*Biochimica et Biophysica Acta*, 408 (1975) 143-153
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BBA 46993

# PROBING THE KINETICS OF PHOTOSYSTEM I AND PHOTOSYSTEM II FLUORESCENCE IN PEA CHLOROPLASTS ON A PICOSECOND PULSE FLUOROMETER

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(Received April 7th, 1975)

## SUMMARY

Picosecond fluorescence kinetics of pea chloroplasts have been investigated at room temperature using a pulse fluorometer with a resolution time of $10^{-11}$ s. Fluorescence has been excited by both a ruby and neodymium-glass mode-locked laser and has been recorded within the 650 to 800 nm spectral region.

We have found three-component kinetics of fluorescence from pea chloroplasts with lifetimes of 80, 300 and 4500 ps, respectively. The observed time dependency of the fluorescence of different components on the functional state of the photosynthetic mechanism as well as their spectra enabled us to conclude that Photosystem I fluoresces with a lifetime of 80 ps ($\tau_{\mathrm{I}}$) and Photosystem II fluoresces with a lifetime of 300 ps ($\tau_{\mathrm{II}}$). Fluorescence with a lifetime of 4500 ps ($\tau_{\mathrm{III}}$) may be interpreted as originating from chlorophyll monomeric forms which are not involved in photosynthesis.

It was determined that the rise time of Photosystem I and Photosystem II fluorescence after 530 nm photoexcitation is 200 ps, which corresponds to the time of energy migration to them from carotenoids.

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## INTRODUCTION

A number of laboratories are involved in the study of the mechanism of conversion of light electromagnetic energy into the energy of chemical bonds in organic matter during photosynthesis. As is evident from the literature, the initial phases of photosynthesis which determine the character of this process proceed at time intervals of $10^{-8}$ and $10^{-13}$ s and are associated with absorption of light quanta, energy transfer from bulk chlorophyll and accessory pigments to the reaction centers as well as with photo-induced charge separation [1–4]. Evidently, it is of importance to study experimentally the processes which occur within the $10^{-8}$ to $10^{-13}$ s time domain. Up to now the technique of phase and pulse fluorometry with a resolution time up to $5 \cdot 10^{-10}$ s was used for this purpose [5–6]. With the advent of lasers it became possible to improve the known methods of the pulse fluorometric technique [7–8] and to develop new methods for measuring decay kinetics of pigments and dyes in the excited electronic state.

Through the use of the methods involving the most sensitive instruments a number of investigators have succeeded in recording the decay kinetics of in vivo chlorophyll fluorescence [9–10]. This permitted us to proceed to the subsequent study of the decay of fluorescence of different components, the existence of which had been predicted earlier but could not be proved directly by the phase fluorometric technique.

In this respect, of greatest interest is the work of Seibert and co-workers [9–10] using $CS_2$ with a pulse instrument resolution time of about $10^{-11}$ s, a picosecond laser excitation and an optical Kerr gate. The results obtained show that there are two fluorescing components in chloroplasts: $\tau_I$ less than 10 ps and $\tau_{II}$ of about 300 ps associated with the proper fluorescence of Photosystem I and Photosystem II, respectively.

Early work with the phase fluorometric technique have shown that under the action of inhibitors [11], low temperatures [12–14], at light-induced saturation of photosynthesis, during greening of etiolated leaves there is correlation between the life-time of total chlorophyll fluorescence and the intensity of processes consuming light energy in photosynthesis. In the present work an attempt is made using a sensitive pulse fluorometer with an electron-optical image converter to study a relationship between the photosynthetic processes in chloroplast and decay kinetics of Photosystem I and Photosystem II fluorescence under different conditions of light excitation.

## MATERIALS AND METHODS

### *Pulse fluorometer*

The resolution time of a pulse fluorometer is determined by the pulse duration of actinic light, as well as by the resolution time of the recording system. At present, to study the ultrafast processes of deactivation of excited states, both solid-state and dye Q-switched mode-locked lasers are used widely as light excitation sources, the principle of their operation having been discribed earlier [15–16]. Indirect methods for measuring light flashes in the picosecond range are now in wide use [17–19], while electron-optic image convertors are used rather rarely for direct measurement of picosecond light pulses [20, 21].

The scheme of pulse fluorometer applied in our experiments is shown in Fig. 1.

To excite fluorescence of the sample 9 both ruby and Nd-glass mode-locked lasers were used. As activation sources, the RL2B ruby rod, 170 mm long and 10 mm in diameter, with leucosapphire tips and the LGS-2B-2 glass rod with an admixture of neodymium, 302 mm long and 15 mm in diameter, were employed. The ends of the rods were cut at Brewster's angle. A cuvette furnished with cryptocyanine solute in ethanol, with optical density $\mu$ at $\lambda = 694$ nm, $\mu = 0.4$, was provided to modulate the ruby laser, and a polimethine dye, No. 3955, solution in nitrobenzene, with optical density $\mu$ at $\lambda = 1060$ nm $\mu = 0.35$ to modulate the Nd-glass laser.

Light outputs of the ruby and Nd-glass lasers pass through $KH_2PO_4$ second-harmonic generator crystals 3 with as much as 10% conversion of the fundamental frequency into the second harmonic. A typical laser flash consist of about 30 pulses

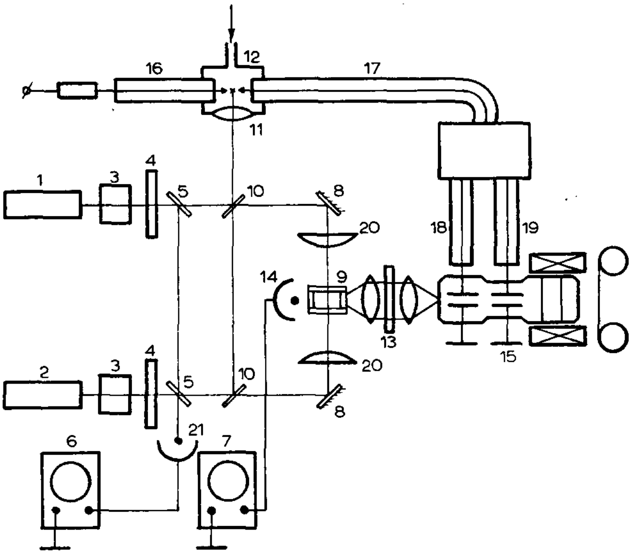

Fig. 1. Scheme of the pulse fluorometer. 1 and 2, ruby and Nd-glass laser; 3, $KH_2PO_4$ crystals; 4, glass filters; 5 and 10, beam diverting glass plates; 8, mirrors; 6 and 7, oscilloscopes; 9, cuvette containing the solution under investigation; 11, focusing system; 12, spark-gap; 13, system of image transfer; 14 and 21, photocells; 15, electron-optical image convertor; 16–19, cable lines; 20, cylindrical lenses.

separated from each other by the cavity round-trip time of about 10 nsec.

Thus, fluorescence could be initiated by picosecond laser pulses at 1060, 694, 530 and 347 nm. The emission at the required wavelength was obtained by passing light through light glass filters 4. For observation of the actinic light, a portion of it was diverted by means of glass plates (5) onto a photocathode of the F-21 coaxial photocell. To check the system for proper alignment, the actinic light pulses were detected and displayed on the screen of an oscilloscope, and the pulse shape was observed visually and recorded photographically. The main portion of actinic light followed its path through glass plates (5 and 10), and dielectric mirrors to the sample in cuvette (9).

Fluorescence could be recorded either through the photo-cell (14), oscilloscope (7) chain or through an electron-optical image convertor. If an oscilloscope was used for the purpose of recording, light was absorbed by photocells, types F-13 and F-21, with multi-alkali and oxygen-cesium cathodes, respectively. In integral sensitivities of the photocells were as high as 400 $\mu$A/lumen and 40 mcA/lumen, for recording purpose we used the oscilloscope with a 2000 MHz passband, this allowed us to obtain a resolution time of $5 \cdot 10^{-10}$ s.

An electron-optical image convertor was used for measuring fast kinetics with the quantum yield of fluorescence of less or about $10^{-4}$. In this case a portion of actinic light diverted by glass plates (10) and focused by system 11 was applied to a gaseous medium of spark gap (12), which acted as a control pulse generator.

Without going into details, we would like to emphasize that with this generator it is possible to obtain a scan time ranging from zero to several tens of nanoseconds.

The main portion of the laser emitted light passed via glass plate (5) to a cuvette containing a sample solution. By passage through a number of cylindrical lenses light was collimated into a narrow beam, 0.2 mm wide. Fluorescence was excited in a small volume on the front face of the cuvette. To protect the cathode of the electron-optical image convertor from the action of actinic light, the fluorescence emission directed to the measuring system was oriented by an angle of 90° to the actinic light pathway. A pulse width of the actinic light emitted by the Nd-glass laser was $5 \cdot 10^{-12}$ s as determined by tracks of two-photon luminescence. Recording of these pulses on the fluorometer (Fig. 2a, σ) showed that the rise-time of the pulse of actinic light at a level of 0.1–0.9 of maximum amplitude is 8 ps and the fall-time is 12 ps. Pulse duration at a half a peak is $1.2 \cdot 10^{-11}$ s. Consequently, the resolution time of the fluorometer operating in conjunction with an electron-optical image convertor is $1.2 \cdot 10^{-11}$ s, the accuracy being 20 %.

To determine the sensitivity of a photochronograph a considerably weakened actinic light emission was applied to the cathode of the electron-optical image convertor. We have found that with a scan rate of $10^4$ km/h (corresponding to a resolution time of $10^{-11}$ s) the fluorometer sensitivity enables to measure light pulses of $5 \cdot 10^{-12}$ s and of a peak power of $10^{-11}$ J. Accordingly, for measuring long-term processes (corresponding to lower scan rates) the fluorometer sensitivity is higher.

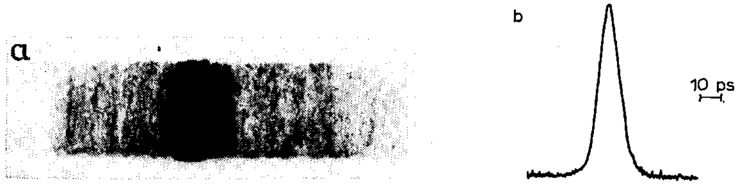

Fig. 2. Densitogram (a) and microphotogram (b) of an exciting pulse obtained with the use of an electron-optical image convertor.

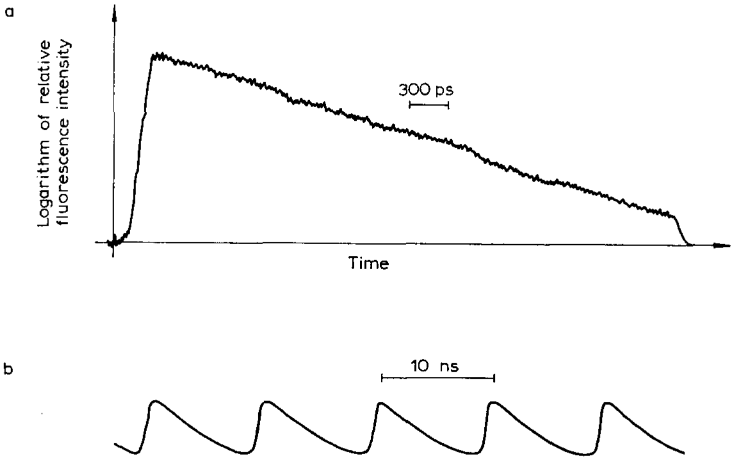

Fig. 3. Kinetics of chlorophyll fluorescence in ethanol. Densitogram and oscillogram obtained with the use of the pulse fluorometer and measured: (a) on an electron-optical image convertor and (b) on the oscilloscope.

The spectral sensitivity of the electron-optical image convertor is conditioned by the type of a photocathode (C-I) and corresponds to 350 to 1200 nm.

To excite the fluorescence from in vivo chloroplasts we used light pulses having the energy density not exceeding $10^{-4}$ J/cm$^2$. For in vitro experiments the pulse energy density might be increased to $10^{-1}$ J/cm$^2$. To demonstrate the technical characteristics of the fluorometer in the experiments in vitro, we have shown the densitograms and oscillograms (Fig. 3) illustrating the decay of fluorescence of chlorophyll "a" solutions.

### *Chloroplasts*

For the experimental purposes we have taken chloroplasts from the leaves of 6–7-day pea seedlings. The plants were grown in the $\frac{1}{2}$N Knopp culture medium with a 16-h photo-period. The light intensity was 10 000 lux. Chloroplasts were isolated according to Arnon [22]. The plants were first stored on ice for 1 h. The leaves cut into small pieces were ground in an isolating medium (40 ml of $H_2O$, 0.35 M NaCl in 0.2 M Tris/HCl buffer solution, pH 7.8, containing 10 mM sodium ascorbate). The resultant slurry was filtered through one layer of linen into a cooled centrifuge glass. To eliminate any intact cells, cell walls or other particles the liquid was centrifuged for 7 min at $1000 \times g$. The sediment was homogenized in the same glass upon addition of 2–3 ml of the chloroplast isolation medium. After washing once in the isolation medium, the chloroplasts were again sedimented for 7 min at $1000 \times g$. The plastids sediment was suspended in several millilitres of the isolation medium; as a result 0.1 ml of suspension contained 0.05 to 0.09 mg of chlorophyll.

## RESULTS

### *Decay of in vivo chlorophyll fluorescence (pea chloroplasts)*

After excitation of chloroplasts by picosecond pulses at 530 nm with band filters transparent in the long wavelength spectral region $\lambda \geqslant 730$ nm, we recorded one decay component with the rise-time of fluorescence being $t_R = 200$ ps and a lifetime of $\tau_I = 80$ ps, whereas for shorter wavelengths $\lambda \geqslant 650$ nm, we recorded components with the lifetime of $\tau_{II} = 300$ ps and $\tau_{III} = 4500$ ps and the same fluorescence rise-time of $t_R = 200$ ps (Fig. 4 (2), (3)).

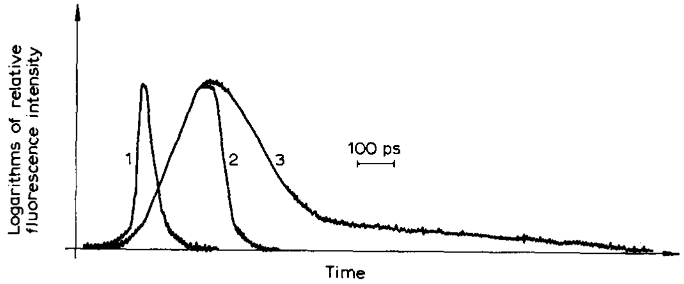

Fig. 4. Kinetics of the fluorescence decay in pea chloroplasts as measured on a pulse fluorometer. 1, $\lambda_{exc} = 694$ nm, $\lambda_{obs} \geqslant 730$ nm; 2, $\lambda_{exc} = 530$ nm, $\lambda_{obs} \geqslant 730$ nm; 3, $\lambda_{exc} = 530$ nm, $\lambda_{obs} \geqslant 650$ nm. On the ordinate axis logarithms of relative fluorescence intensity are plotted as determined on densitograms of films from electron-optical image convertor screen.

When excited with picosecond pulses at 694.3 nm chloroplasts demonstrate only one fluorescing component in a spectral region of $\lambda \geqslant 730$ nm and $\tau_I = 80$ ps (Fig. 4 (1)). In this condition the fluorescence rise-time $t_R$ was about 10 ps, i.e. within the resolution time of the instrument.

Through the use of glass filters it became possible to observe the decay kinetics of different components in the spectral region of their maximal fluorescence [23]. Thus, for the components having lifetimes of $\tau_{II} = 300$ ps and $\tau_{III} = 4500$ ps the fluorescence is maximal at 660 to 680 nm wavelengths, whereas the component with $\tau_I = 80$ ps emits it at $\lambda \geqslant 730$ nm. The data obtained suggest that the components with $\tau_I = 80$ ps and $\tau_{II} = 300$ ps correspond to the fluorescence of both Photosystems I and II. To support this view, experiments were made with well known inhibitors affecting photosynthetic processes and particularly the functional state of Photosystem I and Photosystem II. In the experiments aimed to measure $\tau_I$ fluorescence was excited by light at 694 nm and was recorded at the wavelengths longer than 730 nm. $\tau_{II}$ and $\tau_{III}$ components were excited by light at 530 nm and fluorescence was measured at wavelengths $\lambda \geqslant 650$ nm.

### *3-(3,4-Dichlorophenyl)-1,1-dimethylurea (DCMU) effect*

3-(3,4-Dichlorophenyl)-1,1-dimethylurea is known to be an inhibitor of Photosystem II blocking an electron flow from the primary acceptor. It has been reported that using a phase fluorometer a DCMU-induced increase in the quantum yield and fluorescence lifetime have been observed [24–25].

In our experiments we have observed a 2-fold time increase of the decay kinetics of the second fluorescing component $\tau_{II}$ from 300 to 600 ps due to the effect of $10^{-4}$ M DCMU.

On the other hand, the time dependence of the first and the third fluorescing components, as well as the fluorescence rise-time have remained unchanged under the DCMU effect.

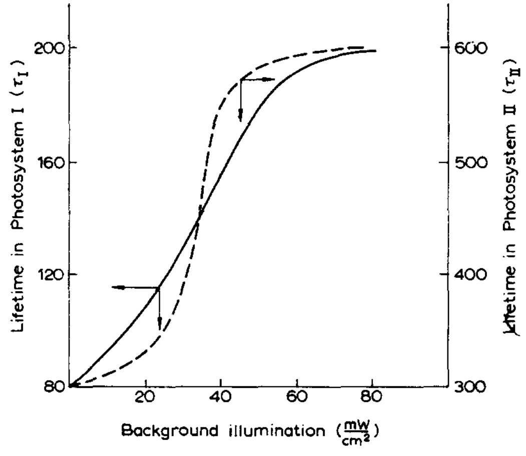

Fig. 5. Fluorescence lifetime (ps) of Photosystem I ($\tau_I$) and Photosystem II ($\tau_{II}$) as a function of background illumination by a helium-neon laser.

### *Influence of background illumination*

Early works on photosynthesis showed that the light intensity increase causes the saturation of this process followed by increase in the fluorescence quantum yield and lifetime values [26–28]. This effect was considered to be due to the reduction of primary acceptor ($Q \rightarrow Q^-$) by photoactive centers (P) in Photosystem II. The complex of $PQ^+$ with oxidized acceptors (Q) can be regarded as chemical traps, in other words, fluorescence-quenching centers.

We have made experiments with the aim of investigating the influence of the background illumination on the fluorescence time of intact chloroplasts and isolated particles in both Photosystem I and Photosystem II.

Simultaneously by ESR measurements [29] we have studied the dependence of the degree of oxidation of Photosystem I on the light intensity. With the increase

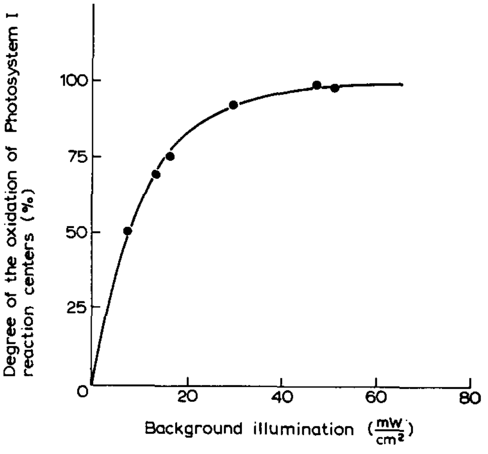

Fig. 6. Dependence of the degree of the oxidation of Photosystem I reaction centers of subchloroplasts particles cn the intensity of background illumination.

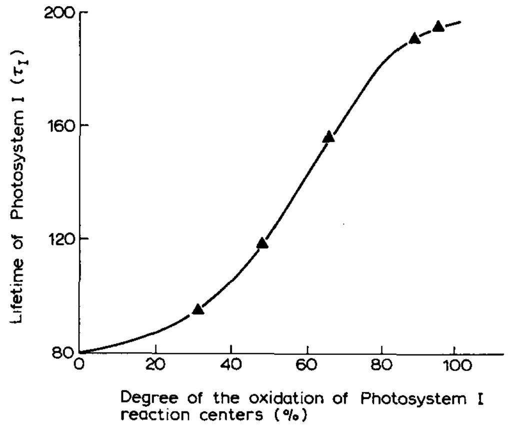

Fig. 7. Dependence of the fluorescence lifetime (ps) of Photosystem I light absorbing pigments in subchloroplast particles on the degree of reaction center oxidation.

of the intensity of background illumination up to 70 mW/cm$^2$ we have observed $\tau_I$ increase of isolated particles in Photosystem I from 80 ps to 200 ps and $\tau_{II}$ from 300 to 600 ps, both $\tau_I$ and $\tau_{II}$ values being saturated at high light intensities (Figs 5–7).

### *Alcohol effect*

Polar organic solvents are known to suppress photosynthetic activity of chloroplasts and at high solvent concentrations completely separate pigment molecules from chloroplast membranes. Such an action of ethanol, acetone and pyridine also causes an increase of the life-time of the total fluorescence [11].

In our experiments, an enhanced ethanol concentration resulted in an increase of the amplitude of the fluorescence component with the lifetime of $\tau_{III} = 4500$ ps and, on the contrary, in a decrease of the amplitude of the fluorescence components with lifetimes of $\tau_I$ and $\tau_{II}$, respectively, the decay times for three of them remaining unchanged.

At a 60 % ethanol concentration the fluorescence of free chlorophyll prevailed in the decay kinetics (Fig. 8, c.f. Fig. 3).

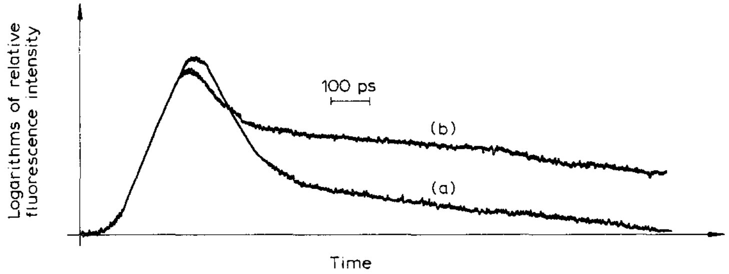

Fig. 8. Kinetics of the fluorescence decay of chloroplasts upon addition of 20 % and 60 % ethanol ("a" and "b", respectively). Excitation at $\lambda = 530$ nm, observation at $\lambda \geq 650$ nm. Ordinate plots as on Fig. 4.

## DISCUSSION

The data obtained on the fluorescence decay and effect of inhibitors on the primary reactions of photosynthesis enabled us to conclude that in chloroplasts there are three fluorescing centers, two of which are associated with both Photosystems I and II and the third one may be attributed either to the fluorescence of newly formed chlorophyll monomeric forms not involved in photosynthesis or fluorescence of monomeric chlorophyll formed when the chloroplasts are damaged in the course of their isolation. Decay kinetics of Photosystem I and Photosystem II measured in our experiments and the observed lifetimes $\tau_I$ and $\tau_{II}$ are in general agreement with the results obtained earlier by M. Seibert [9–10] and with the theoretical calculations made by other authors [30]. However, the precise values measured in our work i.e., $\tau_I = 80$ ps and $\tau_{II} = 300$ ps differ from those stated by these authors: $\tau_I \leq 30$ ps, $\tau_{II} \simeq 1400$ ps (Borisov) and $\tau_I \leq 10$ ps, $\tau_{II} \simeq 300$ ps (Seibert).

For the time being it is hard to explain the discrepancy between the absolute values of the decay time and fluorescence rise-time of Photosystem I excited by 530 nm light obtained by ourselves and by Seibert. Presumably, a difference in the detecting systems and specific features of picosecond laser excitation contribute to this. It is known that light intensities may cause self-bleaching of solutions and induce super luminescence leading to the distortion of the decay kinetics, particularly when measured in the direction of the actinic light beam. We believe that by measuring the fluorescence emission at right angles to the actinic beam (Fig. 1) combined with the use of glass filters, we have succeeded in eliminating these drawbacks.

Apparently the delayed fluorescence rise at 530 nm light excitation is associated with energy transfer with a time of 200 ps from carotenoids to fluorescing chlorophyll molecules in Photosystem I and Photosystem II. In our samples optical densities of carotenoids and chlorophyll at 530 nm are $D_{car} = 0.475$, $D_{chl} = 0.05$. This as well as the similarity of the absorption spectra of Photosystem I and Photosystem II enable us to conclude, that within a resolution time ($1.2 \cdot 10^{-11}$ s) energy from carotenoids to Photosystem I and Photosystem II is transferred at the same rate.

It is well known that a quantum yield of Photosystem II fluorescence is higher by one order of magnitude than that of Photosystem I. Taking into consideration these data and the spectral sensitivity of the photocathode of the electron-optical image convertor in the spectral regions of the maximal fluorescence emission of different components, we can estimate the ratio of their intensities as $J_{II} : J_I : J_{III} = 1 : 10^{-1} : 10^{-4}$, i.e., the fluorescence of the component with $\tau_{II} = 300$ ps is as much 10 times more intense than that of the component $\tau_I = 80$ ps and as much as $10^4$ times as intense as that of the component with $\tau_{III} = 4500$ ps. Using a well known equation governing the mean lifetime in a multi-component emission system:

$$\tau_{mean} = \frac{J_I \cdot \tau_I + J_{II} \cdot \tau_{II} + \cdots + J_i \cdot \tau_i}{J_I + J_{II} + \cdots + J_i}$$

together with the amplitude-time characteristic of each component we obtain:

$$\tau_{mean} \simeq 300 \text{ ps}$$

This shows that the above values are close to these [12, 30, 32] for the decay time of the total fluorescence from in vivo chlorophyll. Note, that in case of the phase fluorometric technique the measured lifetime values includes the fluorescence rise time, whereas the values of $\tau_I$ and $\tau_{II}$ determined by the laser pulse method correspond to the pure fluorescence decay. With a fluorescence rise-time of 200 ps ($t_R$) taken into account, the total time will equal to $\tau_m + t_R = 0.5$ ns which is close to $\tau$ determined earlier by phase methods. Undoubtedly, that the direct measurement of the decay kinetics of each photosystem separately makes it possible to study primary processes causing their deactivation.

For the investigation of the photosynthetic mechanism using the pulse or phase fluorometric technique, it is supposed that a considerable decrease in the lifetime of in vivo chlorophyll as compared with its solutions is related to an effective participation of an excited pigment in a primary photochemical reaction [11–14, 32–35], thus generating an electron flow in the photosynthetic chain. In order to account for the dependence of the quantum yield of fluorescence of in vivo chlorophyll in Photosystem II on the intensity of photosynthesis Duysens has formulated an idea according to which photochemical centers with oxidised primary acceptors Q act as fluorescence quenchers in photosynthesis [35].

Thus an increase of the actinic light intensity has to cause an increase of $\tau$ and quantum yield of fluorescence in Photosystem II. In fact our measurements (Fig. 5) show that $\tau_{II}$ for Photosystem II increases by 2–3-fold with an increase of light intensity saturating at about 70 mW/cm$^2$. As seen from Figs 5–7 the same is true for Photosystem I. The curves of $\tau_I$ for Photosystem I and $P^+/P$ dependency on the actinic light intensity $I_0$ are similar and saturated at the same value of $I_0$. It is worth noting that at light saturating intensities extreme values of $\tau_{II}$ in Photosystem II and $\tau_I$ in Photosystem I still remain 10–25 times lower than those of chlorophyll solutions (Figs 5 and 3). The same is true for $\tau_{II}$ for Photosystem II increasing from 300 ps up to 600 ps under the effect of 3-(3,4-dichlorphenyl)-t,1 dimethylurea applied at concentrations of $10^{-4}$ M which block the electron flow between Photosystem II at a site of inhibitor action so that all Photosystem II centers become "closed".

In other words, under conditions when both photoactive centers are not able to donate electrons to the electron chain, the deactivation of the singlet excited electron state for Photosystem I and Photosystem II still occurs with considerably high efficiency: $\tau$ varies from 200–600 ps.

Of course such deactivation of "inactivated" centers may be due to the heat dissipation of electron energy. On the other hand as follows from previous measurements, [30, 31], a quantum yield of primary photochemical charge separation is rather high sometimes reaching even 95–100 %. Provided this is also true for our preparations, one may conclude that under normal light conditions such heat deactivation of "inactivated" centers would lead to the sharp drop of expected quantum yield values.

To solve this controversy we assume that the observed decrease of $\tau$ values in vivo as compared with in vitro experiments may be due to the primary transfer of singlet excited P molecules into the metastable (triplet) state, occuring after the energy, migrated in the chlorophyll antenna, reaches active centers.

There are different ways to explain such an increase of the probability of the $S \rightarrow T$ transition in P molecules as compared with isolated chlorophyll molecules.

One can mention here the influence of a heavy metal atom (Fe) located in the protein part of the primary acceptor and/or singlet-singlet interactions between several P molecules included in the active center. Evidence to confirm this possibility will, of course, be looked for in the future.

It follows from this hypothesis that S → T transitions in the "inactivated" photochemical centers still occurs approximately with the same probability although they are unable to generate electron flow in the electron chain. The observed 2–3-fold increase of $\tau$ values under these conditions may be brought about by the corresponding changes of conformation and molecular interactions in such "inactivated" state of photochemical centers.

In other words oxidised molecules of the primary acceptor may not be direct quenchers of singlet excited states and therefore their number may have no direct relevance to the changes of $\tau$ values under different light exposures. One may suggest that electron carries located near active centers can only play their role by governing the S → T transitions in the complex of the active center with the primary acceptor through conformational changes accompanying the functioning of the electron transport chain.

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