Photochemistry and Photobiology Vol. 33, pp. 97 to 101

0031-8655/81/0101-0097$02.00/0

ESTIMATION OF ENERGY DISTRIBUTION AND REDISTRIBUTION AMONG TWO PHOTOSYSTEMS USING PARALLEL MEASUREMENTS OF FLUORESCENCE LIFETIMES AND TRANSIENTS AT 77 K

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(*Received* 2 *May* 1980; *accepted* 16 *July* 1980)

Abstract—A single-sample method for estimating energy distribution and redistribution among the two photosystems using fluorescence lifetimes and transients at 77 K is presented. In this method, α (the fraction of photons absorbed by photosystem I, PSI) is $F_{1(\alpha)}/(F_{1(\alpha)} + (\tau_{F\,1(M)}/\tau_{F\,2(M)}) \cdot F_{2(M)})$ where, $F_{1(\alpha)}$ is the fluorescence intensity from PSI excited by photons initially absorbed by the latter, $\tau_{F\,1(M)}$ and $\tau_{F\,2(M)}$ are the maximum lifetimes of fluorescence from chlorophyll-*a* in PSI (1) and II (2), and, $F_{2(M)}$ is the maximum fluorescence intensity from PSII (P level). Analysis of the intensities and lifetimes of wavelength resolved fluorescence of thylakoids (pH 7.0), with and without cations, leads to the following conclusions: The addition of 10 m*M* Na^+ to cation-depleted thylakoids (pH 7.0) increases α by $\sim 10\%$, while the subsequent addition of 10 m*M* Mg^{2+} leads to three principal concomitant changes (in the order of importance): a 50% decrease in PSII to PSI energy transfer, a 20% increase in other radiationless losses, and a 10% decrease in α.

INTRODUCTION

The discovery that Mg^{2+} and other divalent cations enhance chlorophyll-*a*‖ fluorescence in thylakoids at room temperature (Homann, 1969) and increase the ratio of short to long wavelength fluorescence at 77 K (Murata, 1969) has stimulated much research (Barber, 1976; Williams, 1977; Arntzen, 1978; Wong and Govindjee, 1979). It was observed by Gross and Hess (1973) that low concentrations ($\leqslant 10$ m*M*) of monovalent cations added to cation-depleted, sucrose-washed thylakoids produced the opposite effect (also see VanderMeulen and Govindjee, 1974; Wydrzynski *et al.*, 1975). The above changes are commonly referred to as the 'cation effects'.

Butler and Kitajima (1975a,b) introduced a model of the photochemical apparatus of photosynthesis which included parameters to describe the distribution of excitation energy between photosystem I (PSI) and PSII: namely, α and β, the relative cross sections of PSI and PSII, respectively, where $\alpha + \beta = 1.0$ and $k_{T(21)}$, the rate constant for energy transfer from PSII and PSI. The model was used to determine how these parameters were affected by the presence of divalent cations from fluorescence measurements of chloroplasts at 77 K. However, in order to determine energy distribution, the method of analysis required that measurements be made on pairs of samples, one frozen in the absence and one frozen in the presence of divalent cations. Later, methods were devised by Ley and Butler (1976, 1977) and Strasser and Butler (1977a, b) by which the energy distribution parameters could be determined in an individual frozen sample, including such samples as intact leaves or algal cells, from parallel measurements of absorption and fluorescence excitation spectra at 77 K.

We introduce here a new single-sample method for estimating the energy distribution and redistribution parameters using parellel fluorescence lifetime and transient data at 77 K. Applying this analysis to the cation effects, we have evaluated, for the first time, the effects of 10 m*M* Na^+ to sucrose-washed (cation-depleted) thylakoids. Our results reveal an Na^+-induced decrease ($\sim 10\%$) in the fraction of quanta absorbed by PSII and a slight increase in the efficiency of excitation energy transfer from PSII to PSI. The reverse effects obtained upon the subsequent addition of 10 m*M* Mg^{2+} confirm qualitatively the conclusions of Butler and Kitajima (1975a), but show three concomitant changes (in order of importance): a 50% decrease in energy transfer from PSII to PSI, a 20% increase in the radiationless losses and a 10% decrease in α (fraction of light absorbed by PSI).

THEORETICAL CONSIDERATIONS

It was assumed in the bipartite model of Butler and Kitajima that the light-harvesting Chl-*a*/*b* protein complex (Chl LH) served primarily as additional

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‖ Abbreviations: Chl-*a*, chlorophyll-*a*; PSI, photosystem I; PSII, photosystem II.

antenna Chl for PSII (Butler and Kitajima, 1975a; Butler, 1979). A more eleborate tripartite model was formulated by Butler and Strasser (1977) in which Chl LH was assumed to be a separate bed of antenna Chl which could transfer excitation energy to either PSII or PSI. However, an analysis of the fluorescence of PSII and Chl LH from chloroplasts at 77 K in the context of the tripartite model (Butler and Strasser, 1978) showed that Chl LH transferred energy almost exclusively to PSII and confirmed the general validity of the simpler bipartite model which will be used here.

Following the general scheme and nomenclature of Butler and Kitajima (1975a, b), the various processes by which excitation energy is utilized or dissipated will be indicated by first-order rate constants, k, with appropriate subscripts to denote the particular process. Capital letters in the subscript will be used to indicate deexcitation processes which occur in the antenna Chl: F for fluorescence, D for nonradiative decay and T for transfer to a reaction center; and lower case letters will denote deexcitation processes which occur at the reaction center Chl: p for photochemistry, d for nonradiative decay and t for transfer back to the antenna Chl. In each case the numeral 1 or 2 will follow the letter to indicate whether the process is occurring in PSI or PSII. In addition, energy transfer from the antenna of PSII to PSI will be denoted by the subscript T(21).

The probability, ψ, that a process will occur is determined by quotient of the rate constant for that process divided by the sum of the rate constants for all competing processes. For example, the probability for energy transfer from PSII to PSI is

$$\psi_{T(21)} = k_{T(21)}/\Sigma k_2 \tag{1a}$$

where

$$\Sigma k_2 = k_{F2} + k_{D2} + k_{T2} + k_{T(21)}$$

Special note must be taken of the state of the PSII reaction centers. If a PSII reaction center is open (i.e. in the P680·Q state) it is assumed that excitons arriving at the reaction center will be used for photochemistry, i.e. that $k_{p2} \gg k_{d2}$ or k_{t2} so that $\psi_{p2} \approx 1.0$. However, if the reaction center is closed (the $P680 \cdot Q^-$ state) photochemistry cannot occur, $k_{p2} = 0$, and the exciton is either dissipated by nonradiative decay in the reaction center Chl, k_{d2}, or is returned to the PSII antenna, k_{t2}, where the various antenna processes can again compete. At closed PSII centers

$$\psi_{t2} = \frac{k_{t2}}{k_{t2} + k_{d2}} \quad \text{and} \quad \psi_{d2} = \frac{k_{d2}}{k_{t2} + k_{d2}} \tag{1b}$$

Owing to the return of excitation energy from closed reaction centers, the yields (or probabilities) for the various dissipative processes in the antenna of PSII increase as the reaction centers close. The yields of such processes, noted as ϕ, all increase from a minimum value, to be noted by (0) in the subscript, when the PSII reaction centers are all open to maximum values, denoted (M), when the reaction centers are all closed. As an example

$$\phi_{T(21)(0)} = \psi_{T(21)} \tag{1c}$$

$$\phi_{T(21)(M)} = \psi_{T(21)}(1 - \psi_{T2}\psi_{t2})^{-1} = \psi_{T(21)} \cdot E_2 \tag{1d}$$

where E_2 is the enhancement factor which results from the closure of the PSII reaction centers.

It should be noted that although the concept of excitation cycling is invoked in the above derivation, the enhancement factor can arise from any process in which excitation passes through the PSII antenna complex many times, e.g. between two antenna domains which have a non zero probability for back transfer. The lifetimes of fluorescence from PSII can be expected to change to the same extent that the yield of fluorescence changes. Thus

$$\tau_{F2(0)} = (\Sigma k_2)^{-1} \tag{2a}$$

and

$$\tau_{F2(M)} = \tau_{F2(0)} \cdot E_2 \tag{2b}$$

Expressing $\tau_{F2(0)}$ and ψ_{T2} in terms of rate constants and simplifying, Eq. 2b may be rewritten as

$$\tau_{F2(M)} = [k_{D2} + k_{F2} + k_{T(21)} + k_{T2}(1 - \psi_{t2})]^{-1} \tag{2c}$$

This implies that the energy recycling resulting from reaction center closure effectively reduces the rate constant for excitation transfer from the PSII antenna to the reaction center from k_{T2} to $k_{T2}(1 - \psi_{t2})$. It is clear from Eqs 1a and 2a that if $\psi_{T(21)}$ and $\tau_{F2(0)}$ are known, the value of $k_{T(21)}$ can be obtained.

In the case of PSI, the lifetime of fluorescence at 77 K has been reported to be independent of the redox state of the reaction center (Butler *et al.*, 1979) so that

$$\tau_{F1(0)} = \tau_{F1(M)} = (\Sigma k_1)^{-1} \tag{3}$$

where $\Sigma k_1 = k_{D1} + k_{F1} + k_{T1}$. The above statement assumes exclusion of excitation cycling in PSI and of the component of PSII to PSI transfer as the latter is too fast (~ 140 ps) (see Campillo *et al.*, 1977).

Estimation of α

If we denote the rate of absorption of photons by PSI and PSII as $I_1 = \alpha I$ and $I_2 = \beta I$, respectively, where I is the rate of absorption by the entire photochemical apparatus, α can be defined as

$$\alpha = \frac{I_1}{I_1 + I_2} = \frac{\alpha}{\alpha + \beta} \tag{4}$$

Defining the fluorescence produced by photons initially absorbed by PSI as $F_{1(\alpha)}$

$$F_{1(\alpha)} = I_1 \cdot \psi_{F1} \tag{5a}$$

or

$$I_1 = F_{1(\alpha)}/\psi_{F1} \tag{5b}$$

Similarly, the maximum fluorescence from PSII occurs when the reaction centers are closed so that excitation cycling is maximum and the quanta input to PSII is operationally equal to $I_2 \cdot E_2$ (*cf.* Eq. 1c), in which case

$$F_{2(M)} = I_2 \cdot E_2 \cdot \psi_{F2} \tag{6a}$$

and

$$I_2 = F_{2(M)}/(E_2 \cdot \psi_{F2}) \tag{6b}$$

Substituting Eqs 5b and 6b in Eq. 4, and simplifying

$$\alpha = \frac{F_{1(\alpha)}}{F_{1(\alpha)} + F_{2(M)} \cdot \psi_{F1}/(\psi_{F2} \cdot E_2)} \tag{7}$$

By definition, $\psi_{F1} = k_{F1}/\Sigma k_1 = k_{F1} \cdot \tau_{F1(0)}$ (*cf.* Eqs 1a and 2a), and since $\tau_{F1(0)} = \tau_{F1(M)}$, one obtains

$$\psi_{F1} = k_{F1} \cdot \tau_{F1(M)} \tag{8}$$

Similarly, by Eq. 2b

$$\psi_{F2} \cdot E_2 = k_{F2} \cdot \tau_{F2(0)} \cdot E_2 = k_{F2} \cdot \tau_{F2(M)} \tag{9}$$

Hence, by substituting Eqs 8 and 9 in Eq. 7, we have

$$\alpha = \frac{F_{1(\alpha)}}{F_{1(\alpha)} + \frac{k_{F1}}{k_{F2}} \cdot \frac{\tau_{F1(M)}}{\tau_{F2(M)}} \cdot F_2(M)} \tag{10}$$

By assuming identical rate constants of fluorescence for Chl-*a* in PSI and PSII, $k_{F1}/k_{F2} = 1$, Eq. 10 becomes

$$\alpha = \frac{F_{1(\alpha)}}{F_{1(\alpha)} + \frac{\tau_{F1(M)}}{\tau_{F2(M)}} \cdot F_{2(M)}} \tag{11}$$

Alternatively, if $F_{1(\beta)(0)}$ is defined as the fluorescence from PSI sensitized by quanta absorbed in PSII and transferred to PSI when the PSII reaction centers are all open

$$F_{1(\beta)(0)} = I_2 \cdot \psi_{T(21)} \cdot \psi_{F1} \tag{12a}$$

or

$$I_2 = F_{1(\beta)(0)}/(\psi_{T(21)} \cdot \psi_{F1}) \tag{12b}$$

so that by substituting for I_1 and I_2 in Eq. 4 using Eqs 5b and 12b, respectively, and simplifying, we obtain the Strasser and Butler (1977b) Eq.

$$\alpha = \frac{F_{1(\alpha)}}{F_{1(\alpha)} + \frac{1}{\psi_{T(21)}} \cdot F_{1(\beta)(0)}} \tag{13}$$

Using the condition that $\alpha + \beta = 1$, β can be calculated. Then by Eqs 5a and 12a

$$\frac{F_{1(\alpha)}}{F_{1(\beta)(0)}} = \frac{\alpha}{\beta \psi_{T(21)}}$$

giving

$$\psi_{T(21)} = \frac{\alpha}{\beta} \cdot \frac{F_{1(\beta)(0)}}{F_{1(\alpha)}} \tag{14}$$

The theoretical calculated parameters and the experimental quantities needed for our present analysis are described under Results and Discussion.

RESULTS AND DISCUSSION

Comparison of Chl-a fluorescence lifetimes and intensities at 77 K in thylakoids with and without cations

Table 1 reproduces essentially the experimental findings of Wong *et al.* (1979), but it includes both the

Table 1. Cation effects on Chl-*a* fluorescence lifetimes and intensities at 77 K

Sample	Lifetime, τ (ns)* $\tau(F686_{(M)})$	$\tau(F695_{(M)})$	$\tau(F370_{(M)})$	Fluorescence intensities†	F690	F730	Normalized ratios‡ (actual ratios in parentheses) $\tau(F686_{(M)})/\tau(F730_{(M)})$	$\tau(F695_{(M)})/\tau(F730_{(M)})$	$F690_{(M)}/F370_{(M)}$
Salt-depleted	0.42	0.77	2.02	'O'	59	266	—	—	—
				'M'	100	323	0.72 (0.21)	0.81 (0.38)	0.65 (0.31)
+ 10 m*M* NaCl	0.43	0.77	2.16	'O'	56	347	—	—	—
				'M'	100	426	0.69 (0.20)	0.76 (0.36)	0.48 (0.23)
+ 10 m*M* NaCl + 10 m*M* $MgCl_2$	0.60	0.99	2.10	'O'	59	219	—	—	—
				'M'	133	276	1.00 (0.29)	1.00 (0.47)	1.00 (0.48)

Washed thylakoids suspended in 100 m*M* sucrose containing 0.4 m*M* Tris–HCl at pH 7.6, with a final Chl concentration of 25 μg/mℓ and pH 7.0 ± 0.02 (see Wong *et al.*, 1978); samples frozen in a 1 mm cuvette submerged in liquid nitrogen in Dewar flask; fluorescence measured from front surface. Average of five separate measurements from three batches of chloroplasts; the same trend for the cation effects existed in every set of samples (after Wong *et al.*, 1979).

*Fluorescence was detected through interference filters at 686 nm (half band-width, 6.8 nm) for $\tau(F686_{(M)})$, at 695 nm (half band-width, 6.3 nm) for $\tau(F695_{(M)})$, and at 730 nm (half band-width, 8.4 nm) for $\tau(F370_{(M)})$ in combination with a Schott RG5 cut off filter (thickness, 3 mm). λ excitation, 632.8 nm; frequency, 75 MHz; 40 mW/cm^2 (1.7×10^9 photons/cm^2 pulse); phase shift method (after Wong *et al.*, [1979]).

†Fluorescence intensities were measured under conditions similar to that in *; the fluorescence intensities were corrected for photocathode sensitivity, monochromator transmission characteristics and stray light. 'O' stands for minimum and 'M' for maximum fluorescence. $F690_{(M)}$ for any sample was normalized according to the value of $[\tau(F686_{(M)}) + \tau(F696_{(M)})]/2$ for the corresponding sample.

‡These ratios are for the closed reaction centers; normalized to 1.00 for the $Na^+ + Mg^{2+}$ sample.

Table 2. Effects of cations on the excitation distribution and redistribution parameters in thylakoids

Sample	α	β	ψ_{F2}	$\psi_{T(21)}$	$\psi_{D2} + \psi_{T2}$	Calculated $F690_{(M)}/F730_{(M)}$
Salt-depleted	0.36	0.64	0.02	0.25	0.73	0.29
10 m*M* NaCl	0.40	0.60	0.02	0.27	0.71	0.24
10 m*M* NaCl 10 m*M* + $MgCl_2$	0.33	0.67	0.02	0.13	0.85	0.48

In the table, α was calculated by Eq. 11 and $\beta = 1 - \alpha$. $\psi_{F2} = \tau_{F2(0)}/\tau_0$, where $\tau_{F2(0)} = \tau_{F2(M)}$. $F690_{(0)}/F690_{(M)}$, and τ_0 (the lifetime of fluorescence in the absence of competition was taken to be 15.2 ns (Brody and Rabinowitch, 1957); $\psi_{T(21)}$ was calculated by Eq. 14, and $(\psi_{D2} + \psi_{T2})$ was obtained using the condition $\psi_{D2} + \psi_{F2} + \psi_{T(21)} + \psi_{T2} = 1$. $F690_{(M)}/F730_{(M)}$ was calculated as: $[\beta \cdot \tau(F690_{(M)})/\tau(F730_{(M)}]/[\alpha + \beta \cdot \psi_{T(21)} \cdot E_2]$. For the definition of symbols, see Theoretical Considerations, and for other details, see text.

fluorescence intensity and lifetime data for sucrose washed, 10 m*M* Na^+, and 10 m*M* Na^+ plus 10 m*M* Mg^{2+} thylakoids at pH 7.0, and at 77 K, needed for the present analysis. To facilitate comparison between samples, $F690_{(M)}$ in Table 1 was normalized according to the value of $[\tau(F686_{(M)}) + \tau(F696_{(M)})]/2$ for the corresponding sample. Addition of 10 m*M* Na^+ to cation-depleted thylakoids (at pH 7.0) caused no change in $\tau(F695_{(M)})$ and $\tau(F686_{(M)})$; it increased F730 by 32%, but $\tau(F730_{(M)})$ by only 7%. Subsequent addition of 10 m*M* Mg^{2+} caused a 40% increase in $\tau(F686_{(M)})$ and a 29% increase in $\tau(F695_{(M)})$; it decreased F730 by 36% but $\tau(F730_{(M)})$ by only 3%. Thus, a large discrepancy between lifetimes and intensities occurred at 730 nm. This phenomenon was also seen when $\tau(F686_{(M)}/\tau(F730_{(M)})$ was compared with $F690_{(M)}/F370_{(M)}$: addition of Na^+ caused no significant change in the ratios, but it decreased the intensity ratios by ~ 26%. Since $\tau(F730_{(M)})$ did not significantly change, the above changes were explained by changes in fluorescence efficiency of PSII.

Calculation of electronic excitation energy distribution, redistribution and dissipation processes

Using the results in Table 1 and the relations appearing at the end of Theoretical Considerations, the fractions of quanta partitioned to PSI and PSII—α and β, respectively—and the efficiency of energy transfer from PSII to PSI, $\psi_{T(21)}$, were calculated. For these calculations, $\tau(F690_{(M)})$ was approximated as $[\tau(F686_{(M)}) + \tau(F695_{(M)})]/2$, i.e. 0.6, 0.6, and 0.8 ns for the salt-depleted, Na^+, and $Na^+ + Mg^{2+}$ samples, respectively. Assuming the lifetimes and intensities of the fluorescence at 690 nm are proportional, the ratios of the 0 to P level lifetimes, $\tau(F690_{(0)})/F690_{(M)}$, would be equal to the intensity ratios $F690_{(0)}/F690_{(M)}$; thus, values for $\tau(F690_{(0)})$ could be obtained. These values were 0.35, 0.34, and 0.35 ns for the three samples in the order above. Then, the ratio of $\tau(F690_{(0)})$ to τ_0, the intrisic lifetime of Chl-*a* fluorescence, taken as 15.2 ns [Brody and Rabinowitch (1957)], gave the fluorescence efficiency, ψ_{F2}. Finally, since $\psi_{F2} + \psi_{T(21)} + \psi_{D2} + \psi_{T2} = 1$, the sum $\psi_{D2} + \psi_{T2}$—collectively referred to here as other radiationless processes—was obtained (see vertical column 6, Table 2).

Table 2 summarizes the results of our analysis; α (photons into PSI) was obtained by using Eq. 11, where $\tau_{F1(M)}$, $\tau_{F2(M)}$ and $F_{2(M)}$ were the measured values of $\tau(F730_{(M)})$, $\tau(F690_{(M)})$ and $F690_{(M)}$, and $F_{1(\alpha)}$ was

$$F730_{(M)} - \frac{F730_{(M)} - F730_{(0)}}{F690_{(M)} - F690_{(0)}} \cdot F690_{(M)}$$

(Strasser and Butler, 1977b); β (photons into PSII) $= 1 - \alpha$; ψ_{F2} was calculated as $\tau(F690_{(0)})/\tau_0$; and, $\psi_{T(21)}$ (efficiency of energy transfer from PSII to PSI) was calculated according to Eq. 14, with $\alpha, \beta, F_{1(\alpha)}$ as calculated above, and $F_{1(\beta)(0)} = F730_{(0)} - F1_{(\alpha)}$. The main findings were: (a) Mg^{2+} induced a decrease in the efficiency of energy transfer from PSII to PSI ($\psi_{T(21)}$)—50% change (vertical column 5); (b) Mg^{2+} induced an increase in the sum of efficiencies of non-radiative de-excitation in the PSII antenna and of energy transfer from this antenna to the reaction center ($\psi_{D2} + \psi_{T2}$)—~ 20% change (vertical column 6), and (c) cations affected the initial distribution of quanta to the photosystems—~ 6% decrease in β by Na^+, and ~ 12% subsequent increase by Mg^{2+}. The last column in Table 2 shows that the expected values of $F690_{(M)}/F730_{(M)}$ (calculated from the equation shown in the legend of Table 2) corresponded closely to the measured ratios in Table 1, demonstrating that the calculated energy distribution and redistribution parameters were consistent with the observations.

CONCLUDING REMARKS

Using the new equation for α, derived here, Wong *et al.* (1980) have extended the analysis to thylakoids suspended at two other pH values (6.2 and 8.8); the results at pH 6.2 are similar to those at pH 7.0 reported here. However, at pH 8.8, addition of Na^+ to the cation-depleted thylakoids leads to a decrease,

instead of an increase, in α while the further addition of Mg^{2+} to the Na^{+}-containing sample leads to decrease as also observed here. The effects of cations on $\psi_{T(21)}$ at the pH 6.6 and 8.8 are similar to those observed here for pH 7.0.

Changes in α imply that the physical size of PSI could change, presumably by a closer (or farther) association of the antenna to the core PSI complex as suggested by PSII by polarization of fluorescence studies (Wong and Govindjee, 1979). Whether these changes are followed by changes in trapping or losses or both cannot be answered yet although we assume that changes in α produce the same final results as changes in $\psi_{T(21)}$ (also see Wong *et al.*, 1978). In the latter case, Wong *et al.* (1980) found that decreases in non-cyclic PSI activity, upon Mg^{2+} addition, were about half as much as increases in non-cyclic PSII activity suggesting that some PSI, that are not engaged in non-cyclic reactions, may receive energy from PSII.

Acknowledgement—We thank the Biomedical grant (1980–1981), provided through the School of Life Sciences, University of Illinois at Urbana, for financial support.

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