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Comparative Gas Exchange of Four California Beach Taxa

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Summary. Laboratory gas exchange measurements were conducted on four pioneering beach species from southern California. *Atriplex leucophylla* (Moq.) D. Dietr., a C₄ species, had a photosynthetic temperature optimum substantially higher than leaf temperatures normally experienced on the beach during the primary growing season. The C₃ species, *Cakile maritima* Scop., *Ambrosia chamissonis* Less. and *Abronia maritima* Nutt. ex Wats., had photosynthetic temperature optima close to their growth temperature and higher photosynthetic rates than the C₄ species at normal field growth temperatures. *Atriplex leucophylla* had higher mesophyll conductances which resulted in higher water use efficiencies at all measurement temperatures. Leaf chlorophyll and protein contents were not correlated with photosynthetic rates. The possible significance of water use efficiency is discussed in relation to the characteristics of the beach habitat.

Introduction

Little is known about the photosynthetic characteristics of beach species or the adaptive significance of C₄ photosynthesis to a cool beach environment. C₄ photosynthesis has generally been thought to infer high photosynthetic rates, particularly in warm arid environments (Larcher, 1975; Black, 1971). However, Ehleringer and Bjorkman (1977) suggested that a C₃ plant would have a greater potential for carbon gain at low temperatures and light intensities when there is sufficient moisture. The purpose of this research was to compare the gas exchange characteristics of C₃ and C₄ beach species in order to obtain further knowledge concerning the adaptive significance of C₄ photosynthesis to the cool beach environment as well as to gain information about the autecology of beach species.

The four species that I used for this research are *Atriplex leucophylla* (Moq.)

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D. Dietr., *Cakile maritima* Scop., *Abronia maritima* Nutt. ex Wats. and *Ambrosia chamissonis* Less. These species represent an array of life forms, growth habits, leaf morphologies and photosynthetic pathways. *Atriplex leucophylla* exhibits the C₄ di-carboxylic acid pathway of photosynthesis while the other three species have the C₃ pathway. *Cakile maritima* is an introduced annual whereas the other three species are native perennials. *Ambrosia chamissonis* is semi-deciduous, progressively losing leaves throughout the summer, while *Atriplex* and *Abronia* are evergreen. *Abronia*'s leaves are succulent, relatively large (2–4 cm across) and entire, while those of *Ambrosia* and *Cakile* are dissected and generally less succulent.

The field temperature, water and salinity relations of these species at Trancas Beach near Malibu, California have been reported previously (De Jong, 1978). For the various species, mean daylight leaf temperatures ranged from 13.4 to 14.2° C in the winter and 20.9 to 22.7° C in the summer. *Atriplex* and *Cakile* underwent the greatest seasonal changes in xylem sap tension whereas *Abronia* and *Ambrosia* exhibited very little seasonal variation in xylem sap tension. All taxa grow primarily in the winter and spring months when temperatures are cooler but water is less limiting. *Atriplex* and *Cakile* tend to be distributed more seawardly than *Abronia* and *Ambrosia* (Barbour et al., 1975) and thus occupy the less stable, more saline zone of the beach.

Materials and Methods

Seeds of *Atriplex leucophylla*, *Cakile maritima*, *Abronia maritima*, and *Ambrosia chamissonis* were collected from the Trancas Beach study site (De Jong, 1978) during the summer of 1975 and germinated in flats during the fall of 1976. When the seedlings were in the cotyledon stage, each plant was transplanted into a 12 cm plastic pot containing a fertilized potting mixture of sand, peat and vermiculite in a 30:6:12 mix and placed in a greenhouse.

At least 4 weeks prior to gas exchange measurements, the plants were transferred from the greenhouse to an I.S.C.O. E 3A growth chamber equipped with 400 watt metal halide lamps and 100 watt incandescent lamps that gave a quantum flux at the level of the leaves of 45–60 nanoEinsteins cm⁻² s⁻¹. The chamber was set on a 16-h photoperiod with 18° C days and 12° C nights and a 5° C wet bulb depression. While in the growth chamber, the *Cakile*, *Abronia*, and *Ambrosia* plants were watered regularly with deionized water and once a week with full-strength Hoagland's solution. The *Atriplex* plants were watered 3 times a week with fullstrength Hoagland solution plus 4000 ppm artificial sea salt (Rila Products). Previous growth studies showed that *Atriplex leucophylla* grows optimally at salt concentrations between 3000 and 6000 ppm. A separate set of plants were grown for analyzing the response of *Abronia* and *Atriplex* to differing CO₂ concentrations. These plants were grown in tall (25 cm), narrow (6 cm) pots filled with coarse beach sand and continuously subirrigated with 1/4-strength Hoagland solution (the *Atriplex* subirrigation solution contained an additional 6000 ppm of sea salt).

All gas exchange measurements were made on an open system gas analysis apparatus similar to the system described by Augustine et al. (1976). The assimilation chamber was a 2.8 l rectangular Plexiglass box with a finned aluminium heat exchange block as a bottom, through which water is circulated for temperature control. A squirrel-cage blower mounted in the rear of the chamber provided rapid heat exchange and maximum boundary layer conductances.

Air flow through the chamber was regulated with needle valves and monitored with an electronic mass flow meter (Technology Inc. Model LFC-3).

Leaf temperatures were controlled by regulating the rate at which cold water was circulated

through the heat exchange block on the bottom of the chamber. Abaxial leaf surface temperatures were monitored with 0.08 mm enamel-insulated iron and constantan thermocouple junctions.

Light was provided by two 1000 W quartz-iodide lamps (Norelco type FCN) mounted in fan-cooled reflector housings with a polystyrene diffusing filter and a 2.6 cm water filter to remove infra-red radiation. Irradiances were controlled by vertical adjustment of the lamps or with Plexiglas neutral density filters. Irradiances were measured in the plane of the leaves inside the chamber with a fiber optic light pipe extending through the wall of the chamber and connected to a quantum sensor (Lambda Inst. Co.). This system was periodically calibrated against a second quantum sensor placed inside the chamber in the plane of the leaf.

Gas mixtures of known CO₂ concentration were obtained by mixing CO₂ free air and 1% CO₂ in nitrogen with precision needle valves. The gas stream was humidified and then dehumidified to a known dew point temperature in a thermostated glass condenser. The humidity of the air stream leaving the assimilation chamber was measured with a solid state relative humidity sensor (Weather/Measure HM 111) that was frequently calibrated by diverting gas directly from the dew point condenser to the humidity sensor, bypassing the assimilation chamber.

CO₂ concentrations of the gas streams were measured with a differential infra-red CO₂ analyzer (Beckman Inst. Co. Model 865). Interference from water vapor was eliminated by dehumidifying the air stream first to a 3° C dew point and then with magnesium perchlorate. The CO₂ analyzer was calibrated daily with a precision gas mixing pump (H. Wösthoff O.H.G. type M 201a-F) and gases of known CO₂ concentration.

Measurements were made on single intact leaves of *Cakile* and *Ambrosia*. One to three leaves were used on a single stem for *Abronia*, and whole stems were used for *Atriplex*.

Photosynthetic response to light flux was measured by first exposing leaves to saturating irradiances and then decreasing irradiance in seven or more steps to complete darkness, while holding other factors constant.

Responses to temperature were measured in two directions from the temperature optimum for CO₂ exchange. For some leaves, temperatures were initially set near the growth temperature and then increased in 2–3° C intervals to well above the thermal optimum for CO₂ exchange. In other measurements, temperatures were started initially equal to growth temperature, raised to a point above the optimum for photosynthesis and then decreased in 2–3° C intervals to 10° C or below.

Photosynthetic responses to CO₂ concentration were determined by initially exposing the leaves to 300–330 $\mu\text{l l}^{-1}$ CO₂ concentrations. After steady state gas exchange rates were attained at this level, input CO₂ concentrations were increased to 600 $\mu\text{l l}^{-1}$ and then decreased in steps to approximately 300, 200, 150, 75, and 0 $\mu\text{l l}^{-1}$ respectively. The absolute input CO₂ concentrations and gas analyzer zero were checked at each step. The gas analyzer was carefully calibrated to correct for changes in sensitivity at varying background CO₂ concentrations.

Photosynthesis, transpiration, leaf conductance and intercellular CO₂ pressure were calculated from CO₂ and water vapor flux measurements according to procedures outlined by Jarvis (1971). Mesophyll conductance (C_m) was calculated from the initial, linear portion of the CO₂ dependence curve.

Responses to each factor were measured on a minimum of three plants for each taxon. These data were pooled and a polynomial regression program was used to fit a response curve to the factor.

Approximately 0.8 g of leaf tissue was ground in glass homogenizers with 10 ml of a 90% acetone, 10% dilute, NH₄OH (1%) solution at 0° C and centrifuged for 15 min at 12,000 $\times g$. The supernatant was collected and the pellet was resuspended in 80% acetone and recentrifuged for 15 min at 12,000 $\times g$. This supernatant was combined with the first and absorption at 663 and 645 nm was determined in a spectrophotometer (Zeiss M4QII). For protein determination, the pellet was resuspended in 5 ml of 0.1 N NaCl. One ml of this suspension was then allowed to react with 4 ml of Biuret reagent (Itzhaki and Gill, 1964) for 30 min at room temperature and then centrifuged at 12,000 $\times g$ for 10 min. Absorption at 540 nm was then determined. Chlorophyll contents were calculated according to Bruinsma (1961) and are expressed on a fresh leaf area basis. The total protein contents were calculated by comparing absorption at 540 nm with a standard curve for the Biuret reaction with bovine serum albumin and are expressed on a leaf area basis.

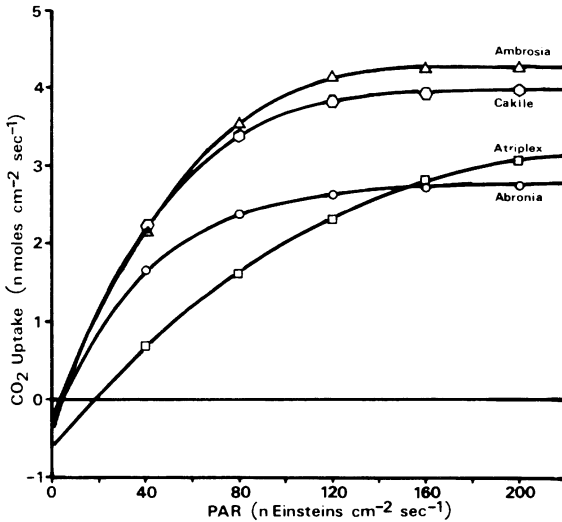


Fig. 1. The light response of photosynthesis of four California beach taxa. Standard deviations about the regressions were *Ambrosia*=0.28, *Cakile*=0.14, *Atriplex*=0.18, and *Abronia*=0.11. Symbols are not actual data points but only serve to identify the curves

Results

Photosynthetic responses of the four taxa to light is shown in Figure 1. Responses for *Abronia* and *Ambrosia* were determined at 19° C, *Cakile* at 21° C and *Atriplex* at 25° C. *Ambrosia* and *Cakile*, both C₃ plants, had higher photosynthetic rates than *Atriplex* at all light levels near full sunlight. *Abronia*, *Ambrosia* and *Cakile* approached light saturation near 100–120 nanoEinsteins cm⁻² s⁻¹. *Atriplex* had a more gradual response and approached light saturation near 200 nanoEinsteins cm⁻² s⁻¹.

Figure 2 shows the photosynthetic response of the four taxa to temperature. *Abronia* and *Ambrosia* exhibited temperature optima for photosynthesis near 20° C while that for *Cakile* was slightly higher, at 22° C. *Atriplex* had a relatively broad, flat response to temperature above 20° C with maximum rates near 28° C.

Figure 3 depicts the temperature responses of leaf conductance to water vapor that were measured simultaneously with the photosynthetic responses to temperature shown in Figure 2. The C₃ taxa, *Abronia*, *Ambrosia* and *Cakile*, had conductances that were nearly twice those of *Atriplex*, the C₄ species, at their respective temperature optima for photosynthesis. The leaf conductance of *Atriplex* was relatively unaffected by high temperatures, whereas the other species all showed marked stomatal closure in response to high temperature.

The effect of intercellular CO₂ pressures on photosynthesis for each of the four species is shown on Figure 4. As is typical for C₄ plants, the CO₂ compensation point for *Atriplex leucophylla* was near zero, whereas the three C₃ species have CO₂ compensation points at 30–40 μbar. The low CO₂ compensation

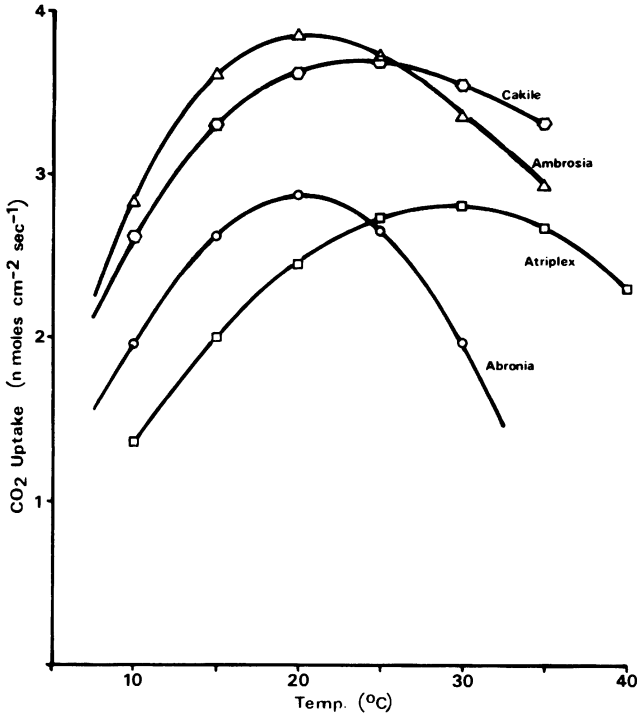


Fig. 2. The temperature response of photosynthesis of four California beach taxa. Standard deviations about the regressions were *Cakile*=0.35, *Ambrosia*=0.32, *Atriplex*=0.18, and *Abronia*=0.27. Symbols are not actual data points but only serve to identify the curves

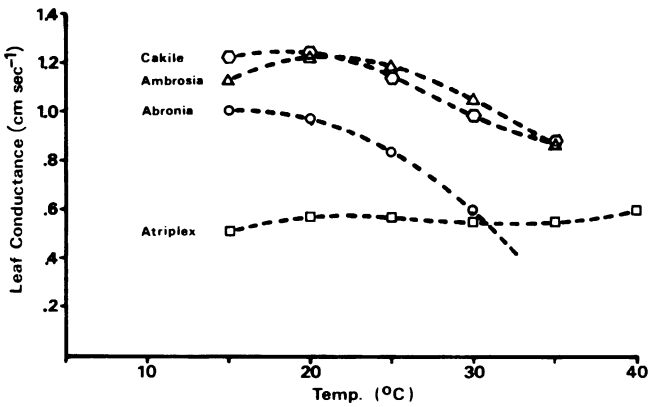


Fig. 3. The temperature response of leaf conductance to water vapor measured simultaneously with the photosynthetic responses shown in Figure 2. Standard deviations about the regressions were *Cakile*=0.19, *Ambrosia*=0.24, *Abronia*=0.24, and *Atriplex*=0.06. Symbols are not actual data points but only serve to identify the curves

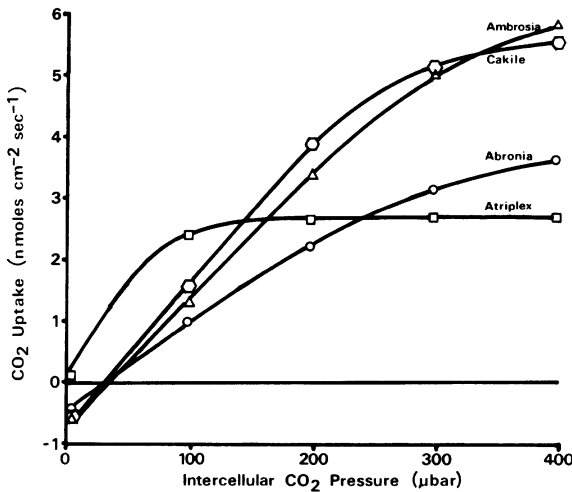


Fig. 4. The effect of intercellular CO_2 pressure on photosynthesis of four California beach taxa. Standard deviations about the regressions were *Ambrosia*=0.11, *Cakile*=0.25, *Abronia*=0.15, and *Atriplex*=0.19. Symbols are not actual data points but only serve to identify the curves

Table 1. A summary of the gas exchange characteristics of four California beach taxa (C_1 and C_m measured near T_{opt})

	\bar{x} max P_{net} $n \text{ mole cm}^{-2} \text{ s}^{-1}$	$P_s T_{\text{opt}}$ $^{\circ}\text{C}$	C_1 cm s^{-1}	C_m cm s^{-1}	P/T at 20°C $\text{mg CO}_2/\text{gm H}_2\text{O}$
<i>Abronia maritima</i>	2.8	20	0.95	0.33	17.8
<i>Ambrosia chamissonis</i>	4.0	20	1.23	0.56	18.7
<i>Cakile maritima</i>	3.7	22	1.21	0.50	17.4
<i>Atriplex leucophylla</i>	2.9	28	0.56	0.83	26.2

point and the relatively steep initial slope of the CO_2 dependence curve allow *Atriplex* to attain maximum photosynthetic rates at intercellular CO_2 pressures near $100 \mu\text{bar}$ while the C_3 taxa were not CO_2 saturated a intercellular CO_2 pressures below $400 \mu\text{bar}$. The C_3 taxa generally maintained intercellular CO_2 pressures of $200\text{--}250 \mu\text{bar}$ under normal ambient CO_2 conditions.

Table 1 summarizes the basic differences between the various taxa with regard to gas exchange. The photosynthetic water use efficiencies were normalized to a standard 10 mbar vapor pressure deficit to eliminate differences in transpiration that are caused by conducting measurements at slightly different vapor pressure deficits. From Table 1, it is clear that *Atriplex leucophylla* maintains higher water use efficiencies than the C_3 taxa at 20°C even though this temperature is nearer the photosynthetic temperature optima for the C_3 taxa. Although not shown, the differences in water use efficiency between the C_3 and C_4 taxa become more pronounced at higher temperatures.

Table 2. Leaf protein and chlorophyll contents of four California beach taxa expressed on an area basis

	Leaf protein content mg cm ⁻²	Leaf chlorophyll content µg cm ⁻²
<i>Abronia maritima</i>	9.0 ± 1.5	83.5 ± 8.4
<i>Ambrosia chamissonis</i>	2.9 ± 0.5	80.5 ± 8.4
<i>Cakile maritima</i>	4.5 ± 0.7	52.6 ± 5.8
<i>Atriplex leucophylla</i>	4.7 ± 0.9	89.3 ± 6.5

In Table 2, the leaf protein and chlorophyll contents are expressed on an area basis so they can be interpreted with respect to the photosynthesis measurements. *Ambrosia* had the lowest leaf protein contents even though its photosynthetic rates were highest. There are no clear cut differences between the protein levels of *Atriplex* when compared with those of the C₃ taxa on an area basis.

There were no significant differences in mean chlorophyll contents between the four taxa.

Discussion

The four California beach species under study—*Abronia maritima*, *Ambrosia chamissonis*, *Cakile maritima* and *Atriplex leucophylla*—all have relatively high photosynthetic capacities when grown under controlled growth chamber conditions. The maximum photosynthetic rates of *Atriplex leucophylla*, the C₄ species, were less than 75% of the maximum rates of the most productive C₃ species, *Ambrosia chamissonis*. Although the C₄ photosynthetic pathway is generally thought to confer higher photosynthetic rates (Larcher, 1975; Black, 1971), recent work by Mooney et al. (1977) and Ehleringer et al. (1976) has shown that some C₃ desert species have photosynthetic rates equal to, or higher than, the most productive C₄ plants. A similar situation appears to exist among California beach species.

The C₃ beach taxa attain maximum photosynthetic rates at substantially lower temperatures and light intensities than the C₄ taxon from the same habitat. *Atriplex leucophylla* had a photosynthetic temperature optimum substantially above the C₃ species which had optima near the daylight temperatures normally experienced in their natural habitat.

The temperature response of photosynthesis of C₄ and C₃ *Atriplex* species from the north Atlantic coast (Bjorkman, 1975) show trends similar to Pacific coast plants. *Atriplex sabulosa* (C₄) had a photosynthetic temperature optimum near 30° C whereas *Atriplex glabriuscula* had its temperature optimum near 24° C when both were grown at 16° C day/10° C night. In general, cool-climate C₄ species appear to maintain higher photosynthetic temperature optima than C₃ species from the same habitat. This, however, does not necessarily mean that C₄ plants are less suited for such environments. Photosynthetic rates (Bjork-

man, 1975) or water use efficiencies of C_4 species may be higher than those of C_3 species at the photosynthetic temperature optima of the C_3 taxa.

It is well established that C_4 plants are generally superior to C_3 plants at using low CO_2 concentrations in intercellular leaf spaces and that this generally results in higher water use efficiencies (Bjorkman et al., 1975; Szarek and Ting, 1975). The present study supports this conclusion and shows that the cool-climate *Atriplex leucophylla* is able to maintain photosynthetic water use efficiencies substantially higher than naturally associated C_3 species at relatively low temperatures and vapor pressure deficits even though it has lower photosynthetic rates at these temperatures.

The higher water use efficiency of *Atriplex* (Table 1) may contribute to its ability to become established in the spring and grow through extended rainless summer periods on a rather small, shallow root system. In a previous paper (De Jong, 1978), I presented evidence indicating that *Atriplex* relies on a small, but continuous, supply of water that moves up from a fresh water table below. *Abronia maritima* and *Ambrosia chamissonis* have deeper roots and utilize the more abundant water supply at lower levels near the water table. *Cakile maritima* generally dies during the dry summer months except for a few plants that may have been able to extend their roots down to sufficient water supply. Subsequent field observations in 1977 suggest that *Abronia* and *Ambrosia* only become established in years when there are late spring or early summer rains, which enable the seedlings of these species to extend their roots deep enough to reach permanent water. *Atriplex* establishment appears to be less dependent on late spring rains.

Research on east coast salt marsh species shows that C_4 grasses have higher nitrogen use efficiencies (ratio of photosynthesis to nitrogen content) than C_3 grasses (Dunn, personal communication). My results do not substantiate that pattern with regard to total leaf protein in dicotyledonous beach species. There were no clearcut differences between C_3 and C_4 taxa with regard to protein content. However, it may be noteworthy that the three more salt tolerant taxa — *Atriplex*, *Abronia* and *Cakile* — (Barbour and De Jong, 1977) all have higher protein contents per unit leaf area than *Ambrosia* which had the highest photosynthetic rates. This suggests that there may be a "cost" in terms of protein associated with salt tolerance that is unrelated to photosynthetic potential.

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