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Thermal Acclimation of Photosynthetic Electron Transport Activity by Thylakoids of *Saxifraga cernua*[1]

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ABSTRACT

Thermal acclimation by *Saxifraga cernua* to low temperatures results in a change in the optimum temperature for gross photosynthetic activity and may directly involve the photosynthetic apparatus. In order to test this hypothesis photosynthetic electron transport activity of *S. cernua* thylakoids acclimated to growth temperatures of 20°C and 10°C was measured *in vitro*. Both populations exhibited optimum temperatures for whole chain and PSII electron transport activity at temperatures close to those at which the plants were grown. Chlorophyll *a* fluorescence transients from 10°C-acclimated leaves showed higher rates in the rise and subsequent quenching of variable fluorescence at low measuring temperatures; 20°C-acclimated leaves showed higher rates of fluorescence rise at higher measuring temperatures. At these higher temperatures, fluorescence quenching rates were similar in both populations. The kinetics of State 1-State 2 transitions in 20°C- and 10°C-acclimated leaf discs were measured as changes in the magnitude of the fluorescence emission maxima measured at 77K. Leaves acclimated at 10°C showed a larger F730/F695 ratio at low temperatures, while at higher temperatures, 20°C-acclimated leaves showed a higher F730/F695 ratio after the establishment of State 2. High incubation temperatures also resulted in a decrease in the F695/F685 ratio for 10°C-acclimated leaves, suggesting a reduction in the excitation transfer from the light-harvesting complex of photosystem II to photosystem II reaction centers. The relative amounts of chlorophyll-protein complexes and thylakoid polypeptides separated electrophoretically were similar for both 20°C- and 10°C-acclimated leaves. Thus, photosynthetic acclimation to low temperatures by *S. cernua* is correlated with an increase in photosynthetic electron transport activity but does not appear to be accompanied by major structural changes or different relative amounts in thylakoid protein composition.

Thermal acclimation of photosynthetic activity, usually measured as changes in the optimum temperature for photosynthesis resulting from a change in growth temperature, has been demonstrated in a number of species from diverse environments (for reviews, see Refs. 4 and 25). From an ecological viewpoint, the potential, or capacity for thermal acclimation is considered to be an important strategy for maximizing carbon fixation and seasonal net productivity, particularly by species native to areas which are subject to considerable temperature fluctuations during the growth season (8, 13). Thermal acclimation would appear to be important for some plants indigenous to arctic and alpine regions (5). Plants growing in these areas complete their life cycle over a relatively short growing season during which temperatures become progressively cooler shortly after germination and can fluctuate widely at any time during the season (9, 21). Most reports documenting physiological mechanisms involved in thermal acclimation have examined species subjected to moderate-to-high seasonal temperatures (4). Studies on low-temperature acclimation (10°C or less) are few and have been, for the most part, confined to species which display low-temperature or freezing tolerance and may not necessarily possess the potential for photosynthetic acclimation (25). Additional studies on low temperature acclimation could be valuable to determine whether the physiological mechanisms underlying high-temperature acclimation differ from those involved in low-temperature acclimation (4).

In a previous report, we have demonstrated the potential for photosynthetic and respiratory thermal acclimation to low temperatures by the arctic plant, *Saxifraga cernua* (21). Changes in the optimum temperature for gross photosynthesis were evident for plants grown at one temperature and shifted to either a lower or higher temperature. These results suggested that the physiological mechanism underlying the change in the optimum temperature for CO_2 fixation may involve the photosynthetic apparatus, and not merely depend on changes in respiratory activity, as suggested for some species (9).

In the present study, we have characterized changes in the temperature-dependency of photosynthetic electron transport activity of *S. cernua* acclimated at 10 or 20°C. Acclimation of the photosynthetic apparatus was probed by monitoring *in vitro*, uncoupled whole-chain and partial reactions of electron transport from isolated thylakoid membranes, changes in the Chl *a* fluorescence transients (the Kautsky effect) from intact leaf tissue, and changes in the temperature-dependency of the State 1-State 2 transition which are reported to be closely associated with PSII and PSI activity (11). Changes in the relative amounts of the Chl-protein complexes and thylakoid polypeptides from plants acclimated to the two temperatures were also measured using electrophoretic techniques.

MATERIALS AND METHODS

Plant Material

Growth conditions for the germination of *Saxifraga cernua* from asexual bulblets at 10 or 20°C under continuous (24-h)

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illumination have been previously described (22). Plants were grown for a minimum of 6 weeks.

Preparation of Isolated Thylakoid Membranes

Thylakoid membranes were prepared from 5 g fresh weight of leaf tissue homogenized in a Sorval Omni-Mixer for 7 s. The grinding medium contained 0.33 M sorbitol, 50 mM NaCl, 5 mM $MgCl_2$, 1 mM EDTA, 0.1% BSA, and 50 mM Hepes-KOH buffer (pH 7.5). Prior to homogenization, the grinding medium was frozen to a consistency of slush and all subsequent isolation procedures were performed at 4°C. The brei was filtered through eight layers of cheesecloth and two layers of Miracloth and the filtrate centrifuged at 1300*g* for 6 min. The supernatant was discarded and the pellet gently resuspended in an incubation medium containing 0.1 M sorbitol, 50 mM NaCl, 5 mM $MgCl_2$, and 50 mM Hepes buffer at pH 7.5. The suspension was centrifuged again at 500*g* for 5 min. The resulting pellet was then resuspended in 2 mL of incubation medium and stored on ice. *In vitro* measurements of photochemical activities were made from this stock.

Measurements of *in Vitro* Electron Chain Activity in Isolated Thylakoid Membranes

Photochemical activity was measured polarographically with a Clark-type oxygen electrode as described previously (20). The custom-made incubation cuvette was enclosed in a Plexiglas water jacket that provided temperature control. Actinic light was supplied by a 100-W incandescent bulb focused on the cuvette surface through a water-filled boiling flask. The photon fluence rate, measured with a Li-Cor quantum meter, was 135 $\mu E/m^2/s$. The electrode collar was designed to allow small (5–50 μL) additions of solutions with a 50-μL Hamilton syringe. A thylakoid suspension of 3 mL, containing 15 to 20 μg Chl, was used for all measurements. Chl concentrations were determined according to MacKinney (18).

Whole-chain electron transport activity was measured as oxygen consumption in the presence of 0.1 mM methyl viologen. Rates of uncoupled photosynthetic electron transport were obtained by the addition of 10 mM methylamine hydrochloride; endogenous catalase activity was inhibited by the addition of 1 mM NaN_3. Electron transport through PSII only was assayed as O_2 release in the presence of 0.23 mM *N,N,N′,N′*-tetramethyl-*p*-phenylenediamine, 1.5 mM $Fe(CN)_6$, and 10 μM dibromothymoquinone. The rate of electron transport through PSI was measured as oxygen consumption in the presence of 60 μM 2,6-dichlorphenolindophenol, 2 mM Na-ascorbate, 0.1 mM methyl viologen, 10 μM DCMU, and 100 μg/mL superoxide dismutase.

The above reactions were measured over a range of temperatures from 0 to 35°C following 3 min preincubation in the dark at each reaction temperature. Because of the temperature-dependent change of oxygen solubility in the incubation solution and temperature sensitivity of the membrane probe, the oxygen electrode was calibrated at each measuring temperature. The electrode was calibrated in air-saturated water held at the measuring temperature. Oxygen was then depleted from the sample using excess sodium dithionite. The signal from the electrode was recorded on a strip-chart recorder.

Measurements of Chl *a* Fluorescence Transients

The procedure for obtaining both the fast transients of fluorescence induction and the slower oscillations during fluorescence quenching to steady state levels have been previously described (22). Briefly, the fluorescence signal was measured using a microspectrophotometer equipped with epifluorescence and a temperature-controlled microscope stage. In the present study a Keithley 604 amplifier was used in the single-ended mode in order to improve the signal-to-noise ratio of the fast transients which were recorded on a storage oscilliscope. The tissue was dark-adapted for 5 min at measuring temperatures greater than 15°C and for 15 min at measuring temperatures below 15°C, prior to excitation with blue light. Rates of the fluorescence rise were measured between D and P.

Measurements of State 1-Stage 2 Transitions by Low Temperature Fluorescence Emission Spectra

The procedure for the incubation of leaf discs to establish State 1 and a transition to State 2, and the preparation of 'diluted powders' from mesophyll tissue for the 77°K fluorescence emission spectra measurements using a fluorescence spectrofluorometer have been previously described (19). For the present study, leaf discs were first adapted to State 1 by illumination with light 1 (wavelength > 700 nm) or maintained in the dark at room temperature for 60 min followed by a further 10 min at the incubation temperature. The tissue was sampled prior to illumination with red light (light 2) which was used to induce a State 2 transition. Incubation temperatures during State 1-State 2 transitions were held constant by circulating water from a water-bath through a Tamson heater and immersion cooler.

Electrophoresis of Thylakoid Chl-Protein Complexes and Polypeptides

Separation of the Chl-protein complexes and thylakoid polypeptides from chloroplasts isolated from 10 and 20°C grown *S. cernua* leaves was carried out according to the procedures reported by Huner *et al.* (16). Chl-protein complexes were extracted with lithium dodecyl sulfate (LDS) at a Chl concentration of 4:1 at 0°C and electrophoresed at a constant current of 4 mA at 4°C for 45 min. The separated complexes were scanned with a densitometer at 440 nm. Thylakoid membrane polypeptides were separated by PAGE on a slab gel at a constant current of 18 mA for 3 h at 4°C and stained with Coomassie brilliant blue R-250. The Chl-protein complexes and several of the polypeptides were identified by Dr. N. P. A. Huner (Univ. of Western Ontario, Ont., Can.).

RESULTS

In Vitro Measurements of Electron Transport by Thermally Acclimated Thylakoids

Uncoupled, whole-chain electron transport activity and rates of electron flow through PSI and PSII for the 10 and 20°C grown plant are shown in Figure 1 (A–C). Thylakoids isolated from leaves acclimated at 10°C showed higher trans-

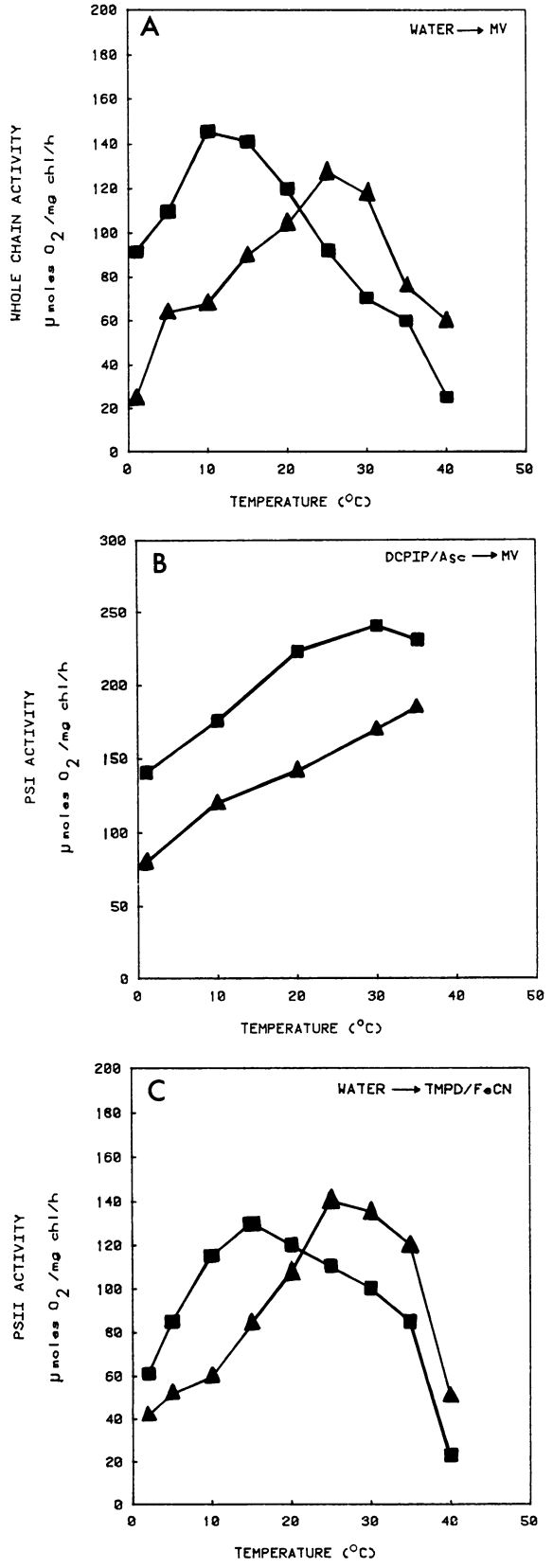

Figure 1. Temperature-dependency of uncoupled (A) whole-chain, (B) PSI, and (C) PSII electron transport for thylakoids isolated from 20°C-acclimated (▲) and 10°C-acclimated (■) leaves. The results are from (A) 5, (B) 12, and (C) 5 separate experiments, respectively.

port rates for whole-chain electron transport below 20°C than did thylakoids isolated from 20°C leaves. The optimum temperatures for maximum whole chain transport for 10°C- and 20°C-grown plants were 10 and 25°C, respectively (Fig. 1A). At low measuring temperatures, *i.e.* 1°C, whole-chain electron transport rates by thylakoids grown at 10°C were 4.2 times higher than rates measured from 20°C-grown plants. At higher temperatures, *i.e.* 40°C, whole-chain transport rates decreased to 16 and 42% of their optima for thylakoids isolated from 10°C- and 20°C-acclimated plants, respectively. Hence, the temperature to which the plants were acclimated significantly altered the temperature response for whole-chain electron transport activity.

Figure 1B shows the temperature-dependency of uncoupled electron transport through PSI for thylakoids isolated from plants grown at 10 and 20°C. Both populations of acclimated chloroplasts showed a near-linear increase in electron transport up to 30°C. Growth at 10°C resulted in an increase in rates of PSI activity of about 40%, independent of the measuring temperature.

Figure 1C shows the temperature-dependent profile for electron transport activity by PSII which was qualitatively similar to that measured for whole chain electron transport (Fig. 1A). Temperature optima for PSII activity by 10°C- and 20°C-grown plants were 15 and 25°C, respectively. Electron transfer rates through PSII were faster at low temperatures by 10°C-acclimated thylakoids in a manner similar to that observed for whole-chain electron transport.

Thermal Acclimation of Electron Transport Activity Monitored by Chl *a* Fluorescence Induction and Quenching

Typical examples of the Chl *a* fluorescence induction curves from *S. cernua* leaf discs acclimated at 20 and 10°C and measured at several temperatures are shown in Figure 2. At a measuring temperature of 21.3°C, both populations showed typical fluorescence kinetics, as indicated by the clear O-I-D-P transients (for discussion of the transient nomenclature see Ref. 17) and the development of Fv[3] above the 0 level (Fig. 2, A and C). Upon lowering the temperature to 5.0°C, leaf discs acclimated to 20°C failed to show any transients and the development of Fv above the 0 level was significantly reduced (Fig. 2B). In contrast to 20°C-acclimated leaf discs, the induction kinetics from 10°C-acclimated leaves measured at 4.3°C showed minimal reduction in the amount of Fv above the 0 level, and the phases in the transients were still present although less resolved (Fig. 2D). The rate of the fluorescence rise to P, which reflects the reduction of Q (the primary electron acceptor for PSII; 26) by PSII is shown in Figure 3 for 20°C- and 10°C-acclimated leaf discs measured over a range of temperatures. Leaf discs acclimated at 10°C showed higher rates of Q reduction at the lower measuring temperatures, while at higher temperatures, *e.g.* >20°C, the 20°C-acclimated leaves showed higher rates for the development of Fv.

The slower fluorescence transients associated with the Kautsky curves from 10°C- and 20°C-acclimated leaf discs also

[3] Abbreviations: Fv, variable fluorescence; LHCII, light-harvesting chlorophyll a/b protein complex associated with photosystem II.

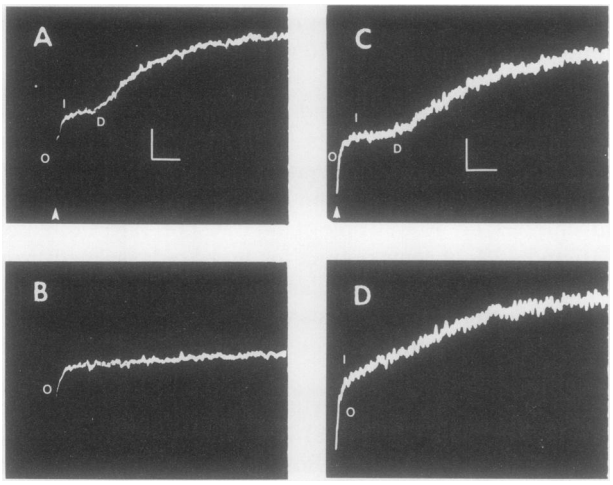

Figure 2. Fast changes in Chl *a* fluorescence induction curves for 20°C-acclimated leaves measured at 21.3°C (A) and 5.0°C (B) and 10°C-acclimated leaves measured at 21.3°C (C) and 4.3°C (D). Horizontal bar = 50 ms; vertical bar = 100 mV. Each panel represents a single trace.

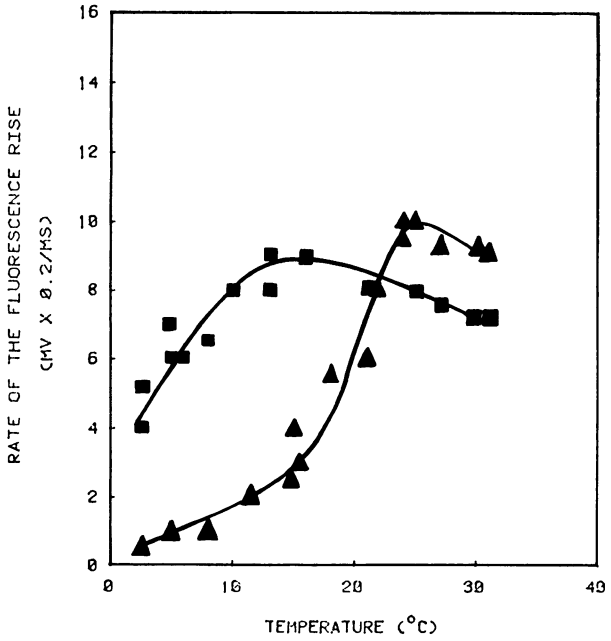

Figure 3. Rate of increase in fluorescence *versus* the measuring temperature for 20°C-acclimated (▲) and 10°C-acclimated (■) leaves. Rates were measured as the increase in variable fluorescence during the first 50 ms of illumination. The results represent 6 separate experiments.

showed differences in the maximum rates of quenching from P to T as a function of temperature (Fig. 4). At 5°C, quenching rates were reduced by 78% compared to rates measured at 21.3°C for 20°C-acclimated leaves, while quenching rates by 10°C-acclimated leaves were reduced about 40%. At measuring temperatures greater than 20°C, quenching rates were similar for both populations.

State 1-State 2 Transitions by Thermally Acclimated Leaves

The kinetics and magnitude of State 1-State 2 transitions, monitored by changes in the F730/F695 ratios obtained from

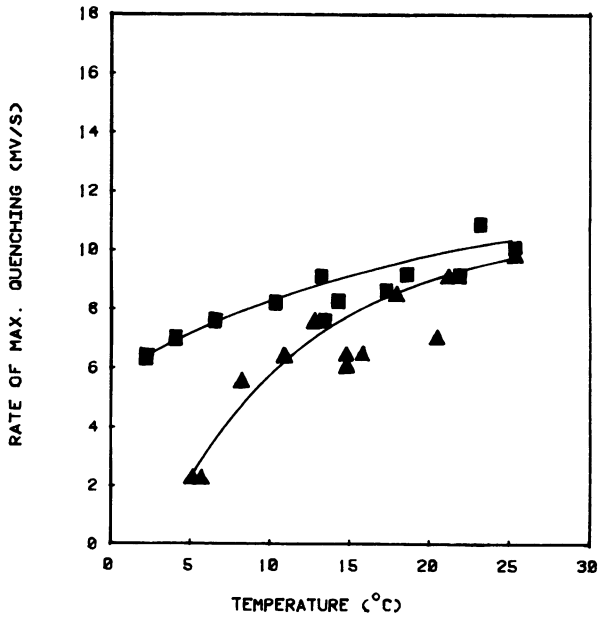

Figure 4. Changes in the maximum rate of fluorescence quenching (-dF/dt, mV/s) from peak P as a function of the measuring temperature for 20°C-acclimated (▲) and 10°C-acclimated (■) leaves. The results represent 6 separate experiments. The lines were plotted using an *n*th-order regression program and are computer-plotted. $r^2 > 0.9$ for each plot.

77K fluorescence emission spectra (19), were measured from 'diluted powders' prepared from leaf discs acclimated to 20 and 10°C at several temperatures (Fig. 5, A–D). Spectra obtained from 10°C- and 20°C-acclimated leaf discs adapted to State 1 showed similar relative peak heights for F730, F695, and F685 emissions (originating from PSI, PSII, and LHCII, respectively; [7]) suggesting that acclimation to either temperature did not alter the relative amounts of these Chl-protein complexes. At both 5 and 10°C, 10°C-acclimated leaf discs showed a greater establishment of State 2 compared to 20°C-acclimated discs (Fig. 5, A and B). At measuring temperatures of 20°C (Fig. 5C), the 20°C-acclimated discs showed a greater establishment of State 2 as indicated by a larger F730/F695 ratio compared to that measured for the 10°C-acclimated discs. In fact, after 15 min at 20°C, the 10°C-acclimated discs showed a decrease in the F730/F695 ratio (Fig. 5C); the decrease in the F730/F695 ratio was much more pronounced at 25°C for 10°C-acclimated discs and reached a steady state level within 10 min of incubation at the higher temperature (Fig. 5D). At 25°C, 20°C-acclimated leaf discs also showed a moderately lower final F730/F695 value although the ratio was still higher than that measured for the 10°C-acclimated leaves (Fig. 5D). Of particular interest was a 14% decrease in the F695/F685 ratio (the emission maxima for PSII and LHCII, respectively) by the 10°C-acclimated leaf discs when measured at 25°C (Fig. 6) which was not observed in the 20°C-acclimated discs (see also Fig. 2C; Ref 19). These results suggest that the magnitude of the State 1-State 2 transition in 10°C-acclimated leaves measured at supraoptimal temperatures is lower than that seen at temperatures closer to which the plant has been acclimated.

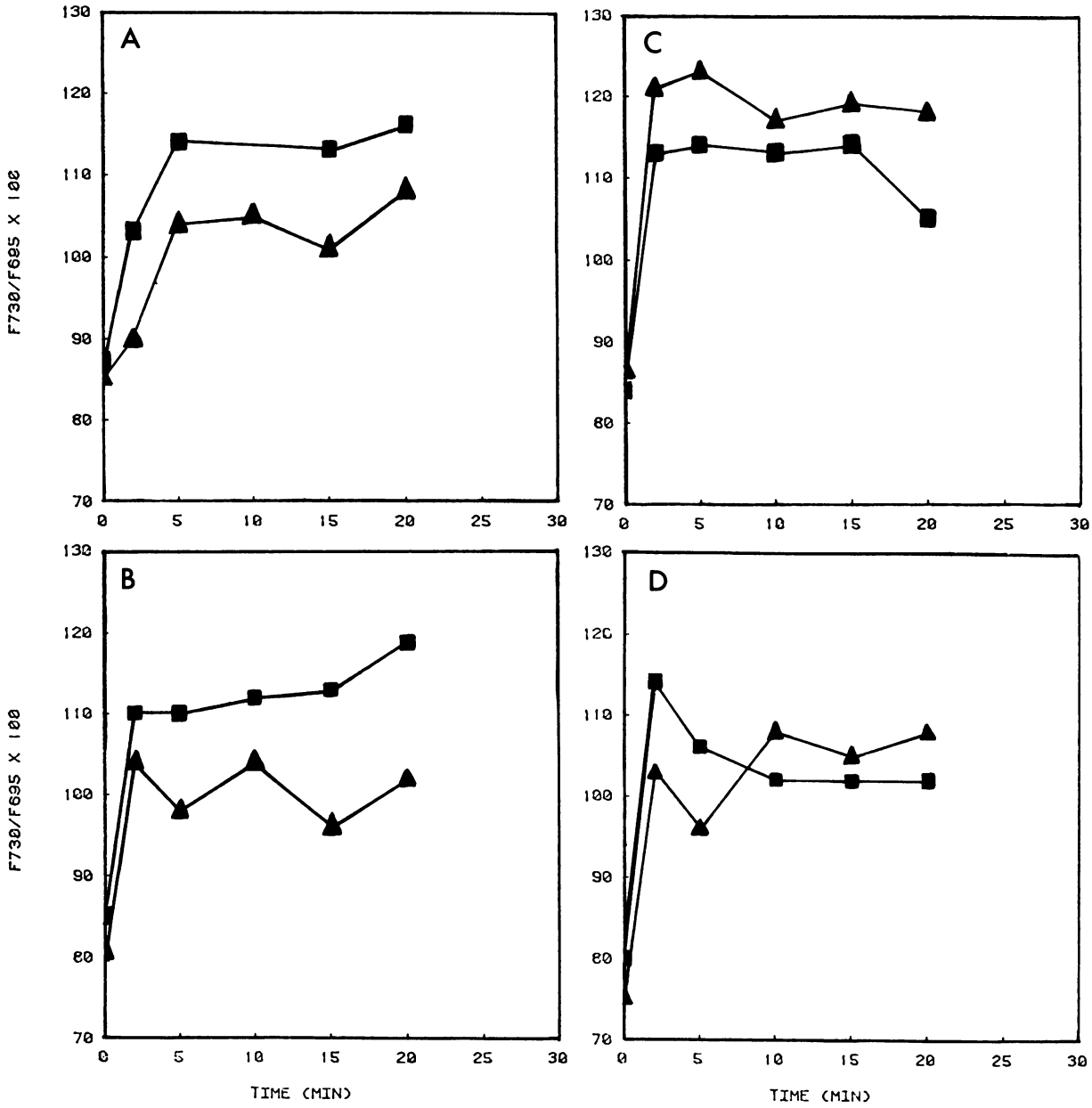

Figure 5. Time courses for changes in the F730/F695 ratios measured from the fluorescence emission spectra obtained at 77 K for 20°C-acclimated (▲) and 10°C-acclimated (■) leaf discs incubated at 5°C (A), 10°C (B), 20°C (C), and 25°C (D). The results are from 15 separate experiments.

Analysis of Thylakoid Polypeptides from Acclimated Leaves

Densitometer traces of Chl-protein complexes separated by gel electrophoresis at 4°C and one-dimensional separation of the thylakoid polypeptides from 10°C- and 20°C-acclimated leaves are shown in Figures 7 and 8, respectively. Electrophoretic separation of the Chl-protein complexes resolved two bands associated with CP1a (P700 Chl *a*-protein; bands 1 and 2 in Fig. 7), two bands representing the oligomeric and monomeric form of the light-harvesting Chl *a*/*b* protein complex (bands 3 and 5 in Fig. 7, respectively), and CPIV (band 4), which is thought to be associated with PSII (14). There were no major differences between the two populations with respect to the relative amounts of Chl-protein complexes. Similarly, separated thylakoid polypeptides resolved by SDS-PAGE from 10°C- and 20°C-acclimated leaves were also identical (Fig. 8).

DISCUSSION

Changes in the optimum temperature for gross photosynthesis in *S. cernua* due to a change in the growth temperature suggest that thermal acclimation results primarily from growth temperature-dependent changes of the photosynthetic apparatus (21). In the present study, we have examined changes in photosynthetic electron transport activity as a

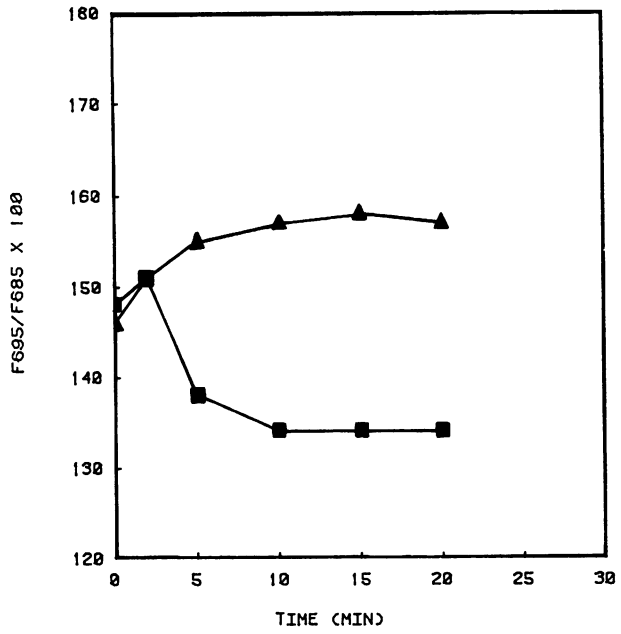

Figure 6. The time course for changes in the F695/F685 ratios of 77K fluorescence maxima following illumination with red light (light 2) for leaves acclimated to 20°C (▲) and 10°C (■).

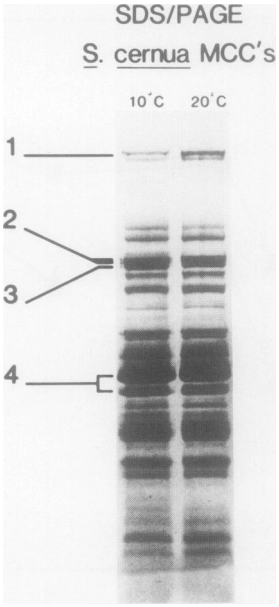

Figure 8. One-dimensional SDS-PAGE separation of thylakoid polypeptides from leaves acclimated to 20°C and 10°C. Several of the polypeptides were identified as (1) CP1 (P700 Chl *a*-protein), (2) the α- and β-subunits of CF_1, (3) the large subunit of ribulose bisphosphate carboxylase, and (4) the 28 and 26 kD apoproteins of LHCII.

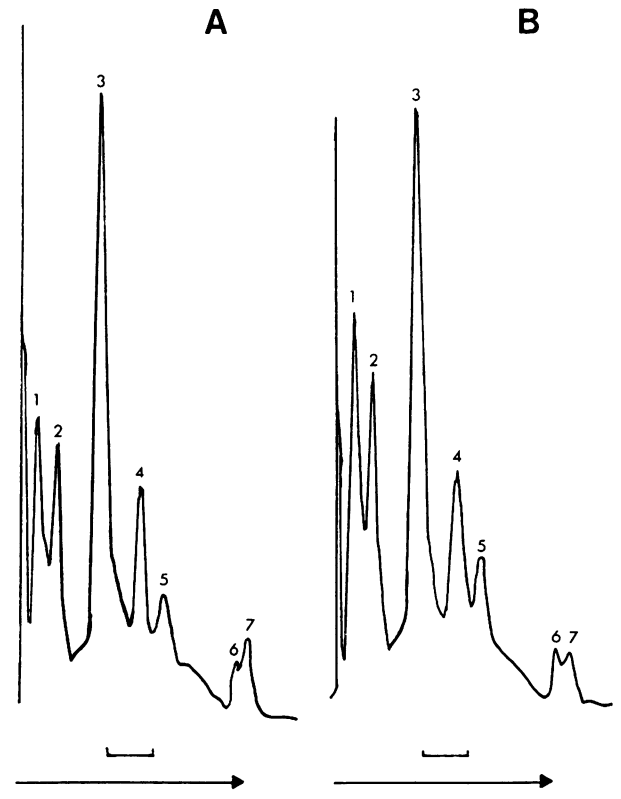

Figure 7. Densitometer tracings from gels of Chl-protein complexes from thylakoids isolated from leaves acclimated to 20°C (A) and 10°C (B). Numbers identifying each peak are given in the text. Bar = 1 cm.

function of the temperature to which the plants have been acclimated. Earlier studies on low-temperature acclimation by both arctic and alpine species have shown equivocal results regarding the role of electron transport in the observed changes on the temperature-dependent photosynthetic activity (6, 29). In contrast, changes in electron transport activity have been correlated with shifts in the photosynthetic optima for species capable of thermal acclimation to high growth temperatures (2, 27). These observations have led to the suggestion that changes in electron transport may not be essential for acclimation to low temperatures (4).

Results from this study clearly show that low temperature acclimation is correlated with a shift in the optimum for photosynthetic electron transport activity to a lower temperature. Furthermore, the data suggest a correlation between the optima for gross photosynthesis (21) and uncoupled whole-chain activity in plants acclimated to 10 and 20°C (Fig. 1A). This supports our previous conclusion regarding a role of the photosynthetic apparatus in low-temperature acclimation (21). Contrasting the temperature-dependency of electron transport activity between whole-chain measurements (Fig. 1A) to the partial-reactions of PSI (Fig. 1B) and PSII (Fig. 1C) transport rates, it would appear that PSII activity is regulating the whole-chain activity as evident by the similar measuring temperatures for optimum rates for 10°C- and 20°C-acclimated thylakoids. In contrast, PSI activity measured in both populations fails to show any optima below 30°C (Fig. 1B). PSI activity in rye plants, measured *in vitro*, also show an increase after a period of cold-hardening compared to non-hardened leaves (15). The increase in PSI activity in 10°C-acclimated thylakoids is intriguing, however, since in some species such as *Larrea divaricata*, a desert shrub native to southwestern United States (2), low growth temperatures resulted in a decrease in PSI activity when measured at low

temperatures. This difference between species indigenous to regions of contrasting thermal regimes may underlie an important physiological feature of acclimation.

In vivo Chl *a* fluorescence reflects changes in the amount of excitation associated primarily with PSII during photosynthetic induction following a dark incubation period (17). The observed reduction in the rate of Fv development and total amount of Fv in 20°C-acclimated plants measured at low temperatures (Fig. 3) suggests that light absorption by PSII and subsequent electron transport are less efficient at low temperatures. This would result in lower transport rates under steady state conditions, similar to that observed for the *in vitro* activity. Thus, acclimation to 10°C reduces the inhibitory effect of low temperatures on PSII activity.

Although fluorescence induction is due primarily to photochemical events associated with PSII, the rate of fluorescence quenching shown in Figure 4 is considered to be due to both reoxidation of plastoquinone by PSI (q_Q or photochemical quenching) and the establishment of the *trans*-thylakoid pH gradient (q_e or nonphotochemical quenching). Therefore, the differences in fluorescence quenching rates measured from leaves grown at 10 and 20°C during a decrease in measuring temperature are more difficult to interpret (for review, see Ref. 28). Although our procedure does not distinguish between the contribution of q_Q and q_e to the quenching rate, the greater PSII and PSI activity demonstrated *in vitro* for 10°C-acclimated thylakoids indicate that both sources of quenching are likely to be more efficient in 10°C acclimated leaves when measured at the lower temperature.

Low-temperature acclimation of photosynthetic electron transport activity in *S. cernua* is further demonstrated by the observed temperature-dependency of State 1-State 2 transitions. It has been proposed that State transitions involve reversible phosphorylation of the LHCII associated with PSII (3). Phosphorylation of LHCII appears to be regulated by the redox state of plastoquinone, which in turn has been shown to be dependent on the ratio of PSI and PSII activities (1). The development of State 2 during a State 1-State 2 transition has been reported to be very sensitive to low temperature (10, 30). Growth at low temperatures has been shown to diminish the inhibition of State transitions observed at low temperatures in *Anacystis nidulans* (24). The results reported here demonstrate a similar phenomenon in a higher plant. Leaves of *S. cernua* acclimated to 10°C show a greater establishment of State 2 when measured at low temperatures (Fig. 5, A and B), an observation consistent with both an increase in *in vitro* PSII activity and a more rapid development of Fv. The reduced magnitude of State 2 as indicated by a lower F730/F695 ratio in leaves acclimated at 20°C observed at low temperatures (Fig. 5, A and B) suggests that the capacity to balance the excitation of PSII and PSI, and thereby optimize electron transport rates, becomes limited at temperatures below which the plant has been acclimated. A similar response by chill-sensitive rice plants exposed to low temperatures has also been reported using a similar experimental approach (23). Hence, an increase in electron transport activity resulting from low-temperature acclimation of PSII may facilitate regulation of energy distribution between the two photosystems and thus represents an important component of the temperature response of gross photosynthesis. This hypothesis is further supported by the *decrease* in the magnitude of State 2 as a function of time by 10°C-acclimated leaves at supraoptimal temperatures (Fig. 5D).

The measurement of State transitions by monitoring changes in the fluorescence emission spectra also provides insight into changes of the energy balance between LHCII and PSII. The decrease of the F695/F685 ratio in 10°C-acclimated leaves at high temperatures during a State 1 to State 2 transition (Fig. 6) may result from the dissociation of some portion of LHCII, such as peripheral LHCII from PSII, resulting in a smaller PSII antenna size. Alternatively, there may be a significant decrease in the rates of energy transfer to PSII (12). In either case, a reduction in excitation transfer from LHCII to PSII may account for, in part, the decrease in State 2 and, as a result, a reduction in electron transport rates.

The lack of any conspicuous differences in the densitometer traces from the separated Chl-protein complexes and the thylakoid polypeptide composition between 20°C- and 10°C-acclimated leaves suggests that photosynthetic thermal acclimation does not involve major structural changes in the protein component of the thylakoid membrane. This would imply that the increase in photosynthetic electron transport activity of leaves acclimated to 10°C and measured at low temperatures results from interactive changes between thylakoid membrane components during electron transport.

Although the present data do not rule out possible changes in enzymic activity associated with the Calvin cycle (4, 25), it is apparent from this study that for *S. cernua*, changes in photosystem activity and reactions associated with energy distribution between PSI and PSII are a component of the observed shift in the optimum temperature for gross photosynthesis to lower temperatures.

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LITERATURE CITED

1. **Allen JF, Bennett J, Steinback KE, Arntzen CJ** (1981) Chloroplast protein phosphorylation couples plastoquinone redox state to distribution of excitation energy between photosystems. Nature **291:** 25–29
2. **Armond PA, Schreiber U, Bjorkman O** (1978) Photosynthetic acclimation to temperature in the desert shrub *Larrea divaricata* II Light-harvesting efficiency and electron transport. Plant Physiol **61:** 411–415
3. **Bennett J** (1984) Chloroplast protein phosphorylation and the regulation of photosynthesis. Physiol Plant **60:** 583–590
4. **Berry J, Bjorkman O** (1980) Photosynthetic response and adaptation to temperature in higher plants. Annu Rev Plant Physiol **31:** 491–543
5. **Billings WD, Mooney HA** (1968) The ecology of arctic and alpine plants. Biol Rev **43:** 481–529
6. **Billings WD, Godfrey PJ, Chabot BF, Bourgue DP** (1971) Metabolic acclimation to temperature in arctic and alpine ecotypes of *Oxyria digyna*. Arct Alp Res **3:** 277–289
7. **Butler WL** (1977) Chlorophyll fluorescence: a probe for electron transfer and energy transfer. *In* A Trebst, M Avron, eds, Photosynthesis I Photosynthetic electron transport and photophosphorylation, Springer-Verlag, New York, pp 149–167
8. **Chabot B** (1979) Metabolic and enzymatic adaptations to low temperatures. *In* LS Underwood, LL Tieszen, AB Callahan, GE Folk, eds, Comparative Mechanisms of Cold Adaptations, Academic Press, New York, pp 283–301

9. **Chapin FS III, Shaver GS** (1985) Arctic. *In* BF Chabot, HA Mooney, eds, Physiological Ecology of North American Plant Communities, Chapman and Hall, New York pp 16–40
10. **Chow WS, Telfer A, Chapman DJ, Barber J** (1981) State 1-State 2 transition in leaves and its association with ATP-induced chlorophyll fluorescence quenching. Biochim Biophys Acta **638:** 60–68
11. **Fork DC, Satoh K** (1986) The control by state transitions of the distribution of excitation energy in photosynthesis. Annu Rev Plant Physiol **37:** 335–361
12. **Griffith M, Huner NPA, Kyle DJ** (1984) Fluorescence properties indicate that photosystem II reaction centers and light-harvesting complex are modified by low temperature growth in winter rye. Plant Physiol **76:** 381–385
13. **Grime P** (1979) Competition and the struggle for existence *In* RM Anderson, BD Turner, LR Taylor, eds, Population Dynamics, Blackwell Science, London, pp 123–139
14. **Haydon DG, Hopkins WG** (1976) Membrane polypeptides and chlorophyll-protein complexes of maize mesophyll chloroplasts. Can J Bot **54:** 1684–1689
15. **Huner NPA** (1985) Acclimation of winter rye to cold-hardening temperatures results in an increased capacity for photosynthetic electron transport. Can J Bot **63:** 506–511
16. **Huner NPA, Krol M, Williams JP, Maissan E, Low PS, Roberts D, Thompson JE** (1987) Low temperature development induces a specific decrease in trans-Δ^3-hexadecenoic acid content which influences LHCII organization. Plant Physiol **84:** 12–18
17. **Krause GH, Weis E** (1984) Chlorophyll fluorescence as a tool in plant physiology II. Interpretation of fluorescence signals. Photosynth Res **5:** 139–157
18. **MacKinney G** (1949) Absorption of light by chlorophyll solutions. J Biol Chem **140:** 315–317
19. **Mawson BT, Cummins WR** (1986) The kinetics of *in vivo* state transitions in mesophyll and guard cell chloroplasts monitored by 77K fluorescence emission spectra. Plant Physiol **82:** 873–879
20. **Mawson BT, Colman B, Cummins WR** (1981) Abscisic acid and photosynthesis in isolated leaf mesophyll cells. Plant Physiol **67:** 233–236
21. **Mawson BT, Svoboda J, Cummins WR** (1986) Thermal acclimation of photosynthesis by the arctic plant *Saxifraga cernua.* Can J Bot **64:** 71–76
22. **Mawson BT, Franklin A, Filion WG, Cummins WR** (1984) Comparative studies of fluorescence from mesophyll and guard cell chloroplasts in *Saxifraga cernua*: analysis of fluorescence kinetics as a function of excitation intensity. Plant Physiol **74:** 481–486
23. **Moll BA, Steinback KE** (1986) Chilling sensitivity in *Oryza sativa*: the role of protein phosphorylation in protection against photoinhibition. Plant Physiol **80:** 420–423
24. **Murata N, Troughton JH, Fork DC** (1975) Relationships between the transition of the physical phase of membrane lipids and photosynthetic parameters in *Anacystis nidulans* and lettuce and spinach chloroplasts. Plant Physiol **56:** 508–517
25. **Oquist G** (1983) Effects of low temperature on photosynthesis. Plant Cell Environ **6:** 281–300
26. **Papageorgiou G** (1975) Chlorophyll fluorescence: an intrinsic probe of photosynthesis. *In* Govindjee, ed, Bioenergetics of Photosynthesis, Academic Press, New York, pp 320–366
27. **Pearcy RW, Berry JA, Fork DC** (1977) Effects of growth temperature on the thermal stability of the photosynthetic apparatus of *Atriplex lentiformis* (Torr) Wats. Plant Physiol **59:** 873–878
28. **Sivak MN, Walker DA** (1985) Chlorophyll *a* fluorescence: can it shed light on fundamental questions in photosynthetic carbon dioxide fixation? Plant Cell Environ **8:** 439–448
29. **Tieszen LL, JA Helgager** (1968) Genetic and physiological adaptation in Hill reaction of *Deschampsia caespitosa.* Nature **219:** 1066–1067
30. **Weis E** (1985) Light- and temperature-induced changes in the distribution of excitation energy between photosystem I and photosystem II in spinach leaves. Biochim Biophys Acta **807:** 118–126