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KINETIC ANALYSIS OF THE CHLOROPHYLL FLUORESCENCE INDUCTIONS FROM CHLOROPLASTS BLOCKED WITH 3-(3,4-DICHLOROPHENYL)-1,1-DIMETHYLUREA

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Summary

1. The induction of Photosystem II chlorophyll fluorescence from chloroplasts blocked with 3-(3,4-dichlorophenyl)-1,1-dimethylurea and uncoupled with gramicidin has been measured.

2. In agreement with other authors it was found that the addition of cations to chloroplasts suspended in a low-cation medium not only stimulated the intensity of fluorescence but also changed the shape of the induction from being nearly exponential to being sigmoid.

3. A new theory of the photosynthetic unit of Photosystem II (Paillotin, G. (1976) J. Theor. Biol. 58, 237—252) was used to analyse the fluorescence inductions.

4. A comparison of the results of the Paillotin model with the experimental data suggests that excitation energy is not able to migrate between all the photosynthetic units of a photosynthetic domain. However, it is concluded that excitation energy may migrate from one photosynthetic unit to another, and that the energy migration is in competition with other processes leading to the decay of the excitation within Photosystem II.

5. It is suggested that the size of the "functional" photosynthetic unit, defined as the number of chlorophyll molecules that may communicate with a reaction centre, is variable.

Introduction

One of the oldest and most fundamental concepts in current models of the primary processes of photosynthesis is that of the photosynthetic unit [1,2]. In higher plants the photosynthetic unit is thought to consist of about 300

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Abbreviation: DCMU, 3-(3,4-dichlorophenyl)-1,1-dimethylurea.

light-harvesting chlorophyll molecules associated with a reaction centre, but it is not yet clear whether the photosynthetic unit is a physical structure or whether it represents a statistical average of the pigment bed taken as a whole.

A range of models for the photosynthetic unit of Photosystem II has been put forward (see ref. 3 for review). At one extreme is the separate unit model [4,5] where the photosynthetic unit is regarded as an isolated entity: excitation energy may not be transferred into or out of such a separate unit. At the other extreme is the uniform pigment matrix model (the statistical or lake model) [6,7]. In this model the Photosystem II pigment bed is thought of as being completely uniform, over which excitation energy can migrate freely to encounter any of the randomly distributed reaction centres. Intermediate models have also been proposed, either postulating excitation migration between separate units [8—11], or the idea of a group of units (a "photosynthetic domain") within which free excitation energy migration is possible [10,12].

In principle it is possible to distinguish between these models by analysing the kinetics of the closing of Photosystem II reaction centres by light. One convenient way in which this may be done is by following the induction of Photosystem II chlorophyll fluorescence which is a measure, albeit an indirect one, of the concentration of closed Photosystem II reaction centres [13,14], provided secondary electron transport is blocked by 3-(3,4-dichlorophenyl)-1,1-dimethylurea (DCMU). A simple model [8] predicts that under these conditions an assembly of separate photosynthetic units should exhibit an exponential fluorescence induction, but that if inter-unit energy migration takes place then the induction should be more sigmoid. Generally speaking, fluorescence inductions have been found to be sigmoid (see, for example, ref. 15), suggesting some inter-unit excitation energy migration.

However, the recent appearance of new experimental observations and a new and more developed theory have made necessary a re-examination of models of the photosynthetic unit. The experimental observations were made in the course of investigations into the cation-induced increase in fluorescence of Photosystem II chlorophyll from isolated chloroplasts (see ref. 16 for review). In DCMU-blocked chloroplasts the induction of fluorescence is approximately exponential when the intensity of fluorescence is low, but becomes more sigmoid when fluorescence is stimulated by the addition of cations. This observation has been made by several authors [17—23]. Such a change in the shape of the fluorescence induction indicates, using the simple model mentioned above [8], a change in inter-unit energy migration.

The new theory of the photosynthetic unit has been presented by Paillotin [24]. The principal assumptions of the theory are (a) Photosystem II is divided into n photosynthetic domains each containing r reaction centres, (b) an open reaction centre need not be a perfect trap for excitation energy, (c) a closed reaction centre may act as a sink for excitation energy and (d) all of the f_o level of fluorescence * originates in Photosystem II. This last assumption has both

* The following notation is used to describe the induction of fluorescence: f_o is the intensity of fluorescence observed on first illuminating the chloroplasts. The fluorescence above the f_o level is variable fluorescence, f_v, and is a function of time. Its maximum value ($t \rightarrow \infty$) is f_{vmax}. Total fluorescence f_t is the sum of f_o and f_v; $f_{tmax} = f_o + f_{vmax}$. Fluorescence yields are denoted by ϕ with the appropriate subscript.

experimental [6,7,15,25] and theoretical [26] support, although several authors have argued that at least a part of the f_o level of fluorescence is unconnected with Photosystem II [9,21,27,28]. The "islet effect" is not taken into account.

The main results of the theory can be split into two parts:

(1) Assuming that excitation energy may migrate freely between all photosynthetic units in a domain, it is easily shown that the relationship between the relative yield of variable fluorescence, ϕ_v, and the fraction of closed Photosystem II reaction centres $(1-Q)$ is

$$\phi_v = \frac{(1-p)(1-Q)}{1-p(1-Q)} \tag{1}$$

where

$$p = f_{vmax}/f_{tmax} \tag{2}$$

(see also ref. 30); p governs both the shape of the graph of ϕ_v versus $(1-Q)$ and the shape of the fluorescence induction. Eqn. 1 is identical to that derived by Joliot and Joliot [8], except that in this case p does not describe excitation energy migration from one unit to another. The physical meaning of p can be seen by writing f_{vmax} and f_{tmax} in terms of rate constants, whence

$$p = \frac{K_Q^{(O)} - K_Q^{(P)}}{K_F + K_H + K_Q^{(O)}} \tag{3}$$

where $K_Q^{(O)}$ is the rate constant for energy capture by an open reaction centre, $K_Q^{(P)}$ is the rate constant for energy capture by a closed reaction centre and K_F and K_H are the rate constants for fluorescence and radiationless deactivation respectively. Eqn. 3 shows that p is a measure of the efficiency of energy trapping compared to the other de-excitation processes in a unit with an open reaction centre.

(2) Assuming that excitation energy may migrate from one photosynthetic unit to another but is not necessarily able to migrate over the whole domain, it may be shown that the relationship between ϕ_v and $(1-Q)$ has the same algebraic form as Eqn. 1, but in this case

$$p = \omega \frac{f_{vmax}}{f_{tmax}} \tag{4}$$

where ω is essentially the yield of energy transfer out of a unit with a closed reaction centre to another unit, and is given by

$$\omega = \frac{L'}{L' + K_F + K_H + K_Q^{(P)}} \tag{5}$$

where L' is the rate constant for excitation energy transfer from one unit to another. Eqn. 4 shows that in this case the shape of the fluorescence induction is governed by two factors: competition between trapping and other processes (f_{vmax}/f_{tmax}) and the yield of excitation energy transfer between photosynthetic units (ω).

An expression for the initial (maximum) yield of photochemistry, χ, is also derived [24]:

$$W \cdot \frac{S}{f_{vmax}} \cdot \chi = \text{number of reaction centres} = \text{constant} \quad (6)$$

where S is the total area over the fluorescence induction, W is the rate of light-induced excitation formation in Photosystem II, and the number of Photosystem II reaction centres is assumed invariant (see also ref. 21). In addition, the time course of the induction is given by Eqn. 1 and

$$W\chi t = p(1 - Q) - (1 - p) \ln Q \quad (7)$$

(see also ref. 8). Eqn. 7 can also be used to calculate the half rise-time of the fluorescence induction, $t_{1/2}$, which is given by

$$t_{1/2} = \frac{1}{W\chi}\left\{\frac{p}{2-p} - (1-p)\ln\left(\frac{1-p}{2-p}\right)\right\} \quad (8)$$

In this article we have analysed the induction of Photosystem II chlorophyll fluorescence from DCMU-blocked chloroplasts, whilst using the cation effect [16] to vary the shape of the induction. The results of the analysis are compared with the predictions of the Paillotin theory outlined above.

Materials and Methods

Intact chloroplasts were isolated from 10-day old peas by the method of Stokes and Walker [31]. The chloroplasts were osmotically shocked in distilled water and resuspended in a medium containing 0.33 M sucrose, 10 mM KCl and 20 mM tricine, pH 7.0, together with the required concentration of $MgCl_2$. Gramicidin ($5 \cdot 10^{-7}$ M final concentration) and DCMU ($5 \cdot 10^{-5}$ M final concentration) were added to the chloroplasts prior to experimenting.

Fluorescence measurements were made in an apparatus already described [32], except that the oscilloscope was replaced by a transient recorder (Datalab model 905) and chart recorder. The concentration of chlorophyll in the chloroplast suspensions was 10 $\mu g \cdot ml^{-1}$ as estimated by Arnon's method [33].

Results

Fig. 1 illustrates typical variable fluorescence inductions from osmotically shocked chloroplasts suspended in a medium containing 0.33 M sucrose, 10 mM KCl, 20 mM tricine, pH 7.0, and the concentration of $MgCl_2$ as indicated in the legend. The chloroplasts were blocked with DCMU and uncoupled with gramicidin (the latter compound being added to avoid any effects of the high-energy state on chlorophyll fluorescence [34]). Fig. 1 shows that the addition of $MgCl_2$ to chloroplasts changes the shape of the induction from being nearly exponential to being sigmoid [17–23]: Table I indicates that at the same time variable fluorescence is stimulated nearly 3-fold. In addition the f_o level is slightly increased by the addition of $MgCl_2$.

Differences in the shape of the inductions shown in Fig. 1 are also evident in Fig. 2 where the fractional variable fluorescence ϕ_v is plotted against the

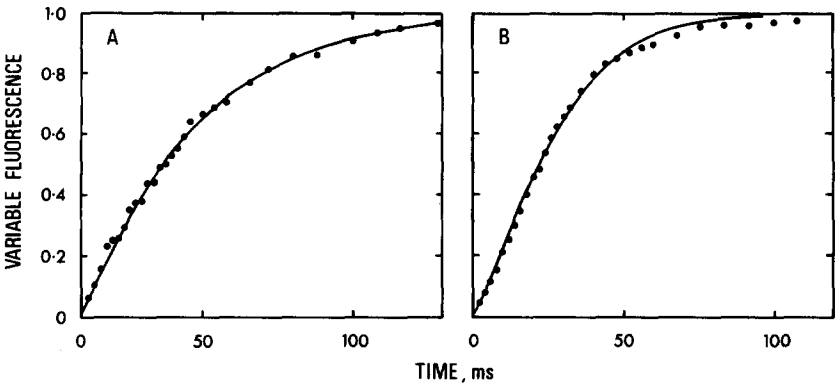

Fig. 1. The induction of variable fluorescence from chloroplasts uncoupled with gramicidin ($5 \cdot 10^{-7}$ M) and blocked with DCMU ($5 \cdot 10^{-5}$ M), suspended in a medium containing no $MgCl_2$ (A) or 2 mM $MgCl_2$ (B). The points are experimental data, the lines represent theoretical plots derived from Eqns. 1 and 5 and are normalised to match the experimental points at $\phi_v = 0.6$. Maximum variable fluorescence is normalised to unity in each case; Table I gives absolute values.

fraction of closed Photosystem II reaction centres $(1 - Q)$. The fraction of closed reaction centres was estimated from the fraction of the complementary area over the induction curve removed at any time [13]. It can be seen from Figs. 1 and 2 that a more sigmoid induction corresponds to a more concave ϕ_v versus $(1 - Q)$ characteristic. The curvature of the plots shown in Fig. 2

TABLE I

DATA FROM CHLOROPHYLL FLUORESCENCE INDUCTIONS TAKEN FROM DCMU-BLOCKED CHLOROPLASTS SUSPENDED IN MEDIA CONTAINING DIFFERENT CONCENTRATIONS OF $MgCl_2$

$MgCl_2$ (mM)	f_o	f_{vmax}	f_{tmax}	p [a]	S/f_{vmax} [b]	f_{vmax}/f_{tmax}	$t_{1/2}$ [c] (ms)	ω	χ [d]	χ [e]
0	18.5	20.5	39.0	0.09 ± 0.07	18.2	0.526	14.0	0.17	99.5	100.2
	21.5	18.5	40.0	0.03 ± 0.08	16.9	0.462	12.5	0.06	106.9	109.1
	22.0	18.0	40.0	0.10 ± 0.06	19.3	0.450	15.5	0.22	93.6	90.8
0.1	27.5	27.0	54.5	0.14 ± 0.08	15.6	0.495	11.5	0.28	115.8	124.6
	28.0	25.0	53.0	0.08 ± 0.08	15.3	0.472	12.0	0.17	118.1	116.3
0.3	25.0	48.0	73.0	0.31 ± 0.05	12.9	0.658	10.0	0.48	140.6	156.0
	25.0	46.7	71.7	0.30 ± 0.05	12.8	0.651	10.0	0.46	140.9	154.8
	24.5	45.0	69.5	0.29 ± 0.04	12.8	0.647	10.0	0.46	141.8	154.6
0.5	24.0	56.2	80.2	0.39 ± 0.05	13.4	0.701	10.8	0.56	135.2	151.0
	24.0	55.0	79.0	0.34 ± 0.05	12.9	0.696	10.3	0.49	139.8	154.2
	24.5	52.5	77.0	0.40 ± 0.05	13.3	0.682	10.5	0.58	136.1	154.9
2.0	23.0	59.5	82.5	0.36 ± 0.07	14.2	0.721	11.0	0.50	127.1	145.1
	23.0	59.5	82.5	0.39 ± 0.07	14.0	0.721	11.3	0.54	129.3	144.0
	23.0	58.0	81.0	0.44 ± 0.05	13.5	0.716	11.0	0.61	134.3	151.0

[a] p is estimated by taking pairs of values of ϕ_v and $(1 - Q)$ and inserting them in Eqn. 1, using values of $(1 - Q) \leq 0.06$ (see text). The standard error shown is the standard error of the mean of individual values calculated.

[b] S is the complementary area over the fluorescence induction, given by Eqn. 8.

[c] $t_{1/2}$ is the half-rise-time of the fluorescence induction.

[d] Calculated from Eqn. 5.

[e] Calculated from Eqn. 7. The mean of the first three values (no $MgCl_2$ added) was taken as 100.

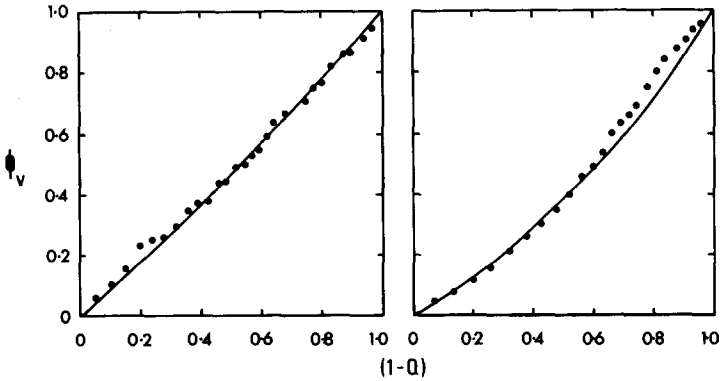

Fig. 2. The relative variable fluorescence ϕ_v plotted as a function of the fraction of closed Photosystem II reaction centres $(1 - Q)$. The points are experimental data; the solid lines represent theoretical curves (Eqn. 1), using for p values of 0.09 (A) and 0.39 (B). These values of p are the mean of values calculated by taking pairs of points ϕ_v and $(1 - Q)$ from the data and using Eqn. 1. Values of $(1 - Q) \leqslant 0.6$ only were used, see text.

can be quantified by inserting in Eqn. 1 a series of pairs of experimental values of ϕ_v and of $(1 - Q)$ to evaluate the parameter p. However, care has to be taken when making this evaluation because of errors which may be introduced by the "islet effect" [29]. This effect predicts that at high values of p and of $(1 - Q)$ the experimental points and the theoretical points from Eqn. 1 will not agree, because the spatial distribution of closed reaction centres in the photosynthetic domain will become inhomogeneous. To avoid these errors, p was estimated from pairs of values of ϕ_v and $(1 - Q)$ where $(1 - Q) < 0.6$, and then an average taken. The average values of p for each induction are presented in Table I. The comparison of experimental points and theoretical curves shown in Fig. 2 indicates that the errors introduced by the "islet effect" are not significant for $p = 0.09$, but are more marked for $p = 0.39$.

Table I also shows values of the ratio f_{vmax}/f_{tmax} for each induction. According to Eqn. 2 if excitation energy is assumed to be able to migrate freely between all the photosynthetic units of a domain, p should be equal to f_{vmax}/f_{tmax}. However, comparison of the values of p and of f_{vmax}/f_{tmax} shows that this is not so.

The second hypothesis of inter-unit energy migration suggests that the parameter p is the product of two factors, ω (a measure of inter-unit excitation energy transfer) and f_{vmax}/f_{tmax} (Eqn. 4). Values of ω have been derived from the experimental data, and are shown in Table I. It can be seen that ω increases when fluorescence intensity increases.

Table I also gives values of χ, the relative initial yield of photochemistry of Photosystem II. The values have been estimated in two ways. Firstly, from Eqn. 6, using f_{vmax} and the total complementary area over the induction curve, S, given by

$$S = \int_0^\infty (f_{vmax} - f_v)\, dt \qquad (9)$$

Secondly, Eqn. 8 enables χ to be evaluated from the half-rise-time of the fluo-

rescence induction and p. Table I shows that χ increases with increase in fluorescence intensity.

Eqn. 7, taken with Eqn. 1, enables theoretical fluorescence inductions to be calculated. Theoretical curves are shown in Fig. 1, where good agreement is obtained with the experimental points when p is low. At higher values of p (Fig. 1B) the discrepancies at high values of ϕ_v may be qualitatively accounted for by the "islet effect" [29].

Discussion

The theory of the photosynthetic unit proposed by Paillotin [24], and outlined in the Introduction is a valuable new tool in the analysis of fluorescence induction data from Photosystem II. The theory presents several relationships (Eqns. 1—8) which may be compared directly with experimental data. In the experiments described here the data have been obtained from kinetic analysis of fluorescence inductions in DCMU-blocked chloroplasts where the shape of the induction has been modified by use of the cation effect [16].

The Paillotin theory [24] puts forward two hypotheses for the character of excitation energy migration between the photosynthetic units of a domain. On the one hand, energy migration can be completely unhindered, in which case Eqn. 2 applies; the parameter p of Eqn. 1 represents the competition between trapping at the reaction centre and other deactivation processes (Eqn. 3) and is given by f_{vmax}/f_{tmax}. On the other hand, excitation energy migration may be limited for some reason (see below) so that the excitation may only visit a few units within the domain. In this case Eqn. 4 applies and p represents the product of two factors: f_{vmax}/f_{tmax} as before and ω, the yield of excitation energy transfer from one photosynthetic unit to the next. It can be seen from Table I that the values of p and f_{vmax}/f_{tmax} are not in accord, and thus the experimental data do not support the hypothesis of excitation energy migration throughout the entire photosynthetic domain.

The hypothesis of limited inter-unit energy migration leads to Eqns. 4—8. Eqn. 6 (see also ref. 8) taken with Eqn. 1 gives theoretical inductions, which agree well with experimental data (Fig. 1), except at high values of p (Fig. 1B) where the "islet effect" [29] would be expected to introduce errors.

Eqn. 3 enables an estimate to be made of ω, the yield of inter-unit energy transfer, and Eqns. 6 and 8 give two methods of calculating χ, the initial yield of photochemistry of Photosystem II. Fig. 3 shows the dependence of ω and χ, together with ϕ_o and ϕ_{tmax}, on the concentration of $MgCl_2$ in the chloroplast suspending medium. It can be seen in Fig. 3 that, at least at low concentrations of $MgCl_2$, all four parameters increase with increasing $MgCl_2$ concentration. At higher concentrations ($\geqslant$0.25 mM) ϕ_o is depressed [21] whilst ω, ϕ_{tmax} and χ all reach essentially steady levels.

Some insight into the mechanism of the cation-induced changes in all four yields may be gained from inspection of their defining equations:

$$\phi_0 = \frac{K_F}{K_F + K_H + K_Q^{(0)}} \qquad \chi = \frac{K_Q^{(0)}}{K_F + K_H + K_Q^{(0)}}$$

$$\phi_{tmax} = \frac{K_F}{K_F + K_H + K_Q^{(P)}} \qquad \omega = \frac{L'}{K_F + K_H + L' + K_Q^{(P)}} \tag{10}$$

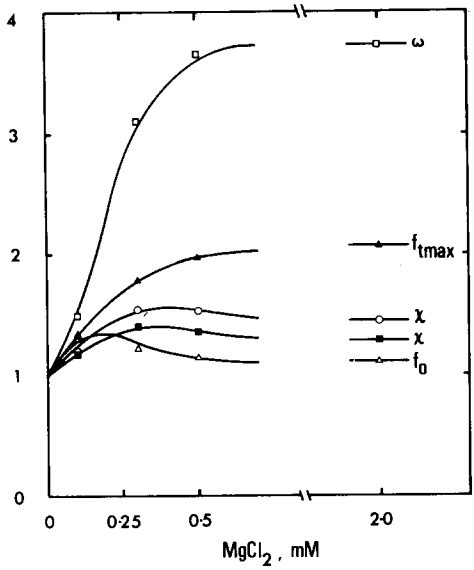

Fig. 3. The dependence on $MgCl_2$ concentration of ϕ_o, ϕ_{tmax}, ω and χ. χ was calculated both from Eqn. 7 (open circles) and from Eqn. 5 (closed squares).

The factor L' only occurs in the expression for ω [24]. From these equations it can be seen that the increases in ϕ_o, ϕ_{tmax}, χ and ω at low $MgCl_2$ concentrations can be accounted for most easily by a cation-induced decrease in K_H (which here represents the sum of the rate constants for radiationless de-excitation and spillover to Photosystem I). This is in agreement with other authors [16]. The decrease in ϕ_o at high $MgCl_2$ concentrations can be accounted for by an additional cation-induced increase in $K_Q^{(O)}$, which might be due to an increase in the rate constant for radiationless de-excitation at the reaction centre [30].

The most interesting conclusion of these experiments, however, is that the yield of inter-unit energy transfer, ω, is less than unity and is a variable parameter. The observation that ω is not unity may be accounted for by either of two hypotheses. In the first hypothesis the pigments contained in Photosystem II are assumed to be homogeneously distributed in space, and migration of the excitation energy is assumed to be limited by the lifetime of the excitation, that is, the excitation decays before it has time to migrate from one unit to another [5]. Alternatively, it may be supposed that the chlorophyll molecules that compose the Photosystem II pigment bed have a specific spatial arrangement where the centre of the unit is composed of the reaction centre and the long-wavelength-absorbing chlorophyll *a* species, whilst the periphery of the unit is made up of the short-wavelength species [24,35]. In this way the photosynthetic unit presents a type of potential well, and intermolecular excitation energy transfer from the periphery of the unit to the centre is more probable than energy transfer from the centre to the periphery [35]. Thus, in this case, energy migration from one unit to another is restricted by the architecture of the pigment bed. The data presented in this article do not allow a choice to be made between these two hypotheses.

But the data also show that ω is variable, dependent on the relative magnitude of the rate constants of all processes within the photosynthetic unit. Therefore, irrespective of whether the Photosystem II pigment bed is composed of a spatially homogeneous or inhomogeneous pigment distribution, the variability of ω indicates that the size of the functional photosynthetic unit (that is, those chlorophyll molecules that can communicate with a reaction centre) is variable.

The conclusions presented in this article represent an extension of the original hypothesis of Joliot and Joliot [8] where energy transfer between photosynthetic units was proposed. Here it has been shown that inter-unit energy transfer is a variable parameter. The model does not have recourse to the other hypothesis put forward to account for a sigmoid fluorescence induction [36—38] in which it is assumed that each (separate) photosynthetic unit requires two quanta to close the reaction centre. This hypothesis is particularly difficult to reconcile with the evidence that an exponential induction (representing a one-quantum process) can be converted to a sigmoid induction (representing a two-quantum process [36—38] by changing the chloroplast suspending medium.

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