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CELL BIOPHYSICS

Levels of Regulation of Photosynthetic Processes

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Abstract—Basic mechanisms of kinetic regulation of photosynthetic processes are considered. These mechanisms provide strict light-dependent regulation of electron transport in photosynthetic reaction centers and more flexible regulation at the level of interaction between photosystems, transmembrane fluxes of ions, and coupling with dark reactions of the Calvin cycle. A generalized mathematical model was constructed. This model consolidates the modern knowledge about photosynthetic processes in higher plants. The general principles of multilevel regulation of photosynthetic processes are discussed.

Key words: regulation, photosynthesis, mathematical models, chlorophyll fluorescence induction curve

INTRODUCTION

The regulatory properties of biological processes are determined by their spatial and temporal hierarchy. For example, the time span of photosynthetic processes ranges from 10^{-12} s (absorption of light quanta by chlorophyll molecules, primary charge separation) to several days (whole plant growth).

Biological systems of all levels of hierarchy are far from thermodynamic equilibrium. They are also open for fluxes of matter and energy. The kinetic processes taking place in biological systems are nonlinear. Therefore, in addition to relaxation processes, various spatiotemporal behavioral patterns (including multistationary, oscillation, and quasi-stochastic) can be implemented in these systems. Implementation of a given regulation mechanism is determined by its specific place in the spatiotemporal hierarchy and by the characteristics of the effector.

In kinetic models, the process of photosynthesis is regulated by modification of system parameters (usually, the rate constants of individual reactions) induced by external or internal factors. Internal factors may change at different hierarchial levels. For example, they can be determined by the genetic program or by the changes in the physiological state of the plant. In a mathematical model, this corresponds to changes of variables of another (usually, slower) level of the temporal hierarchy. From the standpoint of the process of interest, these slow variables are regulatory parameters. This change in model parameters can be associated with regulatory mechanisms of two types.

According to the first mechanism, the rate constants are modified to provide changes in the steady-state concentrations of reagents and relaxation times against the background of invariable qualitative characteristics of system behavior. According to the second mechanism, variation of parameters brings the system to a bifurcation border, thereby changing the qualitative characteristics of the system behavior. This can be implemented as a step transition from one stationary state to another or transition from the relaxation behavior pattern to oscillating or quasi-stochastic. The qualitative changes in the system behavior can also be caused by transition through a separatrix in phase space. This can cause stepwise changes in the steady-state parameters of the system or limiting cycle amplitude in the autooscillation system.

It is probable that the system response to external factors is determined by the degree of the system complexity and its incorporation into more sophisticated

Abbreviations: PS, photosystem; PRC, photosynthetic reaction center(s).

systems of regulation. Further in this work we consider phosynthesizing organisms. These systems have been studied at the Department of Biophysics, Biology Faculty, Moscow State University, for many years.

The system of the primary processes of photosynthesis is located in chloroplast thylakoids of algae and higher plants or in bacterial chromatophores. This system is one of the most comprehensively studied biological systems. In recent decades, the fine details of the structural and functional organization of this system have been discovered. The three-dimensional structure of many components of the photosynthetic electron transport chain was reconstructed with atomic resolution from the X-ray diffraction data [1]. In recent years the mechanism of the functional activity of ATP synthase was suggested. This enzyme transforms the energy of the photosynthetic transmembrane gradient of protons into the energy of chemical bonds of ATP [2].

The majority of experimental studies on the molecular elements of the photosynthetic system were performed using isolated structural fragments: bacterial photosynthetic reaction centers (PRC), photosystems I and II (PS I and PS II, respectively). These studies provided information about the sequences of electron transport reactions along the photosynthetic chain and their correlation with electron-vibrational interactions.

The photosynthetic system fragments are integral pigment–protein complexes. Interaction between components of these complexes can be described by sets of simultaneous differential equations (linear with respect to the probability of the states of these complexes) [4, 5]. There are methodological approaches to univalent identification of the parameters of such models [6]. The rate constants of electron transfer at individual segments of the electron transport chain were estimated in such reduced systems.

Mathematical models of electron transfer reactions were constructed and identified on the basis of experimental studies of PS I and PS II fragments of higher plants, chromatophores and reaction centers of photosynthesizing bacteria. The results of mathematical simulation showed that there are at least two types of organization and regulation of photosynthetic electron transport chain, which differ from one another in the character of interaction between constituent components [6–9].

The first type is the light-induced regulation within multienzyme pigment–protein complexes of photosynthetic reaction centers. The structure and functions of these complexes were brought to an optimum level during evolution. Both structural and functional parameters of these systems are stable, and the pigment–protein complexes isolated from biological membranes by various methods maintain native activity within a broad range of environmental factors. Their kinetic characteristics (including the ability to undergo conformational transitions) are highly stable, because they are embedded into a protein–lipid core. Light is the main factor of regulation of the activity of these systems. Absorption of a light quantum causes charge redistribution over the primary photoactive pair and triggers conformational transition of the protein components of the system. This transition prevents electron transfer reversion and energy dissipation by fluorescence.

In all photosynthetic objects studied thus far (PS I and PS II fragments of higher plants, chromatophores and reaction centers of photosynthesizing bacteria of various species) transition from dark to light conditions was accompanied by an increase in the efficiency of electron escape from the primary photosynthetic pair. Obviously, light-induced regulation may play a physiologically significant role. Like allosteric regulation of enzymatic catalysis, the light-induced regulation of photosynthetic activity is mediated by the conformational mobility of enzymes.

Another type of regulation of photosynthetic activity is implemented at the site of interaction between the PS II plastoquinone and cytochrome complex and between the PS I plastocyanin and cytochrome complex, i.e., at the electron transport chain sites mediated by mobile carriers. Diffusion processes play a crucial role in the electron transfer regulation at these sites. Under variation of external conditions, the electron transfer rate constants at these sites may change by several orders of magnitude. The electron transport rate at these sites is regulated by such intracellular factors as cell matrix viscosity, pH, endogenous inhibitors, metabolites, etc.

Thus, the physiological state of a biological organism can be changed not only at the level of

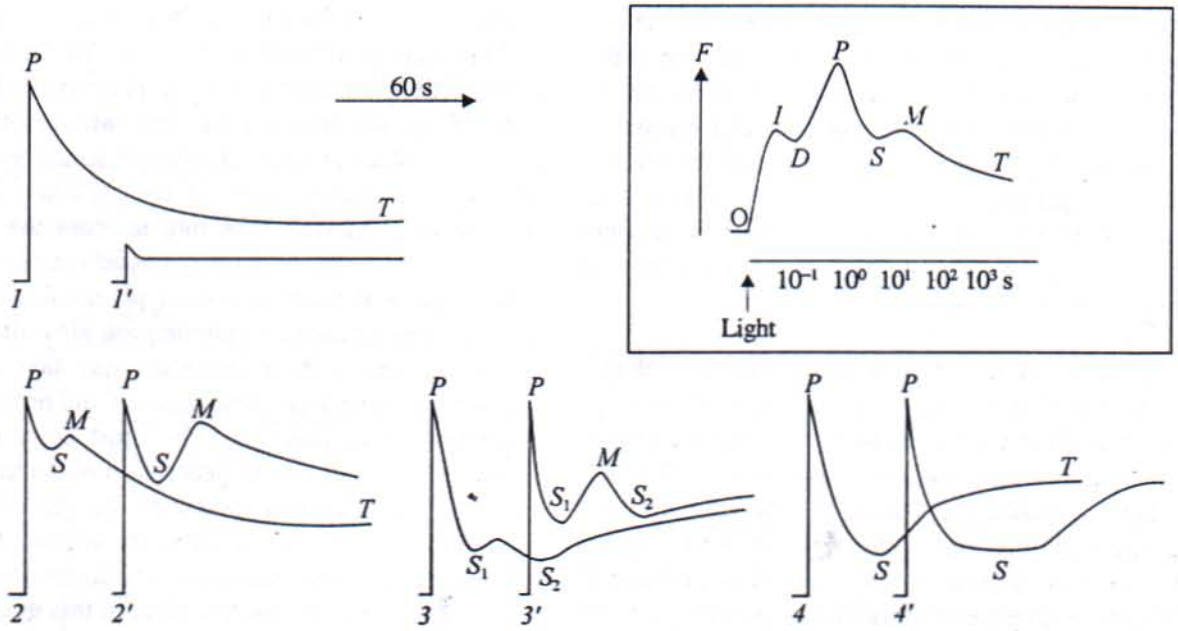


Fig. 1. Different kinetic patterns of chlorophyll fluorescence induction kinetics (slow phase) as recorded in individual cenobia of the green alga *Scenedesmus quadricauda*. Schematic typical chlorophyll *a* fluorescence induction curve and conventional notation of its phases are shown in the insert.

biosynthesis (e.g., biosynthesis and degradation of chlorophyll molecules) but also at the level of changes of intracellular parameters. In terms of kinetic models, this regulation is manifested as changes in the rate constants of interaction of PRC complexes with secondary donors and acceptors. In other words, this regulation corresponds to changes in the input and output rate constants, i.e., the rate constants determining the steady-state levels and kinetics of individual PRC states. Therefore, characteristics of PRC processes (fluorescence, delayed luminescence, etc.) can be used as indicators of the state of the photosynthetic organism in general.

ANALYSIS OF FLUORESCENCE KINETICS

The fluorescence induction curve is a well-known indicator of the functional state of the photosynthetic apparatus. Prompt fluorescence increase segments (millisecond time range) are thought to be associated with the processes in the PS II reaction center [1, 10], whereas slow fluorescence decay (second time range) are usually associated with the processes of generation of the transmembrane electrochemical gradient of protons on thylakoid membranes. This gradient was found to modify the electron distribution over the photosynthetic electron transport chain, thereby affecting the fluorescence intensity and activity of the Calvin cycle enzymes.

In the preceding work [11] we studied the slow induction phase patterns of fluorescence of individual algal cells during culture growth. Typical curves of fluorescence induction as measured within the time scale of several minutes are shown in Fig. 1. Curves *1* and *1′* have one sharp maximum *P*, which is followed by a phase of exponential decline of the fluorescence intensity. These cells can be attributed to an active type of photosynthesis. Curves *3*, *3′* and *4*, *4′* contain one or two minima *S* and a high steady-state plateau of fluorescence intensity, which is indicative of low photosynthetic activity. These cells can be attributed to a less active type of photosynthesis. Curves *2* and *2′* belong to an intermediate type of photosynthesis.

The results of microfluorescence analysis of the distribution of fluorescence induction curve patterns in populations of microalgae obtained by Pogosyan *et al.* [11] can be regarded as an example of regulation of photosynthetic activity of individual algal cells during culture growth. The initial stage of culture growth is characterized by significant diversity of the fluorescence induction curve shapes. Cells with both simple relaxation kinetics and low steady-state level of fluorescence (active photosynthesis) and nonmonotonic

relaxation kinetics and high steady-state level of fluorescence (inactive photosynthesis) are observed at this stage of culture growth. At the stage of unlimited linear growth, most cells are characterized by active photosynthesis. At the stage of stationary growth, the diversity of patterns of the fluorescence kinetics increases again. The population of cells with nonmonotonic relaxation kinetics and high steady-state level of fluorescence increases.

Analysis of a simple mathematical model [12, 13] revealed that transition from active to inactive photosynthesis can be associated with electron transport decoupling from carbon assimilation in the Calvin cycle. Detailed simulation of coupling between the primary photosynthetic reactions and CO_2 fixation confirmed this suggestion and allowed calculation of some quantitative parameters of this process. The results of model analysis showed that ion fluxes are the main contribution to the fluorescence induction curve pattern formation. Efficiency of ion fluxes determines the degree of coupling between electron transport and generation of the transmembrane potential. It is well known that the transmembrane potential of protons is an energy source for ATP synthase and the cycle of photosynthetic reactions of CO_2 fixation.

GENERAL MODEL OF PHOTOSYNTHETIC PROCESSES

To provide more accurate evaluation of the contribution of individual reactions (electron transport, transmembrane ion transport, generation of transmembrane electrochemical potential of protons, and coupling between light and dark photosynthetic reactions) we constructed a detailed mathematical model. This model is based on the contemporary concepts of structure and functions of the photosynthetic apparatus.

A broad range of mathematical models of individual fragments of the complicated system of photosynthetic reactions are described in the literature. For example, there are mathematical models of superfast (10^{-12}–10^{-9} s) processes of light absorption, migration of excited states, and primary charge separation [15–17]. Other mathematical models consider less fast (millisecond) processes of electron transport through so-called two-electron gates at the level of the secondary quinone acceptor of PS II (Q_B) [18]. There are also models of proton transport through the thylakoid membrane [19]. Calvin cycle enzymatic reactions were simulated in [20, 21]. All these models contain detailed description of photosynthetic reactions of specific time ranges. The other photosynthetic reactions are simplified more or less significantly. In addition, virtually none of the presently available mathematical models take into account the dependence of some primary photosynthetic reactions on the electrochemical transmembrane potential. Ion fluxes through the thylakoid membrane are also often disregarded. However, these processes may have a significant effect on various parameters of the primary photosynthetic reactions [22]. The most comprehensive model of the processes of generation of the transmembrane electrochemical potential on the thylakoid membrane and its dissipation in the system of the primary photosynthetic reactions was suggested in [23]. However, ion fluxes are described in this model by an empirical expression, whereas the light reactions of photosynthesis are simulated using the simplified model suggested in [18].

We suggest a new approach to the problem of simulation of photosynthetic processes in chloroplasts of higher plants. This approach is based on detailed kinetic description of the catalytic cycles of major pigment–protein complexes involved in the system of the primary photosynthetic reactions. The dependence of some stages of electron transfer on the electrochemical transmembrane potential and the pH gradient on the thylakoid membrane is taken into account in this model. The analysis of the model is based on the principle of the theory of metabolic control [24].

The model considered in this work describes the photosynthetic processes in three compartments of chloroplasts: thylakoid membrane, intrathylakoid lumen, and chloroplast stroma. The majority of components of the photosynthetic electron transport chain are attributed to specific chloroplast compartments. For example, the thylakoid membrane contains PS I, PS II, and all intermediates of the Q-cycle; the chloroplast stroma contains ATP, ADP, NADP(H), and all intermediates of the Calvin cycle; and the intrathylakoid lumen contains plastocyanin, a mobile electron carrier. The primary processes of electron transfer along the photosynthetic electron transport chain are accompanied by transport of both positively and negatively charged ions through the thylakoid membrane. The transmembrane transport of ions may play a significant role in energy transformation in

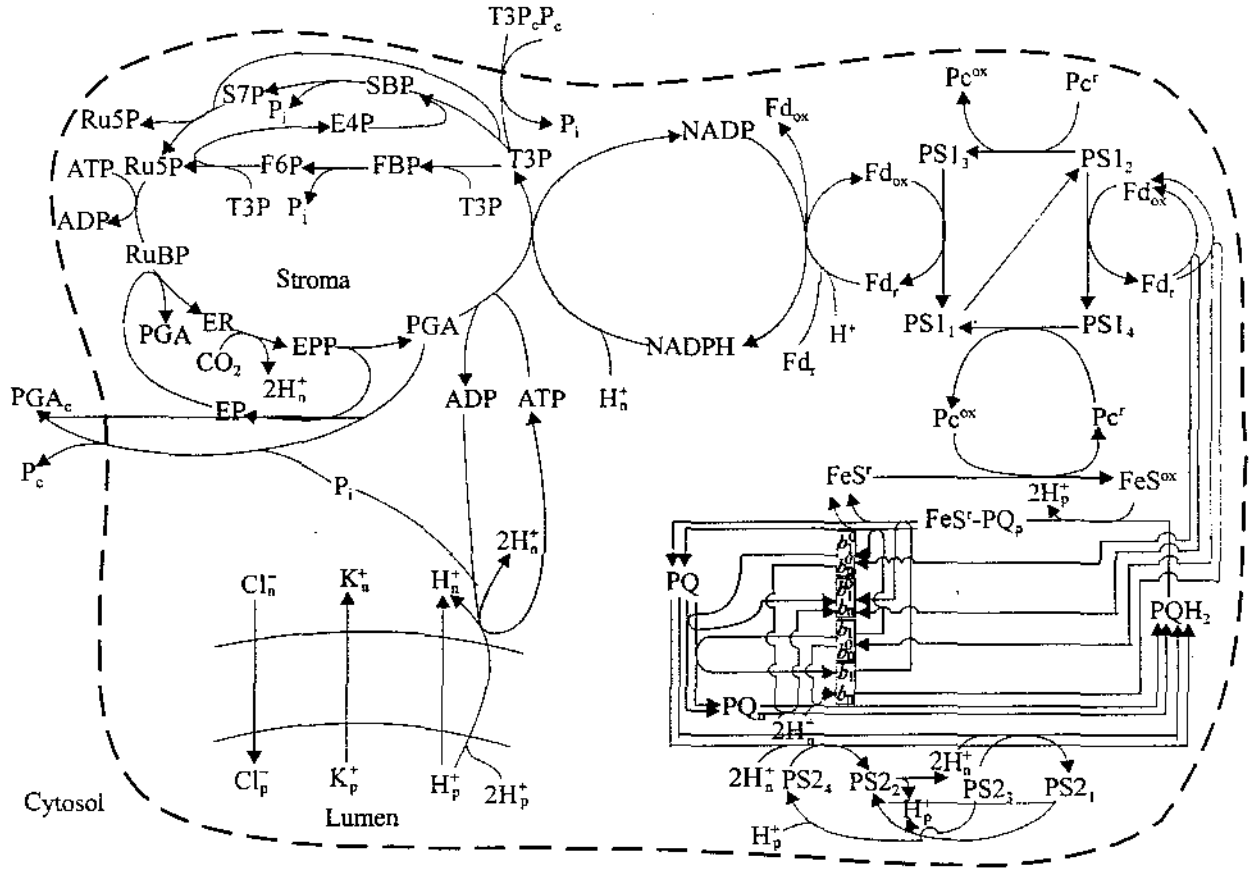
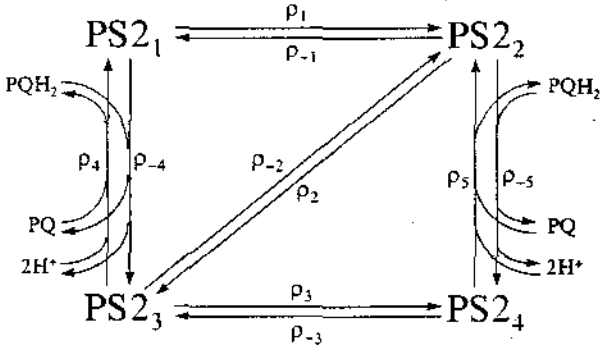


Fig. 2. Diagram of a comprehensive mathematical model of photosynthetic processes in chloroplasts of green plants.

photosynthesis, because it is directly associated with generation of the transmembrane electrochemical potential on the thylakoid membrane. The model considered in this work allows for transmembrane transport of Cl^-, K^+, and H^+ between stroma and lumen. The volumes of these compartments differ from one another. The volume ratio of stroma:thylakoid membrane:lumen is 10:1:1.



State diagram for photosystem II.

The diagram of the mathematical model of interaction between the processes of photosynthetic electron transport, generation of the transmembrane electrochemical potential, and cycle of CO_2 assimilation is shown in Fig. 2.

The mathematical model shown in Fig. 2 was constructed taking into account the fact that the reaction centers of PS I and PS II are integral multienzyme complexes. The state of the electron transport chain within PRC was described using the probability equations of the states of these complexes [5, 6].

The interaction between the model components at the diffusion-controlled sites was described using the acting mass equations or the Michaelis–Menten equation. The ATP-synthase reaction rate equation was based on the minimal kinetic scheme of reactions of ATP synthesis and hydrolysis. The electrogenic transmembrane transport of Cl^- and K^+ was described using equations derived in [25–27] within the framework of Eyring's model of ion transport through a three-barrier channel.

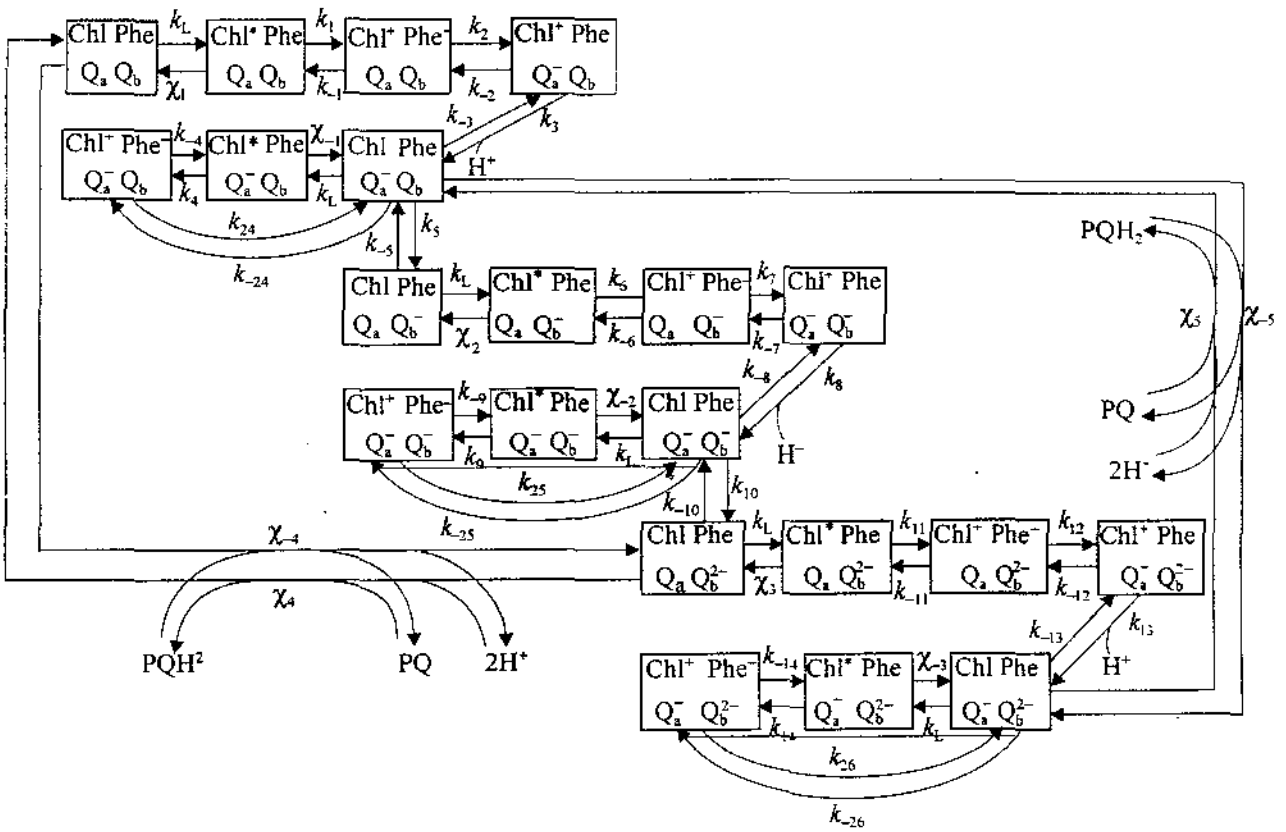


Fig. 3. Catalytic cycle catalyzed by reaction center of photosystem II.

A detailed scheme of the catalytic cycle of the photosynthetic reaction center of PS II is shown in Fig. 3 as an example of such models.

If the hierarchy of the reaction rates of this system is taken into account, the scheme shown in Fig. 3 can be reduced to the four-state diagram displayed on the preceding page.

In this diagram each state $PS2_i$ corresponds to the sum concentration of several states represented in the general scheme (Fig. 3). In other words:

$$PS2_1 = \begin{bmatrix} Chl & Phe \\ Q_a & Q_b \end{bmatrix},$$

$$PS2_2 = \begin{bmatrix} Chl^* & Phe \\ Q_a & Q_b \end{bmatrix} + \begin{bmatrix} Chl^+ & Phe^- \\ Q_a & Q_b \end{bmatrix} + \begin{bmatrix} Chl^+ & Phe \\ Q_a^- & Q_b \end{bmatrix} + \begin{bmatrix} Chl\ Phe \\ Q_a^- \ Q_b \end{bmatrix} + \begin{bmatrix} Chl^* & Phe \\ Q_a^- & Q_b \end{bmatrix} + \begin{bmatrix} Chl^+ & Phe^- \\ Q_a^- & Q_b \end{bmatrix} + \begin{bmatrix} Chl\ Phe \\ Q_a \ Q_b^- \end{bmatrix},$$

$$PS2_3 = \begin{bmatrix} Chl^* & Phe \\ Q_a & Q_b^- \end{bmatrix} + \begin{bmatrix} Chl^+ & Phe^- \\ Q_a & Q_b^- \end{bmatrix} + \begin{bmatrix} Chl^+ & Phe \\ Q_a^- & Q_b^- \end{bmatrix} + \begin{bmatrix} Chl\ Phe \\ Q_a^- \ Q_b^- \end{bmatrix} + \begin{bmatrix} Chl^* & Phe \\ Q_a^- & Q_b^- \end{bmatrix} + \begin{bmatrix} Chl^+ & Phe^- \\ Q_a^- & Q_b^- \end{bmatrix} + \begin{bmatrix} Chl & Phe \\ Q_a & Q_b^{2-} \end{bmatrix},$$

$$PS2_4 = \begin{bmatrix} Chl^* & Phe \\ Q_a & Q_b^{2-} \end{bmatrix} + \begin{bmatrix} Chl^+ & Phe^- \\ Q_a & Q_b^{2-} \end{bmatrix} + \begin{bmatrix} Chl^+ & Phe \\ Q_a^- & Q_b^{2-} \end{bmatrix} + \begin{bmatrix} Chl & Phe \\ Q_a^- & Q_b^{2-} \end{bmatrix} + \begin{bmatrix} Chl^* & Phe \\ Q_a^- & Q_b^{2-} \end{bmatrix} + \begin{bmatrix} Chl^+ & Phe^- \\ Q_a^- & Q_b^{2-} \end{bmatrix}.$$

The corresponding set of simultaneous differential equations for the $PS2_i$ states can be written as:

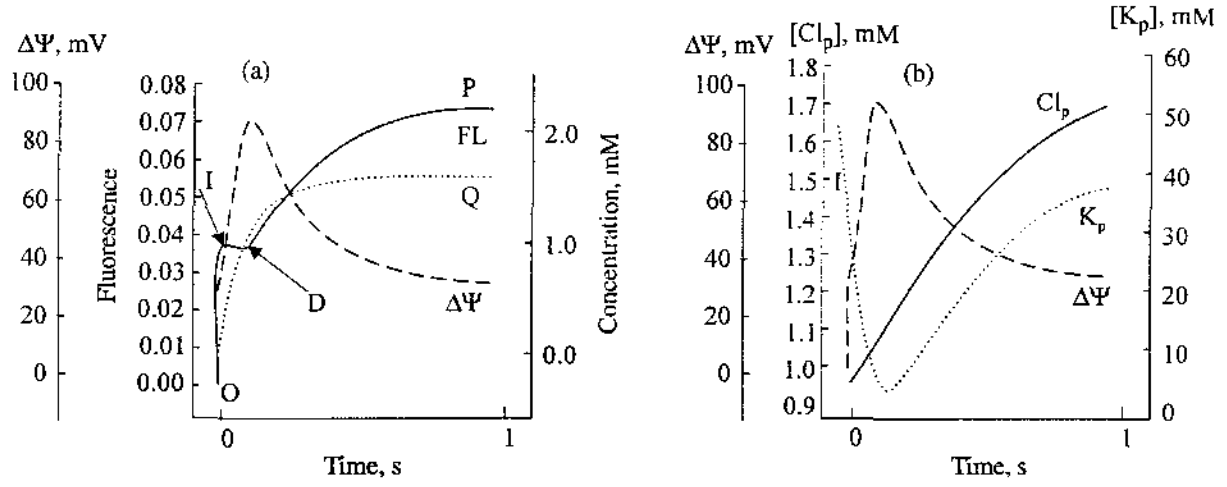


Fig. 4. (a) Initial segment of chlorophyll fluorescence induction curve calculated from reduced model of PS II. O, I, D, and P are the main kinetic phases of the initial segment of the chlorophyll fluorescence induction curve (see insert to Fig. 1). $\Delta\psi$ and Q are kinetic curves of the transmembrane electrical potential and sum concentrations of the PS II states with reduced acceptor complex Q_AQ_B. (b) Kinetic curves of the transmembrane electrical potential $\Delta\psi$ and concentrations of K^+ and Cl^- ions (K_p, Cl_p) in thylakoid lumen.

$$PS2_1 : \dot{y}_1 = \rho_{-1}[H_p^+]y_2 + \rho_4 y_3[PQ][H_n^+]^2 - (\rho_1 + \chi_{-4}[PQH_2])y_1,$$

$$PS2_2 : \dot{y}_2 = \rho_1 y_1 + \rho_5 y_4[PQ][H_n^+]^2 + \rho_{-2} y_3[H_p^+] - (\rho_{-1}[H_p^+] + \rho_{-5}[PQH_2] + \rho_2)y_2,$$

$$PS2_3 : \dot{y}_3 = \rho_2 y_2 + \rho_{-4} y_1[PQH_2] + \rho_{-3}[H_p^+]y_4 - (\rho_{-2}[H_p^+] + \rho_4[PQ][H_n^+]^2 + \rho_3)y_3,$$

$$PS2_4 : \dot{y}_4 = \rho_3 y_3 + \rho_{-5}[PQH_2]y_2 - (\rho_{-3}[H_p^+] + \rho_5[PQ][H_n^+]^2)y_4.$$

Rate constants ρ are functions of the rate constants of slow stages (k_{Lj}, $\chi_{\pm k}$; $j = 1, ..., 6$; $k = 4, 5$) and equilibrium constants $K_i = \dfrac{k_i}{k_{-i}}$ of fast stages (notation and numeration of rate constants correspond to those in Fig. 3):

$$\rho_{-1} = \frac{\chi_1 / R_1}{K_1K_2K_3K_5}, \quad \rho_1 = k_{L1}$$

$$\rho_{-2} = \frac{\chi_2 / R_2}{K_6K_7K_8K_{10}}, \quad \rho_2 = k_{L3} / R_1,$$

$$\rho_{-3} = \frac{1 / R_3}{K_1K_2K_3} \frac{\chi_1\chi_5\chi_{-4}k_{L5}}{\chi_{-5}\chi_4k_{L1}}, \quad \rho_3 = k_{L5} / R_2,$$

$$\rho_{-4} = \chi_{-4}, \quad \rho_4 = \chi_4 / R_2,$$

$$\rho_{-5} = \frac{\chi_{-5} / R_1}{K_5}, \quad \rho_5 = \chi_5 / R_3,$$

where

$$R_1 = 1 + \frac{1}{K_5} + \frac{1}{K_3K_5} + \frac{1}{K_2K_3K_5} + \frac{1}{K_1K_2K_3K_5} + \frac{k_{L2}(1 + K_4)}{\chi_{-1}K_5},$$

$$R_2 = 1 + \frac{1}{K_{10}} + \frac{1}{K_8K_{10}} + \frac{1}{K_7K_8K_{10}} + \frac{1}{K_6K_7K_8K_{10}} + \frac{k_{L4}(1 + K_9)}{\chi_{-2}K_{10}},$$

$$R_3 = 1 + \frac{1}{K_{13}} + \frac{1}{K_{12}K_{13}} + \frac{k_{L6}(1 + K_{14})}{\chi_{-3}} + \frac{1}{K_1K_2K_3} \frac{\chi_1\chi_5\chi_{-4}k_{L5}}{\chi_3\chi_{-5}\chi_4k_{L1}}.$$

Within the framework of the PS II model considered as part of a multicomponent compartmentalized

model of photosynthesis, we managed to demonstrate the role of transmembrane ion fluxes in the formation of the pattern of the initial segment of the chlorophyll fluorescence induction curve (Fig. 4). The method of construction and study of subsystems in this model of PS II is described in more detail elsewhere [14, 28].

About 100 model parameters were estimated quantitatively. Some of them were directly measured in independent experiments or calculated indirectly. Some parameters were identified in model experiments.

This model is planned to be used to assess the photosynthetic apparatus changes induced by unfavorable conditions. These calculations will be performed using experimental data on chlorophyll fluorescence in various physiological states of plants.

CONCLUSION

Comparison of the results of detailed mathematical simulation of individual photosynthetic complexes [3, 4, 15, 17] with mathematical simulation of these complexes incorporated into a sophisticated system of interacting components [5, 8, 28] and with reduced models of interaction between photosynthetic processes [12, 14, 23] showed that the regulatory properties of these systems depend on the complexity hierarchy level of the system. This conclusion is valid for any complex hierarchial system.

Rigid control is typical of the level of photosynthetic reaction centers. A quantum of light induces a strictly determined succession of events of charge redistribution and conformational changes. These processes are directed toward effective and fast transfer of an electron outside the primary photosynthetic pair. The PRC structure is sufficiently standard. Photosynthetic reaction centers of PS I, PS II, and bacterial photosystem are similar to each other. External parameters (pH, redox potential, medium viscosity, etc.) have little if any effect on the PRC activity. Usually, the kinetic patterns of the PRC reactions are reduced to simple relaxation.

More flexible regulation is observed at the level of interaction between PS I and PS II. Diffusion stages of this regulation significantly depend on pH, redox potential, medium viscosity, etc. Therefore, the processes of interaction between photosystems can be regulated during plant growth both at the cellular level and at the level of the whole organism. Kinetic patterns of these processes are more elaborate. They may contain several maxima, giving rise to typical shapes of fluorescence induction curve within the time span of several minutes.

Even more fine and sophisticated mechanisms are involved in regulation of interaction between the primary processes of photosynthesis and the Calvin cycle of CO_2 assimilation. Oscillation dynamics of some variables in this case implies the presence of pools and feedback loops. These properties allow for the dark reactions of CO_2 fixation and biosynthesis of sugars regardless of the presence of background illumination. These processes can be supported by the ATP energy accumulated both in the primary processes of photosynthesis and during respiration.

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