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ANALYSIS OF THE SLOW PHASES OF THE IN VIVO CHLOROPHYLL FLUORESCENCE INDUCTION CURVE

CHANGES IN THE REDOX STATE OF PHOTOSYSTEM II ELECTRON ACCEPTORS AND FLUORESCENCE EMISSION FROM PHOTOSYSTEMS I AND II.

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Summary

An analysis of the photo-induced decline in the in vivo chlorophyll a fluorescence emission (Kautsky phenomenon) from the bean leaf is presented. The redox state of PS II electron acceptors and the fluorescence emission from PS I and PS II were monitored during quenching of fluorescence from the maximum level at P to the steady state level at T. Simultaneous measurement of the kinetics of fluorescence emission associated with PS I and PS II indicated that the ratio of PS I/PS II emission changed in an antiparallel fashion to PS II emission throughout the induction curve. Estimation of the redox state of PS II electron acceptors at given points during P to T quenching was made by exposing the leaf to additional excitation irradiation and determining the amount of variable PS II fluorescence generated. An inverse relationship was found between the proportion of PS II electron acceptors in the oxidised state and PS II fluorescence emission. The interrelationships between the redox state of PS II electron acceptors and fluorescence emission from PS I and PS II remained similar when the shape of the induction curve from P to T was modified by increasing the excitation photon flux density. The contributions of photochemical and non-photochemical quenching to the in vivo fluorescence decline from P to T are discussed.

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Abbreviations: ΔpH, proton concentration gradient; F_{685}, F_{718}, F_{745}, F_{770}, fluorescence emission at 685, 718, 745 and 770 nm, respectively; PQ, plastoquinone; PS I, Photosystem I; PS II, Photosystem II.

Introduction

It is widely accepted that the kinetics of PS II fluorescence emission, induced when photosynthetic organisms are excited by continuous irradiation, can provide information of in vivo photosynthetic processes. However the full potential of this analytical tool has not been realised because of our limited knowledge of the physico- and bio-chemical mechanisms which affect in vivo fluorescence emission. On irradiation of leaf tissue a rapid rise in PS II fluorescence to an initial level, generally termed O, is followed by a slower increase to a maximal level, P; fluorescence is then quenched to a level S. Under low levels of irradiation an increase in fluorescence occurs from S to M and is finally followed by a slow quenching phase from M to the steady-state fluorescence level at T (Fig. 2 shows such a typical fluorescence induction curve).

In vitro studies on broken chloroplasts have shown that fluorescence emission can be influenced by the redox state of PS II electron acceptors [1—5], proton [6] and other cation [7—13] electrochemical gradients across the thylakoid membranes and the ATP concentration in the external environment of the thylakoid [14,15]. Changes in the external cation concentration are thought to produce alterations in the distribution of excitation energy between PS I and PS II chlorophyll complexes [16—20] and recently Briantais et al [6] have demonstrated that fluorescence quenching can be induced by increasing the intra-thylakoid proton concentration. Changes in the distribution of excitation energy between PS I and PS II have been shown to occur during the initial rapid O → P phase of the fluorescence induction curve of a bean leaf and have been attributed to changes in primary photosynthetic charge separation across the thylakoid membrane rather than to ion-flux induced mechanisms because of the rapid nature of the changes [21]. However, during the much slower P → T fluorescence quenching phase changes in the rate of electron transport occur [4,22,23] and thus modifications of both cation electrochemical gradients across the thylakoid membrane and stromal ATP concentration would be predicted. In the present study we examine changes in the relative fluorescence emission from PS I and PS II, the redox state of PS II electron acceptors and O_2 evolution during the P → T phase of the PS II fluorescence induction curve obtained from a bean leaf, and discus the possible regulatory interrelationships between these parameters.

Materials and Methods

Plants of *Phaseolus vulgaris* were grown from seed in a glasshouse at 20°C. All measurements were made at room temperature (21°C) on intact primary leaves 21 days from sowing the seed in John Innes No. 2 potting compost.

Leaves were directly excited with 632.8 nm radiation produced from a 5 mW helium-neon laser (Spectra-Physics) through a 632.8 nm interference filter (Ealing Beck) after dark adaptation for 30 min. Photon flux density at the leaf surface was monitored using a quantum sensor (LI-PIOS, Lambda Instrument Corporation) and attenuated using glass neutral density filters (Ealing Beck). Simultaneous measurements of fluorescence emission at 685 and 770 nm were made from the excited upper leaf surface using bifurcated fibre optic light

pipes. Fluorescence at 685 nm was measured through a 685 nm interference filter (Balzer) and at 770 nm through a high radiance monochromator (Applied Photophysics) with entry and exit slits of 5 mm and 10 nm, respectively. Measurements of fluorescence emission at 718 and 745 nm were made through the monochromator with the same slit settings. Hamamatsu R446 photomultiplier tubes were used to detect fluorescence. Fluorescence kinetics were recorded using transient recorders (Datalab DL905 or Gould Advance OS4100) which were triggered on opening of the electronic shutter (Ealing Beck) coupled to the helium-neon laser.

During the course of the fluorescence induction curve additional 632.8 nm irradiation was provided by a second 5 mW helium-neon laser (Scientifica and Cook Electronics) through a 632.8 nm interference filter (Ealing Beck) using a beam splitting cube (Ealing Beck). The kinetics of 685 nm fluorescence by the excitation addition were recorded using two transient recorders with different sweep times; this enabled accurate determination of the fast F_{O2} and slower F_{P2} levels of fluorescence (refer to Fig. 3). The transient recorders were triggered on opening of the electronic shutter.

Fluorescence emission spectra were measured from the surface of leaf samples which had been preirradiated for approx. 10 min with 100 μmol photons $\cdot$ $m^{-2} \cdot s^{-1}$ of 632.8 nm radiation in order to attain the steady state fluorescence level at T (see Fig. 2). Bifurcated fibre optic light guides were used to transmit the excitation radiation to and the fluorescence from the leaf surface. Fluorescence was detected with the photomultiplier described above after transmission through a scanning high radiance monochromator (Applied Photophysics) with entry and exit slits of 1.25 mm and 5 nm, respectively.

Relative rates of O_2 evolution were determined from 0.5 cm diameter leaf discs by placing them directly onto a Clark-type O_2 electrode (Yellow Springs Instruments Co. Inc.) [24]. The lower surfaces of the leaf discs were gently abraided with a fine nylon toothbrush prior to assay in order to reduce cuticular resistance to gas exchange. Such leaf discs showed identical fluorescence induction characteristics to intact, attached leaves.

Fluorescence emission spectra of chloroplasts, isolated by a previously described method [25], were determined from the surface of a thin smear of of chloroplast suspension (containing 150 μg chlorophyll $\cdot$ cm^{-3}) on a glass slide using the same experimental conditions as described above for the leaf.

Results

The characteristic room temperature fluorescence emission spectrum of the bean leaf at steady state fluorescence level, T, is shown in Fig. 1. The emission bands with maxima at 689 and 745 nm are generally considered to be from chlorophyll a species associated with PS II and PS I respectively [5,20,26,27]. The emission from the leaf at 745 nm relative to 689 nm is unusually large compared to that observed in the previously published spectrum of a pea leaf [20], and may possibly be partially due to the greater self-absorption of emission at wavelengths below 700 nm. However, self-absorption phenomena cannot totally account for the relatively large 745 nm emission from the bean leaf, since a thin film of chloroplasts isolated from a bean leaf, which has a markedly

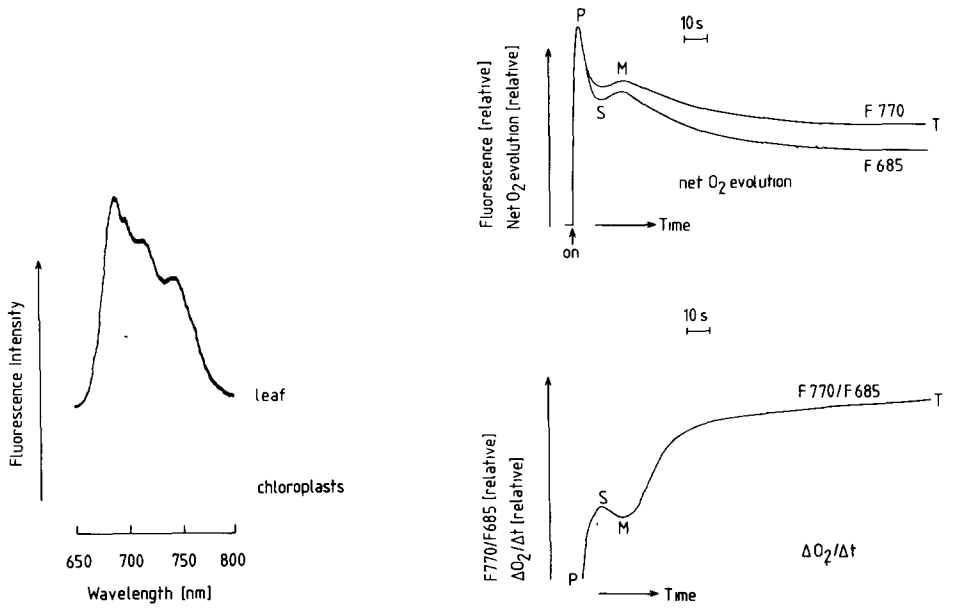

Fig. 1. Fluorescence emission spectra of a bean leaf (———) and a thin layer of isolated bean leaf chloroplasts (· · · · · ·) at 21°C. The chloroplast preparation contained 150 μg chlorophyll · cm^{-3}. Samples were exposed to 100 μmol photons · m^{-2} · s^{-1} of 632.8 nm irradiation for 10 min prior to measurement to ensure that a steady-state fluorescence level had been achieved.

Fig. 2. Kinetics of fluorescence emission at 685 and 770 nm measured simultaneously from a bean leaf. (↑) indicates excitation of leaf with 100 μmol photons · m^{-2} · s^{-1} of 632.8 nm radiation. Changes in net O_2 evolution, the rate of O_2 evolution ($\Delta O_2/\Delta t$) and the 770/685 nm fluorescence emission ratio (F_{770}/F_{685}) are shown during fluorescence quenching. P, S, M and T represent specific points on the 685 nm fluorescence induction curve.

reduced sample thickness compared to the leaf and must effectively minimise self-absorption artefacts, also exhibited a significant 745 nm emission relative to 689 nm (Fig. 1). The presence of a distinct shoulder at ca. 718 nm in the emission spectrum of the leaf made it desirable to monitor PS I emission at 770 nm, rather than 745 nm, in order to avoid large contamination of signals by emission from the component(s) giving rise to the 718 nm shoulder.

The kinetics of fluorescence emission at 685 and 770 nm, determined simultaneously on excitation of the dark-adapted leaf with low intensity radiation (approx. 100 μmol photons · m^{-2} · s^{-1} of 632.8 nm irradiation), the 770/685 nm fluorescence emission ratio (F_{770}/F_{685}), the net O_2 evolution and the rate of O_2 evolution ($\Delta O_2/\Delta t$) from the leaf throughout the fluorescence induction curve are shown in Fig. 2. The similar nature of the kinetics of F_{770} and F_{685} suggest that a common factor(s) regulates the fluorescence emission from both photosystems in a similar way. If changes in F_{685} were solely attributable to modification of the relative excitation distribution between PS I and PS II, then F_{770} would be expected to show antiparallel changes to F_{685}.

The possibility that F_{685} was regulated by the redox state of PS II electron acceptors was examined by determining the amount of variable fluorescence generated at 685 nm when the leaf was exposed to additional irradiation at

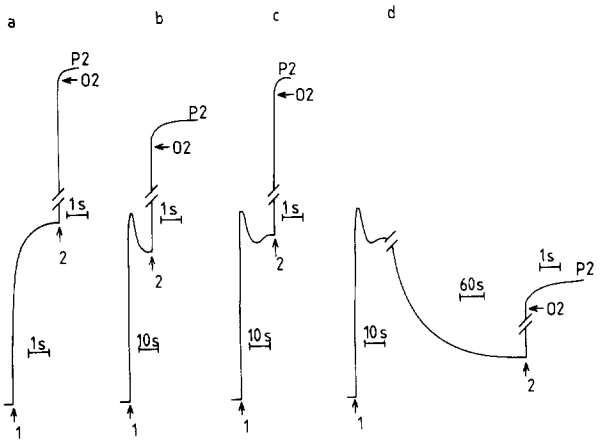

Fig. 3. Procedure for estimating the redox state of PS II electron acceptors. The leaf was initially excited with 100 μmol photons · m^{-2} · s^{-1} of 632.8 nm radiation (↑1), and then subjected, at a given point on the 685 nm fluorescence induction curve, to an additional excitation of 100 μmol photons · m^{-2} · s^{-1} (↑2). a, shows the second excitation (↑2) at point P on the induction curve; b, shows this excitation at point S; c, shows this excitation at point M; and d, shows this excitation at the steady-state fluorescence level T. F_{O2} represents the fluorescence level at O2, reached on completion of opening of the electronic shutter, and F_{P2} represents the maximum fluorescence level achieved at P2 after addition of the second excitation to the leaf. Resolution of F_{O2} was made using a transient recorder taking 1000 sample points within 100 ms on excitation of the leaf with laser 2 (data not shown in this figure); F_{P2} was determined using a longer sweep time. Note the difference in the time base for different sections of the figure. Estimation of the redox state of PS II electron acceptors is made from the ratio F_{V2}/F_{O2}, where F_{V2} is the variable fluorescence, given by $F_{P2} - F_{O2}$, generated on addition of the second laser. Normalization of F_{V2} on F_{O2} removes the possibility of changes in the variable fluorescence indicating non-photochemically induced changes in fluorescence yield.

various points throughout the F_{685} induction curve. The experimental procedure for this technique is illustrated in Fig. 3; the variable fluorescence generated on addition of the second excitation, F_{V2}, being determined from the difference in F_{685} at points O2 and P2 ($F_{V2} = F_{P2} - F_{O2}$). On irradiation of thylakoids at room temperature the rate of reduction of PS II electron acceptors has been shown to be considerably greater than the rate of electron flow from these acceptors to PS I [28], thus F_{V2} will be related to the proportion of electron acceptors in the oxidised state. When $F_{V2} = 0$ all the PS II traps are reduced. Normalization of F_{V2} on F_{O2} removes the possibility of changes in F_{V2} indicating non-photochemically induced changes in the 685 nm fluorescence yield. Thus, throughout this paper F_{V2}/F_{O2} is taken as indicative of the redox state of PS II electron acceptors. Fig. 4 shows that the kinetics of F_{685} exhibit antiparallel changes to F_{V2}/F_{O2} during P → T quenching and suggests that changes in the redox state of PS II electron acceptors make a major contribution to changes in F_{685} and F_{770} during the P → T phase of the induction curve.

It has been demonstrated that the redox state of the major secondary PS II electron acceptor, PQ, can be modified in isolated thylakoids by excitation intensity; high photon flux densities can maintain the PQ pool in a highly reduced state [2]. In principle such a technique can be used to modify the redox state of PQ in the intact leaf. Excitation of the dark-adapted bean leaf with a high photon flux density (approx. 1000 μmol photons · m^{-2} · s^{-1} of

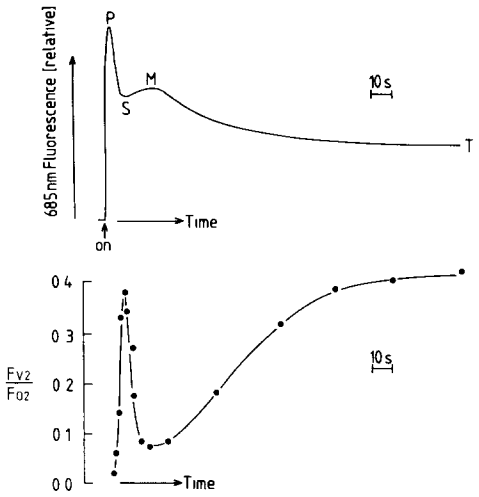

Fig. 4. Changes in F_{V2}/F_{O2} (as determined by the method illustrated in Fig. 3) throughout the P to T phase of the 685 nm fluorescence induction curve generated by exposing a bean leaf to 100 μmol photons · m^{-2} · s^{-1} of 632.8 nm radiation.

632.8 nm irradiation) enabled analysis to be made of the fluorescence induction curve with PQ being potentially maintained in a maximally reduced state. Under such conditions a monotonous quenching from P → T for both F_{685} and F_{770} is obtained (Fig. 5); no S → M rise, characteristic of non-saturating intensities being observed. Determination of F_{V2}/F_{O2} throughout the P → T phase of this induction curve showed that the proportion of PS II electron acceptors reduced increased marginally immediately after P but there then followed an unexpected progressive reoxidation of the acceptors during the course of the induction curve to T. At steady state fluorescence, T, under the high excitation energy, F_{V2}/F_{O2} = 0.22 (see Fig. 5), whilst at the lower excitation energy used in Fig. 4 F_{V2}/F_{O2} = 0.39, indicating that although the higher excitation energy maintained the PS II traps in a more reduced state, it does not effect a total trap closure at T. When leaves were exposed to excitation energies of laser 1 above 2000 μmol photons · m^{-2} · s^{-1}, the changes observed in F_{V2}/F_{O2} through out P → T quenching were similar to those observed with 1000 μmol photons · m^{-2} · s^{-1} (see Fig. 5) and show that at T such high excitation energies did not produce total PS II trap closure, a significant fraction of PS II electron acceptors remained oxidised.

The kinetics of 770 nm emission from bean leaves excited with high levels of irradiation were similar to those at 685 nm, although clearly not identical since F_{770}/F_{685} changed during P → T quenching (Fig. 5). The changes observed in F_{770}/F_{685} were again similar to those in F_{V2}/F_{O2} suggesting a possible relationship between the redox state of PS II electron acceptors and fluorescence emission from PS I and PS II.

The presence of components in the fluorescence emission spectrum having emission maxima at approx. 718 nm and 745 nm (Fig. 1) raised the question of whether the kinetics of emission at 745 nm were identical to those at 718 nm. The experiments described above involving the kinetics of F_{770} were repeated

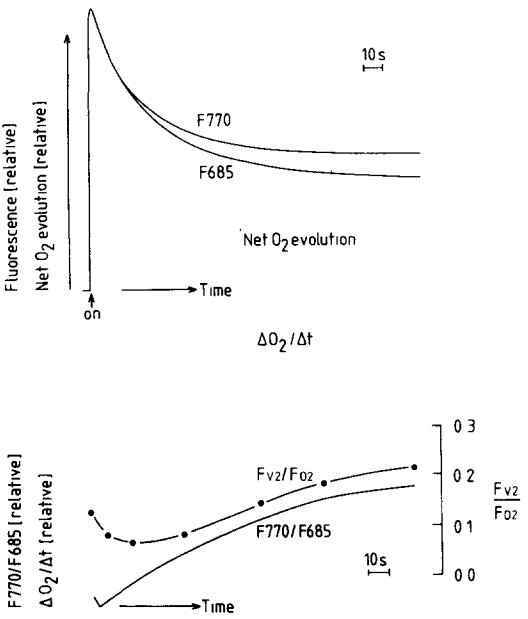

Fig. 5. Kinetics of fluorescence emission at 685 and 770 nm measured simultaneously from a bean leaf on exposure to 1000 μmol photons · m^{-2} · s^{-1} of 632.8 nm radiation. Changes in net O_2 evolution, F_{770}/F_{695} (———), the rate of O_2 evolution, $\Delta O_2/\Delta t$, (· · · · ·) and F_{V2}/F_{O2} (· — · — ·) are shown during fluorescence quenching from P to T. F_{V2}/F_{O2} was determined by the method illustrated in Fig. 3.

for F_{718} and F_{745}. The kinetics observed for F_{718} and F_{745} were similar to those of F_{770} at both high and low irradiation levels, and changes in F_{718}/F_{685} were qualitatively identical to those observed for F_{770}/F_{685}, suggesting that the chlorophyll components associated with the emission bands at 718 and 745 nm appear to be either identical or energetically closely coupled.

Discussion

This study has demonstrated that the redox state of PS II electron acceptors is a major regulatory factor in determining F_{685} during the P → T phase of the induction curve of bean leaves. At P under moderate irradiation the PS II electron acceptors are almost totally reduced since F_{V2}/F_{O2} is close to O (see Fig. 4). However, a rapid reoxidation of the PS II traps occurs after P and is presumably associated with an increased rate of electron flow from PQ to PS I. Such a hypothesis is consistent with the relatively high value of $\Delta O_2/\Delta t$, which is indicative of the rate of non-cyclic electron transport, observed after P (see Fig. 2). Similarly, the reduction of the PS II traps occurring between S and M on the induction curve is also consistent with the low values of $\Delta O_2/\Delta t$ observed during this phase. An increasing rate of non-cyclic electron flow after M can account for the reoxidation of PS II acceptors during M → T quenching.

The similarity in the kinetics of F_{685} and F_{770} during P → T quenching suggests that the redox state of PS II traps may play a major role in regulating emission from PS I. As PQ becomes oxidised the utilisation of excitation energy within PS II for photochemistry will increase, making less energy avail-

able for other PS II deexcitation process, i.e. energy transfer from PS II to PS I, PS II fluorescence and thermal deactivation, thus reoxidation of PQ will be associated with a decrease in both F_{685} and F_{770}. However, as the variable fluorescence at 770 nm, which is attributable to energy transfer from PS II, constitutes a considerably smaller fraction of the total fluorescence at 770 nm than is the case for 685 nm emission, a proportionally greater decrease in F_{685} than F_{770} must occur as PS II traps become reoxidised, with the result that F_{770}/F_{685} must increase. At both moderate (see Fig. 2) and high (see Fig. 5) excitation levels F_{770}/F_{685} is found to increase as PQ reoxidation occurs during fluorescence quenching. Clearly the redox state of PS II traps is a major factor in determining changes in F_{770}/F_{685}, however a comparison of changes in F_{770}/F_{685} (see Fig. 2) and F_{V2}/F_{O2} (see Fig. 4) during P → T quenching under moderate excitation shows that although the kinetics of both parameters are similar some significant differences are evident. For example, the magnitude of F_{V2}/F_{O2} is similar at P and M, and at S and T, however this is not the case for F_{770}/F_{685}; also the relative rate of increase of F_{770}/F_{685} immediately after M is considerably greater than that of F_{V2}/F_{O2}. Such differences imply that factors other than the redox state of the PS II traps also modify F_{770}/F_{685} during the induction curve. Changes in F_{770}/F_{685} which are not directly dependent upon changes in F_{V2}/F_{O2} could be produced by modification of stromal cation and ATP concentrations.

In vitro studies have related cation-induced modifications of energy distribution to PS I relative to PS II to changes in both the direct distribution of quanta absorbed by the light-harvesting chlorophyll *a/b* complexes to PS I and PS II [29] and the yield of energy transfer from PS II to PS I [30,31]. During P → T quenching changes in both non-cyclic and cyclic electron flow will modify the ΔpH across the thylakoid membranes [32,33], resulting in changes in the displacement and efflux of Mg^{2+} and other cations into the stroma [13,20, 34,35]. Increasing stromal cation concentrations may modify the microconformation of the membrane and the organization of the photochemical apparatus [11,16,36—39] with excitation energy distribution between the two photosystems being affected in favour in PS I. The suggestion that a large ΔpH across the thylakoid membrane produces fluorescence quenching by increased thermal deactivation of excited PS II chlorophyll molecules [18] is compatible with our observations, however no direct evidence for this is provided from this study.

ATP induced quenching of F_{685} in isolated chloroplasts is accompanied by an increase in the fraction of absorbed energy transferred to PS I and appears to be dependent upon the activation of a protein kinase by reduced PQ, which then effects the phosphorylation of the light-harvesting chlorophyll *a/b* complexes resulting in increased excitation of PS I [15]. Such ATP induced quenching could be implicated in vivo from the data presented in this paper. At P and M on the induction curve of the bean leaf PQ is highly reduced (see Fig. 4), thus ATP induced quenching of PS II fluorescence with a parallel increase in PS I emission may be implicated in P → S and M → T quenching. The possible involvement of ATP in the regulation of excitation energy distribution between PS I and PS II offers an attractive physiological mechanism by which the leaf can modify the rate of non-cyclic relative to cyclic electron transport and thus control the ATP : NADPH ratio within the cell.

Although currently we may only speculate, using information obtained from in vitro studies, on the nature of the complex interactions between the stroma and the thylakoid in vivo, it is evident that the activation of carbon metabolism (via the associated changes in stromal ATP and NADPH levels which also control the rate of electron transport) may play an important role in regulating the fluorescence emission quenching characteristics of the intact leaf by the mechanisms discussed above. Quantitation of the contribution of each of the factors determining the fluorescence quenching in vivo is required for further elucidation of this important problem.

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