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Comparative Gas Exchange and Growth Responses of C₃ and C₄ Beach Species Grown at Different Salinities

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Summary. Comparative laboratory gas exchange and relative growth rate experiments were conducted on three native California coastal strand species at four salinity treatment levels. Relative mesophyll conductance sensitivities to salinity of *Atriplex leucophylla* (Moq.) D. Dietr. (C₄) and *Atriplex californica* Moq. in D.C. (C₃) were nearly identical. Mesophyll conductances of both species were stimulated by moderate levels of salinity. Mesophyll conductances of *Abronia maritima* Nutt. ex Wats. (C₃) were highest in the absence of salinity and depressed by increasing levels of salinity. Increasing levels of salinity generally decreased net photosynthesis and leaf conductances but increased water use efficiencies. The C₄ species, *Atriplex leucophylla*, had higher mesophyll conductances and water use efficiencies at all salinity levels than the C₃ species. The effects of salinity on relative growth and net assimilation rates of greenhouse grown plants were not directly correlated with the effects on net photosynthesis measured in the laboratory. Growth of *Abronia maritima* was greatly stimulated by low levels of salinity whereas photosynthesis was substantially inhibited. The possible significance of C₄ photosynthesis in relation to salinity is discussed.

Introduction

Although much ecophysiological research concerning the adaptive significance of C₄ photosynthesis in relation to light, temperature and water use efficiency has been done on salt tolerant species (Björkman, 1975; Caldwell et al., 1977; Ehleringer and Björkman, 1977; Pearcy, 1976), little is known about the adaptive significance of the C₄ pathway in relation to salinity. Gale and Poljakoff-Mayber (1970) have reported the stimulation of mesophyll conductances by NaCl in the C₄ plant, *Atriplex halimus*, which may be related to the effects of salinity

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on carboxylation enzymes in these plants (Osmond and Greenway, 1972). On the other hand, Caldwell (1974) cited several studies in which C_3 desert halophytes had rates of photosynthesis or growth that were comparable to C_4 halophytes. C_3 species have also been reported to be less sensitive to salinity than C_4 species from the same habitat (Mahall and Park, 1976; Tiku, 1976).

This paper compares the gas exchange and growth characteristics of *Atriplex leucophylla* (C_4), *Atriplex californica* (C_3), and *Abronia maritima* (C_3) in response to salinity. The purpose of this research was three-fold: 1) to determine if there are any inherent differences in the sensitivities of either photosynthetic pathway to salinity; 2) to ascertain if there are gas exchange characteristics of either pathway that have an adaptive significance in relation to salinity; and 3) to test if the differences in gas exchange characteristics can be correlated with growth responses to salinity.

Methods

The three taxa used in this study are evergreen perennial strand taxa native to the California coast. *Atriplex leucophylla* (Moq.) D. Dietr. and *Abronia maritima* Nutt. ex Wats. occur on open ocean beaches. *Atriplex californica* Moq. in D.C. is generally found on more protected beaches. Both *Atriplex* species have salt glands on their relatively thin, small leaves, whereas *Abronia* develops large, thick, succulent leaves in response to salinity.

Seeds of *Atriplex leucophylla* and *Abronia maritima* were collected from Trancas Beach near Malibu and Morro Bay, California, respectively. Seeds of *Atriplex californica* were collected from Indian Beach on Tomales Bay, California. All species were initially germinated and grown in sand-filled germination flats.

Seedlings were transplanted into tall (25 cm), narrow (6 cm diameter) pots containing sterilized, very coarse beach sand (>60% by wt. composed of grains >1 mm) and subirrigated with 1/4-strength Hoagland solution plus an appropriate amount of artificial sea salt (Rila Products) to bring the solutions to the desired osmotic potential (0, -5, -10, -20 bar). (Note: the osmotic potential of the 0 bar solution was actually slightly below 0 bar due to the nutrient solution.) Electrical conductivity of the salt solutions was monitored with an electrical conductivity meter (Lab-line Inst. Inc.) and all the solutions were changed weekly. The electrical conductivities were converted to osmotic potentials by calibrating the solutions with a thermocouple psychrometer (J.R.D. Merrill Inc.). In the high salt treatments, salt concentrations were slowly increased over the period of a week to prevent shock.

Plants used for the relative growth rate experiments were grown in the greenhouse during the fall of 1976. Light intensities were generally between 50 and 100 nanoEinstein $\text{cm}^{-2} \text{s}^{-1}$.

Mature plants for the gas exchange experiments were transferred from the greenhouse to an I.S.C.O. growth chamber set for a 16 h photoperiod with 18° C days and 12° C nights. Light levels were between 45–55 nanoEinstein $\text{cm}^{-2} \text{s}^{-1}$. The plants were grown under these growth chamber conditions at the appropriate salinity levels a minimum of 3 weeks prior to conducting the gas exchange measurements.

All gas exchange measurements were made on an open system gas analysis apparatus described in more detail elsewhere (De Jong, 1978). CO_2 exchange was measured with a Beckman Model 865 infrared gas analyser. Water vapor concentrations were measured with a relative humidity sensor (Weather Measure Model HM 111) held at a constant temperature. Flow rates were monitored with an electronic mass flow meter (Technology Inc., Model LFC-3). Leaf temperatures were measured with fine wire iron-constantan thermocouples. Light was provided by two 1000-W quartz-iodide lamps (Norelco type FCN). Calibration of the CO_2 analyzer at various CO_2 concentrations was accomplished with a precision mixing pump (H. Wösthoff O.H.G. type M 201a-F).

The photosynthetic responses of each taxon at each of four salinity treatments were determined under saturating light conditions by initially exposing the leaves to 300–330 $\mu\text{l l}^{-1}$ CO_2 concentra-

tions. After steady state gas exchange was attained at this level, the input concentration was increased to 600 $\mu\text{l l}^{-1}$. Following this, the input CO₂ concentrations were decreased in steps to approximately 300, 200, 150, 75, and 0 $\mu\text{l l}^{-1}$ respectively. The gas exchange measurements were made near the photosynthetic temperature optimum for each taxon: 19° C for *Abronia maritima* and *Atriplex californica* and 25° C for *Atriplex leucophylla*. Photosynthesis (P_{net}), transpiration (T), leaf conductance (C_l), and intercellular CO₂ pressures were calculated from CO₂ flux, water vapor flux and leaf temperature measurements according to Jarvis (1971). Mesophyll conductance (C_m) was calculated from the slope of the linear portion of the line representing the effect of changing intercellular CO₂ concentrations on the rate of CO₂ uptake as described by Jarvis (1971).

The CO₂ responses of a minimum of three plants for each taxon were measured at each salinity level. The data from all three plants of a given taxon and salinity level were pooled and a polynomial regression program was used to fit a curve to the pooled data for each species. The standard deviation lines in CO₂ response and mesophyll conductance figures represent the standard deviations about the regressions.

Xylem sap tensions of a minimum of three plants per species and salinity treatment were measured with a pressure chamber (Scholander et al., 1965). "Predawn" measurements were made in the morning before the lights in the growth chamber came on. "Afternoon" measurements were made after the lights had been on in the growth chamber for a minimum of 8 h.

Five plants from each taxon at each of four salinity levels were harvested four times at 8 day intervals. The initial harvest occurred when plants were approximately 1 month old. Roots, stems, and leaves of each plant were harvested and their dry weight recorded.

Relative growth rates (RGR) and leaf area ratios (LAR) were calculated according to West et al. (1920);

$$\text{RGR} = \frac{\ln W_2 - \ln W_1}{t_2 - t_1},$$

and

$$\text{LAR} = \frac{L_1 + L_2}{W_1 + W_2}.$$

Net assimilation rates (NAR) were calculated according to Gregory (1926);

$$\text{NAR} = \frac{\ln L_2 - \ln L_1}{t_2 - t_1} \times \frac{W_2 - W_1}{L_2 - L_1}.$$

The mean whole plant dry weight (W) was used for each sampling interval. The leaf area of fresh leaves per unit of dry leaf weight was determined from a sample of leaves from each taxon at each salinity level. Leaf dry weight was then converted to fresh leaf area (L) for calculations of LAR and NAR.

Results

The CO₂ dependence curves of each of the three taxa at the no-salt treatment level are shown in Figure 1. As is typical of C₄ plants (Krenzer et al., 1975), *Atriplex leucophylla* had a CO₂ compensation point near zero and approached CO₂ saturation at fairly low internal CO₂ pressures (100 μbars). At normal ambient CO₂ concentrations, *Abronia maritima* had photosynthetic rates that were comparable to *Atriplex leucophylla*, however these rates occur at much higher intercellular CO₂ pressures of 200–250 μbars . *Atriplex californica* had maximum photosynthetic rates at normal ambient CO₂ concentrations that were less than half those for the other two species. Both *Abronia maritima* and *Atriplex californica* had CO₂ compensation points substantially above zero

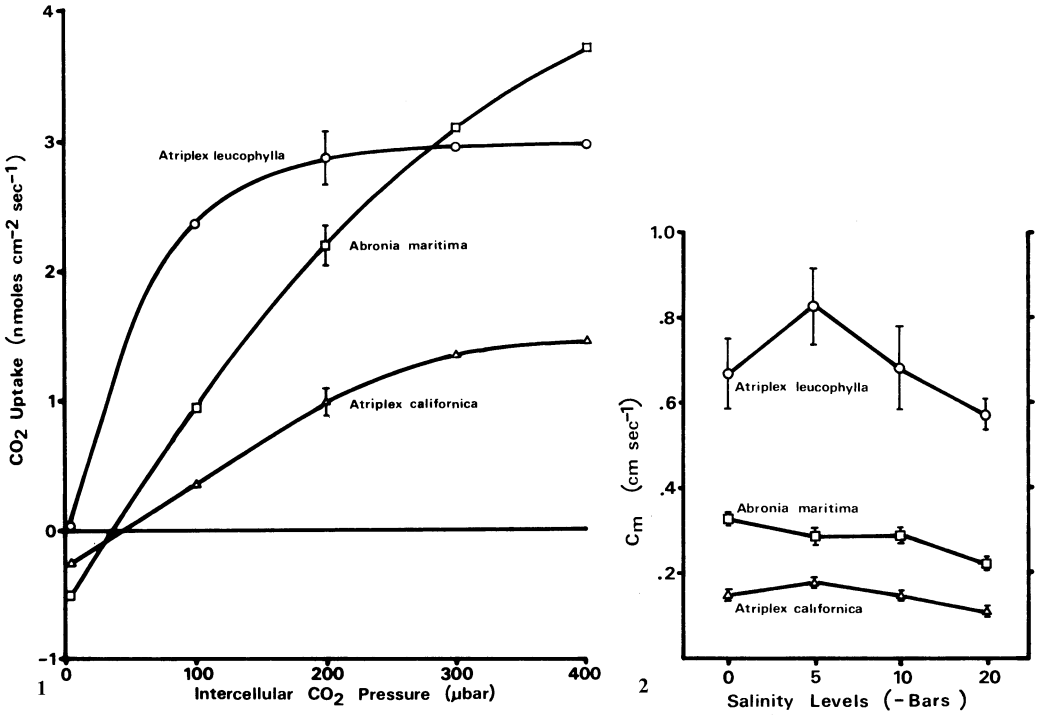


Fig. 1. Photosynthetic CO₂ responses of the three taxa to intracellular CO₂ pressures at the 0-salt treatment level. The vertical bars represent standard deviations about the regressions. The symbols only serve to identify the lines and are not actual data points

Fig. 2. Mesophyll conductances of the three taxa at four salinity levels. Vertical bars represent standard deviations

and approached CO₂ saturation at or above 400 µbars CO₂ pressure. The CO₂ response curves for each of the three taxa at the four salinity levels are similar to those depicted in Figure 1 except for the steepness of the initial slopes and the maximum photosynthetic rates attained.

The effect of salinity on mesophyll conductance (C_m) is shown in Figure 2. As can be seen from the initial slope of the CO₂ dependence curves in Figure 1, the mesophyll conductances of *Atriplex leucophylla* are much larger than those of the C₃ taxa. The mesophyll conductances of both *Atriplex* species increased at the -5 bar salinity level but were negatively affected by higher salinity concentrations. For the succulent C₃, *Abronia maritima*, all salinity levels decreased mesophyll conductance. Although absolute effects on mesophyll conductances varied greatly between species and salinity levels, the relative effects of increasing salinity on the mesophyll conductance were quite similar in each species (Fig. 3).

Figure 4 shows the effect of increasing salinity on photosynthesis (P_{net}), leaf conductance (C_l) and water use efficiency (P/T) in the three species at normal ambient external CO₂ concentrations. The water use efficiencies were normalized to a standard 10 mbar vapor pressure deficit to eliminate differences

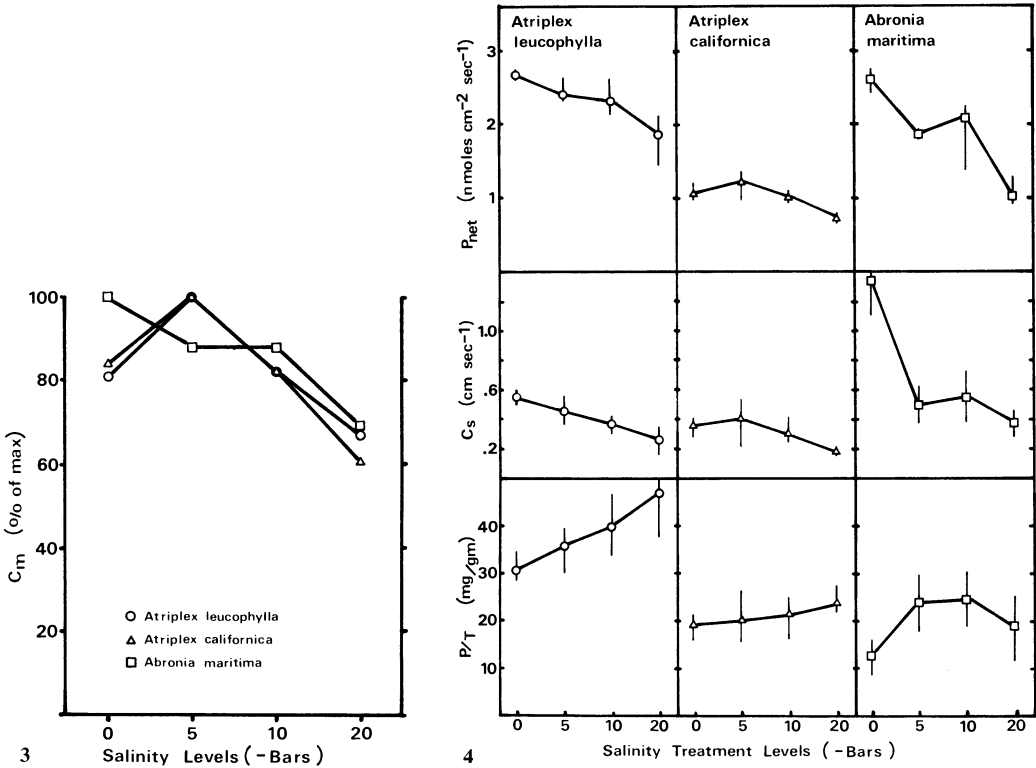


Fig. 3. Relative mesophyll conductances of the three taxa at four salinity levels

Fig. 4. Net photosynthesis, leaf conductances to water vapor and water use efficiencies of the three taxa at four salinity levels. Vertical bars represent ranges about the means

in transpiration that are caused by slightly different vapor pressure deficits in different measurements.

The higher salinity levels generally depressed both photosynthesis and leaf conductance but the effect of salinity on leaf conductance to water vapor was greater than that on CO₂ fixation so water use efficiency generally increased. From Figures 2 and 4 it can be seen that each of the three taxa appears to have a different relationship between photosynthetic rate and water use efficiency in the absence of salt. *Atriplex leucophylla* has relatively high photosynthetic rates, high mesophyll conductances, moderate leaf conductances and high water use efficiencies. *Atriplex californica* has low photosynthetic rates, relatively low mesophyll and leaf conductances but maintains moderate water use efficiencies. *Abronia maritima* has relatively high photosynthetic rates, moderate mesophyll conductances, high leaf conductances and low water use efficiencies. The steep drop in leaf conductance caused by the initial increase in salinity in *Abronia maritima*, makes its water use efficiency comparable to that of *Atriplex californica* but still lower than that of *Atriplex leucophylla*.

Table 1. Xylem sap tensions in the three species grown in the growth chamber at four salinity treatment levels. Measurements were taken at “dawn” just prior to when the lights came on, and in the “afternoon” after the lights had been on a minimum of 8 h

	Salinity treatment level (-bar)	Xylem sap pressure potential (-bar)	
		“dawn”	“afternoon”
<i>Atriplex leucophylla</i>	0	7.0+1.0	8.8+5.3
	5	10.9+0.2	15.1+0.5
	10	12.3+1.9	17.5+0.7
	20	21.4+0.2	27.3+1.8
<i>Atriplex californica</i>	0	15.7+0.7	19.5+0.0
	5	16.7+0.5	20.5+0.5
	10	19.7+0.8	22.4+1.9
	20	25.0+0.3	29.2+0.7
<i>Abronia maritima</i>	0	4.9+0.1	11.0+1.7
	5	11.3+2.0	16.4+2.4
	10	16.3+1.1	19.6+1.1
	20	30.3+2.9	32.0+1.0

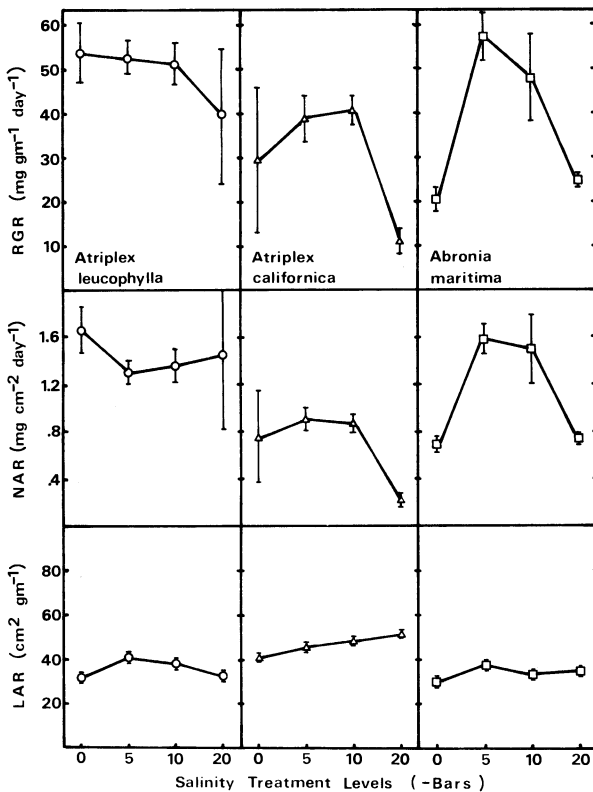


Fig. 5. Relative growth rates, net assimilation rates and leaf-area ratios of the three taxa at four salinity levels. Vertical bars represent standard errors

Table 1 shows the mean "predawn" and "afternoon" xylem sap pressure potentials of the plants grown under different salinity treatments in the growth chamber. The pressure potentials of *Atriplex leucophylla* and *Abronia maritima* are quite similar at each of the respective salinity levels. Both species show a substantial decrease in potential with each increasing level of salinity. Xylem sap potentials in *Atriplex californica* are relatively low even when grown without the addition of any artificial sea salt to the growth medium.

The results of the growth experiments are shown in Figure 5. *Atriplex leucophylla* maintained higher relative growth rates (RGR) at all salinity levels and was least affected by high salinities. The RGR's of *Atriplex californica* and *Abronia maritima* were sharply reduced by the highest salt concentrations. The low RGR's of *Abronia maritima* in the absence of salt appear anomalous since the photosynthetic rate of *Abronia* was the highest in the absence of salt. Perhaps growth was limited by lack of a particular nutrient that was available in the artificial sea salt at higher salt concentrations or by a lack of general salts that are required to develop enough turgor to stimulate growth. The leaves of *Abronia* plants grown without salt appeared flacid when compared to the salt-grown plants.

Similar trends can be seen in the net assimilation rates (NAR) of the three species except that the high salinities tend to increase NAR in *Atriplex leucophylla*. At the intermediate salinities the relative differences in NAR's between taxa are more comparable to the photosynthetic rates than are RGR's. The RGR's of *Atriplex californica* are more comparable to those of the other two taxa than are the photosynthetic rates. This is a result of the higher leaf area ratios (LAR) of *Atriplex californica* relative to the other species and indicates the importance of allocation patterns for interpreting the growth responses of plants (Slatyer, 1970).

Table 2 indicates the effect of the different salinity levels on the allocation patterns in each taxa. *Atriplex leucophylla* invests less into roots but more into stems than the other two species. The -5 bar salinity treatment caused a sharp reduction in relative root dry weights in all taxa, with an increased

Table 2. The effect of salinity on mean dry weight allocations expressed as a percent of total dry weight

		Salinity treatment levels (- bar)			
		0	5	10	20
<i>Atriplex leucophylla</i>	roots	26.27 ± 1.10	17.33 ± 1.95	17.13 ± 1.88	20.20 ± 2.70
	stems	30.30 ± 1.56	26.50 ± 0.55	27.86 ± 0.65	28.10 ± 0.30
	leaves	43.93 ± 1.18	56.20 ± 1.47	55.12 ± 1.37	50.70 ± 2.26
<i>Atriplex californica</i>	roots	49.53 ± 1.36	43.90 ± 3.89	44.50 ± 2.11	45.17 ± 1.29
	stems	8.60 ± 0.53	9.97 ± 1.62	10.07 ± 1.07	10.27 ± 0.42
	leaves	41.70 ± 0.93	46.03 ± 2.25	45.40 ± 1.10	44.53 ± 1.02
<i>Abronia maritima</i>	roots	45.50 ± 0.49	28.40 ± 2.90	25.37 ± 3.12	30.73 ± 2.87
	stems	9.03 ± 0.27	14.27 ± 2.33	12.83 ± 2.52	6.90 ± 1.21
	leaves	45.43 ± 0.57	57.30 ± 0.81	61.80 ± 0.62	62.33 ± 1.67

percentage of dry weight going to the leaves. The percentage of dry weight allocated to the stems remained fairly constant across all salinities within a taxon.

Discussion

The relative effects of salinity on mesophyll conductance in the two *Atriplex* taxa are virtually identical and the relative magnitude of the effects are similar to those for *Abronia*. This indicates that, in these taxa, neither the C₃ or C₄ pathway is inherently more sensitive to salinity than the other.

However, the lack of differential sensitivity does not imply that both pathways are equally adapted to saline habitats. Rates of CO₂ flux are dependent on the CO₂ pressure gradient between the leaf and air, and the leaf conductance to CO₂. Like other C₄ plants (Björkman, 1975; Hatch, 1976) the high carboxylation efficiency of *Atriplex leucophylla* allows it to maintain relatively high rates of photosynthesis at low intercellular CO₂ pressures. These low intercellular CO₂ pressures increase the CO₂ pressure gradient between the leaf and the air so that high rates of CO₂ flux are maintained with moderate leaf conductances. The C₃ species have lower carboxylation efficiencies and therefore are more limited by leaf conductance than is the C₄ species. In the absence of salinity, *Atriplex leucophylla* and *Abronia maritima* had similar rates of net photosynthesis; however, the leaf conductances of *Atriplex leucophylla* were less than half those of *Abronia maritima*. When salt was added to the growth medium, xylem sap pressure potential decreased and leaf conductances decreased. Because of the differences in CO₂ pressure gradients between the leaf and the air in the C₃ and C₄ species, the salinity-induced decreases in leaf conductance had a larger effect on the rate of net photosynthesis of *Abronia maritima* than *Atriplex leucophylla*.

The effect of salinity on net photosynthesis and leaf conductance of *Atriplex californica* are not as evident as in the other C₃ species, *Abronia maritima*. This is apparently related to the unique water relations of *Atriplex californica*. Even in the absence of salinity this species has xylem sap pressure potentials that may have been low enough to limit stomatal opening (Hsiao, 1973) and thus maintained low conductances to water vapor. Xylem sap pressure potentials of *Atriplex californica* were substantially affected only at the highest salinity treatment level and this effect is reflected in decreased leaf conductances and rates of net photosynthesis.

If the interpretation of these data is correct, it is apparent that plants having the C₄ photosynthetic pathway may have an advantage in saline environments because of high carboxylation efficiencies that enable them to maintain high rates of photosynthesis when leaf conductance is limited by osmotically induced water stress. In this study, water use efficiency (P/T) is a relative measure of the ability to fix carbon at a specific rate of leaf-conductance-dependent water loss. The water use efficiency data indicate the superior ability of the C₄ species to fix carbon for a given amount of water loss when compared

to the C₃ species. However, it is important to note that the higher water use efficiencies of *Atriplex leucophylla* relative to *Abronia maritima* do not confer any photosynthetic advantage when leaf conductances are not limited by water stress.

The effect of salinity on the relative growth and net assimilation rates of the greenhouse-grown plants are not directly correlated with the effect of salinity on net photosynthesis of the plants measured in the laboratory. As noted above for *Abronia maritima*, factors other than photosynthesis appear to play a large role in determining the growth potential of these plants. However, there is one factor in particular that may have obscured the relationship between photosynthetic potential and growth in these experiments. The growth experiments were conducted at light intensities below 100 nanoEinsteins cm⁻² s⁻¹, a level which would severely limit photosynthesis in *Atriplex leucophylla* but be closer to light saturation for the C₃ taxa (De Jong, 1978). The laboratory gas exchange experiments were all carried out at saturating light intensities and thus the laboratory photosynthetic measurements did not actually represent the rates of photosynthesis that were possible under the greenhouse light conditions. Since low light would limit photosynthesis in *Atriplex leucophylla* more than in the C₃ taxa, this may explain why *Atriplex leucophylla* had higher laboratory photosynthetic rates but lower net assimilation rates than *Abronia maritima* under greenhouse conditions. Similarly, this may explain the lack of correspondence in the magnitude of difference between the NAR's of *Atriplex leucophylla* and *Atriplex californica*, compared to their photosynthetic rates at intermediate salinity levels.

The dry weight allocation patterns show that *Atriplex leucophylla* had a lower percentage of its dry weight in roots than the C₃ taxa. This indicates that the C₄ plants may need fewer roots relative to the rest of the plant because of their higher water use efficiency. However, this may be misleading since the two C₃ taxa had more well developed central tap roots, and this morphological distinction may have accounted for the difference in relative root dry weights between the taxa. Unfortunately, total water uptake per plant was not measured.

Some of the differences in gas exchange and growth characteristics that are exhibited by the various species appear to be associated with differences in the overall biology of the genus rather than a particular photosynthetic pathway. The gas exchange response patterns of *Atriplex leucophylla* and *Atriplex californica* to salinity are similar to those reported by Gale and Poljakoff-Mayber (1970) for *Atriplex halimus* grown in NaCl solutions. They reported that increased salinities caused general decreases in photosynthesis and leaf conductance and that low salinity levels (above -9 bars osmotic potential) increased mesophyll conductances, but higher salinity levels (below -9 bars osmotic potential) decreased mesophyll conductances.

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