Dynamics of electron transfer within and between PS II reaction center complexes indicated by the light-saturation curve of in vivo variable chlorophyll fluorescence emission

Havaux, Michel; Strasser, Reto

Photosynthesis Research **31**: 149–156, 1992.

Regular paper

Dynamics of electron transfer within and between PS II reaction center complexes indicated by the light-saturation curve of in vivo variable chlorophyll fluorescence emission

Michel Havaux[1] & Reto J. Strasser[2]
[1]*Département de Physiologie Végétale et Ecosystèmes, Centre d'Etudes de Cadarache, F-13108 Saint-Paul-lez-Durance, France*; [2]*Laboratoire de Bioénergétique, Station de Botanique, Université de Genève, CH-1254 Lullier-Genève, Switzerland*

Received 5 August 1991; accepted in revised form 26 November 1991

Key words: chlorophyll fluorescence, Photosystem II, reaction center, environmental conditions

Abstract

The dynamics of light-induced closure of the PS II reaction centers was studied in intact, dark-adapted leaves by measuring the light-irradiance (I) dependence of the relative variable chlorophyll fluorescence V which is the ratio between the amplitude of the variable fluorescence induced by a pulse of actinic light and the maximal variable fluorescence amplitude obtained with an intense, supersaturating light pulse. It is shown that the light-saturation curve of V is a hyperbola of order n. The experimental values of n ranged from around 0.75 to around 2, depending on the plant material and the environmental conditions. A simple theoretical analysis confirmed this hyperbolic relationship between V and I and suggested that n could represent the apparent number of photons necessary to close one reaction center. Thus, experimental conditions leading to n values higher than 1 could indicate that, from a macroscopic viewpoint, more than one photon is necessary to close one PS II center, possibly due to changes in the relative concentrations of the different redox states of the PS II reaction center complexes at the quasi-steady state induced by the actinic light. On the other hand, the existence of environmental conditions resulting in n noticeably lower than 1 suggests the possibility of an electron flow between PS II reaction center complexes.

Abbreviations: F_0 and F_m – minimal and maximal levels of chlorophyll fluorescence emission, respectively; F_p – peak fluorescence induced by a pulse of actinic light; I – incident light irradiance (in $W\,m^{-2}$); PS II – Photosystem II; P_{680} – PS II reaction center; Q_A and Q_B – primary and secondary (stable) electron acceptors of PS II; V – relative variable chlorophyll fluorescence ($V = (F_p - F_0)/(F_m - F_0)$)

Introduction

Electron transport on the acceptor side of Photosystem II (PS II) proceeds through a two-electron gating mechanism, with the reaction center (P_{680}) of PS II donating an energized electron to the primary quinone-type acceptor (Q_A) to form Q_A^- which is reoxidized by a two-electron acceptor Q_B (Mathis and Rutherford 1987, Hansson and Wydrzynski 1990). After receiving two electrons, Q_B^{2-} is protonated to form hydroquinone which is released and substituted by a molecule from the plastoquinone pool. Thus, the reaction scheme can be written as follows

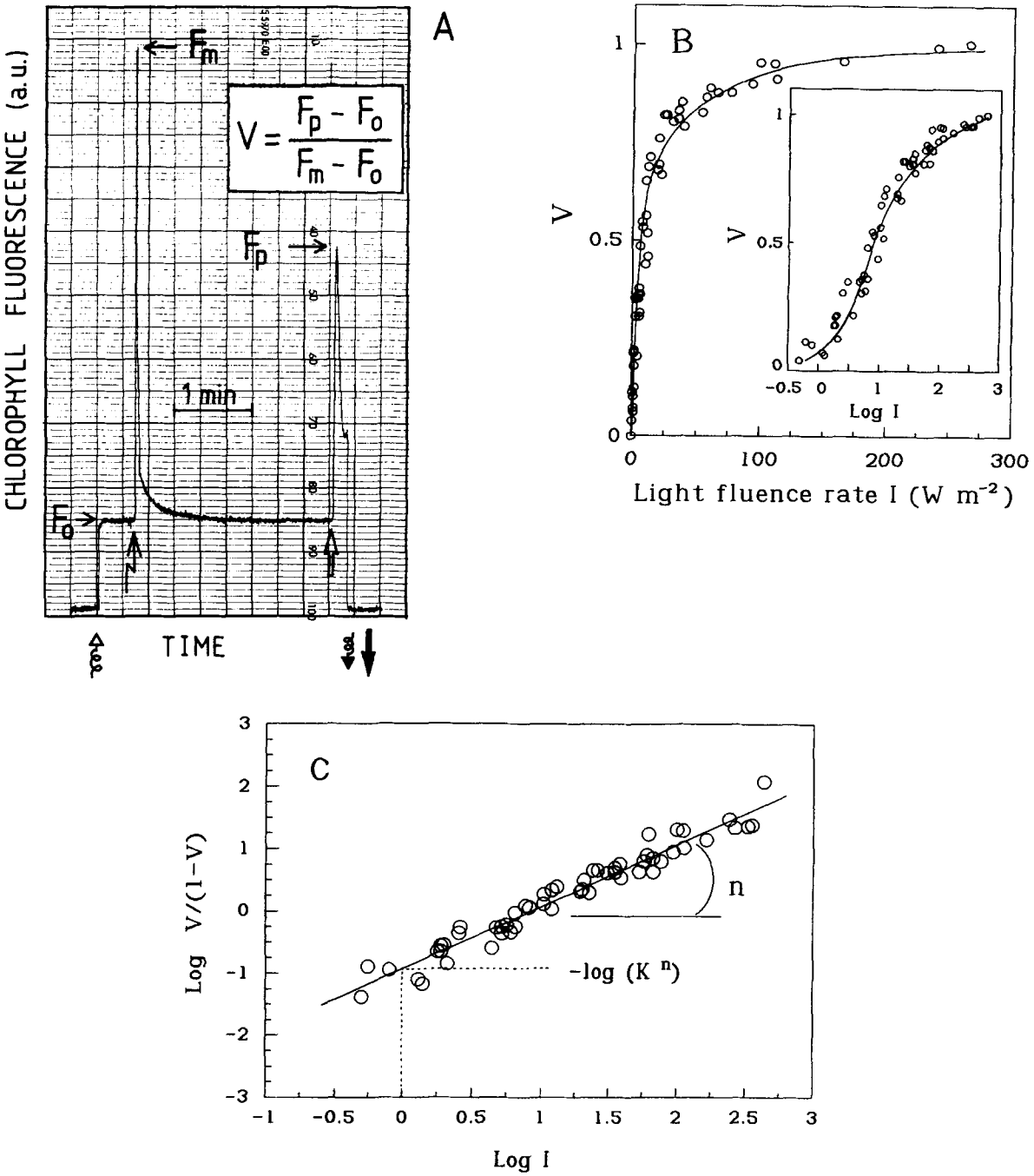

Fig. 1. (A) Typical signal of modulated chlorophyll fluorescence (arbitrary units) emitted at 685 nm by an intact leaf (pea). The F_0, F_m and F_p levels, used to calculate the relative variable fluorescence V, were obtained by applying, respectively, a weak modulated yellow light (870 Hz, 585 ± 12 nm, <0.025 W m^{-2}; ⇕, on; ⇓, off), a 1-s pulse of intense blue-green light (400–600 nm, 600 W m^{-2}, ⇑) and a blue-green actinic light of 3.5 W m^{-2}(⇑, on; ⇓, off). The leaf was previously dark-adapted for around 1 h prior to the fluorescence measurements. (B) Relative variable 685-nm chlorophyll fluorescence V in spinach leaves (grown for 5 weeks in short days of 8-h light) illuminated with various fluence rates (I) of a blue-green actinic light. Each point represents an different leaf. Inset: a semi-log plot of V vs. I. (C) Plot of the logarithm of the $V/(1 - V)$ ratio as a function of the logarithm of I (with I expressed in W m^{-2}). The slope of the linear relationship gives the order n of the hyperbol V vs. I whereas the intercept with the y-axis gives the logarithm of $1/(K^n)$.

$$P_{680}Q_AQ_B \xrightarrow{h\nu} P_{680}Q_A^-Q_B \quad (1)$$

$$P_{680}Q_AQ_B^- \xrightarrow{h\nu} P_{680}Q_A^-Q_B^- \quad (2)$$

$$P_{680}Q_AQ_B^{2-} \xrightarrow{h\nu} P_{680}Q_A^-Q_B^{2-} \quad (3)$$

This scheme does not account for the existence of inactive PS II reaction centers which are unable to transfer electrons efficiently from Q_A^- to Q_B (Black et al. 1986, Melis 1991). In the state $P_{680}Q_A^-$ (see products of reactions (1)–(3)), a reaction center complex cannot accept another electron and is thus 'closed', i.e., photochemically inactive. It is assumed that excitation energy transferred to a closed center is transferred back to the associated antenna chlorophylls, increasing the energy flux through the PS II dissipative pathways, including fluorescence (Butler and Kitajima 1975, Butler 1978). Thus, a transitory closure of all the PS II reaction centers by a short pulse of intense, photosynthetically saturating, light results in the maximal fluorescence yield (F_m) whereas, in a dark-adapted leaf with all PS II reaction centers in the 'open' configuration $P_{680}Q_A$, the chlorophyll fluorescence yield is minimal (F_0) (see Fig. 1A). When an intermediate, subsaturating light is used, the induced variable fluorescence ($F_p - F_0$) is indicative of a (transitory) steady-state level of Q_A^-/Q_A. The relationship between variable chlorophyll fluorescence and Q_A redox state is, however, not linear due to energy exchanges between PS II units (Joliot and Joliot 1964, Strasser 1981).

Using intact leaves or algae exposed to various experimental conditions, we have measured the amplitude of variable chlorophyll fluorescence as a function of the irradiance of the actinic light and analyzed the *shape* of the light-response curve of the relative variable fluorescence V. It is shown that the plot of V versus light irradiance is a hyperbola of order n, with n considerably varying with the plant material and its physiological state. Using a simple theoretical approach, we show that n can be interpreted as the apparent number of photons required to transform an open center into a closed one. The existence of situations where $n < 1$ suggests the possibility of a physico-chemical cooperativity among electron acceptors of PS II.

Materials and methods

Plant material

Most of the experiments were performed on intact leaves taken from spinach plants (*Spinacea oleracea* L., cv. Nobel) grown from seeds for 4 to

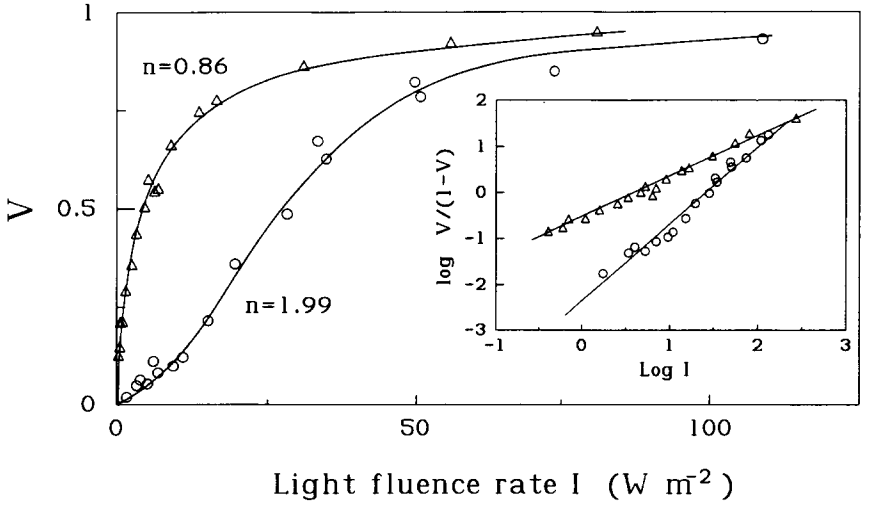

Fig. 2. Light-irradiance dependence of the relative variable chlorophyll fluorescence V in spinach leaves (grown for 5 weeks in a 5-h light/19-h dark cycle) preadapted to darkness (△) or to a dim blue-green light of 1.5 W m^{-2} (○). Inset: plot of log $V/(1-V)$ vs. log I.

5 weeks under controlled environmental conditions as described by Degli Agosti et al. (1990). For purposes of comparison, other plant species, including tomato (*Lycopersicum esculentum* L.), pea (*Pisum sativum* L.), cucumber (*Cucumis sativus* L.) and the unicellular alga *Chlamydomonas reinhardtii* were also examined. The growth conditions have been previously described (Havaux et al. 1990, Govindjee et al. 1991). The leaves or algae were dark-adapted for at least 1 h before the fluorescence measurements.

Chlorophyll fluorescence measurements

In vivo modulated chlorophyll fluorescence was measured at 685 nm using a MFMS fluorometer (Hansatech, Kings Lynn, UK), as previously described (Havaux et al. 1991). Intact leaves, previously adapted to darkness (unless specified otherwise, cf. experiment shown in Fig. 2), were suddenly illuminated with a blue-green light, inducing variable chlorophyll fluorescence emission (Kautsky effect). The fluence rate of the actinic light was adjusted using neutral density filters. The peak fluorescence F_p thus obtained (see Fig. 1A) was compared with the initial (F_0) and maximal (F_m) fluorescence levels allowing the relative variable fluorescence V to be determined:

$$V = (F_p - F_0)/(F_m - F_0) \quad \text{with } 0 \leq V \leq 1 \qquad (4)$$

The light-intensity dependence curves of V was analyzed using the commercial non-linear regression data analysis computer program ENZFITTER (Leatherbarrow 1987). All fluence rates were measured with a YSI-Kettering lightmeter (model 65A, Yellow Springs Instr., Yellow Springs, Ohio, USA).

Results

In Fig. 1B, the relative variable fluorescence V, measured in spinach leaves, was plotted as a function of the fluence rate I of the actinic light, yielding a hyperbola-like curve. Considering a hyperbola of order n, we have:

$$V = I^n/(C + I^n) \qquad (5)$$

with $C = K^n$ where K is a constant which corresponds to the light irradiance leading to $V = 0.5$. Equation (5) can be rewritten in a logarithmic form as follows:

$$\log V/(1 - V) = n \log I - \log(K^n) \qquad (6)$$

Thus, the plot of $\log V/(1 - V)$ versus $\log I$ is linear with a slope equal to n and an intercept with the y-axis equal to $-\log(K^n)$. Figure 1C shows that, indeed, plotting the logarithm of the $V/(1 - V)$ ratio, calculated from the data of Fig. 1B, as a function of the logarithm of I gives a very good linear relationship, confirming the hyperbolic nature of the light-intensity curve of V. From this plot, it was determined that the hyperbola was of order 1 ($n = 1.01 \pm 0.04$) and the light fluence rate for half-saturation of V was around 8.5 W m^{-2} ($K = 8.48 \pm 0.36$). This latter value of K can also be derived from the semi-log plot presented in the inset of Fig. 1B. Table 1 shows data obtained with other plant species. An interesting observation was that the V vs. I curve was a first-order hyperbola for pea only; in all the other species examined, n was significantly higher than 1, indicating a sigmoidal curve. Table 1 shows also that K strongly differs from one species to the other, ranging from 2.9 (pea) to 7 (*Chlamydomonas*). Although this latter variability can reflect a true difference between species, it could also be due to the growth conditions which are known to affect the light-satura-

Table 1. Values of the K and n parameters of the hyperbolic relationship between the relative variable chlorophyll fluorescence V and the actinic light fluence rate I ($V = I^n/(K^n + I^n)$) in tomato, pea and cucumber leaves and in the unicellular alga *Chlamydomonas reinhardtii*. Data obtained with spinach leaves grown under three different light conditions are also shown. All fluorescence measurements were done at 25 °C. Data are mean values ± standard deviations. The number of experiments is given in parentheses

	K	n	$C = K^n$
Tomato (17)	6.65 ± 0.65	1.24 ± 0.03	10.48
Pea (25)	2.90 ± 0.24	1.00 ± 0.05	2.90
Cucumber (21)	3.67 ± 0.24	1.16 ± 0.07	4.52
Chlamydomonas (19)	7.04 ± 0.61	1.20 ± 0.09	10.40
Spinach			
5-h light/day (20)	3.67 ± 0.52	0.78 ± 0.08	2.76
8-h light/day (15)	6.18 ± 0.59	1.06 ± 0.08	6.89
continuous light (26)	7.54 ± 0.57	1.08 ± 0.06	8.86

tion characteristics of photosynthesis (Anderson 1986) and which might be optimal for some of the species examined and not for the others. The experiments presented below, which examine the effects of changing light and temperature conditions on the characteristics of the hyperbolic relationship between V and I, support this latter idea.

Light conditions

In Table 1, there is a comparison of spinach leaves grown under different light conditions. It was observed that lowering the quantity of light received by the plants during growth strongly decreased the value of both K and n, so that a hyperbola of order lower than 1 ($n = 0.78$) was obtained for leaves grown with a very short photoperiod of 5 h. This hyperbola is displayed in Fig. 2, showing also the effects of adapting the leaves to a weak light (instead of darkness) prior to the fluorescence analysis. Clearly, this preillumination treatment of the leaves transformed the hyperbola into a sigmoidal curve characterized by $n = 2$ and noticeably increased K.

Temperature

Figure 3 shows that it was also possible to markedly modify the light-saturation curve of V by changing the leaf temperature. Moderately elevated temperature (38 °C) drastically decreased the slope (n) of the linear plot of $\log V/(1-V)$ versus $\log I$ whereas chilling temperature (13 °C) increased it. Inversely, K markedly increased at 38 °C and decreased at 14 °C, indicating that changes in K and n are not correlated.

Discussion

The presented data show that the light-saturation curve of V is a hyperbola of order n, with n ranging from values substantially lower than 1 to values close to 2, depending on the plant material and the environmental conditions. In recent studies, the light response of variable fluorescence was analyzed differently. For example, Carpentier et al. (1991) have assimilated the light saturation curve of variable fluorescence emission from thylakoid membranes to a Michaelis–Menten curve whereas Genty et al. (1990) have used an exponential curve to describe the flash-energy dosage curve of chlorophyll fluorescence yield in preilluminated leaves. Clearly, none of these mathematical expressions can be considered as a general description of the phenomena in vivo since (i) a first-order hyperbola

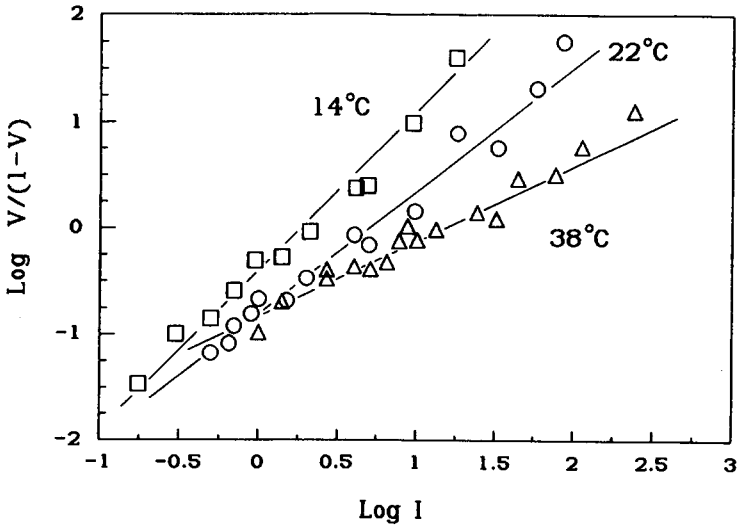

Fig. 3. Plot of the logarithm of the $V/(1-V)$ ratio as a function of the logarithm of the actinic light fluence rate I (W m^{-2}) in spinach leaves at three different temperatures (22, 14 or 38 °C). Slopes (n): 1.27 at 14 °C; 1.05 at 22 °C and 0.74 at 38 °C. Intercept with the y-axis allows the fluence rate (K) for half-saturation of V to be determined: 2.55 at 14 °C, 9.1 at 22 °C and 13.3 at 38 °C.

was experimentally observed in some cases only (e.g., Fig. 1), thus representing a particular situation, and (ii) the sigmoidal shape observed in other cases (e.g., in preilluminated leaves as in Fig. 2) cannot be described by an exponential.

Theoretical meaning of n

The hyperbolic nature of the relationship between V and I can be demonstrated, considering that, for a short time interval (e.g., a light pulse of a few seconds, as used in this study), a quasi equilibrium between open and closed systems is established as a function of the light intensity:

$$P_{680}Q_A \underset{n \text{ electrons}}{\overset{n.h.\nu + n \text{ electrons}}{\rightleftharpoons}} P_{680}Q_A^- \qquad (7)$$

As the incident light fluence rate (I) determines the concentration of excited chlorophyll pigments and assuming that the excitation energy flux to the PS II reaction centers is proportional to this latter concentration, the constant K_{eq} of the quasi-equilibrium of reaction (7) is given by the following expression

$$K_{eq} = \frac{[P_{680}Q_A] \cdot I^n}{[P_{680}Q_A^-]} = \frac{([P_{680}Q_A]^{total} - [P_{680}Q_A^-]) \cdot I^n}{[P_{680}Q_A^-]} \qquad (8)$$

In reality, K_{eq} is the product of the equilibrium constants of the n individual steps constituting reaction (7). Equation (8) can be rewritten

$$\frac{[P_{680}Q_A^-]}{[P_{680}Q_A]^{total}} = \frac{I^n}{K_{eq} + I^n} \qquad (9)$$

If there is no cooperativity between the antennae of different PS II units, V is a direct measure of the fraction of closed reaction center $B = [P_{680}Q_A^-]/[P_{680}Q_A]^{total}$ and, consequently, Eq. (9) gives the (hyperbolic) relationship between V and I.

For the general case where the probability p_{22} of energy changes between PS II units is different from 0, it has been demonstrated (Strasser 1981) that

$$V = B/(1 + k(1 - B)) \quad \text{with } k = ((F_m - F_0)/F_0)\, p_{22} \qquad (10)$$

or

$$B = (1 + k)V/(1 + kV) \qquad (10A)$$

Therefore, combining Eqs. (9) and (10A), we have

$$V = \frac{I^n}{K_{eq}(1 + k) + I^n} \qquad (11)$$

Consequently, the experimental constant $C = K^n$ of Eq. (5) corresponds to $K_{eq}(1 + k)$ and the light irradiance for the half-saturation of V is equal to $\sqrt[n]{K_{eq}(1 + k)}$ whose value is dependent on the saturation characteristics of the photosynthetic apparatus including, for example, the redox state of the plastoquinone pool.

Equations (9) and (11) indicate that, independently of the fact that PS II units cooperate or not, the relationship between V and I is a hyperbola of order n, as found experimentally. According to Eq. (7) and following the concept presented in a previous paper by one of us (Strasser 1990), n can be interpreted as the average number of photons required to transform an open PS II center into a closed one. Our experiments have shown that this number is dependent on the environmental conditions and can be substantially different from unity.

n *values higher than 1*

It is clear that the closure of a PS II reaction center through reaction (1), (2) or (3) requires one photon only. However, if we consider the series of reactions (1) + (2) or (2) + (3), the transformation of $P_{680}Q_AQ_B$ into $P_{680}Q_A^-Q_B^-$ or $P_{680}Q_AQ_B^-$ into $P_{680}Q_A^-Q_B^{2-}$ requires 2 photons and, for the series of reactions (1) + (2) + (3), three photons are necessary to obtain the closed state $P_{680}Q_A^-Q_B^{2-}$ from the open state $P_{680}Q_AQ_B$. If the proportions between the reaction center species involved in reactions (1), (2) and (3) (i.e., the ratios $(PQ_AQ_B + PQ_A^-Q_B)/(PQ_AQ_B^- + PQ_A^-Q_B^-)/(PQ_AQ_B^{2-} + PQ_A^-Q_B^{2-})$) remain constant during the quasi-steady state established at

the peak fluorescence level (F_p), reactions (1), (2) and (3) can be considered as isolated and, consequently, $n = 1$. However, in the case where the above proportions changed during the observed 'steady-state' at F_p, some reaction centers will appear as if 2 or 3 photons were necessary to close them and hence, from a macroscopic point of view, the average number of photons necessary to close the PS II centers will be above 1. Thus, the magnitude of n (when $n > 1$) could depend on the extent of the light-induced changes in the concentrations of the various forms of PS II reaction center complexes. Possibly, those changes may be related to the heterogeneity of PS II. It is well documented that a significant fraction of PS II centers is impaired in its ability to transfer electrons from Q_A to Q_B and that there is a dynamic interplay between active and inactive centers (Black et al. 1986, Melis 1991). In particular, it has been shown that light can activate the Q_B-non-reducing PS II complexes into active, Q_B-reducing complexes (Guenther and Melis 1990, Guenther et al. 1990). Consequently, this photoactivation process could progressively increase electron transfer from Q_A^- to Q_B and thus, modify the equilibria shown in reactions (1) to (3). Obviously, some environmental constraints (e.g., low temperature) favored the above-mentioned changes.

n *values lower than 1*

An interesting result was that, under certain environmental conditions, the order of the hyperbola V vs. I was noticeably lower than 1, thus suggesting that less than one exciton was apparently necessary to transform Q_A into Q_A^-. This is possible if one assumes, as in a previous work (Strasser and Greppin 1981), a physico-chemical cooperativity between PS II reaction center complexes, so that a PS II reaction center complex can accept an electron from a neighbour PS II center either directly (from Q_B^- or Q_B^{2-}) or via intermediates. Figure 4 shows an example of such a mechanism which is presented here as a working hypothesis only, in order to illustrate the theoretical possibility of closing more than one reaction center with one absorbed photon. In this hypothetical model, the oxidized reaction center pigment P_{680}^+ is re-reduced (reaction (a) in Fig. 4) by an electron from the long-lifed state $P_{680}Q_AQ_B^{2-}$ (thus competing with the normal electron donor Z); the resulting formation of $P_{680}Q_AQ_B^-$ will change the equilibrium (b) (see Fig. 4), increasing the concentration of $P_{680}Q_A^-Q_B$ and, therefore, more than one closed reaction center is formed with only one excitation event in an open center. It remains, however, to demonstrate that oxidized P_{680} can be really re-reduced by reduced Q_B. Another possibility, previously suggested by Strasser (1990), could be an electronic interaction between PS II reaction centers and the partially reduced environment.

An intriguing fact is that the conditions which resulted in decreased n (e.g., mild heat stress (Fig. 2) or low light conditions during growth

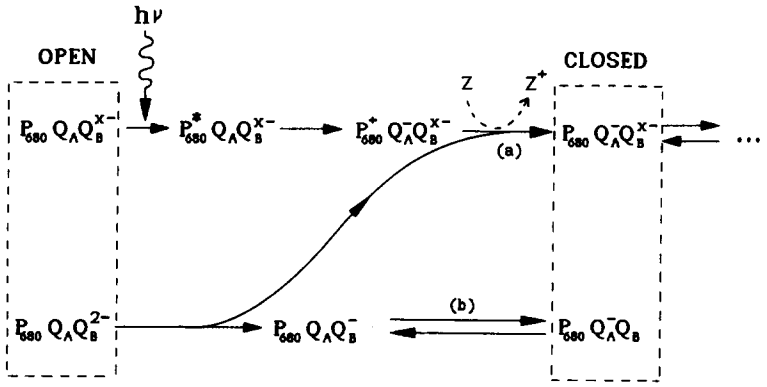

Fig. 4. Hypothetical mechanism for the closure of more than one PS II reaction center with only one excitation event in an open PS II center. P_{680} is the PS II reaction center pigment; Q_A and Q_B are, respectively, the primary and secondary electron acceptors of PS II. The superscript x can be 0, 1 or 2.

(Table 1)) correspond to conditions which are known to favor apparition of inactive, Q_B-non-reducing PS II centers. Indeed, Cao and Govindjee (1990) have recently demonstrated that heat alters the ratio of active to inactive PS II centers in thylakoid membranes, with a preponderance of inactive centers at high temperature. Similarly, low light conditions are believed to favor accumulation of inactive centers (Melis 1991). Conversely, transfer of plants from dark to light has been observed to result in light-activation of non-reducing centers to a Q_B-reducing form (Guenther and Melis 1990, Guenther et al. 1990) and, in this study, preillumination of leaves brought about a marked increase in the n value. Those correlations could suggest that the hypothesized electron transfer between reaction center complexes and the reduction of the apparent number of photons required to close a reaction center might be somehow related to the accumulation of inactive centers.

In conclusion, irrespective of the exact molecular mechanisms determining the value of n, the analysis of the characteristics of the light-saturation curve of V presented here reveals a variability in the dynamics of PS II reaction centre closure in vivo. The various shapes of light-intensity curve of V presumably reflect different responses of the acceptor side of PS II to environmental conditions, with specific effects on the electron transfers within or between PS II reaction center complexes.

References

Anderson JM (1986) Photoregulation of the composition, function and structure of thylakoid membranes. Ann Rev Plant Physiol 37: 93–136

Black MT, Brearley TH and Horton P (1986) Heterogeneity in chloroplast Photosystem II. Photosynth Res 8: 193–207

Butler WL (1978) Energy distribution in the photochemical apparatus of photosynthesis. Ann Rev Plant Physiol 29: 345–378

Butler WL and Kitajima M (1975) Fluorescence quenching in Photosystem II of chloroplasts. Biochim Biophys Acta 376: 116–125

Cao J and Govindjee (1990) Chlorophyll *a* fluorescence transients as an indicator of active and inactive Photosystem II in thylakoid membranes. Biochim Biophys Acta 1015: 180–188

Carpentier R, Owens TG and Leblanc RM (1991) Simultaneous saturation of variable fluorescence yield and photoacoustically monitored thermal emission in thylakoid membranes. Photochem Photobiol 53: 565–569

Degli Agosti R, Bonzon M and Greppin H (1990) Carbohydrates evolution in spinach plants during early acclimation to various changes in photoperiod. Archs Sci Genève 43: 401–417

Genty B, Harbinson J, Briantais J-M and Baker NR (1990) The relationship between non-photochemical quenching of chlorophyll fluorescence and the rate of Photosystem 2 photochemistry in leaves. Photosynth Res 25: 249–257

Govindjee, Schwarz B, Rochaix J-D and Strasser RJ (1991) The herbicide-resistant D1 mutant L275F of *Chlamydomonas reinhardtii* fails to show the bicarbonate-reversible formate effect on chlorophyll *a* fluorescence transients. Photosynth Res 27: 199–208

Guenther JE and Melis A (1990) Dynamics of Photosystem II heterogeneity in *Dunaliella salina* (green algae). Photosynth Res 23: 195–203

Guenther JE, Nemson JA and Melis A (1990) Development of PS II in dark grown *Chlamydomonas reinhardtii*. A light-dependent conversion of $PS II_\beta$, Q_B-non reducing centers to $PS II_\alpha$, Q_B-reducing form. Photosynth Res 24: 35–46

Hansson O and Wydrzynski T (1990) Current perceptions of Photosystem II. Photosynth Res 23: 131–162

Havaux M, Strasser RJ and Greppin H (1990) In vivo photoregulation of photochemical and nonphotochemical deactivation of Photosystem II in intact plant leaves. Plant Physiol Biochem 28: 735–746

Havaux M, Strasser RJ and Greppin H (1991) A theoretical and experimental analysis of the q_P and q_N coefficients of chlorophyll fluorescence quenching and their relation to photochemical and nonphotochemical events. Photosynth Res 27: 41–55

Joliot A and Joliot P (1964) Etudes cinétiques de la réaction photochimique libérant l'oxygène au cours de la photosynthèse. CR Acad Sci Paris 258: 4622–4625

Leatherbarrow RJ (1987) Enzfitter Manual. Elsevier, Amsterdam

Mathis P and Rutherford AW (1987) The primary reactions of Photosystems I and II of algae and higher plants. In: Amesz J (ed) Photosynthesis, pp 63–96. Elsevier, Amsterdam

Melis A (1991) Dynamics of photosynthetic membrane composition and function. Biochim Biophys Acta 1058: 87–106

Strasser RJ (1981) The grouping model of photosynthesis: Heterogeneity of photosynthetic units in thylakoids. In: Akoyunoglou G (ed) Photosynthesis. Proc 5th Internat Congress on Photosynthesis, Vol III, pp 727–737. Balaban Internation Science Services, Philadelphia

Strasser RJ (1990) The dynamics of variable fluorescence of photosynthetic systems at 77 K correlated to redox carriers Q_A/Q_B. In: Baltscheffsky M (ed) Current Research in Photosynthesis, Vol I, pp 615–618. Kluwer, Dordrecht

Strasser RJ and Greppin H (1981) Primary reactions of photochemistry in higher plants. In: Akoyunoglous G (ed) Photosynthesis. Proc 5th Internat Congress on Photosynthesis, Vol III, pp 717–725. Balaban International Science Services, Philadelphia