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Analysis of Light Curve Shape for Delayed Chlorophyll Fluorescence in a Cell

E. M. Sorokin

Timiryazev Institute of Plant Physiology, USSR Academy of Science, Moscow

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Abstract

The shape of a light curve of intensity, $F_d(I)$, (or quantum yield ρd (I)) for delayed chlorophyll "a" fluorescence in a cell was theoretically analysed. It has been shown that depending on a number of parameters $F_d(I)$ (or $\rho_d(I)$) variations are described by two qualitatively different curves. In one case $F_d(I)$ is convex upwards all along its length, i.e. F_d is a monotonically increasing (ρ_d – monotonically decreasing) function of excitation light intensity, I. In the second case $F_d(I)$ is S-shaped and $\rho_d(I)$ has a maximum. One specific conclusion has been that the change in electron transport velocity on the reduction side of PS II must result in the transition from one type of curve to the other. Experimental data from the literature which are in agreement with this conclusion are cited.

Introduction

The phenomenon of prolonged luminescence in photosynthetizing organisms was discovered by Strehler and Arnold [1]. In green plants and algae its spectral composition is identical to that of chlorophyll "a" fluorescence (π_{max} = 685 nm with vibrational satellite of this band being in the region of 710-730 nm) [2-4] (see, however [5]), its duration is by several orders of magnitude greater [1, 5-9] and quantum yield, as a rule, by several orders of magnitude smaller [6, 7, 8, 10] than those of chlorophyll "a" fluorescence.

Identity of their spectral compositions is evidence of the fact that both types of luminescence result from deactivation of one and the same excitation state of chlorophyll "a" molecules. A predominant part of observable fluorescence in green plants and algae is known to be due to

chlorophyll "a" molecules in the pigment matrices of photosynthetic units (PSU) in photosystem II (PS II) [11, 12]. This makes it possible to analyse the data on the fluorescence of these photosynthetizers taking into account photosystem II only.

Model

The data available at present enables us to represent schematically the interrelationship between PS II and the noncyclic electron transport chain as it is shown in Fig. 1. Vertically (Fig. 1a) it shows a photosynthetic unit, i.e. a set of light-collecting and fluorescent chlorophyll molecules (crosses) and reaction centre (PA). Horizontally it represents components of the electron transport chain: H_2O decomposition system, plastoquione pool PQ, primary electron donor P and acceptor A, etc. Both subsystems, i.e. PSU and the electron transport chain have, as it were, a common intersection point equally belonging to both of them. This node element, on the one hand, acts in the neutral PA form as the reaction centre and, on the other, its charged components P^+ and A^- constantly localized in space are the initial driving force of oxidation-reduction processes in the electron transport chain at different sides of the reaction centre.

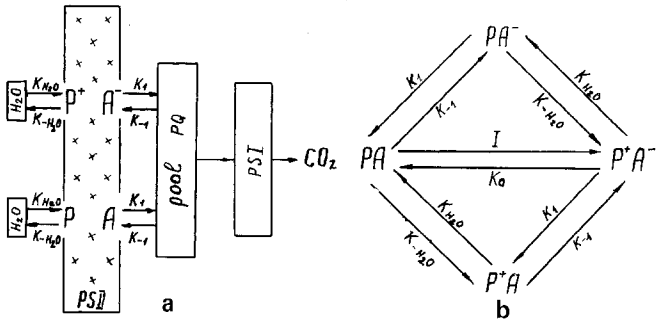

Figure 1. Diagrams of interrelation between PS II and non-cyclic electron transport chain (a) and of reaction centre state sequence (b).

The sequence of elements taking place here is approximately as follows. Due to light quantum absorption one of the PSU pigment matrix molecules is transferred to the singlet excitation state. From here on excitation energy starts to migrate over the pigment matrix. This process continues until the excitation quantum is captured by one of the reaction centres or released as a fluorescence quantum in one of the light-collecting molecules. At the expense of the absorbed energy in the PA centre (Fig. 1b) the electron is transferred from the primary donor P (assumed to be a chlorophyll "a" molecule) on to an as yet unidentified

primary acceptor A. The structural arrangement of the centre ensures that this separated pair of different sign charges remain stabilized. Then the charged forms of molecules making part of the reaction centre, now independently of one another, enter oxidation-reduction (heterogeneous) processes taking place at different sides of the photosynthetic membrane: P^+ receives electrons from the H_2O decompostion system which is in the inner thylakoid cavity [13] and A^- donates its electron to the plastoquinone pool on the external side of the membrane [13]. Because of the independence of A^- oxidation and P^+ reduction processes, the centre as a whole may be in four different charged forms: PA, P^+A^-, PA^- and P^+A. The last three cannot capture electron excitation energy from light-collecting molecules and hence they determine the so called "closed" state of the centre. After the act of charge separation, but still before one of the elements of the centre with two different charges P^+A^- has time to interact with its partners in the electron transport chain, back electron transfer from A^- to P^+ may take place in it, with energy stored in P^+A^- causing the excitation of the singlet level of a chlorophyll molecule P ($P^+A^- \xrightarrow{k_0} P^-A$). From here energy can further migrate to the light-collecting molecules. Having originated in this way the electron excitation quantum of the PSU pigment matrix is either reabsorbed in the same or some other centre or released in the form of a fluorescence quantum. These very quanta constitute delayed fluroescence. Its duration will not be determined by the time of energy migration along the PSU which is approximately equal to 10^{-9} sec and determines the observable duration of chlorophyll "a" fluorescence *in vivo*. It will be mainly determined by the lifetime of the centre with two different charges P^+A^- i.e. by the lifetime of its excitation source. This latter time depends only on rate constants which cause the centre in the form of P^+A^- (k_{H_2O}, k_1, k_0) to disappear. The reciprocal of their total value is by several orders of magnitude greater than the time of electron excitation energy migration over the PSU. Thus delayed fluorescence differs from fluorescence proper only in its excitation mechanism.

Theory

For the described model in [14] we have set up a system of kinetic equations which satisfactorily describes the observed dependences of stationary intensities (quantum yields) of non-cyclic electron transport, normal and delayed fluorescence on the excitation light intensity, i.e. the light curves of corresponding quantities [15]. Agreement of calculations with experiment is observed only for the so-called multicentral PSU model, where several reaction centres are combined into one functional system at the level of electron excitation energy migration [16, 17]. The relationships analysed below concern this very model.

If the back electron transfer from reduced plastoquinone molecules to oxidized molecules of the primary acceptor A is neglected, i.e. if we assume that $k_{-1} =$ (Fig. 1b), then, for the given model, delayed fluorescence intensity F_d will in the following manner be dependent on the excitation light intensity I [15]:

$$F_d = M \frac{\rho_0}{1 - L\alpha} \cdot k_0 \cdot Q \cdot \frac{k_{\Delta(p^+a^-)}}{k_{\Delta\alpha}} (\alpha - \alpha_1), \tag{1}$$

where α, which is equal to or less than unity, is the root of the equation

$$I\epsilon(1-\alpha) = k_{\Delta\alpha} (\alpha - \alpha_1) (\alpha_2 - \alpha). \tag{2}$$

The dependence of quantum yield ρ_d (equal, as defined, to the ratio of the intensity F_d to the intensity of light absorbed by the given photosystem $I\epsilon MQ$) on α is given by the equation:

$$\rho_d = \frac{\rho_0}{1 - L\alpha} \cdot \frac{k_0}{k_{\Delta(P^+a^-)}} \cdot \frac{1-\alpha}{\alpha_2 - \alpha} \tag{3}$$

The notations in (1) – (3) are:

M is the PSU concentration per unit volume;

Q is the number of reaction centres per PSU;

I is the excitation light intensity expressed as number of quanta per cm^2 per sec;

ϵ is the effective cross-section for capture of monochromatic light quanta by the light-collecting molecules, ascribed to one reaction centre;

$$\alpha = \frac{P^+A^- + P^+A + PA^-}{PA + P^+A + P^+A + PA^-} = \frac{P^+A^- + P^+A + PA^-}{MQ}$$

is the fraction of centres in the closed state (the fraction of closed centres in each PSU is assumed to be, with sufficient degree of accuracy, equal to α);

$$\alpha_1 = P^+A_{eq}/MQ = k_{-H_2O}/(k_{H_2O} + k_{-H_2O})$$

is the equilibrium (dark) value of α;

$$L = \frac{kQ(1-\alpha)}{k_f + k_t + kQ(1-\alpha)}$$

is the quantum yield for excitation capture by centres when all of them are in the open state, i.e. when $\alpha = \alpha_1 = 0$, and

$$1/\alpha_2 = \frac{L}{1 + \dfrac{(1-L)k_0}{K_{\Delta(p^+a^-)}}}$$

is the effective value of the yield when there is back electron transfer in the centres:

$$1/k_{\Delta(p^+a^-)} = \frac{k_1 + k_{-H_2O}}{k_1(k_1 + k_{H_2O} + k_{-H_2O})}$$

is the average (relaxation) lifetime of centres in P^+A^- form with respect to the processes of electron transfer in the transport chain only:

$$1/k_{\Delta\alpha} = \frac{(k_1 + k_{H_2O} + k_{-H_2O})^2 - (k_{H_2O} + k_{-H_2O})(k_1 + k_{-H_2O})}{k_1(k_{H_2O} + k_{-H_2O})(k_1 + k_{H_2O} + k_{-H_2O})}$$

is the average (relaxation) lifetime of centres in closed state, i.e. in P^+A^-, P^+A and PA^- states, with respect to electron transfer in the transport chain only; k_1, k_{H_2O}, k_{-H_2O} and k_0 are the first order rate constants for processes shown in Fig. 1: kQ, k_f, k_t are the excitation capture rates of emissive (k_f) and non-emissive (k_t) deactivation for light-collecting PSU molecules.

The term

$$MQ \frac{k_{\Delta(p^+ + a^-)}}{k_{\Delta\alpha}} (\alpha - \alpha_1)$$

in (1) denotes for the concentration of centres with different charges, P^+A^-, as expressed through α. When multiplied by the velocity of electron back transfer in k_0 centres, it describes the intensity of electron excitation quanta generation in PSU due to this process. A part of this intensity, determined by the value of the fast fluorescence quantum yield $\rho = \rho_0/(1 - L\alpha)$, will constitute the intensity of delayed fluorescence. Its quantum yield is expressed as the product of the ratio of the intensity of light-collecting molecule excitation by the centres to the intensity of their excitation by light quanta

$$\left(\frac{k_0(1-\alpha)}{k_{\Delta(p^+a^-)}} \cdot \frac{1-\alpha}{\alpha_2 - \alpha} \right)$$ and the yield ρ.

The intensity of electron excitation states generated by light quanta is expressed in (3) with the help of (2) through α. Expression (2) is a

balance equation between the number of light quanta, effectively absorbed by the centres in a time unit ($I\varepsilon(1-\alpha)/(\alpha_2-\alpha)$) and the number of electrons transported along the electron transport chains in the same time ($k_{\Delta\alpha}(\alpha-\alpha_1)$).

As it is seen from (1) – (3), delayed fluorescence kinetics depends on a great number of parameters. This great number of parameters results from the fact that it includes not only the entire kinetics of excitation capture by the centres and that of fast fluorescence but also the kinetics of oxidation-reduction processes occurring on different sides from the reaction centre.

Using formulae (1) – (3) it is not difficult to plot light curves for delayed fluorescence intensity, $F_d(I)$, and quantum yield $\rho_d(I)$. The character of dependences of $F_d(I)$ and $\rho_d(I)$ at some particular values of parameters L, k_{H_2O}, k_{-H_2O}, k_1 and k_0 is illustrated by the graphs in Fig. 2. From those we see that $F_d(I)$ has an inflection point ($F_{d,i}$) and $\rho_d(I)$ has a maximum ($\rho_{d,m}$). Such kind of $F_d(I)$ and $\rho_d(I)$ dependences, which we shall arbitrarily refer to as the "S-type", are observed in intact organisms or, with sufficiently intensive electron flow, in isolated chloroplasts.

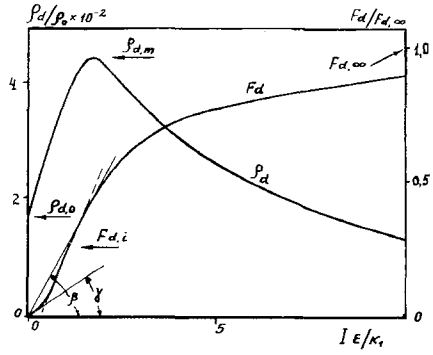

Figure 2. Calculated light (F_d) and quantum yield (ρ_d) intensity curves for delayed fluorescence.

However this is not the only form. Calculations show [18] that, along with the S-type, $F_d(I)$ can aquire the shape without an inflection point. In this case $F_d(I)$ all along its length is convex upwards and, correspondingly, ρ_d is a monotonically decreasing function of I. We shall arbitrarily call such curves "Γ-type" or "Γ-form" curves. Let us then

consider the factors which produce S- and Γ-forms. For this purpose it will be helpful to introduce the quantity:

$$l = \frac{k_{\Delta(p^+a^-)}}{k_0 + k_{\Delta(p^+a^-)}} = \frac{\dfrac{k_1\,(k_1 + k_{H_2O} + k_{-H_2O})}{k_1 + k_{-H_2O}}}{k_0 + \dfrac{k_1\,(k_1 + k_{-H_2O} + k_{-H_2O})}{k_1 + k_{-H_2O}}} \tag{4}$$

This defines the fraction of centres in the P^+A^- form which are not subjected to the back electron transfer, whereas 1–l is the quantitative expression of the fraction of centres with the P^+A^- form in which this process does take place.

Besides, to exclude the variation of F_d amplitude from (1), we shall divide it by the intensity F_d in the region of light saturation. This is obtained when $\alpha = 1$. Let then $\tilde{F}_d = F_d/F_{d,\infty}$, where $F_{d,\infty}$ is the value of F_d at $\alpha = 1$. In equation (2) we shall use dimensionless intensity $\tilde{I} = I\epsilon L l/k_{\Delta\alpha}$ and measure the quantum yield ρ_d in units of $\rho_\infty = \rho_0/(1-L)$, i.e. referring it to the quantum yield of fast fluorescence at $\alpha = 1$, and designating the value of ρ_d/ρ_∞ ratio as $\tilde{\rho}_d$.

Taking into account (4) we get:

$$1/\alpha_2 = \frac{Ll}{1 - L + Ll} \tag{5}$$

Then, in accordance with (4) and (5) and the newly introduced designations, equations (1), (2) and (3) will correspondingly assume the forms:

$$\tilde{F}_d = \frac{1 - L}{1 - \alpha_1} \cdot \frac{\alpha - \alpha_1}{1 - L\alpha}, \tag{6}$$

$$\tilde{I}(1 - \alpha) = (\alpha - \alpha_1)/[1 - L + Ll\ (1 - \alpha)]\,, \tag{7}$$

$$\tilde{\rho}_d = \frac{1 - L}{L} \cdot \frac{1 - \alpha}{1 - L\alpha} \cdot \frac{1 - l}{1 - L + Ll\ (1 - \alpha)}\,, \tag{8}$$

This clearly suggests that the shape of $F_d(I)$ and $\rho_d(I)$ dependences can be defined by a set of three parameters: L, l and α_1.

As $\frac{\partial\alpha}{\partial I}$ nowhere equals zero, i.e. α is monotonical function of I, we can, with the help of (8) and taking $\frac{\partial\tilde{\rho}_d}{\partial\tilde{I}} = 0$, find the value of $\alpha = \alpha_m$ (corresponding to the maximum on the $\rho_d(I)$ curve) as a function of parameters L and l.

$$\alpha_m = 1 - \frac{1 - L}{L\sqrt{l}}. \tag{9}$$

With $l = 1$, α_m reaches its highest value equal to $2 - 1/L$. On the other hand, it is obvious the α_m cannot be smaller than α_1. In other words, the region of α_m values lies within the $\alpha_1 \leqslant \alpha_m \leqslant (2 - 1/L)$ interval, its length being defined by the values of L and α_1. With the decrease of L the upper value of α_m will also decrease and, naturally, there may come a moment when $\alpha_1 = 2 - 1/L$. It follows that the S-shape of $F_d(I)$ manifests itself only when $L > 1/(2 - \alpha_1)$, i.e. when $L \geqslant 0.5$.

Thus, the necessary condition for the existence of S-type of $F_d(I)$ dependence is a certain value of quantum yield of the excitation captured by reaction centres from light-collecting molecules, viz. $L = kQ/(k_f + k_t + kQ)$ must be greater than 0.5. This occurs when the fast fluorescence quantum yield ρ_∞/ρ_0 has changed more than twice with the conditions when all the centres are open ($\rho_0 = k_f/[k_f + k_t + kQ(1 - \alpha)]$, where $\alpha = \alpha_1 = 0$) having become such that all of them are closed ($\rho_\infty = k_f/[k_f + k_t + kQ(1 - \alpha)]$, where $\alpha = 1$). At $L < 0.5$ ($\rho_\infty/\rho_0 < 2$), $F_d(I)$ is Γ-shaped. ($L > 0.5$ is also a necessary condition for the sigmoid nature of the dependences of electron transport and fluorescence quantum yields on excitation intensity I.)

Let then $L > 0.5$. From (9) and the stipulation that $\alpha_1 \leqslant \alpha_m$ we get that the S-type of curve occurs if

$$l \geqslant \left[\frac{1 - L}{L(1 - \alpha_1)}\right]^2 \tag{10}$$

Fig. 3 shows the region of L and l values within which this inequality is valid.

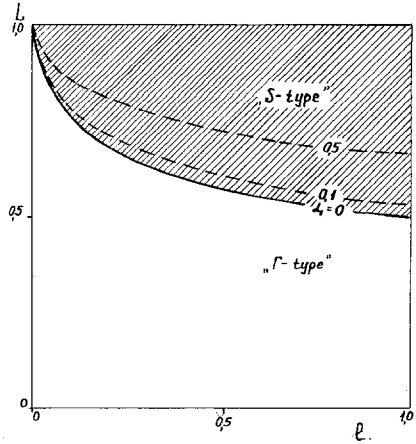

Figure 3. Regions of S- and Γ-types of $F_d(I)$ (or $\rho_d(I)$) light curves.

To better define the S-type curve region we can introduce a quantitative measure of its sigmoidality. Let us take this measure to be the ratio of the ρ_d yield at maximum ($\rho_{d,m}$) to its initial value ($\rho_{d,o}$), i.e. $\rho_{d,m}/\rho_{d,o}$. To obtain the dependence of this ratio on L, l and α_1 it is

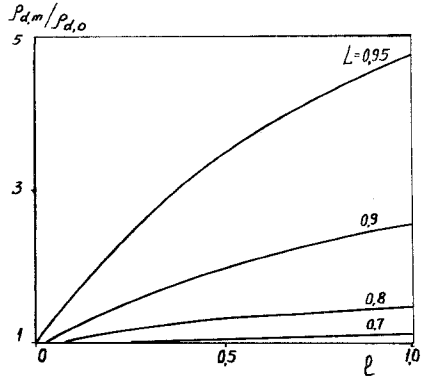

Figure 4. Dependence of $F_d(I)$ curve sigmoidality on l at constant $\alpha_1 = 0.1$ and different L values.

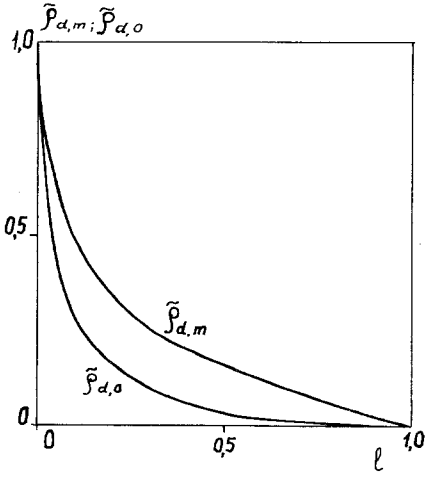

Figure 5. Variation of quantum yield values ρ_d at a maximum ($\rho_{d,m}$) and the beginning of light curve ($\rho_{d,o}$) depending on l. Calculated from (8) for L = 0.95 and $\alpha = 0.1$. (Dependence of $\rho_{d,o}$ on l is followed from (8) when $\alpha = \alpha_1$ and $\rho_{d,m}$ when $\alpha = \alpha_m = 1 = 1 - (1-L)/(L\sqrt{l})$.)

necessary to substitute $\alpha = \alpha_m$ from (9) for $\rho_{d,m}$ and $\alpha = \alpha_1$ for $\rho_{d,o}$ into (8).

After this we get:

$$\frac{\rho_{d,m}}{\rho_{d,o}} = \frac{1 - L\alpha_1}{L(1 - L)(1 - \alpha_1)} \cdot \frac{1 - L + Ll(1 - \alpha_1)}{(1 + \sqrt{l})^2}. \quad (11)$$

Graph (11) is shown in Fig. 4. The $\rho_{d,m}/\rho_{d,o}$ value is expressed by the ratio of the tangents of the inclination angles formed by two lines tangent to the $F_d(I)$ curve and intersecting at the origin of coordinates ($\rho_{d,m}/\rho_{d,o} = tg\beta/tg\gamma$) (See Fig. 2). The increase of sigmoidality with the increase of l is due to a sharper decrease of $\rho_{d,o}$ as compared to $\rho_{d,m}$. This can be easily seen on the graph in Fig. 5, which shows the curves of $\tilde{\rho}_{d,m}$ and $\tilde{\rho}_{d,o}$ variations as a function of l.

$F_d(I)$ variation can thus be described by two qualitatively different curves. In one case (Fig. 3) (small l and any L) F_d is a monotonically increasing function of I("T-type"), in the other ($L > 0.5$ and large l) $F_d(I)$ is described by a sigmoid curve ("S-type"). Therefore, when $L > 0.5$ and l varies within broad limits, there must be a transition from one type of curves to the other.

Comparison with Experiment and Discussion

Fig. 6 shows the data obtained by Bonaventura and Kindergan [5] on intact and diuron (DCMU) poisoned cells of the green single-cell alga *Chlorella pyrenoidosa.*

First of all, we see that in intact cells the main part of the $F_d(I)$ light curve is indeed sigmoid. The absence of an intermediate plateau (which we see on Fig. 6 at $\lambda = 690$ nm) on the calculated curves in Fig. 2 is explained by the fact that we have neglected the back electron transfer from reduced plastoquinone molecules to the oxidized primary acceptor A molecules, taking in our calculations $k_{-1} = 0$. Generally speaking, k_{-1} cannot be a constant value, as it must include the change in the degree of plastoquinone reduction when passing from darkness to light. Under the conditions of complete and prolonged darkening it inevitably becomes equal to zero, because plastoquinone molecules reduced in light will sooner or later be oxidized in darkness, at least due to the back electron transfer in the centres. It is difficult to take into account the value of the k_{-1} changes, but one can hope that it is not large compared to the other values, characterizing electron transport, so that its contribution can be neglected.

Secondly, we see that in the presence of diuron $F_d(I)$ dependence has the Γ-shape. Diuron is known to block electron transfer from A^- on to the plastoquinone, decreasing k_1 by 2-3 orders of magnitude (i.e. practically to zero). But, if $k_1 \to 0$, then, proceeding from (4) with

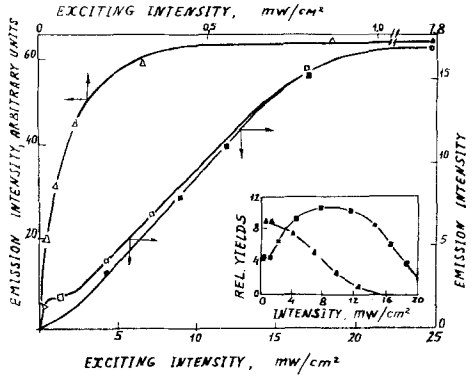

Figure 6. Dependence of delayed fluorescence intensity on excitation light intensity with $\lambda = 488$ nm in intact [light and black squares] and diuron (3.10^{-5} M) poisoned [light triangle] *Chlorella pyrenoidosa* cells. Delayed fluorescence was recorded 2 msec after illumination in the 690 nm [light and black triangles] and 730 nm [black square] regions. The inset illustrates dependence of O_2 emission quantum yields (black triangle) and delayed fluorescence at 730 nm (black square) on excitation intensity in intact cells. Taken from (5) Figures 6 and 7.

$k_{-H_2O} \neq 0$, 1 also tends to zero. In this case, as it is seen from the graph in Fig. 3, the $F_d(I)$ curve must be transformed from the S- to the Γ-type. This is actually observed in experiment. At the same time, since diuron apparently also, and not to a smaller extent, blocks the back electron transfer from the reduced plastoquinone on to the oxidized primary acceptor A, the intensity of F_d, in the region of the intermediate plateau, drops to zero.

Data on the $F_d(I)$ shape transformation, but this time in the opposite direction, are cited in the paper by Venediktov et al. [19]. Fig. 7 shows the $F_d(I)$ dependences taken from [19] which were obtained on pea chloroplasts before and after phenozinemetasulphate (PMS), flavinmononucleotide (FMN) and ferricyanide were added. Stationary non-cyclic electron flow is known to be practically absent in isolated chloroplasts, when there is no acceptor ($k_1 \cong 0.5$ sec^{-1} [20]). In this case the Γ-shape of the $F_d(I)$ curve should be and actually is observed (Fig. 7). Introduction of electron acceptors results in the increase of k_1 (e.g., in the presence of 0.25 mM of NADP, $k_1 = 40$ sec^{-1} [21]), and therefore, also, in the increase of I, which should be and actually is accompanied by the transformation of the Γ-shape of the curve into the S-shape (Fig. 7).

The question of delayed fluorescence intensity behaviour in the region of light saturation and at the beginning of the light curve with the inhibition and stimulation of non-cyclic electron transport was previously considered by us [22] and also found to be in complete

agreement with calculations. All this gives reason to believe that the model of the primary photosynthesis processes in PS II described above reflects, with sufficient adequacy, the regularities of delayed fluorescence kinetics of chlorophyll "a" observed in a cell. It should be especially stressed that the model is based on the concept of there being only one source of delayed fluorescence, which is considered to be the process of back electron transfer in the centres. The complexity and diversity of kinetic manifestations of delayed fluorescence is, in our case, explained not by the superposition of luminescences of different origin but by the dependence of this phenomenon on several processes of different nature whose kinetics, in one way or another, it reflects. It is also explained by the organization of the systems in which these processes are taking place.

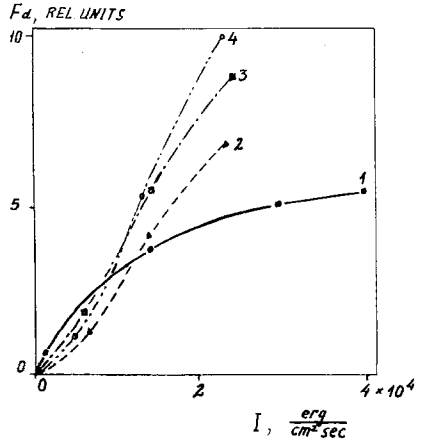

Figure 7 Dependence of delayed fluorescence on excitation light intensity with $\lambda \geqslant 640$ nm in suspension of pea chloroplasts. Chloroplasts were isolated using the method described in (23). Delayed fluorescence was recorded 3 msec after illumination 1 – in isolation medium; 2 – with 0.1 mcM of phenazinemetasulphate; 3 – with 0.1 mcM of flavinmononucleotide; 4 – with 3.5 mcM of ferricyanide. Taken from (19) Figure 5.

It should be mentioned too that a principal objection against the assumption that there is only one source of delayed fluorescence is inherent in the observation of Bonaventura and Kindergan [5] on the absence of a maximum in the F_d spectrum for diuron poisoned *Chlorella* cells in the 730 nm region. However, Shuvalov and Litvin [4] who measured F_d spectra on diuron poisoned leaves of higher plants observed the maximum. Therefore, the question of the spectral composition of delayed fluorescence in higher plants and algae in the presence of diuron is, as we see it, at present still open.

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