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Effects of salinity on growth and photosynthesis of three California tidal marsh species

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Summary. The comparative responses of photosynthesis and growth to salinity were investigated for two C_3 and one C_4 species native to the tidal marshes of the San Francisco Bay-Sacramento River estuary of Northern California. At low salinities (0 or 150 meq l^{-1}), where photosynthetic rates were maximal for all species, the C_4 grass *Spartina foliosa* maintained the highest photosynthetic capacity and the C_3 stem-succulent shrub *Salicornia virginica* the lowest; photosynthetic rates of the C_3 sedge *Scirpus robustus* were intermediate. Differences in photosynthetic responses to intercellular CO_2 pressure and temperature were consistent with those generally observed between C_3 and C_4 plants.

CO_2 uptake was reduced at salinities above 150 meq l^{-1} in *Scirpus* and 300 meq l^{-1} in *Spartina*. In contrast, *Salicornia* exhibited no inhibition of CO_2 uptake even at 450 meq l^{-1} salinity. Analysis of the responses to intercellular CO_2 partial pressures showed that the inhibition of photosynthesis by high salinity in both *Spartina* and *Scirpus* is primarily accounted for by reduced photosynthetic capacity of the mesophyll, and secondarily, by reduced leaf conductances.

Species differences in relative growth rate (RGR) almost exactly opposed the differences in photosynthetic rates; the highest RGR was found in *Salicornia* and the lowest in *Spartina*. This reversal is accounted for by the greater allocation to photosynthetic shoots in *Salicornia*, which more than compensated for the lower photosynthetic capacity per unit surface area. RGR was more sensitive to salinity than photosynthetic rate in all three species, but the same relative sensitivities held. For *Scirpus*, reduced leaf elongation rates and changes in allocation patterns account for the greater limitation by salinity of RGR than of photosynthesis, and may be a primary factor restricting productivity of this species in saline habitats.

Introduction

The physiological ecology of the tidal marsh vegetation of the California coast has not been studied as extensively as that of the Atlantic coast of North America and of Europe. The tidal marshes of California, however, offer an interesting system for ecophysiological investigations because of the generally high salinity levels and the large seasonal changes in salinity due to the lack of summer precipitation. Moreover, these marshes have only a few dominant species which occur in well defined zones that appear to correspond to differences in salinity and tidal immersion (Mahall and Park 1976a, b, c). Previous studies have documented the zonation patterns (Hinde 1954; Atwater et al. 1980) and species differences in growth and water relations as influenced by the seasonal salinity changes (Ustin et al. 1982).

In the research reported here, we compared photosynthetic and growth responses to salinity of three marsh species: *Spartina foliosa,* Trin. a C_4 grass species, *Salicornia virginica* L., a succulent C_3 shrub species, and *Scirpus robustus,* Pursh. a C_3 sedge. The first two are common in the highly saline tidal marshes of San Francisco Bay with *Spartina* occupying the low marsh at elevations from about mean sea level to mean high tide level and *Salicornia* occurring in the higher marsh (Mahall and Park 1976a). *Scirpus,* in contrast, is more common in the brackish water marshes occurring further inland in the Sacramento River estuary (Atwater et al. 1980). At some sites, such as the Sonoma Creek Marsh at the northern extension of the San Francisco Bay system (Ustin et al. 1982), all three species occur together with *Scirpus* occupying an intermediate zone between the other two species.

The objectives of this research were to determine how these contrasting species differ in their photosynthetic responses to salinity and how these differences relate to growth responses. Analysis of the photosynthetic responses were obtained primarily by examining intercellular CO_2 partial pressure dependence curves for photosynthesis. These curves define a "demand function" (Raschke 1979) related to the capacities for carboxylation, electron transport, etc. in the leaf (Farquhar and Sharkey 1982) and a "supply function" determined primarily by stomatal conductance. This analysis allowed separation of the effects of salinity into stomatal and mesophyll components.

Materials and methods

Seeds and rhizomes of *Scirpus robustus* and rhizomes of *Spartina foliosa* were collected from Sonoma Creek Marsh or San Pablo Bay, while seeds and rhizomes of *Salicornia virginica* and *Scirpus robustus* were obtained from Suisun Marsh, located approximately 40 km E of Sonoma Creek Marsh in the Sacramento River Delta. The magnitudes and

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seasonal patterns of salinity are similar in the *Salicornia* zones of both marshes (Mall 1969; Ustin et al. 1982).

Plants of *Salicornia, Spartina,* and *Scirpus* were regenerated from rhizome sections in sand irrigated with a modified Hoagland's solution and transplanted into 7 × 30 cm pots containing a perlite and sand mixture. The pots were subirrigated by partial immersion into tanks containing 26 l of aerated nutrient solution. Each tank contained up to 15 plants. After the plants were established, the nutrient solutions were gradually salinized with an artificial sea salt mixture (Rila mix) up to 150, 300 or 450 meq l^{-1}; the control treatment consisted of unsalinized Hoagland's solution. The solutions were changed every 2 weeks and the pots were leached regularly to insure uniform concentrations. All measurements were made after development of new leaves under the final salinity regimes.

Plants were grown in a greenhouse with supplemental light supplied by 1,500 W metal-halide arc lamps for 15 h per day. Photon flux densities (PFD) and air temperatures were recorded periodically using a LI-COR Inst., Inc. quantum sensor and copper-constantan thermocouples, respectively, connected to a Campbell Scientific CR21 Micrologger. On clear days, which predominated during the measurement period, photon fluxes were 1,300 μmol m^{-2} s^{-1} and the daily total 43 mol m^{-2}. On cloudy days the values were 750 μmol m^{-2} s^{-1} and 27 mol m^{-2}, respectively. Evaporative cooling kept daytime air temperatures between 27 and 32° C; night temperatures were 15 to 19° C.

Photosynthetic CO_2 and water vapor exchange rates were measured with an apparatus similar to that described by Pearcy (1977). A single attached leaf of *Scirpus* or *Spartina* or a branch of *Salicornia* was enclosed within a glass-windowed circular brass chamber with a thermostatted water jacket in the base and the lid. A fan maximized the boundary layer conductances and heat exchange between the leaf or branch and the chamber. Leaf or branch temperatures were measured with 0.7 mm diameter copper-constantan thermocouples. Light was measured with a silicon cell mounted on the lid of the chamber. Air of known CO_2 concentration was supplied to the chamber by mixing CO_2-free air and 1% CO_2 from compressed air cylinders with calibrated metering valves or rotameters. Humidity was controlled by condensation to a known dewpoint in a thermostatted condenser. The flow rate was measured with either a mass flowmeter (Flow Technology, Inc.) or with a differential pressure transducer (Validyne Engineering, Inc.) mounted across a flow restrictor made from a scintered glass disc. CO_2 concentrations were determined with a differential infrared gas analyser (Beckman Inst., Inc. model 865 or Horiba, Inc. model VIA 500-R) and water vapor concentration with a solid-state relative humidity probe (Weathermeasure model HM-111P). Light was supplied by a 1,500 W metal-halide lamp, and intensities controlled with wire screen filters.

Leaf conductances to CO_2 (g_l') were calculated from the simultaneous measurements of CO_2 and water vapor exchange using the equations given by Wong et al. (1978), which yield molar flux units for conductances. Mesophyll conductances to CO_2 (g_m') were calculated from the initial slopes of curves of photosynthetic rate versus intercellular CO_2 partial pressure [$p(CO_2)$] as outlined by Jarvis (1971). Expression of intercellular CO_2 as a mole fraction gave molar flux units for g_m'. The method outlined by Farquhar and Sharkey (1982) was used to calculate the relative limitation to CO_2 uptake imposed by g_l'. In this method the relative limitation, l_s, is calculated from:

$$l_s = \frac{A_o - A}{A_o}$$

where A_o equals the expected photosynthetic rate if g_l' were infinitely high and A is the measured photosynthetic rate at the normal atmospheric CO_2 partial pressure (rate at 32.5 ± 1.0 Pa). Since at an infinite g_l' there would be no CO_2 partial pressure difference between the atmosphere and cell walls, values of A_o were determined from CO_2 dependence curves at 32.5 Pa intercellular $p(CO_2)$. For *Spartina,* this required extrapolation of several of the curves since g_l' decreased strongly at high CO_2 and kept intercellular $p(CO_2)$ below 32.5 Pa.

Gas exchange rates and g_l' were calculated on the basis of the surface area of one side of the leaf in *Scirpus* and *Spartina* and, so that the measurements were comparable, using half of the round shoot surface area in *Salicornia.*

Relative growth rates (RGR) were measured using seedlings selected for uniformity of size. Growth conditions in these experiments were the same as those used for the photosynthesis measurements. After the gradual salinization period, the plants were allowed to equilibrate for 7–10 days. Harvests of 4–5 plants each were then made at 7–10 day intervals and weights were determined after oven drying. RGR was then calculated for each harvest interval and the average was calculated to give an overall mean for the growth period. Ash contents were determined by combustion of dried tissue samples at 500° C for 8 h in a muffle furnace.

Results

Light and temperature dependence curves illustrate the comparative photosynthetic responses of *Spartina, Scirpus* and *Salicornia* in the absence of salinity stress. The light dependence responses (Fig. 1) were similar for all three species and differed mainly in the rates of photosynthesis and the higher light compensation point in *Salicornia.* None of these species showed a clear saturation of photosynthesis

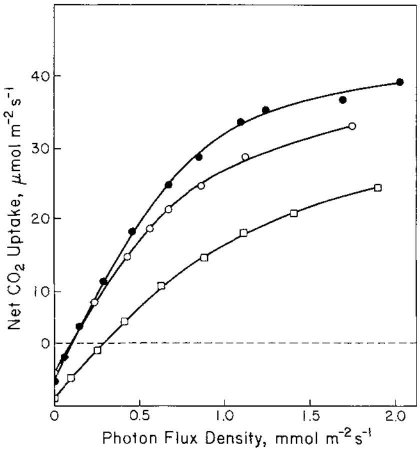

Fig. 1. Photosynthetic CO_2 uptake as a function of PFD for *Spartina foliosa* (●), *Scirpus robustus* (○), and *Salicornia virginica* (□). The measurements were made at 30° C leaf temperatures, 32.0 Pa CO_2 pressures, and a VPD of 0.5–1.0 kPa

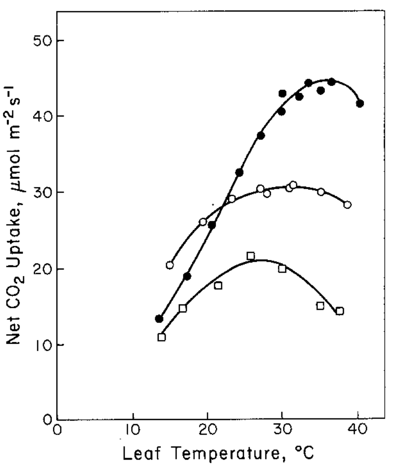

Fig. 2. Photosynthetic CO_2 uptake as a function of leaf temperature for *Spartina foliosa* (●), *Scirpus robustus* (○), and *Salicornia virginica* (□). The measurements were made at PFD of 1.7 to 2.0 mmol m^{-2} s^{-1}, 32.0 Pa CO_2 pressures, and a VPD of 0.5–1.0 kPa. The plants were from the same treatments as in Fig. 1

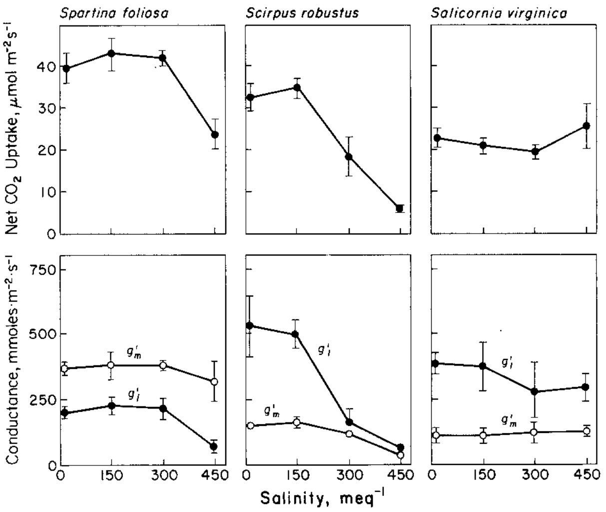

Fig. 4. Effect of salinity on CO_2 uptake, leaf (g'_l) and mesophyll conductances (g'_m) of *Spartina foliosa, Scirpus robustus,* and *Salicornia virginica*

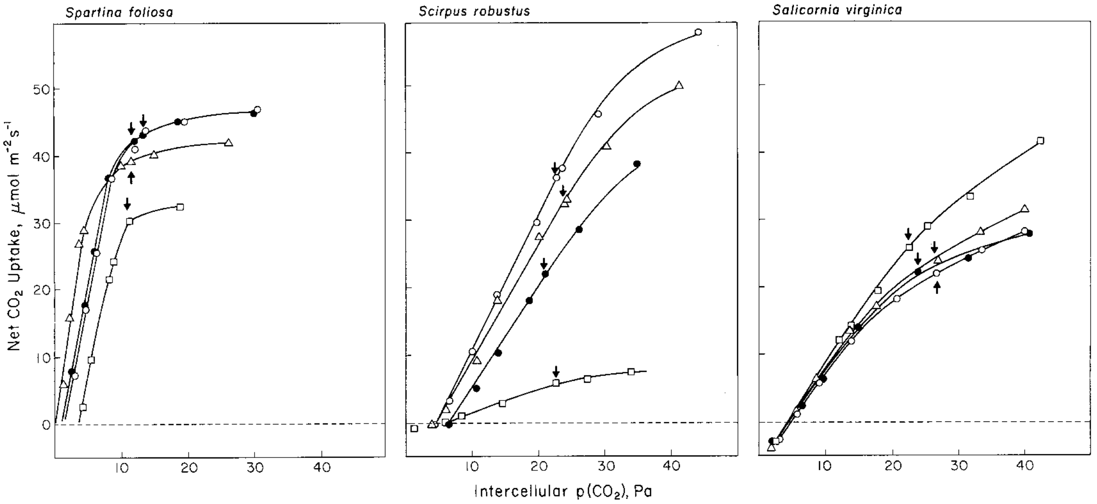

Fig. 3. Photosynthetic CO_2 uptake as a function of intercellular CO_2 pressure for *Spartina foliosa, Scirpus robustus,* and *Salicornia virginica* grown at 0 (△), 150 (○), 300 (●) or 450 (□) meq l^{-1} salt concentrations. The arrows indicate the intercellular $p(CO_2)$ and photosynthetic rate at an atmospheric $p(CO_2)$ of 32.5±1.0 Pa. The measurements were made at high PFD (1.7 to 2.0 mmol m^{-2} s^{-1}), 30° C leaf temperatures, and a VPD of 0.5–1.0 kPa

even at PFD equivalent to full sunlight, presumably due to the high photosynthetic capacities in *Spartina* and *Scirpus* and the poor geometry for light interception of *Salicornia*. Respiration rates and light compensation points were also much higher in *Salicornia* than either *Scirpus* or *Spartina*. Maximum photosynthetic rates occurred at leaf temperatures of about 25° C in *Salicornia*, 30° C in *Scirpus*, and 35° C in *Spartina* (Fig. 2). Photosynthetic rates were highest in *Spartina* at high temperatures and *Scirpus* at low temperatures, while *Salicornia* had the lowest rates at all temperatures.

The effects of the salinity treatments on the photosynthetic responses are best illustrated by the response curves to intercellular CO_2 partial pressure (Fig. 3). Arrows indicate the net CO_2 uptake and intercellular $p(CO_2)$ at ambient $p(CO_2)$. As is characteristic of C_4 plants, *Spartina* exhibited steep initial slopes of the response curves at low intercellular $p(CO_2)$ and an abrupt transition to saturation at higher intercellular $p(CO_2)$. The CO_2 compensation point was near zero for the plants grown at 0 meq l^{-1}, as is typical of C_4 plants, but shifted to 3.5±1.4 Pa at 450 meq l^{-1}. Salinity did not affect the initial slopes of the CO_2 response curves but did affect the CO_2-saturated photosynthetic capacity.

Both *Scirpus* and *Salicornia* (Fig. 3) exhibited CO_2 responses typical of C_3 plants, with high CO_2 compensation points and only a slight tendency for saturation at high intercellular $p(CO_2)$. For *Salicornia*, the effect of salinity on the CO_2 response was relatively small and the curves differed principally in the degree of curvature at high intercellular $p(CO_2)$ rather than in the initial slopes or CO_2 compensation points. In contrast, salinities above 150 meq

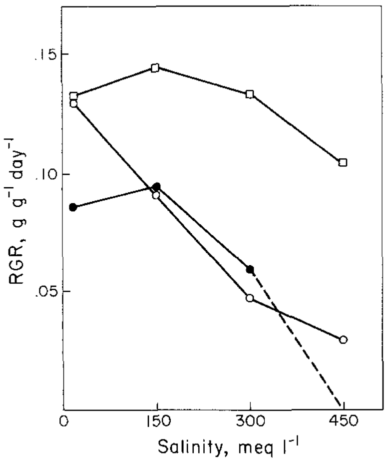

Fig. 5. Relative growth rates of *Spartina foliosa* (●), *Scirpus robustus* (○), and *Salicornia virginica* (□) as a function of salinity

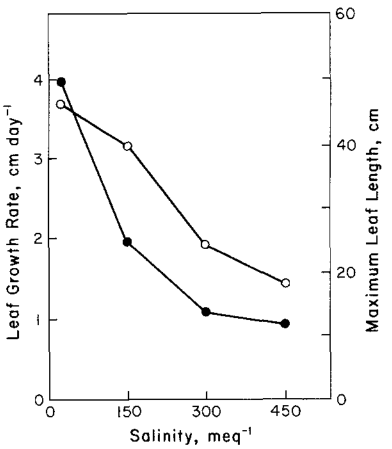

Fig. 6. Leaf elongation rate (○) and maximum leaf length (●) of *Scirpus robustus* as a function of salinity

Table 1. Dry weights and root/shoot ratios (R/S) at the end of the growth period for plants grown under different salinity treatments. Weights are in g ± 1 SD

		Salinity (meq l^{-1})			
		0	150	300	450
Spartina	Total wt	1.28 ± 0.58	1.62 ± 0.40	0.51 ± 0.13	–
	R/S	0.51	0.53	0.63	
Scirpus	Total wt	4.87 ± 0.36	2.05 ± 0.74	0.88 ± 0.34	0.45 ± 0.10
	R/S	0.65	0.56	1.21	1.92
Salicornia	Total wt	2.42 ± 0.82	4.23 ± 0.77	3.66 ± 0.63	1.41 ± 0.33
	R/S	0.49	0.25	0.33	0.33

l^{-1} had a large effect on the CO_2 responses of *Scirpus*. The primary effect was a reduced initial slope of the CO_2 response curves and at 300 and 450 meq l^{-1} a slightly increased CO_2 compensation point.

Analysis of g'_l and g'_m (Fig. 4) also shows that the effects of salinity differed considerably among the species. For *Spartina*, g'_m was greater than g'_l and was not significantly affected by salinity, whereas g'_l was strongly reduced at 450 meq l^{-1}. However, l_s, the limitation actually imposed by g'_l was quite small, ranging from 10 to 15% in 0 to 300 meq l^{-1} and increased to only 30% at 450 meq l^{-1} salinity treatments. Thus, while the decreased g'_l contributed to reduced photosynthetic rates of *Spartina* at 450 meq l^{-1}, lower photosynthetic capacity in the CO_2 saturated portion of the response curve was primarily responsible for the observed reduction in photosynthetic rate. The salinity-induced changes in g'_l appear to act in concert with changes in the mesophyll limitations on CO_2 uptake, so that intercellular $p(CO_2)$ remains at the transition from CO_2 limitation to CO_2 saturation.

The CO_2 response curves for *Scirpus* also indicated that the primary effect of salinity was on the mesophyll limitations on photosynthetic capacity. This was especially apparent at 450 meq l^{-1}, where photosynthetic rates at 32.5 Pa intercellular $p(CO_2)$ were only 20% of those at 150 meq l^{-1}. The decrease in g'_l closely paralleled photosynthetic capacity so that intercellular $p(CO_2)$ remained relatively constant at 22 to 24 Pa. Calculation of l_s at each salinity showed that it increased from 27 to 40% from 0 to 300 meq l^{-1} but decreased to only 19% at 450 meq l^{-1}.

Salicornia showed no consistent patterns of changes in photosynthetic rates, g'_m or g'_l in response to salinity. Photosynthetic capacity in *Salicornia* was relatively independent of salinity over this range, increasing to slightly higher values at 450 meq l^{-1} than at lower salt concentrations. Calculation of l_s showed that it was relatively constant at 15 to 17% at salinities up to 300 meq l^{-1} but increased to 35% at 450 meq l^{-1}.

Substantial differences in the salinity dependence of RGR (Fig. 5) and final plant dry weights (Table 1) were also apparent. Maximum RGR was highest in *Salicornia* and lowest in *Spartina*, a relationship opposite that found for CO_2 uptake rates. For *Salicornia*, RGR was stimulated by 150 and 300 meq l^{-1} and showed only a modest decline at 450 meq l^{-1}. The dried shoots of *Salicornia* consisted of 26% ash for plants grown at 0 meq l^{-1}, and about 41% ash for the plants grown at higher salinities. These differences in ash content account for 50 and 100% of the increase in final dry weights of the plants grown at 150 and 300 meq l^{-1}, respectively, as compared to those grown at 0 meq l^{-1}. At 150 meq l^{-1}, the remaining 50% of the increased final dry weight of *Salicornia* is accounted for by the increased RGR. *Spartina* also showed an increase in RGR and final dry weight at 150 meq l^{-1}, but higher salinities inhibited both quantities. At 450 meq l^{-1}, little growth occurred after the first two weeks and most seedlings died. Growth of *Scirpus* was inhibited at all salinities.

Comparison of the relative effects of salinity on RGR revealed a close parallel with its effects on photosynthesis, except that growth was always more sensitive. Thus, in *Sali-*

cornia growth was inhibited above 300 meq l^{-1}, while photosynthetic rates were not affected. All levels of salinity inhibited growth in *Scirpus*, while photosynthesis was inhibited only at concentrations greater than 150 meq l^{-1}. In *Scirpus*, the fact that growth was more sensitive to salinity than photosynthetic rate was probably due to increasing allocation to below-ground structures at high salinities, as indicated by the root/shoot ratios (Table 1), and to inhibition of photosynthetic surface area expansion. As shown in Fig. 6, both the rates of leaf elongation and the final leaf lengths in *Scirpus* were greatly reduced by salinity.

Discussion

The light, temperature, and CO_2 responses of photosynthesis for *Spartina, Scirpus,* and *Salicornia* are similar to those obtained in comparisons of other C_4 and C_3 species native to saline habitats (De Jong 1978; De Jong et al. 1982; Giurgevich and Dunn 1979). At salinities not inhibitory to CO_2 uptake, the C_4 species, *Spartina*, is characterized by higher light-saturated photosynthetic capacities, a higher temperature optimum for CO_2 uptake, much higher mesophyll conductances, and lower leaf conductances than either of the C_3 species. However, *Scirpus* has a higher intrinsic photosynthetic capacity at high intercellular $p(CO_2)$. Thus, the higher CO_2 uptake rates in *Spartina* at normal ambient CO_2 levels result from the greater efficiency of utilization of low intercellular $p(CO_2)$ rather than from an intrinsically greater photosynthetic capacity.

The effects of salinity stress on CO_2 exchange are usually analyzed by simply comparing changes in g'_m and g'_l. In most halophytes investigated so far, g'_m is relatively independent of salinity, while g'_l is considerably reduced (Gale and Poljakoff-Mayber 1970; Longstreth and Strain 1977; De Jong 1978). The results shown in Fig. 4 indicate that *Scirpus* and *Spartina* exhibit this response. However, analysis of the limitations from the CO_2 dependence curves following the approach of Farquhar and Sharkey (1982) shows that both stomatal and mesophyll limitations contribute to the reduced photosynthetic performance at high salinities. Where salinities are sufficient to strongly limit CO_2 uptake, the primary effect appears to be on the mesophyll. In *Spartina,* the changes in CO_2-saturated photosynthetic rates and the CO_2 compensation point, photosynthetic components which are not included in the calculation of g'_m, appear to account for nearly all of the changes in photosynthetic rate which occur in response to salinity. Thus, the effects of salinity on photosynthesis in *Spartina* are probably at the metabolic rather than the diffusional level. In *Scirpus* too, the CO_2 response curves show that salinity has a major effect on the limitations to CO_2 uptake in the mesophyll but the stomata, however, also play an important role in the responses to salinity, since l_s increases with increasing salinity up to 300 meq l^{-1}. However, at 450 meq l^{-1}, the reduction in photosynthetic rate due to lower g'_l was actually less than at other salinities because of the low inherent photosynthetic capacities of the mesophyll. Among these species, only *Salicornia,* the most halophytic species, shows no inhibition in photosynthetic rate or g'_m and little change in g'_l with increasing salinity.

The increase in the CO_2 compensation point of *Spartina* at high salinity suggests either a large stimulation of respiration or some breakdown in the C_4 mechanism. Giurgevich and Dunn (1979) reported high CO_2 compensation points under field conditions in a Georgia salt marsh for the short form of *Spartina alterniflora,* whereas the tall form, growing in less saline sites, had low compensation points. While salinity can stimulate respiration (Epstein 1972), it is unlikely that the increase could be large enough to cause the shift in the CO_2 compensation point observed in the plants grown at 450 meq l^{-1}. The metabolic effect may be localized in the bundle sheath cells, since the RuBP carboxylase-oxygenase reactions potentially determining a compensation point and determining the CO_2 saturated photosynthetic capacity are localized there (Berry and Farquhar 1978). The lack of a salinity effect on the initial slope (g'_m) of the CO_2 response curves, which is presumably controlled by PEP carboxylase activities in the mesophyll cells, is consistent with this hypothesis.

RGR is ultimately a function of total photosynthetic capacity as determined by leaf photosynthetic rate and the proportional allocation to photosynthetic versus non-photosynthetic tissues. Comparisons of photosynthetic and growth responses to salinity among the three species clearly illustrate the importance of differences in allocation patterns, especially since photosynthetic rates and RGR were inversely related. Low RGR in *Spartina*, despite the high photosynthetic rates, was due to the low allocation to photosynthetic tissue as compared to the other species. The large allocation to stems in *Spartina* is probably necessary to keep the leaves above water level as much as possible and to resist mechanical damage during tidal flooding. Similarly, the high RGR of *Salicornia* can be accounted for by high allocation to photosynthetic tissue, which more than compensates for the low photosynthetic rates.

Comparisons within each species show that growth was always more sensitive to salinity than was photosynthesis, suggesting that photosynthesis, while certainly contributing to the growth response, is not the primary factor determining RGR in these species. These patterns of growth are consistent with the responses of other halophytes where comparisons have been made (Gale and Poljakoff-Mayber 1970; De Jong 1978; Winter 1979).

The differences in physiological and growth responses found in the three species correlate well with differences in field distribution and behavior. Midsummer salinities are much higher in the high marsh where *Salicornia* occurs than in the low marsh where *Spartina* is found (Mahall and Park 1976a; Ustin et al. 1982). Mahall and Park (1976c) suggest that *Spartina* is excluded from the high marsh by salinity while *Salicornia* is excluded from the low marsh by tidal flooding effects on seedling survival. Furthermore, they suggest that both species are less abundant in the intermediate zone because both high salinities and tidal flooding occur there. Our results demonstrate that *Salicornia* is much more tolerant of high salinities than *Spartina*, in terms of both growth and photosynthesis. The occurrence of *Scirpus* in the ecotone between *Spartina* and *Salicornia* is an intriguing paradox, since its photosynthetic and growth responses are more sensitive to moderate salinity levels than those of either *Salicornia* or *Spartina*. Indeed, midsummer salinities in the *Scirpus* zone are sufficient to inhibit strongly growth and photosynthesis of *Scirpus*. Field measurements have shown that g'_l values for *Scirpus* are quite low during the summer, supporting the view that photosynthetic gas exchange may be strongly limited (Ustin et al. 1982). However, these marshes have high salinities only during the summer; spring salinities are much lower because of higher fresh-water runoff into San Francisco Bay and leaching in the marsh due to the heavy winter precipitation. *Scirpus* completes vegetative growth during this spring period of lower salinities, whereas *Spartina* and especially *Salicornia* are more active during the late spring and summer (Ustin et al. 1982). The rapid growth of *Scirpus* at low salinities and the high photosynthetic rates at low temperatures would appear to favor this kind of seasonal growth pattern and allow survival of *Scirpus* in these marshes.

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