

The hidden function of photosynthesis: a sensing system for environmental conditions that regulates plant acclimation responses

Thomas Pfannschmidt · Chunhong Yang

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Abstract Plants convert light energy from the sun into chemical energy by photosynthesis. Since they are sessile, they have to deal with a wide range of conditions in their immediate environment. Many abiotic and biotic parameters exhibit considerable fluctuations which can have detrimental effects especially on the efficiency of photosynthetic light harvesting. During evolution, plants, therefore, evolved a number of acclimation processes which help them to adapt photosynthesis to such environmental changes. This includes protective mechanisms such as excess energy dissipation and processes supporting energy redistribution, e.g. state transitions or photosystem stoichiometry adjustment. Intriguingly, all these responses are triggered by photosynthesis itself via the interplay of its light reaction and the Calvin–Benson cycle with the residing environmental condition. Thus, besides its primary function in harnessing and converting light energy, photosynthesis acts as a sensing system for environmental changes that controls molecular acclimation responses which adapt the photosynthetic function to the environmental change. Important signalling parameters directly or indirectly affected by the environment

are the pH gradient across the thylakoid membrane and the redox states of components of the photosynthetic electron transport chain and/or electron end acceptors coupled to it. Recent advances demonstrate that these signals control post-translational modifications of the photosynthetic protein complexes and also affect plastid and nuclear gene expression machineries as well as metabolic pathways providing a regulatory framework for an integrated response of the plant to the environment at all cellular levels.

Keywords Photosynthesis · Environmental sensing · Light-harvesting chlorophyll *a/b* complexes · Redox regulation · Metabolism · Acclimation responses

Abbreviations

Chl	Chlorophyll
CP	Chloroplast
CSK	Chloroplast sensor kinase
Cyt <i>b₆f</i>	Cytochrome <i>b₆f</i> complex
FTR	Ferredoxin–thioredoxin oxidoreductase
LHC	Light-harvesting systems
LHCIIb	The major light-harvesting chlorophyll <i>a/b</i> complexes of photosystem II
LTR	Long-term response
PAR	Photosynthetic active radiation
PEP	Plastid encoded RNA polymerase
P-	Phosphorylated LHCIIb
LHCIIb	
PQ	Plastoquinone
PS	Photosystem
PTK	Plastid transcription kinase
RC	Reaction centre
RubisCO	Ribulose-1,5-bisphosphate carboxylase/oxygenase
SIG1	Sigma factor 1

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T. Pfannschmidt (✉)
Junior Research Group “Plant acclimation to environmental changes: Protein analysis by MS”, Department of Plant Physiology, Institute of General Botany and Plant Physiology, Friedrich-Schiller-University Jena, Dornburger Str. 159, 07743 Jena, Germany
e-mail: thomas.pfannschmidt@uni-jena.de

C. Yang (✉)
Key Laboratory of Photobiology, Institute of Botany, Chinese Academy of Sciences, Beijing, China
e-mail: yangch@ibcas.ac.cn

Introduction

Photosynthesis is the process by which photoautotrophic organisms harvest the light energy of the sun and use it to generate ATP and NADPH + H⁺. These molecules are subsequently used in metabolism as sources of energy or reducing power in order to drive growth, development and reproduction. Heterotrophic organisms depend on the sun as energy source as well since they obtain their energy by feeding on other organisms generating complex food chains which always are based on photosynthetic organisms. Therefore, photosynthesis fuels all life on Earth with energy with the very rare exception of chemolithoautotrophic organisms. Without photosynthesis, no complex ecosystems and higher life forms including men would exist (Blankenship 2002; Buchanan et al. 2002).

In eukaryotic photoautotrophs, photosynthesis takes place in specialised cell organelles, the chloroplasts (CP). These emerged from an endosymbiotic event about two billion years ago in which a photoautotrophic cyanobacteria-like ancestor was incorporated by a heterotrophic eukaryotic cell. In a subsequent and long-ongoing evolutionary process, this ancestor lost its autonomy by transfer of most of its genes to the nucleus of the host and was established as a permanent part of the cell. Therefore, the photosynthetic apparatus of nowadays' eukaryotes and free-living prokaryotes still exhibits many similarities (Martin et al. 2002; Stoebe and Maier 2002; Herrmann et al. 2003).

In general, photosynthesis consists of two functional parts: a light reaction in which the sun light is harvested and used to generate ATP and NADPH and a subsequent dark reaction (basically the Calvin–Benson cycle) in which these molecules are used to synthesise energy-rich carbohydrates from CO₂ and H₂O. The light reaction is performed by the photosynthetic apparatus which consists of photosystem (PS) II, the cytochrome *b₆f* complex (Cyt *b₆f*) and PSI. These are multi-protein complexes which bind a high number of co-factors including chlorophylls for light-harvesting and redox-active co-factors for electron transfer reactions. The three complexes are electrochemically connected in series by the mobile electron carrier plastoquinone (connecting PSII and Cyt *b₆f*) and plastocyanin (connecting Cyt *b₆f* and PSI). All together these elements generate a sunlight-driven electron transport chain which transfers electrons and protons from H₂O to NADP⁺. This chain is located in a membrane system of high three-dimensional complexity, the thylakoids. These separate the inner part of chloroplasts into the lumen inside of the thylakoids and the stroma outside of it. During the light-driven electron transport protons are enriched in the lumen generating a strong lumen acidification and a pH gradient towards the stroma. It generates the proton motif force which is used by the chloroplast ATPase to synthesise ATP. NADPH + H⁺ and ATP are subsequently

used by the enzymes of the Calvin–Benson cycle to fix CO₂ and generate triose-phosphates which are finally exported from the chloroplast (Aro and Andersson 2001).

Besides its principal function as energy converter, however, photosynthesis possesses a second less obvious function which is of highest importance for the plant: it serves as a sensing system for environmental changes. The light reaction is mainly based on processes which require light but are largely temperature-independent. In contrast, the dark reaction is based on enzymatic reactions which are light-independent but very temperature- and substrate-sensitive. For optimal function, these two parts of photosynthesis need to be highly balanced. Since plants are sessile life forms, they are fully exposed to their surrounding environment and any fluctuation in it. Therefore, any abiotic and biotic factor influencing either the light harvesting or the enzymatic efficiency of the Calvin–Benson cycle can cause a disturbance of the balance between light and dark reactions which subsequently results in a change of photosynthetic efficiency. Thus, changes in the photosynthetic rate mirror environmental changes and hence photosynthesis serves as a sensing system for it (Pfannschmidt 2003). It has been calculated that an improvement of photosynthesis could largely contribute to optimisation of yield and biomass production in crop plants (Murchie et al. 2009; Zhu et al. 2010; Parry et al. 2011). A deeper understanding on how photosynthetic efficiency is maintained under highly variable conditions, therefore, is of valuable interest in this context. This review highlights the idea of a sensing function of photosynthesis by focussing on selected examples and recent advances in photosynthetic acclimation.

The role of photosynthetic efficiency in triggering acclimation to environmental cues

The property of photosynthesis that its functional efficiency serves as an environmental sensing system for the plant has been already recognised by Arnon who called it “the grand design of photosynthesis” (Arnon 1982; Anderson et al. 1995). This sensing function triggers a number of acclimation responses which effectively adapt the photosynthetic process to changing environmental cues and, by this means, help to maintain photosynthesis as efficient as possible. In the last decade, photosynthetic acclimation became a highly dynamic research field not only because of the identification of many novel regulatory components using genetic approaches via *Arabidopsis* mutants, but also because the general interest in maintaining and improving crop yield despite the global change problem increased very much (Horton et al. 2001; Pfannschmidt 2003; Kanervo et al. 2005; Walters 2005; Long et al. 2006; Eberhard et al. 2008; Zhu et al. 2010). Many environmental cues affect

either the light or the dark reaction and have been extensively studied under laboratory conditions. However, in natural environments, most of these factors occur in parallel and have combinatorial effects on photosynthesis which create influences on electron transport being very different from laboratory set-ups. Thus, a future challenge will be a careful integration of data obtained under controlled laboratory conditions and results from experiments under free-fluctuating field conditions (Mishra et al. 2012). Most prominent factors affecting photosynthesis in the field are light, temperature and water availability and these will be discussed in more detail below to illustrate the sensor function of photosynthesis.

Changes in illumination intensity are the most obvious parameter affecting photosynthesis as it directly concerns the light-harvesting capacity of the photosynthetic apparatus (Fig. 1). The intensity of incident irradiation can change within seconds to minutes because of leaf movement or clouding or within hours, days or months due to daily and seasonal changes. Sudden increases in light intensity can cause an over-excitation of the photosynthetic apparatus which subsequently can lead to photodamage and oxidative stress. Therefore, a number of photoprotective mechanisms exist which buffer or even prevent such over-excitation or repair the damage (Baena-Gonzalez and Aro 2002; Holt et al. 2004; Takahashi and Badger 2011).

In dense plant populations such as crop fields, forests or meadows, strong light gradients exist which are caused by shading from the top most layer of leaves which absorb a large proportion of the photosynthetic active radiation (PAR). These light gradients include a large decrease in light intensity and a concomitant strong shift in the light quality towards the far-red wavelengths spectrum. This weak far-red-enriched light environment is the typical illumination for ~60–80 % of all leaves in dense plant populations. It causes an imbalance in excitation energy distribution between the two photosystems. Short-term and long-term acclimation responses exist which re-direct parts of the excitation energy towards the rate-limiting photosystem in order to counteract the excitation imbalance (Terashima and Hikosaka 1995; Dietzel et al. 2008).

Light also controls the activity of the dark reaction (Fig. 1). With the onset of day light in the morning, the photosynthetic electron transport chain becomes activated and the final electron acceptors are reduced. A ferredoxin–thioredoxin oxidoreductase (FTR) now can transfer reducing power from ferredoxin to thioredoxins (a large family of small, redox-active, soluble regulatory proteins) which in turn reduce redox-active dithiol groups within the regulatory γ -subunit of the ATPase and a number of Calvin–Benson cycle enzymes (e.g. the FBPase) as well as entry enzymes of other important metabolic pathways in the chloroplast. This reduction activates the enzymes and initiates ATP production and the dark reaction representing the prototypes of

light-dependent regulation of metabolic processes which include many more biosynthetic pathways besides reductive carbohydrate metabolism, e.g. lipid biosynthesis (Buchanan and Balmer 2005; Schürmann and Buchanan 2008; Dietz and Pfannschmidt 2011).

Changes in temperature have a less obvious but equally strong impact on photosynthesis as light (Fig. 1). A decrease in temperature typical for moderate climate regions (for instance from 20 to 10°C) will reduce the activity of the Calvin–Benson cycle enzymes by 50 %. This usually results in a lower demand for the reduction equivalent NADPH_2 and causes its subsequent accumulation. This in turn can lead to a limitation of the electron end acceptor of the electron transport chain NADP^+ which might result in an over-reduction of the chain and a final over-excitation of the photosynthetic apparatus. Thus, in a low temperature environment, a moderate or low light intensity can result in the same over-excitation of photosynthesis as high light intensities in a warm environment. The excitation pressure on the photosynthetic apparatus therefore is always a consequence of the combined impact of both light and temperature. Most dramatic examples for such a situation are the evergreen forests of the northern hemisphere which have to withstand bright sunny days at temperatures far below 0°C. Plants in such ecosystems therefore developed a number of mechanisms which help the plant to acclimate photosynthesis to such temperature decreases and its combinatorial effects with light (Huner et al. 1998; Ensminger et al. 2006).

A warm climate in principle appears to have positive effects on photosynthesis and plant growth as long as enough water is present as visible from the strong plant growth in the tropics. However, high temperatures can become detrimental if water is limited (Fig. 1). Under such conditions, drought and/or salinity stress forces the plants to close the stomata which might limit the CO_2 uptake. Lack or limitation of this essential substrate of RubisCO can slow down or even stop the Calvin–Benson cycle and can result in a depletion of NADP^+ quite similar to a temperature decrease. Again this can cause over-reduction and over-excitation of the photosynthetic apparatus. Many plants from arid and semi-arid areas therefore developed adaptive strategies in morphology and acclimation mechanisms to deal with this special situation including the C4 or CAM syndromes (Chaves et al. 2009; Ghannoum 2009; Lawlor and Tezara 2009).

It must be noted that the scenarios depicted above are to some degree simplified in order to demonstrate the principle that the photosynthetic function can integrate several environmental parameters. Other endogenous processes like photorespiration or cyclic electron transport around PSI can also contribute to this. Furthermore, many other environmental factors exist beside the examples mentioned above which all have detrimental effects on photosynthesis. This includes (1) nutrient deprivation such as iron, copper or

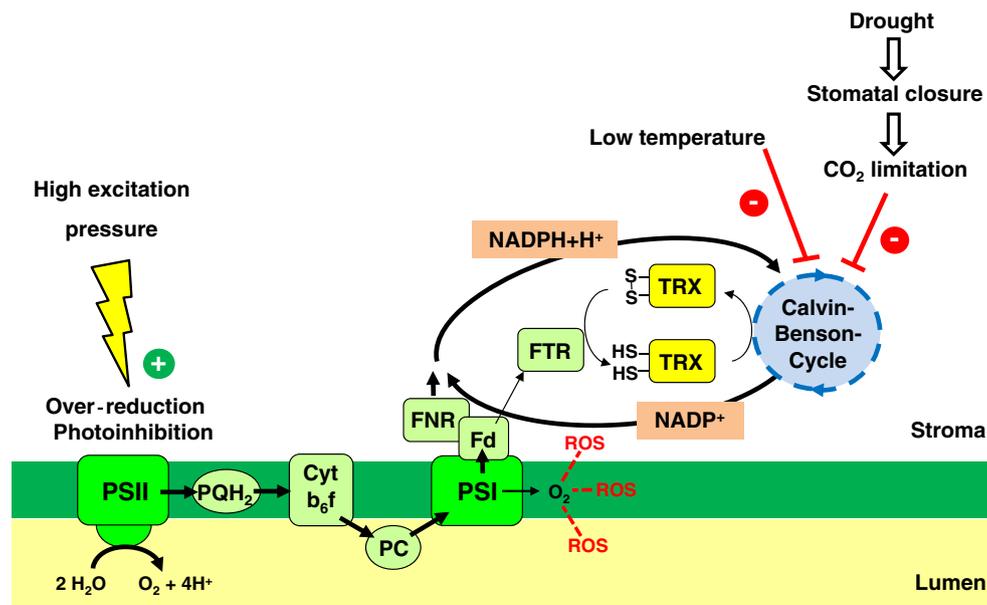


Fig. 1 Interacting effects of light, temperature and drought on electron transport efficiency. The scheme depicts the light-dependent photosynthetic electron transport chain and the enzyme-dependent dark reaction coupled to each other by the $\text{NADPH} + \text{H}^+/\text{NADP}^+$ redox couple and the FTR/thioredoxin system. *Black arrows* indicate electron flow and *red bars* repression of the Calvin–Benson cycle. High excitation pressure (indicated by a *flash*) occurs under high light or combinations of illumination with low temperatures and/or drought which both

decrease dark reaction efficiency. Repression of the Calvin–Benson cycle leads to a feedback inhibition of photosynthetic electron flow by limited regeneration of the final electron acceptor NADP^+ . Under high light, this leads to over-reduction of the electron transport chain (including a reduced PQ pool), photoinhibition of PSII and increased ROS production at PSI. For further functional details and abbreviations, see text

sulfur depletion affecting co-factor generation essential for photosynthetic electron transport (for instance in iron–sulfur clusters), (2) heavy metal accumulation which inhibits enzyme activities and promotes unwanted hydroxyl radical formation via the Fenton reaction or (3) herbivore or pathogen attack resulting in down-regulation of photosynthesis by induction of reactive oxygen species and various stress response programmes including cell death. They all possess numerous connections to other sensing mechanisms in plant cells located in the nucleus, cytosol and plasmamembrane representing research fields of its own and are not covered by this review here. Therefore, the interested reader is referred to other reviews specifying these topics in more detail (Shcolnick and Keren 2006; Zhao and Qi 2008; Burkhead et al. 2009; Baena-Gonzalez 2010; Pourrut et al. 2011).

Sensing the change—variation in photosynthetic function mediates responses to environmental cues

The overall commonality under all environmental situations described above is the fact that they all affect in a first step the redox state of photosynthetic electron transport components or electron end acceptors and, if not counterbalanced or released, induce the generation of various types of reactive oxygen species or redox-active radicals which subsequently cause

oxidative damage and initiate defense or stress responses (Mittler et al. 2011). Photosynthetic acclimation responses to environmental cues are confined to the first step and aim to counterbalance the unfavourable environmental condition by reconfiguration of the photosynthetic apparatus. They can be clearly distinguished from stress or defense responses by the fact that they are fully reversible and solely dependent on photosynthesis as trigger and regulator. The decisive control parameters appear to be the redox states of the plastoquinone (PQ) pool and the electron end acceptor NADP^+ and/or alternative redox systems like thioredoxins, peroxiredoxins or NtrC. Besides the structural reconfiguration in the photosynthetic apparatus itself in recent years, the picture emerged that these signals in parallel control nuclear and plastid gene expression as well as a fine-tuning of metabolism. Thus, photosynthetic acclimation is not restricted to photosynthesis itself but outreaches to coupled cellular processes such as gene expression or metabolite pools resulting in an integrated response to the environment at all cellular levels (Dietz and Pfannschmidt 2011).

Light harvesting, state transition and photoprotection—short-term acclimation responses to the changing environment

The photosynthetic apparatus of eukaryotes consists of PSII and PSI (Barber 2006; Melkozernov et al. 2006; Amunts

and Nelson 2009). Each photosystem consists of two parts: a reaction centre super-complex and the light-harvesting systems (LHCs) (Caffarri et al. 2009; Kouril et al. 2011). During evolution, photosynthetic eukaryotes including plants have developed photosystems characterised by reaction centres (RCs) which are quite conserved between different species and light-harvesting systems that exhibit a high degree of diversity (Durnford et al. 1999). The light-harvesting antennae have been developed to highly coordinated pigment protein complexes that can, on the one hand, transfer the energy effectively from the outer light-harvesting complexes to the reaction centre (Szabo et al. 2008) and, on the other hand, dissipate over-excitation under strong light conditions (Nathan 2011). In this respect, the light-harvesting protein complexes are not only responsible for harvesting and transferring light energy to the reaction centre, but they are also important for maintaining the structure of photosynthetic membranes (Standfuss et al. 2005), for dissipation of excess excitation energy (Johnson 2011), for regulating the size of the macro-pigment protein super-complexes (Lambrev et al. 2011) and for regulation of photosystem stoichiometries (Allen 2003). In conclusion, LHCs are an integral part of a sensitive system detecting light distribution and over-excitation in the thylakoid membrane (Liu et al. 2008; Yang et al. 2008; Johnson 2011).

LHCs have developed at first from FeS-type RC light-harvesting systems in cyanobacteria to phycobilisome-like antenna systems, which divided into red and green algae systems (Kozioł et al. 2007), and then to the light-harvesting pigment protein complexes of PSII and PSI of plants. The process of adaptation of photosynthetic proteins to high light intensities and over-excitation is characterised by the evolution of the light-harvesting complexes from the prokaryotic light-harvesting antenna system to the eukaryotic system, namely from the ring-shaped RC–LH system, through the prokaryotic phycobilisome chlorophyll (Chl) *a/b* and Chl *a/c* LHC system and finally to the eukaryotic system. In this way, the photosystem with phycobilisome has been developed to the light-harvesting system of PSII and PSI where the charge separation takes place and the different photo-protection processes are regulated (Durnford et al. 1999).

In higher plants and green algae, LHCs are encoded by a group of nuclear genes, translated in the cytosol, imported into plastids and subsequently transported to the thylakoid membrane after post-translational modification, where they construct different pigment–protein complexes and the antenna system for PSI or PSII called LHCI and LHCII, respectively (Jansson 1999; Durnford et al. 2003). The antenna system of PSII is composed of the minor antennas and the major antennas (LHCIIb). LHCIIb is a multi-functional pigment–protein complex which is essential for adjusting the absorption, distribution and conversion of the

solar energy in the thylakoid membrane under different light conditions. The high resolution structural analysis of LHCIIb at near atomic level (Liu et al. 2004; Standfuss et al. 2005) illuminates that the proteins of LHCIIb contain three trans-membrane α -helices, one amphiphilic α -helix and a super-secondary structure in the luminal region which plays an important role in sensing over-excitation (Yang et al. 2008). As co-factors, the LHCIIb binds eight Chl *a* and six Chl *b*, two lutein molecules in the middle of the complexes, one neoxanthin molecule at the interface of two LHCIIb trimers and one violaxanthin that is converted to zeaxanthin via the xanthophyll cycle under excess light conditions. The LHCIIb-bound pigments are coordinated as clusters which enable LHCIIb to transfer the excitation energy effectively to the reaction centre of PSII where the charge separation takes place and the electron transport chain starts. The pigments of the LHCIIb monomer are constructed into seven pigment clusters at the stromal side and the six pigment clusters at the luminal side (Liu et al. 2004; Novoderezhkin et al. 2005). This highly coordinated pigment arrangement in the LHCIIb enables efficient long distance energy transfer in the thylakoid membrane (Novoderezhkin et al. 2005; Georgakopoulou et al. 2007).

Besides harvesting solar energy, the light-harvesting complexes are also important in protecting photosynthetic membranes under strong illumination, wherein the structural adjustment is ultimately important for the functional regulation (Fig. 2) (Liu et al. 2008; Romanowska et al. 2008). One of the Lhc gene products, PsbS, is a 22-kDa and four-transmembrane helices protein, which is found to be the most important protein in adjusting structural and functional relationships of LHCIIb. It could be demonstrate that PsbS is responsible for sensing the high proton concentration in the lumen and that it triggers a response that protects the photosynthetic reaction centre from photodamage (Fig. 2) (Li et al. 2000; Szabo et al. 2005). This short-term protection mechanism dissipates excess excitation energy as heat and is called non-photochemical quenching (NPQ) (Niyogi 1999). Two glutamate residues in the luminal region of PsbS are important in sensing the high proton concentration generated in the thylakoid lumen upon excess excitation. They trigger the photoprotective function, including effects on the rigidity of the grana membrane and the macro-organisation adjustment of the LHCIIb structure in the thylakoid membrane, which in turn leads to different fluorescence quenching mechanisms (Allen 2003; Li et al. 2004; Niyogi et al. 2005; Kiss et al. 2008; Johnson and Ruban 2010; Ruban and Johnson 2010). Besides inter-molecular LHCIIb interactions, the intra-molecular structural change is also crucial in adjusting the structure for functional regulation. The protonation of the luminal loop in LHCIIb affects the conformation of the neoxanthin which leads to changes in fluorescence efficiency and trimer–trimer interaction

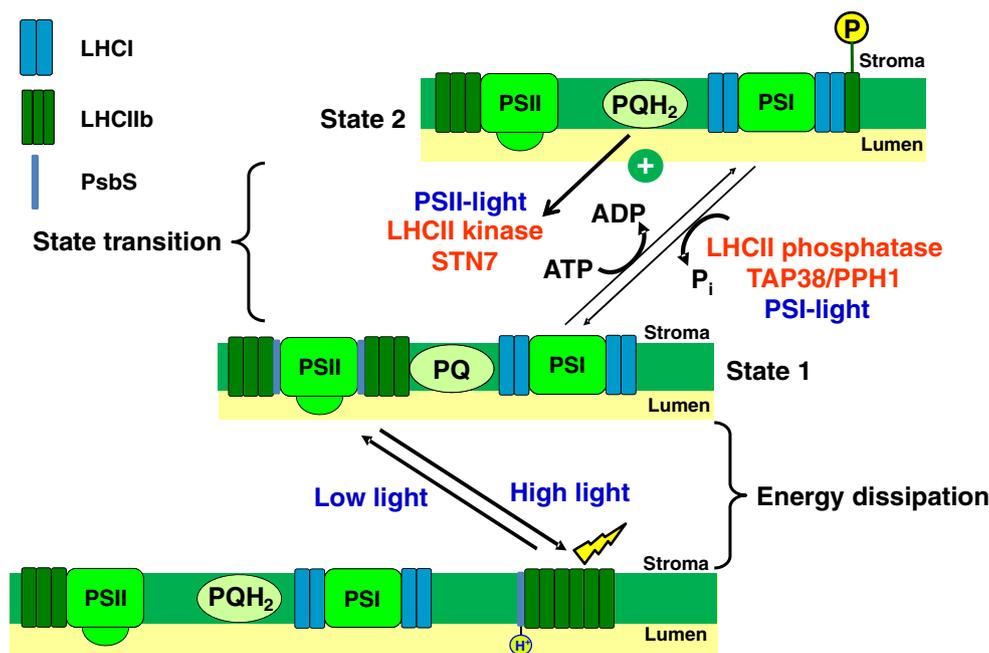


Fig. 2 Roles of the major light-harvesting complexes of photosystem II in light harvesting, energy distribution and dissipation. The major light-harvesting complex of PSII is a pigment–protein complex important for acclimation to changing light environments. PsbS is an important protein in dissipation of excess excitation energy. Under normal light conditions, PsbS is not protonated and LHCIIb functions as a light-harvesting protein that transfers energy to the RCs. Under excessive light conditions, PsbS is protonated which causes the migration of PsbS to LHCIIb. The macrostructure of LHCIIb is changed and switches to function as an energy dissipater that turns the excitation energy to heat (*lower part*: indicated by yellow arrow). Under different

light qualities, the reversible phosphorylation of LHCIIb is of great significance in distributing the excitation energy between PSI and PSII. When the light condition leads to enhanced excitation of PSII (PSII light), the plastoquinone pool becomes reduced and activates the LHCIIb-kinase STN7 and LHCIIb is phosphorylated (P-LHCIIb). As a result, the P-LHCIIb is detached from PSII and migrates to PSI and redistributes more excitation energy to PSI. When the light condition favours PSI (PSI light), the plastoquinone pool becomes oxidised and STN7 is inactivated. P-LHCIIb is then dephosphorylated by the phosphatase TAP38/PPH1 and the LHCIIb switches from state 2 back to state 1 and transfers more excitation energy to PSII

(Dall'Osto et al. 2007). It has been demonstrated that the anti-parallel structure in the super-secondary structure of LHCIIb plays important roles in keeping the conformation of the neoxanthin–Chl *b* niche that regulates the energy transfer efficiency of LHCIIb, and it is therefore important in adjusting the structure and the function of the complex under different environmental conditions (Liu et al. 2008).

It has been observed that a heptameric association of LHCIIb in the thylakoid membrane undergoes flexible and reversible structural changes under different conditions (Dekker et al. 1999). LHCIIb appears to possess a built-in property to undergo reversible structural changes in response to changes in temperature or light intensity in the environment (Garab et al. 1988; Barzda et al. 1996; Istokovics et al. 1997). It is proposed that the aggregation of LHCIIb causes conformational changes in the LHCIIb that regulate the fluorescence efficiency of the complexes (Horton et al. 1991; Walters and Horton 1994; Moya et al. 2001; Horton et al. 2008). It has been accepted that the aggregation of LHCIIb reduces the fluorescence efficiency of the complexes (Mullineaux et al. 1993; Miloslavina et al. 2008), but recent data imply that the physical size of

LHCIIb is not necessarily a factor influencing the fluorescence efficiency of the complexes (Lambrev et al. 2011).

The phosphorylation of the light-harvesting complexes provides another mechanism for regulating the energy absorption, transfer and conversion in the thylakoid membrane (Allen 2003). The LHCIIb distributes the captured solar energy in a balanced manner between PSII and PSI via phosphorylation/dephosphorylation mechanisms which are regulated by the redox state of plastoquinone pool (Allen 2003; Aro and Ohad 2003). Reduction of the plastoquinone pool activates a Cyt *b₆f* bound, membrane-embedded kinase called Stt7 in *Chlamydomonas* and STN7 in *Arabidopsis*, which is required for phosphorylation of LHCIIb. This triggers state transitions, redistributes the excitation energy between PSII and PSI and regulates the electron transport efficiency in the thylakoid membrane (Depege et al. 2003; Bellafiore et al. 2005; Tikkanen et al. 2006; Hemschemeier and Happe 2011; Pesaresi et al. 2011; Rochaix 2011). The state transition, firstly discovered in 1969 with algae (Bonaventura and Myers 1969; Murata 1969), is a short-term regulatory response of LHCIIb to different light qualities to regulate the energy distribution in the thylakoid membrane (Fig. 2) (Allen

2003). The phosphorylated LHCIIB detaches from PSII and migrates to PSI which induces “state 2”, resulting in distribution of excitation in LHCIIB to PSI, while dephosphorylation of LHCIIB by the phosphatase TAP38/PPH1 (Pribil et al. 2010; Shapiguzov et al. 2010) results in reattachment of LHCIIB to PSII and recovers a “state 1” situation that transfers the excited energy to PSII. Thus, state transitions counteract excitation imbalances between PSII and PSI by purely post-translational means (Allen 2005a).

In conclusion, in order to cope with the ever-changing environment, light-harvesting pigment–protein complexes of PSII and PSI have developed different mechanisms, which enable the LHC to regulate its structural–functional relationships. The molecular mechanism of LHCIIB to regulate its different functions is realised via changes in the macro-molecular structures in the membrane and the phosphorylation–dephosphorylation of LHCIIB (Allen 2005b; Horton et al. 2008). This multi-functional characteristic ensures highly efficient light harvesting and sensibility against the situations of over-excitation (Bassi and Caffarri 2000; Szabo et al. 2008; Varkonyi et al. 2009).

Redox control of gene expression and long-term acclimation responses

Energy dissipation and state transitions are post-translationally controlled short-term acclimation responses being most important in the leaves at the top layers of a canopy where they can be exposed to direct sunlight and experience very sudden and strong changes in illumination intensity. In contrast, the light environment within a canopy is characterised by a relatively stable and weak light intensity. In addition, this light is enriched in far-red wavelengths due to the selective absorption of PAR from the upper leaf layers (Dietzel et al. 2008). This creates a strong imbalance in excitation which favours the activity of PSI and limits that of PSII. State transitions are not sufficient for a complete redistribution of excitation energy under these conditions. Therefore, plants perform a long-term response (LTR) in which the photosystem stoichiometry is adjusted in favour of the rate-limiting photosystem, i.e. PSII (Allen and Pfannschmidt 2000). Functionally, this has the same but longer lasting effect as state transitions (Chow et al. 1990). However, in contrast to the short-term response, it requires corresponding changes in the expression of the genes encoding the respective photosystem subunits. Since the photosynthetic apparatus of chloroplasts is comprised of nuclear and plastid encoded subunits, this requires that (1) the redox signals are transduced to the gene expression machineries in the nucleus and plastid and that (2) the gene expression events in the two compartments must be coordinated (Fey et al. 2005a). In mustard, it could be demonstrated that the pacemaker of photosystem stoichiometry adjustment is the

transcriptional control of the chloroplast genes *psaA* and *psbA* which encode the core proteins of PSI and PSII, respectively. Light quality treatments using PSI or PSII light in combination with inhibitors of photosynthetic electron transport revealed that a reduced PQ pool activates *psaA* transcription while an oxidised one activates *psbA* (Pfannschmidt et al. 1999a, b). In pea and *Arabidopsis*, similar results were obtained (Tullberg et al. 2000; Fey et al. 2005b). This provided experimental evidence for the hypothesis that organelles retained genes because their regulation depends on the functionality of the energy-transducing membranes (Allen 1993). However, how the redox state of the PQ pool is sensed and how the signal is transduced to the level of gene expression is still under investigation. Recent data indicated that the thylakoid kinase STN7 is required not only for state transitions but also for the LTR (Bonardi et al. 2005). Since the activity of this kinase depends on the redox state of the PQ pool being activated upon reduction, it would be an ideal redox sensor for the LTR; however, since the true phosphorylation target of STN7 is still unknown, it remains to be elucidated how the signal transduction chain proceeds at this step. Mutant analyses suggest that the signalling pathways for gene expression and state transition diverge at or directly after this kinase (Pesaresi et al. 2009). The chloroplast sensor kinase (CSK) is a second kinase which has been identified to be involved in the redox control of transcriptional regulation and which could play an inter- or counteracting role in this event (Puthiyaveetil et al. 2008). In the yeast two-hybrid system, it interacts with itself, with sigma factor 1 (SIG1) and with the plastid transcription kinase (PTK) which belongs to the class of casein-kinase 2 enzymes (Puthiyaveetil et al. 2010). Based on this observation, a model proposes that CSK is activated by auto-phosphorylation when the PQ pool becomes oxidised under PSI light and, subsequently, phosphorylates both SIG1 and PTK. SIG1 has been postulated to be responsible for recognition of *psa* gene promoters and redox regulation of it (Shimizu et al. 2010). SIG1 phosphorylated by CSK, therefore, would be an effective repressor of *psa* gene transcription while phosphorylated PTK is inactive under these conditions. Upon reduction of the PQ pool (e.g. under PSII light), CSK would become inactive and a dephosphorylated SIG1 would allow increased transcription from *psa* promoters driving photosystem stoichiometry adjustment. At the same time, PTK would become active and would phosphorylate PEP subunits and other sigma factors. In vitro, this results in a non-specific repression of plastid transcription (Tiller and Link 1993) which, however, would be not favourable under these conditions. Intriguingly, chloroplast run-on transcription assays suggested that not only phosphorylation but also reduction of the plastid transcription machinery is an important determinant of its activity (Steiner et al. 2009). It appears that a second, thiol-dependent signal

interacts with the phosphorylation-dependent signal having a strong influence on chloroplast transcription. Recent proteomic data, indeed, identified a novel thioredoxin called TrxZ, which was initially identified as a component of the transcriptionally active chromosome of plastids (Pfalz et al. 2006) and turned out later to be an essential subunit of the PEP complex (Schroter et al. 2010). This thioredoxin could be a potential target for thiol-dependent regulation of the PEP complex; however, this functional connection requires further investigation. Interestingly, in the yeast two-hybrid system, TrxZ revealed an interaction with two chloroplast-located phosphofructokinase-like enzymes called FLN1 and 2 (Arsova et al. 2010). The function of both is not known yet, but FLN1 is also a PEP subunit pointing to the likely possibility that phosphorylation- and thiol-dependent regulation of plastid transcription converge at this point (Schroter et al. 2010).

Early studies demonstrated that photosynthetic redox signals have also an impact on transcription and translation of some nuclear photosynthesis genes in plants (Oswald et al. 2001; Yang et al. 2001; Petracek et al. 1997, 1998; Karpinski et al. 1997; Karpinski et al. 1999; Sheramati et

al. 2002) and a variety of other photosynthetic organisms (Pfannschmidt 2003). More sophisticated studies in *Arabidopsis* using array technologies indicated that light quality-dependent regulation in the nucleus covers several hundreds of genes (Piippo et al. 2006; Fey et al. 2005b). Interestingly, this redox regulation was not limited to photosynthesis genes as originally expected, but it extended to all major gene groups including genes for gene expression, signalling and regulation. The most prominent gene group, however, was that for metabolism genes suggesting an adjustment of metabolic pathways parallel to the reconfiguration of the photosynthetic apparatus. A drawback in this study was that the gene expression profile was obtained at a time point when the LTR was finished and an equilibrium in gene expression was reached. In order to identify primary regulated genes, a kinetic array study was performed which obtained the gene expression changes at different time points after inducing the redox signal in the electron transport chain (Bräutigam et al. 2009). This revealed high dynamics in the gene expression response, but confirmed that metabolism genes responded in a specific way to the photosynthetic redox signals. Intriguingly, the identified

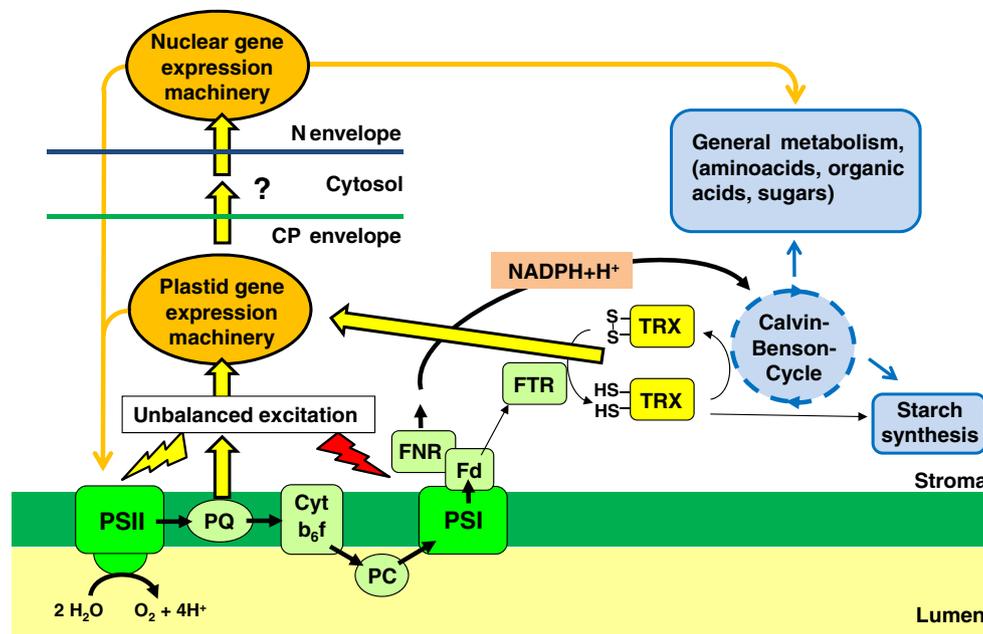


Fig. 3 Long-term acclimation at the level of gene expression and metabolism. The scheme depicts the photosynthetic electron transport chain as in Fig. 1 and some metabolic pathways coupled to it either by reduction equivalents or by metabolites. The Calvin–Benson cycle is central to this regulation being sensitive to photosynthetic redox signals from the thioredoxin system as well as from the availability of NADPH + H⁺. Unbalanced excitation of the two photosystems caused by light quality gradients which typically occur in dense plant populations disturbs the balance between light and dark reactions. In the long-term redox, signals from the PQ pool and the thioredoxin system (indicated by yellow arrows) affect the plastid gene expression

machinery (for details, see text). The signals extend also to the nuclear gene expression machinery by still unknown pathways (indicated by question mark). This requires a transfer across the CP envelope, a passage through the cytosol and a transfer across the nuclear (N) envelope. Coordinated gene expression in both compartments provides gene products which are used to reconfigure the photosynthetic apparatus and various biosynthetic pathways in the chloroplast (indicated by an orange arrow). Acclimation of the photosynthetic apparatus serves to counteract the excitation imbalances while acclimation of the metabolism adapts the efficiency of biosynthetic pathways to the changes in photosynthesis

primary gene targets revealed only very few overlap with gene expression responses to reactive oxygen species or photoreceptor-mediated light signals suggesting that this redox regulation of genes represents a distinct signalling mechanism or network although some interaction with photoreceptor-mediated signalling cannot be excluded at this stage of investigation.

In order to understand if these transcript profiles reflected true functional consequences in response to the environment, determination of corresponding metabolites in *Arabidopsis* was performed in parallel. Metabolite profiles of PSI and PSII light-grown plants were markedly distinct from each other, but could be transferred into each other by shifting the plants between the respective growth lights (Bräutigam et al. 2009). The starch content turned out to be a robust marker for the respective metabolic state. In PSI light, it was about 40–50 % lower than in PSII light being consistent with electron micrographs from chloroplasts isolated from corresponding tissues (Wagner et al. 2008). Interestingly, this variation of starch contents was completely abolished in the *Arabidopsis stn7* mutant lacking the LTR (Bräutigam et al. 2009). This indicates that the growth light condition not only affects photosynthesis but also the corresponding metabolic state of the plants. This physiological redox control of metabolic states is consistent with the observation that leaf metabolism can be re-directed in the presence of DTT (Kolbe et al. 2006). In summary, these observations provide evidence that metabolism and photosynthesis are adjusted in parallel contributing to an integrated response of the plant to the light quality change (Fig. 3). The LTR, therefore, is not restricted to photosynthesis alone but includes biochemical pathways functionally coupled to photosynthesis. This provides potential targets for enzymatic engineering of photosynthetic acclimation responses which eventually improve plant growth performance especially in plant communities with high density of individuals such as crop fields.

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