GROWTH AND PHOTOSYNTHETIC RESPONSES OF SCAEVOLA SERICEA, A HAWAIIAN COASTAL SHRUB, TO SUBSTRATE SALINITY AND SALT SPRAY

G. GOLDSTEIN,[1,]* D. R. DRAKE,† C. ALPHA,* P. MELCHER,* J. HERAUX,* AND A. AZOCAR‡

*Department of Botany, University of Hawaii, 3190 Maile Way, Honolulu, Hawaii 96822; †Department of Biology, Georgia Southern University, Statesboro, Georgia 30460; and ‡CIELAT, Facultad de Ciencias, Universidad de Los Andes, Merida, Venezuela

Growth patterns, water relations, and photosynthetic traits in *Scaevola sericea* plants grown under different levels of substrate salinity and salt spray were studied. *Scaevola sericea* is a dominant shrub species in coastal strand ecosystems throughout the tropical and subtropical Pacific and Indian Oceans. Seventy-two cuttings from two coastal sites on the island of Oahu (Hawaii) were grown in a greenhouse under six treatments that resulted from the combination of three levels of substrate salinity (0, 100, and 335 mOsm kg^{-1}) and two levels of simulated salt spray (0 and 1200 mg salt m^{-2} d^{-1}). Several characteristics of *S. sericea* were strongly affected by substrate salinity but only weakly affected by salt spray. New stem and leaf biomass per plant decreased by ca. 65% as substrate salinity increased from 0 to 335 mOsm kg^{-1}; photosynthetic rates decreased by only 20% over the same salinity range. Leaf sap osmolarity increased 300 mOsm kg^{-1} as substrate salinity changed from 0 to 335 mOsm kg^{-1}, allowing the maintenance of a constant soil-to-leaf osmotic potential gradient favorable for water uptake even at higher salinity levels. Carboxylation capacity, determined by the initial slope of net CO$_2$ assimilation–intercellular CO$_2$ concentration relationships, remained constant for plants grown under different levels of salinities. The $\delta^{13}C$ of leaves increased from −29.2‰ to −26.3‰ with increasing salinity and was associated with lower stomatal conductances but nearly unchanged photosynthetic rates. *Scaevola sericea* is capable of substantial growth and physiological responses, which apparently are required to maintain a positive carbon balance in coastal habitats characterized by large temporal and spatial variations in substrate salinity and salt spray levels.

Introduction

Plants from coastal strands are often subject to heavy loads of salt spray and a shifting sandy substrate with low water-holding capacity and variable salinity. Seeds of few species germinate and grow successfully under such adverse environmental conditions, and thus plant cover and species diversity tend to be low in such coastal habitats. Coastal substrate salinity is extremely variable, ranging from 0.1% to 3% (Barbour et al. 1985). The salinity of sea water in Hawaii is ca 3.4% w/v. Salinity in the 2%–3% range can be detrimental to growth of halophytic species (Ungar 1991). The salinity of the substrate depends on the vertical distance to the sea level, topography, and rainfall. Some variation in salinity values reported in the literature may be explained by the units used to express interstitial substrate salinity because values expressed per gram of soil often underestimate salinity content relative to values expressed as salt dissolved in soil water.

Salt spray is another principal limiting factors in the coastal strand (Oosting and Billings 1942; Oosting 1945; Boyce 1954; Barbour and De Jong 1977; Barbour 1978). Droplets of salt spray tend to have a salt content similar to that of sea water and may vary in distribution according to wind speed, topography, distance back from the tide line, and height above sea level. The amount of airborne salt that accumulates on leaf surfaces also depends on the orientation, distribution, and size of leaves. For example, larger amounts of salt accumulate on vertical leaves than on horizontal ones (Barbour et al. 1985). The persistence of salt

spray on a leaf surface is a function of the amount and frequency of rainfall. A heavy rainfall may wash off accumulated salt. However, if precipitation is absent, a thin layer of salt may precipitate on the leaf surface following evaporation of the salt spray water. Besides being a potential limiting factor for plant growth, salt spray may be beneficial by providing nutrients (Barbour and De Jong 1977) or changing the soil pH by the addition of cations (Parsons 1981).

Scaevola sericea Vahl (syn. *Scaevola taccada* Roxb) is a dominant shrub in coastal strand ecosystems throughout the tropical and subtropical Pacific and Indian Oceans (Tomlinson 1986). In the Hawaiian archipelago, *S. sericea* is common on all major islands (Wagner et al. 1990). The leaves and the young stems tend to be succulent and fleshy, respectively. Initial research on aspects of the reproductive biology of this species indicates that it possesses some adaptations for existing in a saline environment. For example, the fruits float in sea water; viability of mature seeds is not substantially affected by exposure to sea water for long periods of time; and seeds treated with saline solutions germinate rapidly after exposure to fresh water (Lesko and Walker 1969). These characteristics of the seed responses to sea water may partially explain the wide distribution of *S. sericea*. Despite the potential importance of salt spray and soil salinity as limiting environmental factors in the coastal habitats of *S. sericea*, the degree of tolerance and the physiological responses to above- and belowground salinity of this species is not known.

Environmental salinity is known to affect the growth of *S. sericea* seedlings adversely (Alpha et al. 1996). The purpose of this study was to assess the effects of salinity stress on the growth of relatively

mature *S. sericea* plants and then determine what physiological mechanisms allow the plants to respond to this salinity stress. Large morphological variation of *S. sericea* leaves, observed in natural habitats with different substrate salinities and salt spray loading, indicated that this species is capable of substantial morphological and physiological adaptations. The underlying hypothesis of this study is that substantial phenotypic plasticity is required to maintain continuous growth activity of perennial plants in coastal habitats characterized by variable physical conditions. *Scaevola sericea* plants were grown on sandy soils in a greenhouse and subjected to different levels of soil salinity and simulated salt spray. Growth was monitored over the duration of the experiment and water relations and photosynthetic gas exchange characteristics were studied at the end of the experiment. Also, carbon isotope ratios were analyzed and stomatal regulation of CO_2 and water vapor exchange were measured.

Material and methods

Two or three young stem sections of *Scaevola sericea* were obtained from ca. 40 plants, half at Makapu'u Point and half at Sandy Beach, on the island of Oahu in May 1994. Beach sand was also collected at these sites. Cuttings were placed into flats of washed sand inside a mist room and misted for 6 s every 2 min. The rooted cuttings were transplanted to 7-cm-diameter pots filled with a sand and perlite mixture and were allowed to grow in a greenhouse under 50% shade cloth. After 4 wk, the plants were transplanted into 4-L pots of sand and grown for two more weeks before beginning the experiments.

The plants were randomly allocated to six treatments, each treatment containing 12 plants. The six treatments resulted from the combination of three levels of substrate salinity (0, 100, and 335 mOsm kg^{-1}, corresponding to 0.0, 0.3, and 1.0% salinity [w/v] or 0, 0.25, and 0.83 MPa at sea level and 25°C, respectively) and two levels of salt spray (0 and 1200 mg salt m^{-2} d^{-1}). The high level of salt spray was similar to the highest values observed on *S. sericea* plants in the field (Alpha et al. 1996). Rates of accumulation of salt spray in the field were measured along a 50-m transect running landward from the high tide line through a population of *S. sericea*. To measure rates of salt accumulation in the field, we marked three leaves (50 cm above the ground) on both the windward and leeward sides of each plant intersected by the transect and rinsed their surfaces with deionized water. After 1 wk of typical onshore tradewinds weather with no rain, leaves were harvested and immersed in 10 mL of deionized water for 1 min. The electrical conductivity of the resulting solution was measured with a conductance meter (YSI model 32, Yellow Springs Instruments, Inc., Yellow Springs, Ohio), allowing calculation of the solution's salinity (conductivity [mmho] × 0.064 [constant] = salinity (% w/v); Jackson 1958). After determining the projected leaf surface area, the average number of mg (NaCl) m^{-2} d^{-1} was calculated. Salt loading intensities were generally higher near the ocean, on the windward side of the plant, and on plants on high ground. The greatest loading intensity was recorded on the windward side of a plant on a dune crest.

The salt spray was applied to the greenhouse plants (sprayed plants) twice a week with a hand sprayer, containing filtered sea water that produced a very fine mist. Salinity of the spray applications was monitored by spraying leaves of extra plants, then washing the leaves and measuring the conductivity of the rinse water as before. The plant leaves were rinsed every 2 wk to simulate rain events and to avoid high levels of salt accumulation on the leaf surfaces. Total salt load prior to rinsing was 16,800 mg m^{-2}, which resulted in an average of salt spray loading of 1200 mg m^{-2} d^{-1}. Plants in the 0 spray treatments (nonsprayed plants) were sprayed with deionized water in the same fashion. All plants (sprayed and nonsprayed) were watered with their appropriate substrate solutions immediately after spraying to flush the soil and prevent contamination.

The plants were slowly brought into the substrate salinity treatments over a period of 2 wk. Filtered sea water was obtained periodically, and stock solutions of 100 and 335 mOsm kg^{-1} sea water were prepared weekly. A stock solution of 1/100 standard concentration of a commercial NPK fertilizer was used as supplementary nutrient solution for all substrate salinity treatments. To avoid accumulation of salts in the substrate, the plants were thoroughly irrigated every 2 d with the sea water solution until excess water drained from the bottom of the pots. The locations of the plants on the greenhouse bench were randomly changed twice every week.

After 8 wk of treatment a portable photosynthesis system (LI6200, Li-Cor, Lincoln, Nebr.) was used to obtain net CO_2 assimilation (A), stomatal conductance to water vapor (g_{wv}), and intercellular CO_2 concentration (c_i) values for the youngest fully expanded leaves of five plants in each treatment. Measurements of these leaves were obtained from 900 to 1300 hours during three consecutive days. These leaves were then removed from the plants and oven-dried at 60°C for 3 d. The dried leaves were finely ground and sent to the Stable Isotope Laboratory at Boston University for $\delta^{13}C$ determinations. Stable carbon isotope composition was expressed as the $^{13}C/^{12}C$ ratio relative to that of the PeeDee belemnite standard with a precision of ±0.20‰.

The relationship between A and c_i was determined for three plants per treatment on the youngest fully expanded leaf of each plant with a PACsys 9900 gas exchange system (Data Design Group, La Jolla, Calif.). A light source fitted with infrared filters was used to maintain photosynthetically active radiation levels inside the cuvette at 600 μmol m^{-2} s^{-1}, approximate light saturation for the species (unpublished results). Leaf temperature and vapor pressure differences between the leaf and air (VPD) were maintained at 25°C and 0.5 kPa, respectively. CO_2 levels were changed in steps of 100–200 μmol mol^{-1}, from 1200 to 50 μmol mol^{-1}. Calculations of A, g_{wv}, and c_i were based on equations from Farquhar et al. (1982). The Michaelis Menten equation [$A = A_{max} (m + c_i)/(m + c_i + K)$] was fitted to the A-c_i relationships, with m and K as parameters. Optimum temperature for photosynthesis and saturating light levels was determined in experiments prior to obtaining A-c_i response curves. The A-c_i relationships were used to calculate the relative limitation to net CO_2 assimilation (l_s) imposed by stomata according to Farquhar and Sharkey (1982) as follows: $l_s = (A_o - A)/A_o$, where A_o is the expected net CO_2 assimilation when the stomatal conductance is infinitely high and A is the measured net CO_2 assimilation at normal atmospheric CO_2 concentrations (350 μmol mol^{-1}).

Upon finishing the gas exchange measurements, all plants were harvested and the number of branches and leaves, total leaf surface area, total leaf fresh weight, and total dry weight of leaves and stems per plant was recorded only for tissues

Table 1

Analyses of variance of morphological and physiological traits from Scaevola sericea plants exposed to different substrate salinity and salt spray treatments

Plant trait	Substrate salinity		Salt spray		Interactions		
	F-statistic	$P <$	F-statistic	$P <$	F-statistic	$P <$	ANOVA
Stem dry wt. (g)	26.92	0.001	...	...	...	...	1 way
Leaf dry wt. (g)	88.12	0.001	...	...	...	...	1 way
Shoot dry wt. (g)	82.65	0.001	...	...	...	...	1 way
LMA (g m^{-2})	54.65	0.001	...	...	...	...	1 way
Leaf water (g m^{-2})	0.49	ns	4.27	ns	...	...	2 way
Leaf area (cm^2)	80.25	0.001	...	...	...	...	1 way
Osmolarity (mOsm kg^{-1}) ...	370.12	0.001	54.58	0.001	0.4	ns	2 way
δ^{13}C (‰)	25.72	0.001	5.85	0.05	0.17	ns	2 way
g_{wv} (mol m^{-2} s^{-1})	23.45	0.001	...	...	...	...	1 way
A (μmol m^{-2} s^{-1})	3.44	ns	4.92	ns	...	...	2 way

Note. Responses of plant traits to substrate salinity and salt spray were analyzed by two-way ANOVA. In cases where only substrate salinity or salt spray produced a significant main effect, treatments were combined and reanalyzed using a one-way ANOVA. LMA is leaf mass per unit area, leaf water is leaf water content on a unit surface area, osmolarity is leaf osmolarity, g_{wv} is stomatal conductance, and A is net CO_2 assimilation. $n = 12$ plants per treatment, except for δ^{13}C, g_{wv}, and A, where $n = 5$.

produced during the experiment. There were no significant differences in initial stem length among plants assigned to different treatments (one-way ANOVA, $F = 0.88$, $P = 0.496$). Leaf thickness, surface area, and osmotic potential were determined for the youngest fully developed leaf in each plant. Leaf surface area was measured with a leaf area meter (LI 3000A, Li-Cor). Leaf cell sap osmolarity was measured with a freezing point depression osmometer (μ-Osmette 5004, Precision Systems, Inc., Natick, Mass.). The leaves were squeezed inside a section of Tygon tubing with a C-clamp, and a 50-μL aliquot of leaf cell sap was withdrawn with a micropipette and immediately placed in the chamber of the osmometer.
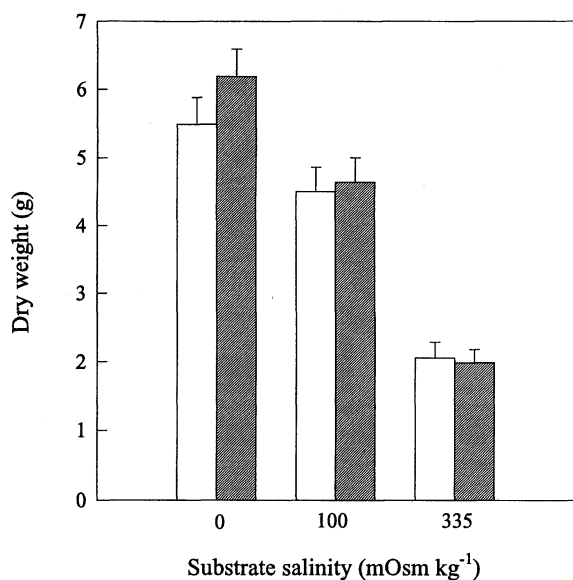

Fig. 1 Aboveground biomass per plant produced since treatment began as a function of substrate salinity for Scaevola sericea exposed to spray containing 0 (open bars) and 1200 mg m^{-2} d^{-1} (dashed bars) of sea water salt. The segments on each bar indicate one SE above the mean.

The MINITAB 8.2 statistical package (Minitab, Inc., State College, Pa.) was used for statistical analysis. The data were evaluated with regard to normality, skew, and spread. When necessary, the data for leaf area, branch number, and all dry mass values were square-root transformed to correct for unequal variances and normality. Responses to both substrate salinity and salt spray were analyzed by two-way ANOVA. In cases where only substrate salinity or spray produced a significant main effect, treatments were combined and reanalyzed using a one-way ANOVA.

Results

Several characteristics of Scaevola sericea plants were strongly affected by substrate salinity but only weakly affected by salt spray (table 1). Eight out of 10 characteristics showed statistically significant effects due to substrate salinity, but only two showed significant effects due to salt spray. For example, new stem and leaf biomass per plant decreased by ca. 65% as substrate salinity increased from 0 to 335 mOsm kg^{-1} (fig. 1). The decrease was significant ($P < 0.001$) for plants under both salt spray and non–salt spray treatments. Sprayed plants tended to exhibit higher aboveground biomass than nonsprayed plants only at 0 mOsm kg^{-1} substrate salinity (fig. 1).

Leaf sap osmolarity increased ca. 300 mOsm kg^{-1} as substrate salinity changed from 0 to 335 mOsm kg^{-1} (fig. 2). Leaf osmolarity and substrate salinity, therefore, changed in an approximately similar (1 : 1) fashion. This led to the same soil-to-leaf osmotic potential gradients in the 0 to 335 mOsm kg^{-1} salinity range. Salt spray also had a significant effect on leaf sap osmolarity (table 1; fig. 2); however, its contribution to the increase in osmotically active solutes on the leaves was smaller than substrate salinity. Leaf water content expressed on an area basis, however, was not affected by leaf sap osmolarity (fig. 3) or the salinity treatments (table 1), indicating that the increase in sap osmolarity
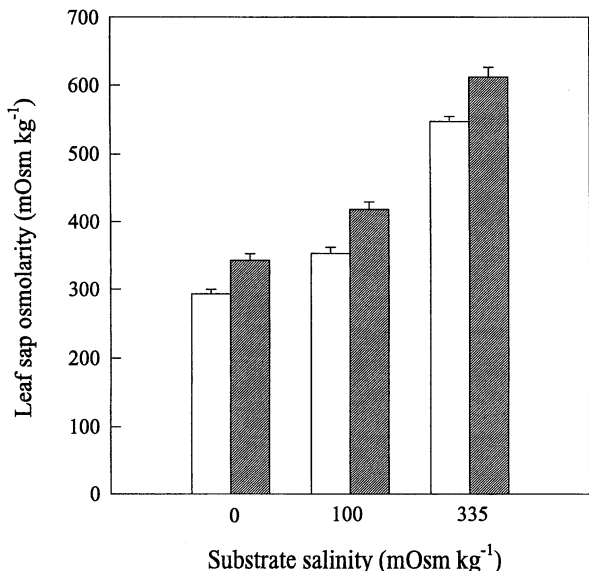
Fig. 2 Leaf sap osmolarity as a function of substrate salinity for *Scaevola sericea* exposed to spray with 0 (open bars) and 1200 mg m^{-2} d^{-1} (dashed bars) of sea water salt. The segments on each bar indicate one SE above the mean.
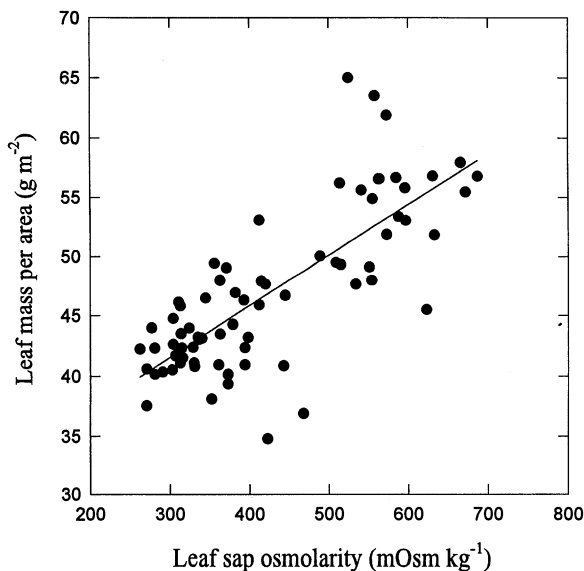

Fig. 4 Leaf mass per area (specific leaf mass) as a function of leaf sap osmolarity for *Scaevola sericea* grown under different salinity treatments ($r^2 = 0.59$).

with increasing substrate salinity resulted from the net increase in osmotically active solutes rather than the passive decrease in water content of the leaf tissues. Leaf water content expressed on a dry weight basis was also independent of substrate salinity and therefore not significantly correlated with leaf sap osmolarity (data not shown). Leaf mass per unit surface area (LMA) tended to increase linearly with increasing leaf sap osmolarity from 40 to 60 g m^{-2} (fig. 4).

The $\delta^{13}C$ of the leaves increased from $-29.2\%o$ to $-26.3\%o$ with increasing salinity (table 2). Increasing
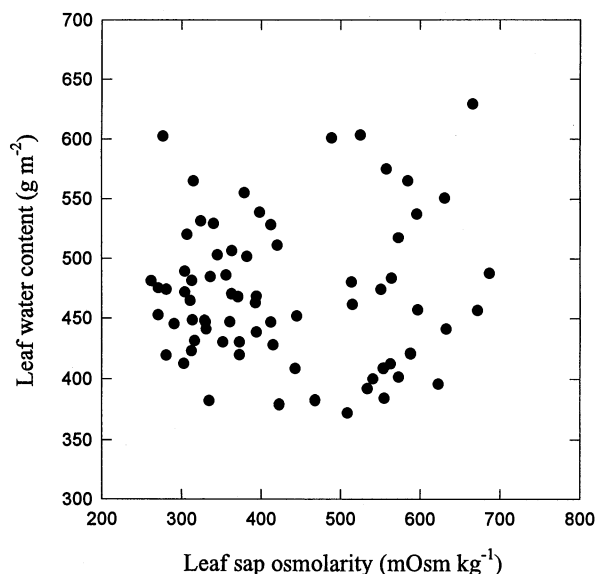

Fig. 3 Leaf water content, expressed on a leaf area basis, as a function of leaf sap osmolarity for *Scaevola sericea* grown under different salinity treatments ($r^2 = 0.001$).

substrate salinity resulted in less discrimination against ^{13}C (higher $\delta^{13}C$ values), with salt spray having a minor effect. The foliar $\delta^{13}C$ roughly increased $1\%o$ for every 100 mOsm kg^{-1} increase in leaf sap osmolarity. The higher $\delta^{13}C$ values at higher substrate salinity were apparently the result of lower stomatal conductances rather than higher photosynthetic rates (fig. 5). Net assimilation rates only decreased by 20% over a $5\%o$ change in foliar $\delta^{13}C$, while g_{wv} decreased by 60% over the same $\delta^{13}C$ range. Substantially lower g_{wv} at high salinity should result in both higher instantaneous intrinsic water use efficiency (A/g_{wv}), and higher $\delta^{13}C$ values.

The initial slope of the net CO_2 assimilation–intercellular CO_2 concentrations (A-c_i) relationships remained constant for plants grown under different salinities (fig. 6), indicating that the carboxylation efficiency was not affected by either substrate salinity or salt spray. The CO_2-saturated photosynthetic capacity and the CO_2 compensation point were also apparently not markedly different for plants subjected to the different above- and belowground salinity levels. The highest photosynthetic rates (ca. 10 μmol m^{-2} s^{-1})

Table 2

EFFECT OF SUBSTRATE SALINITY AND SALT SPRAY ON CARBON ISOTOPE RATIOS ($\delta^{13}C$) OF *SCAEVOLA SERICEA* LEAVES

Substrate salinity (mOsm kg^{-1})	Salt spray	
	0 mg m^{-2} d^{-1}	1200 mg m^{-2} d^{-1}
0	-29.20 ± 0.34	-28.36 ± 0.42
100	-28.40 ± 0.32	-27.82 ± 0.18
335	-26.78 ± 0.29	-26.30 ± 0.33

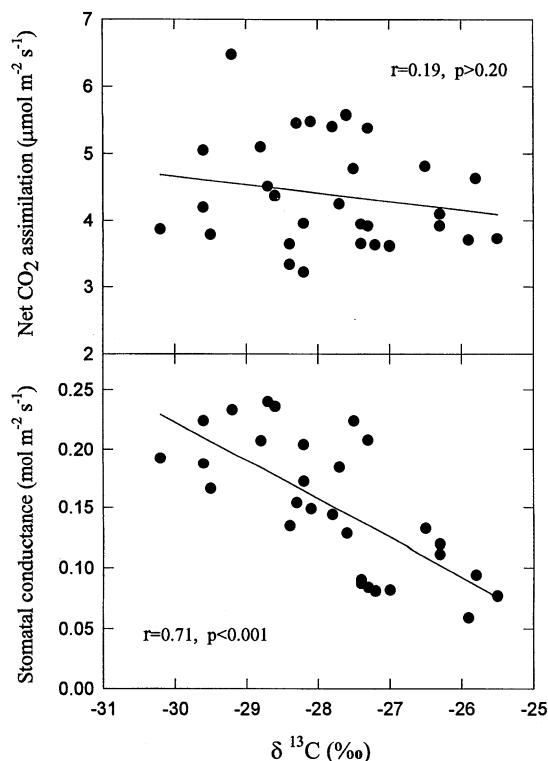Note. Values of $\delta^{13}C$ in $\%o$ represent means $\pm$ standard errors ($n = 5$).

Fig. 5 Net CO_2 assimilation and stomatal conductance to water vapor as a function of carbon isotope ratios ($\delta^{13}C$) for *Scaevola sericea* grown under the different salinity treatments.

were above 400 μmol mol^{-1} CO_2 for plants grown at 0 and 100 mOsm kg^{-1} substrate salinity. Stomatal conductances were very low for the plants grown at 335 mOsm kg^{-1} salinity. It was not possible to obtain c_i values higher than 400 μmol mol^{-1} for the salinity-stressed plants because stomata tended to close tightly at high CO_2 concentrations. The PACsys 9900 gas exchange system simultaneously utilized the incoming flow rate of dry air and transpirational water loss from the leaves enclosed in the cuvette to control humidity. Even though a large leaf surface area was enclosed in the cuvette, low transpiration rates made it impossible to increase c_i values above 400 μmol mol^{-1} without changing VPDs. The operational point (c_i and A at ambient CO_2 concentrations), in contrast, decreased with increasing salinity for the nonsprayed plants, and it was virtually independent of salinity for the sprayed plants (fig. 6).

The limitation to CO_2 uptake imposed by stomatal conductance in *S. sericea* increased from 9% at 0 mOsm kg^{-1} salinity to 29% in the 335 mOsm kg^{-1} salinity treatment for nonsprayed plants (table 3). The stomatal limitation for the sprayed plants was somewhat higher, ranging from 19% to 34% in the 0–335 mOsm kg^{-1} salinity range. The g_{wv} at atmospheric CO_2 concentration declined from 0.15 to 0.06 μmol m^{-2} s^{-1}, and from 0.07 to 0.04 μmol m^{-2} s^{-1}, for the sprayed and nonsprayed plants, respectively (table 3). The stomatal conductance to CO_2 was actually 38%

Intercellular CO_2 concentration
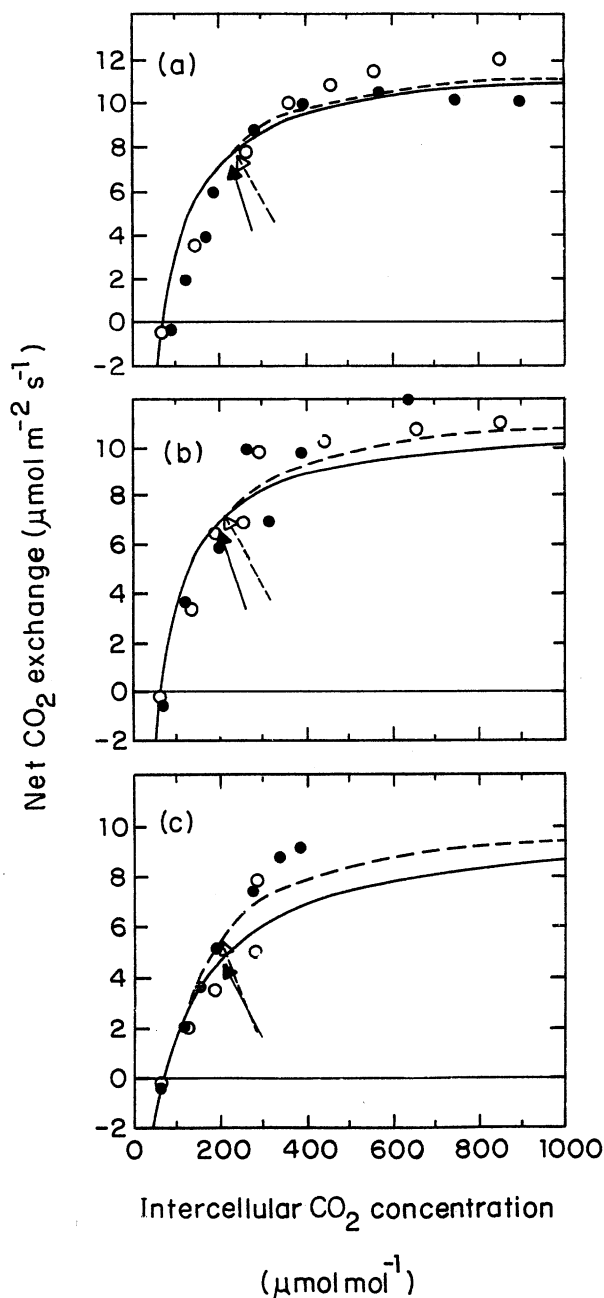
$(\mu mol\, mol^{-1})$

Fig. 6 Net CO_2 assimilation as a function of intercellular CO_2 concentration for *Scaevola sericea* grown at 0 (a), 100 (b), and 335 (c) mOsm kg^{-1} substrate salinity and exposed to salt spray containing 0 (○ and solid lines) and 1200 mg m^{-2} d^{-1} (● and dashed lines) of sea water salt. The arrows indicate the intercellular CO_2 concentration and photosynthetic rate at an atmospheric CO_2 of 350 μmol mol^{-1} (open arrow heads indicate nonsprayed treatments, while filled arrow heads indicate sprayed treatments). The measurements were made at a photosynthetic photon flux density of 600 μmol m^{-2} s^{-1}, 25°C leaf temperature and a VPD of 0.5 kPa.

lower when g_{wv} was corrected for differences in CO_2 diffusivities between water vapor and CO_2. As expected, the intercellular CO_2 levels at atmospheric CO_2 (350 μmol mol^{-1}) decreased with increasing salinity; however, the decline of A and A_0 was relatively small

Table 3

GAS EXCHANGE PARAMETERS OBTAINED FROM A-c_i RELATIONSHIPS OF SCAEVOLA
SERICEA GROWN UNDER DIFFERENT SUBSTRATE SALINITY AND SALT SPRAY LEVELS

Gas exchange parameters	Salt spray					
	0 mg m^{-2} d^{-1}			1200 mg m^{-2} d^{-1}		
	Substrate salinity (mOsm kg^{-1})			Substrate salinity (mOsm kg^{-1})		
	0	100	335	0	100	335
l_s	9	16	29	19	28	34
T	55	50	80	90	70	70
c_i	240	210	190	200	180	170
A_o	8.4	8.4	6.8	8.2	8.2	7.6
A	8.2	7.4	5.2	6.2	7.0	5.6
g_{wv}	0.15	0.08	0.06	0.07	0.05	0.04
g_m	0.06	0.07	0.06	0.07	0.07	0.07

Note. l_s in % is the relative stomatal limitation as defined by Farquhar and Sharkey (1982); T in μmol mol^{-1} is the CO_2 compensation point; c_i is the intercellular CO_2 concentration in μmol mol^{-1} at atmospheric CO_2 (350 μmol mol^{-1}); A_o in μmol m^{-2} s^{-1} is the potential photosynthetic rate at infinite stomatal conductance; A in μmol m^{-2} s^{-1} is the actual photosynthetic rate at atmospheric CO_2; g_{wv} in mol m^{-2} s^{-1} is stomatal conductance to water vapor at atmospheric CO_2; and g_m is mesophyll · conductance in mol m^{-2} s^{-1}. Values are means ($n = 3$).

(7% and 10%, respectively, with increasing substrate salinity by 335 mOsm kg^{-1}; table 3), particularly for the sprayed plants. Mesophyll conductance (calculated from the initial slopes of the A-c_i relationships (Jones 1992), as opposed to intercellular CO_2 levels, was independent of substrate salinity and salt spray levels.

Discussion

Detrimental effects of salinity on plant growth result from direct effects of ion toxicity or indirect effects of dissolved ions, particularly Na$^+$ and Cl$^-$, on the substrate water potential. To avoid water deficits at high salinity, halophytic plants accumulate saline ions in shoots, particularly in leaf tissues. Salinity tolerance at the cellular level involves compartmentalization of excess saline ions required for osmotic adjustment in vacuoles, coupled with production and accumulation of nontoxic, usually nitrogenous, compatible solutes in the cytoplasm (Berry and Downton 1982; Ungar 1991). By these means a plant can sustain a water potential gradient from soil to plant that is favorable for water uptake. *Scaevola sericea* can maintain a large and fairly constant soil-to-leaf osmotic potential gradient for various levels of substrate salinity. Clearly the increased osmolarity of the cell sap resulted from osmotic adjustment (net production of osmotically active solutes) and not the effect of passive water loss. Leaf water content of *S. sericea* leaves did not significantly decrease with increasing salinity. Osmotic adjustment is an energy-requiring process that sequesters photoassimilates that could otherwise be used for processes directly related to leaf expansion and growth.

The growth rates of halophytes are to some extent insensitive to variation in salinity within the 0 to 335 mOsm kg^{-1} range. Several halophytic species, such as *Aster tripholium, Atriplex triangularis, Salicornia bra-*

chystachya, and *Spartina alterniflora,* show increased dry mass production when grown at 335 mOsm kg^{-1} external salinity compared with growth at 0 mOsm kg^{-1} salinity (Drake and Ungar 1989; Ungar 1991). Most halophytic species achieve only marginal growth increments above sea water concentration levels but are able to tolerate hypersaline conditions up to ca. 1675 mOsm kg^{-1} soluble salts (about 5% sea water salinity) for at least short periods of time. Glycophytes, in contrast, have much lower tolerance limits, usually less than 335 mOsm kg^{-1} total soluble salts in the soil solution. *Scaevola sericea* exhibits its maximum growth rate at 0 mOsm kg^{-1}, but it was still able to maintain appreciable growth rates at 335 mOsm kg^{-1}. Even though tolerance of *S. sericea* to higher salinity levels was not tested in this study, the growth rate response to substrate salinity appears to be intermediate between that of halophytes and that of glycophytes. Some morphological characteristics of *S. sericea,* such as high leaf specific mass when grown at high external salinity, are more typical of halophytic species.

Increased salinity usually results in a decrease in photosynthetic rates, not only in glycophytes but also in halophytes, which are supposed to be very tolerant and relatively insensitive to saline ions in the soil. Salinity stress can decrease the photosynthetic activity of a halophytic plant by inducing partial stomatal closure, decreasing carboxylation efficiency and/or CO_2-saturated photosynthesis, and inhibiting the light reaction mechanism (Ungar 1991). The decline in photosynthetic rates in most plants growing in saline habitats results from a tighter stomatal control of gas exchange rather than from a change in carboxylation efficiency or CO_2-saturated photosynthesis (Ishikawa et al. 1991). *Scaevola sericea* grown at high salinity exhibits

very little inhibition of CO_2 assimilation even at 335 mOsm kg^{-1} substrate salinity. While stomatal conductance decreases threefold with increasing salinity, mesophyll conductance and carboxylation efficiency, in contrast, are not substantially affected by changes in salinity. The limitation actually imposed by stomata on CO_2 assimilation of *S. sericea* is quite small, particularly for the nonsprayed plants, ranging from 9% to 16% in 0 and 100 mOsm kg^{-1} and increasing to only 29% in the 335 mOsm kg^{-1} salinity treatment. Stomatal limitations are slightly higher for the sprayed plants at 335 mOsm kg^{-1} substrate salinity, consistent with the small photosynthetic decline observed at higher salinity. The main consequence of lower g_{wv}'s at higher salinity is the decrease of c_i. The decline of c_i at higher salinity is also consistent with the increase in $\delta^{13}C$ of the *S. sericea* leaves at higher salinity. Like *S. sericea, Salicornia virginica* also exhibits no inhibition of CO_2 uptake at high salinity (Pearcy and Ustin 1984). Results of gas exchange measurements at different salinities in this study are consistent with both the portable and the laboratory photosynthesis systems. The relatively lower *A* values observed with the portable system results from a lower irradiance during measurements under the shade cloths of the greenhouse benches.

Scaevola sericea growing at higher substrate salinities results in a higher long-term water use efficiency as measured by $\delta^{13}C$. *Scaevola sericea* seedlings (Alpha et al. 1996) and other coastal or halophytic plants also respond strongly to higher substrate salinity by increasing the $\delta^{13}C$ of their leaf tissues (Guy et al. 1989; Walter and Sinclair 1992). More positive $\delta^{13}C$ in *S. sericea* is associated with maintenance of nearly constant photosynthetic rates while g_{wv} declines. Likewise, Geber and Dawson (1990) and Meinzer et al. (1992*a*) report that, in an annual weed and in Hawaiian *Metrosideros polymorpha,* respectively, more variation in g_{wv} than in *A* leads to strong differences in A/g_{wv} and $\delta^{13}C$. In contrast, genotypic variation in A/g_{wv} (and therefore in $\delta^{13}C$) in peanut results from variation in photosynthetic capacity at similar levels of g_{wv} (Wright et al. 1988). Similarly, the increase in $\delta^{13}C$ in two shade-tolerant tropical species, *Piper cordulatum* and *Psychotria limonensis,* growing under higher irradiance in treefall gaps results from an increase in *A* associated with a smaller increase in g_{wv} (Jackson et al. 1993).

Few characteristics of *S. sericea* plants are affected by salt spray. Osmolarity of the leaf tissues, in particular, increases significantly at all levels of substrate salinity for the plants subjected to salt spray loading, probably due to foliar absorption of NaCl and other ions. *Scaevola sericea* seedlings, in contrast, are strongly affected by salt spray (Alpha et al. 1996). Because salt spray intensity in the field increases with height above the ground (Barbour et al. 1985) the ability to tolerate spray may be less critical for seedlings than for older plants. Even though the salt contained in the wet depositions could have been absorbed di-

rectly by the twigs or via root uptake, it is likely that leaves and young stems are the primary route of salt spray incorporation into the leaf tissues. Boyce (1954) showed that salt enters the leaf tissues via small cuts and abrasions in the leaf cuticle produced by the leaves flapping in the wind in the natural environment. Such injuries might be reduced or absent in the young cuttings grown out in the greenhouse and thus may have led to higher spray tolerances than would be the case in nature. The ability of plants to take up water and nutrients directly by leaf and young stem tissues is well known. For example, Katz et al. (1989) have shown that a substantial uptake of water and solute ions occurs through the bark and foliage of *Picea abies.* Using fluorescent dyes they find that one of the pathways of solute incorporation into the twigs is the radially oriented ray tissue of the young stems. Other authors find that stomata and leaf cuticles are also important pathways for water and solute uptake from dry and wet depositions (Pearson and Stewart 1993). Salt spray may have beneficial effects on the plant growth of coastal plants. Barbour and De Jong (1977) observe that salt spray promotes growth of *Lathyrus littoralis,* probably due to the nutrient input from the spray. Seneca (1972) and Maze and Whalley (1992) also find that biomass of coastal plants increases with salt spray applications. In our study, increased biomass production with salt spray is only observed in *S. sericea* plants irrigated with tap water. At higher substrate salinity, biomass increments of sprayed and nonsprayed plants are similar, probably due to the overriding effect of substrate salinity on the growth and physiology of *S. sericea* plants. Similarly, Rozema et al. (1982) find that airborne salinity increases the dry matter production of coastal sand dune species under conditions of low soil fertility.

Dry matter increments were clearly more sensitive to salinity levels than were CO_2 assimilation rates, indicating that photosynthesis is not the primary factor contributing to the growth response in *S. sericea.* Although, in general, actual incorporation of C affects the growth potential of a plant, the proportional allocation to photosynthetic versus nonphotosynthetic tissues and the use of photoassimilates for maintenance functions such as osmoregulation are important determinants of dry-matter increments. The pattern of *S. sericea* growth is similar to that of other halophytes where growth tends to decrease more than photosynthesis with increasing salinity (Long and Baker 1986). If salinity stress causes a reduction in leaf area, biomass production of plants will be reduced even though net assimilation rates remain constant. High leaf specific mass (perhaps due to higher nitrogen and chlorophyll content per unit leaf area) at high salinity may have contributed in maintaining photosynthetic rates of *S. sericea* leaves, despite lower stomatal conductance. The constancy in photosynthetic behavior per leaf for plants subjected to long-term stress conditions has been observed for factors other than salinity. For example, net assimilation rates of coffee plants grown

under different soil water availability conditions are nearly equal at the end of a 120-d experiment, while the total leaf surface area per plant decreases substantially with decreasing soil water content (Meinzer et al. 1992b). It appears that, similarly to the coffee plants, the maintenance of nearly constant photosynthetic characteristics on a unit leaf area basis through maintenance of a smaller total leaf area may constitute a major mode of adjustment to higher salinity levels in S. sericea.

The results from this study indicate that substrate salinity had a stronger effect on the growth and physiology of S. sericea than did salt spray. The effect of salt spray, though minor, still affected some characteristics of the plant, such as the osmotic potential of leaf tissues. Higher concentration of osmotically active solutes at higher salinities helped to maintain an adequate soil-to-leaf water potential gradient favorable for water uptake under salt stress conditions. The carboxylation capacity of the leaves and other characteristics of the photosynthetic apparatus were not substantially affected by the salinity treatments, indicating that continuous photosynthesis was possible under a wide range of substrate salinity and salt spray levels. Increases in water use efficiency at high salinity, as measured by gas exchange and carbon stable isotope ratios, were the consequence of lower stomatal conductances rather than an increase in leaf photosynthetic capacity. All of this indicated that S. sericea was capable of substantial growth and physiological responses, which apparently was required to maintain a positive carbon balance and continuous growth in coastal habitats characterized by large temporal and spatial variations in substrate salinity and salt spray levels. At the same time, these responses may partially explain the wide geographical distribution of S. sericea in coastal habitats throughout the tropical and subtropical Pacific and Indian Oceans.

Acknowledgments

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