



# Diurnal water relations of inland and coastal halophytic populations from Pakistan

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The diurnal water relations of three halophytic species common to both inland and coastal habitats in saline flats of Karachi, Pakistan were studied. The first hypothesis was that species with different adaptation modes [leaf succulent (*Suaeda fruticosa* (L.) Forssk.), re-creting (*Atriplex griffithii* Moq. var. *stocksii* Boiss.) and non-re-creting (*Heliotropium curassavicum* L.)] have different patterns of water relations. The second hypothesis was that the coastal populations were more stressed in comparison to inland populations. The first hypothesis was rejected because the overall diurnal variation pattern of water relations was similar in all three species. There were quantitative differences in all parameters studied in various species from inland and coastal populations, and species also showed some individual differences in their responses to stress. The second hypothesis was accepted because coastal populations were generally more stressed in comparison to inland populations.

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## Introduction

Salinity tolerance involves mechanisms at different levels, i.e. the molecular (enzymes, membranes), the cellular (osmotic adjustment, compartmentation) and the organ and whole plant level (water relations, transpiration, co-ordinated growth and reproduction) (Jeschke & Wolf, 1993). The present paper addresses one aspect of the whole plant mechanism, i.e. water relations. Halophytes have the ability to adapt to saline conditions by adjusting osmotically to the increasing salinity levels (Riehl & Ungar, 1983; Karimi & Ungar, 1984; Clipson *et al.*, 1985; Khan *et al.*, 1998 *a,b,c*). They are capable of adjusting their water potential to the soil water potential conditions in their habitat (Ustin *et al.*, 1982; Riehl & Ungar, 1983). Resistance against drought and salinity is decisive for primary productivity of saline communities in arid areas (Nagy *et al.*, 1995). Dicotyledenous halophytes (*Suaeda fruticosa*, *S. maritima*, *Atriplex griffithii*)

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exhibit optimal growth at moderate salinities (about 200 mol m<sup>-3</sup> NaCl) accompanied by an increase in succulence, as well as other morphological changes (Hajibaghiri *et al.*, 1984; Khan *et al.*, 1998a,b). Under such saline conditions, halophyte leaf osmotic potentials are maintained at more negative levels than those of the external medium, largely by the accumulation of Na<sup>+</sup> and Cl<sup>-</sup> (Flowers, 1975). Water relations have been seen as important determinants of the growth response (Flowers *et al.*, 1977; Munns *et al.*, 1983) and at higher salinities growth reduction might be caused by a reduced ability to adjust osmotically as a result of the saturation of the solute uptake systems (Clipson *et al.*, 1985).

Diurnal variation in the water relations of plants have been widely reported (Acevedo *et al.*, 1979; Devitt *et al.*, 1997; Fordyce *et al.*, 1997; Oatham, 1997; Mills *et al.*, 1997; Rhizopoulou *et al.*, 1997). Halophytes (*Atriplex polycarpa*, *A. confertifolia* and *Eurotia lanata*) showed a daily rhythm in plant water potentials, with higher values in the early morning and evening and lower water potentials from late morning to afternoon (Moore *et al.*, 1972; Sankary & Barbour, 1972; Ustin *et al.*, 1982). However, *Atriplex hymenalytra* growing in Death Valley does not show such a marked variation in water potential (Mooney *et al.*, 1977). Leaf stomatal conductance usually exhibits a more or less continued decline over a wide range of osmotic potentials extending from -15 to -40 bars (Bunce, 1977).

The present study was conducted on three perennial halophyte species, found in both inland and coastal habitats. These species also vary in their adaptation to high salinity stress. *Atriplex griffithii* is a recreting species and comparatively less ion accumulating (Khan *et al.*, 1998a). It is an osmoconformer, i.e. its osmotic potential becomes more negative with an increase in stress. *Heliotropium currasavicum*, on the other hand, does not have any mechanism to excrete salt. It has some level of succulence. The response of this species can be either as an osmoconformer or as an osmoregulator. *Suaeda fruticosa* is a leaf succulent halophyte and is known to accumulate a large amount of ions (Khan *et al.*, 1998b). It is expected to make its water potential very negative with the onset of salinity and would not change relative to external osmotic pressure (osmoregulator). Coastal habitats are more stressful due to high salinity and strong coastal winds. We tested the following two hypotheses: (1) halophytic species that vary in their adaptation to salt will also show different patterns of water relations; and (2) coastal populations will be more stressed than inland populations.

## Materials and methods

### *Site*

The inland population was located on saline flats (28 dS m<sup>-1</sup>) on the University of Karachi campus (about 15 km from the coast). The coastal population was sampled on the Arabian Sea coast (45 dS m<sup>-1</sup>) at Sands Pit, Karachi. The area is classified as subtropical maritime desert (latitude 24° 48' N, longitude 65° 55' E) and receives monsoon rains with an average rainfall of about 220 mm year<sup>-1</sup>. Temperature ranges from 22 to 36°C.

### *Plant material*

All the species studied have both coastal and inland distribution. *Atriplex griffithii* is a salt recreting, short, robust perennial shrub, restricted to moderately saline regions. It reproduces predominantly through seeds which germinate on salinities of up to 400 mM

NaCl (Khan & Rizvi, 1994), and can grow on salinities of up to 360 mM NaCl (Khan *et al.*, 1998a). *Suaeda fruticosa* is a leaf succulent species that attains a height of about 60 cm. It is the most common species found in both inland and coastal salt marshes and deserts. This species is reported to germinate on salinities of up to 400 mM NaCl (Khan & Ungar, 1998) and can grow in 1000 mM NaCl (Khan *et al.*, 1998b). *Heliotropium curassavicum* grows as a herb or sometimes as a low shrubby plant. It is a perennial, glabrous halophyte with fleshy stems and leaves which turn black when dried. It is usually found in highly saline areas.

### *Diurnal water relations*

Diurnal trends in osmotic relations were recorded during October 1994. Leaf water potentials were measured using a dew point microvoltmeter (Model HR-33, Wescor Inc., Logan, Utah) on leaf disks 5 mm in diameter placed in the sample chamber. Osmotic potential was measured by the pressed sap method using filter paper instead of leaf disks in the microvoltmeter. Stomatal conductance was measured with a cycling diffusion porometer (Model AP-4, Delta-T Devices Limited, Cambridge). Relative humidity, air temperature and light intensity were measured with the sensor on the porometer. All readings were taken at pre-dawn (0600h), post-dawn (0700h), noon (1200h), before sunset (1700h) and after sunset (1900h) on fully expanded mature leaves. Soil pH was measured with an Ion 85 Ion Analyzer (Radiometer, Copenhagen) and conductivity was measured with a conductivity meter (Radiometer, Copenhagen). Soil texture was determined by the hydrometer method (Boyucous, 1956).

## Results

### *Diurnal variation in light intensity in inland and coastal populations*

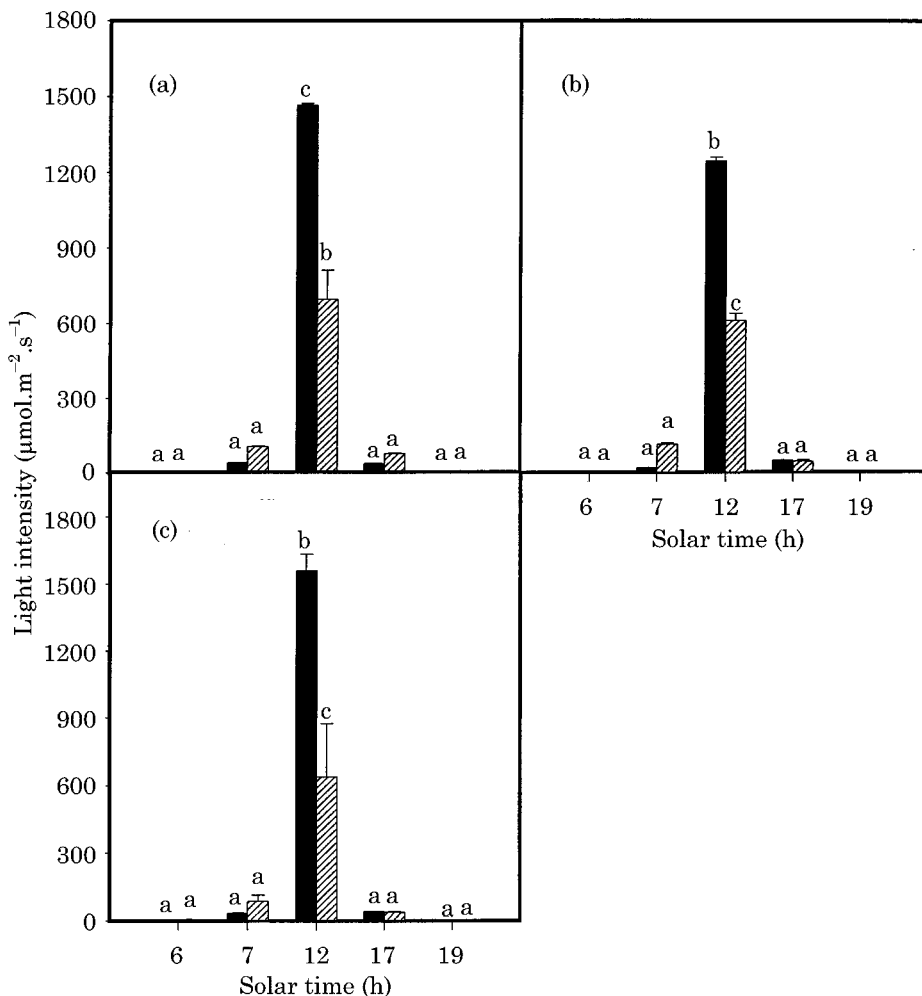
Light intensity was higher for the inland population than for the coastal population (Fig. 1).

### *Effect of the time of the day on the pressure potential of halophytes*

A three-way ANOVA of the pressure potential indicated a significant ( $p < 0.0001$ ) main effect of site, species and time of day, and their interactions (Table 1). A one-way ANOVA of the water relations revealed that time affected the pressure potentials of *S. fruticosa* (inland:  $F = 10.82$ ,  $p < 0.0001$ ; coastal:  $F = 14.5$ ,  $p < 0.01$ ), *A. griffithii* (inland:  $F = 14.5$ ,  $p < 0.0001$ ; coastal:  $F = 14.8$ ,  $p < 0.0001$ ) and *H. curassavicum* (inland:  $F = 221.8$ ,  $p < 0.0001$ ; coastal:  $F = 10.3$ ,  $p < 0.0001$ ). Pressure potentials of *A. griffithii*, *S. fruticosa* and *H. curassavicum* decreased rapidly after sunrise, reached their minimum levels by noon and gradually increased thereafter (Fig. 2). The inland populations showed higher pressure potentials than coastal populations.

### *Effect of the time of the day on the osmotic potential of halophytes*

A three-way ANOVA of osmotic potential indicated a significant ( $p < 0.0001$ ) main effect of site, species and time of day, and their interactions (Table 1). A one-way ANOVA of the water relations revealed that time significantly affected the osmotic



**Figure 1.** Light intensity measurements at pre-dawn, post-dawn, noon, afternoon and after sunset for various species in both inland (■) and coastal (▨) communities. (a) *Atriplex griffithii*; (b) *Suaeda fruticosa*; (c) *Heliotropium currasavicum*. Bars represent mean  $\pm$  standard error. Bars with different letters are significantly different at  $p < 0.005$ ; Bonferroni test.

potentials of *S. fruticosa* (inland:  $F = 149.8$ ,  $p < 0.0001$ ; coastal:  $F = 101.4$ ,  $p < 0.0001$ ), *A. griffithii* (inland:  $F = 148.8$ ,  $p < 0.0001$ ; coastal:  $F = 1424.8$ ,  $p < 0.0001$ ) and *H. currasavicum* (inland:  $F = 182.7$ ,  $p < 0.0001$ ; coastal:  $F = 55.8$ ,  $p < 0.0001$ ). The osmotic potential of all species decreased at sunrise, reached its minimum at midday and gradually increased later (Fig. 3). Osmotic potential was generally more negative in coastal populations of *A. griffithii* and *S. fruticosa*; however, this difference was substantially greater at midday in *A. griffithii*. There was no difference in osmotic potentials of the inland and coastal populations of *H. currasavicum*.

#### *Effect of the time of the day on the water potential of halophytes*

A three-way ANOVA of water potential indicated a significant ( $p < 0.0001$ ) main

Table 1. Result of three-way analysis of variance of characteristics by species (Sp), site (S) and time (T) of treatments

Dependent variable	Independent variable						
	Sp	S	T	S × Sp	Sp × T	S × T	Sp × T × S
Light intensity	1.84 <sup>NS</sup>	57.9 <sup>***</sup>	483.5 <sup>***</sup>	1.1 <sup>NS</sup>	1.5 <sup>NS</sup>	76.1 <sup>***</sup>	0.8 <sup>NS</sup>
Water potential	137.6 <sup>***</sup>	2990 <sup>***</sup>	1981 <sup>***</sup>	102 <sup>***</sup>	140 <sup>***</sup>	213 <sup>***</sup>	204 <sup>***</sup>
Osmotic potential	88 <sup>***</sup>	980 <sup>***</sup>	1278 <sup>***</sup>	183 <sup>***</sup>	156 <sup>***</sup>	207 <sup>***</sup>	192 <sup>***</sup>
Pressure potential	7.8 <sup>**</sup>	538 <sup>***</sup>	104 <sup>***</sup>	9.2 <sup>***</sup>	3.1 <sup>**</sup>	32.8 <sup>***</sup>	6.9 <sup>***</sup>
Stomatal conductance	1010 <sup>***</sup>	0.38 <sup>NS</sup>	733 <sup>***</sup>	411 <sup>***</sup>	121 <sup>***</sup>	49 <sup>***</sup>	130 <sup>***</sup>

Numbers represent *F* values: NS = not significant; \*\* =  $p < 0.001$ ; \*\*\* =  $p < 0.0001$ .

effect of site, species and time of day, and their interactions (Table 1). A one-way ANOVA of the water relations revealed that time significantly affected the water potentials of *S. fruticosa* (inland:  $F = 319.8$ ,  $p < 0.0001$ ; coastal:  $F = 123.2$ ,  $p < 0.0001$ ), *A. griffithii* (inland:  $F = 315.6$ ,  $p < 0.0001$ ; coastal:  $F = 3821.6$ ,  $p < 0.0001$ ) and *H. curassavicum* (inland:  $F = 455.4$ ,  $p < 0.0001$ ; coastal:  $F = 63.3$ ,  $p < 0.0001$ ). Water potentials of all species became progressively more negative with the increase in sunlight and reached their lowest values at midday (Fig. 4). The water potentials of coastal populations of *A. griffithii* and *S. fruticosa* were higher than the inland populations. *Heliotropium curassavicum* showed a significant difference in water potential between inland and coastal populations during sunrise and sunset.

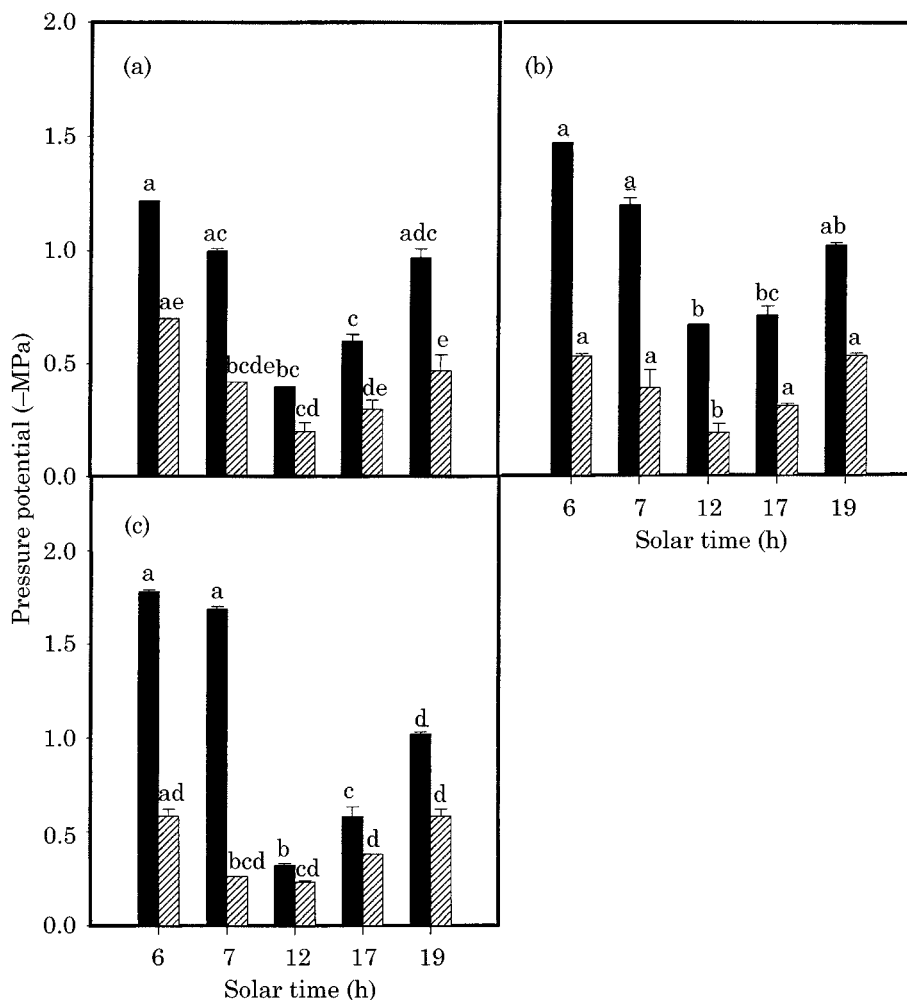
#### Effect of the time of the day on the stomatal conductance of halophytes

A three-way ANOVA of stomatal conductance indicated a significant ( $p < 0.0001$ ) main effect of species, time of day, and their interactions (Table 1). Variation in the site had no significant effect on stomatal conductance. A one-way ANOVA of water relations revealed that time significantly affected the stomatal conductance of *S. fruticosa* (inland:  $F = 75.2$ ,  $p < 0.0001$ ; coastal:  $F = 35.9$ ,  $p < 0.0001$ ), *A. griffithii* (inland:  $F = 651.3$ ,  $p < 0.0001$ ; coastal:  $F = 38.2$ ,  $p < 0.0001$ ) and *H. curassavicum* (inland:  $F = 85.7$ ,  $p < 0.0001$ ; coastal:  $F = 410.3$ ,  $p < 0.0001$ ). Stomatal conductance decreased with sunrise in all three species studied, reaching its lowest at midday (Fig. 5). Coastal populations of *A. griffithii* and *S. fruticosa* were the most stressed, while inland populations of *H. curassavicum* were the most stressed.

## Discussion

There is a great deal of variation in the environmental conditions of coastal and inland sites in Karachi, Pakistan. Humidity was highest on the coast with little variation during the day. The inland site, on the other hand, has a relatively low humidity but a great deal of diurnal variation. Temperature ranged from 22 to 36°C at the coastal site and was slightly higher at inland sites. Light intensity of the inland population was twice ( $1300 \mu\text{mol m}^{-2} \text{S}^{-1}$ ) as high as the coastal populations, pH was more alkaline at the coastal site and the vapour pressure deficit was higher at the coastal site ( $-4.34$  MPa) than at the inland site ( $-2.33$  MPa).

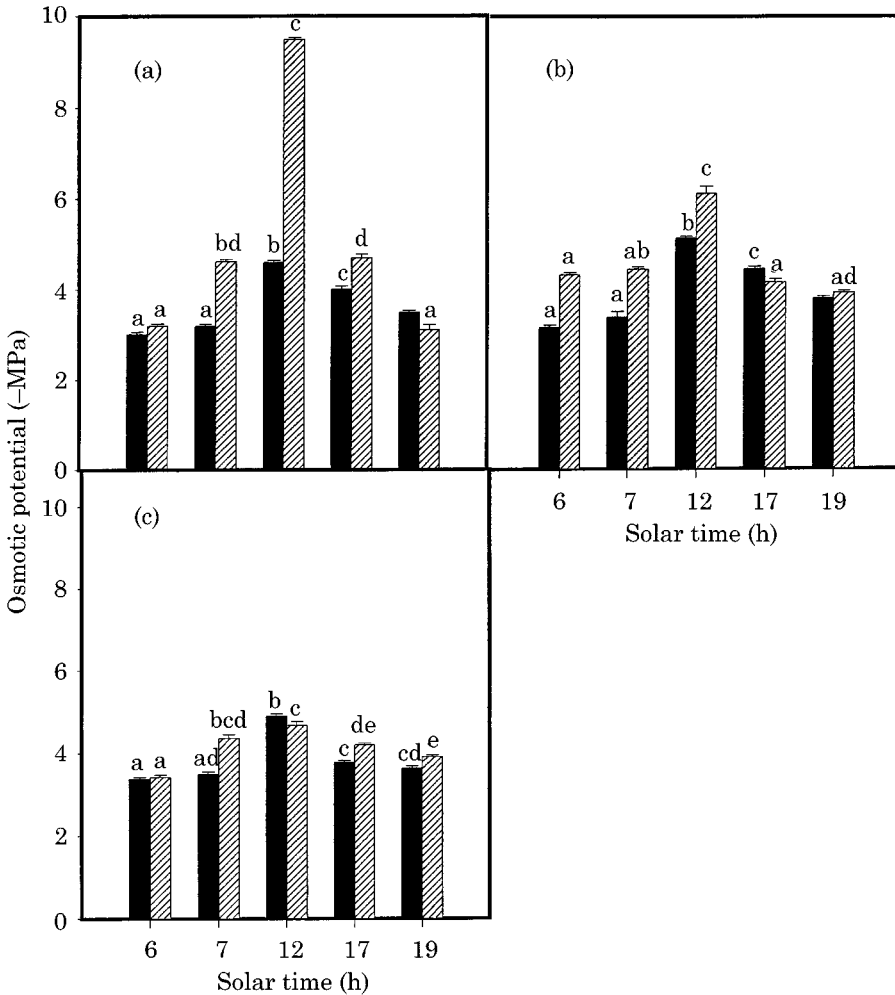
We tested two hypotheses. The first hypothesis was that different halophytic species would follow different patterns of water relations. These species have different methods of adaptation to salinity, varying from leaf succulence (*Suaeda fruticosa*), recretting (*Atriplex griffithii* var. *stocksii*), or non-recretting and succulent (*Heliotropium*



**Figure 2.** Pressure potential at pre-dawn, post-dawn, noon, afternoon and after sunset for various species in both inland (■) and coastal (▨) communities. (a) *Atriplex griffithii*; (b) *Suaeda fruticosa*; (c) *Heliotropium curassavicum*. Bars represent mean  $\pm$  standard error. Bars with different letters are significantly different at  $p < 0.005$ ; Bonferroni test.

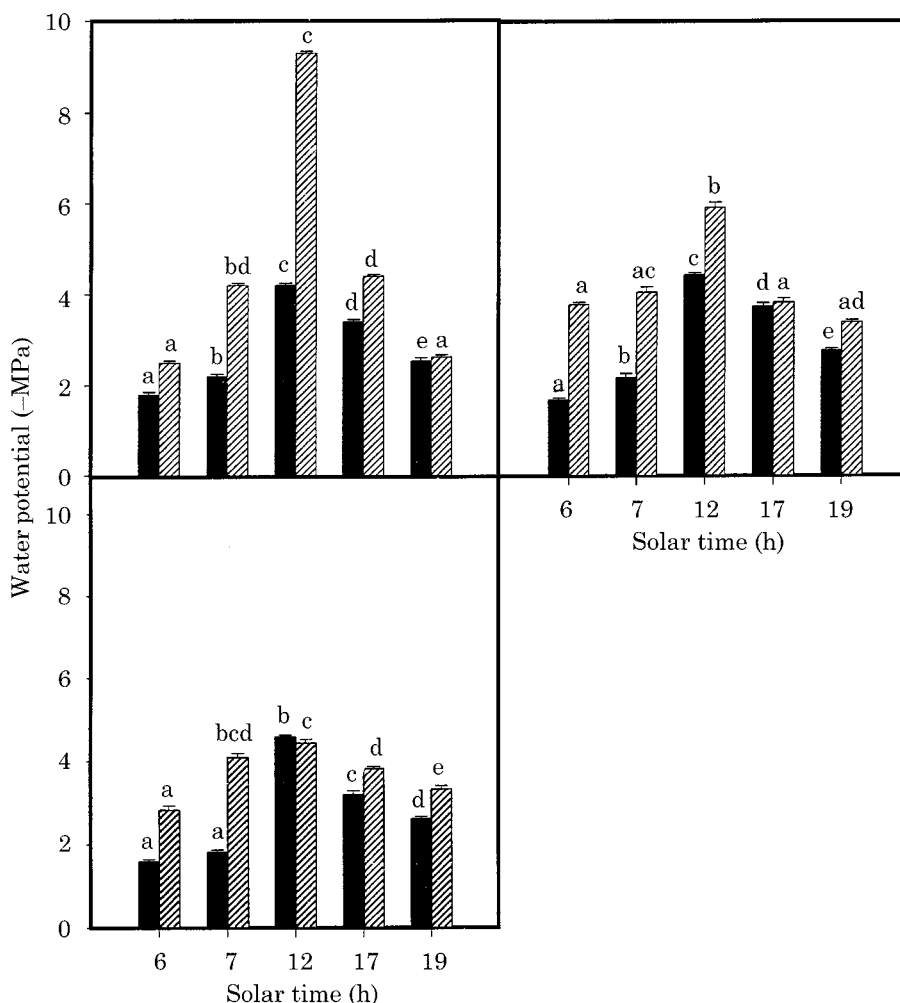
*curassavicum*). The overall pattern for all water relation parameters was similar in all species, thereby rejecting our first hypothesis. Osmotic and water potentials decreased as the day progressed, were lowest at noon, and then increased gradually during the afternoon. The water and osmotic potentials of *Atriplex griffithii* were more negative at noon compared to *Suaeda fruticosa* and *Heliotropium curassavicum*. Our data showed that despite the differences in the strategies for osmotic adaptation, they all acted like osmoconformers. The second hypothesis was that coastal populations will be more stressed in comparison to inland populations and this was generally found. A three-way ANOVA showed that site significantly ( $p < 0.0001$ ) affected all the parameters of water relations. This difference could also be due to the high salinity of the coastal medium ( $45 \text{ dS m}^{-1}$ ) compared to  $28 \text{ dS m}^{-1}$  in inland sites.

Ackerson *et al.* (1977) found that osmotic potential was generally less than leaf water



**Figure 3.** Osmotic potential at pre-dawn, post-dawn, noon, afternoon and after sunset for various species in both inland (■) and coastal (▨) communities. (a) *Atriplex griffithii*; (b) *Suaeda fruticosa*; (c) *Heliotropium currasavicum*. Bars represent mean ± standard error. Bars with different letters are significantly different at  $p < 0.005$ ; Bonferroni test.

potential when adequate soil water was available, resulting in significant turgor. As soil water became limiting, osmotic potential decreased but not as rapidly as leaf water potential, causing loss in turgor. This is in agreement with our data. Significant differences in osmotic potential existed between inland and coastal sites and also among the three species. Sankary & Barbour (1972) found that as the soil water content declined, the water potential in the root and shoot declined, with the difference between the two remaining more or less constant at -10 to -14 bar. Plant water potential commonly varies throughout the day and is lowest at about noon or early afternoon, recovering to higher values in the evening. Ustin *et al.* (1982) showed that halophytes such as *Spartina*, *Scirpus* and *Salicornia* all showed a daily rhythm in plant water and osmotic potentials, with higher values in the morning and evening and more negative values from late morning to noon. They also showed that plant species were



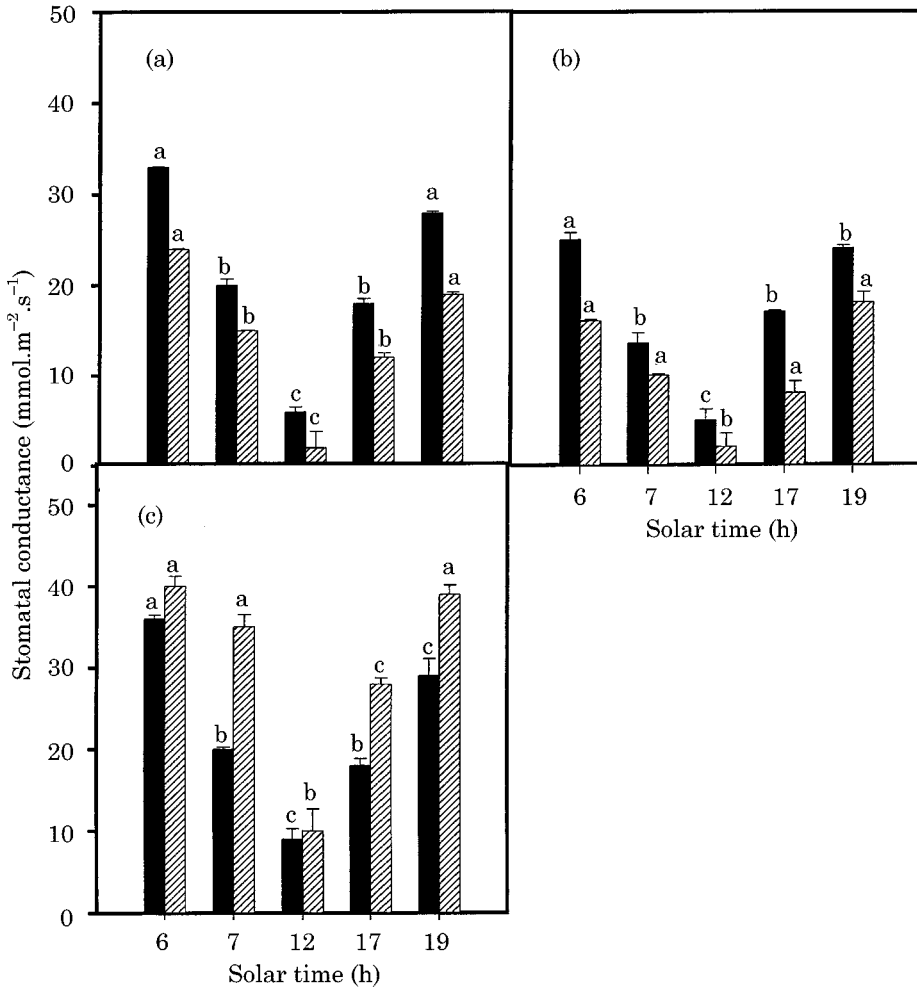
**Figure 4.** Water potential at pre-dawn, post-dawn, noon, afternoon and after sunset for various species in both inland (■) and coastal (▨) communities. (a) *Atriplex griffithii*; (b) *Suaeda fruticosa*; (c) *Heliotropium currasavicum*. Bars represent mean  $\pm$  standard error. Bars with different letters are significantly different at  $p < 0.005$ ; Bonferroni test.

able to lower their osmotic potential and reduce leaf stomatal conductance to conserve water as salinity stress increased. Bradbury (1990) reported that xylem pressure potential of stressed *Acacia nilotica* changed little from morning to noon and increased to more positive values.

Stomatal conductance decreased after sunrise and stayed that way until sunset. Salt-tolerant species showed a low stomatal conductance under high salinity and drought stress (Sharma, 1977; Werner, 1990; Gordon, 1993; Aziz & Khan, 1998). This low stomatal conductance decreased the rate of CO<sub>2</sub> accumulation and uptake and rate of respiration, and increased xylem tension (Ball & Farquhar, 1984).

In summary, the water relations of perennial halophytes showed similar patterns of variation in all parameters, and plants at the coastal locations appeared to be more stressed than plants at inland locations.





**Figure 5.** Stomatal conductance at pre-dawn, post-dawn, noon, afternoon and after sunset for various species in both inland (■) and coastal (▨) communities. Bars represent mean  $\pm$  standard error. Bars with different letters are significantly different at  $p < 0.005$ ; Bonferroni test.

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