Photosynthetic Acclimation to Temperature in the Desert Shrub, *Larrea divaricata*

I. CARBON DIOXIDE EXCHANGE CHARACTERISTICS OF INTACT LEAVES[1]

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ABSTRACT

Larrea divaricata, a desert evergreen shrub, has a remarkable ability to adjust its photosynthetic temperature response characteristics to changing temperature conditions. In its native habitat on the floor of Death Valley, California, plants of this C_3 species when provided with adequate water are able to maintain a relatively high and constant photosynthetic activity throughout the year even though the mean daily maximum temperature varies by nearly 30 C from winter to summer. The temperature dependence of light-saturated net photosynthesis varies in concert with these seasonal temperature changes whereas the photosynthetic rate at the respective optimum temperatures shows little change.

Experiments on plants of the same age, grown at day/night temperatures of 20/15, 35/25, and 45/33 C with the same conditions of day length and other environmental factors, showed a similar photosynthetic acclimation response as observed in nature. An analysis was made of a number of factors that potentially can contribute to the observed changes in the temperature dependence of net CO_2 uptake at normal CO_2 and O_2 levels. These included stomatal conductance, respiration, O_2 inhibition of photosynthesis, and nonstomatal limitations of CO_2 diffusive transport. None of these factors, separately or taken together, can account for the observed acclimation responses. Measurements under high saturating CO_2 concentrations provide additional evidence that the observed adaptive responses are primarily the result of changes in intrinsic characteristics of the photosynthetic machinery at the cellular or subcellular levels. Two apparently separate effects of the growth temperature regime can be distinguished: one involves an increased capacity for photosynthesis at low, rate-limiting temperatures with decreased growth temperature, and the other an increased thermal stability of key components of the photosynthetic apparatus with increased growth temperature.

Warm deserts are characterized by periods of exceptionally high temperatures in summer and cool temperatures in winter. Many plants which inhabit these regions are evergreen and maintain photosynthetically active tissue throughout the year. Maintenance of a positive carbon exchange balance under such wide ranges of environmental conditions may require that the plants possess a high photosynthetic acclimation potential. This term is here defined as the ability of a given genotype to change its photosynthetic characteristics in an adaptive manner in response to changes in environmental conditions such as light, temperature, or water regime.

One of the most prominent woody evergreen species of the deserts of the Southwestern United States is *Larrea divaricata* Cav. The photosynthetic performance of this species has been studied previously in some detail (13, 14, 19–22). Strain (19) noted that under natural conditions *Larrea*, of a number of species studied by him, may possess an unusually high photosynthetic acclimation potential to seasonal change in temperature regime.

In the present study the basis for the temperature acclimation process in *L. divaricata* was further explored by analyzing the photosynthetic characteristics of its leaves both in its native habitat on the floor of Death Valley at different times of the year and under a series of controlled regimes in the laboratory.

MATERIALS AND METHODS

The field study site is located on the base of an alluvial fan on the floor of Death Valley, close to the National Park Service Headquarters at Furnace Creek.

This locality is notable for its extremely high summer temperatures. Long term weather records show that the mean daily maximum temperature for July is 46 C, whereas the winters are mild with a mean daily maximum temperature for January of only 18 C. This represents a seasonal change of nearly 30 C. The *L. divaricata* plants maintain photosynthetically active leaves throughout the year both in natural, nonirrigated sites (10) and in our irrigated experimental garden at Furnace Creek (this paper). The results reported here were obtained on 1- to 2-year-old plants grown in the experimental garden (5) where they had been watered once daily throughout their life.

Measurements of photosynthetic gas exchange characteristics were made in January, May, and September using a mobile laboratory described by Björkman *et al.* (5) with modifications as given by Ehleringer and Björkman (8). Single, attached twigs so oriented that all leaves were fully exposed and perpendicular to the light beam were used in all measurements. A 1-kw metal arc lamp (Sylvania) provided the equivalent of full sunlight conditions (170–190 nE cm^{-2} sec^{-1}). Ambient CO_2 pressure in the leaf chamber was kept at 320 to 340 μbar, O_2 at 21%, and water vapor pressure deficit below 25 mbar. The measurements were started at a leaf temperature of 30 C and progressed first to lower temperatures in a stepwise manner. The leaves were then returned to 30 C and when the photosynthesis rate had resumed its original value the measurements progressed to higher temperatures.

Water potential during the course of the experiments was routinely measured on other twigs from the same plant using a pressure bomb (18). Occasional comparisons with leaf water potentials, determined by a thermocouple psychrometric method, showed that there was a close agreement (±1 bar) between the two techniques.

Measurements of photosynthetic characteristics were also made

in the laboratory at Stanford, California on plants grown under a series of controlled growth regimes, using natural daylight. For this purpose seeds were collected from the field plants in Death Valley and seedlings were grown in three different controlled temperature regimes with the same conditions of light regime, water, nutrient, humidity, and CO_2 concentration. The average quantum flux density of the natural light reaching the plants inside the growth chambers was approximately 4,800 μE cm^{-2} day^{-1} (82% of the flux incident on the chambers). The day length during the growth period varied from 10.5 to 12.5 hr. CO_2 was kept constant at 330 ± 10 μbar partial pressure and the humidity at 60 to 70%. Thus, the water vapor pressure deficit was kept below 30 mbar even in the hottest regime. The plants were grown in an equal mixture of Vermiculite and Perlite and a complete nutrient solution was automatically fed six times daily. Leaf temperatures during periods of peak insolation were within 1 C of the air in the intermediate regime, 1 to 2 C warmer than the air in the cool regime, and 1 to 3 C cooler than the air in the hot regime. Root temperature exceeded that of the air by 1 to 4 C in all regimes.

As in the field studies, photosynthesis was measured on attached twigs with three to five pairs of young but fully expanded leaves. The same gas exchange measuring system was also used, except that a 2.5-kw xenon arc lamp served as the light source.

Temperature dependence measurements were always started at the respective daylight growth temperature. Since the temperature range used in the laboratory studies was broad and preliminary experiments showed that exposure of the leaves to either temperature extreme sometimes resulted in changes that were irreversible in the short term, different sets of leaves were used for determinations of photosynthetic temperature dependence below and above the growth temperature. Curves for the temperature dependence of net CO_2 uptake were determined under combinations of normal CO_2 (320–340 μbar) and normal O_2 (21%), normal CO_2 and low O_2 (1.5%), as well as saturating CO_2 (816–918 μbar) and low O_2. Temperature dependence of dark CO_2 evolution was measured at normal CO_2 and normal O_2 only. In all, 24 different sets of leaves were used for the laboratory studies of photosynthetic gas exchange characteristics. Leaf nitrogen content was determined by the micro-Kjeldahl procedure.

RESULTS

Field Studies. The irrigated *L. divaricata* plants in Death Valley maintained relatively high net photosynthetic rates during all seasons (Fig. 1). The rate at optimum temperature for this C_3 species averaged 2.60 nmol of CO_2 cm^{-2} sec^{-1} (41.2 mg of CO_2 dm^{-2} hr^{-1}) which is well above the mean of the rates reported in the literature for both wild and cultivated C_3 species. The stomatal
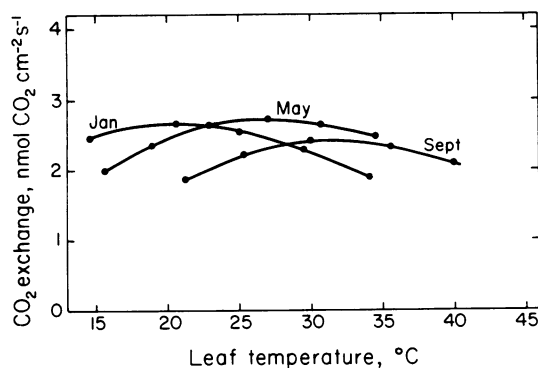

Fig. 1. Temperature dependence of net CO_2 uptake by intact *L. divaricata* leaves during three seasons in Death Valley, California. Measurements were made at 170 to 180 nE cm^{-2} sec^{-1}, 320 to 340 μbar CO_2, 21% O_2, and a water vapor pressure deficit below 25 mbar.

Table I. Environmental and leaf characteristics of *Larrea* plants during different seasons in Death Valley (1975-76)

	Jan.	May	Sept.
Mean daily max. air temp. (C)	20.7	37.2	41.7
Daylength (hour)	10	14	12
Xylem water potential during photosynthesis measurements (bar)	-25.9	-20.4	-33.7
Net photosynthesis at optimum temp. (nmol CO_2 cm^{-2} sec^{-1})	2.65	2.71	2.45
Conductance to H_2O at optimum temperature for net photosynthesis (cm sec^{-1})	0.8	1.1	1.0
Dark respiration at 30 C (nmol CO_2 $cm^{-2}sec^{-1}$)	0.35	0.45	0.40
Leaf nitrogen (mg cm^{-2})	0.47	0.31	0.51
Leaf specific wt. (mg cm^{-2})	18.9	12.7	22.6

conductance to gaseous diffusion also remained high in this desert species throughout the season even though the water potentials (in spite of daily irrigation) were quite low (Table I). In September when the water potential had fallen to −33.7 bar, the stomatal conductance to water vapor transfer was still as high as 1 cm sec^{-1}.

Like the optimum photosynthetic rate and stomatal conductance, leaf dark respiration rates (measured at 30 C) showed no appreciable seasonal change.

In contrast to the constancy during the year of the absolute rates of net photosynthesis at optimum temperature, pronounced seasonal shifts occurred in the temperature dependence of this process. In January when the mean daily maximum temperature was 20 C, the rate of photosynthesis at 20 C was approximately 60% higher than in September when the prevailing air temperature was 40 C and above. Conversely, in September the rate at 40 C was approximately 65% higher than in January. The optimum temperature for net photosynthesis shifted from about 20 C in January to about 32 C in September. The temperature dependence of photosynthesis in May was intermediate between those determined in January and September and in concert with the prevailing leaf temperatures.

Stomatal conductance, measured under a water vapor deficit of less than 25 mbar at all temperatures, was little affected by measurement temperature (data not shown) and, as mentioned above, remained high throughout the season. This strongly indicates that stomata played no role in the observed seasonal shift in the temperature dependence of light saturated photosynthesis.

The quantum yield of net CO_2 uptake, determined at rate-limiting light intensities, 330 μbar of CO_2, 21% O_2, and 30 C remained constant at 0.050 ± 0.002 mol of CO_2/E throughout the year. In contrast to the pronounced seasonal shift in the temperature dependence of light-saturated photosynthesis there was no evidence for any change in the temperature dependence of the quantum yield (data not shown).

Leaf nitrogen content, in per cent of dry weight, showed only a small and statistically insignificant seasonal variation (Table I). Because of a large variation in leaf specific weight there was a considerable variation in the amount of nitrogen per unit leaf area (Table I). It is noteworthy that there was no positive correlation between the rates of light-saturated photosynthesis or dark respiration, and nitrogen content or specific leaf weight when all are expressed on a leaf area basis.

Controlled Environment Studies. In the natural habitat the seasonal change in temperature is concomitant with considerable changes in day length, evaporative demand, and also in the developmental stage of the plants and leaf age. To determine if the temperature regime directly controls the observed seasonal photosynthetic acclimation to temperature and to analyze the nature of this acclimation in greater detail photosynthetic characteristics were also determined on *L. divaricata* plants of similar age (8–12 weeks) and developmental stage, grown at three different controlled temperature regimes but with the same conditions of day length, water, nutrient, humidity, and CO_2 concentration.

The photosynthetic temperature responses of *L. divaricata*

plants grown under the three temperature regimes are shown in Figure 2. These determinations were made, as in the field, under normal CO_2 and O_2 concentrations and high light intensities. The maximum net rates of CO_2 uptake were very similar to those observed in the field and so were the rates of dark respiration (Table II). The temperature dependence of light-saturated photosynthesis shifted with the temperature regime under which the plants were grown in a similar manner as the seasonal shift observed in the field. The low temperature-grown plants exhibited considerably higher rates at low temperatures than did the high temperature-grown plants and vice versa. For example, the rate at 20 C was almost twice as high in the plants grown at this temperature as in the plants grown at the 45 C temperature regime. Conversely, the rate at 45 C was almost twice as high in the plants grown at this temperature of photosynthesis in the plants grown under the 35 C regime was intermediate between the two extremes in all respects. It is thus clear that growth temperature alone is sufficient to effect a similar acclimation in the temperature dependence of net photosynthesis as observed during the different seasons in the native habitat.

It is well known that the rate of dark respiration, measured at a given temperature, in many plants tends to increase with increasing growth temperature, at least on a leaf area basis. This could contribute to a shift in the optimum temperature of net CO_2 uptake. As shown in the lower part of Figure 2 such changes in the dark respiration in *L. divaricata* were much too small to account, to any significant extent, for the differences in the temperature dependence of net photosynthesis.

As was also the case in the field studies stomatal conductance remained high regardless of the growth regime (Table II). Moreover, as illustrated in Figure 3, the stomatal conductances were high and nearly constant at all analysis temperatures. As a result, the intercellular CO_2 pressure merely mirrors the rate of net photosynthesis, reaching its minimum at the photosynthetic temperature optimum. The decline of photosynthesis on either side of this optimum takes place in spite of an increase in intercellular CO_2 pressure. This unequivocally demonstrates that CO_2 diffusion limitation in the gaseous phase can in no part account for the observed temperature-induced shifts in the temperature dependence of photosynthesis. The possibility was also investigated that growing the plants under different temperature regimes somehow influenced the inhibitory effect of 21% O_2 on net photosynthesis ("photorespiration"), causing a shift in the temperature depend-
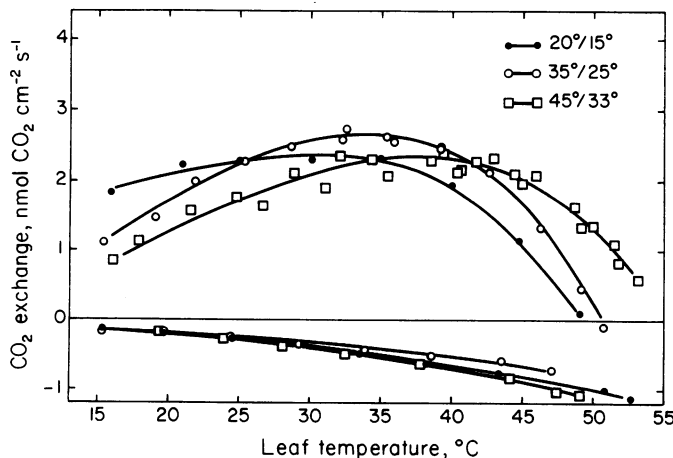
Table II. Leaf characteristics of *Larrea* plants grown under controlled conditions.

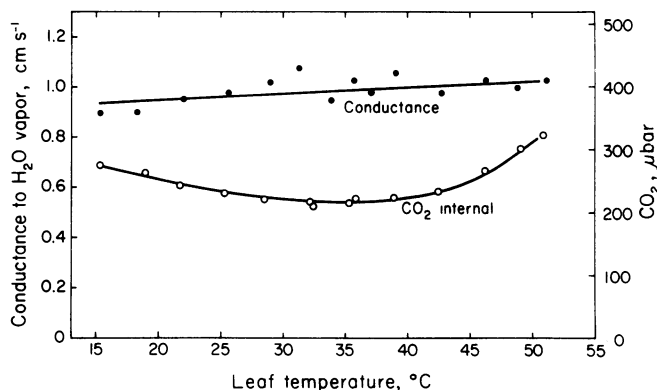|	Growth Temperature (C)		
	20/15	35/25	45/33
Net photosynthesis at optimum temp. (nmol CO_2 cm^{-2} sec^{-1})			
at 21% O_2, 330 μbar CO_2	2.3	2.6	2.4
at 1.5% O_2, saturating CO_2	5.8	6.1	6.1
Conductance to H_2O vapor (cm sec^{-1})			
at 20 C	1.10	0.95	0.65
at 30 C	1.05	0.95	0.90
at 40 C	0.95	1.05	0.95
Dark respiration at 30 C (nmol CO_2 cm^{-2} sec^{-1})	0.38	0.30	0.41
Leaf nitrogen (mg cm^{-2})	0.25	0.20	0.23
Leaf specific wt. (mg cm^{-2})	6.54	6.96	7.94
Chlorophyll content (μg cm^{-2})	40	46	45

FIG. 3. Temperature dependence of leaf conductance to the diffusive transport of water vapor and intercellular CO_2 concentration of photosynthesizing *L. divaricata* leaves grown at a 35/25 C day/night temperature regime. Measurements were made under the same conditions as given in Figure 1.

FIG. 2. Temperature dependence of net CO_2 uptake in the light and respiratory CO_2 release in the dark by intact *Larrea divaricata* leaves, grown in three temperature regimes. Measurements were made under the same conditions as given in Figure 1. Photosynthesis declined with time at temperatures exceeding the respective optima shown in Figure 4. The rates shown are those determined after 10 min at each superoptimal temperature.

ence of net photosynthesis in normal air. The results clearly show that this is not the case. As can be expected with any C_3 species, reducing the O_2 concentration from 21% to 1% while maintaining the CO_2 pressure at 320 μbar increased the net rate of CO_2 uptake by approximately 45% at 30 C. This enhancement decreased at lower and increased at higher measurement temperatures and consequently shifted the temperature optima upward by a few degrees. This effect, however, was quantitatively the same regardless of the regime in which the plants had been grown (data not shown), indicating that no significant differences existed in the relative affinities to CO_2 and O_2 of the ribulose-1,5-bisP carboxylase/oxygenase enzyme or in other possibly limiting aspects of "photorespiratory" metabolism.

Measurements of photosynthesis in a combination of saturating CO_2 and low O_2 permit an analysis of the temperature dependence of CO_2 uptake under conditions where rate restrictions by all CO_2 diffusion processes, including intracellular CO_2 transport, as well as by any O_2 effects, are completely eliminated. Figure 3 shows the temperature dependence of photosynthesis, determined under these conditions. As one would expect, raising the CO_2 from normal to saturating levels caused a large increase in photosynthetic rate in this C_3 plant, especially at higher temperatures. This increase results in a substantial upward shift and a much sharper definition of temperature optimum. The differences in the temperature dependence characteristics among the plants grown under the three different temperatures were even more pronounced than in air of normal CO_2 and O_2.

At measurement temperatures exceeding the optimum for photosynthesis as determined under saturating CO_2 the photosynthetic
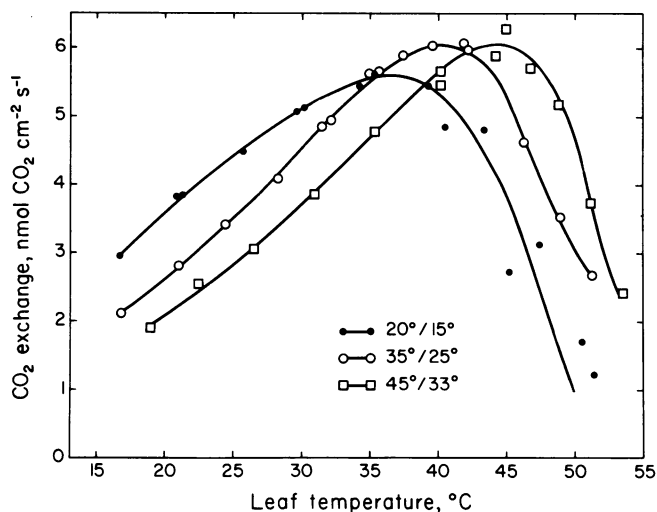
FIG. 4. Temperature dependence of net photosynthesis in an atmosphere of 1.5% and saturating CO_2 by intact leaves of L. divaricata, grown in three temperature regimes. Light intensity was 190 to 200 nE cm^{-2} sec^{-1}. Photosynthesis declined with time at temperatures exceeding the respective temperature optima. The rates shown are those determined after 10 min at each superoptimal temperature.

rate declined with time. This decline was observed both at limiting and saturating CO_2 pressures. The threshold temperatures for such inactivation increased with growth temperature in concert with the temperature optima shown in Figure 4. No time-dependent declines in photosynthetic rate were observed at low measurement temperature irrespective of growing conditions.

Two effects of temperature acclimation on intrinsic photosynthetic characteristics can therefore be distinguished. Growth at low temperature results in an increase in photosynthetic capacity at low temperature whereas growth at high temperature results in an increased temperature stability of the photosynthetic machinery.

DISCUSSION

During the past decade a large number of studies have been conducted concerning the influence of growing or preconditioning plants to different temperature regimes on subsequent photosynthetic performance (2–4, 6, 7, 9, 11, 12, 15–17, 22). In most instances it has been found that growth or preexposure to high temperature results in an upward shift in the photosynthetic temperature optimum and vice versa. This type of response has generally been interpreted as photosynthetic acclimation. However, in many of these studies the shift in the temperature dependence of photosynthesis in relative terms was often accompanied by considerable counteracting changes in photosynthetic capacity in absolute terms, resulting in an inferior rather than a superior over-all performance. The recent work of Pearcy (15, 16) using coastal ecotypes of the C_4 species Atriplex lentiformis well illustrates this point. When these plants were grown at 23 C the rate of photosynthesis at 40 C was 60% of maximum which occurred at 32 C. Growing this same clone at 43 C resulted in an upward shift of the temperature optimum so that the rate at 40 C now was 100% of maximum. However, the absolute rate at 40 C declined to only 0.5 of the rate in the plant grown at 23 C. Such results can evidently not be taken as evidence for photosynthetic acclimation but indicate that the plant is incapable of responding favorably to the high temperature growth regime and actually suffers injury (16). Conversely, when the Death Valley species Tidestromia oblongifolia (which unlike L. divaricata is active only during the hot summer and dormant during the cool winter months) was grown at 40 C the photosynthetic temperature optimum was 43 C

(4). Keeping this species at 16 C resulted in a downward shift in the temperature optimum to about 28 C but in spite of this the absolute rate at 16 C declined to less than one-third of the value for the plant grown at 40 C. Clearly this species lacks the ability to acclimate to low temperature even though a pronounced downward shift in the optimum temperature occurred.

In contrast to these results, the present investigation on the C_3 species, L. divaricata, and Pearcy's recent work on warm desert ecotypes of the C_4 species, A. lentiformis (also from Death Valley), provide unequivocal evidence for photosynthetic acclimation to seasonal changes in temperature regime. The absolute rates of photosynthesis at the respective optimum temperatures remained remarkably constant in the field plants during the different seasons as well as in the plants grown at different temperature regimes under controlled conditions. The shift in photosynthetic temperature dependence obtained in the controlled environment studies closely resemble the seasonal shifts observed in the field, demonstrating further that temperature alone is sufficient to effect the acclimation. It is noteworthy that both L. divaricata and A. lentiformis are evergreen perennial shrubs that remain active throughout the year in their desert environments.

In addition to the problems discussed above, a difficulty encountered in many past attempts to analyze the basis for photosynthetic acclimation to temperature is that net photosynthesis is affected by a number of factors other than the response of intrinsic photosynthetic machinery itself and that these factors may respond independently to temperature. One such factor is stomatal conductance, which may respond to temperature directly. It may also respond indirectly since unless special precautions are taken a change in temperature over a wide range will drastically affect the water vapor pressure deficit. Respiration, and in C_3 plants, the inhibitory effect of O_2 on photosynthesis and associated photorespiratory metabolism are also temperature-dependent processes affecting the rate of net CO_2 uptake.

In the present investigation these factors were taken into account. Changes in stomatal conductance did not contribute even in part to the observed changes in the temperature dependence of net photosynthesis either in the field or in the laboratory studies. Although respiration and especially O_2 inhibition markedly influence both the absolute rates of net CO_2 uptake and the shape of the temperature dependence curves, the effects of these factors were similar regardless of the growth temperature regime.

These results provide strong evidence that the observed temperature acclimation of net CO_2 uptake in L. divaricata is primarily the result of changes in intrinsic photosynthetic characteristics. This is further supported by the results obtained under low O_2 and rate-saturating intercellular CO_2 concentrations where any effects that may result from CO_2 diffusion limitations, extracellular and intracellular, as well as O_2 inhibition, are eliminated. Under these conditions the effect of growth temperature on subsequent photosynthetic performance is perhaps even more pronounced than in an atmosphere of normal CO_2 and O_2 concentration. It is likely that the factors underlying the change in the photosynthetic capacity at low, rate-limiting temperatures are different from those underlying the change in the ability to sustain high photosynthetic activity at high temperatures.

An increased photosynthetic capacity at low temperatures could be achieved simply by an increased quantity of one or several rate-limiting enzymes with no qualitative alterations of these components. The possibility of a qualitative change leading to a higher catalytic activity at low temperature without an increase in quantity cannot be excluded, however. Björkman and Pearcy (6) considered the possibility that ribulose bisP carboxylase may be subject to such quantitative adjustments and in many species the activity and amount of this enzyme have been found to increase with decreased growth temperature (6, and unpublished data by Björkman and co-workers). No quantitative information on this or any other enzyme is available for L. divaricata. However, no

significant differences were found in the leaf nitrogen content of plants grown under the different temperature regimes, neither were any positive correlations found between Chl content or specific leaf weight and photosynthetic capacity at low, rate-limiting temperatures. This indicates that the higher capacity of the *Larrea* plants grown at low temperature is not simply the result of a general increase in the amount of photosynthetic machinery per unit leaf area.

The increased photosynthetic rate at high analysis temperature with increasing growth temperature is undoubtedly related to an increased thermal stability of key components of the photosynthetic apparatus. The basis for this aspect of temperature acclimation is investigated and discussed in the companion report by Armond *et al.* (1).

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