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Effects of high temperature on chlorophyll fluorescence induction and the kinetics of far red radiation-induced relaxation of apparent F_0 in maize leaves

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Abstract

Temperature dependence (25-50 °C) of chlorophyll (Chl) fluorescence induction, far-red radiation (FR)-induced relaxation of the post-irradiation transient increase in apparent F_0, and the trans-thylakoid proton gradients (ΔpH) was examined in maize leaves. Temperatures above 30 °C caused an elevation of F_0 level and an enhancement of F_0 quenching during actinic irradiation. Millisecond delayed light emission (ms-DLE), which reflects the magnitude of ΔpH, decreased strikingly above 35 °C, and almost disappeared at 50 °C. It indicates that the heat-enhanced quenching of F_0 under actinic irradiation could not be attributed mainly to the mechanism of ΔpH-dependent quenching. The relaxation of the post-irradiation transient increase in apparent F_0 upon FR irradiation could be decomposed into two exponential components (τ_1 = 0.7-1.8 s, τ_2 = 2.0-9.9 s). Decay times of both components increased with temperature increasing from 25 to 40-45 °C. The bi-phasic kinetics of FR-induced relaxation of the post-irradiation transient increase in apparent F_0 and its temperature dependence may be related to plastoquinone (PQ) compartmentation in the thylakoid membranes and its re-organisation at elevated temperature.

Additional key words: heat stress; *Zea mays* L.

Introduction

The complicated syndrome of photosynthesis under heat stress can be probed by non-invasive methods such as chlorophyll (Chl) fluorescence measurements. Increased temperature causes an increase in non-photochemical quenching (q_N) (Bilger *et al.* 1987, Georgieva and Yordanov 1994). Heat treatment is believed to limit ATP consumption in the Calvin cycle, which may lead to an accumulation of ΔpH gradient with an increase in high-energy dependent Chl fluorescence quenching (q_E) during actinic irradiation (Bilger *et al.* 1987, Joshi *et al.* 1995). On the other hand, membrane permeability probably increases during heat stress, which may bring about a decrease in ΔpH across thylakoid membranes (Berry and Björkman 1980, Bukhov *et al.* 1999) and consequently a suppression of q_E. In this study, the significance of heat-induced increase of q_E was examined in intact maize leaves by comparing the Chl fluorescence induction curve with ms-DLE, an indicator of trans-thylakoid ΔpH (Evans and Crofts 1973, Xu and Shen 1984). The results suggest that heat-enhanced Chl fluorescence quenching under actinic irradiation could not be ascribed mainly to q_E.

In cyanobacteria (Mi *et al.* 1997) and higher plants (Bukhov *et al.* 1992, Asada *et al.* 1993, Mano *et al.* 1995, Burrows *et al.* 1998, Feild *et al.* 1998, Shikanai *et al.* 1998, Jin *et al.* 2000, Yamane *et al.* 2000) the minimal Chl fluorescence yield (apparent F_0) transiently increases after a light-to-dark transition. This increase in apparent

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Abbreviations: AR – actinic radiation; apparent F_0 – dark level of chlorophyll fluorescence yield measured after light-to-dark transition; Chl – chlorophyll; F_0 – dark level of Chl fluorescence yield measured after dark-adaptation; F_0' – the dip of Chl fluorescence level after the turning off of actinic radiation; F_0^p – the fraction of the post-irradiation transient increase in apparent F_0 that can be quenched by far-red radiation; F_0^s – the steady state level of apparent F_0 during far-red irradiation; FR – far-red radiation; LHC – light-harvesting complex; ms-DLE – millisecond delayed light emission; PQ – plastoquinone; PS – photosystem; q_E – trans-thylakoid-ΔpH-dependent Chl fluorescence quenching; q_N – non-photochemical quenching of Chl fluorescence; ΔpH – proton gradient.
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F_0 can be quenched by FR (Asada *et al.* 1993, Burrows *et al.* 1998, Shikanai *et al.* 1998). It is inhibited by a specific inhibitor of ferredoxin-plastoquinone reductase (Mano *et al.* 1995) or by site mutation of the genes encoding the sub-units of NAD(P)H dehydrogenase complex (Burrows *et al.* 1998, Shikanai *et al.* 1998), and enhanced by specific inhibitor of cytochrome b_6f (Mano *et al.* 1995). The post-irradiation increase in apparent F_0 probably reflected the reduction by reducing equivalents of the intersystem electron transport chain that has been accumulated during actinic irradiation. FR preferentially drives photosystem (PS) 1, depletes electrons from the intersystem chain, and consequently brings about a decrease in Chl fluorescence level. Hence, the analysis of the relaxation of the post-irradiation transient increase in apparent F_0 upon FR irradiation can provide information about the efficiency of energy transfer in PS1 and the structural and functional change in photosynthetic membranes. In this work, the temperature dependence of the FR-induced relaxation of the post-irradiation transient increase in apparent F_0 in an intact maize leaf was investigated.

Materials and methods

Plants of maize (*Zea mays* L.) were grown in Hoagland solution under natural light at temperature range of 13-24 °C. The third fully unfolded leaves were used for measurements.

Chl fluorescence was measured using *PAM101* (*Walz*, Effeltrich, Germany) integrated with a microcomputer. The modulated measuring beam (1-μs duration, 1.6 kHz, peak emission at 650 nm) was 0.05 μmol(photon) m^{-2} s^{-1}. Actinic irradiation (620 μmol m^{-2} s^{-1}) was provided by a halogen lamp. Far-red radiation (>720 nm, 7.3 μmol m^{-2} s^{-1}) was from a halogen lamp filtered by a *GR720* filter (*Schott*, Mainz, Germany). For the measurement of F_m, 1-s saturating pulse [655 nm, 1 200 μmol(photon) m^{-2} s^{-1}] was provided by a LED-array cone (High-Power-LED-Lamp, *Walz*).The abaxial side of an intact attached leaf was pressed on a thermostatted glass platform covered by a piece of black cotton cloth, and the adaxial side of the leaf was placed facing the detector encircled by a piece of plastic foam, as described in Jin *et al.* (2001). The temperature was increased from 25 to 50 °C by 5 °C steps. The dark period between two measurements was 20 min, and the temperature was increased thermostatically within 3 min at the beginning of each dark period.

Measurement of ms-DLE was carried out using a home-equipped apparatus (Xu and Shen 1984, Li and Shen 1995, Wei *et al.* 1998). The outputs were fed to an analogue-digital converter attached to a microcomputer. Intact attached maize leaves treated in the same way as that used for Chl fluorescence measurement were cut into 4.5 cm long sections and inserted into a flat simple cell made of plexiglass, and the ms-DLE was measured immediately at room temperature (22 °C).

Data analysis: Processing of all the digitised records was made using a series of home-designed software. The relaxation of the post-irradiation transient increase in apparent F_0 upon FR irradiation was described by a sum of exponential decaying components with amplitude a_i and decay time τ_i,

$$F(t) = F_0^s + \Sigma a_i \exp(-t/\tau_i) \quad (1)$$

where t represents the time since the turning on of FR, F(t) the level of apparent F_0 as a function of t, and F_0^s the estimated asymptotic level of apparent F_0 under FR irradiation. Experimental points were fitted to Eq. 1 by software based on non-linear Levenberg-Marquardt algorithm as described by Jin *et al.* (2001).

Results and discussion

Temperature dependence of the profile of Chl fluorescence induction, the transient post-irradiation increase in apparent F_0, and its relaxation upon FR irradiation measured in an intact attached maize leaf are depicted in Fig. 1. The post-irradiation transient increase in apparent F_0 was quenched by FR applied 20 s after the turning off of actinic radiation. The values of parameters used to characterise the Chl fluorescence traces in Fig. 1, *i.e.* the dip upon light-to-dark transition (F_0'), the fraction of the post-irradiation increase of apparent F_0 that could be quenched by FR (F_0^p), the steady state level of apparent F_0 during FR irradiation (F_0^s), and the F_0 level before actinic irradiation are shown in Fig. 2. Elevated temperature caused not only a rise of F_0 but also an acceleration of Chl fluorescence quenching under actinic irradiation, and a decline of the Chl fluorescence below the F_0 level at temperatures above 35 °C.

The heat-induced rise of F_0 has been well documented and attributed mainly to the disconnection of light-harvesting complex (LHC) from PS2 (Schreiber and Armond 1978, Armond *et al.* 1980, Yamane *et al.* 1997) and/or to the accumulation of reduced Q_A (Bukhov *et al.* 1990, Cao and Govindjee 1990, Goltsev *et al.* 1994, Havaux 1996, Sazanov *et al.* 1998, Yamane *et al.* 2000). In the present experiment, F_0 could not be quenched by FR (values not shown), indicating that Q_A reduction mechanism was not involved in the heat-induced rise of the original F_0 in maize leaves. Comparative study among various higher plants made by Yamane *et al.* (2000) revealed that the functioning of Q_A reduction mechanism in

the heat-induced enhancement of F_0 was species-dependent. The quenched F_0 could not return to the original level instantly upon the turning off of actinic radiation, as indicated by the observation that the steady state level of apparent F_0 under FR irradiation (F_0^S) dropped below F_0 at temperatures above 35 °C. This was caused by heat-induced quenching of F_0 under actinic irradiation (Bilger *et al.* 1987). F_0 quenching suggests a limitation of energy transfer from LHC2 to PS2 (Bilger and Schreiber 1986), which takes place upon LHC2 phosphorylation (Krause and Behrend 1983, Hodges and Barber 1986).

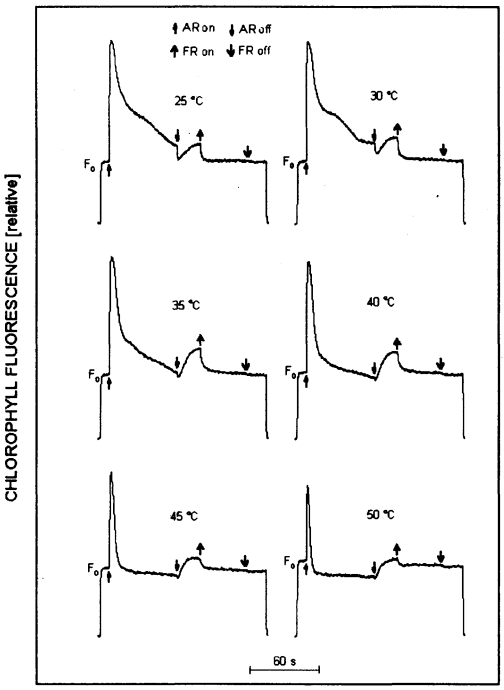

Fig. 1. Effects of elevated temperatures on Chl fluorescence induction, the post-irradiation transient increase in apparent F_0, and its relaxation upon FR irradiation in an intact attached maize leaf. After 50-min dark-adaptation, the leaf was exposed sequentially to a series of step-wise increased temperatures. The measurement was performed after 20-min leaf adaptation to the treated temperatures. *Arrows* indicate switching on (↑) or off (↓) of actinic or FR irradiation.

Heat-induced change in ΔpH across the thylakoid membranes in maize leaves was followed with ms-DLE measurement (Fig. 3). First discovered by Strehler and Arnold (1951) and having been used to probe a variety of parameters which change during adjustment to steady-state photosynthesis (Malkin 1977), ms-DLE generally consists of a fast phase and a subsequent slow increase. The slow phase depends on trans-thylakoid ΔpH proton gradient (Evans and Crofts 1973) and the fast phase is related to a rapid establishment of the thylakoid membrane potential (Wraight and Crofts 1971). Furthermore, Xu and Shen (1984) showed that adding NH_4Cl or nigericin plus K could diminish the intensity of the fast

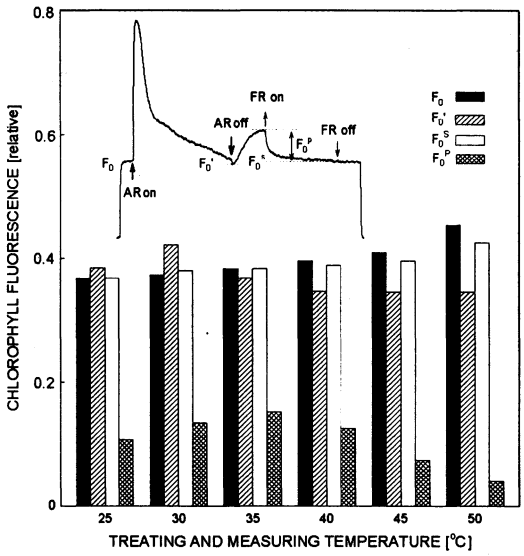

Fig. 2. Quantitative representation of the temperature-dependent Chl fluorescence changes in Fig. 1. F_0 quenching under actinic irradiation was indicated by F_0', which dropped below F_0 at temperatures above 30 °C. Magnitude of the post-irradiation transient increase in apparent F_0 was estimated by the fraction that could be quenched by FR (F_0^P).

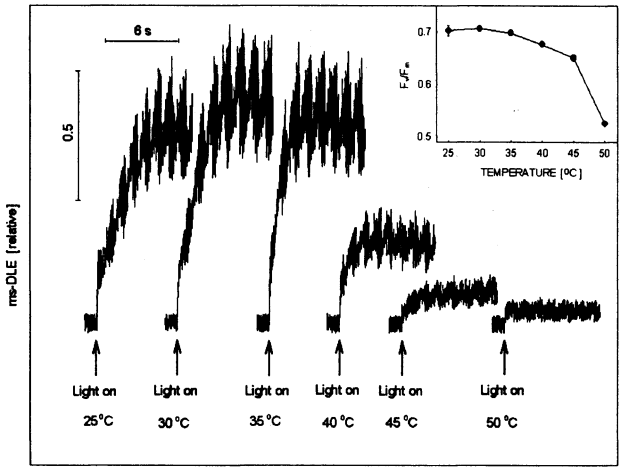

Fig. 3. Effects of elevated temperatures on ms-DLE in maize leaves. The leaves had gone through the same heating and darkening regimes as those used for Chl fluorescence measurement at corresponding temperatures. For details, see Materials and methods. The oscillations were due to instrumental noise. The *inset* demonstrates temperature-dependence of F_v/F_m.

phase; suggesting also a ΔpH-dependence. As shown in Fig. 3, the magnitude of ms-DLE changed slightly with temperature in the range 25-35 °C, strikingly decreased above 35 °C, and almost vanished at 50 °C. Although heat-induced inactivation of PS2 may lead to the inhibition of linear electron transport and consequently a decrease in ΔpH, the temperature-dependence pattern of F_v/F_m (Fig. 3, *inset*) indicates that this effect was not significant at temperatures below 45 °C. Thus, the dimi-

nishing of ms-DLE above 35 °C arose mainly from heat-induced increase in membrane permeability and the resultant abolishment of trans-thylakoid proton gradient, as suggested by Berry and Björkman (1980) and Bukhov *et al.* (1999). The discrepancy between thermal response patterns of ms-DLE and Chl fluorescence induction curve suggests that q_E was not the main mechanism causing the heat-induced quenching of Chl fluorescence during actinic irradiation, especially at temperatures above 35 °C.

Heat stress causes the detachment of LHC2 from PS2 and the subsequent lateral migration of PS2. A portion of LHC tightly bound to it goes to the non-appressed regions, leaving behind the free LHC2 in the appressed membranes (Sundby and Andersson 1985, Sundby *et al.* 1986, Ruban and Trach 1991), which might be transferred to PS1 located in the grana margins (Ruban and Trach 1991), but not necessarily so (Carpentier 1999). Conceivably, it was the quenching related to the heat-induced state transition that accounted for the main part of the enhanced declining of the Chl fluorescence induction curve at elevated temperature (Figs. 1 and 2).

When the actinic irradiation was turned off, non-photochemical reduction of the intersystem chain brought about a transient increase in apparent F_0 (Fig. 1). At temperatures above 30 °C, a substantial fraction of the post-irradiation increase in Chl fluorescence arose from the nullification of light-induced F_0 quenching (Fig. 2). The FR-quenchable portion of the post-irradiation transient increase in apparent F_0, as represented by F_0^P in Fig. 2, went through a maximum around 35 °C. This form of the temperature-dependent pattern might be related to the change in size of the pool of electrons available for the reduction of the intersystem electron transport chain (Jin *et al.* 2000).

As shown in Fig. 4, the kinetics of the FR-induced relaxation in apparent F_0 can be decomposed into two exponentially decaying components. Although FR-irradiation could also induce ΔpH-dependent Chl fluorescence quenching, the effect would be too small under the FR irradiance employed in this experiment (Feild *et al.* 1998). Bi-phasic kinetics of the FR-induced relaxation of apparent F_0 indicates the structural and functional heterogeneity of the thylakoid membranes.

There is growing documentation on the structural and functional heterogeneity of photosynthetic membranes of higher plants. Apart from the heterogeneous distribution of photosystems and other integral protein complexes in thylakoid membranes (Albertsson 2001), PQ compartmentation indicated by difference in rate of photoreduction has also been found in chloroplasts (Joliot *et al.* 1992, Kirchhoff *et al.* 2000). As proposed by Kirchhoff *et al.* (2000), PQ molecules in thylakoid membranes are segregated into micro-domains by large aggregates formed by a hierarchy of specific PS2-LHC2 and LHC2-LHC2 interactions. At least 70 % of PS2 may be located in small domains, with an average number of only 1 to 2 PS2 centres in each domain, while a small fraction of PS2 is located in large domains, with more than 10 PS2 centres in a domain. Such micro-organisation allows rapid shuttling of electrons between PS2 and cytochrome b_6f by PQ diffusion within each micro-domain, but redox equilibration throughout the membrane is slow. The structural and functional difference between the large and the small micro-domains of PQ in thylakoid membranes may result in a variation in the decay-time of FR-induced depletion of electrons accumulated in these domains, as reflected by the bi-phasic kinetics of FR-induced relaxation of the post-irradiation transient increase in apparent F_0.

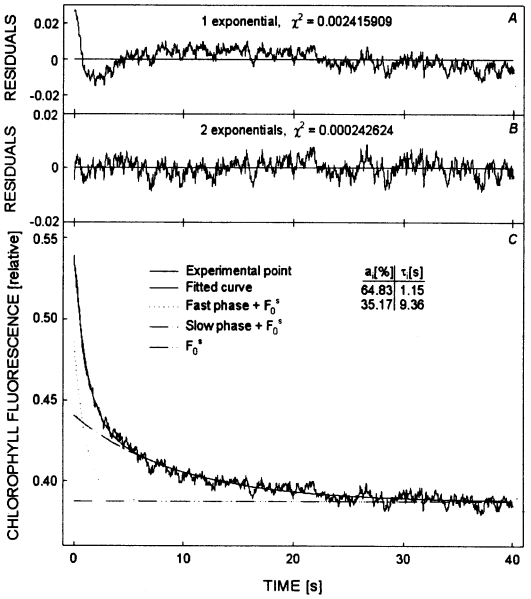

Fig. 4. Relaxation kinetics of the post-irradiation transient increase in apparent F_0 upon FR irradiation in the intact maize leaf. The figure illustrates the fitting procedure and the decomposition with the best fit. *A, B*: Residual plots of the fitting of experimental data to mono- and bi-exponential model, respectively. *C*: Decomposition of the fitted bi-exponential curve, showing the individual contributions of the two kinetic components. The treating and measuring temperature was 35 °C.

The temperature-dependence of the kinetic parameters is shown in Fig. 5. As the temperature increased sequentially from 25 to 50 °C, the fast phase was slowed down and its decay-time increased with temperature up to 45 °C, with a slight decrease above 45 °C. The slow phase, with a decay-time increasing monotonously with temperature in the range from 25 to 40 °C, degenerated at 45 °C, and could not be resolved at 50 °C.

Heat-treatment caused not only the detachment of LHC2 from PS2 but also the randomisation and dissociation of other integral protein complexes in the thylakoid membranes, leading to a re-organisation of PQ compartmentation. Meanwhile, heat-treatment also enhanced random motion of PQ, which in turn muddled PQ diffusion within micro-domains. All these effects would limit the FR-induced oxidation of the PQ pool in the thylakoid

membranes, and thus slow down the relaxation of apparent F_0, or even change the pattern of decay. This interpretation seems contradictory to the observations that the dark re-reduction of $P700^+$ was accelerated by heat treatment (Havaux 1996, Bukhov *et al.* 1999, Jin *et al.* 2001). As an accommodation, heat-induced de-stacking of the thylakoid membranes (Carpentier 1999) may be made easy for reduced ferredoxin molecules to enter into the narrow, crowded space between two neighbouring appressed membranes to reach the cytochrome b_6f complex in the grana, bringing about a promotion of $P700^+$ reduction. Although the direct reaction between ferredoxin and cytochrome *b* has been questioned (Bendall and Manasse 1995), there might be other pathways through which electrons can be transferred from stromal reductants to cytochrome b_6f without the participation of the PQ pool. In *Chlorella sorokiniana*, a redox-active component loosely associated with the stromal surface of cytochrome b_6f complex has been identified, which undergoes redox equilibration with the haem b_H of cytochrome *b*-563 (Lavergne 1983, Joliot and Joliot 1988). Recently, Zhang *et al.* (2001) found the activity of ferredoxin:$NADP^+$ oxidoreductase in spinach chloroplast cytochrome b_6f complex. Since the PQ pool is not involved in all these pathways, the limitation arising from heat-induced randomisation of PQ can be avoided.

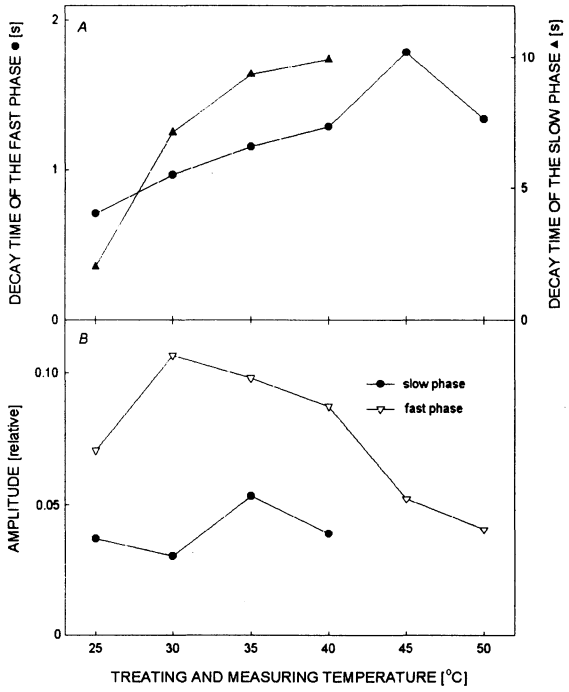

Fig. 5. Temperature dependence of the decay-times (*A*) and amplitudes (*B*) of the exponential components characterising the FR-induced relaxation of the post-irradiation transient increase in apparent F_0 in the intact maize leaf described in Fig. 1. The slow component was not resolved at 45 and 50 °C.

Alternatively, we cannot exclude the possibility that the retardation of FR-induced relaxation of the post-irradiation transient increase in apparent F_0 at high temperatures was caused by the detachment of LHC1 from PS1. We observed that the FR-induced relaxation of the post-irradiation transient increase in apparent F_0 in intact maize leaves was slowed down under lower irradiance by FR (data not shown), indicating that the absorption of radiation may become the rate-controlling step. Although we have not found evidence in the literature, it is conceivable that LHC1 may dissociate from PS1 under severe heat stress, leading to a decrease in functional cross section of the light-harvesting system.

In summary, the present study provides evidence that the ΔpH-dependent quenching is not the dominating mechanism of heat-enhanced quenching of Chl fluorescence induction. As to the kinetic analysis of FR-induced relaxation of the post-irradiation transient increase in apparent F_0, our interpretation is tentative. More investigations are needed before it can be employed as a probe to explore conformational changes in photosynthetic apparatus.

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