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BIOPHYSICS AND MEDICAL PHYSICS

Electron and Proton Transfer in Chloroplasts In Silico. 2: The Effect of Diffusion Limitations on the Process of Photosynthesis in Spatially Inhomogeneous Thylakoids

A. V. Vershubskii* and A. N. Tikhonov**

Department of Biophysics, Faculty of Physics, Moscow State University, Moscow, 119991 Russia

**e-mail: vershoubskiy@mail.ru,*

***e-mail: an_tikhonov@mail.ru*

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Abstract—The lateral mobility of protons and mobile electron carriers (plastoquinone and plastocyanin) is subjected to diffusion limitations; the effect of these limitations on the kinetics of photoinduced pH_i changes has been investigated in the present work for metabolic states 3 (conditions of intensive ATP synthesis) and 4 (the state of photosynthetic control). Computer simulations were based on a mathematical model of electron and proton transport in chloroplasts developed earlier by the authors. Non-uniform distribution of electron carriers and ATP synthase complexes in the membranes of grana and intergranal thylakoids was taken into account in the model. The kinetics of intrathylakoid pH_i changes and the lateral profiles of distribution of the mobile electron transporters in granal and intergranal thylakoids were studied. The formation of non-uniform pH_i profiles (with lumen acidification in the central parts of the grana being substantially slower than in the stromal thylakoids) was shown to occur under the conditions of ATP synthesis. Variation of the diffusion coefficients of intrathylakoid hydrogen ions and mobile electron carriers (plastoquinone and plastocyanin) can have substantial effects on the lateral pH_i profiles and the redox state of the mobile electron carriers.

Keywords: photosynthesis, electron and proton transport, mathematical modeling.

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INTRODUCTION

Thylakoid membranes of chloroplasts incorporate protein complexes that mediate the absorption and transformation of the light energy. Photochemical and biochemical processes initiated by light absorbed by the pigment-protein complexes of photosystems 1 and 2 (PS1 and PS2) incorporated in the thylakoid membrane result in the formation of NADPH and ATP, the terminal products of the "light" stage of photosynthesis [1–4]. The key stage of energy transformation in chloroplasts consists in the generation of a transmembrane difference of electrochemical potentials of hydrogen ions ($\Delta\tilde{\mu}_{H^+}$) due to transmembrane transfer of protons coupled to electron transport. The energy stored as $\Delta\tilde{\mu}_{H^+}$ enables the functioning of the ATP-synthase complexes. In contrast to prokaryotic cells and mitochondria, the transthylakoid pH gradient provides a major contribution to the steady state electrochemical gradient of protons in chloroplasts. The pH difference is defined as $\Delta pH = pH_o - pH_i$, where pH_o and pH_i are the pH values in the stroma and inside the thylakoids, respectively [4, 5]. In addition to its role in energy metabolism (the "proton-driving" force that enables the functioning of ATP synthase), $\Delta\tilde{\mu}_{H^+}$ has regulatory functions. The light-dependent decrease of pH in the intrathylakoid space (pH_i) causes a decrease in the rate of photosynthetic electron transfer and induces non-photochemical quenching of chlorophyll *a* fluorescence [6–8].

As proposed in several earlier studies [2, 9–11], the morphological heterogeneity of the lamellar system of the chloroplasts can account for the lateral difference in pH inside specific compartments (for instance, inside granal and intergranal thylakoids). Lateral diffusion of mobile electron carriers (plastoquinone and plastocyanin) is usually hindered by the presence of numerous protein complexes in the thylakoid membrane and inside the thylakoids. An extensive lamellar system of thylakoid membranes of a chloroplast implies a considerable effect of diffusion limitations on the rate of electron transport, the generation of ΔpH, and the rate of ATP synthesis, since these limitations reduce the rate of diffusion of the mobile electron transporters, as well as the rate of lateral migration of protons. The inhomogeneity of thylakoids, along with the small size of these structures, imposes restrictions on the measurements of local pH values

inside a chloroplast. Mathematical modeling of photosynthesis processes with the specific features of the spatial structure of chloroplasts can serve as a tool for analysis of the effect of diffusion limitations on the distribution of pH along the thylakoid membrane and for the analysis of the effects of the spatial organization of thylakoids on the rate of electron and proton transport and ATP synthesis in chloroplasts.

This study reports computer simulations based on a model developed earlier by the authors [12–16] to characterize the effects of diffusion limitations on the migration of protons and the mobility of plastoquinone and plastocyanin. A spatially inhomogeneous distribution of pH and mobile electron carriers can occur due to diffusion limitations. Variation of diffusion parameters in the system was shown to have a considerable effect on the acidification of the intrathylakoid space and the alkalization of the narrow interthylakoid gap and thus to affect the overall rate of noncyclic electron transport in chloroplasts.

RESULTS AND DISCUSSION

Kinetics of photoinduced changes of intrathylakoid pH_i. A previously developed mathematical model of electron and proton transport processes in heterogeneous photosynthetic systems of the oxygenic type [15, 17] was used for quantitative analysis. The model describes the key stages of linear (non-cyclic) electron transfer and the processes of transmembrane proton transfer coupled to the former process. Lateral heterogeneity of thylakoids and non-uniform distribution of macromolecular protein complexes in the membranes are taken into account in the model, as well as ATP synthesis from ADP and inorganic phosphate (P_i) by the ATP synthase of the F_0F_1 type. A detailed description of the model was given in our earlier study [17]; the variables $H_i(\mathbf{r}, t)$ and $H_o(\mathbf{r}, t)$ that corresponded to the local concentrations of hydrogen ions inside the thylakoids and in the intrathylakoid spaces of the grana were used to describe the processes of proton transport. The diffusion of hydrogen ions in the system can occur in the aqueous phase of the intrathylakoid space and in the narrow gap of the interthylakoid space of the grana. The interaction of hydrogen ions with the proton acceptor buffering groups associated with the internal and external surfaces of the thylakoid membrane was taken into account as well. The buffering groups of the thylakoid membranes can bind protons transported into the thylakoids, thereby creating a specific proton transfer pathway that enables the transfer of protons from the proton-generating centers to ATP synthase complexes.

All these variables were defined as local concentrations of the respective components in the neighborhood of the point **r** at the moment t. A system of kinetic equations that describes the dynamic changes of the concentrations of electron carriers and hydrogen ions, as well as the methodology of the selection of actual rate constants for the elementary stages of electron and proton transport, was described in detail in previously published studies [13, 15].

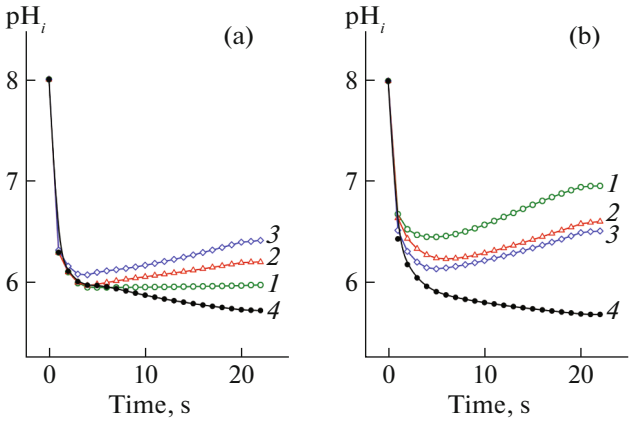

Fig. 1. The kinetics of photoinduced changes of intrathylakoid pH_i for the different values of the model parameter D_{H^+} (the efficient diffusion coefficient for the protons) calculated at the characteristic points $r = 0$ (a) and $r = b$ (b) that correspond to granal and intergranal thylakoids. *1*, *4*, $D_{H^+} = 1$; *2*, $D_{H^+} = 10$; *3*, $D_{H^+} = 100$. Curves *1–3* were calculated for the metabolic state 3 (conditions of intensive ATP synthesis), and curve 4 was calculated for the state of photosynthetic control (no ATP synthesis).

The kinetics of photoinduced pH_i changes for the metabolic states 3 (conditions of intensive ATP synthesis) and 4 (the state of photosynthetic control, no ATP synthesis) at the characteristic points $r = 0$ and $r = b$ that correspond to granal and intergranal thylakoids is illustrated in Fig. 1. The pH value in the stroma was assumed constant (pH_s 8). Curves *1–3* correspond to different values of the model parameter D_{H^+}, the effective diffusion coefficient for protons. In this case, the geometric parameters of the model, that is, the width l_o of the interthylakoid gap and the width l_i that characterized the size of the intrathylakoid space, were not varied during the calculations and were assumed constant with the ratio of the parameters being $l_o/l_i = 0.1$. The initial pH values inside the thylakoids and in the gap prior to the exposure of chloroplasts to light were the same as pH_s, that is, $pH_i(0, r) = pH_o(0, r) = 8$.

As discussed earlier [11, 15], the model developed by the authors revealed the formation of a non-uniform pH_i profile under the conditions of intensive ATP synthesis (metabolic states 3) associated with the outward transfer of protons from the thylakoids through the active ATP synthase complexes. The degree of non-uniformity was largely dependent on the hindrances for the lateral migration of protons (from the center of a grana to its periphery). The presence of a large number of buffer groups capable of

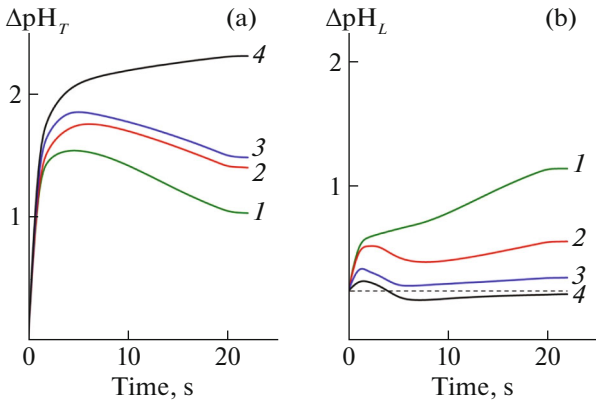

Fig. 2. The kinetics of photoinduced changes of transmembrane (ΔpH_T) and lateral (ΔpH_L) difference of intrathylakoid pH_i calculated for the different values of the model parameter D_{H^+}. Numbering of the curves is the same as in Fig. 1.

hydrogen ion binding in the internal space (lumen) of the thylakoids and on both surfaces of the thylakoid membrane causes a considerable reduction of the rate of lateral diffusion of protons in these compartments (as compared to diffusion in water). The kinetics of photoinduced pH changes in the lumen (pH_i) at the points $r = 0$ and $r = b$ are illustrated in Fig. 1. As evident from the figure, the kinetics of lumen acidification in the center of a grana ($r = 0$) and at the periphery ($r = b$) are substantially different. The pH_i value in the center of the grana drops rapidly by two pH units and varies relatively weakly (Fig. 1a). The kinetics of pH_i changes in the peripheral zone (in the zone of intergranal thylakoids) are non-monotonous: a rapid decrease of the pH_i value by 1.5 units is followed by a relatively slow increase in pH_i caused by the functioning of ATP synthase complexes (Fig. 1b). Gradual alleviation of diffusion limitations on the migration of protons in the lateral direction (curves *2* and *3* correspond to a 10-fold and a 100-fold increase of the effective diffusion coefficient of protons, respectively) makes the kinetic curves for the points $r = 0$ and $r = b$ very similar. As evident from Fig. 1, curve *3* in the panel a is almost equivalent to curve *3* in the panel b; this implies smoothening of the lateral pH_i profile upon an increase of the diffusion coefficient of protons and the attainment of lateral uniformity by the pH profile in the case of a 100-fold increase of the diffusion coefficient. The metabolic state 4 (the state of photosynthetic control) is characterized by a homogeneous pH_i profile (curves *4* in Figs. 1a and 1b). The outward transfer of protons through the ATP synthase complexes is blocked in this case, and therefore the lateral pH profile can become uniform, even in the case of relatively slow lateral diffusion of protons.

The kinetics of photoinduced changes of transmembrane (ΔpH_T) and lateral (ΔpH_L) pH gradients calculated for the metabolic states 3 and 4 is illustrated in Fig. 2. The ΔpH_T value (Fig. 2a) was calculated as $\Delta pH_T = pH_s - pH_i$, whereas the ($\Delta pH_L$ (Fig. 2a) was calculated as $\Delta pH_L = pH_i(r = b) - pH_i(r = 0)$. The results of the calculations shown in Fig. 2 provide a good illustration of the statements on the specific features of the kinetics of photoinduced lumen acidification presented above. An increase of the effective coefficient of lateral diffusion of protons (Fig. 2a, curves *2* and *3*) induced a pronounced increase of the ΔpH_T value, since the intensive outward leakage of protons through the ATP synthase complexes could be compensated by the rapid influx of protons from the granal area of the thylakoid. A decrease of the lateral pH gradient was observed in this case.

The kinetics of the photoinduced changes of the redox state of mobile electron carriers. Electron transfer between the complexes PS2, b_6f, and PS1 is mediated by the diffusion of plastoquinone (PQ) and plastocyanin (Pc) molecules. The hydrophobic plastoquinol (PQH_2) molecules diffuse in the membrane and mediate the transfer of electrons from PS2 to b_6f complexes, whereas the hydrophilic plastocyanin (Pc) molecules diffuse in the lumen and mediate the transfer of electrons from the b_6f complex to PS1. As mentioned in our previous publication [17], the model predicts nonuniform photoinduced stationary profiles of the concentration of the mobile electron carriers plastoquinone and plastocyanin. This statement is illustrated by Fig. 3, where the initial levels of the mobile electron transporters [PQ] and [Pc] are shown by dashed lines and the stationary levels of these transporters are shown by solid lines.

Plastoquinol (PQH_2) molecules diffuse in the lipid phase of the thylakoid membrane and transfer electrons from PS2 to b_6f complexes. However, it is necessary to mention that protein complexes account for at least 70% of the area of thylakoid membranes [9]. Collisions of plastoquinone molecules with unsurmountable barriers formed by the macromolecular protein complexes restrict the lateral movement in the membrane [18, 19]. The effective diffusion coefficient of plastoquinone in the thylakoid membrane is at least two or three orders of magnitude lower than that in protein-free lipid membranes, due to the factors described above [20]. The nature of the limiting stage of electron transport in the plastoquinone segment of the chain has remained a matter of discussion for many years. PQH_2 diffusion from PS2 to the b_6f complex and its oxidation are proposed as the rate-limiting stages [21]. The lateral profiles of the relative concentration of the oxidized form of plastoquinone ([PQ]) calculated for the different values of the diffusion coefficient of plastoquinone in the thylakoid membrane under the conditions of intensive ATP synthesis (state 3) are shown in Fig. 3a. A nonuniform lateral

profile of [PQ] is apparently established at a reduced rate of plastoquinone diffusion (curve *1*). This profile corresponds to the concentration of reduced plastoquinone in the granal thylakoid membranes being higher than in the stromal thylakoid zone. An increase in the coefficient of PQ diffusion is associated with a considerable increase of the relative content of the oxidized form in the grana (curves *2* and *3*). The latter finding is in good agreement with the well-known experimental data that pointed at the high mobility of plastoquinol molecules in the thylakoid membrane densely packed with protein complexes under a wide range of experimental conditions (pH, ionic strength, and temperature of the chloroplast incubation medium) (see reviews [22, 23].) In this case, the transfer of PQH_2 molecules from PS2 to the cytochrome b_6f complex is not the rate-limiting stage in the functioning of the chain of electron transfer between PS2 and PS1.

The mobility of plastocyanin in the lumen of granal thylakoids can be limited by steric barriers for Pc diffusion. The distance between the internal surfaces of the adjacent thylakoid membranes is relatively small (10–20 nm). As shown by Kirchhoff et al. [18], Pc diffusion inside the compressed granal thylakoids can be hindered by the PS2 protein complexes that protrude strongly into the lumen. The densely packed PS2 complexes with voluminous water-splitting domains that protrude into the luminal gap reduce the space for the migration of plastocyanin molecules that have a size of approximately 4 × 4 × 3 nm. The gap between the opposite edges of the water-degrading complexes protruding from the membrane should be at least 3 nm in order to provide for efficient percolation of Pc inside the lumen of granal thylakoids. Therefore, plastocyanin diffusion in the lumen can be strongly hindered by the fragments of PS2 protein complexes protruding into the lumen. The rate of Pc diffusion will depend on the lumen width and the diffusion distance. Rapid diffusion of plastocyanin molecules within the lumen enable a fast connection between b_6f complexes and the remote PS1 complexes upon thylakoid swelling. Kirchhoff et al. [18] provided experimental evidence of deceleration of electron transfer between PS2 and PS1 in the case of hindered Pc diffusion. They observed two stages of cytochrome *f* oxidation in chloroplasts of dark-adapted *Arabidopsis thaliana* plants. The presence of a slow phase of cytochrome *f* photooxidation implied that restricted diffusion of plastocyanin in the lumen hindered the electron transfer from the b_6f complex located in granal thylakoids to PS1. Lumen width increased two times upon photoinduced thylakoid swelling; this change was accompanied by strong acceleration of photoinduced cytochrome *f* oxidation [18]. Thylakoid swelling that provides additional volume for the spreading of Pc molecules in the lumen of granal thylakoids and facilitates lateral diffusion of Pc from the b_6f complexes to PS1 could explain this result.

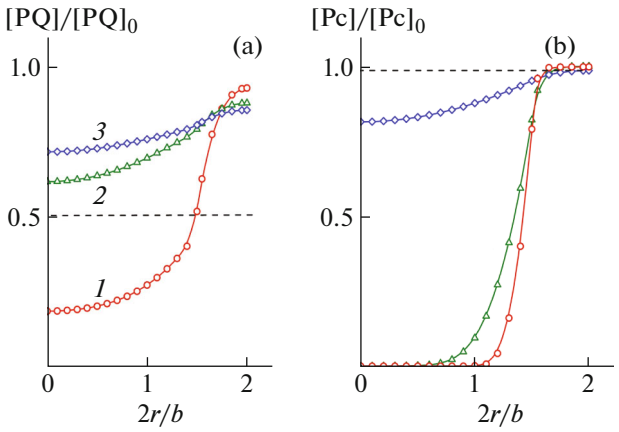

Fig. 3. The lateral profiles of the concentrations of the oxidized form of (a) plastoquinone PQ and (b) plastocyanin Pc in the stationary state 3. The dashed lines illustrate the initial distribution of the profiles of electron transporters ($t = 0$) and the solid lines illustrate the final distribution. Curves *1–3* correspond to different values of the dimensionless parameters D_{PQ} (a) and D_{Pc} (b) that characterize the respective diffusion coefficients of the mobile transporters: (a): (*1*) 1; (*2*) 5; (*3*) 10 and (b): (*1*) 1; (*2*) 10; (*3*) 100. The dimensionless variable $2r/b$ characterizes the distance from the center of the grana (see [17] for a detailed discussion).

The specific features of Pc oxidation kinetics listed above could be described within a model we developed. Stationary lateral profiles of oxidized plastocyanin (Pc) calculated for different values of the diffusion coefficient D_{Pc} are shown in Fig. 3b. The profile of oxidized plastocyanin concentration ([Pc]) is apparently non-uniform and almost independent of the metabolic state of the chloroplast and the mobility of protons. If the initial conditions correspond to an oxidized Pc pool, exposure to light evokes complete reduction of the Pc pool in the granal area, whereas almost all Pc molecules in the lumen of intergranal thylakoids remain in the oxidized state (curve *1*). Smoothening of the Pc profile and an increase of its uniformity (curve *3*) is only observed upon a dramatic (~100-fold) increase in the coefficient D_{Pc} of plastocyanin diffusion.

The kinetics of photoinduced changes in the concentrations of the oxidized forms of PQ and Pc molecules calculated for the metabolic states 3 and 4 in the characteristic points ($r = 0$ and $r = b$) that correspond to granal and intergranal thylakoids is illustrated in Fig. 4. The differences between the kinetics of PQH_2 oxidation in the center of a grana and on the edge of a thylakoid are obvious (Fig. 4a). The concentration of oxidized plastoquinone in the stromal area of a thylakoid increases more quickly and reaches a higher level than that in the granal area. This is due both to non-uniform distribution of PS2 complexes in the thylakoid membrane and insufficiently fast diffusion of

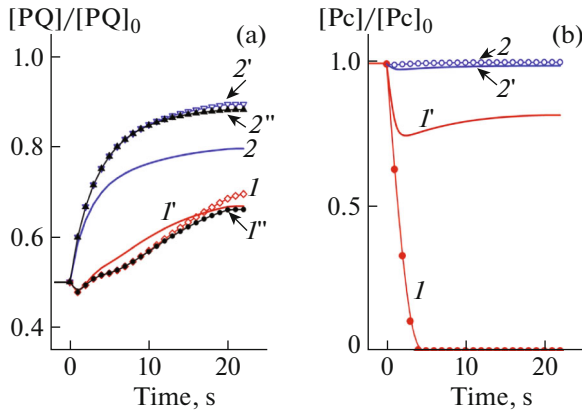

Fig. 4. The kinetics of photoinduced changes of concentrations of the oxidized forms of plastoquinone (a) and plastocyanin (b) calculated for the metabolic states 3 (curves *1*, *1*', *2*, and *2*') and 4 (curves *1*" and *2*") at the characteristic points $r = 0$ (curves *1*, *1*', and *1*") and $r = b$ (curves *2*, *2*', and *2*") that correspond to granal and stromal thylakoids. Curves *1*' and *2*' illustrate the case of rapid diffusion of the respective transporters (the same conditions as for curves *3* in Fig. 3). Curves *1* and *1*" for plastocyanin (b) are identical, as well as curves *2* and *2*".

PQH_2 molecules in the lateral direction. A tenfold increase of the effective diffusion coefficient for plastoquinone renders the differences in the kinetics of PQH_2 oxidation at the edge (curves *2* and *2*') less pronounced than those in the center (curves *1* and *1*').

Redox transformations of plastocyanin in the center of a grana and at the periphery are substantially different (Fig. 4b). If almost all of the molecules of the plastocyanin pool are oxidized at the initial time point, reduced Pc^- molecules accumulate rather quickly at the center of a grana, whereas the vast majority of Pc molecules at the periphery remain oxidized. However, our calculations demonstrated that the character of kinetic curves of plastocyanin concentration had a relatively slight dependence on the diffusion coefficient of Pc molecules. Let us also emphasize that the kinetic curves for Pc are virtually identical in the metabolic states 3 and 4 (data not shown)

CONCLUSIONS

Regulatory mechanisms associated with photoinduced changes of stroma and lumen pH are of special interest for research on the regulation of photosynthetic electron transport in chloroplasts [24–26]. Changes in the intrathylakoid pH are among the key factors that control electron flow between PS2 and PS1. A photoinduced pH_i decrease leads to deceleration of electron transfer at the ETC segment associated with the b_6f complex and triggers a mechanism that promotes the dissipation of energy in the light-harvesting antenna of PS2 to prevent overexcitation of PS2 reaction centers and excessive acidification of the lumen. These protective mechanisms account for the metabolic stability of the photosynthetic apparatus of chloroplasts upon changes in environmental conditions, such as the variation of illumination intensity or gas composition of the atmosphere.

Modeling of electron and proton transport processes with the lateral heterogeneity of the lamellar system revealed the possibility of formation of nonuniform pH profiles in granal and intergranal thylakoids of chloroplasts. The shape of the profiles depended on the metabolic state of the chloroplasts and the rate of hydrogen ion diffusion in the vicinity of the membrane inside and outside the thylakoids [11–15]. Calculations performed within our model showed that the rate of electron transfer at the plastoquinone segment of ETC was affected by the intrathylakoid pH value (pH_i), which determined the rate of PQH_2 oxidation by the cytochrome b_6f complex and by the pH_o value in the interthylakoid gap that determined the rate of PQ reduction in PS2 [11–15]. Alkalization of the interthylakoid gap evoked by the uptake of protons upon the reduction of PQ molecules by PS2 localized in granal thylakoids can reduce the rate of PS2 turnover. The intensity of ATP synthesis in chloroplasts was also shown [13] to depend on topological features of the thylakoids (for instance, the presence of elongated fragments characterized by a lower rate of longitudinal diffusion of protons). The results of the calculations provide a diffusion limitation-based explanation for the dependence of the rate of ATP synthesis on the ionic strength of the incubation medium [27–29].

In conclusion, let us emphasize that the modeling of diffusion-controlled stages of electron and proton transport in a distributed heterogeneous system of chloroplasts described in our previous study [17] and in the present study showed that the geometry characteristics of thylakoids and diffusion limitations could have substantial effects on the distribution of pH along the thylakoid membrane and the redox state of the mobile electron carriers (plastoquinone and plastocyanin). The release of diffusion limitations can occur due to structural rearrangements of the thylakoids that, in their turn, can affect the efficiency of photosynthetic processes and the regulation of energy balance in the chloroplasts. Lateral migration of protein complexes, photoinduced thylakoid swelling or compaction, and the density of thylakoid packing in the grana can affect the transfer of electrons between PS2 and PS1 and other photosynthesis phenomena. All these structural changes can be referred to as photoinduced rearrangements in the lamellar system of the chloroplast. Our future studies will be dedicated to modeling of the dynamics of these processes and the light-dependent changes of thylakoid geometry.

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