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Acclimation of Photosynthetic and Respiratory Carbon Dioxide Exchange to Growth Temperature in *Atriplex lentiformis* (Torr.) Wats.[1]

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ABSTRACT

***Atriplex lentiformis* plants collected from coastal and desert habitats exhibit marked differences in capacity to adjust photosynthetic response to changes in growth temperature. Plants from desert habitats grown at 43 C day/30 C night temperatures had higher CO_2 uptake rates at high temperatures but reduced rates at low temperatures as compared to plants grown at 23 C day/18 C night temperatures. In contrast, growth of the coastal plants at high temperatures resulted in markedly reduced photosynthetic rates at all measurement temperatures.**

Leaf conductances to CO_2 were not important in controlling either the differences in the temperature dependence of net CO_2 uptake or the differences in photosynthetic capacities at any measurement temperature. At low measurement temperatures, differences in photosynthetic capacities among plants acclimated to the contrasting growth regimes were correlated with differences in leaf ribulose diphophate carboxylase activities. At high measurement temperatures, the improved net photosynthetic performance of the high temperature acclimated desert plants appeared to be due to a combination of decreased respiration rates, decreased temperature dependence of respiration, and an apparent increased thermal stability of photosynthetic CO_2 exchange.

Observations under both field and laboratory conditions have established that for many plant species a certain degree of plasticity or capacity for acclimation exists in the photosynthetic response to temperature. Plants preconditioned in different growth temperature regimes or at different seasons exhibit shifts in photosynthetic response that in some cases appear to have adaptive value since the result is enhanced CO_2 uptake rates (2, 16, 17). Despite the many observations, very little information is available in the literature concerning the underlying mechanisms controlling these acclimation responses.

Atriplex lentiformis (Torr.) Wats. is an evergreen phreatophytic shrub native to both hot desert and cool coastal habitats in California. This species possesses the "Kranz" type leaf anatomy characteristic of the C_4 dicarboxylic acid pathway of photosynthesis (15). Under summer field conditions, CO_2 exchange characteristics of the plants in the two habitats contrast markedly with the desert plants possessing nearly a 10 C higher temperature optimum (21). Subsequent laboratory measurements of growth and CO_2 exchange at three temperatures have shown that the desert and coastal plants differ primarily in their capacity to acclimate to high temperatures rather than in genetically fixed temperature responses (19). The large capacity for temperature acclimation in the desert plants and marked contrasts with the coastal plants make *Atriplex lentiformis* an ideal species for studies of the mechanisms involved in photosynthetic temperature acclimation. Here, the results of a detailed analysis of the effects of growth temperature on the CO_2 exchange characteristics of *A. lentiformis* are reported. The objective in this analysis was to characterize the CO_2 exchange responses in terms of the possible rate-limiting steps so that the components of the photosynthetic apparatus involved in the temperature acclimation response could be identified.

MATERIALS AND METHODS

Plants of *Atriplex lentiformis* were established from cuttings collected at coastal and desert sites in southern California. General descriptions of these sites are given elsewhere (19). Experimental plants were established from cuttings taken from the stock clones and were grown in an I.S.C.O. E3A growth chamber. Light was supplied from a mixture of 400 w metal halide and 100 w incandescent lamps that gave an irradiance at the top of the pots of 110 neinsteins cm^{-2} sec^{-1}. All plants were grown in Perlite continuously irrigated from below with a modified Hoagland nutrient solution that was vigorously aerated. Since preliminary experiments established that *A. lentiformis* had maximum growth with 0.12 M NaCl in the nutrient solution, this concentration was used routinely in all experiments. The temperature regimes used in all experiments were either 23 C day/18 C night or 43 C day/30 C night. These regimes were chosen because the day temperatures are similar to those present in the desert habitat in the winter and summer months, as well as in the coastal and desert habitats, respectively, during the summer.

CO_2 exchange measurements were made on single attached leaves with an open system gas exchange apparatus incorporating a Beckman 315B IR CO_2 analyzer modified for differential analysis. The leaf chamber in this system was similar to that illustrated by Björkman and Holmgren (5). Leaf temperatures were measured on the abaxial surface with a 44-gauge copper-constantan thermocouple. A fan mounted in the bottom of the chamber rapidly mixed the chamber atmosphere providing maximum and constant boundary layer conductances. Air was supplied from compressed air cylinders containing 350 to 380 $\mu l\ l^{-1}$ CO_2. Flow rates through the chamber were measured either with a rotameter or with a Validyne differential pressure transducer mounted across a sintered glass disc that acted as a flow restrictor in the air stream. Flow rates were adjusted to give concentrations of 290 and 310 $\mu l\ l^{-1}$ CO_2 in the chamber atmosphere when the plants had high rates of CO_2 uptake. At low temperatures, however, CO_2 concentrations in the chamber were allowed to rise because of the necessity of maintaining adequate flow rates.

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Transpiration rates were determined by measuring the humidity in the exiting air stream with either an EG & G model 880 dew point hygrometer or a Weathermeasure model HMlllp relative humidity sensor. Both systems were frequently calibrated with air streams of known water vapor content. Humidity in the entering air stream was controlled by first humidifying and then dehumidifying in a gas washing bottle and a thermostatted glass condenser, respectively, to a known dew point temperature.

Leaf conductances to CO_2 and the intercellular space CO_2 pressures were calculated according to the procedures of Sestak *et al.* (23) from the simultaneous measurements of water vapor and CO_2 flux. The leaf conductances reported include the contributions of both the boundary layer and stomatal conductances. Preliminary measurements established that the stomata were equally distributed between both leaf surfaces. No attempt was made to correct for any possible errors resulting from differences in conductances of the two surfaces.

The light source for photosynthetic CO_2 exchange measurements was a 2.5 kw short arc xenon lamp. Wavelengths longer than 700 nm were removed by filtering through 15 cm of water and a heat-reflecting interference filter. Irradiances were measured with a silicon photoelectric cell mounted on the lid of the chamber that was frequently calibrated against a Lambda Inst. Co. quantum sensor placed inside the chamber. Irradiances were controlled with neutral density filters.

The temperature dependence of photosynthetic CO_2 exchange was determined by measuring the steady-state rate of CO_2 exchange at 2 C temperature intervals. In order to avoid significant aftereffects of high temperature on the rate of photosynthesis, the following procedure was used. Measurements were always started at the growth temperature, or in the case of the high temperature-grown plants, a few degrees below the growth temperature. The temperature was then increased in steps up to 1 to 3 C above the optimum temperature for CO_2 exchange and then decreased in steps down to 10 C. With other leaves, the temperature was increased in steps up to the maximum temperature where CO_2 exchange was measured. In this way, the sequence of measurements at both high and low temperatures was always from a more to a less favorable temperature regime. Since slight differences in the mean photosynthetic rate in the increasing and decreasing measurement series were present, the mean responses of each series were normalized to the average photosynthetic rate for all plants from a collection location at the growth temperature. Vapor pressure gradients from the leaf to the chamber atmosphere were kept within the range of 5 to 15 mbars at all temperatures.

The temperature dependence of dark respiration was determined with plants left in the dark for 2 to 3 hr prior to the measurements in order to achieve steady rates. The temperature was first lowered from 25 C to 5 C and then increased in steps up to the maximum temperature used. Rates of respiration were always equal at 25 C before and after the reduction in temperature.

RuDP[3] and PEP Carboxylase Activities. Activities of RuDP carboxylase (EC 4.1.1.39) and carboxylase (EC 4.1.1. 31) were determined according to the procedures of Björkman and Gauhl (4).

RESULTS

Figure 1 illustrates the large dependence of photosynthetic CO_2 exchange characteristics of *A. lentiformis* on the growth temperature regime. For the Death Valley plants, growth in the contrasting temperature regimes resulted in no change in the maximum CO_2 exchange rates but nearly a 10 C difference in the photosynthetic temperature optimum. CO_2 uptake rates were higher at high temperatures but lower at low temperatures in the 43/30 C as compared to the 23/18 C grown plants. Steady-state CO_2 exchange rates were not achieved at temperatures above 38 to 39 C with the plants grown at 23/18 C, indicating a thermal inhibition of CO_2 exchange, but occurred up to 45 C and exhibited only a very gradual decline at 47 C in plants from the 43/30 C regime. Plants from the coastal Ventura collection site grown at 23/18 C had CO_2 exchange characteristics that were similar to those of the Death Valley plants in the same regime. Growth of the Ventura plants at 43/30 C resulted in a marked reduction in photosynthetic CO_2 exchange rates at all temperatures. The Ventura plants thus exhibited a lesser capacity to acclimate to high temperatures than the Death Valley plants. There seems to be at least a partial photosynthetic acclimation to high temperatures in these plants since the temperature optimum shifted from 32 to 40 C and steady-state CO_2 uptake rates were maintained to the highest measurement temperature of 43

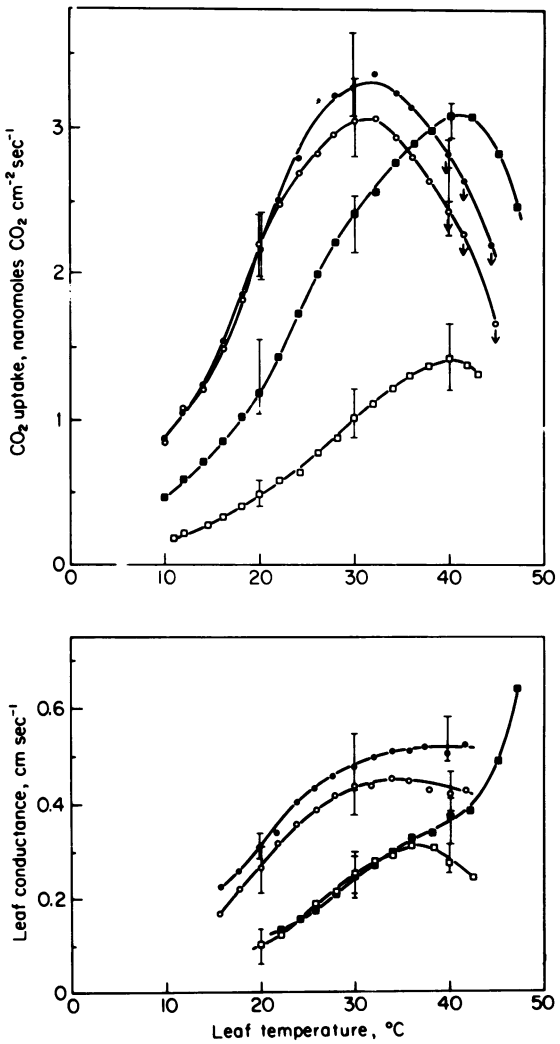

FIG. 1. Temperature dependence of CO_2 uptake (upper) and leaf conductance (lower) for the Death Valley and Ventura plants grown at either 23 C day/18 C night or 43 C day/30 C night temperatures. (●) Death Valley 23 C day/18 C night; (○) Ventura - 23 C day/18 C night; (■) Death Valley 43 C day/30 C night; (□) Ventura 43 C day/30 C night. Vertical bars give ranges for four to seven plants and are representative of those at other temperatures. Arrows indicate non-steady-state rates of CO_2 exchange. All measurements were made at irradiances of 170 to 180 neinsteins cm^{-2} sec^{-1}.

[3] Abbreviations: RuDP: ribulose diphosphate; PEP: phosphoenolpyruvate.

C. It is noteworthy that under the respective high and low growth temperature regimes, the photosynthetic temperature responses of the Death Valley and Ventura plants were similar to curves determined under field conditions in coastal and desert habitats (21).

Leaf conductances to CO_2 (Fig. 1, lower) were strongly dependent on both growth and measurement temperature. Below the thermal optimum for CO_2 uptake, leaf conductances decreased with decreasing temperatures in both growth regimes but were much higher in plants from the 23/18 C regime. Above 36 C, leaf conductances increased markedly in the Death Valley plants but decreased slightly in the Ventura plants grown in the 43/30 C regime. The marked increase in leaf conductance above 36 C in the 43/30 C grown Death Valley plants was not present in desert plants under field conditions (21). High leaf chamber vapor pressures in the laboratory experiments and the growth chamber *versus* field environment are possible contributing factors to the difference in the field and laboratory response. The reasons for the differences in stomatal response at high temperature of the 43/30 C grown Death Valley and Ventura plants are not apparent.

Except for the Ventura plants grown at 43/30 C, the mean intercellular CO_2 partial pressures calculated from the photosynthetic CO_2 fluxes and leaf conductances were lowest at temperatures near or slightly below the thermal optima for CO_2 uptake and increased at either higher or lower temperatures (Fig. 2). For the Death Valley plants, mean intercellular CO_2 partial pressures at the respective thermal optima were similar in the two growth regimes. Growth of the Ventura plants at 43/30 C, however, resulted in markedly increased intercellular CO_2 partial pressures at all temperatures below the thermal optimum despite reduced leaf conductances. Thus, the increased limitations to CO_2 uptake in the mesophyll were clearly much greater than the limitations imposed by the decreased leaf conductances. In the other plants, the increased intercellular CO_2 partial pressures, but reduced CO_2 uptake rates, at temperatures both above and below the thermal optima show that changes in leaf conductance are not responsible for the differences in photosynthetic temperature dependence. Rather, differences in the internal limitations to photosynthesis in the mesophyll must be involved.

Preliminary measurements of the CO_2 concentration dependence of CO_2 uptake with the Death Valley plants from both growth regimes indicated that CO_2 saturation was occurring at intercellular concentrations in the range of 100 to 140 $\mu l\ l^{-1}$ which is similar to the responses of other C_4 plants from arid habitats (6). Thus, mesophyll conductances could not be calculated as the residual conductance without significant error (24).

Arrhenius plots for the temperature dependence of net CO_2 uptake (Fig. 3) show that at temperatures below 16 to 18 C, activation energies ranged from 18 to 21 kcal mol^{-1} for plants in both growth regimes. Plots for the 43/30 C grown plants show a break at 16 to 18 C, but CO_2 uptake continued to follow a logarithmic increase as a function of the reciprocal of absolute temperature giving an activation energy of about 14 kcal mol^{-1}. At temperatures above 26 and 29 C in the Death Valley and Ventura plants, respectively, CO_2 uptake deviated from an Arrhenius relationship indicating an increasing limitation by factors other than those limiting at lower temperatures. This increasing limitation of CO_2 uptake resulting in a deviation from an Arrhenius relationship occurred at much lower temperatures (18 C) in the plants grown at 23/18 C.

Since activities of RuDP carboxylase have been shown to be closely correlated with photosynthetic capacity in a number of C_3 photosynthetic species (3), the activities of this enzyme as well as the other carboxylating enzyme present, PEP carboxylase, were determined (Table I). Marked differences were apparent in the responses of the two enzymes with RuDP carboxylase activities decreasing strongly in response to the higher growth temperature while no consistent pattern was present for PEP carboxylase. For RuDP carboxylase, the increased growth temperature resulted in a 60% decline in activities in the Death Valley plants, but over a 90% reduction in the Ventura plants. In contrast, PEP carboxylase activities showed a slight increase in the Ventura but a slight decrease in the Death Valley plants at high as compared to low growth temperatures.

Dark respiratory acclimation to temperature was also apparent in both the Death Valley and Ventura plants. Increased growth temperatures resulted in decreased dark respiration rates at all temperatures (Fig. 4). The differences were, however, most apparent at temperatures above 30 C. Only small differences were apparent in the responses of the plants from the two collection locations.

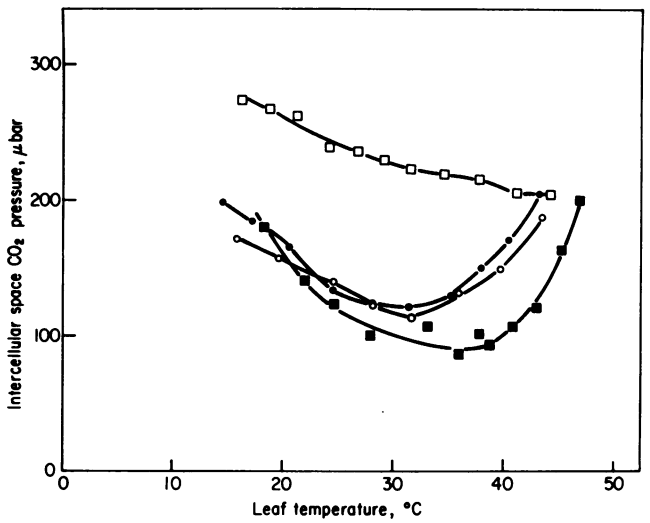

FIG. 2. Mean intercellular space CO_2 pressures as a function of temperature for the Death Valley and Ventura plants grown at 23 C day/30 C night or 43 C day/30 C night temperatures. Symbols and conditions are the same as in Figure 1.

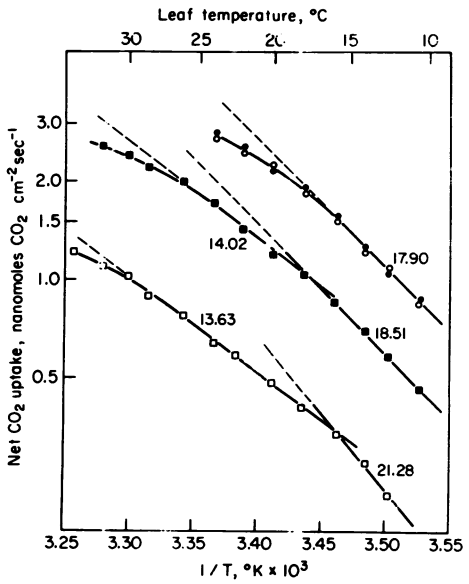

FIG. 3. Arrhenius plots for net CO_2 uptake of the Death Valley and Ventura plants grown at 23 C day/30 C night or 43 C day/30 C night temperatures. Symbols and conditions are the same as in Figure 1.

Table 1. RuDP and PEP carboxylase activities per unit leaf area in leaves of coastal and desert Atriplex lentiformis plants grown in two temperature regimes.

	Growth temp. Day/Night, °C	Activity, nanomoles cm^{-2} sec^{-1} RuDP carboxylase	PEP carboxylase
Death Valley	23/18	2.06[1]	6.20
	43/30	0.83	5.31
Ventura	23/18	2.28	6.77
	43/30	0.13	8.38

[1] each value is the mean of 3 to 5 determinations.

Arrhenius plots for the respiration rates of the Death Valley plants are shown in Figure 5. A single transition from an activation energy of 15.13 kcal mol^{-1} to 12.61 kcal mol^{-1} occurred at 25 C for the plants grown in the coastal regime. In contrast, two transitions occurred at about 27 and 37 C in the Arrhenius plot for the plants grown in the desert regime. Above and below the two transitions, the activation energies were similar to those of the coastal regime grown plants. Between the two transitions, however, the activation energy was much lower at 5.24 kcal mol^{-1}. Arrhenius plots of the respiration rates of the Ventura plants yielded similar results to those presented for the Death Valley plants.

DISCUSSION

Although the factors controlling the temperature response of CO_2 exchange are not well understood, it seems clear that the temperature dependence of net CO_2 uptake is probably the result of the temperature dependence of several rate-limiting steps, with each acting alone or in combination over a limited part of the total temperature range (3). Raschke (22), in line with an earlier model of Hesketh and Baker (14), has proposed that the temperature response of maize can be described in terms of three components: (*a*) an exponentially increasing process that dominates at low temperature; (*b*) an antagonistic process (or several processes) that gradually increases with temperature; and (*c*) an inactivation of the photosynthetic CO_2 exchange apparatus at high temperatures. These processes also seem to describe the temperature response of *A. lentiformis*. Since the acclimation responses involve changes in CO_2 uptake rates in all parts of the temperature response curve, it is likely that at least several rate-limiting processes are involved.

Changes in several processes have been suggested as possible factors controlling acclimation responses. Changes in the O_2 effect on CO_2 uptake have been implicated in the differences in photosynthetic temperature response of *Encelia farinosa* grown in contrasting temperature regimes (17). Since *A. lentiformis* possesses the C_4 dicarboxylic acid pathway and therefore lacks an O_2 effect on photosynthesis, this cannot be of importance here. Changes in the temperature dependence of stomatal conductance as a function of growth temperature appear to control the shifts in temperature dependence of CO_2 uptake of some species (9, 10, 17, 18). Marked effects of growth temperature on stomatal response are apparent in *A. lentiformis*. The different directions of change of intercellular CO_2 concentrations and CO_2 uptake rates, both above and below the temperature optima in both the high and low temperature-grown plants, argue against a role for these differences in stomatal response as a determinant of the shifts in the temperature dependence of CO_2 uptake seen here.

The similar Arrhenius activation energies for CO_2 uptake, regardless of population origin or growth temperature, support the conclusions of Björkman and Pearcy (7) that adaptations in the low temperature part of the temperature dependence curve involve quantitative adjustments in the same rather than changes to different rate-limiting steps. The activation energies determined for CO_2 uptake in *A. lentiformis* are similar to those found for photosynthesis and for RuDP carboxylase activity in a wide variety of other species. At high bicarbonate concentrations, RuDP carboxylase gives an Arrhenius plot with a single transition at about 17 C and activation energies of 18 to 21 and 12 to 14 kcal mol^{-1} at lower and higher temperatures, respectively. The activation energies for CO_2 uptake determined here are thus remarkably similar to those exhibited by RuDP carboxylase. Furthermore, a good correlation is also apparent between CO_2 uptake rates below 25 C and RuDP carboxylase activities; both are lowest in the Ventura plants grown at 43/30 C, intermediate in the Death Valley plants grown at 43/30 C, and highest in

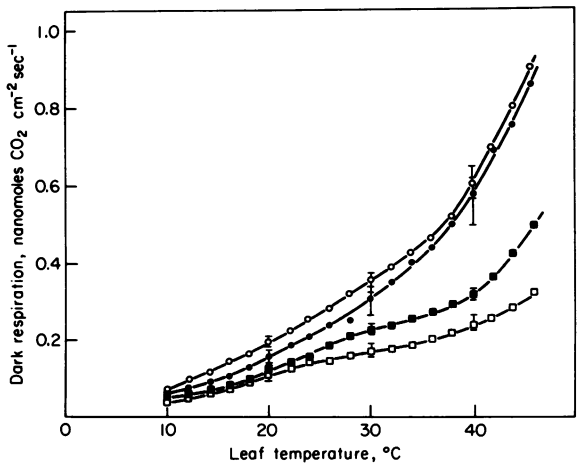

FIG. 4. Temperature dependence of dark respiration in the Death Valley and Ventura plants grown at 23 C day/48 C night or 43 C day/30 C night temperatures. Symbols are the same as in Figure 1. Mean responses and representative ranges for three plants are given.

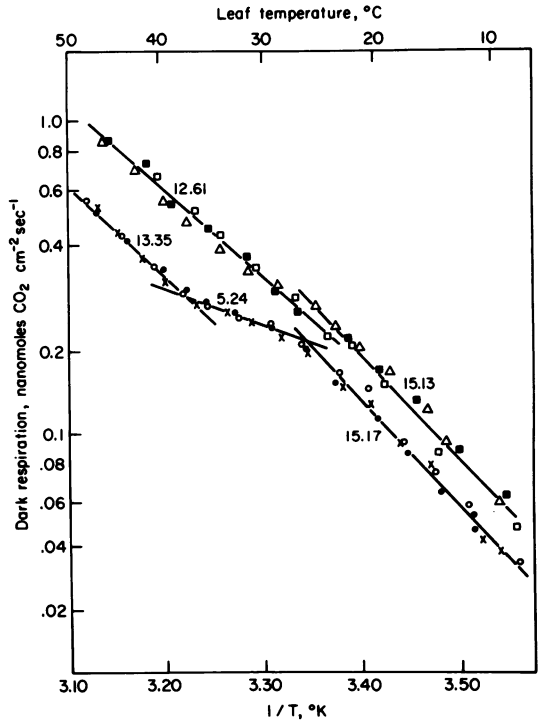

FIG. 5. Arrhenius plots for the respiration rates of the Death Valley plants grown at either 23 C day/18 C night (upper lines) or 43 C day/30 C night (lower lines) temperature regimes. Symbols refer to data from different plants.

plants grown at 23/18 C. These results support the suggestions that RuDP carboxylase may be rate-limiting for CO_2 uptake at low temperatures in C_4 as well as C_3 plants (3) and that the growth temperature-dependent changes in photosynthesis at low measurement temperatures where an Arrhenius relationship is followed may be due to changes in RuDP carboxylase activities (7). Decreased activities of RuDP carboxylase in high as compared to low temperature-grown plants have been demonstrated in other species (8, 24). The results reported here, however, contrast with those reported for cotton acclimated to different temperatures where no correlation could be found between RuDP carboxylase activities and estimates of CO_2 and light-saturated photosynthesis (9).

Because increases in temperature increase enzyme activity, less RuDP carboxylase protein may be required at high growth temperatures, effecting a savings in synthesis and maintenance energy costs. This argument would apply to the responses of the Death Valley plants but clearly the very large reduction in RuDP carboxylase levels in the Ventura plants could limit CO_2 uptake even at high temperatures. Thus, whether the reduction is apparently adaptive or nonadaptive would depend on its magnitude. These changes would be particularly important for RuDP carboxylase which generally represents a large fraction of the total leaf protein in plants.

Synthesis of RuDP carboxylase in rye seedlings has been shown to be sensitive to high growth temperatures (11) because of a heat sensitivity of chloroplast 70S ribosomes in this species (12). Differences in heat sensitivity of the chloroplast 70S ribosomes of the Death Valley and Ventura plants could be one possible explanation for the poor photosynthetic performance of the Ventura plants at high growth temperatures. Although the site of PEP carboxylase synthesis is not known, assembly on 80S ribosomes would account for the marked differences in response of this enzyme and RuDP carboxylase.

Reductions in dark respiration rates that lead to higher net CO_2 uptake rates have been implicated in the improved high temperature performance in warm-acclimated plants for some species (2) but not in others (16). The substantial reduction in dark respiration rates of *A. lentiformis* could contribute to higher net photosynthetic rates at high temperatures in the 43/30 C grown plants provided that CO_2 uptake capacities were not also strongly reduced as occurred in the Ventura plants. Also, the course of net CO_2 uptake of the 23/18 C grown plants with increasing temperature from 30 to 40 C declined possibly in response to the strong increase in the respiration rates. In contrast, photosynthetic rates increased over this temperature interval in the 43/30 C grown plants, possibly due at least in part to the low activation energies and consequently the small increase in respiration rates. The Arrhenius plots show that changes in the rate-limiting steps, as indicated by the much lower activation energy in the 27 to 37 C interval as well as changes in the capacities of other rate-limiting steps at higher and lower temperatures are involved in temperature acclimation of respiration. These respiratory differences can however account for only part of the differences in CO_2 uptake observed at high temperatures since respiration reached steady-state rates at temperatures above 37 C while photosynthesis did not in the 23/18 C grown plants. Thus, the decline in photosynthesis at supraoptimal temperatures must involve a direct inhibition of the photosynthetic apparatus in these plants. The steady CO_2 exchange rates at temperatures out to 45 C indicate that high temperature acclimation in *A. lentiformis* also involves increases in the thermal stability of the photosynthetic CO_2 exchange apparatus. Further studies on differences in thermal stability will be reported in another paper (20).

The similar increases in the temperature optima and apparent thermal stabilities of photosynthesis in the coastal and desert plants were surprising since maximum day temperatures in the coastal habitats rarely exceed 40 C and then for no more than 2- to 3-day periods. The increased thermal stability of the photosynthetic apparatus could be an adaptation to protect against these high temperatures, but only if the changes could occur fast enough. Heat hardening of the photosynthetic apparatus can occur over short time periods in some species (1), but the changes are generally small. Alternatively, since according to taxonomic evidence (13) the coastal populations evolved from those in the desert, only part of the capacity to acclimate to high temperatures may have been lost during evolutionary adaptation to the coastal habitat.

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LITERATURE CITED

1. Bauer H, W Larcher, RB Walker 1975 Influence of temperature stress on CO_2-gas exchange. *In* JP Cooper, ed, Photosynthesis and Productivity in Different Environments. Cambridge University Press pp 557-586
2. Billings WD, PJ Godfrey, BF Chabot, DP Bourque 1971 Metabolic acclimation to temperature in arctic and alpine ecotypes of *Oxyria digyna*. Arctic Alpine Res 3: 277-289
3. Björkman O 1973 Comparative studies on photosynthesis in higher plants. *In* AC Giese, ed, Photophysiology Vol 13. Academic Press, New York pp 1-63
4. Björkman O, E Gauhl 1969 Carboxydismutase activity in plants with and without β-carboxylation photosynthesis. Planta 88: 197-203
5. Björkman O, P Holmgren 1963 Adaptability of the photosynthetic apparatus to light intensity in ecotypes from exposed and shaded habitats. Physiol Plant 16: 889-914
6. Björkman O, HA Mooney, J Ehleringer 1975 Photosynthetic responses of plants from habitats with contrasting thermal environments. Carnegie Inst Wash Yearbook 74: 743-748
7. Björkman O, RW Pearcy 1971 Effect of growth temperature on the fixation *in vitro* in C_3 and C_4 species. Carnegie Inst Wash Yearbook 70: 511-520
8. Chabot BF, JF Chabot, WD Billings 1972 Ribulose-1,5 diphosphate carboxylase activity in arctic and alpine populations of *Oxyria digyna*. Photosynthetica 6: 364-369
9. Downton J, RO Slatyer 1972 Temperature dependence of photosynthesis in cotton. Plant Physiol 50: 518-522
10. Drake BG, FB Salisbury 1972 After effects of low and high temperature pretreatment of leaf resistance, transpiration and leaf temperature in *Xanthium*. Plant Physiol 50: 572-575
11. Feierabend J, C Berger, A Meyer 1969 Spezifische Storung von Entwicking und Enzymbildung der Pflanzen höher Pflanzen durch höhe Wachstumstemperaturen Z Naturforsch 24: 1641-1647
12. Feierabend J, U Schrader-Reichhardt 1976 Biochemical differentiation of plastids and other organelles in rye leaves with a high temperature induced deficiency of plastid ribosomes. Planta 129: 147-153
13. Hall HM, FE Clements 1923 The phylogenetic method in taxonomy: the North American species of *Artemesia*, *Crysothamnus* and *Atriplex*. Carnegie Inst Wash Publ 326. 355 pp
14. Hesketh JE, DBaker 1967 Light and carbon assimilation by plant communities. Crop Sci 7: 285-293
15. Laetsch WM 1968 Chloroplast specialization in dicotyledons possessing the C_4-dicarboxylic acid pathway of photosynthetic CO_2 fixation. Am J Bot 55: 875-883
16. Lange OL, ED Schulze, M Evenari, L Kappen, U Buschbom 1974 The temperature-related photosynthetic capacity of plants under desert conditions. I. Seasonal changes of the photosynthetic response to temperature. Oecologia 17: 97-110
17. Mooney HA, AT Harrison 1970 The influence of conditioning temperature on the subsequent temperature-related photosynthetic capacity in higher plants. *In* CT de Wit, ed, Prediction and Measurement of Photosynthetic Productivity Centre for Agricultural Publishing and Documentation, Wageningen pp 411-417
18. Nelson RE, MM Ludlow, PG Jarvis 1972 Photosynthesis in sitka spruce (*Picea sitchensis* (Bong.) Carr.) II response to temperature. J Appl Ecol 9: 721-745
19. Pearcy RW 1976 Temperature effects on growth and CO_2 exchange rates in coastal and desert races of *Atriplex lentiformis*. Oecologia. 26: 245-255
20. Pearcy RW, JA Berry, DC Fork 1976 Effects of growth temperature on the thermal stability of the photosynthetic apparatus. Plant Physiol In press
21. Pearcy RW, AT Harrison 1974 Comparative photosynthetic and respiratory gas exchange characteristics of *Atriplex lentiformis* (Torr.) Wats. in coastal and desert habitats. Ecology 55: 1104-1111
22. Raschke K 1970 Temperature dependence of CO_2 assimilation and stomatal aperture in leaf sections of *Zea mays*. Planta 91: 336-363
23. Sestak I, J Caksky, P Jarvis, eds, 1971 Plant Photosynthetic Production; Manual of Methods. W. Junk, The Hague
24. Treharne KJ, CF Eagles 1970 Effect of temperature on photosynthetic activity of climatic races of *Dactylis glomerata*. Photosynthetica 4: 107-117