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Hypothesis

Two fundamentally different types of variable chlorophyll fluorescence in vivo

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Abstract Upon onset of saturating continuous light only the first part of the observed polyphasic fluorescence rise follows Q_A reduction (photochemical phase), whereas the remaining part (thermal phases) is kinetically limited by relatively slow reactions with light saturated half-times in the order of 10–50 ms. A simple hypothesis is presented for the interpretation of these fundamentally different types of variable fluorescence. The hypothesis, which is based on the reversible radical pair model of PSII, assumes stimulation of both prompt and recombination fluorescence upon Q_A reduction, with only recombination fluorescence being in competition with nonradiative energy loss processes at the reaction centers. It is proposed that changes in the rate constants of these processes modulate the yield of recombination fluorescence in closed centers, thus causing large variations in the maximal fluorescence yield and also giving rise to the 'thermal phases'. This hypothesis can reconcile numerous experimental findings which so far have seemed difficult to interpret.

Key words: Chlorophyll fluorescence; Photosynthesis; Photosystem II; Reversible radical pair model; Polyphasic fluorescence rise

1. Introduction

Analysis of chlorophyll fluorescence yield has evolved as one of the most successful approaches for noninvasive assessment of photosynthesis in vivo [1,2]. In particular, fluorescence quenching analysis by the so-called saturation pulse method provides information on photochemical energy conversion and nonradiative energy dissipation in PSII [3,4]. This method relies on pulses of saturating light in order to cause rapid closure of reaction centers and to induce maximal fluorescence yield, Fm. It has been shown that the fluorescence rise kinetics in saturating light display two well separated parts (photochemical and thermal phases) [5–8]. The photochemical phase is limited by light absorption and determined by the rate of Q_A reduction, which at the available high light intensities can be completed in less than 1 ms [9]. On the other hand, above a certain light intensity (ca. 1500 μmol quanta m^{-2} s^{-1} photosynthetically active radiation, PAR), the rate of the thermal phases becomes saturated at half-times in the order of 10–50 ms [6].

In Fig. 1 the fluorescence information which may be obtained with different experimental approaches is summarized and the notations of the characteristic fluorescence levels are illustrated. Trace 1 shows a typical slow recording with a PAM fluorometer when a 300 ms pulse of saturating 650 nm light is applied to a dark-adapted sample of spinach chloroplasts. The fluorescence yield is increased from a minimal level, Fo (Q_A fully oxidized), to a maximal level, Fm (Q_A fully reduced and nonphotochemical quenching minimal). When the fluorescence excited by the saturating 650 nm light is directly measured with high time resolution, the polyphasic rise kinetics can be resolved (trace 2, 100 ms scale, and trace 4, 500 μs scale). A rapid rise (Fo–I_1, photochemical phase) is followed by a small dip (visible in trace 2) and the slower thermal phases I_1–I_2 and I_2–Fm. The ratio of the amplitudes of photochemical and photothermal phases is approximately 60:40. In the presence of DCMU, the thermal phases are eliminated (trace 3, 500 μs scale), with the amplitude of the photochemical phase being equivalently increased, while its half-rise time is unchanged (165 μs). The latter finding confirms that under the given conditions the light intensity is sufficiently high to induce full reduction of Q_A in the course of the Fo–I_1 rise in the absence of DCMU. It should be noted that for unknown reasons the maximal yield reached in the presence of DCMU is somewhat variable, depending on chloroplast preparations and DCMU concentration. In previous work on spinach chloroplasts it often did not exceed the I_2 level [6]. When fluorescence yield is assessed by the pump-and-probe method as a function of the dark-time between pump and probe flashes (right panel of Fig. 1), the maximal values correspond to the I_1 and I_2 levels, in the absence and presence of DCMU, respectively. It seems clear that at the shortest dark-time (20 μs with the used set-up) there is nonphotochemical quenching of maximal fluorescence yield which in the presence of DCMU decays within 1 ms ($t_{1/2} \sim 50$ μs). It may be assumed that similar quenching (but possibly with different decay kinetics) is also effective in the absence of DCMU, with relaxation of quenching being superimposed by the increase of photochemical quenching due to Q_A reoxidation. Therefore, the $F_{30\mu s}$ commonly measured by the pump-and-probe method [10] does *not* represent the value of Fm, on which the saturation pulse method is based [3,4].

The mechanism responsible for fluorescence quenching at the I_1 level relative to Fm has been a matter of debate [5–11]. In view of the widespread use of saturation pulse quenching analysis in photosynthesis research, a clarification of this question is important. Here we wish to present a hypothesis to explain transient fluorescence quenching in the presence of Q_A^- which, like the original Klimov-Shuvalov hypothesis [12,13], assumes a substantial contribution of recombination fluorescence to variable fluorescence. The new hypothesis is

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Abbreviations: DCMU, 3-(3,4-dichlorophenyl)-1,1-dimethylurea; PAM, pulse amplitude modulation; PQ, plastoquinone; Q_A and Q_B, primary and secondary quinone acceptors of photosystem II

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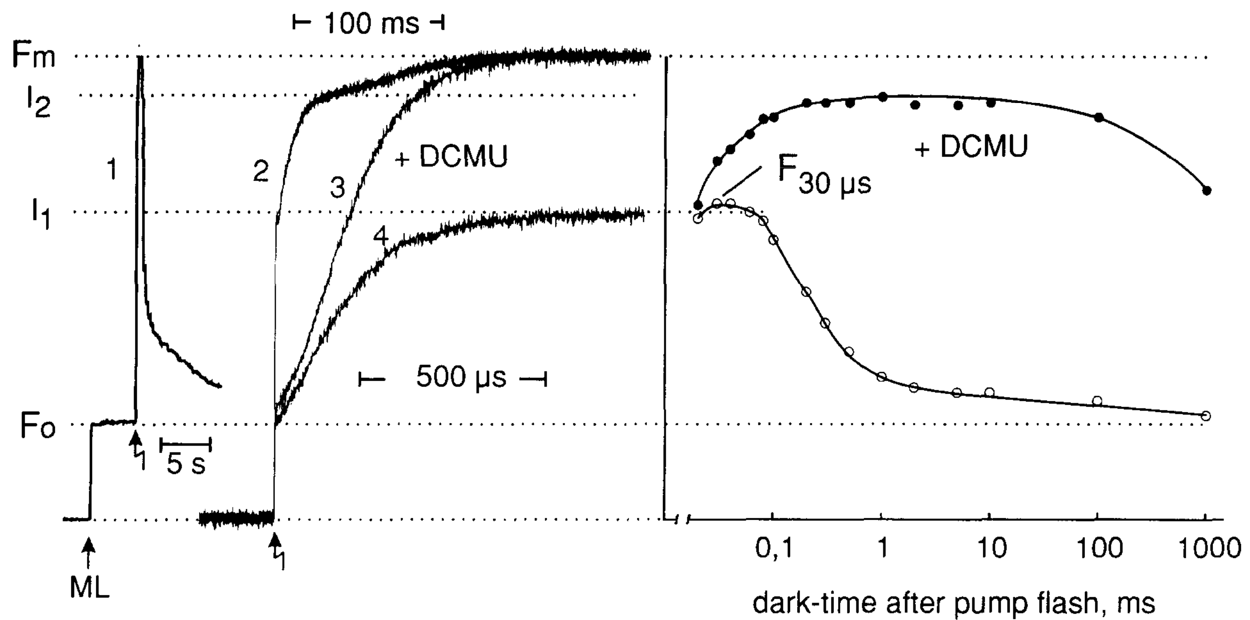

Fig. 1. Assessment of variable chlorophyll fluorescence by different experimental approaches, and notations of characteristic fluorescence levels. All measurements with dark-adapted intact spinach chloroplasts at 0.5 μg Chl ml^{-1} in the same cuvette and optical geometry, as described in [11]. Different sources for fluorescence excitation and detectors for fluorescence emission were applied in order to assess fluorescence yield by the PAM method (trace 1), in continuous light (traces 2–4) and by the pump-and-probe method (right panel). The same high intensity LED array with an intensity of 12 000 μmol m^{-2} s^{-1} PAR served as saturation pulse source in the recordings of traces 1–4 and at the same time as fluorescence excitation source for traces 2–4. DCMU concentration was 5 μM. The pump-and-probe measurements were carried out with the same Xe-PAM Fluorometer (see [42]) with which trace 1 was recorded. The pump flashes were applied via fiberoptics using a separate Xe discharge lamp (half-pulse width 1.5 μs). Fo, minimal fluorescence yield of dark-adapted sample. I_1, first intermediate level reached within 1 ms in saturating continuous light (saturation pulse); I_2, second intermediate level, reached within 50 ms. $F_{30\mu s}$, fluorescence yield measured 30 μs after saturating single turnover (pump) flash with the help of weak (probe) flash. ML, onset of measuring light (Xe-PAM fluorometer), consisting of the same weak (probe) flashes as used for pump-and-probe measurements, with 2 Hz repetition rate. See text for further explanations.

based on the more recent reversible radical pair model of PSII [14]. Arguments are put forward that recombination fluorescence may be preferentially quenched by nonradiative energy loss processes at the level of the primary radical pair, the rate constants of which are variable and transiently stimulated in saturating light.

2. Major points of the hypothesis

In Fig. 2 a simplified scheme of the reversible radical pair model of PSII is shown, as derived from fluorescence lifetime measurements [14,15]. In principle, according to this model numerous parameters may control chlorophyll fluorescence yield, which corresponds to the yield of singlet excitation in PSII, including antenna and reaction centers. In practice, it has been known for some time that the fluorescence yield is substantially increased when Q_A is reduced and within the framework of the reversible radical pair model, this is due to a decrease of the rate constant of primary charge separation k_1 and an increase of the recombination rate $k_{-1}\cdot[P^+Pheo^-]$. Both changes result in an increase of the number of excited states and hence can contribute to so-called variable fluorescence. In the past, the contribution of recombination fluorescence had been considered to be relatively small [14–16], as the available data suggested rather low yields of radical pair formation when Q_A was reduced. However, absorption measurements with PSII core particles led to the conclusion that in principle even in the presence of Q_A^- radical pair formation can take place with high yields [17]. Also more recent evidence suggests that, depending on conditions, substantial rates of radical pair formation in the presence of Q_A^- are possible [18,19]. Hence, when upon the transition from Q_A to Q_A^- the fluorescence yield is increased, part of this increase is due to a decreased rate of charge separation ($k_1\cdot[P^*Pheo]$), while, however, another part may be due to an increased rate of recombination ($k_{-1}\cdot[P^+Pheo^-]$). The reversible pair model predicts that the contribution of the two types of variable

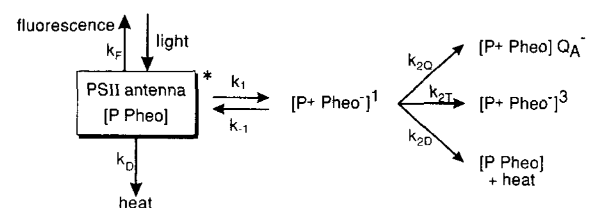

Fig. 2. Simplified scheme of energy conversion in PSII according to the reversible radical pair model, featuring rapid excitation equilibration between the PSII antenna and the reaction center chlorophyll P (P_{680}). Excitation trapping (rate constant k_1), which results in the primary radical pair $[P^+Pheo^-]^1$ in the singlet state, is assumed to be reversible (k_{-1}). Three further reactions of the primary radical pair are considered: k_{2Q}, photochemical energy conversion by electron transfer to Q_A; k_{2T}, spin dephasing resulting in triplet state of radical pair; k_{2D}, nonradiative decay to ground state. Fluorescence yield (rate constant k_F) reflects excitation density in PSII (antenna, including P), which is determined by light absorption, primary radical pair recombination (k_{-1}) and competing nonradiative decay (k_D). Variable fluorescence is defined as the increase in fluorescence yield when the primary stable acceptor, Q_A, is reduced. It is considered to be caused by a decrease in k_1 and an increase in k_{-1}, and to be modulated by k_D, k_{2T} and k_{2D}. See text for further explanations.

fluorescence may display fundamentally different properties with respect to nonradiative dissipation reactions involving the primary radical pair. This is the basis of a hypothesis, which to our knowledge has not yet been explicitly stated, characterised by the following points:

1. If in the presence of Q_A^- the rate constants of nonradiative energy loss processes (k_{2D} and/or k_{2T}) are increased, the resulting decrease in [P^+Pheo^-] will affect the 'recombination type' of variable fluorescence much more than the 'prompt type'.
2. Hence, changes in k_{2D} and k_{2T} may modulate part of the variable fluorescence (recombination type) and leave largely unaffected the other part (prompt type).
3. Changes in k_{2D} and k_{2T} can be due to transient effects (e.g. local fields induced by charge separation, relaxing upon charge stabilization and charge equilibration, including formation of various S-states) or long-lasting/irreversible modifications of the PSII reaction center complex (e.g. by photoinhibition, ageing, chaotropic effects).
4. Following a single turnover flash, or at the I_1 level in saturating continuous light, the PSII center complex is transiently in a state which favors k_{2D} (and/or k_{2T}) and, therefore, the preferential elimination of recombination fluorescence. This state relaxes within 1 ms following a pump flash (at least in the presence of DCMU) and much more slowly (within 30–200 ms) in continuous saturating light (saturation pulse), presumably related to multiple turnovers (see below).
5. The polyphasic rise of fluorescence yield in saturating light reveals the two different types of variable fluorescence via transient preferential suppression of recombination type fluorescence. Phenomenologically, this results in 'fast variable fluorescence' (photochemical phase, in parallel to Q_A^- accumulation) and 'slow variable fluorescence' (thermal phases) mostly reflecting the decay kinetics of quenching of recombination fluorescence.
6. The amplitude of the 'fast variable fluorescence' is determined by k_{2D} and k_{2T} (at the reaction center) as well as by k_D (at the antenna). At constant k_D, with increasing k_{2D} and k_{2T} the 'fast variable fluorescence' will decrease at most to the limit where the recombination type variable fluorescence is completely suppressed and only the prompt type persists.

3. Experimental findings relevant to the proposed hypothesis

In the past, many attempts have been made to interpret the complex fluorescence rise kinetics in saturating light [5–11]. Relevant information comes from experiments in which specific treatments lead to different extents of suppression of the photochemical and thermal phases. In this context, the following findings appear important:

1. Treatments which slow down the donor side of PSII generally suppress the thermal phases without much effect on the photochemical phase [7,20,21]. Inhibition of the water splitting complex by Ca^{2+} depletion leads to an upshift of the redox potential of Q_A. It was suggested that under such conditions, fluorescence quenching is due to a direct charge recombination into the ground state of P680 [22].
2. When intact chloroplasts are irradiated at low temperature (6°C) with strong light (4000 μmol quanta m^{-2} s^{-1}) the resulting decrease in PSII quantum yield (photoinhibition) is paralleled by preferential suppression of the thermal phases (Neubauer and Schreiber, unpublished).
3. Fluorescence quenching at the I_1 level or of $F_{30 \mu s}$ oscillates with period 4 as a function of the number of preilluminating flashes, with quenching being most pronounced upon accumulation of S_2 and S_3 [7,23].
4. Simultaneous measurements of the electrochromic bandshift around 515 nm and of fluorescence upon onset of strong continuous light have revealed that the thermal phases are paralleled by a *decrease* of the electrical field [21].
5. When Q_A reoxidation is inhibited by DCMU, the amplitude of the photochemical phase is increased and the thermal phases are eliminated ([5,6,8], see also Fig. 1).
6. In cyanobacteria and green algae a state 1–state 2 transition results in almost selective suppression of I_1–I_2 [24].
7. Zeaxanthin-dependent nonphotochemical quenching, which is based on an increase of k_D (in the antenna) [25,26], decreases the amplitude of both the photochemical and thermal phases [9,11].
8. Recent fluorescence decay measurements suggest that zeaxanthin independent ΔpH related quenching of Fm is caused by a significant increase in the rate constant k_{2D} and/or k_{2T} [26].

All these experimental findings are in agreement with the above hypothesis, although this statement will need some justification in the case of findings 5 and 6. With the rationale of this hypothesis, and following the model of Fig. 2, it appears that positive charges at the PSII donor side (directed towards lumen) could be a major cause favoring quenching of recombination type variable fluorescence, by stimulating k_{2D} or k_{2T}. Additional causes presently cannot be excluded.

As to the effect of DCMU, this inhibitor presumably acts by preventing multiple turnovers of PSII. While the quenching state which is formed in the presence of DCMU after a saturating single turnover flash was found to relax within 1 ms, it may be assumed that in the absence of DCMU quenching states with longer lifetimes will form as long as charge separation/stabilization is possible, i.e. full relaxation of quenching requires complete exhaustion of the secondary acceptor pools (primarily oxidized PQ). Hence, phenomenologically this quenching resembles 'PQ quenching' [5,27]. However, from the fact that DCMU increases 'fast variable fluorescence' to the I_2 or even the Fm level (see Fig. 1), it may be concluded that a quenching mechanism directly involving the oxidized PQ pool could not be responsible for more than the I_2–Fm phase, which is a minor component of the overall thermal phases.

The finding that state 2 stabilizes quenching at I_1 can be easily reconciled with the above hypothesis, if the detachment of LHCII or of phycobilisomes from PSII causes a modification of the reaction center complex (e.g. dimer to monomer, see [28]), which may well be associated with an increase of k_{2D} or k_{2T}.

It is important to note that only highly active samples with

high PSII quantum yields (high Fv/Fm) display a polyphasic fluorescence rise with a large contribution of thermal phases. Treatments which impair optimal PSII function generally suppress I_1–I_2–P together with Fv/Fm. This points to a delicate balance between potential energy loss at the reaction center (controlled by k_{2D} and k_{2T}) and energy conservation via recombination and chlorophyll reexcitation.

4. Discussion

The significance of the above hypothesis strongly depends on two aspects which have been discussed in the past:

1. Yield of radical pair formation in the Fm state (Q_A reduced). This has to be relatively high in order to account for a relatively large contribution of recombination type variable fluorescence.
2. Rate of nonradiative deexcitation at the radical pair level (k_{2D} and/or k_{2T}). This should be variable, with transiently high rates competing with the rate of recombination to the singlet excited state (k_{-1}).

While in the original work of Shuvalov et al. [13] a high yield of the primary pair with a relatively long lifetime of 4 ns was reported, later results by Schatz, Holzwarth and co-workers [14,16] seemed to exclude that more than 15% of a long-lived primary pair are present (but see [17]). More recent investigations, however, do suggest that, in the presence of Q_A^-, there can be considerable radical pair formation (50–70%, depending on the temperature) and radical pair recombination with $t_{1/2} > 2$ ns [18,19,29,30]. As to the significance of nonradiative deexcitation at the radical pair level, a major role for k_{2T} (spin dephasing followed by decay to the triplet excited state) had been excluded [30,31], until very recently Van Mieghem et al. [18] and Hillmann et al. [19] discovered that substantial triplet formation can occur in the presence of Q_A^-. As the $^3P^*$ lifetime is drastically shortened in the presence of singly reduced Q_A [18], it had escaped detection by earlier EPR measurements [31].

Since chlorophyll fluorescence quenching analysis by the saturation pulse method has become a widespread method for assessment of photosynthesis [1–4], the question of the mechanism causing quenching at the I_I level (or of $F_{30\mu s}$) is of considerable practical importance. The rationale of this method relies on the assumption that nonphotochemical quenching does not change during a pulse of saturating light which induces the Fm state by Q_A reduction. Obviously, there is substantial nonphotochemical quenching at I_1 and in $F_{30\mu s}$ (see Fig. 1), which normally relaxes during the thermal phases (I_1–I_2–Fm). Its relaxation is counteracted, however, by conditions which weaken the PSII donor side [7,20,21]. Within the framework of our hypothesis, at I_1 and in $F_{30\mu s}$ the recombination type variable fluorescence is preferentially quenched due to a transiently high k_{2D} and/or k_{2T}. In this context, it should be noted that according to current electron transfer theory [32] recombination to the triplet state of P_{680} may well be accelerated by a local electric field [18]. Hence, Q_A^- as well as positive charges on the donor side may conspire in the transient stimulation of k_{2T} and transient quenching of recombination type variable fluorescence. Notably, not only the rate of triplet formation but also the rate of triplet quenching appears to be strongly stimulated in the presence of Q_A^- [18]. Therefore, a nonphotochemical quenching mechanism which involves transient triplet formation does not necessarily increase the danger of irreversible damages (e.g. via singlet oxygen [22]).

In 1990 a unifying model of nonphotochemical fluorescence quenching was presented [21] as an attempt to reconcile the evidence for donor side dependent quenching at the reaction center level [7] with that for zeaxanthin-dependent quenching in the antenna [25]. This model already assumed a decisive role for spin dephasing, which is stimulated by local electrostatic forces. Arguments put forward against this model [33] were primarily based on rate constants obtained under non-energized conditions and ignoring the α/β heterogeneity of PSII [34,35]. It should be emphasized that for the sake of simplicity the concept of PSII heterogeneity has not been explicitly incorporated in the formulation of our hypothesis, but a number of reasons can be pointed out suggesting that the recombination type of variable fluorescence may be particularly pronounced in PSIIβ:

1. Due to the smaller antenna size (1/3) the probability of radical pair formation is enhanced in PSIIβ [36].
2. The rate constant of radical pair recombination is particularly high in PSIIβ [35].
3. The lifetime of PSIIβ fluorescence is longer than that of PSIIα [35].

The proposed hypothesis is in agreement with previous suggestions that nonradiative deexcitation at the reaction center level can contribute to the lowering of PSII quantum yield [20–22,37–40]. In the case of photoinhibition, it is quite obvious that the cause of nonphotochemical quenching and of lowered PSII quantum yield cannot be a dissipating process in the antenna (increase of k_D in Fig. 1, e.g. involving zeaxanthin) as this should suppress all phases equally. This is indeed the case with a large part of energy dependent nonphotochemical quenching [11].

In conclusion, the proposed hypothesis is in line with recent insights into the dynamics of primary radical pair reactions in PSII [14–19,29–31] and provides a reasonable framework for the interpretation of numerous experimental findings which have so far appeared difficult to reconcile with each other. More work will be required to substantiate this hypothesis. In particular, time resolved fluorescence spectroscopy should be the method of choice to give evidence in favor or against it. Special attention should be paid to the slowly decaying emission in samples displaying a high Fv/Fm. Furthermore, it will be important to clarify to what extent recombination type variable fluorescence is dominated by emission from PSIIβ. Finally, based on the information from fluorescence lifetime measurements carried out in the characteristic states of Fo, I_1, ($F_{30\mu s}$,) I_2 and Fm, it should be possible to simulate the polyphasic fluorescence rise in saturating light, in analogy with recent work of Trissl and Lavergne [41], who succeeded in the simulation of the fluorescence rise in the presence of DCMU applying the reversible radical pair model [14].

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