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Effect of High Temperature on Photosynthesis in Beans[1]

I. Oxygen Evolution and Chlorophyll Fluorescence

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We studied the effect of increasing temperature on photosynthesis in two bean (*Phaseolus vulgaris* L.) varieties known to differ in their resistance to extreme high temperatures, Blue Lake (BL), commercially available in the United Kingdom, and Barbucho (BA), noncommercially bred in Chile. We paid particular attention to the energy-transducing mechanisms and structural responses inferred from fluorescence kinetics. The study was conducted in nonphotorespiratory conditions. Increases in temperature resulted in changes in the fluorescence parameters nonphotochemical quenching (qN) and photochemical quenching (qP) in both varieties, but to a different extent. In BL and BA the increase in qP and the decrease in qN were either completed at 30°C or slightly changed following increases from 30 to 35°C. No indication of photoinhibition was detected at any temperature, and the ratio of the quantum efficiencies of photosystem II (PSII) and O_2 evolution remained constant from 20 to 35°C. Measurements of 77-K fluorescence showed an increase in the photosystem I (PSI)/PSII ratio with temperature, suggesting an increase in the state transitions. In addition, measurements of fast-induction fluorescence revealed that the proportion of $PSII_\beta$ centers increased with increasing temperatures. The extent of both changes were maximum at 30 to 35°C, coinciding with the ratio of rates at temperatures differing by 10°C for oxygen evolution.

High temperature affects the photosynthetic functions of plants by its effect on the rate of chemical reactions and on structural organization. It has been previously reported that high temperatures are responsible for changes in the thylakoid membrane, altering not only its physicochemical properties, but also its functional organization (Berry and Björkman, 1980). PSII, particularly, is the most sensitive component of the photosynthetic system (Berry and Björkman, 1980; Mamedov et al., 1993). Extreme high temperatures affect the functioning of the O_2-evolving system (Yamashita and Butler, 1968), resulting in the release of functional manganese ions from the complex (Nash et al., 1985). This release may be the result of reductions by peroxides or superoxides (Thomson et al., 1989). PSII also responds to the range of temperatures below those causing inhibition or destruction of the complex, with consequences for thylakoid organization and functioning. Separation of the LHCII from the core center induces destacking of the grana (Gounaris et al., 1984) and temperature-induced migration of the reaction center ($PSII_\beta$) or LHCII (state transition) to the nonappressed region, which would have consequences for the energy redistribution between PSI and PSII.

Most of the information available on the effect of high temperature on photosynthesis, however, is either concerned with long-term responses by which plants are able to modify their photosynthetic functions, increasing both their tolerance and thermal optimum for net CO_2 assimilation, or with individual steps of the process and isolated parts of the photosynthetic machinery. However, considerable fluctuations in temperature occur in the time range of a few minutes to hours and the photosynthetic process has to be adjusted accordingly. This is particularly true for species cultivated in warm seasons in production areas characterized by Mediterranean climates (e.g. beans [*Phaseolus vulgaris* L.]). Consequently, such plants are exposed to changing light and temperatures that reach their highest levels during the few hours around midday.

There are several important questions concerning the effect of high temperature on photosynthesis: Is the response of photosynthesis to temperature controlled? If so, by what mechanism? Do the above alterations in thylakoid membrane function occur under such conditions? If so, are they correlated with altered photosynthetic carbon assimilation?

In this paper, the response of leaf photosynthesis to heat in the short-term in two bean varieties is described. In particular, the effect of high temperature on the functioning of the thylakoid membrane is assessed by means of simultaneous observation of room-temperature fluorescence and O_2 evolution, together with the determination of structural changes upon heating using fluorescence spec-

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Abbreviations: BA, variety Barbucho; BL, variety Blue Lake; F_o, F_v, and F_m, minimal, variable, and maximal fluorescence, respectively; LHCII, light-harvesting complex of PSII; qN, nonphotochemical quenching; qP, photochemical quenching; Q_{10}, ratio of rates at temperatures differing by 10°C; Φ_{CO2}, quantum yield of CO_2 evolution; Φ_{O2}, quantum yield of O_2 evolution; Φ_{PSII}, quantum yield of PSII electron transport.

troscopy. The two varieties used were known to differ in their resistance to extreme high temperature. When exposed to 40°C, BA maintains photosynthetic function longer than BL, as concluded from O_2 evolution and room-temperature fluorescence analysis (C. Pastenes and P. Horton, unpublished data).

MATERIALS AND METHODS

Bean seeds (*Phaseolus vulgaris* L.) BL and BA were sown in 400 cm^3 pots (one plant per pot) containing potting compost (Fison-Levington, Ipswich, UK) and topped with vermiculite (Silvaperl grade 4, Sinclair Horticulture, Lincoln, UK) to reduce water evaporation. The plants were grown in conditions of 300 μmol m^{-2} s^{-1} PAR light from 400-W discharge lamps (Thorne, Ruislip, UK) with a 12-h light/12-h dark photoperiod, 40% RH, and a thermal regime of 20 to 22/15 to 17°C day/night. The plants used for the experiments were 1 month old when the first trifoliate leaves were fully expanded.

O_2 Evolution

O_2 evolution rates were determined simultaneously with fluorescence analysis using a modified Clarke-type O_2 electrode unit (Hansatech, Kings Lynn, UK) as described by Walker (1990). Leaf discs (2.5 cm^2) were placed in the chamber over a capillary matting wetted with CO_2 buffer, pH 9 ($NaHCO_3$-Na_2CO_3), to maintain a high concentration of CO_2.

Chlorophyll Fluorescence

Modulated chlorophyll fluorescence measurements were carried out by means of a fluorimeter (model PAM 101, Heinz Walz, Effeltricht, Germany). The transient closure of PSII reaction centers was accomplished utilizing the saturating-pulse method (Quick and Horton, 1984), which consisted of a 1.5-s pulse of high-intensity light (4000 μmol m^{-2} s^{-1}) from a 500-W tungsten halogen light bulb (General Electric) mounted in a laboratory-built lamp with a heat-reflecting filter. Actinic light was supplied from a halogen lamp (HLX 64–674, Xenophot, Osram, Munich, Germany) mounted in a cold light source (model KL 1500, Schott-Glassware, Mainz, Germany). A multibranched fiberoptic connected the O_2 electrode unit with the emitter-detector unit (model 101 ED, Walz), the actinic light, and the saturating high-intensity light. F_o and F_m fluorescence were determined at the beginning of the measurements (dark-adapted leaves) and in steady-state fluorescence emission and O_2 evolution. The fluorescence quenching parameters qP and qN were calculated according to the method of van Kooten and Snel (1990): $qP = (F_m' - F_s)/(F_m' - F_o')$ and $qN = 1 - (F_m' - F_o')/(F_m - F_o)$.

Fast Kinetics Fluorescence

Leaf discs of 1 cm^2 were cut from attached leaves previously heated for 30 min and immersed in a solution of 50 μM DCMU at the same temperature for another 45 min in complete darkness. The leaf discs were then transferred to the leaf chamber for fluorescence determination. The fluorescence induction kinetics were determined using a fluorimeter (Walz) equipped with a data acquisition system (DA 100, Walz). The light intensity was 250 μmol m^{-2} s^{-1} from a 500-W tungsten halogen light bulb (General Electric) mounted in a laboratory-built lamp with a heat-reflecting filter. The shutter was automatically operated by the fluorimeter system. The sampling rate was set to 17 μs and the illumination to 0.3 s, slightly longer than the time necessary to reach F_m. The relative concentration of $PSII_\alpha$ and $PSII_\beta$ (Melis and Homann, 1976; Melis, 1989) were calculated using the data-acquisition software.

Low-Temperature Fluorescence

Leaf discs were inserted in the sample holder for 77-K fluorescence, and given 5 min of dark adaptation prior to immersion in liquid N_2. Measurement of 77-K fluorescence was carried out as described by Ruban and Horton (1994).

Heat Treatment

For all of the experiments, attached first trifoliated leaves were enclosed (on a wet surface) in a temperature-controlled darkened chamber in air, and the temperature was adjusted to the required level at a rate of 0.5 to 1°C/min by means of a circulating water bath. A constantan-copper thermocouple was placed below the leaf to record temperature. Once the required temperature had been reached, the leaf was kept in the chamber for at least 30 min, completing at least 1 h of darkness from the time of transfer from the growth room to the time measurements were taken. All of the experiments were carried out on leaf discs cut from the temperature-treated leaves. Fluorescence and O_2 evolution were measured for a combination of different temperatures: 20, 25, 30, and 35°C; and light intensities: 200, 800, and 1200 μmol m^{-2} s^{-1}. Variations from this protocol are described in the text when necessary.

RESULTS

O_2 Evolution and Room-Temperature Fluorescence

For all temperatures from 20 to 35°C, the gas-exchange rate and the fluorescence parameters were constant for at least 3 h (data not shown). Therefore, after being dark-adapted, the samples were heated for 1 to 3 h before leaf discs were taken for measurements. A similar response of O_2 evolution rate for both varieties was observed when the temperature was increased from 20 to 35°C at every light intensity (Fig. 1). In high light, the greatest increase in O_2 evolution was observed between 20 and 30°C, with the rate approaching saturation at 35°C. At low light intensity, O_2 evolution remained nearly constant as the temperature was increased to 35°C.

The qP increased in high light, but the magnitude of the change was different between varieties (Fig. 1). In BL, qP varied to a greater extent than in BA when the temperature was increased from 20 to 35°C in high light. In BL, qP increased slightly from 30 to 35°C, whereas BA reached the maximum at 30°C and was maintained at 35°C. As ex-

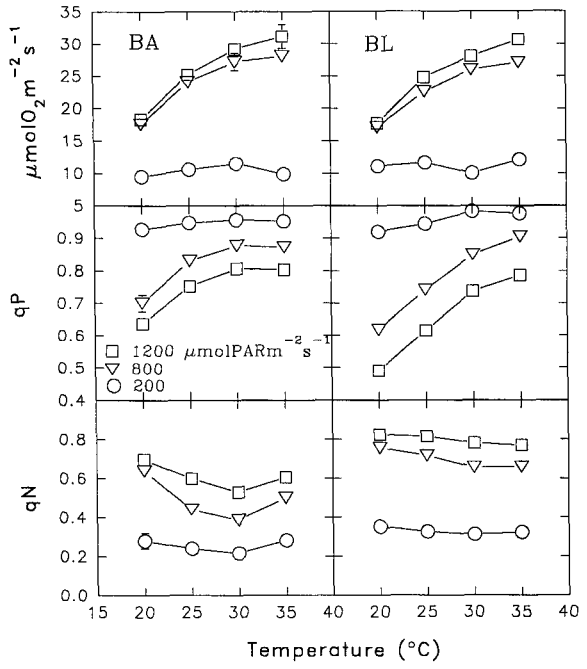

Figure 1. O_2 evolution, qP, and qN (upper, middle, and lower panels) in BA (left) and BL (right) upon increases in temperature from 20 to 35°C at different light intensities. Each point represents the average and SE of at least five samples.

pected, the qN changed in an opposite direction to qP at high temperatures (Fig. 1). In the range of 20 to 30°C the lower levels of qP in BL were accompanied by higher qN. Also in BL, qN decreased when the temperature was increased from 20 to 30°C and was maintained up to 35°C. In BA, the same parameter decreased markedly when the temperature was increased from 20 to 30°C, but increased again when temperature was increased to 35°C. Over the same range of temperatures, no significant variations in qP and qN were detected at low light intensity in either of the varieties. At 200 μmol m^{-2} s^{-1} the flattened responses in O_2 evolution and fluorescence parameters as the temperature was increased from 20 to 35°C are consistent with the established fact that temperatures above the range that induces chilling injury and below the range that causes heat damage do not affect the maximum quantum yield in nonphotorespiring conditions (Ehleringer and Björkman, 1977).

The variations in qP and qN when the temperature was increased from 20 to 35°C in high light confirms previous observations (Weis and Berry, 1988; Bruggemann, 1992). Such variations imply that the proportion of open reaction centers increases at the same time that the energy dissipation by nonphotochemical means decreases; therefore, not only does the efficiency of O_2 evolution increase (Fig. 1), but also the efficiency of electron transport through PSII increases.

According to Genty et al. (1989), Φ_{PSII} is proportional to the product of qP and the efficiency of excitation capture by open PSII centers, denoted as F_v/F_m. This concept is based on the assumption that nonphotochemical energy dissipation does not occur in the reaction center. Φ_{PSII} has been shown to be linearly related to Φ_{CO2} and Φ_{O2} in leaves under nonphotorespiratory conditions (Genty et al., 1989; Seaton and Walker, 1990), and therefore can be used as a probe of noncyclic electron transport (Genty et al., 1989). Figure 2 shows the relationship between Φ_{PSII} and Φ_{O2} in BA and BL. Linearity was maintained when the temperature was varied from 20 to 35°C in samples illuminated with 800 and 1200 μmol m^{-2} s^{-1}. In low-intensity light, however, Φ_{O2} increased more than Φ_{PSII}, similar to reports by Öquist and Chow (1992) measuring Φ_{O2} in C_3 and C_4 species, by Harbinson et al. (1990) with Φ_{CO2} in peas, and by Seaton and Walker (1990) in several species under different light intensities. Such an effect makes the slope of the Φ_{PSII}/Φ_{O2} ratio for BL, by variations in light only, lower than that observed for variations in temperature in high light; however, they are similar to those observed in BA (Fig. 2) when only Φ_{O2} values smaller than 0.04 are considered.

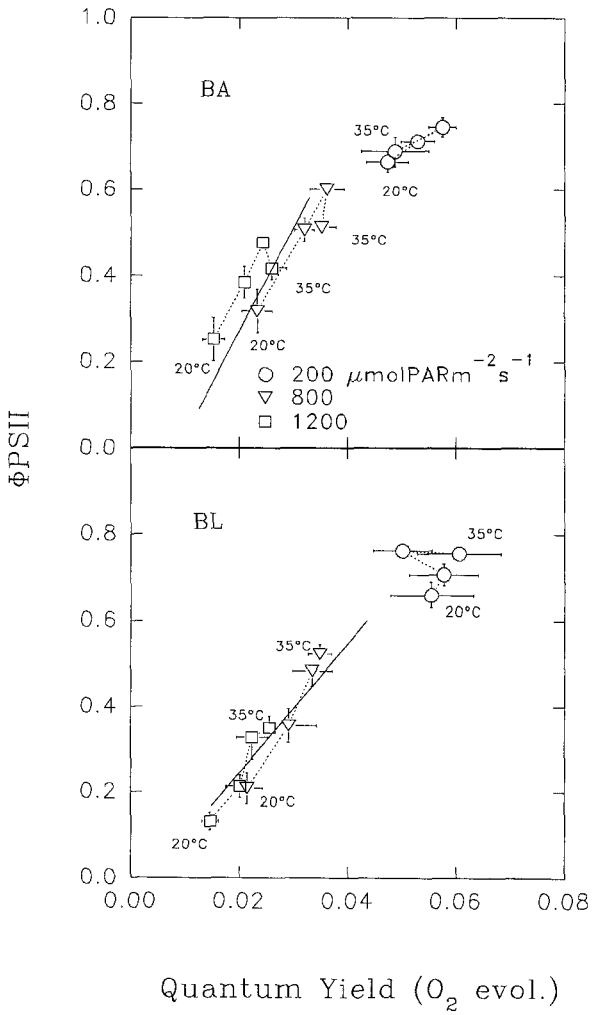

Figure 2. Relationship between Φ_{PSII} and Φ_{O2} in BA and BL with increasing temperature at different light intensities. The solid lines represent the regression from measurements at 20°C and different light intensities from 400 to 1200 μmol m^{-2} s^{-1} PAR. Each point represents the average and SE of at least five samples.

Mechanisms of Nonphotochemical Energy Dissipation

The incidence of photoinhibition of photosynthesis with increases in temperature from 20 to 35°C was assessed by measuring the F_v/F_m ratio in dark-adapted leaf discs previously illuminated with 1200 μmol m^{-2} s^{-1} for 30 min. After the illumination at different temperatures, the leaf discs were put on a wet surface at 20°C for another 30 min, after which the fluorescence was determined. This method avoided any temperature-dependent effect on the recovery from photoinhibition (Greer et al., 1991). This protocol was based on the fact that photoinhibition results in a decline in the maximal quantum yield of photosynthesis (Powles, 1984), a parameter closely correlated to the ratio F_v/F_m (Adams et al., 1990). There were no significant differences in the F_v/F_m ratio from leaf discs of both varieties measured after increases in temperature from 20 to 35°C (data not shown). Therefore, temperature does not have any significant effect on the incidence of photoinhibition in either bean variety under the experimental conditions used.

Another reversible component of qN is the state transition, in which energy absorbed by PSII is redistributed to PSI after phosphorylation of the LHCII. The ratio of emission at 688 to 689 nm compared with that of 733 to 734 nm at 77 K was used to examine variations in the redistribution of excitation energy between both photosystems (Horton and Black, 1981). Despite the distortion of the fluorescence spectrum by reabsorption that occurs in leaves because of their high chlorophyll concentration, it was still possible to measure the relative emission intensities from PSI and PSII, since the chlorophyll content did not change during the experiment (data not shown). For completely dark-adapted samples, the PSI/PSII ratio increased only at 40°C (Fig. 3A); however, after illumination the ratio increased continuously from 20 to 35°C, suggesting that a significant light-dependent state transition had occurred (Fig. 3B)

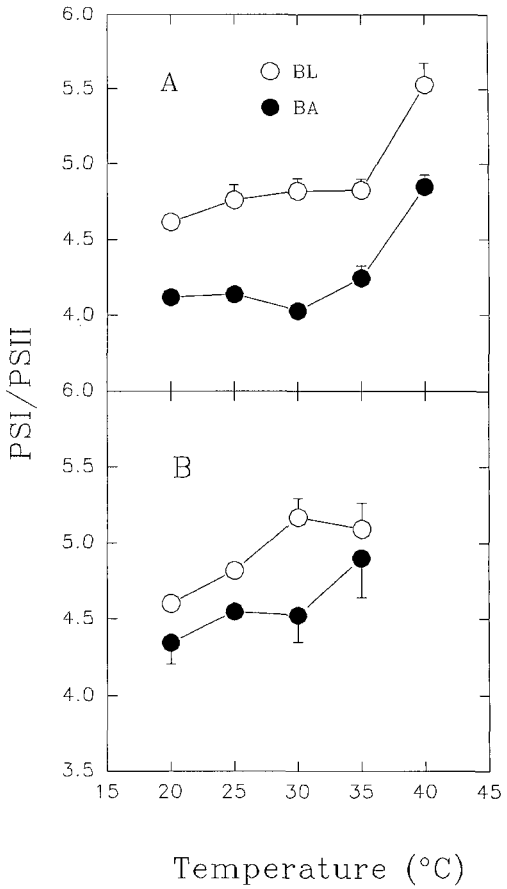

Figure 3. Changes in 77-K fluorescence emission ratio PSI/PSII in BA and BL. A, Measurements were carried out in samples heated in darkness at temperatures from 20 to 40°C. B, Measurements were carried out on preilluminated samples at temperatures from 20 to 35°C. Each point represents the average and SE of at least four samples.

Fast Kinetics of Fluorescence Induction

The effect of temperature on the proportion of $PSII_\alpha$ and $PSII_\beta$ following an increase in temperature from 20 to 35°C in darkness was investigated. In both varieties, there was a moderate increase in the relative concentration of $PSII_\beta$ centers when the temperature was increased from 20 to 30°C (Fig. 4); a sharper increase was observed when the temperature was increased to 35°C. These results are similar to those reported by Sundby et al. (1986) after heating spinach chloroplasts. The amplitudes of F_m and F_o were not affected by the change in temperature, indicating that the differences in $PSII_\beta$ were not due to artifacts arising from inaccurate determinations of the maximum F_v. Again, the lack of change in chlorophyll content or physical characteristics of the leaf enable these measurements to be used to establish changes in the relative proportion of $PSII_\beta$, although absolute values cannot be given.

DISCUSSION

As expected, the maximum rate of photosynthesis increased with the increase in temperature from 20 to 35°C. The Q_{10} values at 1200 μmol m^{-2} s^{-1} declined as the temperature was increased from 20 to 30°C in BA and BL. This indicates that despite the increase in O_2 evolution with increases in temperature, a restriction of photosynthesis occurs as the temperature approaches 35°C, giving rise to a temperature "optimum"; this was expected because of previous data (Weis and Berry, 1988). This restriction in photosynthesis was not associated with a decrease in its maximum quantum yield, and at low light intensity photosynthesis did not change with temperature; this was also expected because of previous observations (Ehleringer and Björkman, 1977).

There was no evidence of a photoinhibitory change in photosynthetic efficiency at higher temperature. However, changes in qN were observed, which differed between the two bean varieties. The decline in qN between 20 and 30°C most likely reflected a decrease in qE, the major component of qN at 20°C. Such a decline in qE would arise either from an increased ATP consumption or from a failure to maintain a pH gradient due to increased H^+ permeability of the thylakoid. The latter has not been directly investigated, although the more rapid dark relaxation of qE at 30°C

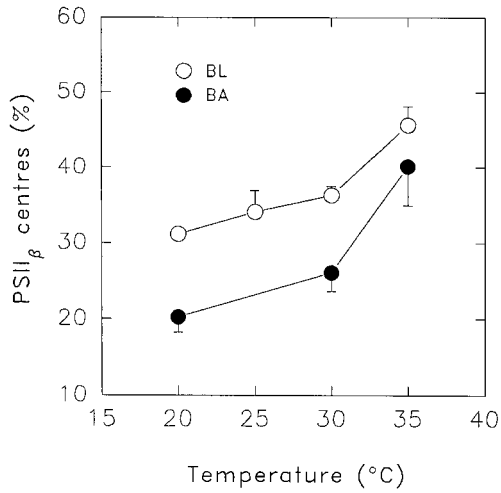

Figure 4. Relative concentration of $PSII_\beta$ centers upon heating in BA and BL. Each point represents the average and SE of at least four samples.

compared with 10°C has been explained previously by an increased rate of H^+ efflux from the thylakoid (Gilmore and Björkman, 1994). The increase in qN at higher temperatures is unlikely to be due to qE, but could be due to state transitions.

It is important to note that the increase in the quantum yield of O_2 evolution in both bean varieties was linearly correlated with the quantum yield of PSII electron transport under high-intensity light (Fig. 2). Such a relationship, however, is curvilinear under low-intensity light, similar to that observed before as Φ_{O2} or the Φ_{CO2}/Φ_{PSII} ratio and attributed to the occurrence of a different mechanism of non-photochemical energy dissipation (Öquist and Chow, 1992), an alternative electron sink, or variable dark respiration, all of which vary with light intensity (Harbinson et al., 1990). A maintenance of the linearity upon temperature was reported before by Oberhuber and Edwards (1993) in a C_3 species measuring Φ_{CO2} and Φ_{PSII} in low and high light (300 and 1100 μmol m^{-2} s^{-1}, respectively), by Krall and Edwards (1991) in maize at constant light intensity, and by Cornic and Ghashghaie (1991) measuring CO_2 assimilation at constant light intensity. Data shown in Figure 2 provide additional evidence that the increase in the quantum efficiency of PSII electron transport is followed by a proportional increase in gas exchange with increasing temperature, this time measuring O_2 evolution in combination with varying high light intensities (800 and 1200 μmol m^{-2} s^{-1}). The fact that the temperature-induced changes follow the same relationship as those induced by alterations in light intensity suggests that in this temperature range, regulated adjustments in photosynthetic electron transport and photoprotective energy dissipation occur. The data do not, however, provide any clues as to where within the photosynthetic process these restrictions occur.

There is evidence from the data shown in Figures 3 and 4 that changes occur in the organization of the thylakoid membrane between 30 and 35°C. There was also a change in PSI/PSII fluorescence ratio consistent with the occurrence of a state transition, as well as an increase in the proportion of $PSII_\beta$ centers. It is clear that the state transitions, observed as the ratio of fluorescence emission by PSI and PSII, are increased by temperature, but that the increase is light-dependent in the temperature range of 20 to 35°C. Figure 3 shows that no changes in the PSI/PSII emission ratio were incurred by heat in the absence of illumination, except at 40°C. This is not the case with the increase in the relative concentration of $PSII_\beta$ centers, which were detected in the absence of light. These centers, which have a smaller antenna size and are located in the nonappressed thylakoid regions (Melis et al., 1988), have been suggested to be a reserve pool of PSII to replace photoinhibited PSII centers (Melis, 1985; Tyystjarvi and Aro, 1990). However, the β centers created by heat treatment are unlikely to have such a role; rather, they are formed by the disconnection of LHCII from PSII (Sundby et al., 1986).

The functional effect of the occurrence of state transitions and $PSII_{\alpha\text{-}\beta}$ conversion is less clear. On one hand, state transitions involve redirection of energy to PSI, but there seems to be no agreement whether the redirected energy is used in PSI photochemistry (Horton and Black, 1981; Horton and Lee, 1984; Telfer et al., 1984). As for $PSII_{\alpha\text{-}\beta}$, it seems to be considered as an effect of increased temperatures to protect PSII from photoinhibition by decreasing absorption cross-section, more so than a mechanism of energy transfer to PSI (Sundby et al., 1986; Anderson and Andersson, 1988). Ruban (1991) and Ruban and Trach (1991) have found, however, that energy is transferred independently of state transitions to PSI from PSII internal antenna chlorophylls upon heating of chloroplasts to 40°C.

Comparing data shown in Figures 3 and 4, it is clear that increases in the proportion of $PSII_\beta$ are not necessarily associated with energy transfer to PSI by itself, since no change in the proportion of PSI/PSII fluorescence emission at 77 K were detected in darkness. The opposite has been reported before, showing that the 77-K PSI/PSII ratio increases with heat in darkness (Weis, 1985), similar to what happens in the bean varieties studied at 40°C (Fig. 3). However, it is difficult to discriminate the origin of such changes. In fact, the effect of such high temperature on the unstacking of chloroplasts (Gounaris et al., 1984; Doltchinkova et al., 1986) would mean that PSII-LHCII and PSI complexes would randomize their distribution, making energy redistribution, independent of state transitions and PSII heterogeneity, more likely, similar to a decrease in cation concentration in chloroplasts (Horton and Black, 1983). A model has been put forward by Timmerhaus and Weis (1990) to explain the conflicting reports on the effect of energy transfer from PSII to PSI due to state transitions and PSII heterogeneity. They propose that phosphorylated LHCII moves away from PSII, and at high temperatures PSII moves away from the grana region, leaving behind the LHCII complex. Both reorganizations would not imply reassociation with PSI, however. When occurring simultaneously the phospho-LHCII may connect $PSII_\beta$ with PSI and allow spillover of excitation energy between them. This model is in agreement with the finding that temper-

ature-dependent increases in the proportion of $PSII_\beta$ centers occurs independently from state transitions, the latest being light-mediated in the bean varieties.

The physiological significance of such an effect is not established, although it may be hypothesized that its role is to protect PSII from photodamage or to stimulate a PSI cyclic electron flow that results in an enhanced rate of H^+ translocation. This may be necessary to offset the increased H^+ leakage from the thylakoid. Alternatively, these changes may have no adaptive value, and may simply be deleterious responses to elevated temperature that are the cause of the decline in Q_{10} for photosynthetic O_2 evolution.

In summary, the results presented are further evidence that temperature induces changes in chloroplasts, but most importantly, that these changes occur well below the threshold at which high temperature inhibits photosynthesis irreversibly. It is also shown that such changes, namely state transitions and PSII heterogeneity, are simultaneous with the lowest Q_{10} of photosynthesis measured as O_2 evolution. In the following paper the response of carbon assimilation is described and its relationship to the changes in thylakoid function described here are explored.

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