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Effects of Growth Temperature on the Thermal Stability of the Photosynthetic Apparatus of *Atriplex lentiformis* (Torr.) Wats.[1,2]

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ABSTRACT

High growth temperatures induced a substantial increase in the thermal stability of the photosynthetic apparatus of *Atriplex lentiformis*. This was manifested as a much reduced inhibition of light-saturated photosynthesis and the initial slope of the light-dependence curves by exposure to high temperatures in high as compared to moderate temperature-grown plants. Heat treatment at 46 C of leaves from moderate temperature-grown plants resulted in a marked reduction in photosystem II activities of chloroplasts isolated from them. In contrast, heat treatment of leaves from high temperature-grown plants resulted in no reduction of photosystem II activities. *In vivo* estimates of photosystem II functioning, the 515 nm light-induced absorbance change, and the ratio initial to maximum fluorescence (F_0/F_{max}) indicated a similar increase in the thermal stability of photosystem II in high temperature-grown plants.

The high summer temperatures of some deserts, which can often exceed 40 C and may reach 50 C or higher, can impose a severe constraint upon plant growth and productivity, even when adequate water is available. These temperatures are well above the thermal optimum for CO_2 uptake for temperate zone plants as well as species predominantly active during the cooler seasons in the desert (3, 8). It is becoming evident, however, that at least some summer active desert species have physiological adaptations that allow for high rates of CO_2 uptake at high temperatures (7, 21). For example, *Tidestromia oblongifolia* has a thermal optimum for CO_2 uptake which exceeds 40 C. This species, however, is not capable of growth at cool temperatures and is not photosynthetically active during the mild spring and winter months (5).

In contrast to species predominantly active during one season, evergreen desert species that are active throughout the year must possess a broad thermal tolerance or must be capable of acclimation to the seasonal changes in the temperature regime. Recent experiments have shown that many desert species that are active under seasonally variable temperatures possess a capacity to acclimate to the prevailing temperature regime (8, 16). Despite these observations, however, there is little in the literature concerning the mechanisms underlying temperature acclimation, particularly those involved in high temperature responses.

Atriplex lentiformis (Torr.) Wats. is a phreatophytic evergreen shrub that occurs in the hot interior deserts of California and possesses the C_4 pathway of photosynthesis. Previous experiments in both the field and laboratory have shown that growth temperature has a substantial effect on the photosynthetic performance of these plants (19-21). Growth at high temperatures resulted in a substantially greater photosynthetic temperature optimum, increased rates of CO_2 uptake at high temperatures, but decreased rates at low temperatures as compared to the responses of low temperature-grown plants. Differences in photosynthetic performance at low temperatures appear to be related principally to changes in RuDP carboxylase activity in the leaves (20). In this paper, we show that an important factor leading to a higher temperature optimum for CO_2 uptake and the ability to maintain high CO_2 uptake rates at high temperatures is an increase in the thermal stability of the photosynthetic apparatus of the high temperature-grown plants as compared to that of low temperature-grown plants, and we report studies of the physiological basis of this increased tolerance to high temperatures.

MATERIALS AND METHODS

Plant Material. Plants were propagated from rooted cuttings of *A. lentiformis* shrubs collected near Saratoga Spring, Death Valley, Calif. (19), and were grown either in a growth chamber (ISCO E-3A) equipped with metal halide plus incandescent lamps providing 110 neinsteins cm^{-2} sec^{-1} or in naturally lit, temperature-controlled phytocells (6). All plants were grown in Perlite that was continuously irrigated with a modified Hoagland nutrient solution. Temperature regimes used were selected to provide conditions similar to those experienced in the native desert environment in early spring (23/18 C, day/night) or midsummer (43/30 C).

CO_2 Exchange. CO_2 exchange and leaf conductance measurements were made with an open system gas analysis apparatus incorporating a single leaf chamber and an IR CO_2 analyzer (Beckman, 315b) set up for differential analysis. A solid state relative humidity sensor (Weathermeasure Corp. model HM111P) was used for determining water vapor fluxes and leaf conductances. Detailed descriptions of the procedures and the apparatus are reported elsewhere (19).

Photosystem I and II Activities. PSI and II activities were measured with chloroplasts isolated from leaves by homogenization in a mortar with 7 ml buffer/g leaf tissue. The isolation buffer consisted of 50 mM Tricine (pH 7.6), 0.4 M sucrose, 10 mM KCl, and 19 mM $MgCl_2$. The brei was filtered through Miracloth and centrifuged at 1,500*g* for 3 min. The resulting pellet was resuspended in isolation buffer containing 1 mg/ml of BSA to a final Chl concentration of 60 to 100 μg/ml. Chl concentrations were determined according to the procedure of Arnon (2).

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PSII activities were determined from the decrease in absorbance of DCPIP[4] at 590 nm upon illumination of chloroplast suspension. The measurements were made in a Beckman DU 2 spectrophotometer modified for crossbeam illumination. Actinic light was supplied from a 300 w quartz iodide lamp and was filtered through 3 cm of water to remove heat and a red filter (Schott RG 665) to remove wavelengths shorter than 600 nm. The photomultiplier was protected from the actinic light with a 590 nm (Ditric Opics) interference filter. The output from a recording attachment on the spectrophotometer was converted to absorbance units with a log amplifier and recorded on a strip chart recorder. An experimentally determined molar extinction coefficient for DCPIP of 15,960 M^{-1} cm^{-1} at 590 nm was used to calculate activities. Assays were conducted in a 1-cm path length cuvette thermostatted at 25 C. The final assay mixture consisted of 40 mM Tricine (pH 7.6), 7.6 mM KCl, 7.6 mM $MgCl_2$, 30 μM DCPIP, 33 mM methylamine, and chloroplasts equivalent to 3 to 5 μg Chl. The final reaction volume was 1.3 ml.

PSI activities were determined as the photoreduction of NADP, measured at 340 nm, with ascorbate and DCPIP as an electron donor system. Measurements were made in a Perkin-Elmer spectrophotometer with a crossbeam illumination attachment. Actinic light was supplied from a 150 watt quartz iodide lamp that gave an intensity of 40 neinstein cm^{-2} sec^{-1}. The photomultiplier was protected with the appropriate filters to block the actinic light but pass the 340 nm measuring beam. The final reaction mixture contained 50 mM Na-phosphate (pH 7.6), 160 mM NH_4Cl, 30 μM DCPIP, 30 mM Na-ascorbate, 1.6 mM NADP, 0.1 mM DCMU, 0.1 mg ferredoxin, and chloroplasts equivalent to 10 to 15 μg Chl. The final reaction mixture volume was 1 ml.

Fluorescence Measurements. The fluorescence yield was measured in leaves that had been infiltrated under a 25-mm Hg vacuum with water containing 10 mM DCMU. The leaves were immersed in water in a well stirred temperature-controlled cuvette, and blue actinic light (0.16 neinstein cm^{-2} sec^{-1}, Schott 9860 filter) was provided from above with a rapid acting (half-open time, 2 m sec) mechanical shutter. Fluorescence emission was collected from the front surface with a photomultiplier shielded with a 682 nm interference filter (Balzers) and two red cutoff filters (Schott, RG 665). The initial (F_0) and final (F_{max}) fluorescence levels were recorded during a 6-sec illumination using an oscillographic recorder. The dark period between illuminations was 24 sec, which was long enough to permit full recovery of the F_0 level.

515 nm Absorbance Change. The 515 nm absorbance change was determined in intact leaves using an apparatus that has been described previously (9). The leaf was positioned over the photomultiplier in a temperature-controlled water-jacketed chamber. Leaf temperatures were measured with a copper constantan thermocouple appressed to the lower surface. Actinic light in the 650 to 700 nm range was supplied from an incandescent lamp filtered with a red (Corning, 2030) and a calflex C (Balzars) filter that gave an intensity of 1.2×10^5 ergs cm^{-2} sec^{-1}. The leaf was illuminated for 3 sec which was sufficient for the maximum development of the second, slower phase of the 515 nm absorbance change (24). The maximum steady-state level of this slower phase, as recorded on an oscillographic recorder, was taken as a measure of the 515 nm absorbance change. Three to four actinic light exposures with 4-sec dark intervals in between were required to establish reproducible absorbance changes and all measurements were made after these initial exposures.

RESULTS

At high measurement temperatures, the photosynthetic rates of *A. lentiformis* plants grown at 23/18 C are limited by temperature. Figure 1 shows the effect of increasing temperatures on the time course of CO_2 uptake for a cool temperature-grown plant. Above 30.9 C, the apparent thermal optimum for this plant, stepwise increases in temperature resulted in stepwise changes to lower steady-state rates of CO_2 uptake up to a temperature of 38 C. These changes in CO_2 uptake rates were generally reversible upon returning the plant to the optimum temperature, although occasionally stomatal closure occurred. At temperatures above 38 C, the initial stepwise decrease was followed by a time-dependent decline in CO_2 uptake that was dramatically stimulated by the further increases in temperature. Lowering the temperature resulted in a small recovery of CO_2 exchange rates to level markedly below that present before exposure to high temperatures. No further recovery occurred for periods of up to several hr; however, there was some further recovery overnight. Clearly, exposure of the leaves to temperatures of 46 C results in an irreversible damage to the capacity for CO_2 uptake in these plants.

Figure 2 shows a time course for CO_2 uptake with step increases in temperature for a plant grown at 43/30 C temperatures. The apparent temperature optimum for CO_2 uptake in this plant was 40.9 C, or about 10 C higher than that of the 23/18 C-grown plant. Increases in temperature above the optimum resulted in lower but steady-state CO_2 exchange rates out to the highest measurement temperature of 46 C. In other experiments where temperatures were increased to 47 C, a slow long term decline was apparent. Thus, the long term inhibition of CO_2 uptake present from 38 to 47 C in the 23/18 C-grown plants did not occur in plants grown at 43/30 C temperatures until measurement temperatures above 46 C were reached. The reduction in rates was at least partially reversible upon lowering of the temperature back to 39 to 40 C but stomatal closure prevented a direct determination of the amount of recovery.

Leaf conductances to water vapor exchange showed little change with temperature with leaves from plants grown at either temperature, except that conductances of the cool temperature-grown plants increased markedly at higher temperatures. Thus, the thermal inhibition of CO_2 uptake cannot be attributed to stomatal closure, and is most likely due to changes occurring in the mesophyll or metabolic steps.

Since there is some evidence that the light reactions and electron transport may be particularly thermally sensitive components of photosynthetic apparatus (5, 23), the effects of high temperature on the light dependence of CO_2 uptake were inves-

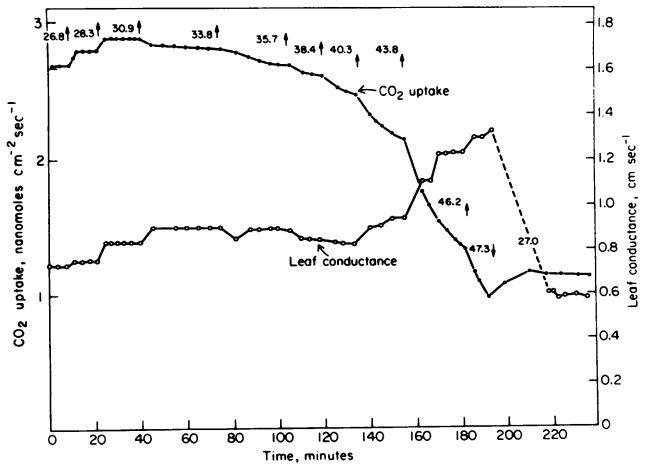

FIG. 1. Changes in photosynthetic CO_2 uptake and leaf conductance as a function of time at increasing temperatures for *A. lentiformis* grown at 23/18 C temperatures. Arrows indicate the time and direction of temperature change which occurred at a rate of 1 C/min. The numbers refer to the final steady-state temperature (C). Measurements were made at a saturating irradiance of 180 neinsteins cm^{-2} sec^{-1} and a CO_2 concentration of 295 μl l^{-1} at 30.9 C to 325 μl l^{-1} at 47.3 C.

[4] Abbreviation: DCPIP: 2,6-dichlorophenol-indophenol.

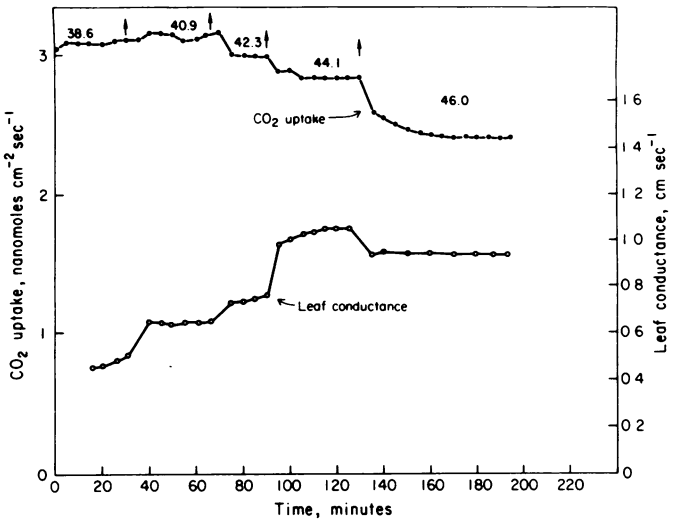

FIG. 2. Changes in photosynthetic CO_2 uptake and leaf conductance as a function of time at increasing temperatures for *A. lentiformis* grown at 43 day/30 C night temperatures. Symbols and conditions are the same as in Figure 1 except that CO_2 concentrations varied from 305 μl l^{-1} at 40.9 C to 318 μl l^{-1} at 46 C.

tigated. In order to separate the irreversible component of the thermal inhibition from other high temperature effects, all measurements were made at a noninhibitory temperature (27 C) before and after exposure of the leaf to high temperatures. For this, the light dependence of CO_2 uptake was first measured at 27 C. Temperatures were increased up to 46 to 47 C and light-saturated photosynthetic rates were allowed to decline to about 50% of the initial values. The temperature was then lowered to 27 C and the light dependence was redetermined. Figure 3 shows the initial slopes of the light dependence curves for a plant grown at 23/18 C temperatures. Exposure to high temperatures that result in an inhibition of light-saturated CO_2 uptake rates clearly also results in an irreversible inhibition of the initial slope of the light dependence curve. In contrast, similar treatments to the leaves of the 43/30 C-grown plants resulted in a small change in dark respiration but no effect of the initial slope of the light curve (Fig. 4). Thus, growth at high temperatures resulted in a substantially more thermally stable light-harvesting apparatus, paralleling the effects observed at light-saturating intensities. The slopes of the photosynthesis *versus* incident light intensity curves are a function of the quantum efficiency of photosynthesis and the efficiency of light absorption by the leaf. Since no visual changes in apparent Chl contents occurred during the course of the experiments, it seems likely that the reduction in slope represents a reduction in quantum efficiency.

Experiments were conducted to determine the site of the damage to the photosynthetic apparatus of *A. lentiformis*. A number of studies have examined the effect of heating isolated chloroplasts on their subsequent capacity for PSI, PSII, and photophosphorylation (4, 11, 17). Recent evidence indicates that the integrity of the chloroplast envelope as well as the composition of the suspending medium may significantly modify the apparent thermal stability of the isolated chloroplasts (15, 18, 22). These results suggest that studies with isolated chloroplasts may not show the same thermal stability as the intact tissue. That this is true is indicated in Table I. For a 46 C treatment, 6 min for isolated chloroplasts causes almost as much reduction as 25 min given to the intact leaf before chloroplast isolation. Furthermore, preliminary experiments showed that chloroplasts from the high temperature-grown plants were also rapidly inactivated. Because of these differences, we chose to examine the effects of heat treatment of the intact tissue. In order to provide a control on the variations in activity of chloroplasts from leaf to leaf, leaves to be treated were split in half along the mid rib. One half was heated; the other half was used as a control. Separate preparations of chloroplasts were obtained from the two halves and the relative change in the assayed activities was determined.

Assays of PSII activity showed a substantial inhibition by heat treatment. Figure 5 shows the effect of pretreatment time at 46

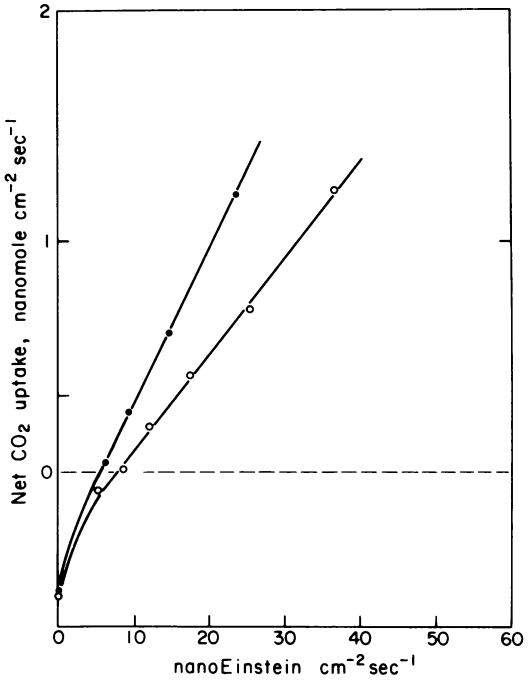

FIG. 3. Light dependence of CO_2 uptake at low intensities before (●) and after (○) heat treatment at 47 C for *A. lentiformis* grown at 23 day/18 C night temperatures. Both curves were determined at 27 C.

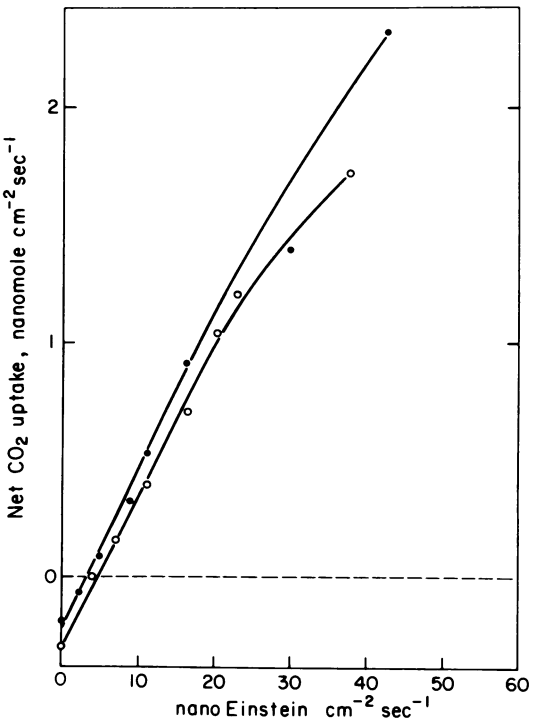

FIG. 4. Light dependence of CO_2 uptake at low intensities before (●) and after (○) heat treatment at 47 C for *A. lentiformis* grown at 23 day/18 C night temperatures. Both curves were determined at 27 C.

Table I

Effect of DPC as an Electron Donor to Photosystem II in Chloroplasts Isolated from Heat Treated Leaves and in Heat Treated Isolated Chloroplasts

The assay procedures were as described in the methods except that the assay buffer consisted of 50 mM Na-phosphate, pH 6.7, and 10 mM KCl. All heat treatments were at 46 C.

Electron Donor	Treatment Time	DCPIP reduction	Control
	min	μmol mg Chl^{-1}hr^{-1}	%
Control			
H_2O	0	299	-
Leaves			
H_2O	25	65	22
DPC	25	202	68
Chloroplasts			
H_2O	6	84	28
DPC	6	234	78

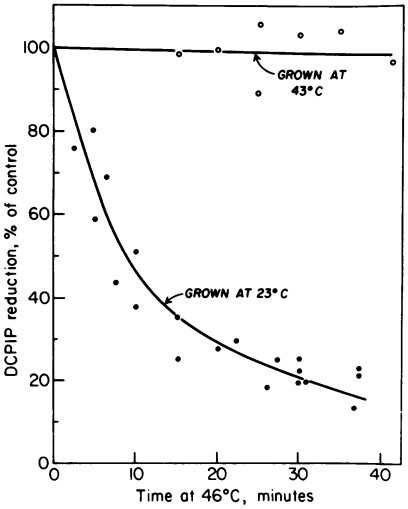

FIG. 5. Rates of DCPIP reduction by isolated chloroplasts as a function of time of heat treatment of leaves at 46 C. Rates for the chloroplasts isolated from a heated leaf half are expressed relative to those for the chloroplasts from the unheated leaf half. Mean rate of DCPIP reduction for the controls was 690 μmol mg Chl^{-1} hr^{-1} for the 23/18 C-grown plants and 584 μmol mg Chl^{-1} hr^{-1} for the 43/30 C-grown plants.

C on the light-saturated rate of uncoupled PSII activity of chloroplasts isolated from heated leaves. Activities were strongly inhibited in chloroplasts from leaves grown at 23 C day/18 C night temperatures but no inhibition was apparent in the chloroplasts isolated from the leaves of the 43 C day/30 C night-grown plants. Thus, higher growth temperatures resulted in a marked increase in the apparent thermal stability of PSII.

Figure 6 shows the effect of a heat treatment of leaves at 46 C on the light dependence of PSII. Damage caused by high temperatures clearly results in a reduction in both the light-limited and the light-saturated portions of the curve. These results are similar to the observed effects of high temperature on the light dependence of CO_2 exchange in intact leaves, and suggest that at least one of the sites damaged by high temperature *in vivo* is within PSII.

The substantial stimulation of PSII activities by diphenylcarbazide in chloroplasts heat-treated *in vitro* has been taken as evidence that the site of thermal inhibition lies in the electron transport chain from water to PSII (26). Table I shows that the addition of diphenylcarbazine results in a similar recovery of photosystem II activities in chloroplasts isolated from heat-treated leaf halves and in chloroplasts heat-treated *in vitro*, but full recovery of activities was not achieved in either case. The mechanism of thermal damage appears to be similar in both cases, however.

Assay of PSI activity of heat-treated and control leaf halves indicated no damage to this capacity by a heat treatment which resulted in substantial damage to the capacity for complete photosynthesis (data not shown). This is consistent with other work which has shown that PSI activity of isolated chloroplasts is heat-stable (4, 14).

We have examined two approaches to assaying the integrity of PSII in the intact tissue as a possible supplement or alternative to studying PSII activity of chloroplasts isolated by the split leaf technique. Light-induced absorption changes that are maximum in chloroplasts or leaves around 515 nm provide a sensitive indicator of the functional state of PSII. The changes are produced by shifts in absorption spectra of Chl as well as carotenoids and have been attributed to the establishment of an electrical field across the thylakoid membrane (25). The slower phase occurring after 1 to 3 sec can be largely abolished with DCMU and is much reduced in far red actinic light (12), indicating an origin in the functioning of PSII.

Figure 7 shows the time course of the magnitude of the 515 absorbance change at 47 C for high and low temperature-grown plants. The maximum absorbance change occurred at 25 C regardless of the growth conditions, and all values were expressed relative to this. For the low temperature-grown plants, an increase in temperature from 25 to 47 C resulted in an initial large reduction of about 50% in the magnitude of the 515 nm change followed by a slower but continued decline until after 17 min the absorbance change was only 10% of the initial value. No recovery was apparent over periods of up to 1.5 hr after returning the leaf to 25 C. In contrast, the magnitude of the 515 nm change initially decreased by only about 20% with the increase in temperature and then remained essentially constant for up to 17 min in the high temperature-grown plants. Clearly, the 515 nm absorbance change is much less inhibited by high temperatures in leaves from high temperature-grown plants indicating a higher *in vivo* thermal stability of PSII in high as compared to low temperature-grown plants.

The variable yield of Chl fluorescence from intact leaves provides an additional approach which may indicate the functional state of PSII *in vivo*. The fluorescence yield reflects the oxidation and reduction of the primary electron acceptor, "Q," in PSII and thus provides an indicator of electron transport (10). The rise in fluorescence upon illumination is characterized by a rapid increase to an initial level (F_0), followed by a slower increase as Q is reduced. In the presence of DCMU, which blocks oxidation of Q by electron transport intermediates, fluorescence rises over a few tenths of a sec to a maximum level. Previous studies have shown that heat treatment of chloroplasts or leaves results in an irreversible increase in the ratio of the

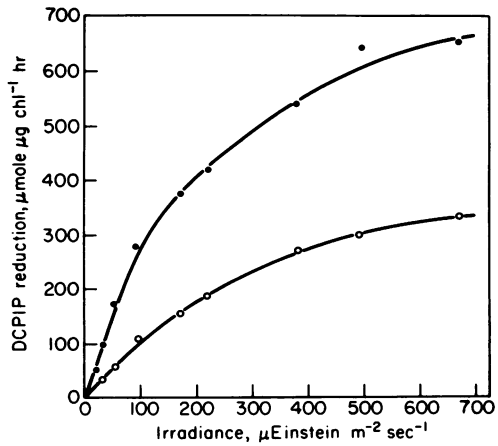

FIG. 6. Light dependence of DCPIP reduction by chloroplasts isolated from heat-treated (○) and unheated (●) leaf halves from *A. lentiformis* plants grown at 23/18 C temperatures.

initial to maximum fluorescence, which correlates with inhibition of PSII electron transport (4, 13).

The effect of increasing temperature at 1 C/min on the ratio of F_0/F_{max} for both high and low temperature-grown plants is shown in Figure 8. In the low temperature-grown plants, the ratio remained stable from 20 to 37 C and then rose sharply as temperatures were increased above 40 C. In contrast, no increase in the ratio was apparent until temperatures above 45 C were reached with the high temperature-grown plants. In both cases, the change in the ratio resulted predominantly from an increase in F_0 while F_{max} changed only slightly. If these measurements accurately reflect the thermal stability of PSII *in vivo*, then growth at high temperatures results in a shift in the critical temperature for thermal inhibition to some 5 to 8 C higher temperatures, which is in good agreement with the responses of CO_2 uptake by intact leaves.

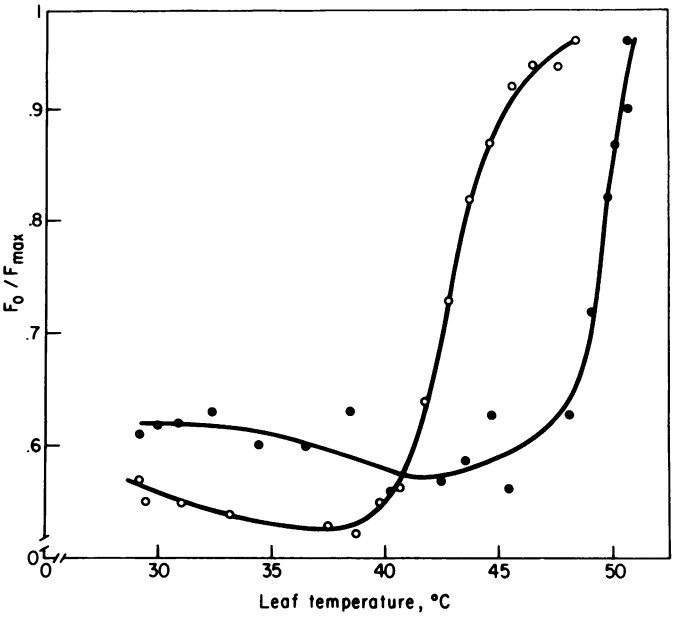

FIG. 8. Effect of increasing temperatures on the rate of initial to maximum fluorescence (F_0/F_{max}) in leaves of *A. lentiformis* grown at 45/30 C (●) or 20/15 C (○) temperatures. Temperatures were increased at a constant rate of 1 C/min.

DISCUSSION

A. lentiformis can undergo substantial acclimations in photosynthetic response to temperature that result in an improvement in the CO_2 uptake rates at the growth temperatures. When acclimated to high growth temperatures, the improved photosynthetic rates result at least in part from an increased thermal stability of the photosynthetic apparatus. The results reported here show that this increased thermal stability of light-saturated CO_2 uptake is correlated with an increased thermal stability of the quantum efficiency of CO_2 uptake and the light-harvesting reactions of the photosynthetic apparatus as indicated by both *in vitro* and *in vivo* measures of the thermal stability of PSII.

Considerable evidence is accumulating that photosynthesis and in particular the light-harvesting reactions of photosynthesis are one of, if not, the most thermally labile steps in cellular metabolism in most plants. Direct comparisons have shown that photosynthesis is inhibited at temperatures several degrees below that required for inhibition of other processes such as respiration (5), protoplasmic streaming (1), and resistance to loss of ions across the tonoplast membrane (4). Direct comparative measurements have shown that the soluble enzymes involved with CO_2 fixation have a much greater thermal stability than do the membrane-dependent light-harvesting reactions, PSII and cyclic photophosphorylation (15). Variations in the apparent thermal stability of photosynthesis have been shown in comparisons between a number of different plant species. A good correlation was shown between the thermal stability of photosynthetic CO_2 uptake and measures of PSII thermal stability in species native to cool coastal and hot desert habitats (6). In *A. lentiformis*, similar differences in thermal stability clearly can be induced by growth temperature.

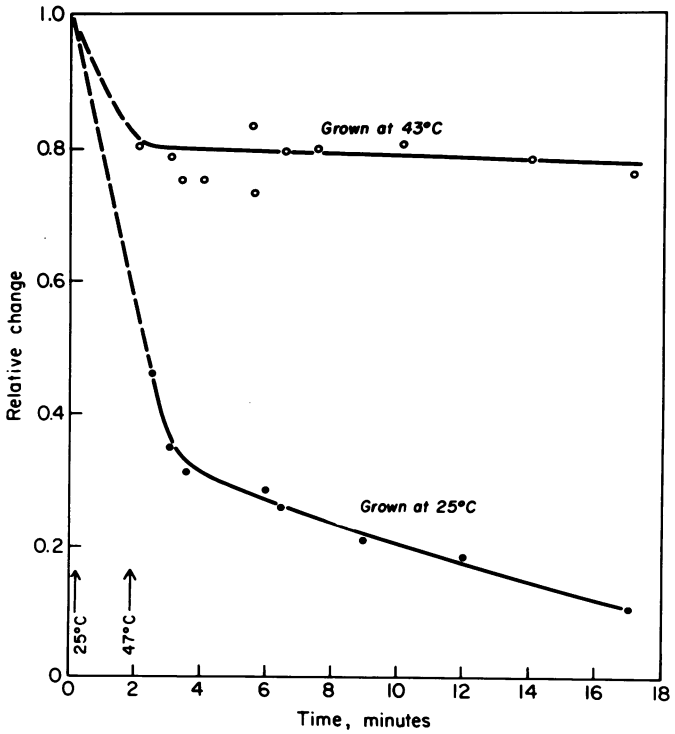

FIG. 7. Time dependence of the magnitude of the slow phase of the 515 nm absorbance change in leaves from *A. lentiformis* plants grown at day temperatures of 25 or 43 C. Each point is the relative absorbance change measured after 3 sec exposure to the actinic light. Absorbance changes are expressed relative to the maximum that occurred at 25 C in all plants.

The similar nature and temperature sensitivity of the inhibition of PSII *in vivo* would be sufficient to account for the observed effects of heat damage on the intact leaf. Clearly, however, other photosynthetic activities might also be involved. Studies with isolated chloroplasts have shown that cyclic photophosphorylation is also rapidly inactivated by heat (22). With *A. lentiformis*, we observed (data not shown) that electron transport became increasingly uncoupled, as measured by methylamine stimulation of DCPIP reduction, with increasing time of heat treatment of the leaves. Methylamine stimulation of DCPIP reduction was lost at about the same rate as the loss of uncoupled PSII rates. Clearly, similar increases in heat stability of phosphorylation and PSII electron transport must result from increases in growth temperature, suggesting the possibility that common mechanisms are involved in the heat inactivation and the changes in heat stability of both processes. The localization of PSII in the thylakoid membranes as well as the similarity of action of heat treatment and lipid-specific reagents (17) suggest that properties of the thylakoid membrane system and in particular the membrane lipids may be important in determining the heat stability of these processes.

The large increases in thermal stability of PSII and photosynthetic CO_2 uptake in *Atriplex lentiformis* seem to be of considerable adaptive significance. This species is evergreen and active during both the cool winter and hot summer months in the

desert. The shift to an increased thermal stability of the photosynthetic apparatus with increased growth temperatures results in a substantial improvement in CO_2 uptake at the growth temperature that could permit maintenance of high year-around productivities.

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