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REVIEW

Induction events and short-term regulation of electron transport in chloroplasts: an overview

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Abstract Regulation of photosynthetic electron transport at different levels of structural and functional organization of photosynthetic apparatus provides efficient performance of oxygenic photosynthesis in plants. This review begins with a brief overview of the chloroplast electron transport chain. Then two noninvasive biophysical methods (measurements of slow induction of chlorophyll *a* fluorescence and EPR signals of oxidized P_{700} centers) are exemplified to illustrate the possibility of monitoring induction events in chloroplasts in vivo and in situ. Induction events in chloroplasts are considered and briefly discussed in the context of short-term mechanisms of the following regulatory processes: (i) pH-dependent control of the intersystem electron transport; (ii) the light-induced activation of the Calvin–Benson cycle; (iii) optimization of electron transport due to fitting alternative pathways of electron flow and partitioning light energy between photosystems I and II; and (iv) the light-induced remodeling of photosynthetic apparatus and thylakoid membranes.

Keywords Photosynthesis · Chloroplasts · Induction events · Regulation of photosynthetic electron transport

Abbreviations

b_6f	Cytochrome b_6f complex
CBC	Calvin–Benson cycle
Chl	Chlorophyll
CEF1	Cyclic electron flow around photosystem I
EPR	Electron paramagnetic resonance
ETC	Electron transport chain
ISP	Iron-sulfur protein
Fd	Ferredoxin
FNR	Ferredoxin-NADP-oxidoreductase
FQR	Ferredoxin-quinone-reductase
FRL	Far-red light
HL	High light
LEF	Linear electron flow
LHCI	Light-harvesting complex I
LHCII	Light-harvesting complex II
LL	Low light
MV	Methylviologen
NDH	NAD(P)H dehydrogenase complex
NPQ	Non-photochemical quenching
PAM	Pulse-amplitude modulation
pmf	Proton motive force
PSI	Photosystem I
PSII	Photosystem II
PTOX	Plastoquinol terminal oxidase
P_{700}	Reduced form of electron donor of PSI
P_{700}^{+}	Oxidized form of electron donor of PSI
Pc	Plastocyanin
PQ	Plastoquinone
PQH_2	Plastoquinol
ROS	Reactive oxygen species
SIF	Slow induction of fluorescence
Tr	Thioredoxin
TrR	Thioredoxin reductase
VDE	Violaxanthin de-epoxidase
Vx	Violaxanthin
WL	White light
WOC	Water-oxidizing complex
WWC	Water–water cycle
Zx	Zeaxanthin
ΔpH	Transthylakoid pH difference

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Introduction

Photosynthesis is one of the most important biological processes in Biosphere, which provides assimilation of atmospheric CO_2 and produces molecular oxygen (O_2) at the expense of light energy. Oxygenic photosynthetic organisms (cyanobacteria, algae, plants) have two photosystems, Photosystem I (PSI) and Photosystem II (PSII), which, operating in tandem, extract two electrons from H_2O molecule using the water-oxidizing complex (WOC) of PSII and transfer them via the intersystem electron transport chain (ETC) to PSI and further to $NADP^+$, the terminal electron acceptor of PSI. Electron transport is coupled to generation of the transthylakoid difference in electrochemical potentials of protons, $\Delta\widetilde{\mu}_{H^+}$ (often termed as the proton motive force, *pmf*), which serves as the driving force for actuation of the ATP synthase (Mitchell 1966). The operation of the ATP synthase (CF_0–CF_1 complex) results in the production of ATP from ADP and inorganic phosphate (P_i). The products of the light-induced stages of photosynthesis (ATP and NADPH) are used in reductive biosynthetic reactions of the Calvin–Benson cycle (CBC) and other metabolic cycles and processes (Edwards and Walker 1983).

Flexibility of the photosynthetic apparatus is a very important property the photosynthetic organisms, which provides their efficient performance under natural conditions. High reactivity of photosynthetic ETC in response to rapid (on the timescale ranging from seconds to a few minutes) fluctuations in the light environment and variations in atmospheric CO_2 should facilitate sustainable development of photosynthetic organisms and their survival under light stress and inclement environment conditions (Kasahara et al. 2002; Allakhverdiev and Murata 2004; Murata et al. 2007, 2012; Li et al. 2009; Demmig-Adams et al. 2012; Foyer et al. 2012; Tikkanen et al. 2012, 2014; Rochaix 2014). Photosynthetic electron transport, as well as other processes of energy transduction in oxygenic photosynthesis, depends on illumination prehistory (dark-adaptation time, variations of environment gases, temperature). Activities of several CBC enzymes and other biochemical systems are regulated by light. The transition from darkness to light induces redox changes in the chloroplast ETC and causes the induction of photosynthetic enzymes involved in redox poise (Edwards and Walker 1983; Scheibe 2004). Transition events of electron transport and other metabolic processes are usually termed as "induction phenomena" (Edwards and Walker 1983). The time-courses of induction events, as well as the rate of photosynthetic apparatus adaptation to darkness, reflect the ability of photosynthetic systems to react rapidly to fluctuations of light intensity. The capacity of photosynthetic apparatus for fast response to variable environment would determine their viability and survival under extreme conditions. It has been, for instance, found that drastic fluctuations in light intensity is a potent stress factor that can cause photoinhibition and irreversible injuries to PSI and PSII (Allakhverdiev and Murata 2004; Gill and Tuteja 2010; Tikkanen et al. 2012; Kono and Terashima 2014; Kono et al. 2014; Sejima et al. 2014). Rapid response of photosynthetic ETC to fluctuations in the light environment, operating on the proper timescale, should facilitate sustainable development of photosynthetic organisms and their survival under light stress and severe environment conditions. For instance, fluctuations of light within the timescale of a few seconds would not cause dramatic changes in operation of the CBC, because its activation in the light and inactivation in the dark take more time (within several tens of seconds to 20 min) (Buchanan 1980, 1991; Edwards and Walker 1983; Pearcy 1990). Otherwise, variations of light intensity within minutes may be critical for CO_2 fixation in the CBC. Fluctuations of light with the cycle of dozen minutes to hours may be an important factor, which influence stomata conductance (Cardon and Berry 1992; Willmer and Fricker 1996; Morison 1998; Lawson et al. 2002).

Induction events reflect different mechanisms of electron transport control and regulation of metabolic processes in photosynthetic systems, which provide the short-term acclimation of photosynthetic apparatus to variable environmental conditions (Edwards and Walker 1983; Kramer et al. 2004; Cruz et al. 2005a, b; Eberhard et al. 2008; Dietz and Pfannschmidt 2011; Demmig-Adams et al. 2012; Foyer et al. 2012; Tikkanen et al. 2012; Kangasjärvi et al. 2014; Rochaix 2014). In this review, the induction events in chloroplasts are considered in the context of the feedback regulation of electron transport. After a brief overview of structural and functional organization of the chloroplast ETC, the analysis of the problem is focused on the feedbacks responsible for flexibility of photosynthetic apparatus to changes in the environment conditions. Short-term mechanisms of regulation (within a few minutes or dozens of minutes) of electron transport are achieved by cooperation of several feedbacks: (i) electron transport control governed by the light-induced variations of the lumen and stromal pH, (ii) partitioning of light quanta between PSI and PSII ("state transitions"), (iii) light-induced activation of the CBC enzymes, (iv) redistribution of electron fluxes between alternative pathways of electron transport (noncyclic/cyclic/pseudocyclic electron transport), and (v) the light-induced remodeling thylakoid membranes in chloroplasts. These processes are considered below in the context of short-term mechanisms of up- and down-regulations of photosynthetic electron transport.

Photosynthetic chain of electron transport

In photosynthetic systems of oxygenic type, the energy of light quanta absorbed by the pigment–protein complexes of PSI and PSII is converted into the energy of separated charges, providing electron transfer from the water molecule oxidized by the WOC complex of PSII to $NADP^+$ reduced by PSI. Figure 1 schematically depicts a variety of electron transport pathways in chloroplasts. Reaction centers PSI and PSII are interconnected via the membrane-bound cytochrome b_6f complex and mobile electron carriers, plastoquinone (PQ) and plastocyanin (Pc): $H_2O \rightarrow$ PSII $\rightarrow$ PQ $\rightarrow b_6f \rightarrow$ Pc $\rightarrow$ PSI $\rightarrow NADP^+$. Electron transport complexes are embedded into the thylakoid membranes, which form closed vesicles situated under the chloroplast envelope. Electron transfer along the ETC is accompanied by alkalization of the stroma and acidification of the intrathylakoid lumen. Some peculiarities of the structural and functional organization of basic multisubunit protein complexes involved in the intersystem electron transport (PSI, PSII, and b_6f complexes) are briefly considered below.

Photosystem I

The multisubunit pigment–protein complex of PSI catalyzes electron transfer from plastocyanin (or cytochrome c_6 in cyanobacteria) on the lumenal side of the thylakoid membrane to a mobile electron carrier ferredoxin (or flavodoxin) on the stromal side of the membrane (see for review Brettel 1997; Fromme et al. 2001; Nelson and Yocum 2006; Amunts et al. 2007; Shelaev et al. 2010, and references therein). A special pair of chlorophyll (Chl) molecules (Chl_{1A} and Chl_{1B}), located at the interface of PSI subunits PsaA and PsaB, forms the primary electron donor named P_{700} (Fig. 1). The light-induced excitation of PSI is followed by charge separation between P_{700} and the primary electron acceptor. Electron carriers on the acceptor side of PSI are arranged as two quasi-symmetric cofactor branches (A-branch and B-branch). Each branch consists of two chlorophyll molecules (Chl_{2A} and Chl_{3A} in A-branch; Chl_{2B} and Chl_{3B} in B-branch) and one phylloquinone molecule (A_{1A} or A_{1B}, respectively). The two branches converge at the electron acceptor F_X (one of three $[Fe_4S_4]$ clusters of PSI, F_X, F_A, and F_B). Reduced phylloquinone (A_{1A} or A_{1B}) donates electron to F_X. Electron transport through PSI is asymmetric (at least under certain experimental conditions in cyanobacterial PSI), with the majority of electron transfer taking place through the A-branch of cofactors (Cohen et al. 2004; Dashdorj et al. 2005; Savitsky et al. 2010; Mula et al. 2012). From the reduced F_X, the electron is transferred to ferredoxin (Fd) via the membrane-bound redox centers F_A and F_B ($F_X \rightarrow F_A \rightarrow F_B \rightarrow$ Fd). Reduced Fd molecules (Fd^-) deliver two electrons to $NADP^+$ via the ferredoxin-NADP-oxidoreductase (FNR). Oxidized center P_{700}^+ accepts electron from reduced Pc, which, in turn, accepts electron from the cytochrome b_6f complex.

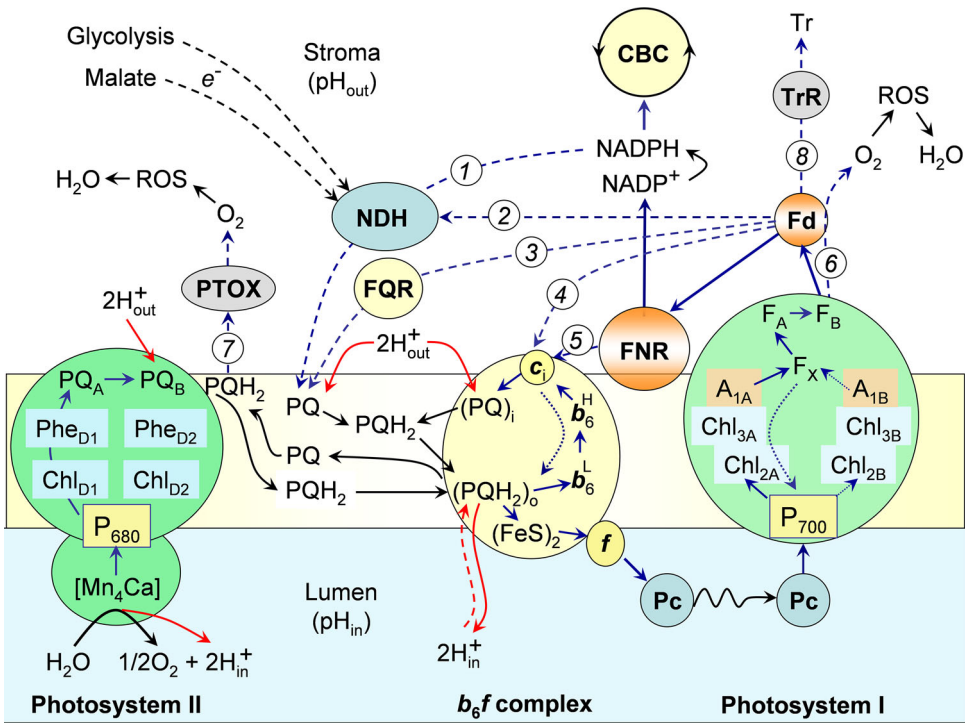

Fig. 1 A scheme of photosynthetic electron transport pathways and the arrangement of protein complexes (photosystem I, photosystem II, cytochrome b_6f) in the thylakoid membrane (modified Fig. 1 from Tikhonov 2014). See the list of abbreviations and text for notations and other details

Photosystem II

PSII contains the photoreaction center with the primary electron donor P_{680} (a special pair of chlorophylls, $P_{D1}P_{D2}$) and the water-oxidizing complex (WOC) (Nelson and Yocum 2006; Barber 2008; Guskov et al. 2009; Umena et al. 2011; Cardona et al. 2012). WOC catalyzes the cleavage of water and formation of atmospheric dioxygen ($H_2O \rightarrow 1/2O_2 + 2H^+ + 2e^-$). Excited P_{680} center (P^*_{680}) donates electron to the A-branch of electron carriers, which involves chlorophyll (Chl_{D1}) and pheophytin (Phe_{D1}) molecules (Fig. 1). Reduced pheophytin delivers electron to tightly bound PQ molecule (primary plastoquinone, PQ_A). Reduced quinone PQ_A^- donates an electron to the secondary quinone PQ_B ($PQ_A^-PQ_B \rightarrow PQ_APQ_B^-$). WOC includes the water-splitting cluster [Mn_4Ca] and a nearby tyrosine residue Y_Z, which serves as a mediator of electron transfer from WOC to photooxidized center P^+_{680}. Two electrons consecutively extracted from the water molecule are used to reduce PQ_B to PQ_BH_2. The second electron transferred to PQ_B^- from the WOC provides the double reduction of the secondary quinone ($PQ_A^-PQ_B^- \rightarrow PQ_APQ_B^=$) and induces its protonation due to the uptake of two protons from stroma ($PQ_B^= + 2H^+_{out} \rightarrow PQ_BH_2$). The affinity of PQ_BH_2 to PSII decreases and PQ_BH_2 dissociates from PSII in exchange for a new oxidized PQ molecule ($PQ_BH_2 + PQ \rightarrow PQ_B + PQH_2$) (Cardona et al. 2012; Müh et al. 2012). As a result of double actuation of PSII, two protons are translocated from the stroma to the intrathylakoid lumen per one PQ molecule reduced by PSII ($H_2O + PQ + 2H^+_{out} \rightarrow 1/2O_2 + PQH_2 + 2H^+_{in}$).

Cytochrome b_6f complex

Diffusing in the thylakoid membrane, PQH_2 reaches the cytochrome b_6f complex (plastoquinol:plastocyanin oxidoreductase), which belongs to the cytochrome *bc* family of multisubunit electron transport complexes (see for review Berry et al. 2000; Crofts 2004; Cramer et al. 2006, 2011; Hasan et al. 2013; Tikhonov 2014). The cytochrome b_6f complex is a central component of the chloroplast ETC, which mediates electron transfer between PSII and PSI by oxidizing PQH_2 and reducing Pc. This complex is considered as a functional homodimer of multisubunit monomers. Each monomer consists of eight polypeptide subunits, including the iron–sulfur protein (ISP), the cyt b_6 and cyt f proteins (Fig. 1). The catalytic functions of the b_6f complex are served by the iron–sulfur cluster [Fe_2S_2] of the ISP, and three hemes: the low-potential heme b_6^L and the high-potential heme b_6^H of the cyt b_6 protein, and the cyt f heme. The b_6f complex contains two binding centers for PQH_2 and PQ molecules: Q_o-site (PQH_2 oxidase) and Q_i-site (PQ reductase). The two-electron oxidation of PQH_2 occurs at the catalytic center Q_o placed in the cavity at the interface between the cyt b_6 subunit and the ISP. This center is oriented toward the lumenal side of the thylakoid membrane; PQH_2 oxidation is accompanied by the release of two protons into the bulk phase of the thylakoid lumen.

According to the Q-cycle mechanism suggested by Peter Mitchell (1976), the oxidation of quinols (PQH_2 in chloroplasts and UQH_2 in photosynthetic bacteria and mitochondria) is a bifurcated reaction: one electron is transferred to a high-potential chain and the other to a low-potential chain (Berry et al. 2000; Crofts 2004; Crofts et al. 2000, 2013; Mulkidjanian 2005; Osyczka et al. 2005; Cramer et al. 2006, 2011; Tikhonov 2014). The first electron is transferred to Pc through the high-potential redox chain, which consists of the ISP and cyt f ($PQH_2 \rightarrow ISP \rightarrow$ cyt $f \rightarrow$ Pc). The second electron is directed through the hemes: b_6^L and b_6^H to reduce PQ at the quinone reductase Q_i-site on the stromal side of the b_6f complex ($PQH^\bullet \rightarrow b_6^L \rightarrow b_6^H \rightarrow PQ$). In this center, two successive steps of PQ reduction are accompanied by binding two protons taken from the stroma: ($PQ + 2e^- + 2H^+_{out} \rightarrow PQH_2$). Protonated molecule PQH_2 dissociates from the Q_i-site; then it can bind to the Q_o-site on the lumenal side of the b_6f complex. As a result of PQH_2 turnover around the b_6f complex, two protons are translocated from stroma to the lumen per one electron ($H^+/e^- = 2$) transferred from PQH_2 to P^+_{700} through the high-potential chain ($ISP \rightarrow$ cyt $f \rightarrow$ Pc $\rightarrow P^+_{700}$). It has been suggested that stroma-exposed quinone-binding center Q_i may be involved in the cyclic route of electron transfer around PSI (see for review Allen 2003; Munekage et al. 2004; Alric et al. 2005; Shikanai 2007; Alric 2010). Electrons from the acceptor side of PSI might return to the quinone-reductase center Q_i via Fd, FNR, and/or heme c_i (an atypical heme c_i is located nearby the stromal side of the thylakoid membrane, Kurisu et al. 2003; Stroebel et al. 2003).

Standing at the crossroad of electron transport pathways, the b_6f complex plays an important role in the sustainability of photosynthetic processes, providing efficient functioning, high flexibility, and adaptability of photosynthetic apparatus in plants. Under a wide range of experimental conditions (pH, ionic strength, and temperature), the PQH_2 formation in PSII and its lateral diffusion within the thylakoid membrane do not limit the overall rate of the intersystem electron transport (Haehnel 1976; Tikhonov et al. 1984; Tikhonov 2013, 2014). These processes occur much faster ($\tau_{1/2} < 2$–5 ms) than PQH_2 oxidation after its binding to the b_6f complex ($\tau_{1/2} \geq 10$–20 ms). The overall rate of the intersystem electron transport is limited by the endergonic reaction of electron transfer from PQH_2 to the ISP. Pc diffusion into the thylakoid lumen and its

interaction with P_{700}^{+} may occur much more rapidly ($\tau_{1/2} < 200$ μs, at ambient temperatures) than electron transfer from PQH_2 to Pc via the b_6f complex (Stiehl and Witt 1969; Witt 1979; Haehnel 1984). However, under certain conditions, e.g., in the initial stage of electron transport induction, diffusion-controlled processes may pose restrictions to the long-range steps of the intersystem electron transport (Lavergne and Joliot 1991; Lavergne et al. 1992; Kirchhoff 2008, 2013, 2014).

PQH_2 oxidation at the Q_o-site of the b_6f complex represents the "bottle-neck" link in the ETC between PSII and PSI, which controls the overall rate of the intersystem electron transport. The feedback control of PQH_2 oxidation by the b_6f complex is governed by the intrathylakoid pH (see for review Tikhonov 2012, 2013, 2014; Järvi et al. 2013). The acidification of the lumen causes deceleration of PQH_2 oxidation, thus impeding the intersystem electron transport. Two other mechanisms of the feedback regulation of electron flow through the b_6f complex include (i) "state transitions" associated with the light-induced redistribution of solar energy between PSI and PSII, and (ii) redistribution of electron fluxes between alternative pathways (noncyclic electron flow to $NADP^+$ and cyclic electron transport around PSI). These mechanisms are considered below in more details.

Structural peculiarities of the chloroplast lamellar system

As noted above, under a wide range of experimental conditions, diffusions of mobile electron carriers (PQ, Pc) do not limit the intersystem electron transport in chloroplasts (see for review Tikhonov 2013, 2014). However, some peculiarities of structural organization of photosynthetic ETC in chloroplasts could pose restrictions to diffusion of mobile electron carriers (Kirchhoff et al. 2000, 2004, 2008; Tremmel et al. 2003; Kirchhoff 2013, 2014), limiting the intersystem electron transport from the outset of illumination of dark-adapted chloroplasts (Kirchhoff et al. 2011). In chloroplasts, the multiprotein complexes PSI, PSII, and b_6f are distributed nonuniformly between the granal and stromal thylakoids (Albertsson 2001; Dekker and Boekema 2005; Kouril et al. 2012). Stacked thylakoids of grana are enriched with PSII and the light-harvesting complex II (LHCII), whereas most of the PSI and CF_0–CF_1 complexes are localized in the membranes of unstacked stroma-exposed thylakoids, grana margins, and grana end membranes. In contrast to PSI and PSII, the cytochrome b_6f complexes are distributed almost uniformly throughout all the domains of the chloroplast lamellae (see cartoon in Fig. 2). About 55 % of the b_6f complexes are localized in appressed membranes of grana, and about 45 % complexes are distributed over the stromal lamellae, in the margins and grana end membranes (Albertsson 2001). Although significant amounts of PSI, PSII, and b_6f complexes are laterally segregated in the thylakoid membrane, most of them are in close contact. The amount of PQ molecules is about 10 times higher than that of PSI or PSII (Stiehl and Witt 1969; Witt 1979; Haehnel 1984).

Noninvasive biophysical methods of monitoring induction events

In this section, I will exemplify noninvasive biophysical methods for monitoring induction events in oxygenic photosynthesis based on the fluorometry and electron paramagnetic resonance (EPR) techniques. These methods allow the experimenter to perform noninvasive studies of photosynthetic processes in vivo and in situ in optically dense samples (e.g., in leaves).

Oximetric measurements

The long-standing investigations of gas-exchange processes in leaves present numerous examples of induction events in oxygenic photosynthesis (see for review Laisk 1977; Edwards and Walker 1983; Laisk et al. 1989, and references therein). Below, I consider one example of using the EPR technique for monitoring changes in the partial pressure of O_2 within the leaf interior, which occur due to respiration and light-induced evolution of O_2. Figure 3 compares the time-courses of the light-induced production of O_2 in dark-adapted and pre-illuminated bean leaves, as monitored by a specific O_2-sensor (paramagnetic fusinite particles) injected into the leaf (Ligeza et al. 1997). The use of fusinite particles, as O_2-sensors, allowed for direct measurements of O_2 concentration in the leaf interior. Consumption of O_2 due to respiration of leaves in the dark manifests itself as an increase in the magnitude of the EPR signal of fusinite particles; evolution of O_2 during illumination attenuates the signal amplitude (Fig. 3). In dark-adapted (30 min) leaves placed into water-filled closed cell, the light-induced increase in O_2 in the leaf interior becomes visible only after a certain lag-phase (curve *1*). After short adaptation to darkness (curve *2*), the light-induced evolution of O_2 is observed immediately after switching the light on, without any delay. Such a difference between the dark-adapted and pre-illuminated leaves is a pictorial manifestation of induction events in leaves.

Diagram in Fig. 4 summarizes different processes of O_2 consumption and O_2 evolution in the plant cell. Mitochondrial respiration in darkness causes gradual depletion

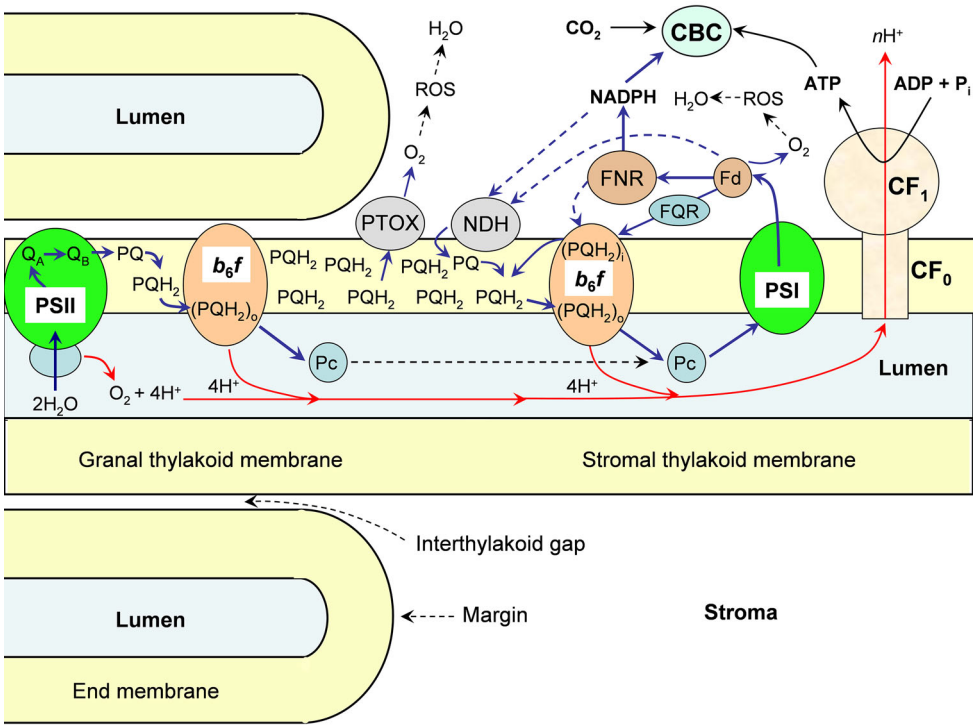

Fig. 2 A scheme of arrangement of photosynthetic electron transport complexes (PSI, PSII, b_6f, FNR, NDH, PTOX, FQR) and the ATP synthase (CF_0–CF_1) in the granal and stroma-exposed thylakoids (modified Fig. 4 from Tikhonov 2014). See the list of abbreviations and text for notations and other details

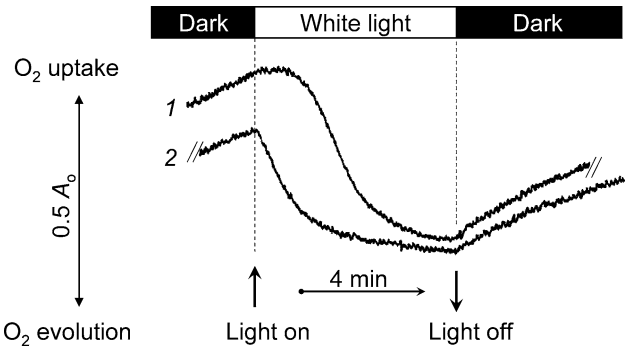

Fig. 3 Light-induced production of O_2 and O_2 uptake in the dark inside bean leaves. The typical patterns of the time-courses of the light-induced changes in the amplitude of the oxygen-sensitive EPR signal from fusinite particles injected into a bean leaf are shown. Samples were placed into the water-filled closed chamber; therefore, O_2 could be accumulated inside the leaf. Curves *1* and *2* correspond to the first and the second cycles of illumination, respectively. Before the first illumination (intensity of light focused on the sample was about 160 W/m^2), a sample (4 mm × 5 mm piece of the leaf placed in the closed chamber) was adapted to the dark for about 30 min. Curve *2* is the continuation of curve *1*. A_0, the amplitude of the EPR spectrum of fusinite particles injected into the leaf equilibrated with air. Modified Fig. 3 from Ligeza et al. (1997)

of O_2 in the leaf interior. Illumination induces the O_2 production by PSII; however, restricted outflow of electrons to the CBC during the induction phase hampers the overall rate of the intersystem electron transport, thereby attenuating the net yield of O_2 in PSII. Also, at low activity of the CBC in the initial phase of photosynthesis induction, electrons from PSI are diverted to alternative channels of electron outflow: (i) cyclic electron transport around PSI and (ii) electron flow to O_2 (Mehler 1951). The latter leads to O_2 reduction and its final conversion to water (the so-called water–water cycle, WWC, see Asada 1999 for review). With the light-induced CBC activation, linear electron transport would not limit the O_2 production by PSII; on the other hand, the electron flow to O_2 (the Mehler reaction) will go down. Therefore, the net balance of gas-exchange reactions will gradually changes in favor of O_2 evolution (Fig. 3).

It is important to note that under the normal physiological conditions, when the leaf is exposed to air, there are no visible changes in the level of O_2 inside the leaf, neither in the dark nor during illumination (Ligeza et al. 1997). This means that ventilation of the leaf interior is sufficient for maintaining the O_2 partial pressure practically on the same level, both in the dark or during illumination. Such good ventilation of the leaf interior, along with a high permeability of thylakoid membranes for molecular oxygen (Ligeza et al. 1998), should protect leaf tissues against the dangerous increase in the level of O_2 evolved by chloroplasts.

Note that there are other processes directed to avoid light stress that would reveal themselves as induction events of photosynthesis in dark-adapted plants. Along with the mechanisms of electron transport control mentioned in Introduction, these processes include: the light-induced remodeling of photosynthetic apparatus (Chuartzman et al.

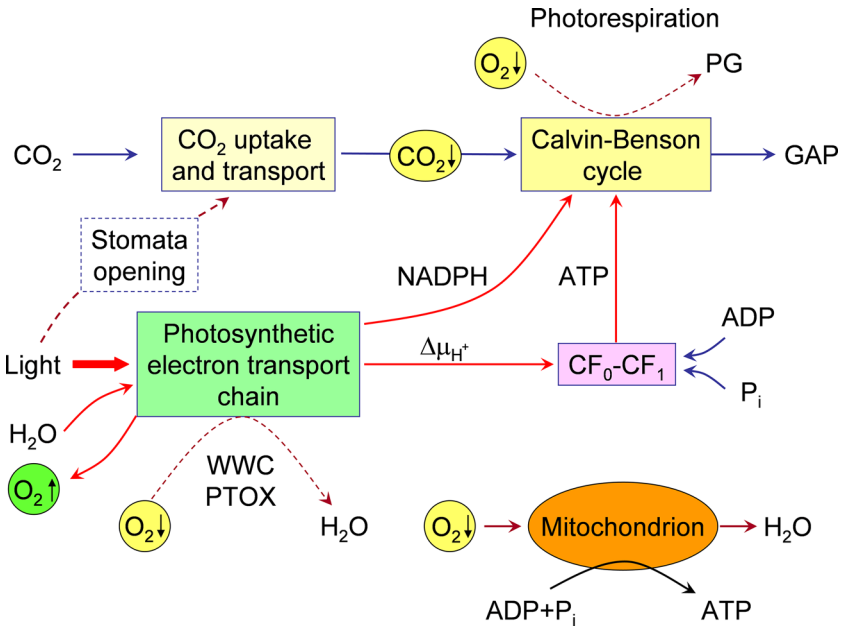

Fig. 4 Simplified block-diagram of the light-induced processes involved in gas-exchange reactions in the plant cell. *GAP* glyceraldehyde 3-phosphate, *PG* 2-phosphoglycolate

2008; Iwai et al. 2010a; Kirchhoff et al. 2011; Nagy et al. 2011, 2013; Los et al. 2013; Garab 2014), stomata opening/closure (Cardon and Berry 1992; Willmer and Fricker 1996; Morison 1998; Lawson et al. 2002), and relocation of chloroplasts within the plant cell (avoidance effects, see for review Kasahara et al. 2002; Takagi 2003; Wada et al. 2003; Kong and Wada 2011).

Slow induction of chlorophyll a fluorescence

Chlorophyll (Chl) *a* fluorescence provides a powerful signature of photosynthetic processes in vivo, in situ and in vitro. The use of Chl *a* fluorescence to monitor photosynthetic performance in plants and algae is widely spread (see for references reviews by Schreiber 1986, 2004; Govindjee 1995; Lazar 1999; Maxwell and Johnson 2000; Baker and Oxborough 2004; Papageorgiou and Govindjee 2004; Baker 2008; Stirbet and Govindjee 2011, 2012; Schreiber et al. 2012; Goltsev et al. 2014; Kalaji et al. 2014). In this section, I briefly outline the kinetics of slow induction of Chl *a* fluorescence (SIF), which is widely used as a convenient method for express-monitoring induction events in leaves and algae.

Figure 5 illustrates how induction of oxygenic photosynthesis manifests itself in the time-course of Chl *a* fluorescence. This figure shows the typical pattern of the fluorescence induction in dark-adapted (10 min) *Hibiscus rosa-sinensis* leaves, as measured according to a standard PAM-fluorometry (pulse-amplitude modulation) protocol (Schreiber 1986, 2004; Schreiber et al. 1986, 2012). In response to first saturating flash, the fluorescence yield

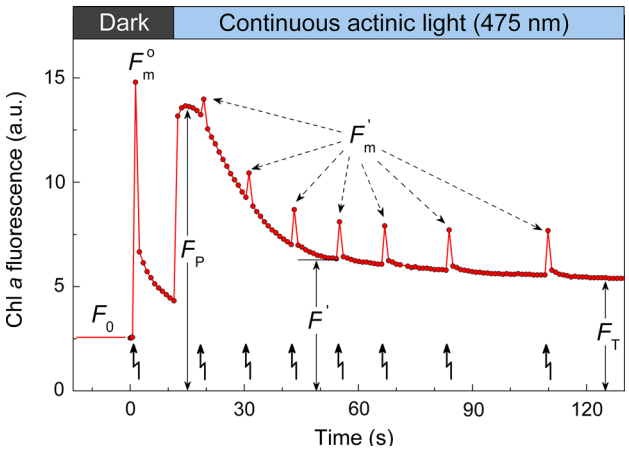

Fig. 5 Light-induced changes in Chl *a* fluorescence in dark-adapted *Hibiscus rosa-sinensis* leaves exposed to saturating light pulses (indicated by broken vertical arrows) and continuous actinic light (475 nm, 300 μmol photons m^{-2} s^{-1}) used for assaying non-photochemical fluorescence quenching (parameter *NPQ*) and photochemical activity of PSII (parameters Φ_{PSII} and q_P). Prior to the application of first saturating light pulse, pre-illuminated leaf was adapted to the dark for 10 min. Modified Fig. 1 from Kuvykin et al. (2011)

increases from the initial level F_0 up to the maximal level F_m^0 and then gradually decays. After switching on a continuous actinic light, the fluorescence yield rises to the transient maximum F_P and then gradually decays toward the steady-state level F_T. Such a nonmonotonic time-course of Chl *a* fluorescence is known as the Kautsky effect (Kautsky and Hirsch 1931) or "slow induction of fluorescence" (see for review Govindjee 1995; Lazar 1999; Stirbet and Govindjee 2011). A rise of Chl *a* fluorescence

($F_0 \rightarrow F_P$ transition) reflects the light-induced reduction of electron carriers on the acceptor side of PSII (primary plastoquinone PQ_A and secondary plastoquinone PQ_B) and the reduction of electron carriers in the intersystem ETC beyond PQ_A and PQ_B (mainly the PQ pool; van Gorkom et al. 1974; Kurreck et al. 2000; Tóth et al. 2007; Kalaji et al. 2014; Schansker et al. 2014).

A further decrease in the yield of fluorescence ($F_P \rightarrow F_T$ transition) can be caused by up- and down-regulatory processes: (*i*) an increase in photochemical quenching of Chl *a* fluorescence due to reoxidation of PSII acceptors caused by acceleration of electron transport on the acceptor side of PSI (e.g., due to the light-induced activation of the CBC), and/or (*ii*) an enhancement of non-photochemical quenching (NPQ) of Chl *a* fluorescence associated with an increase in energy dissipation as heat in LHCII induced by energization of chloroplasts. Along with the gradual decrease in the fluorescence yield tested by weak probing flashes ($F_P \rightarrow F_T$ transition), the fluorescence intensity measured in response to a train of saturating pulses (parameter $F_m^{'}$) also declines, which is considered as a clear manifestation of NPQ development during illumination (Schreiber 1986, 2004). After cessation of illumination, $F_m^{'}$ gradually recovers to its initial level F_m^0 peculiar to dark-adapted leaves (not shown). The post-illumination rise of $F_m^{'}$ reflects the NPQ release in the dark.

Development of NPQ is one of the most important mechanisms of plant protection against light stress (see for review Demmig-Adams 1990, Horton et al. 1996; Li et al. 2009; Horton 2012; Jahns and Holzwarth 2012; Ruban et al. 2012). The light-induced generation of NPQ and its decay in the dark occur at different timescales (Hodges et al. 1989; Nilkens et al. 2010; Demmig-Adams et al. 2012; Jahns and Holzwarth 2012). The rapid phase of NPQ (within ~1–2 min) provides a prompt response of photosynthetic apparatus to sunflecks. This component of NPQ, which is usually termed as *qE*-component, is triggered by the light-induced decrease in the intrathylakoid pH (Rees et al. 1989, 1992; Noctor et al. 1991; Horton et al. 1996). In photosynthetic eukariots, a central role in development of NPQ belongs to PsbS subunit of PSII and the xanthophylls cycle. Along with the energy-dependent component *qE*, there are slowly developing (~10–30 min) and slowly relaxing (~10–60 min) components of NPQ, which have been collectively termed by Jahns and Holzwarth (2012) as *qZ*-component, because its contribution to NPQ strictly depends on zeaxanthin (Zx) level in leaves (Johnson et al. 2008; Nilkens et al. 2010). The development of NPQ accelerates and enhances upon de-epoxidation of violaxanthin (Vx) to Zx, while NPQ relaxation in darkness becomes slower. De-epoxidation of Vx (Vx → Zx) occurs within minutes; epoxidation of Zx (Zx → Vx) occurs within minutes to hours (or even several days under severe stresses, Adams et al. 1995; Demmig-Adams et al. 2012). The light-induced development of *qZ* allows supporting an elevated dissipation of energy after relatively long periods of dark adaptation of pre-illuminated leaves (so-called "sustained" NPQ, Ruban and Horton 1995; Adams and Barker 1998; Adams and Demmig-Adams 2004). The long-term sustained NPQ is peculiar for evergreen species upon plant transfer from low light (LL) to high light (HL), when a state of photosynthetic apparatus allowing for maximal levels of thermal dissipation of light energy is continuously maintained ~24 h a day.

Along with de-epoxidation/epoxidation reactions in the xanthophylls cycle, the slowly developing and slowly relaxing component of NPQ may also reflect other light-induced events in chloroplasts ("state transitions" and photoinhibition, which are related to so-called *qT* and *qI* components of NPQ, respectively). The three components of NPQ (*qE*, *qT*, and *qI*) can be distinguished on the basis of NPQ relaxation in the dark (Hodges et al. 1989). The light-induced redistribution of light quanta between photosystems ("state transitions"), which is associated with the relocation of LHCII complexes from PSII to PSI (Allen 1992; Wollman 2001; Minagawa 2011; Tikkanen and Aro 2012; Rochaix 2014), will lead to a decrease in the yield of Chl *a* fluorescence emitted by PSII (the *qT*-component of NPQ). This component relaxes in the dark within minutes. This mechanism of the feedback regulation of the light energy partitioning between PSII and PSI usually manifests itself at LL and moderate light illumination (Quick and Stitt 1989). Photoinhibition of PSII (the *qI*-component of NPQ, Őquist et al. 1992; Baker 2008) also contributes to a decrease in the yield of Chl *a* fluorescence. This component of NPQ relaxes very slowly (several dozens of minutes or longer).

The use of PAM-fluorometry technique allows deriving parameters which characterize photochemical activity of PSII: the operating efficiency of PSII, Φ_{PSII}, and photochemical quenching, q_P. Φ_{PSII} characterizes quantum yield of PSII; q_P is proportional to open PSII. Parameters Φ_{PSII} and q_P are widely used to describe photosynthetic performance of chloroplasts (Oxborough and Baker 1997; Maxwell and Johnson 2000; Baker and Oxborough 2004; Baker 2008). In particular, linear electron flow (LEF) can be evaluated as $J_{LEF} = PPFD \times \alpha_2 \times \Phi_{PSII}$, where PPFD is the photosynthetically active photon flux density (μmol photon m^{-2} s^{-1}) of absorbed light and α_2 is a partitioning factor that accounts for the energy distribution between PSII and PSI. The typical patterns of time-courses of the fluorescence parameters Φ_{PSII}, q_P, and q_{NPQ} measured in dark-adapted *Hibiscus rosa-sinensis* leaves are shown in Fig. 6. In response to switching on actinic light, parameter Φ_{PSII} rapidly drops from the initial level $\Phi_{PSII} \approx 0.8$ to a minimum and then gradually rise toward a

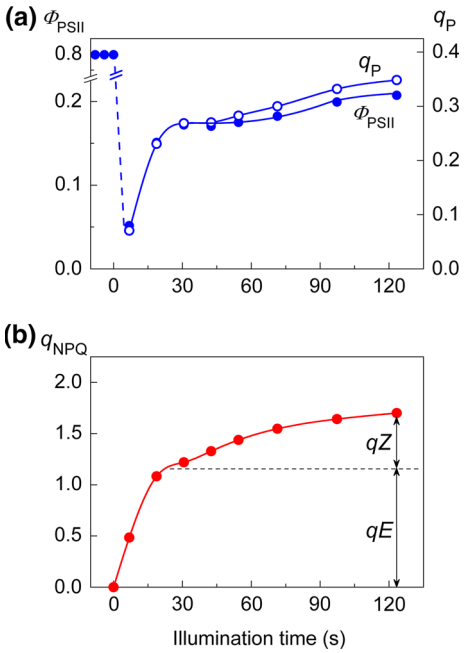

Fig. 6 Time-courses of the fluorescence parameters Φ_{PSII} and q_P (**a**), and q_{NPQ} (**b**) in dark-adapted (10 min) *Hibiscus rosa-sinensis* leaves (modified Fig. 8 from Kuvykin et al. 2011). Fluorescence parameters Φ_{PSII}, q_P, and q_{NPQ}, which are widely used to characterize the state of photosynthetic apparatus, were calculates as follows: $q_{NPQ} = (F_m^o - F_m')/F_m'$ (non-photochemical quenching of Chl *a* fluorescence), $\Phi_{PSII} = (F_m' - F')/F_m'$ is the quantum yield of PSII photochemical activity, and $q_P = \frac{F_m' - F'}{F_m' - F_0/((F_m^0 - F_0)/F_m^0 + F_0/F_m')}$ is the current proportion of open PSII centers (Oxborough and Baker 1997). See text for explanation of *qE* and *qZ* components of NPQ

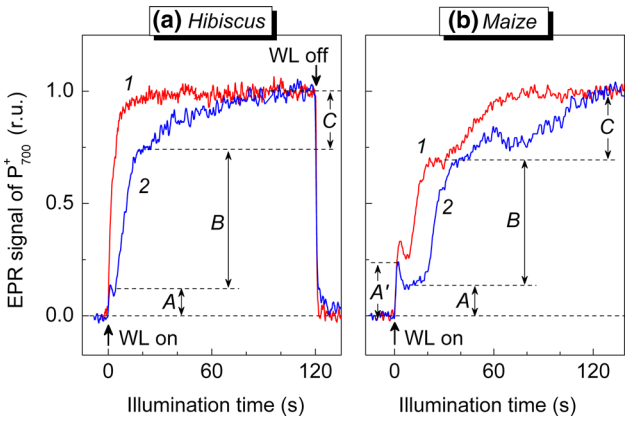

Fig. 7 The typical patterns of P_{700} photooxidation kinetics in *Hibiscus rosa-sinensis* leaves (**a**) and in maize (**b**) leaves. **a** Pre-illuminated specimens of *Hibiscus rosa-sinensis* leaves adapted to the dark for 0.5 min (*curve 1*) or 8 min (*curve 2*). Before dark adaptation, each sample was pre-illuminated with WL for 1 min. Modified Fig. 3B from Kuvykin et al. (2011). **b** Pre-illuminated specimens of maize leaves were adapted to the dark for 1.5 min (curve *1*) or 16.5 min (curve *2*). Before dark adaptation, each sample was pre-illuminated with WL for 2 min. Modified Fig. 1 from Vishnyakova et al. (2000)

steady-state level. The immediate decrease in Φ_{PSII} and q_P (Fig. 6a) reflects a rapid reduction of electron carriers on the acceptor side of PSII and in the intersystem segment of the ETC (the PQ pool, Baker and Oxborough 2004). A subsequent slow increase in Φ_{PSII} and q_P can be accounted for by the light-induced activation of the CBC and concomitant acceleration of electron outflow from PSI, which eventually results in gradual reoxidation of the PQH_2 pool. A slow phase of the Φ_{PSII} increase may be explained by gradual attenuation of PSII activity caused by the light-induced development of NPQ. Actually, this phase correlates with a slow rise of the NPQ parameter q_{NPQ}. It is noteworthy that a similar multiphase kinetics of electron transport processes is observed in the case of P_{700} photooxidation in dark-adapted leaves measured by the EPR method (Fig. 7).

Measurements of photosynthetic electron transport by the EPR method

The EPR method provides another convenient means for monitoring electron transport in optically dense specimens, in particular, in plant leaves. This method is readily suitable for monitoring the redox state of P_{700}, because oxidized centers P_{700}^+ give characteristic EPR signal (Webber and Lubitz 2001). For illustration how induction events can be monitored by the EPR method, consider kinetics of P_{700} photooxidation in *Hibiscus rosa-sinensis* (C_3 plant) and maize (C_4 plant) leaves (Fig. 7). In both cases, after sufficiently long adaptation of pre-illuminated leaves to darkness ($t_{ad} \geq$ 1–5 min, depending on species), the time-course of P_{700} photooxidation shows three distinct phases, *A*-*B*–*C*. An initial jump of P_{700}^+ (the overshoot *A*′–*A*) is followed by the lag-phase (phase *A*), which duration increases with the dark-adaptation time. The lag-phase is followed by subsequent *S*-shaped oxidation of P_{700} (phase *B*). The third phase of P_{700}^+ induction (phase *C*) corresponds to comparatively slow rise of P_{700}^+ toward a steady-state level. After ceasing the illumination, the EPR signal of P_{700}^+ disappears due to electrons donated to P_{700}^+ by reduced ETC. Illumination of leaves after sufficiently short dark period ($\leq$ 30 s) results in fast monotonous oxidation of P_{700}. In this case, the separation between phases *A*, *B*, and *C* disappears. The reader can find other examples of the influence of pre-illumination history on the kinetics of P_{700}^+ induction in the leaves of higher plants in (Joliot and Joliot 2005, 2006; Hald et al. 2008b; Bulychev and Vredenberg 2010; Bulychev et al. 2010).

The difference in kinetic behavior of P_{700} in dark-adapted and pre-illuminated leaves is caused by de-energization of chloroplasts in the dark (dissipation of ΔpH) and adaptive changes in chloroplasts. For example, the CBC metabolites might be present in larger amounts in pre-illuminated samples (these metabolites can persist for long periods in darkness, Edwards and Walker 1983; Scheibe 2004; Foyer et al. 2012), thus favoring a faster activation of

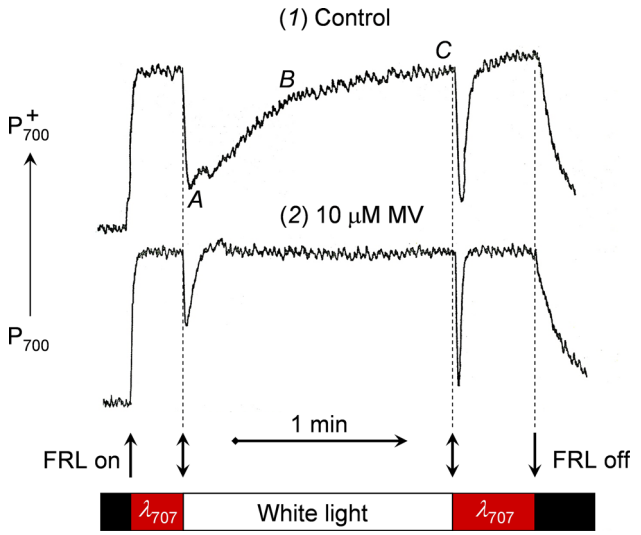

Fig. 8 Effect of methylviologen (MV) on the light-induced redox transients of P_{700} in dark-adapted (10 min) *Hibiscus rosa-sinensis* leaves induced by far-red (λ_{707}) and white light illumination (after Ryzhikov and Tikhonov 1988)

the CBC. The multiphase kinetics of P_{700} photooxidation in dark-adapted leaves correlates with the kinetics of electron flow through PSII as characterized by parameters Φ_{PSII} and q_P derived from the fluorescence data (Fig. 6a). EPR and fluorometry methods for monitoring electron transport are complementary each other, providing information about the states of PSI and PSII, respectively. It should be noted that both methods reveal similar peculiarities of electron transport during the induction phase in dark-adapted leaves. In both cases, we observe a multiphase kinetics of the light-induced changes in P_{700}^+ concentration and fluorescence parameters Φ_{PSII} and q_P, which reveal relatively fast (~15–30 s) and relatively slow (~2 min) phases. Analysis of experimental data on P_{700}^+ induction in photosynthetic systems of oxygenic type (Maxwell and Biggins 1976, 1977; Tikhonov et al. 1981; Ryzhikov and Tikhonov 1988; Vishnyakova et al. 2000; Joliot and Joliot 2005, 2006; Laisk et al. 2005, 2007, 2010; Hald et al. 2008b; Bulychev and Vredenberg 2010; Bulychev et al. 2010; Bulychev 2011; Kuvykin et al. 2011), as well as the results of computer simulation (Tikhonov and Vershubskii 2014) allowed the attribution of different phases of P_{700} photooxidation to feedback regulation events in chloroplasts. The interplay of different regulatory events during the induction of P_{700}^+ is considered below.

Light-induced activation of the CBC

The light-induced activation of the CBC reactions is one of the crucial factors of electron transport regulation in intact chloroplasts. Illumination of chloroplasts activates key enzymes of the reductive pentose phosphate cycle prior to achieve high rates of CO_2 assimilation (Buchanan 1980, 1991; Edwards and Walker 1983; Mott and Berry 1986; Woodrow and Berry 1988; Andersson 2008; Foyer et al. 2012). The light-induced activation of the CBC is a striking example of pH- and redox-dependent regulation of metabolic processes in photosynthetic organisms, which have significant impact on the overall rate of linear (non-cyclic) electron transport. In the initial stage of induction, when the CBC is inactive, the outflow of electron from PSI to $NADP^+$ is limited due to the over-reduction of the NADP pool and slow consumption of NADPH. Acceleration of NADPH consumption in the active CBC causes efficient regeneration of $NADP^+$, thereby facilitating LEF.

Figure 8 illustrates how the light-induced activation of the CBC stimulates photooxidation of P_{700} in *Hibiscus rosa-sinensis* leaves (Ryzhikov and Tikhonov 1988). Far-red light (FRL, $\lambda_{max} = 707$ nm), which is absorbed preferentially by PSI, induces relatively fast oxidation of P_{700}. Change-over the FRL to white light (WL), exciting efficiently both PSI and PSII, induces rapid reduction of P_{700}^+ due to electrons donated by PSII via the intersystem ETC. The drop of P_{700}^+ is followed then by relatively slow re-oxidation of P_{700} (Fig. 8, phase *A*-*B*–*C*). Reoxidation of P_{700} during the action of WL is caused mainly by gradual activation of the CBC, which releases the impediment to electron outflow from PSI to $NADP^+$. Actually, injection of methylviologen (MV) into the leaf significantly accelerates reoxidation of P_{700} (Maxwell and Biggins 1976, 1977; Ryzhikov and Tikhonov 1988). MV acts as efficient mediator of electron transfer from PSI to O_2, to allow for rapid outflow of electrons from PSI, thereby promoting photooxidation of P_{700}. The overshoot in the time-course of P_{700} transients observed in MV-treated leaves can be explained, at least partly, by pH_{in}-dependent regulation of the intersystem electron transport (Tikhonov et al. 1981). The acidification of the thylakoid lumen can cause deceleration of electron flow from PSII to PSI due to (i) attenuation of PSII activity caused by NPQ and (ii) slowing down of PQH_2 oxidation by the b_6f complex. In the next section, these mechanisms of electron transport control are described in more details.

Consider how the regulatory processes in the intersystem segment of ETC might contribute to P_{700}^+ induction in control (untreated) leaves (Fig. 8, phase *A*–*B*–*C*). The rate of the intersystem electron transport can be inferred from the kinetics of post-illumination reduction of P_{700}^+ after abruptly cutting the light off (Rumberg and Siggel 1969; Tikhonov et al. 1981, 1984; Harbinson and Hedley 1989). Figure 9 shows how the half-time ($t_{1/2}$) of post-illumination reduction of P_{700}^+ depends on illumination time in

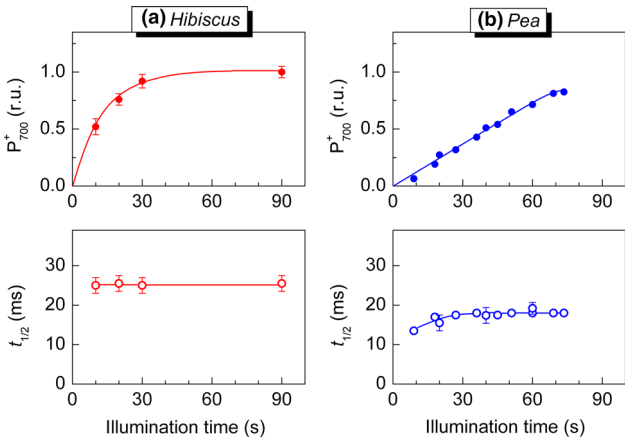

Fig. 9 Time-courses of P_{700} photooxidation (top boxes) and half-times (t_{12}) of P^+_{700} post-illumination decay (bottom boxes) as measured in dark-adapted *Hibiscus rosa-sinensis* leaves (panel **a**, modified after Ryzhikov and Tikhonov 1988) and in dark-adapted pea leaves (panel **b**, experimental data are taken from Fig. 9 of the study by Harbinson and Hedley 1993)

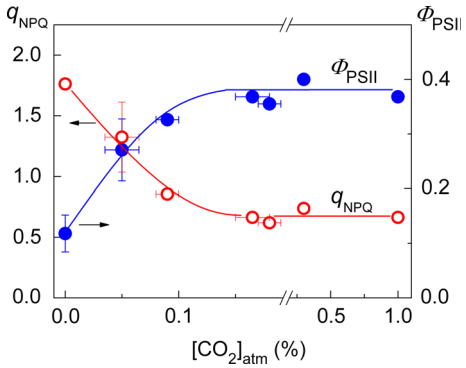

Fig. 10 Steady-state values of the fluorescence parameters q_{NPQ} and Φ_{PSII} versus the concentration of CO_2 in the air surrounding the leaf. Effects of atmospheric CO_2 on the fluorescence parameters Φ_{PSII} and q_{NPQ} were measured in *Hibiscus rosa-sinensis* leaves (Modified Fig. 10 from Kuvykin et al. 2011)

Hibiscus rosa-sinensis (Ryzhikov and Tikhonov 1988) and pea (Harbinson and Hedley 1993) leaves. In both species, kinetic parameter $t_{1/2}$ does not change after ~10–20 s of illumination, although a level of P^+_{700} continues to increase. This indicates that the rate of electron flow to P^+_{700} does not change during the induction phase (at least in the interval from 10 to 90 s), whereas the concentration of oxidized centers P^+_{700} markedly increases (Fig. 9). This suggests that the acceleration of electron outflow from PSI to the CBC is one of the main factors that determine the *A–B–C* phase of P^+_{700} induction, while the rate of the intersystem electron flow remains almost the same already after 10-s illumination of leaves.

Activation of the CBC is associated with the feedback redox- and ion-dependent regulation of electron transport. Redox-dependent changes in activities of the CBC enzymes are mediated through the thioredoxin/thioredoxin reductase system (Holmgren 1985; He et al. 2000; Serrato et al. 2013). In the initial period of P^+_{700} induction in dark-adapted leaves, the acceptor side of PSI becomes easily over-reduced due to limited consumption of NADPH in the CBC. At the excess of reductants, electron flow will be diverted from reduced Fd to alternative routes of electron transport (Fig. 1), including (i) cyclic electron flow around PSI (CEF1, pathways 1–5), (ii) electron flow to O_2 (the Mehler reaction, pathway 6, and PTOX-mediated reduction of O_2, pathway 7) which is involved into the water–water cycle (WWC), and (iii) electron flow to thioredoxin (Tr) via the thioredoxin reductase (TrR) (pathway 8). Reduced Tr activates other photosynthetic enzymes, including those of the CBC (Michelet et al. 2013) and the ATP synthase (Bakker-Grunwald and van Dam 1974; He et al. 2000; Bald et al. 2001; Mills 2004; Feniouk and Yoshida 2008).

An important role in activation of the CBC belongs to the light-induced alkalization of stroma (Werdan et al. 1975; Flügge et al. 1980; Gardemann et al. 1986; Mott and Berry 1986). The stromal pH_{out} increases with illumination of chloroplasts ($pH^{dark}_{out} \approx 7.0-7.2 \rightarrow pH^{light}_{out} \approx 7.8-8.0$; Heldt et al. 1973; Robinson 1985) due to proton consumption upon the $NADP^+$ reduction and protonation of reduced plastoquinone ($PQ^= + 2e^- + 2H^+_{out} \rightarrow PQH_2$). Protonation of PQ occurs at the acceptor side of PSII and at the Q_i-center of the cytochrome b_6f complex (Fig. 1). Alkalization of stroma would stimulate activity of Rubisco, because its affinity for CO_2 increases with the rise of pH_{out} (Werdan et al. 1975; Flügge et al. 1980; Edwards and Walker 1983; Mott and Berry 1986). The light-induced increase in pH_{out} is also accompanied by elevation of stromal concentration of Mg^{2+}, which occurs in response to proton consumption in stroma and other ion-exchange processes—translocation of Cl^- and Ca^{2+} ions across the thylakoid membrane (see for references Barber 1976; Buchanan 1980; Edwards and Walker 1983). An increase in stromal Mg^{2+} may serve as a factor of activation of Rubisco, which is the key enzyme of the CBC. Thus, the redox- and ion-dependent activations of the CBC enzymes would stimulate the consumptions of NADPH and ATP and, as a consequence, to accelerate the outflow of electrons from PSI to the CBC.

Enrichment of atmosphere with CO_2 also stimulates the CBC turnover, promoting the consumption of NADPH and releasing limitations to LEF on the acceptor side of PSI (see, e.g., Foyer et al. 1990, 2012; Paul and Foyer 2001; Sage et al. 2002). Stimulating effect of CO_2 on LEF is illustrated in Fig. 10 (Kuvykin et al. 2011), which shows

that electron flow through PSII increases with the rise in atmospheric CO_2.

pH-Dependent regulation of the intersystem electron transport

The light-induced generation of the transthylakoid pH difference (ΔpH) is another important factor of electron transport control that can manifest itself during the induction phase. In chloroplasts, the ΔpH value is a major component of *pmf* (Johnson and Ruban 2014), although under certain conditions one cannot ignore the contribution of the transmembrane difference of electric potentials (Δψ) (Cruz et al. 2001, 2005a, b; Kramer et al. 2003). The light-induced acidification of the lumen ($pH_{in}\downarrow$) reveals itself as one of the key factors of down-regulation of electron transport in chloroplasts (see for review Kramer et al. 1999, 2003; Tikhonov 2012, 2013, 2014). There are two basic mechanisms of pH_{in}-dependent regulation of the intersystem electron flow. One of them is realized at the level of PQH_2 oxidation by the b_6f complex. Another mechanism is associated with attenuation of PSII activity due to NPQ (Demmig-Adams 1990; Muller et al. 2001; Murata et al. 2007; Li et al. 2009; Solovchenko 2010; Takahashi and Badger 2011; Demmig-Adams et al. 2012; Horton 2012; Jahns and Holzwarth 2012; Ruban et al. 2012; Tikkanen et al. 2012; Zaks et al. 2013).

"Photosynthetic control" of electron transport in chloroplasts

The mechanism of pH_{in}-dependent regulation of the intersystem electron flow is at the basis of the so-called photosynthetic control phenomenon (see for review Foyer et al. 1990, 1992, 2012; Harbinson et al. 1990; Kramer et al. 1999; Tikhonov 2012, 2013, 2014). According to Foyer et al. (2012), the term "photosynthetic control" describes the short- and long-term mechanisms that regulate reactions in the photosynthetic ETC so that the rates of ATP and NADPH production are coordinated with their utilization in metabolism. Traditionally, the term "photosynthetic control" implies that the rate of electron transport depends on the chloroplast phosphorylation potential, $P = [ATP]/([ADP] \times [P_i])$ (Kraayenhof 1969; Kobayasi et al. 1979a), which value determines the mode of the ATP synthase operation. This notion stems from the classic work by Chance and Williams (1956) who coined terminology for classification of mitochondrial metabolic states.

Rigorously speaking, the very idea that phosphorylation potential "controls" the rate of photosynthetic electron transport tacitly implies that steady-state values of *P* and *pmf* are close to thermodynamic equilibrium. It should be noted, however, that *P* and *pmf* may be out of equilibrium. Kobayasi et al. (1979b) reported that the phosphorylation potential in intact chloroplasts was not in equilibrium with the chloroplast *pmf*. Therefore, they concluded that the intrathylakoid pH_{in}, not the phosphorylation potential, was a factor in the control of the rate of electron transport in intact chloroplasts. In any event, however, the *P* and pH_{in} values may be interconnected. The proton-driven ATP synthase is a reversible molecular machine (Boyer 1993, 1997; Stock et al. 2000; Feniouk and Yoshida 2008; von Ballmoos et al. 2009; Nakanishi-Matsui et al. 2010; Romanovsky and Tikhonov 2010) capable of functioning in two regimes, either as the ATP synthase ($H^+_{in} \rightarrow H^+_{out}$, ATP formation) or as the ATPase (ATP hydrolysis, $H^+_{out} \rightarrow H^+_{in}$). At the surplus of ADP and P_i (metabolic state 3), efficient ATP synthesis is accompanied by stoichiometric drain of protons from the thylakoid lumen to stroma ($nH^+_{in} \rightarrow nH^+_{out}, n = 5$), which precludes too strong acidification of the lumen ($pH_{in} \geq 6$–6.2). In this case, chloroplasts retain a high rate of electron transport, which is comparable with rapid electron flow in uncoupled chloroplasts where $pH_{in} \approx pH_{out}$ (state 5). More significant acidification of the thylakoid lumen occurs in the state of "photosynthetic control" (metabolic state 4) when the overall flux of protons through CF_0–CF_1 tends to zero. After acute shortage of ATP synthesis substrates (ADP and/or P_i) and accumulation of surplus amounts of ATP, the overall production of ATP becomes negligible. Actually, when chloroplasts reach state 4, both reactions catalyzed by the ATP synthases (the ATP formation and the ATP hydrolysis) are balanced, and, therefore, the overall production of ATP and the proton flux through the CF_1–CF_0 complexes are virtually zero. This provides more significant acidification of the lumen in state 4 ($pH_{in} < 6$) compared with state 3 ($pH_{in} \geq 6$–6.2) (Tikhonov et al. 1981, 2008; Tikhonov and Timoshin 1985; Nishio and Whitmarsh 1993; Kramer et al. 1999; Trubitsin and Tikhonov 2003).

Figure 11 illustrates how the intersystem electron transport decelerates upon the state 3 → state 4 transition in isolated bean thylakoids (class B chloroplasts). During illumination of control chloroplasts (without added ADP), electron flow to P^+_{700} decreases, rapidly attaining a steady-state level. The slowing down of electron flow occurs due to back-pressure from the protons accumulated inside the thylakoids on the reaction of PQH_2 oxidation by the b_6f complex. In the presence of added ADP, the rate of electron flow remains high during the first 20 s of illumination, because the proton drain through CF_0–CF_1 prevents chloroplasts from too strong acidification of the lumen ($pH_{in} \approx 6.0$–6.2 at $pH_{out} = 7.8$–8.0). It should be noted, however, that ΔpH generated in state 3 (ΔpH ≈ 1.6–2.0)

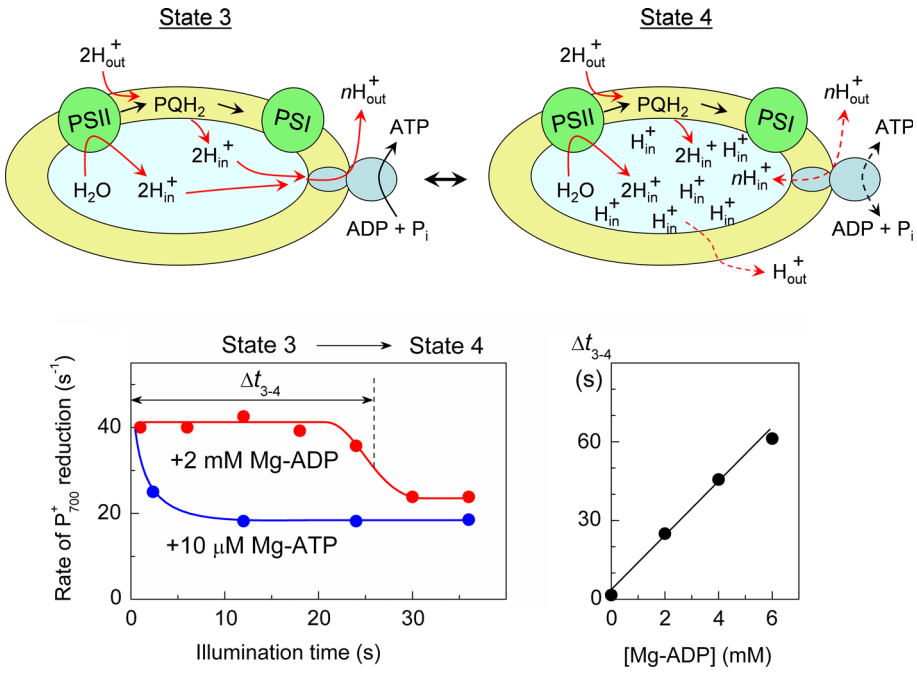

Fig. 11 The time-courses of the rate of electron flow from PSII to P_{700}^{+} in isolated bean chloroplasts with different additions of Mg-ATP and Mg-ADP and the dependence of the metabolic state 3 duration (parameter Δt_{3-4}) on the initial concentration of Mg-ADP in the chloroplast suspension (after Tikhonov 2012)

is quite sufficient to sustain intensive ATP synthesis (see for review Tikhonov 2012, 2013). Owing to a moderate acidification of the lumen, electron flow in metabolic state 3 remains high. Then, after the conversion of most ADP molecules to ATP, pH_{in} decreases (state 3 → state 4 transition), and electron transport decelerates. The duration of state 3 (parameter Δt_{3-4}) increases with the ADP concentration added to chloroplasts (Fig. 11). Class B chloroplasts have $pH_{in} \sim 5.2–5.7$ at $pH_{out} = 7.8–8.0$ ($\Delta pH \sim 2.1–2.6$) in state 4 (Tikhonov 2012, 2013).

How acidic becomes the lumen in illuminated chloroplasts in situ? Direct measurements of ΔpH in chloroplasts in situ with conventional pH-indicators face insuperable obstacles (see for review Tikhonov 2012). In this case, however, pH_{in} can be derived from the kinetics of post-illumination reduction of P_{700}^{+} which depends on pH_{in} (Rumberg and Siggel 1969; Tikhonov et al. 1981, 1984; Harbinson and Hedley 1989). Kinetic data suggest a moderate acidification of the thylakoid lumen in the leaves of different plant species, $pH_{in} \approx 6–6.2$ (Ryzhikov and Tikhonov 1988; Kramer et al. 1999). Schönknecht et al. (1995) evaluated ΔpH from the data on the CO_2 uptake and chlorophyll fluorescence in spinach leaves. Under conditions that allow high rates of photosynthesis (0.2 % CO_2; 1 % O_2), they found that $\Delta pH \sim 1.8–2.6$, increasing with light intensity. Taking into account that stromal pH is close to pH 8.0 (Heldt et al. 1973; Robinson 1985), these estimates suggest the intrathylakoid $pH_{in} \sim 5.4–6.2$.

pH-Dependent modulation of PSII activity

A rather strong acidification of the lumen under the light stress conditions, where light input exceeds the capacity of both photosystems, could be harmful to photosynthetic apparatus. Along with the pH_{in}-dependent control of PQH_2 oxidation, there is another mechanism which prevents the over-acidification of the lumen and protects chloroplasts against photodamage. The light-induced acidification of the lumen ($pH_{in} \leq 5.5–6.2$) induces the attenuation of PSII activity due to dissipation of excess energy in LHCII. A decrease in pH_{in} causes protonation of lumen facing acidic residues of "pH_{in}-sensors," initiating events that enhance NPQ. In vascular plants, there are two basic mechanisms of NPQ induction: (*i*) activation of the xanthophyll cycle reactions resulting in Vx conversion to Zx (Demmig-Adams 1990; Müller et al. 2001; Li et al. 2009; Demmig-Adams et al. 2012; Jahns and Holzwarth 2012; Murata et al. 2012; Ruban et al. 2012), and (*ii*) structural changes in granal thylakoids induced by the PsbS protein caused by protonation of its glutamic acid residues in the lumen-exposed loops (Li et al. 2000, 2002, 2004; Kiss et al. 2008; Kereïche et al. 2010; Ikeuchi et al. 2014). These events induce conformational changes in LHCII, creating a quenching channel for dissipation of excess energy to heat. Thus, generation of NPQ prevents from too strong acidification of the lumen, thereby decreasing the probability of damage to the photosynthetic apparatus under the solar stress conditions (Allakhverdiev and Murata 2004; Murata et al. 2007,

2012). Both mechanisms of pH_{in}-dependent regulation of electron transport, the light-induced deceleration of PQH_2 oxidation and NPQ generation, are characterized by close pK values (~6.0–6.5) (Tikhonov et al. 1981, 1984; Hope et al. 1994; Pfündel and Dilley 1993; Pfündel et al. 1994), providing similar contribution to down-regulation of the intersystem electron flow in chloroplasts.

NPQ development at different CO_2 concentrations and light intensities

Development of NPQ depends on various factors that have an impact on photosynthetic electron transport. NPQ is regulated by the needs of photosynthetic apparatus. For instance, depletion of CO_2 induces a marked rise in NPQ (Fig. 10) caused by lessening the operation of CF_0–CF_1 at low consumption of ATP in the CBC. The latter will reduce the proton drain from the lumen to stroma, which would manifest itself as an enhancement of NPQ: $CO_2\downarrow \rightarrow$ CBC$\downarrow \rightarrow$ ATP$\uparrow \rightarrow$ CF_0–$CF_1\downarrow \rightarrow \Delta pH\uparrow \rightarrow$ NPQ$\uparrow$. Otherwise, acceleration of LEF with the increase in CO_2 concentration (≥0.15 %), which is well documented as a rise in Φ_{PSII}, is accompanied by essential decrease in NPQ (Fig. 10), indicating a decrease in ΔpH. Stimulation of LEF releases NPQ due to acceleration of the proton drain through CF_0–CF_1 as a result of intensive consumption of ATP in the CBC: $CO_2\uparrow \rightarrow$ CBC$\uparrow \rightarrow$ ADP$\uparrow \rightarrow$ CF_0–$CF_1\uparrow \rightarrow \Delta pH\downarrow \rightarrow$ NPQ$\downarrow$.

Variation in light intensity is another factor that has influence on NPQ. At low light (LL), which is insufficient to saturate photosynthesis, generation of NPQ is insignificant, as a rule. At high light (HL), which intensity exceeds potential capacities of PSII and PSI, generation of NPQ may be significantly higher than at LL. In order to illustrate this point, let us compare induction of NPQ in dark-adapted *Tradescantia* leaves by actinic light of different intensities (Samoilova et al. 2011; Ptushenko et al. 2013). Figure 12 shows the time-courses of NPQ induction during illumination of *T. sillamontana* leaves with the HL (800 μmol photons m^{-2} s^{-1}) or LL (30 μmol photons m^{-2} s^{-1}) (Ptushenko et al. 2013). HL illumination causes the two-phase growth of NPQ, which is peculiar to dark-adapted *Arabidopsis* leaves (Jahns and Holzwarth 2012). The rapid phase qE ($t_{1/2}$ ~ 30 s) relates to the energy-dependent component of NPQ induced by ΔpH generation. The slow phase qZ ($t_{1/2}$ ~5–10 min) can be attributed to de-epoxidation of Vx and other processes (e.g., state transitions and/or photoinhibition of PSII). At LL illumination, when a potential hazard to photosynthetic apparatus is insignificant, NPQ generation is significantly smaller than at HL, and the slow phase of NPQ generation is absent.

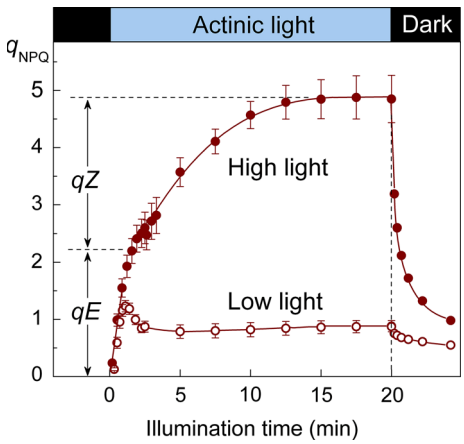

Fig. 12 Time-courses of NPQ development in dark-adapted *T. sillamontana* leaves exposed to high (800 μmol photons m^{-2} s^{-1}) or low (30 μmol photons m^{-2} s^{-1}) actinic light (modified Fig. 3 from Ptushenko et al. 2013)

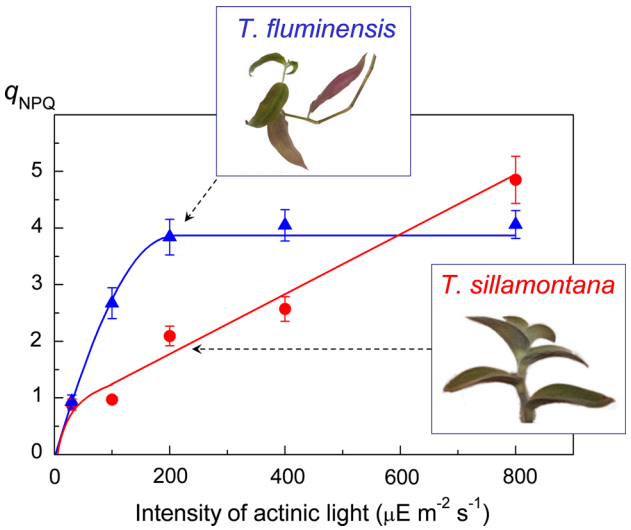

Fig. 13 Effects of actinic light intensity on steady-state values of NPQ developed after 20-min illumination of *T. fluminensis* and *T. sillamontana* leaves (after Samoilova et al. (2011), Fig. 1, and Ptushenko et al. (2013), Fig. 4)

Figure 13 compares the light curves of steady-state NPQ generated in *Tradescantia* species of different ecological groups, *T. fluminensis* (shade-tolerant species) and *T. sillamontana* (light-resistant species). These species show markedly different responses to light. In *T. fluminensis* leaves, NPQ attains saturation at lower light (≈ 200 μmol photons m^{-2} s^{-1}) than in *T. sillamontana*. Another difference between the species concerns their "memory" about exposition to light.[1] In *T. fluminensis*, the post-illumination relaxation of NPQ occurs markedly slower than

[1] Here and below, the term "memory" is used colloquially to characterize the rate of post-illumination relaxation of NPQ: a slow decay of NPQ corresponds to long "memory" of photosynthetic apparatus about plant illumination.

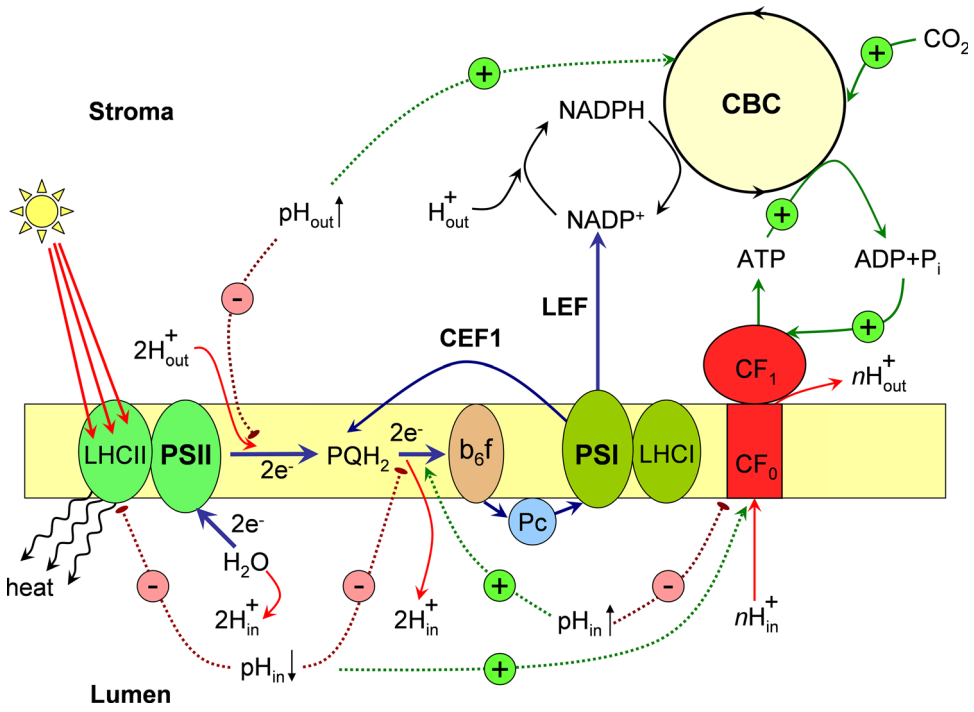

Fig. 14 A scheme of positive (+) and negative (−) feedbacks that determine pH-dependent regulation of electron transport between PSII and PSI

in *T. sillamontana* (Ptushenko et al. 2013). The rapid component of NPQ decay, related to ΔpH dissipation in the dark, is characterized by characteristic time $\tau_E \approx 50$–60 s in *T. fluminensis* and $\tau_E \approx 30$ s in *T. sillamontana*. The slow component of NPQ decay (which amplitude increases with the actinic light intensity) equals to $\tau_Z \approx 14$–28 min in *T. fluminensis* and $\tau_Z \approx 10$–18 min in *T. sillamontana*. These results can be interpreted in context of interspecies differences between the plants of the same genus which belong to contrast ecological groups. Shade-tolerant plant *T. fluminensis* has soft hairless leaves; it colonizes an extraordinary wide range of light environment, ranging from completely exposed to deeply shaded areas. Being adapted to grow at shady places, this plant should be ready to meet fluctuations of environment light. High sensitivity of shade-tolerant species to low and moderate light, as well their relatively long "memory" about illumination, can smooth negative effects of environment light fluctuations. Fleshy leaves of light-resistant species (*T. sillamontana*, the inhabitant of semi-desert regions of Mexico and Peru) reveal high NPQ only at HL illumination (Fig. 13). Due to adaptive selection, this plant acquired capacity for growth at strong light, demonstrating a high potential to withstand HL-induced photoinhibitory damage and the ability to survive at significant variations of light intensity.

Summing up, the light-induced changes in pH_{in} play a major role in regulation of the intersystem electron flow. Acidification of the lumen decelerates the oxidation of PQH_2 by the b_6f complex and attenuates the PSII activity due to losses of light energy in LHCII as heat. Figure 14 shows a general scheme of positive and negative feedbacks that regulate electron transport in chloroplasts. Dashed lines marked by the sign "+" indicate positive feedbacks, which stimulate the CBC and ATP synthesis. The sign "−" denotes pH-dependent negative feedbacks that cause deceleration of electron transport due to kinetic limitations at the level of the b_6f complex and attenuate PSII activity due to energy dissipation in LHCII. Note that the effect of the lumen acidification on PQH_2 oxidation is comparable with the pH-dependent decrease in PSII activity due to NPQ. Both mechanisms of down-regulation of the intersystem electron transport prevent the excessive acidification of the thylakoid lumen, the over-excitation of PSII, and the over-reduction of electron carriers on the acceptor side of PSI.

Alternative pathways of electron transport

The feedback regulation of electron transport on the acceptor side of PSI is associated with redistribution of electron fluxes, which provides optimal functioning of photosynthetic apparatus and its efficient interaction with other metabolic systems. There are diverse pathways of electron transport, where electrons donated by PSI are delivered to different metabolic channels. Apart from the mainstream electron flow to the CBC ("linear" electron flow to $NADP^+$, LEF), the electron flux may be diverted to cyclic routes around PSI (CEF1). According to a widely spread point of view, CEF1 helps to sustain required ratio between ATP and NADPH (ATP/NADPH = 3/2) used for

CO_2 assimilation in the CBC (see for review Bendall and Manasse 1995; Finazzi et al. 1999; Allen 2003; Johnson 2005, 2011; Breyton et al. 2006; Joliot and Joliot 2005, 2006; Shikanai 2007; Alric 2010). LEF alone cannot provide this ratio. In the meantime, CEF1 driven by PSI alone (without the reduction of $NADP^+$) would contribute to generation of *pmf*, providing generation of "extra" ATP molecules. Thus, the splitting of electron flow into LEF and CEF1 will maintain the stoichiometry ATP/NADPH = 3/2 required for CO_2 fixation in the CBC.

Additional channel of electron outflow from PSI is associated with pseudocyclic electron transport (so-called "water–water" cycle: $H_2O \rightarrow$ PSII $\rightarrow$ PSI $\rightarrow O_2 \rightarrow H_2O$), which includes the Mehler reaction of O_2 reduction by PSI (Mehler 1951). The Mehler reaction leads to the production of superoxide radicals, $O_2^{\bullet-}$, converted to H_2O_2 and O_2 ($2O_2^{\bullet-} + 2H^+ \rightarrow H_2O_2 + O_2$). In chloroplasts, the H_2O_2 molecules produced via the dismutation of $O_2^{\bullet-}$ radicals (catalyzed by the thylakoid membrane-attached superoxide dismutase) are reduced to water by ascorbate-specific peroxidase (Asada 1999). In the leaves of higher plants, up to 30 % of electrons donated by PSI may be drained to O_2 (Asada 1999; Miyake and Yokota 2000; Kuvykin et al. 2008). In marine organisms, this process can reach $\approx$40–50 % of overall electron flow driven by PSII (see for review Eberhard et al. 2008). Similarly to CEF1, the water–water cycle (WWC) has a photoprotective role due to scavenging reactive oxygen species and dissipation of excess energy, and may help in balancing the proper levels of ATP and reductants (see for review Asada 1999; Ort and Baker 2002; Miyake 2010).

Cyclic electron transport around photosystem I

Several routes of cyclic electron transfer around PSI (Fig. 1, pathways 1–5) have been considered in the literature. Electrons from PSI may be recycled to PQ from either NADPH or reduced Fd (Fd^-). The "long" route of CEF1 involves the chloroplast NAD(P)H-dehydrogenase (NDH). The "short" pathway relates to electron transfer from Fd^- to PQ molecule bound to the b_6f complex without the participation of NDH. Recent genetic and biochemical studies clarified the physiological role of CEF1 and helped to elucidate the participation of different proteins in electron transport around PSI (see for review Shikanai 2007).

The NDH-dependent route of CEF1 is assumed to pass through the NDH complex, which returns electrons from NADPH (and/or NADH) to the intersystem ETC. Genetic and biochemical data give unequivocal evidence for a participation of the chloroplast NDH in CEF1 (Endo et al. 1998; Shikanai et al. 1998; Joet et al. 2001). The NDH complexes involved into CEF1 have been found in the chloroplast genome (Ohyama et al. 1986; Shinozaki et al. 1986) and also in cyanobacteria (Ogawa and Mi 2007; Battchikova et al. 2011). The participation of NDH in CEF1 is supported by its location in the stromal lamellae close to PSI (Sazanov et al. 1996) and the finding of elevated levels of NDH proteins in the bundle sheath cells of C_4 plants which lack PSII and which are characterized by high levels of CEF1 (Kubicki et al. 1996). Biochemical data indicate that the NDH and PSI complexes can form a supercomplex in higher plants (Peng et al. 2008, 2009) and cyanobacteria (Kubota et al. 2010). NADPH can donate electrons to the intersystem ETC in the presence of Fd in ruptured chloroplasts isolated from higher plants (Gins et al. 1982; Munekage et al. 2002, 2004; Okegawa et al. 2008). This suggests that NADPH might serve as electron donor to NDH (Fig. 1, pathway 1) and participate in CEF1 along the following chain of electron transfer reactions: PSI $\rightarrow$ Fd $\rightarrow$ FNR $\rightarrow$ NADPH $\rightarrow$ NDH $\rightarrow$ PQ $\rightarrow$ b_6f. Nevertheless, the nature of the electron donor to NDH is still a matter of debate. According to an alternative model suggested by Johnson (2011), reduced Fd can also feed electrons to the PQ pool in the stromal lamellae via the NDH-dependent route (Fig. 1, pathway 2). There are indications that chloroplast NDH can accept electrons directly from reduced Fd (Yamamoto et al. 2011; Leister and Shikanai 2013). Genetic and biochemical data demonstrate that NDH also mediates electron transfer from stromal reductants to PQ (Burrows et al. 1998).

Most of CEF1 models suggest that "short" pathways are mediated via the cytochrome b_6f complex (Fig. 1, pathways 3–5). In the Q_i-center on the stromal side of the b_6f complex, PQ molecule reduces to PQH_2 accepting two electrons from different chains. One electron is donated by the high-potential heme b_6^H, which belongs to the low-potential branch of the b_6f complex (see for review Cramer et al. 2006, 2011; Crofts et al. 2013; Tikhonov 2014). The second electron may come to the Q_i-center from the acceptor side of PSI. It has been suggested that an atypical heme c_i located on the stromal side of the b_6f complex could be directly involved into PQ reduction (Kurisu et al. 2003; Stroebel et al. 2003; Alric et al. 2005; Cramer et al. 2006, 2011; Hasan et al. 2013). Nevertheless, the nature of the immediate electron donor to PQ molecule at the Q_i-site (FQR, FNR, or Fd?) is still under debate (Alric et al. 2005; Shikanai 2007; DalCorso et al. 2008; Iwai et al. 2010a; Johnson 2011).

One of the ways to return electron from reduced Fd to PQ implies the participation of elusive ferredoxin-plastoquinone-reductase (FQR, Bendall and Manasse 1995): PSI $\rightarrow$ Fd $\rightarrow$ FQR $\rightarrow$ PQ $\rightarrow$ b_6f (Fig. 1, pathway 3). Analysis of knockout mutants of *Arabidopsis* has demonstrated that the products of two genes, *PGR5* (proton gradient regulation) and *PGRL1* (*PGR5*–like protein 1), are necessary for induction of NPQ and protection of PSII from

photoinhibition. These proteins may be involved into Fd-dependent CEF1 in eukaryotes (Tagawa et al. 1963; Munekage et al. 2002, 2004, 2008; Shikanai 2007; Iwai et al. 2010b; Suorsa et al. 2012; Hertle et al. 2013). Plants deficient in one of these proteins show disturbed CEF1. This suggests that *PGR5* and *PGRL1* may be considered as the components of FQR. Hertle et al. (2013) have demonstrated that *PGRL1* is the redox regulated protein, which accepts electrons from Fd^-. The *PGR5* protein is required for electron transfer from Fd^- to *PGRL1*. *PGR5*–dependent regulation of electron transport and generation of ΔpH is crucial for protection of PSI against photodamage induced by rapidly changing light intensities (Munekage et al. 2008; Suorsa et al. 2012). Another model of Fd-dependent CEF1 assumes that electron returns from PSI to PQ at the Q_i-center of the b_6f complex directly from either Fd^- or/and FNR (Fig. 1, pathways 4 and 5, respectively). The formation of a supercomplex FNR-b_6f (see for review Benz et al. 2010) might facilitate electron flow along the pathway 5.

Taken together, CEF1 is important for fine-tuning the energy and redox balance in chloroplasts, despite the fact that the relative contribution of CEF1 to energy supply may be insignificant as compared to LEF. In higher plants, the contribution of CEF1 to steady-state photosynthetic electron transport comprises about 10 % of the overall electron flow driven by PSI and PSII (Eberhard et al. 2008). More significant efficiency of CEF1 (up to 50 % of the overall electron flow) has been reported for *C. reinhardtii* (Forti et al. 2003). However, even a relatively small contribution of CEF1 to generation of ΔpH may be enough to supplement ATP formation, providing thus the well-balanced ATP/NADPH ratio in chloroplasts. Comparing the contributions of LEF and PGR5-dependent CEF1 to total ΔpH generation for induction of NPQ, Sato et al. (2014) predict that the contribution of CEF1 varies in the range 60–80 %. Also, there are experimental data indicating that CEF1 is essential for effective responses to significant fluctuations of light intensity, avoiding the risk of photodamage to chloroplasts (Suorsa et al. 2012; Kono and Terashima 2014; Kono et al. 2014).

Molecular oxygen as electron sink: water–water cycle

Photosynthetic electron transport in plants strongly depends on the presence of O_2 in surrounding air (Sage et al. 2002; Foyer et al. 2012). Interacting with the chloroplast ETC, O_2 can influence the redox status of ETC. For instance, deficit of O_2 could result in accumulation of reduced electron carriers both on the acceptor side of PSI and between PSII and PSI. It is well-known fact (Mehler 1951; Ort and Baker 2002) that O_2 can serve as an alternative electron sink in PSI (Fig. 1, pathway 6). When O_2 rather than $NADP^+$ acts as a terminal electron acceptor in PSI, it is eventually reduced to water during operation of pseudocyclic WWC: $H_2O \rightarrow PSII \rightarrow PSI \rightarrow O_2 \rightarrow H_2O$ (Asada 1999; Heber 2002). Accepting electrons from PSI, O_2 will retard the over-reduction of the acceptor side of PSI, thereby promoting photooxidation of P_{700}. In de-aerated leaves and cyanobacteria, the over-reduction of PSI acceptors would hamper in P_{700} photooxidation (see, e.g., Trubitsin et al. 2003, 2005; Kuvykin et al. 2008, 2011).

Another way of O_2 participation in photosynthetic electron transport may be associated with the operation of the plastoquinol terminal oxidase (PTOX), which provides electron sink from PQH_2 to O_2 (Fig. 1, pathway 7) when the PQ pool is over-reduced (see for review Peltier and Cournac 2002; McDonald et al. 2011). PTOX plays a major role in the control of the stromal redox poise. Also, it is thought that PTOX is capable of modulating the balance between LEF and CEF1 during the CBC deactivation phase that follows a light to dark transition (Trouillard et al. 2012).

Figures 15, 16, and 17 illustrate the effects of O_2 on photosynthetic electron transport in oxygenic photosynthesis. As one can see, depletion of O_2 induces a decrease in P_{700}^+ concentration observed in de-aerated leaves (Fig. 15). Diminished concentrations of P_{700}^+ in de-aerated samples can be explained, in principle, by two factors: (i) an impediment to electron outflow from PSI, and (ii) efficient feeding of P_{700}^+ with electrons donated by over-reduced PQH_2 pool. Aeration promotes the outflow of electrons to O_2, precluding the over-reduction of photosynthetic ETC and stimulating photooxidation of P_{700}. In the leaves of C_3 plants, the O_2 effects manifest themselves clearly at ambient and low concentrations of CO_2 in air (≤0.06–0.08 %, Kuvykin et al. 2011).

Cyanobacteria provide us with another pictorial sample of aeration/de-aeration effects in oxygenic photosynthesis. Cyanobacteria contain both the photosynthetic and

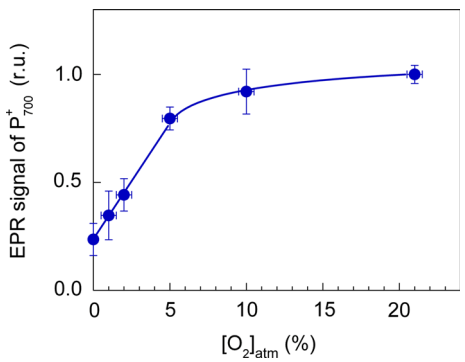

Fig. 15 Effect of atmospheric oxygen on the steady-state level of P_{700}^+ in *Hibiscus rosa-sinensis* leaves illuminated with white light. Modified Fig. 5 from Kuvykin et al. (2011)

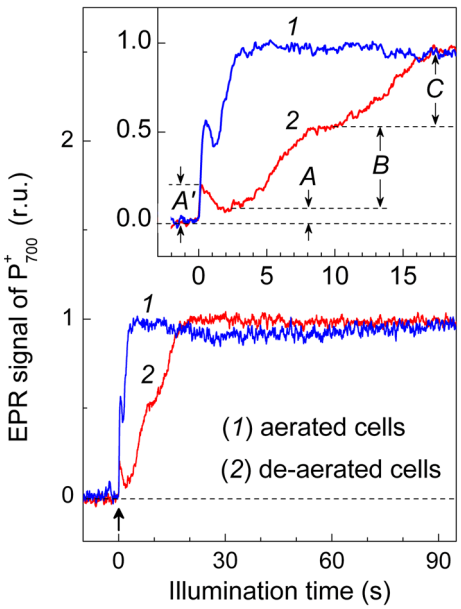

Fig. 16 Kinetics of P_{700} photooxidation in aerated (*1*) and de-aerated (*2*) suspensions of dark-adapted (10 min) cells of cyanobactrium *Synechocystis* sp. PCC 6803. Cells were incubated either in a gas-impermeable quartz cuvette (*1*) or inside a gas-permeable plastic tube (*2*). Deprivation of molecular oxygen in the suspension of cells placed inside the quartz cuvette occurs due to O_2 consumption by the terminal oxidases in the thylakoid and cytoplasm membranes of cyanobacterial cells. Inside the gas-impermeable cuvette suspension was equilibrated with atmospheric O_2. Modified Fig. 2 from Trubitsin et al. (2005)

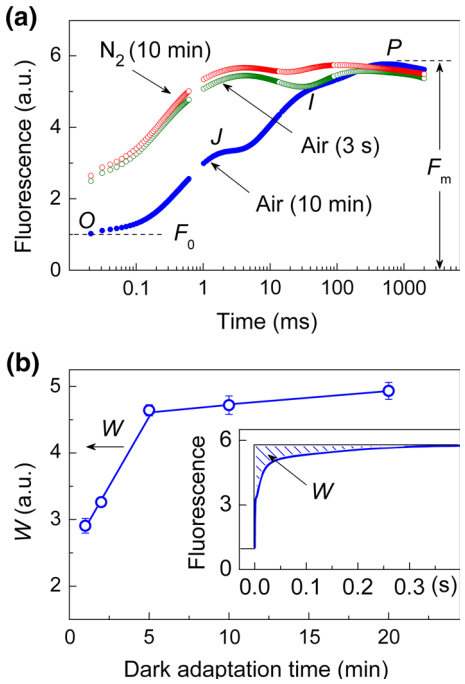

Fig. 17 Fast transients (*O–J–I–P* curve) of the Chl *a* fluorescence in *Hibiscus rosa-sinensis* leaves adapted to darkness in air (for 10 min or 3 s) or in N_2 (for 10 min) atmosphere (**a**), and the plot of the fluorescence parameter *W* versus the dark-adaptation time for samples exposed to air (**b**). Modified Fig. 7 from Kuvykin et al. (2011)

respiratory ETCs in the same membranes (Schmetterer 1994; Mullineaux 2014). Dark-incubation of cyanobacteria, when photosynthetic ETC is inactive, may cause significant deprivation of O_2 in the cell suspension due to respiration (Trubitsin et al. 2003, 2005). Oxygen-dependent interrelations between photosynthetic and respiratory ETC manifest themselves in P^+_{700} induction kinetics. Figure 16 shows time-courses of P_{700} photooxidation in dark-adapted cyanobacterial cells (*Synechocystis* sp. PCC 6803). Aerated samples (Fig. 16, curve 1) show that the initial phase of P_{700} oxidation is followed by a certain drop of P^+_{700} and subsequent rise of P^+_{700} toward a steady-state level. Deprivation of oxygen during pre-incubation of cells in gas-impermeable quartz cuvette causes significant retardation of P^+_{700} induction (Fig. 16, curve 2). In this case, marked photooxidation of P_{700} is observed only after significant delay, when the light-induced regeneration of O_2 begins to stimulate the efflux of electrons from cyanobacterial ETC to O_2 (curve 2, phases *B* and *C*). Simultaneous measurements of the P^+_{700} signal and O_2 production has demonstrated that there is a strong correlation between P_{700} oxidation and O_2 accumulation in the suspension of cyanobacterial cells (Trubitsin et al. 2003, 2005). Note that in the initial stage of P^+_{700} induction, when pseudocyclic WWC is diminished, electrons from PSI can be redirected, at least partly, to CEF1. Thus, cyanobacteria might retain their photosynthetic activity under the oxygen deficiency conditions.

Effects of oxygen depletion can also be explained in terms of redistribution of electron fluxes between photosynthetic and respiratory chains. In cyanobacteria, both chains share common electron carriers, including the PQ pool and the b_6f complex. In aerated cells, the terminal oxidases cyt *bd* and cyt aa_3 compete with P^+_{700} for electrons from the PQH_2 pool ($PQH_2 \rightarrow$ cyt *bd* $\rightarrow O_2$) and cyt c_6 (cyt $c_6 \rightarrow$ cyt $aa_3 \rightarrow O_2$), thereby decreasing the electron flux to P^+_{700} ($PQH_2 \rightarrow$ cyt $b_6f \rightarrow$ cyt c_6/Pc $\rightarrow P^+_{700}$). Therefore, in de-aerated cells the intersystem pool of electron carriers will be more reduced than under aerobic conditions, thus leading to a decrease in the level of P^+_{700}.

Effects of dark adaptation on the redox state of PSII

The ability of O_2 to accept electrons from different segments of ETC also manifests itself in effect of dark adaptation on Chl *a* fluorescence in leaves. Information on the redox state of electron carriers on the acceptor side of PSII can be easily derived from the *O–J–I–P* test widely used in photosynthesis research (Lazar 2003; Tóth et al. 2007;

Kalaji et al. 2014). Figure 17a compares typical *O-J-I–P* patterns measured in dark-adapted leaves exposed to air (control) or to N_2 atmosphere. In dark-adapted control (aerated) samples, we observe typical multiphasic induction curve characterized by the ratio $F_v/F_m \approx 0.83$, where $F_v = F_m - F_0$ is a variable component and F_m is a maximal level of fluorescence, which value is typical of dark-adapted leaves of C_3 plants (Bjorkman and Demmig 1987; Johnson et al. 1993). Repeated illumination of samples after a short dark interval ($t_{ad} = 3$ s) yields the ratio $F_v/F_m \approx 0.56$. In this case, the initial level of fluorescence (F_0) is markedly higher than after a rather long adaptation to the dark ($t_{ad} \sim 10$ min). This is because the short-term adaptation to the dark (a few seconds) may be insufficient for efficient oxidation of the PQH_2 pool in pre-illuminated leaves. It is likely that PQH_2 oxidation in the dark occurs through slowly operating PTOX complexes (Peltier and Cournac 2002; McDonald et al. 2011). Actually, adaptation of pre-illuminated leaves to the dark under anaerobic conditions does not lead to oxidation of electron carriers on the acceptor side of PSII, when the major part of electron carriers localized between PSII and PSI (mainly the PQ pool) remain reduced even after sufficiently long adaptation to the dark. This conclusion is supported by the *O–J–I–P* test (Fig. 17a), which shows that 10-min adaptation of pre-illuminated leaves in N_2 atmosphere does not lead to relaxation of photosynthetic apparatus as observed in aerated samples. As a measure for oxidized pool of electron carriers between PSII and PSI, one can use parameter *W* (the area over the *O–J–I–P* curve normalized to F_m value, Fig. 17b, see also Lazar 1999; Strasser et al. 2004). In *Hibiscus rosa-sinensis* leaves, dark adaptation for 5 min ensures almost complete reoxidation of the PQ pool (Karavaev and Kukushkin 1975; Kuvykin et al. 2011).

Kinetic mechanism of light-induced redistribution of electron fluxes

Distribution of electrons between alternative pathways (CEF1 and WWC) should optimize the operation of photosynthetic apparatus. Well-balanced electron fluxes and optimal ATP/NADPH output ratio may be crucial for normal operation of chloroplasts. For instance, too high CEF1 activity could result in depletion of ADP, while too little will result in over-reduction of the chloroplast ETC (Kramer et al. 2004). The mechanisms of fine tuning alternative electron transport pathways may be realized by variations of stromal ADP or ATP levels (Joliot and Joliot 2006), the redox state of NADPH/$NADP^+$ (Munekage et al. 2004), the availability of PSI electron acceptors (Breyton et al. 2006), and/or by means of redox modulation of proteins involved in CEF1 (Michelet et al. 2013). In general, distribution of electron fluxes between alternative pathways (LEF, CEF1, and WWC) is controlled by competition for reducing equivalents; the redox status of the chloroplast ETC will determine partitioning the electron fluxes. Competition for reduced Fd seems to be the major control point for branching electron flows at the acceptor side of PSI (Ivanov et al. 1998; Hald et al. 2008a, b). Plants with over-expressed Fd reveal increased capacity for CEF1 (Yamamoto et al. 2006). Under particular conditions, peculiar to initial stages of photosynthesis induction in dark-adapted chloroplasts, the contribution of CEF1 may be significant and even prevail over LEF (Joliot and Joliot 2005; Laisk et al. 2005, 2007, 2010), supporting generation of ΔpH and ATP synthesis during the induction phase. With the CBC activation, CEF1 would decrease and steady-state LEF will prevail over CEF1. The over-reduction of the acceptor side of PSI would also stimulate the reduction of thioredoxin, thus activating the thioredoxin-dependent enzymes (Motohashi et al. 2006; Dietz and Pfannschmidt 2011; Serrato et al. 2013).

Dynamics of electron flux partitioning during the induction period has been simulated within the framework of our kinetic model described earlier (Vershubskii et al. 2011; Tikhonov and Vershubskii 2014). Figure 18 compares the patterns of light-induced changes in the overall electron flux through PSII (J_{PSII}) and partial electron fluxes on the acceptor side of PSI (J_{LEF}, J_{CEF1}, and J_{WWC}) simulated for chloroplasts. The model predicts that during the induction period the electron flux from PSII to the PQ pool (J_{PSII}) changes nonmonotonically: after the initial jump, J_{PSII} gradually decays owing to pH_{in}-dependent mechanisms of down-regulation of the intersystem electron transport. In the same time, there occurs a substantial redistribution of electron fluxes on the acceptor side of PSI. In the initial stage, electron flux to $NADP^+$ (J_{LEF}) is small, while CEF1 (J_{CEF1}) displays a rather strong flux. Relatively low initial flux J_{LEF} is explained by hindrance to LEF caused by the over-reduction of the NADP pool at low activity of the CBC in dark-adapted chloroplasts. During the induction phase, there is also noticeable contribution of the electron flux from PSI to O_2 (J_{WWC}). Results of numerical experiments based on our kinetic model (Fig. 18) are consistent with the current notion that CEF1 and WWC provide bypasses to avoid the over-reduction on the acceptor side of PSI. After a certain lag, when the CBC becomes activated, the relative contribution of the linear electron flux J_{LEF} increases, whereas alternative fluxes gradually decline (Fig. 18).

Light-induced remodeling of photosynthetic apparatus

Structural changes in thylakoids have significant impact on photosynthetic performance of chloroplasts. Lateral migration of multisubunit protein complexes, light-induced

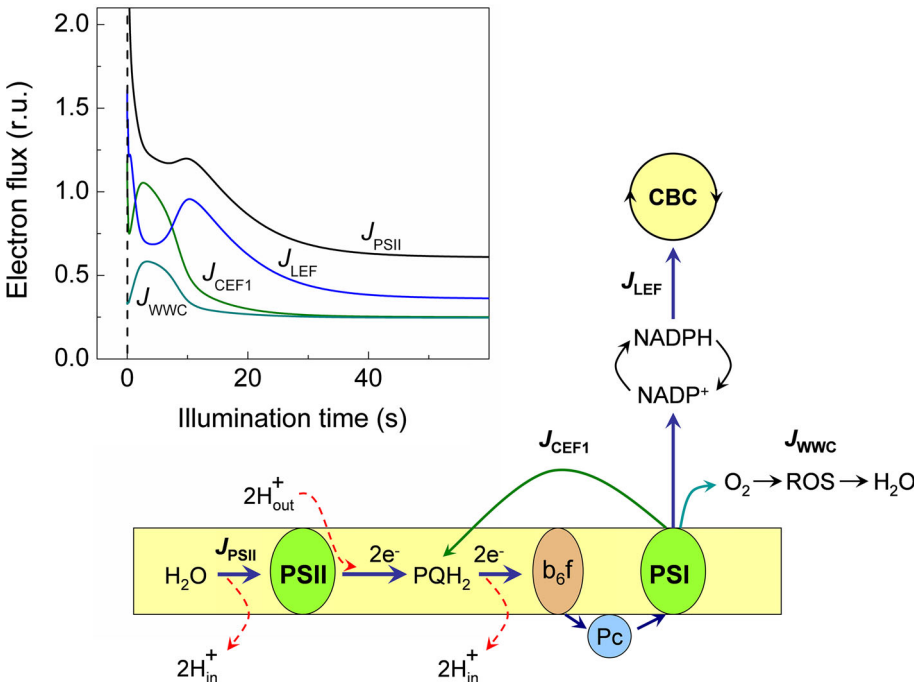

Fig. 18 Computer modeling of the light-induced redistribution of electron fluxes (J_{PSII}, J_{LEF}, J_{CEF1}, and J_{WWC}) during illumination of dark-adapted chloroplasts (*top*, adopted from Tikhonov and Vershubskii 2014)

swelling/shrinkage, and stacking/unstacking of thylakoids may be directly involved in induction events and regulation of energy balance and electron transport between PSII and PSI. In a broad sense, all these structural changes may be termed, in general, as the light-induced remodeling of the chloroplast lamellar system. Below, I briefly outline some of architectural switches that may have impact on the ETC performance in chloroplasts.

State transitions

It is common knowledge that over-reduction of the PQ pool serves as a signal about the "traffic jam" on the electron transport way between PSII and PSI (see for review Allen 1992, Haldrup et al. 2001; Wollman 2001; Finazzi et al. 2002; Murata 2009; Lemeille and Rochaix 2010; Minagawa 2011; Tikkanen et al. 2011; Tikkanen and Aro 2012, 2014; Rochaix 2014). The light-induced reduction of the PQ pool induces activation of a protein kinase that catalyzes phosphorylation of LHCII, leading to redistribution of light energy in favor of PSI at expense of PSII (State I → State II transition). This process is triggered by PQH_2 binding to the Q_o-site of the b_6f complex (Vener et al. 1997; Zito et al. 1999; Finazzi et al. 2001). According to conventional point of view, phosphorylated LHCII complexes dissociate from the PSII-LHCII supercomplex localized preferentially in granal thylakoids and migrate to associate with PSI, thereby increasing the light-harvesting capacity of PSI. There are biochemical (Zhang and Scheller 2004) and electron microscopy (Kouril et al. 2005) data in favor of relocation of phosphorylated LHCII from PSII to PSI and formation of the PSI-LHCI-LHCII supercomplex. In plant chloroplasts, there are three forms of LHCII trimers, which differ from each other in respect of their association with PSII ("strong," "moderate," and "loose" binding to PSII, Galka et al. 2012; Hofmann 2012). It is likely that it the loosely bound form of phosphorylated LHCII that dissociates from PSII and migrates to PSI (Iwai et al. 2010a). Novel insights into LHCII phosphorylation and state transitions have been considered in recent studies (Tikkanen et al. 2011; Tikkanen and Aro 2012, 2014).

State transitions are reversible processes controlled by the ETC redox state. The over-reduction of the intersystem ETC induces State I → State II transition and concomitant gain of PSI activity, providing the reoxidation of the PQH_2 pool. In the dark and at LL illumination, the light-harvesting capacity of PSII recovers (State II → State I transition) due to dephosphorylation of LHCII by chloroplast phosphatases. This allows dephosphorylated LHCII to return back to PSII-enriched grana domains and to gain light absorption by PSII.

A molecular device, which controls state transitions, is inherent to the b_6f complex and specific protein subunits bound to it. PQH_2 binding to the Q_o-site induces activation of the LHCII kinase (Vener et al. 1997; Zito et al. 1999; Finazzi et al. 2001). Putative molecular mechanism of the kinase activation caused by PQH_2-induced structural changes in the core of the b_6f complex has been suggested in (Hasan et al. 2013). However, the exact mechanisms by

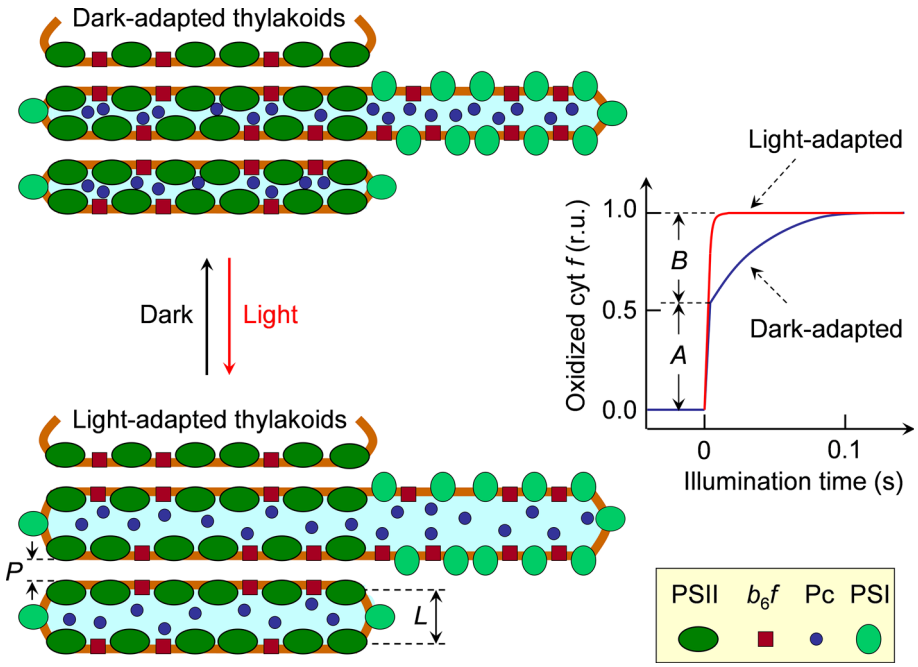

Fig. 19 A sketch of chloroplast remodeling associated with the light-induced swelling of thylakoids. Parameters *L* and *P* denote the surface-to-surface width of the lumen (*L*) and the distance between the neighboring thylakoids of grana (*P*), respectively. Right panel demonstrates schematically the time-courses of cytochrome *f* oxidation upon illumination of dark-adapted and light-adapted chloroplasts according to kinetic data presented in Fig. 4 of the work by Kirchhoff et al. (2011)

which PQH_2 activates the LHCII kinase and triggers a chain of events leading to state transitions are yet unknown. In *C. reinhardtii*, the transduction of a signal for operation of the LHCII kinase is mediated through the protein kinase Stt7 (Lemeille et al. 2009), which has an ortholog STN7 in land plants (Bellafiore et al. 2005). There are good reasons to believe that the Stt7/STN7 kinase is the redox-regulated enzyme which redox state may be regulated by electron carriers beyond PSI (e.g., ferredoxin and thioredoxin) through the membrane-bound thiol oxidoreductases (Lennartz et al. 2001; Motohashi and Hisabori 2006; Dietz and Pfannschmidt 2011; Serrato et al. 2013). A signal transmitted to the LHCII kinase from the over-reduced pool of electron carriers on the acceptor side of PSI is thought to promote dephosphorylation of the kinase and eventually induces an increase in the light-harvesting capacity of PSII.

Taken together, the two modes of the reversible control of the LHCII kinase activity provide a proper balance of energy partitioning between PSI and PSII: (i) activation of the LHCII kinase induced by PQH_2 binding to the Q_o-site, (ii) deactivation of the enzyme upon the over-reduction of the acceptor side of PSI. This allows avoiding a "traffic jam" in the intersystem ETC. Reversible relocation of LHCII provides a short-term response (in the minute range) to variations of light intensity, providing the optimal balance of absorbed light energy between PSI and PSII to be sustained upon fluctuations of environment light. Capacity of photosynthetic apparatus for energy redistribution upon state transitions depends on the species of photosynthetic organism. In unicellular green algae *C. reinhardtii*, a gain in energy absorption by PSI in State II is significantly higher (about 80 %, Delosme et al. 1996) than in plants (about 15–20 %, Allen 1992).

Light-induced remodeling of thylakoids

Let us now consider examples of architectural changes in chloroplasts, associated with swelling/shrinkage of thylakoids that can influence on photosynthetic electron transport. Lateral mobility of Pc within the lumen of granal thylakoids may be restricted due to steric constraints to Pc diffusion. The face-to-face distance between the inner surfaces of opposite thylakoid membranes is relatively short, $L \leq$ 10–20 nm (Dekker and Boekema 2005; Kirchhoff 2014). According to Kirchhoff et al. (2011), diffusion of Pc within the shrunken thylakoids of grana may be hindered due to over-crowding the granal thylakoids with PSII complexes. Densely packed PSII complexes, with voluminous WOC domains protruding to the lumen, would reserve small room for Pc molecules. Pc is the 10.5-kDa protein of 4 × 3 × 3 nm sizes (Guss et al. 1986). Therefore, in order to allow for efficient percolation of Pc inside the granal lumen, the gap between the opposite WOCs should not be smaller than 3 nm. Obstructed diffusion of Pc would restrict Pc-mediated electron transfer from the fraction of b_6f complexes localized in granal membranes to PSI complexes localized in stromal membranes. In the meantime, Pc molecules rapidly diffusing in spacious volume of the stromal lumen will provide fast communication between the b_6f and PSI complexes located in stromal domains of thylakoid membranes.

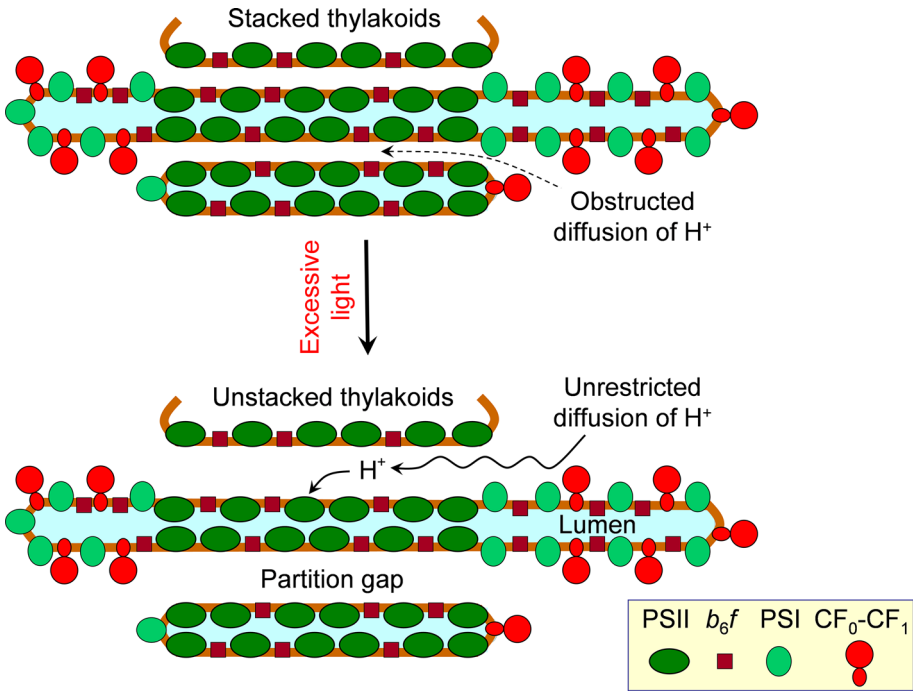

Fig. 20 A sketch of chloroplast remodeling associated with the light-induced destacking of thylakoids

A restricted diffusion of Pc within granal thylakoid lumen has been supported by Kirchhoff et al. (2011), who observed biphasic oxidation of cytochrome *f* in chloroplasts of dark-adapted *Arabidopsis thaliana* leaves. A rapid phase of cytochrome *f* photooxidation induced by saturating light pulse (phase *A* of the kinetic curve, as illustrated in Fig. 19) has been attributed to fast electron transfer from the b_6f complexes located in stromal thylakoids to oxidized PSI centers ($b_6f \rightarrow \text{Pc} \rightarrow \text{P}^{+}_{700}$). The presence of slow phase of cytochrome *f* photooxidation (phase *B*) suggests that electron transfer from the b_6f complexes located in granal thylakoids to PSI is impeded due to obstructed diffusion of Pc within the thylakoids of shrunken grana. The intrathylakoid gap expands upon the light-induced swelling of thylakoids. Kirchhoff et al. (2011) found the twofold increase in the width of the thylakoid lumen in light-adapted *Arabidopsis* chloroplasts. In this case, they observed rapid monophasic kinetics of cytochrome *f* oxidation (Fig. 19). This result can be easily explained, because the light-induced swelling of thylakoids provides additional volume for Pc diffusion within the granal lumen, thereby facilitating a rapid long-range lateral diffusion of Pc from all b_6f complexes to PSI. Characteristic times of architectural switches associated with the thylakoid swelling/shrinkage events lie in the range between tens of seconds and a few minutes (Tychinsky et al. 2004; Tychinsky and Tikhonov 2010; Kirchhoff et al. 2011; Nagy et al. 2013).

As noted above, the b_6f complexes located in granal membranes are thought to be involved solely into LEF, whereas the other b_6f complexes may also participate in CEF1 (Fig. 2). In this connection, it is interesting to note that at least two isoforms of Fd (FdI and FdII) have been found in plant leaves. These isoforms show different activities in linear and cyclic electron transport (Gins et al. 1982; Kurisu et al. 2005; Blanco et al. 2013; Hanke and Mulo 2013). The structural differences between FdI and FdII concern the FNR-binding sites (Kurisu et al. 2005). This results in their functional differences that may influence on the partitioning of electrons between LEF and CEF1. Blanko et al. (2013) have demonstrated that the over-expression of the minor isoform of Fd promotes CEF1 and decreases LEF. Also, along with the lateral migration of phosphorylated LHCII toward PSI (State I → State II transition), there occurs the relocation of a certain fraction of the b_6f complexes toward PSI (Vallon et al. 1991), which is assumed to induce the formation of a large supercomplex (PSI–LHCI–LHCII–b_6f–FNR–PGRL1) engaged in CEF1 (Iwai et al. 2010b).

Reduced mobility of protons within the thylakoid lumen and in the narrow partition between appressed thylakoids of grana may also restrict proton-coupled reactions of electron transport in chloroplasts. Direct measurement of the lateral profiles of pH in the intrathylakoid lumen and along the narrow partition between adjacent thylakoids of grana is almost insuperable experimental task; therefore, we turned to computer simulations of these profiles (Vershubskii et al. 2011; Tikhonov and Vershubskii 2014). Our numerical experiments predict a rather strong alkalization of the interthylakoid gap caused by the proton consumption upon PQ reduction by PSII ($\text{pH}_{\text{gap}} \geq 9.5$–10). This is

because restricted diffusion of protons through the narrow interthylakoid gap ($H^+_{stroma} \rightarrow H^+_{gap}$) cannot equilibrate pH values in the partition and stroma. Significant alkalization of the gap would hinder to protonation of double-reduced form of plastoquinone ($PQ^{2-}_B + 2H^+_{gap} \rightarrow PQ_BH_2$), thereby slowing down the PSII turnover. Unstacking of granal thylakoids should release the constraints to protons diffusion (Fig. 20), stimulating the turnover of PSII. The ion-induced and light-induced stacking and unstacking of thylakoids are well-documented events in chloroplasts (Barber 1979; Kirchhoff et al. 2000; Khatoon et al. 2009; Yamamoto et al. 2013, 2014). Under natural conditions, reversible unstacking of thylakoids could occur within minutes. Results of our numerical experiments (Tikhonov and Vershubskii 2014) predict that unstacking of granal thylakoids might induce a twofold acceleration of PSII turnover due to accelerated diffusion of protons in the partition between granal thylakoids. This prediction is in a good agreement with experimental data concerning the influence of osmotic conditions on electron transport in chloroplasts. Kirchhoff et al. (2000) reported that in stacked thylakoids a large fraction of PQ molecules remained oxidized after the light pulse (about 40 % and 50 % in tobacco and spinach thylakoids, respectively). Otherwise, in destacked chloroplasts nearly all PQ molecules became rapidly reduced by a 120 ms light pulse. The authors explained their result by inability of PQ to migrate rapidly throughout the membrane. Results of our calculations suggest alternative explanation of the stacking/destacking experiment data: in stacked thylakoids the light-induced formation of PQH_2 may be limited by slow diffusion of protons throughout the narrow interthylakoid gap; unstacking of granal thylakoids stimulates diffusion of protons, thereby promoting the light-induced formation of PQH_2.

Concluding points

Short-term mechanisms of electron transport control provide flexibility of photosynthetic apparatus in response to changes in the environmental conditions, which is achieved by cooperation of the following feedbacks operating in different timescales (within tens of minutes).

1. pH-Dependent regulation of photosynthetic electron transport governed by the light-induced acidification of the thylakoid lumen and alkalization of stroma.
2. The light-induced activation of the CBC, which stimulates the outflow of electrons from PSI.
3. Redistribution of electron fluxes between alternative pathways of electron transport (noncyclic/cyclic/pseudocyclic electron transport).
4. Optimal partitioning of light quanta between PSI and PSII.
5. Light-induced remodeling of photosynthetic apparatus and chloroplast architecture.

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