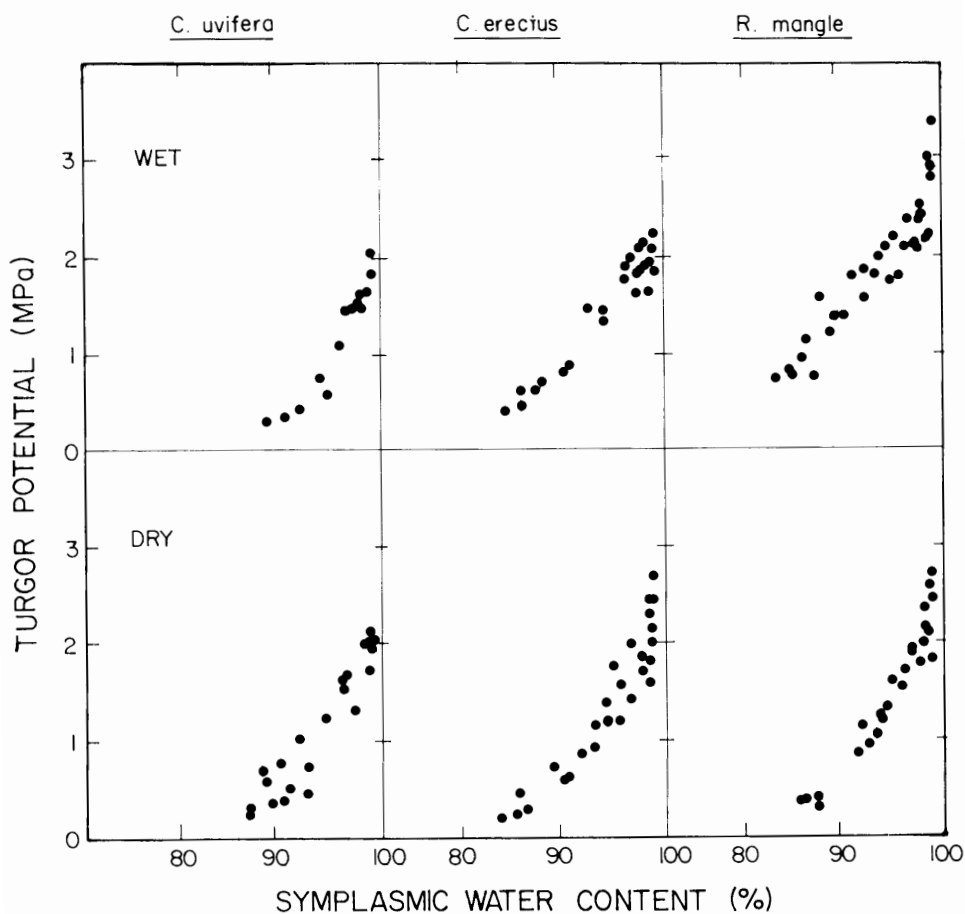

Fig. 4. Turgor potential *v.* symplasmic water content for the three species studied. Upper panels are for the wet season and lower panels for the dry season.

($96 \cdot 8\%$ of the change in Ψ_π^{100}), and *C. erectus* combined both ($44 \cdot 7\%$ due to a decrease of the symplasmic water fraction and $55 \cdot 3\%$ due to an increase in osmotically active solutes).

Relations between turgor potential and symplasmic water content of samples taken during the wet and dry season are shown in Fig. 4. Turgor potential decreased with decreasing symplasmic water content of leaf tissues. The slopes of the relations between turgor potential and SWC appear to be influenced by the salinity of the ground water;

as salinity increased from wet to dry season, the slope of the turgor potential–SWC relation increased in all three species, particularly in *R. mangle* and *C. erectus*. Because the slope of each relation gives a measure of the elasticity of the cell walls, steeper slopes during the dry season indicate that the leaf cell walls were more rigid during this period. Cell wall rigidity also changes along the salinity gradient from coast to further inland. *Rhizophora mangle* had the most rigid cell walls (steeper slopes) while *C. uvifera* had the most elastic ones.

Seasonal changes in the bulk modulus of elasticity (ϵ) are shown in Fig. 5. Cell wall rigidity increased approximately $3 \cdot 0$ MPa for *C. uvifera* and *C. erectus* during the dry season, and approximately $1 \cdot 5$ MPa for *R. mangle*, but these differences are not statistically significant for the latter species.
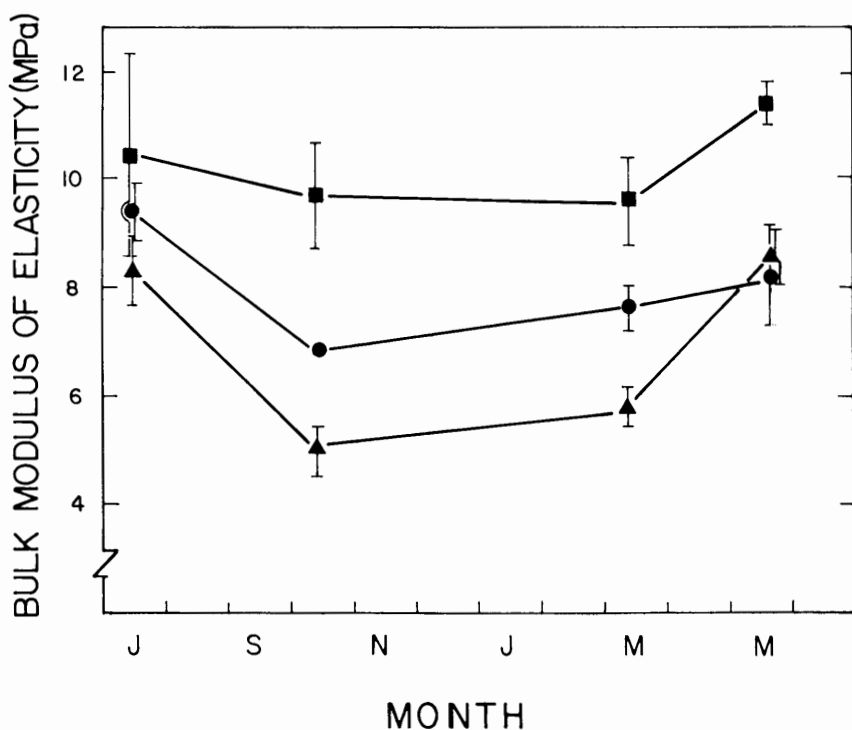

Fig. 5. Changes in the bulk modulus of elasticity (ϵ) during a 1-year period for *Rhizophora mangle* (■), *Conocarpus erectus* (●) and *Coccoloba uvifera* (▲). Vertical bars are standard errors for each month. Absence of bars indicates s.e. was smaller than the symbol.

Discussion

During the dry season leaf osmotic potential decreased in all species regardless of their distribution along the salinity gradient. The greatest changes occurred during the transition periods of August–October and March–May. The extent of osmotic adjustment for these species (c. $1 \cdot 0$ MPa at the turgor loss point) is greater than that reported for grasses (Wilson *et al.* 1980; Henson *et al.* 1982; Pavlik 1984), crops under natural conditions (Turner *et al.* 1978), and various woody shrubs and tree species (Turner 1979; Hinckley *et al.* 1980; Turner and Jones 1980), although extremely high osmotic adjust-

ment values have been reported in the literature. For example *Galactia striata*, a twining pasture legume, showed an osmotic adjustment of 2·3 MPa when submitted to drought (Sheriff *et al.* 1986).

The decrease in osmotic potential at full turgor in *R. mangle* was largely the result of a decrease in symplasmic water content, while changes in osmotic potential of *C. uvifera* resulted from a net increase in osmotically active solutes inside the cells of the leaf tissues (Table 2). *Conocarpus erectus,* which grows in soils of intermediate salinity levels, showed both mechanisms. Pavlik (1984) observed that dune grass species varied in their mechanisms to produce a seasonal reduction in osmotic potential. The reduction in osmotic potential of *Ammophila arenaria* resulted entirely from a decrease in symplasmic water content, while in *Elymus mollis* it was primarily the consequence of an increase in osmotically active solutes. Sobrado and Turner (1983) suggest that this type of osmotic adjustment may result from a decrease in cell size during the dry season, while osmotically active solutes per cell remain constant. The possibility of osmotic adjustment by these two methods may be important because they may require different amounts of energy. Meinzer *et al.* (1986) suggest that an active net increase in osmotically active solutes per cell may be more costly than sequestering the same amount of solutes in a smaller cell volume. If this is true, *C. uvifera* would expend more energy than *R. mangle* to maintain its leaf water potential below that of the soil substrate during periods of high salinity.

To maintain a gradient for water movement from the soil, leaf water potentials of mangroves must be more negative than the osmotic potential of the substrate. A linear relationship was observed between osmotic potential at full turgor and the osmotic potential of the substrate where each species grows (Fig. 2). If negative soil water potentials are maintained at night, then leaf water potentials on certain measurement dates were higher than soil water potential, and a reverse water flow between the plant and soil would be expected. High Ψ_l values were seldom obtained in *R. mangle* and *C. erectus*, although on a few occasions we detected indirect evidence of small reverse flows during brief periods at night (unpublished results). This evidence indicates that, although the total water potential in leaves may occasionally be more positive than the osmotic potential of the soil, seasonal changes in water relations of each mangrove species are finely tuned to seasonal changes in substrate salinity. Chapman (1976) cites further examples where leaf osmotic potentials appear to have been influenced by the osmotic potential of the substrate.

Leaves of all species showed seasonal changes in the elasticity of the cell walls. A decrease in elasticity during the dry season together with a decrease in osmotic potential observed during the periods of high soil salinity may be regarded as mechanisms of turgor maintenance at low soil water potentials. Bolaños and Longstreth (1984) suggest that low elasticity allows a large difference in water potential between soil and leaves to be produced with relatively little water loss. Because it would increase water uptake, this may be of adaptive value in mangrove trees, which possess high intrinsic hydraulic resistances (Field 1984; Goldstein, Rada, Orozco, Azocar, unpublished information).

Data indicate two of the mangrove species were at zero turgor pressure for a few hours near midday during the dry season (Fig. 1), but this may be experimental artifact. Incorrect estimates of turgor pressure could result from incorrect interpretation of the pressure–volume curves (Tyree 1976), or from artifacts produced by hydration of samples prior to measurements (Bolaños and Longstreth 1984; Meinzer *et al.* 1986). Meinzer *et al.* (1986) found a 2·0 MPa difference in estimates of the turgor loss point with hydrating and non-hydrating techniques; differences in our data are less than 0·4 MPa. Comparing pressure–volume curves from hydrated and non-hydrated samples showed the standard hydration technique did not significantly alter the water relation characteristics of the three species studied. Therefore the turgor loss for two species in our data appears real.

The seasonal water economy of these mangrove species is related to both an osmotic and an elastic adjustment. This is shown by the large difference between seasonal changes in osmotic potential at full turgor and at turgor loss for these species (Fig. 1). Variations in osmotic potential at full turgor do not exceed $0 \cdot 5$ MPa, while those at turgor loss reach approximately $1 \cdot 0$ MPa. These differences may be accounted for by the observed changes in cell wall elasticity (Fig. 5). Although the contribution of either osmotic adjustment or cell wall elasticity to turgor maintenance has commonly been investigated, both types of adjustment have rarely been considered as an integrated system. A large drop in water potential results in a relatively small loss of intracellular water in mangroves (Scholander et al. 1966; Scholander 1968), probably because of the relatively inelastic cell walls and because a relatively small change in cell volume causes a low intracellular osmotic potential (Clough et al. 1982).

This study shows that the water relations of mangroves, not only on a seasonal basis but also along the seashore gradient, were affected by salinity levels of the soil. Osmotic potentials and elasticity tend to decrease with a decrease in soil osmotic potential. Reduction in turgor was much less than it would have been if there had been no acclimation to increasing salinity, but turgor loss was not completely avoided during the dry season. This work suggests that increasing water uptake by establishing large leaf–soil water potential gradients is more important for the water economy of whole plants than is midday turgor maintenance. To better understand the water balance of mangrove plants, further research is necessary on hydraulic properties of the vascular system, possible reverse water flows from leaf to soil during brief night-time periods, consequences of turgor loss on the carbon economy, and possible diurnal osmotic adjustment.

Acknowledgments

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