



Review Article

Computer modeling of electron and proton transport in chloroplasts



Alexander N. Tikhonov*, Alexey V. Vershubskii

Faculty of Physics, M.V. Lomonosov Moscow State University, Moscow 119991, Russia

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ABSTRACT

Photosynthesis is one of the most important biological processes in biosphere, which provides production of organic substances from atmospheric CO₂ and water at expense of solar energy. In this review, we contemplate computer models of oxygenic photosynthesis in the context of feedback regulation of photosynthetic electron transport in chloroplasts, the energy-transducing organelles of the plant cell. We start with a brief overview of electron and proton transport processes in chloroplasts coupled to ATP synthesis and consider basic regulatory mechanisms of oxygenic photosynthesis. General approaches to computer simulation of photosynthetic processes are considered, including the random walk models of plastoquinone diffusion in thylakoid membranes and deterministic approach to modeling electron transport in chloroplasts based on the mass action law. Then we focus on a kinetic model of oxygenic photosynthesis that includes key stages of the linear electron transport, alternative pathways of electron transfer around photosystem I (PSI), transmembrane proton transport and ATP synthesis in chloroplasts. This model includes different regulatory processes: pH-dependent control of the intersystem electron transport, down-regulation of photosystem II (PSII) activity (non-photochemical quenching), the light-induced activation of the Bassham–Benson–Calvin (BBC) cycle. The model correctly describes pH-dependent feedback control of electron transport in chloroplasts and adequately reproduces a variety of experimental data on induction events observed under different experimental conditions in intact chloroplasts (variations of CO₂ and O₂ concentrations in atmosphere), including a complex kinetics of P₇₀₀ (primary electron donor in PSI) photooxidation, CO₂ consumption in the BBC cycle, and photorespiration. Finally, we describe diffusion-controlled photosynthetic processes in chloroplasts within the framework of the model that takes into account complex architecture of chloroplasts and lateral heterogeneity of lamellar system of thylakoids. The lateral profiles of pH in the thylakoid lumen and in the narrow gap between grana thylakoids have been calculated under different metabolic conditions. Analyzing topological aspects of diffusion-controlled stages of electron and proton transport in chloroplasts, we conclude that along with the NPQ mechanism of attenuation of PSII activity and deceleration of PQH₂ oxidation by the cytochrome *b₆f* complex caused by the lumen acidification, the intersystem electron transport may be down-regulated due to the light-induced alkalization of the narrow partition between adjacent thylakoids of grana. The computer models of electron and proton transport described in this article may be integrated as appropriate modules into a comprehensive model of oxygenic photosynthesis.

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Abbreviations: PSI and PSII, photosystem I and photosystem II, respectively; P₇₀₀, primary electron donor of PSI; BBC, Bassham–Benson–Calvin cycle; *b₆f*, plastoquinone–plastocyanin–oxidoreductase (*b₆f* complex); CEF, cyclic electron flux; ETC, electron transport chain; Fd, ferredoxin; FNR, ferredoxin–NADP–reductase; FQR, ferredoxin–quinone–reductase; LHCI, light-harvesting complex II; LEF, linear electron flux; NDH, NAD(P)–dehydrogenase; NPQ, non-photochemical quenching; PQ, plastoquinone; PQH₂, plastoquinol; Pc, plastocyanin; *pmf*, proton motive force; Tr, thioredoxin; WWC, water–water cycle (pseudocyclic electron transport); WOC, water-oxidizing complex.

* Corresponding author. Tel.: +7 495 9392973.

E-mail addresses: an.tikhonov@mail.ru (A.N. Tikhonov), vershubskiy@mail.ru (A.V. Vershubskii).<http://dx.doi.org/10.1016/j.biosystems.2014.04.007>

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1. Introduction

Photosynthesis is one of the main biological processes in biosphere, which provides production of organic substances from atmospheric CO₂ and water. The primary processes of photosynthesis are initiated by light absorption in the light-harvesting antenna, followed by migration of energy and charge separation in photoreaction centers. Photosynthetic organisms of oxygenic type (higher plants, algae, cyanobacteria) have two multisubunit pigment–protein complexes, photosystem I (PSI) and photosystem II (PSII) (Nelson and Yocum, 2006). PSI and PSII are interconnected via the membrane-bound cytochrome *b₆f* complex and mobile electron carriers, plastoquinone (PQ) and plastocyanin (Pc) (see cartoon in Fig. 1). The pigment–protein complex of PSII contains the photoreaction center and water-oxidizing complex (WOC). Photoexcitation of PSII leads to the extraction of electrons from water, producing molecular oxygen by WOC, and the reduction of plastoquinone to plastoquinol (PQH₂) (see for review Müh et al., 2012). The cytochrome *b₆f* complex mediates electron transfer between PSII and PSI by oxidizing PQH₂ and reducing Pc (see for review Cramer et al., 2006; Hasan et al., 2013; Tikhonov, 2014). The two-electron oxidation of PQH₂ occurs at the quinone-binding center Q_o on the electropositive (lumenal) side of the thylakoid membrane. This reaction is accompanied by dissociation of two protons into the bulk phase of the thylakoid lumen. Photoexcitation of PSI provides the oxidation of Pc (or cytochrome *c₆* in cyanobacteria) and reduction of ferredoxin (Fd), a mobile electron carrier on the stromal side of the membrane. Ferredoxin reduces NADP⁺ to NADPH via the ferredoxin-NADP-oxidoreductase (FNR) (Benz et al., 2010). Thus, acting in tandem, PSII and PSI provide electron transfer along the photosynthetic electron transport chain (ETC) from water to NADP⁺, the terminal electron acceptor of PSI (H₂O → PSII → PQ → *b₆f* → Pc → PSI → NADP⁺).

In chloroplasts (the energy-transducing organelles of the plant cell), the multisubunit electron transport complexes are embedded into lamellar membranes of thylakoids, closed vesicles situated

under the chloroplast envelope. Electron transport is coupled to translocation of hydrogen ions from the chloroplast stroma to the thylakoid lumen, thus generating the transthylakoid difference in electrochemical potentials of protons, $\Delta\tilde{\mu}_{\text{H}^+}$, which serves as the proton motive force (*pmf*) used to drive ATP synthesis from ADP and P_i (ADP + P_i → ATP) by the CF₀–CF₁ ATP synthase (see for review Mitchell, 1966; Boyer, 1993, 1997; Kramer et al., 1999, 2003; von Ballmoos et al., 2009; Romanovsky and Tikhonov, 2010; Tikhonov, 2013). The products of the light-induced stages of photosynthesis, ATP and NADPH, are used in reductive biosynthetic reactions in the Bassham–Benson–Calvin (BBC) cycle (Edwards and Walker, 1983). The *pmf* value is determined by two components: the pH difference ($\Delta\text{pH} = \text{pH}_{\text{out}} - \text{pH}_{\text{in}}$) and the difference in electric potentials, $\Delta\psi = \psi_{\text{in}} - \psi_{\text{out}}$. Both components of $\Delta\tilde{\mu}_{\text{H}^+}$ are competent as the sources of energy for operation of ATP synthases (Gräber, 1982; Junesche and Gräber, 1991). In chloroplasts, under steady state conditions, ΔpH is a major component of *pmf* (Johnson and Ruban, 2014), although under certain conditions one cannot ignore the contribution of $\Delta\psi$ (Cruz et al., 2001, 2005).

Elucidation of the mechanisms of regulation of electron transport and adaptation of the photosynthetic apparatus to varying environmental conditions is a challenging task of biochemistry and biophysics of photosynthesis (Buchanan, 1980, 1991; Noctor and Foyer, 2000; Kramer et al., 2004; Eberhard et al., 2008; Foyer et al., 2012). Among the diversity of regulatory processes that serve to optimize electron transport in oxygenic photosynthesis, noteworthy are the feedbacks associated with the light-induced changes in the lumen and stroma pH. The light-induced acidification of the lumen (pH_i↓) markedly slows down PQH₂ oxidation by the *b₆f* complex and attenuates the activity of PSII due to the enhancement of energy dissipation in the PSII light-harvesting antenna (see for review Jahns and Holzwarth, 2012; Järvi et al., 2013; Ruban et al., 2012; Tikhonov, 2012, 2013). The light-induced alkalization of stroma (pH_o↑) activates the BBC cycle, thus stimulating the consumption of NADPH and ATP (Werdan et al., 1975; Mott and Berry, 1986; Andersson, 2008). Redox-regulation of

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