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The relationship between the quantum yield of photosynthetic electron transport and quenching of chlorophyll fluorescence

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Measurements of the quantum yields of chlorophyll fluorescence and CO_2 assimilation for a number of plant species exposed to changing light intensity and atmospheric CO_2 concentrations and during induction of photosynthesis are used to examine the relationship between fluorescence quenching parameters and the quantum yield of non-cyclic electron transport. Over a wide range of physiological conditions the quantum yield of non-cyclic electron transport was found to be directly proportional to the product of the photochemical fluorescence quenching (qQ) and the efficiency of excitation capture by open Photosystem II (PS II) reaction centres (F_v/F_m). A simple fluorescence parameter, $\Delta\phi_F/\phi_{Fm}$, which is defined by the difference in fluorescence yield at maximal ϕ_{Fm}, and steady-state ϕ_{Fs}, divided by ϕ_{Fm}, can be used routinely to estimate changes in the quantum yield of non-cyclic electron transport. It is demonstrated that both the concentration of open PS II reaction centres and the efficiency of excitation capture by these centres will determine the quantum yield of non-cyclic electron transport in vivo and that deactivation of excitation within PS II complexes by non-photochemical processes must influence the quantum yield of non-cyclic electron transport.

Introduction

Analyses of the kinetics of chlorophyll fluorescence quenching induced in photosynthetic systems by exposure to light have provided considerable qualitative information on the organization and functioning of the photosynthetic apparatus. Recently, with the development of instruments capable of rapidly resolving the photochemical and non-photochemical fractions of fluorescence quenching [1,2], attempts have been made to quantitate the relationships between fluorescence quenching parameters and electron transport with a view to resolving factors involved in the regulation of electron transport in vivo. At low light intensities it is well established that the rate of electron transfer by PS II reaction centres of isolated chloroplasts is inversely related to the magnitude of the variable fluorescence emission [3,4], and thus it has been argued that a linear relationship between photochemical quenching (qQ) and the quantum yield of non-cyclic electron transport may be expected under light conditions in which the rate of PS II reaction centre turnover is limiting for non-cyclic electron transport. However, a strict linear relationship between these parameters has not been found for barley [5] and sunflower [6] leaves and barley protoplasts [7] over a range of light intensities which were not saturating for photosynthesis. As the rate of non-cyclic electron transport increases with light intensity, an increase in high-energy state quenching (qE), which results from the increased energization of the thylakoid membrane, will occur concomitantly with a decrease in qQ [8]. It has been suggested that this increase in qE produces a reduction in the quantum yield of open PS II reaction centres [5–7,9,10] and can account for a non-linear relationship between qQ and the quantum yield of non-cyclic electron transport. Although the mechanism by which thylakoid energization induces a non-photochemical quenching in PS II is unknown, it is argued that increases in qE could constitute a potential excitation energy drain in PS II which would compete effectively with open PS II reaction centres [6,9,10]. If this hypothesis is correct then it has important implications for the regulation of the rate of PS II electron transport

Abbreviations: PS, Photosystem; qE, high-energy state quenching; qQ, photochemical quenching; ϕ_{CO_2}, quantum yield of CO_2 assimilation; ϕ_e, quantum yield of photosystem II electron transport; ϕ_F, yield of fluorescence (subscripts o, m, s and v define minimal, maximal, steady-state and variable levels).

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and the protection of PS II reaction centres from over-excitation and consequent damage.

In this study we argue that theoretically the quantum yield of non-cyclic electron transport should be directly proportional to the product of qQ and the efficiency of excitation capture by open PS II centres (generally designated as F_v/F_m). Experiments with a range of plants and using changes in light intensity, the time of induction of photosynthesis and the atmospheric CO_2 concentrations to modify the quantum yield of non-cyclic electron transport are used to demonstrate that under almost all of the physiological conditions studied a linear relationship exists between these parameters. Thus, the data presented support the contentions that (i) both the concentration of open PS II reaction centres and the efficiency of excitation energy capture by these open PS II centres will determine the quantum yield of non-cyclic electron transport in vivo, and (ii) changes in any non-photochemical process involved in the deactivation of excitation within PS II complexes must influence the quantum yield of non-cyclic electron transport. The data presented also demonstrate that estimation of changes in the quantum yield of non-cyclic electron transport in vivo can be made from simple measurements of the fluorescence yield at the steady-state and maximal levels.

Materials and Methods

Mature leaf tissue was obtained from plants of red campion (*Silene dioica*), barley (*Hordeum vulgare* var. Clermont) and chlorophyll-*b*-less barley (*H. vulgare* chlorina F-2 mutant), which were grown at 20 °C in a glasshouse supplemented with artificial light to give a minimum photon flux density of 550 $\mu mol \cdot m^{-2} \cdot s^{-1}$ for a 16 h photoperiod. Plants of maize (*Zea mays* L. cv. LG11) were grown at 25 °C from seed sown in John Innes potting compost No. 2 in a controlled environment cabinet (Fi-totron H600, Fisons plc, Loughborough, U.K.) and photosynthetically active radiation was supplied at 250 $\mu mol \cdot m^{-2} \cdot s^{-1}$ during 16 h photoperiods.

Measurements of carbon dioxide assimilation were made on detached monocotyledonous (barley and maize) leaves at 25 °C in a leaf chamber as previously described [11], except that the leaf tissue was illuminated from both sides to ensure that chlorophyll fluorescence and gas exchange measurements were made from populations of chloroplasts in the same physiological state [12]. Dicotyledonous (red campion) leaves were illuminated only on the upper surface. Measurements of modulated chlorophyll fluorescence emission from the upper surface of the leaf were made using a pulse amplitude modulation fluorimeter (PAM-101, H. Walz, Effeltrich, F.R.G.) [13]. The measuring modulated light intensity was approx. 0.1 $\mu mol \cdot m^{-2} \cdot s^{-1}$ and sufficiently low not to produce any significant variable fluorescence.

Dark-adapted leaves were initially exposed to the weak, modulated measuring beam, followed by exposure to a continuous, actinic white light (L1). A 500 ms pulse of high-intensity (10000 $\mu mol \cdot m^{-2} \cdot s^{-1}$) white light (L2) was used to produce a transient closure of the PS II photochemical reaction centres. Far-red light (L3) (190 $\mu mol \cdot m^{-2} \cdot s^{-1}$ at 710–730 nm) was used to produce maximal oxidation of PS II electron acceptors. The protocol for the fluorescence measurements is illustrated in Fig. 1. The initial minimal fluorescence yield ϕ_{Fo} was measured after at least 1 h dark-adaptation of the leaf and the maximal fluorescence yield ϕ_{Fm} was obtained by exposing the leaf sample simultaneously to the actinic light (L1) and the saturating light pulse (L2). The steady-state fluorescence yield, ϕ_{Fs}, was determined in the actinic light, L1. During fluorescence induction or at steady state the yield of fluorescence corresponding to that which would be produced on maximal closure of PS II reaction centres, ϕ_{Fm}, was determined by exposing the leaf to the saturating light pulse, L2. After reaching steady state the fluorescence yield, ϕ_{Fo}, corresponding to that produced on maximal oxidation of the PS II electron acceptors, but yet with a similar amount of non-photochemical quenching to that at ϕ_{Fs}, was determined by exposing the leaf to far-red light (L3) on removal of the actinic light (L1). Photochemical quenching (qQ) was determined essentially as described previously [2] except that quenching of ϕ_{Fo} was taken into account [14].

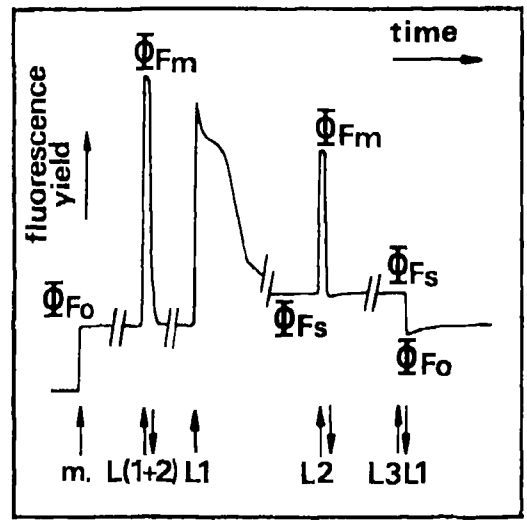

Fig. 1. Experimental protocol for determination of ϕ_F and qQ. L1, white actinic light (variable intensity); L2, white light saturating 500 ms pulse (10000 $\mu mol \cdot m^{-2} \cdot s^{-1}$); L3, far-red light (190 $\mu mol \cdot m^{-2} \cdot s^{-1}$); m., measuring modulated light (0.1 $\mu mol \cdot m^{-2} \cdot s^{-1}$); ↑ indicates light on; ↓ indicates light off.

Results and Discussion

In the context of the experimental protocol shown in Fig. 1 and using the principles stated by Schreiber et al. [2], qQ is determined from:

$$qQ = \frac{\phi_{Fm} - \phi_{Fs}}{\phi_{Fm} - \phi_{Fo}} = \frac{\phi_{Fm} - \phi_{Fs}}{\phi_{Fv}} \quad (1)$$

where ϕ_F defines the yield of fluorescence at the fluorescence level designated by the subscript (see the legend of Fig. 1 for definition of fluorescence levels). The parameter qQ is a measure of the fluorescence quenching that is attributable to the proportion of PS II reaction centres that are in an oxidised or 'open' state.

The efficiency of excitation energy capture by open PS II reaction centres can be defined as ϕ_{Fv}/ϕ_{Fm} if no change in non-photochemical quenching at the reaction centres is assumed [15–17], thus in this case ϕ_{Fv}/ϕ_{Fm} and qQ can be used to determine the excitation energy density being utilized to drive PS II photochemistry, D, where

$$D = \frac{\phi_{Fv}}{\phi_{Fm}} \cdot qQ \cdot I_a \quad (2)$$

and I_a is the photon flux density absorbed by PS II complexes. Using such formulations the quantum yield of PS II electron transport, ϕ_e (i.e. the efficiency of PS II electron transport per quantum absorbed by PS II complexes or PS II photochemical yield), can be defined as:

$$\phi_e = \frac{D}{I_a} = \frac{\Delta\phi_F}{\phi_{Fm}} \quad (3)$$

where

$$\Delta\phi_F = \phi_{Fm} - \phi_{Fs} \quad (4)$$

Hence, it should be possible from measurements only of F_m and F_s, using a modulated fluorescence technique [1,2], to estimate the quantum yield of PS II electron transport. It is evident from Eqns. 2 and 3 that any factor which affects the capture of excitation energy by open PS II reaction centres, i.e. ϕ_{Fv}/ϕ_{Fm}, will modify the quantum yield of PS II electron transport. Changes in excitation energy transfer between PS II complexes would be expected to affect equally the rate of electron transport through PS II and the amplitude of fluorescence; this has been shown experimentally to be the case [4].

In order to test the hypothesis that $\Delta\phi_F/\phi_{Fm}$ equates to the quantum yield of PS II electron transport in leaf tissue, measurements of the fluorescence parameters shown in Fig. 1 and the efficiency of CO_2 assimilation per quantum incident upon the leaf, ϕ_{CO_2}, were made on leaf tissue of *S. dioica*. When leaves of C_3 plants are exposed to low O_2 levels, in order to minimise photorespiration, the rate of CO_2 assimilation provides an estimate of the rate of linear electron transport, i.e.

$$\phi_{CO_2} = \phi_e \cdot \frac{I_a}{I_i} \cdot \frac{1}{k} \quad (5)$$

where I_i is the photon flux density incident upon the leaf and k is the number of electron equivalents required to reduce 1 mol of CO_2. *S. dioica* leaves were exposed to 400 ppm CO_2 and 1% (v/v) O_2 in N_2 for 30 min in the dark or in a photon flux density of 1500 $\mu mol \cdot m^{-2} \cdot s^{-1}$ and then measurements of ϕ_{Fv}/ϕ_{Fm}, $\Delta\phi_F/\phi_{Fm}$, qQ and ϕ_{CO_2} were made at a photon flux density of 34 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (Table I). The pretreatment in high light produced a 14% decrease in ϕ_{CO_2} compared to the dark pretreatment. Eqns. 3 and 5 predict that $\Delta\phi_F/\phi_{Fm}$ should show a close relationship with ϕ_{CO_2}, and it is seen from Table I that this is the case experimentally. It is also evident that both qQ and ϕ_{Fv}/ϕ_{Fm} can exhibit large variations without affecting significantly the predicted proportional relationship between ϕ_{CO_2} and $\Delta\phi_F/\phi_{Fm}$. Since $\Delta\phi_F/\phi_{Fm}$ is the product of ϕ_{Fv}/ϕ_{Fm} and qQ (see Eqns. 2 and 3), these data demonstrate that ϕ_{CO_2} is intimately related to both the efficiency of excitation energy capture by open PS II reaction centres, estimated by ϕ_{Fv}/ϕ_{Fm}, an the concentration of open PS II centres, which is related to qQ. Clearly any non-photochemical deactivation of PS II complexes will influence ϕ_{Fv}/ϕ_{Fm} and thus influence ϕ_{CO_2}. The model predicting the relationship between ϕ_{CO_2} and $\Delta\phi_F/\phi_{Fm}$ has been tested experimentally for a range of C_3 species, and data (not shown) similar to those shown in Table I suggest that the relationship is ubiquitous.

TABLE I

The relationships between the quantum yield of CO_2 assimilation and fluorescence parameters in leaves pretreated in the dark and in high light

Comparison of the fluorescence parameters qQ, ϕ_{Fv}/ϕ_{Fm}, $\Delta\phi_F/\phi_{Fm}$ and ϕ_{CO_2} (see text for definitions) for leaves of *S. dioica* which had been either kept in the dark (Dark) or in a photon flux density of 1500 $\mu mol \cdot m^{-1} \cdot s^{-1}$ (High light) for 30 min prior to exposing the leaves to a photon flux density of 34 $\mu mol \cdot m^{-2} \cdot s^{-1}$ and determining these parameters. The leaves were continuously exposed to 400 ppm CO_2 and 1% O_2 in N_2. The percentage differences between the dark and high light treatments are given in parentheses. The decrease in ϕ_{Fv}/ϕ_{Fm} after the high light treatment was not due to irreversible photoinhibitory damage; the leaves recovered within 1 h of being placed in the dark.

Parameter	Dark	High light	
ϕ_{CO_2}	0.051	0.044	(−13.8%)
qQ	0.690	0.824	(+19.4%)
ϕ_{Fv}/ϕ_{Fm}	0.712	0.526	(−26.1%)
$\Delta\phi_F/\phi_{Fm}$	0.492	0.432	(−12.2%)

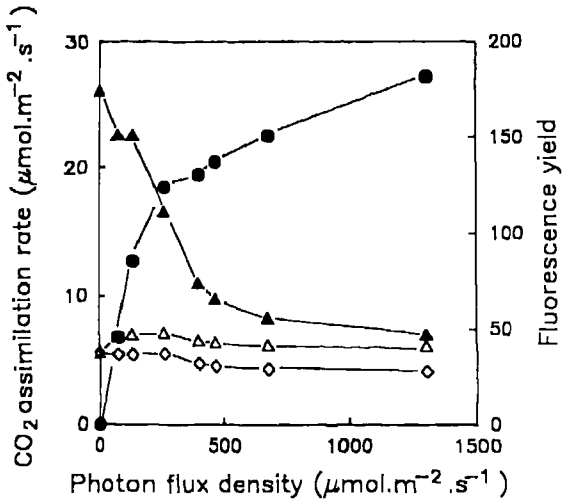

Fig. 2. Changes in the rate of CO_2 assimilation (●) and the fluorescence yields, ϕ_{Fm} (▲), ϕ_{Fs} (△) and ϕ_{Fo} (◇), of a wild-type barley leaf at steady state as a function of light intensity. Measurements were made in 2500 ppm CO_2 and 1% O_2 in N_2.

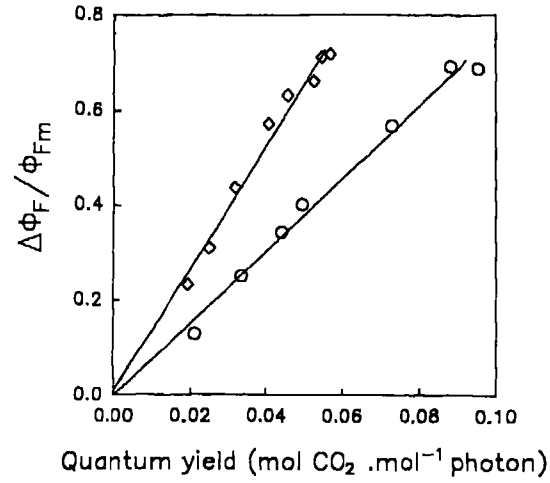

Fig. 4. The relationship between the quantum yield of CO_2 assimilation and the photochemical yield of PS II, i.e. $\Delta\phi_F/\phi_{Fm}$, in a wild-type (○) and a chlorophyll-*b*-less mutant (◇) barley leaf at steady state over the range of light intensities shown in Figs. 2 and 3. Experimental conditions were as for Fig. 2.

The effect of PS II antenna size on the relationship between ϕ_{CO_2} and $\Delta\phi_F/\phi_{Fm}$ was examined by comparing the effects of increasing light intensity on leaves of wild-type barley and a chlorophyll-*b*-less barley mutant, which lacks functional light-harvesting chlorophyll II and exhibits a substantially reduced antenna size of PS II [18]. The changes in the rate of CO_2 assimilation measured in 1% O_2 and 2500 ppm CO_2 in N_2 to minimise photorespiration, ϕ_{Fm}, ϕ_{Fs} and ϕ_{Fo} are shown for the wild type and mutant barley as a function of light intensity in Fig. 2 and Fig. 3 respectively. As expected, at limiting light levels the mutant is less efficient at CO_2 assimilation and has a lower ϕ_{Fm} and ϕ_{Fo}. The predicted linear relationships were observed between ϕ_{CO_2} and $\Delta\phi_F/\phi_{Fm}$ for both the wild-type and mutant leaves, however the gradients of the relationship differed (Fig. 4). Since I_a in Eqn. 5 will be markedly different for the wild-type and mutant, but the light-saturated rates of CO_2 assimilation are similar (Figs. 2 and 3), the constant relating $\Delta\phi_F/\phi_{Fm}$ to ϕ_{CO_2} will be different and related to the difference in PS II antenna size between the two leaf types. Differences in PS II antenna size would be expected to result in differences in ϕ_{Fm}, ϕ_{Fo} and ϕ_{CO_2} at light levels limiting for CO_2 assimilation. It is of note that the ratio of the gradients of $\Delta\phi_F/\phi_{Fm}$ plotted against ϕ_{CO_2} in Fig. 4 for the mutant/wild type is 1.7, which is similar to the ratios of ϕ_{Fm}, ϕ_{Fo} and ϕ_{CO_2} calculated at limiting light levels from Fig. 2 and Fig. 3 for the wild type/mutant.

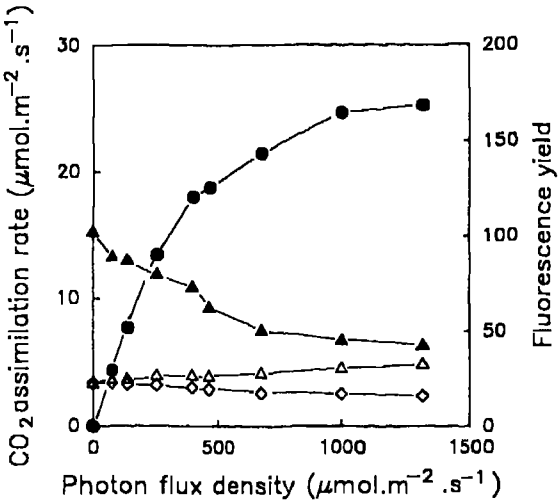

Fig. 3. Changes in the rate of CO_2 assimilation (●) and the fluorescence yields, ϕ_{Fm} (▲), ϕ_{Fs} (△) and ϕ_{Fo} (◇), of a leaf of the chlorophyll-*b*-less barley mutant at steady state as a function of light intensity. Experimental conditions were as for Fig. 2.

The possibility that the relationship between ϕ_{CO_2} and $\Delta\phi_F/\phi_{Fm}$ may be different in leaves of C_4 plants was examined in maize leaves exposed to increasing incident light intensities (Fig. 5). The leaves were exposed to 340 ppm CO_2 and 20% O_2 as C_4 plants exhibit minimal photorespiratory activity in air. A linear relationship was observed between ϕ_{CO_2} and $\Delta\phi_F/\phi_{Fm}$ over a wide range of incident light intensities, however the relationship deviated from linearity at very high light intensities. The rate of CO_2 assimilation in maize changes markedly during the slow induction of photosynthesis after a long dark period and also when at steady state with changes in atmospheric CO_2 concentration [19]. Thus, the relationship $\Delta\phi_F/\phi_{Fm}$ in maize leaves can be examined independently of changes in light intensity by measuring these parameters during the induction of photosynthesis and at steady-state photosynthesis when the atmospheric concentration of CO_2 is changed. The relationship between ϕ_{CO_2} and $\Delta\phi_F/\phi_{Fm}$ during induction of photosynthesis and at different CO_2

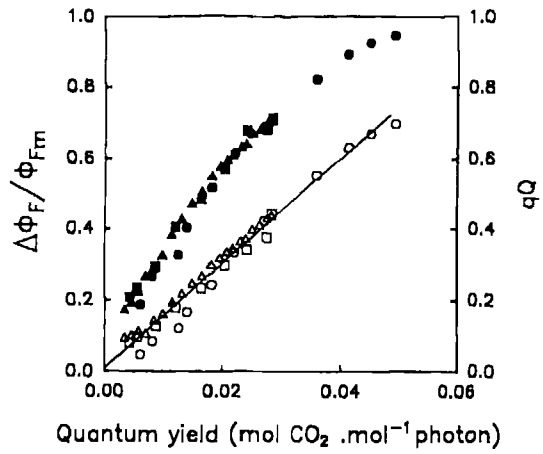

Fig. 5. The relationship between the quantum yield of CO_2 assimilation and the photochemical yield of PS II, i.e., $\Delta\phi_F/\phi_{Fm}$ (○, □, △), and the fluorescence photochemical quenching coefficient, qQ (●, ■, ▲), for a maize leaf at steady state as a function of light intensity (○, ●), in a range of atmospheric CO_2 concentrations (□, ■) or during photosynthetic induction (△, ▲). Measurements were made in air over a photon flux density range of 40–2700 μmol·m^{-2}·s^{-1} (○, ●), over an atmospheric CO_2 concentration range of 30–370 ppm (□, ■) at a photon flux density of 650 μmol·m^{-2}·s^{-1} and during photosynthetic induction (△, ▲) in air at a photon flux density of 650 μmol·m^{-2}·s^{-1}.

concentrations was found to be linear (Fig. 5) with a gradient similar to that observed from data obtained from maize leaves by changing the incident light intensity above the linear region of the light dosage-response curve (see Fig. 5). Thus, it would appear that for maize leaves the predicted direct proportionality between ϕ_{CO_2} and $\Delta\phi_F/\phi_{Fm}$ does occur.

Factors which can modify $\Delta\phi_F/\phi_{Fm}$ independently of ϕ_{CO_2}, or vice versa, will produce a deviation from linearity in the relationship between the two parameters. Changes in $\Delta\phi_F/\phi_{Fm}$ which are independent of ϕ_{CO_2} would involve a differential effect on ϕ_{Fm} and ϕ_{Fs}. Changes in fluorescence quenching by oxidized plastoquinone [20] and by non-photochemically quenched, closed PS II reaction centres [16] would induce such differential changes in ϕ_{Fm} and ϕ_{Fs}. The relationship between $\Delta\phi_F/\phi_{Fm}$ and ϕ_{CO_2} is dependent upon the accuracy with which the fluorescence parameters and ϕ_{CO_2} can be measured. Accurate determination of ϕ_{CO_2} can be difficult due to the problems in estimating the rate of respiration at the light intensity at which the measurement of ϕ_{CO2} is being made. Light-induced inhibition of respiration could account for the non-linearity observed between ϕ_{CO_2} and $\Delta\phi_F/\phi_{Fm}$. Also changes in the proportion of electrons, generated by non-cyclic electron transport, which are utilized by sinks other than CO_2 reduction would result in a change in $\Delta\phi_F/\phi_{Fm}$ but not ϕ_{CO_2}. Similarly, changes in the rate of cycling of electrons around PS II, if this does actually occur, would modify ϕ_{CO_2} differently from $\Delta\phi_F/\phi_{Fm}$. Non-linearity between $\Delta\phi_F/\phi_{Fm}$ and ϕ_{CO_2} would also result if different populations of pigment-proteins contributed to emissions at the F_o and F_m levels and these populations were differentially quenched by non-photochemical quenching processes. This could be the case if PS I pigments contribute significantly to F_o but not F_v. Measurements made on ϕ_{Fo} at 676 nm and wavelengths above 710 nm indicated that the same proportion of non-photochemical quenching of ϕ_{Fo} occurred at 676 nm compared to the longer wavelengths where the contribution of PS I emissions would be greater (data not shown). This would suggest that the contribution of PS I to ϕ_{Fo} is minimal or alternatively that non-photochemical quenching processes affect equally the PS I and PS II pigment matrices involved in emission at the F_0 level.

It is evident from Eqns. 2 and 3 that the quantum yield of non-cyclic electron transport is a function of qQ and ϕ_{Fv}/ϕ_{Fm}, i.e. the concentration of open PS II reaction centres and the efficiency with which photons absorbed by PS II complexes are utilized for photochemistry by these open PS II centres respectively. Consequently if changes in ϕ_{Fv}/ϕ_{Fm} occur, then qQ cannot be used to estimate directly the apparent quantum yield of non-cyclic electron transport. This is clearly seen from data obtained from maize (Fig. 5) and barley (Fig. 6) whereas when the product of qQ and ϕ_{Fv}/ϕ_{Fm} is calculated (this is equivalent to $\Delta\phi_F/\phi_{Fm}$ – see Eqns. 2–4) a linear relationship with ϕ_{CO_2} results.

The data presented in this paper demonstrate unequivocally that the quantum yield of linear electron transport is dependent upon both the concentration of open PS II reaction centres and the efficiency with which these open centres can capture and utilise excita-

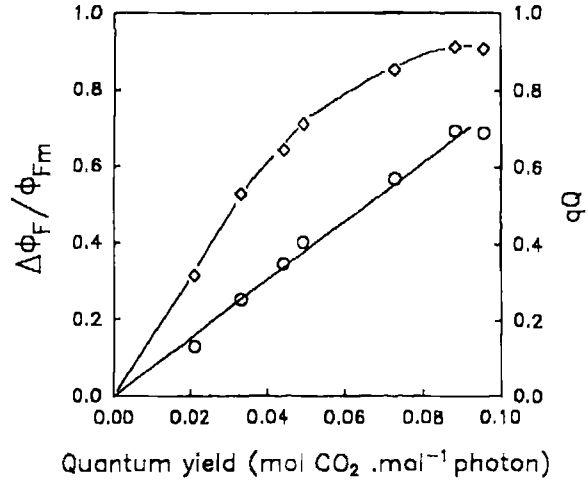

Fig. 6. The relationship between the quantum yield of CO_2 assimilation and the photochemical yield of PS II, i.e. $\Delta\phi_F/\phi_{Fm}$ (○), and the fluorescence photochemical quenching coefficient, qQ (◇), for a wild-type barley leaf at steady state over the range of light intensities shown in Fig. 2. Experimental conditions were as for Fig. 2.

tion energy trapped within PS II complexes. A consequence of this is that the relatively simple fluorescence parameter $\Delta\phi_F/\phi_{Fm}$, defined by $(\phi_{Fm} - \phi_{Fs})/\phi_{Fm}$, can be used to monitor changes in the quantum yield of linear electron transport in vivo. This is particularly important for routine measurements of photosynthetic performance of leaves since there is no requirement to determine ϕ_{Fo} in order to assess the quantum yield of linear electron transport. It is also evident from this study that any factor which affects the efficiency of capture of excitation energy by open PS II reaction centres, e.g. photoinhibition [21] and high-energy state non-photochemical quenching [7,8,22], will modify the rate of electron transport through the PS II centres and also the fluorescence parameters ϕ_{Fv}/ϕ_{Fm} and $(\phi_{Fm} - \phi_{Fs})/\phi_{Fm}$.

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References

1 Ogren, E. and Baker, N.R. (1985) Plant Cell Environ. 8, 539–547.
2 Schreiber, U., Schliwa, U. and Bilger, W. (1986) Photosynth. Res. 10, 51–62.
3 Delosme, R., Joliot, P. and Lavorel, J. (1959) C.R. Acad. Sci. Ser. D Paris 249, 1409–1411.
4 Bennoun, P. and Li, Y.S. (1973) Biochim. Biophys. Acta 292, 162–168.
5 Scholes, J., Horton, P. and Lewis, D. (1987) Research Institute for Photosynthesis, Annual Report, pp. 45–48, University of Sheffield.
6 Weis, E. and Berry, J.A. (1987) Biochim. Biophys. Acta 894, 198–208.
7 Horton, P. and Hague, A. (1988) Biochim. Biophys. Acta 932, 107–115.
8 Quick, W.P. and Horton, P. (1984) Proc. Roy. Soc. Lond. B220, 371–382.
9 Krause, G.H. and Laasch, H. (1987) Progress in Photosynthesis Research (Biggins, J., ed.), Vol. 4, pp. 19–25, Martinus Nijhoff, Dordrecht.
10 Weis, E., Ball, J.T. and Berry, J.A. (1987) Progress in Photosynthesis Research (Biggins, J., ed.), Vol. 2, pp. 553–556, Martinus Nijhoff, Dordrecht.
11 Ireland, C.R., Baker, N.R. and Long, S.P. (1987) Biochim. Biophys. Acta 893, 434–443.
12 Long, S.P., Farage, P.K., Bolhar-Nordenkampf, H.R. and Rohrhofer, U. (1988) Planta, in press.
13 Schreiber, U. (1986) Photosynth. Res. 9, 261–272.
14 Bilger, W. and Schreiber, U. (1986) Photosynth. Res. 10, 303–308.
15 Kitajima, M. and Butler, W.L. (1975) Biochim. Biophys. Acta 376, 105–115.
16 Butler, W.L. and Kitajima, M. (1975) Biochim. Biophys. Acta 376, 116–125.
17 Baker, N.R. and Horton, P. (1987) Photoinhibition (Kyle, D.J., Osmond, C.B. and Arntzen, C.J., eds.), pp. 145–168, Elsevier, Amsterdam.
18 Ghirardi, M.L., McCauley, S.W. and Melis, A. (1986) Biochim. Biophys. Acta 851, 331–339.
19 Ireland, C.R., Long, S.P. and Baker, N.R. (1984) Planta 160, 550–558.
20 Vernotte, C., Etienne, A. and Briantais, J.M. (1979) Biochim. Biophys. Acta 545, 519–527.
21 Bjorkman, O. (1987) Photoinhibition (Kyle, D.J., Osmond, C.B. and Arntzen, C.J., eds.), pp. 123–144, Elsevier, Amsterdam.
22 Krause, G.H., Vernotte, C. and Briantais, J.-M. (1982) Biochim. Biophys. Acta 679, 116–124.