The Dynamics of Photosynthesis

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Abstract

Despite recent elucidation of the three-dimensional structure of major photosynthetic complexes, our understanding of light energy conversion in plant chloroplasts and microalgae under physiological conditions requires exploring the dynamics of photosynthesis. The photosynthetic apparatus is a flexible molecular machine that can acclimate to metabolic and light fluctuations in a matter of seconds and minutes. On a longer time scale, changes in environmental cues trigger acclimation responses that elicit intracellular signaling between the nucleo-cytosol and chloroplast resulting in modification of the biogenesis of the photosynthetic machinery. Here we attempt to integrate well-established knowledge on the functional flexibility of light-harvesting and electron transfer processes, which has greatly benefited from genetic approaches, with data derived from the wealth of recent transcriptomic and proteomic studies of acclimation responses in photosynthetic eukaryotes.

RC: reaction center

PQ: plastoquinone

Fd: ferredoxin

PC: plastocyanin

cyt: cytochrome

cp: chloroplast(s)

Acclimation: process by which organisms modulate gene expression, protein content and metabolic properties to cope with changes in their environment. Photosynthetic acclimation encompasses changes in light harvesting capacity, stoichiometry between antenna protein and RC and/or in the relative stoichiometry between the two photosystems

chl: chlorophyll

INTRODUCTION

With the rapid development of membrane protein crystallography following the pioneering work on bacterial reaction center (RC) structure (67), the 3D structures of all major multimeric proteins for oxygenic photosynthesis have been solved at atomic resolution (see Reference 205 for a review) (**Figure 1*a***). The position and orientation of the major cofactors involved in light harvesting or electron transfer have been identified within these complexes, augmenting our understanding of basic principles that govern light energy conversion within photosynthetic membranes. The most rapid events in light energy collection and charge separation, mainly intraprotein processes, are well understood in a molecular and structural context. However, this is not yet the case for steps requiring interactions among photosynthetic protein complexes, or that rely on diffusion of small molecule/protein electron carriers within the membrane bilayer, like plastoquinones (PQ); in the stroma, like ferredoxins (Fd); or in the lumen, like plastocyanin (PC) or cytochrome (cyt) c_6. Changes in molecular interactions are revealing numerous ways in which photosynthetic processes are regulated, and continued study should generate a refined understanding of supramolecular organization of thylakoid membrane complexes, in particular with high resolution attained through electron tomography (206, 274, 300).

Despite the wealth of structural data available, developing a clear picture of photosynthetic energy conversion under physiological conditions requires placing these molecular structures in their dynamic intra- and extracellular environments. The photosynthetic apparatus can be viewed as a flexible molecular machine that rapidly molds to fluctuating environmental conditions. Intracellular signaling processes triggered by environmental cues have been shown to control distinct patterns of the biogenesis and function of photosynthetic membranes. These signaling processes between chloroplasts (cp) and the nucleo-cytosol combine with direct effects of environmental cues, including nutrient levels, temperature, and light quality or intensity, to coordinate nuclear and plastid gene expression. Thus, the core dynamic of photosynthetic processes bridges functional flexibility of the system with acclimation events that modulate gene expression and polypeptide composition.

The foundation for a new age in photosynthesis research is being set with the use of time-resolved spectroscopic techniques on live organisms, providing unparalleled access to photosynthesis function in vivo, and both experimental and computational methods for integrating changing functionalities with changes in the transcriptome, proteome, and metabolome. Several genome-wide studies of photosynthetic eukaryotes are providing preliminary information on acclimation processes from a systems biology perspective. In this review we provide the reader with a fresh perspective of the complexity and diversity of electron transfer and light-harvesting strategies. We then present a comprehensive view of photosynthetic acclimation processes that are supported by transcriptomic and proteomic data. Although this review deals mostly with the dynamics of cp-based photosynthesis, in some instances the similarity between oxygenic photosynthesis in cyanobacteria and cp-based photosynthetic eukaryotes are discussed with respect to specific issues.

PHOTOSYNTHESIS AS A FLEXIBLE MOLECULAR MACHINE

Genetics and Biophysics Have Shaped Our Current View of Photosynthesis

Biophysical analysis of photosynthetic function has been instrumental to our understanding of light energy conversion by plants and algae. These studies have benefited from genetic approaches that, early on, were critical for identifying mutants aberrant for some aspect of photosynthetic function or regulation. Among the various screens used to probe photosynthetic function, the use of chlorophyll (chl)

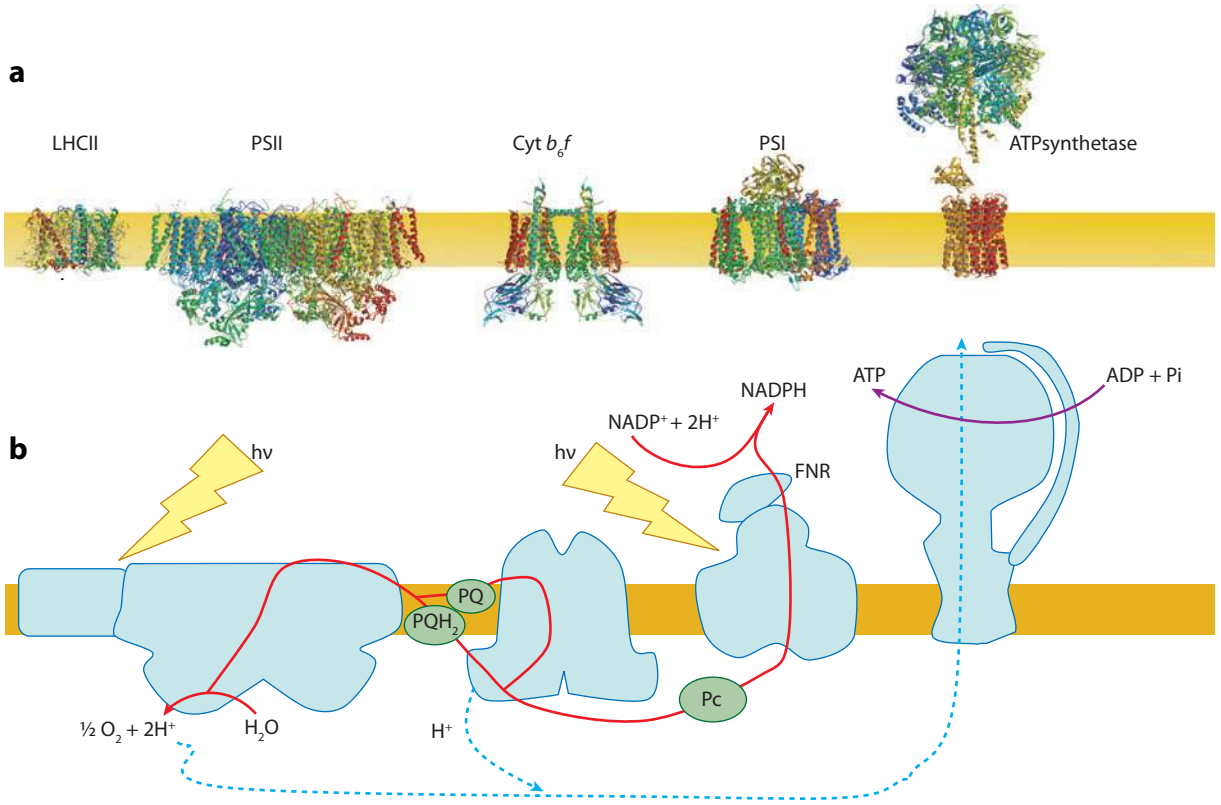


Figure 1

The simple picture of photosynthesis: the major thylakoid membrane proteins support linear electron flow. (*a*) Transmembrane organisation of the major photosynthetic proteins in their native oligomerization state, as resolved by X-ray crystallography (courtesy of Daniel Picot). (*b*) Schematic representation of the pathway for photosynthetic linear electron flow and proton translocation through major protein complexes whose atomic structures are shown in *a*. Electrons are extracted from water on the lumenal side of membranes and transferred to NADP on the stromal side of membranes. Electron transfer is driven by the RC from two distinct photosystems—PSII and PSI—which are the site of a light-induced charge separation between a photosensitive chlorophyll and an acceptor molecule. The intersystem electron carriers consist of a pool of plastoquinone molecules soluble within the lipid bilayer, a transmembrane protein complex—the cyt b_6f complex—comprising an Fe-S cluster and four hemes, a small copper-containing protein, plastocyanin, soluble in the thylakoid lumen, which is replaced by a soluble cyt, c_6, in some photosynthetic organisms. Protons translocated across the membrane during linear electron flow are used by the transmembrane ATP synthase to drive ATP synthesis.

fluorescence has been invaluable because of its nondestructive nature and high sensitivity. Light energy absorbed by photosynthetic pigments is used for photochemistry (charge separation fueling electron transport), or re-emitted by chl as fluorescence, or released as a consequence of thermal dissipation. Changes in fluorescence yield are inversely correlated with the rate of photosynthetic electron transfer (PET). In the 1960s and 1970s, large-scale screening of microalgae for impaired PET was based on changes in the yield of in vivo, steady-state chl fluorescence emission, or on changes in the fluorescence transients upon illumination of dark-adapted samples (33, 34) (**Figure 2*a***). These studies, which set the groundwork for assessing the contribution of individual proteins to light-driven electron flow, were successfully extended to vascular plants. Initially, high fluorescence emission was used to identify mutants altered for their photosynthetic properties (185). Later, screens were expanded to

PET: photosynthetic electron transfer

NPQ: non-photochemical quenching of fluorescence

ΦPSII: fluorescence yield of photosystem II

PS: photosystem

LEF: linear electron flow

monitor functional parameters including non-photochemical quenching (NPQ) and the fluorescence yield of photosystem II (ΦPSII) (90) (see **Figure 2** legend), leading to the identification of genes controlling the dynamics of photosynthetic processes.

In particular, mutants were screened for defective electron flow (302), or NPQ (especially the qE contribution to NPQ) (208, 166) or in alternative pathways for electron transfer (272). Some NPQ mutants exhibited modified regulation of electron flow (e.g., *pgr1* or *pgr5*; reviewed in Reference 271), confirming a tight genetic interplay between PET and photoprotective responses. Mutants impaired for light acclimation were isolated based on their inability to modify photosynthetic yield (ΦPSII) upon transition to high light (307). In addition, mutants with impaired redox signaling, like those in the STT7/STN7/STN8 kinase family, were isolated by monitoring the cells for their ability to adjust to PSII sensitization (through the qT or state transition component of NPQ, see **Figure 2**) as the PQ pool becomes reduced (reviewed in Reference 250). Other screening procedures for identifying chlorophyll biosynthesis mutants involved a visual screen for seedlings with reduced pigmentation (257). Several mutants affected in signaling between the cp and the nucleus were isolated based on their impaired greening behavior (e.g., 145). Mutants with altered cp movement were detected in leaves by measuring local pigment changes in leaf cells following exposure to high-intensity white light (216). Finally, a phytochrome signaling mutant with increased hypersensitivity to red and far-red light has been isolated using a fluorescence imaging screen that revealed increased transcription from a chl *a/b* binding protein–luciferase (*CAB2–LUC*) transgene in *Arabidopsis* (89). In a few other cases, mutant identification was performed using other approaches, i.e., direct measurements of absorption properties of photosynthetic complexes (12), or direct measurements of carbon assimilation [autoradiographic assessment of ^{14}C assimilation (178)]. Our growing understanding of light-harvesting and electron transfer processes is likely to provide new screening procedures based on multiparameter assessments.

Regulation of PET

Over the past 40 years we have gained insights into the kinetics and thermodynamics of PET through spectroscopy, fluorescence, and biochemical and molecular characterizations of photosynthetic processes. The overall picture that has emerged from these studies is consistent with the early proposal of a Z scheme (106), which describes a linear electron flow (LEF) from water to NADP (**Figure 1*b***).

Some unresolved features of electron flow remain, including the mechanism of water oxidation by PSII (reviewed in References 135, 186, 231, 275, 278, 327), the role of a recently discovered c′ heme that likely contributes to PQ oxidation and electron recycling through the cyt b_6f complex (62, 63, 159, 282) or the bidirectionality of electron transfer in PSI (239, 242, 260). Another unresolved issue involves electron diversion at the reducing side of PSI, where several electron sinks compete for reducing equivalents generated by photochemical conversion. As discussed below, electron flow from PSI is a complex, dynamic process (**Figure 3*a***).

PSI, a key site for integration of photosynthesis into the cell's metabolism. Photosynthesis involves light-induced LEF between two photosystems embedded in thylakoid membranes, which work in series to generate ATP from energy stored as a transmembrane, electrochemical proton gradient, and reducing equivalents often in the form of NADPH. Photosynthetically generated ATP and/or NADPH are used in a variety of metabolic processes in the cp, including CO_2 assimilation in the Benson-Calvin cycle, nitrate metabolism, lipid, amino acids, and pigment synthesis and the modulation of gene expression. Different abiotic and biotic stress conditions may decrease the efficiency of light-induced ATP and NADPH generation, leading to electron

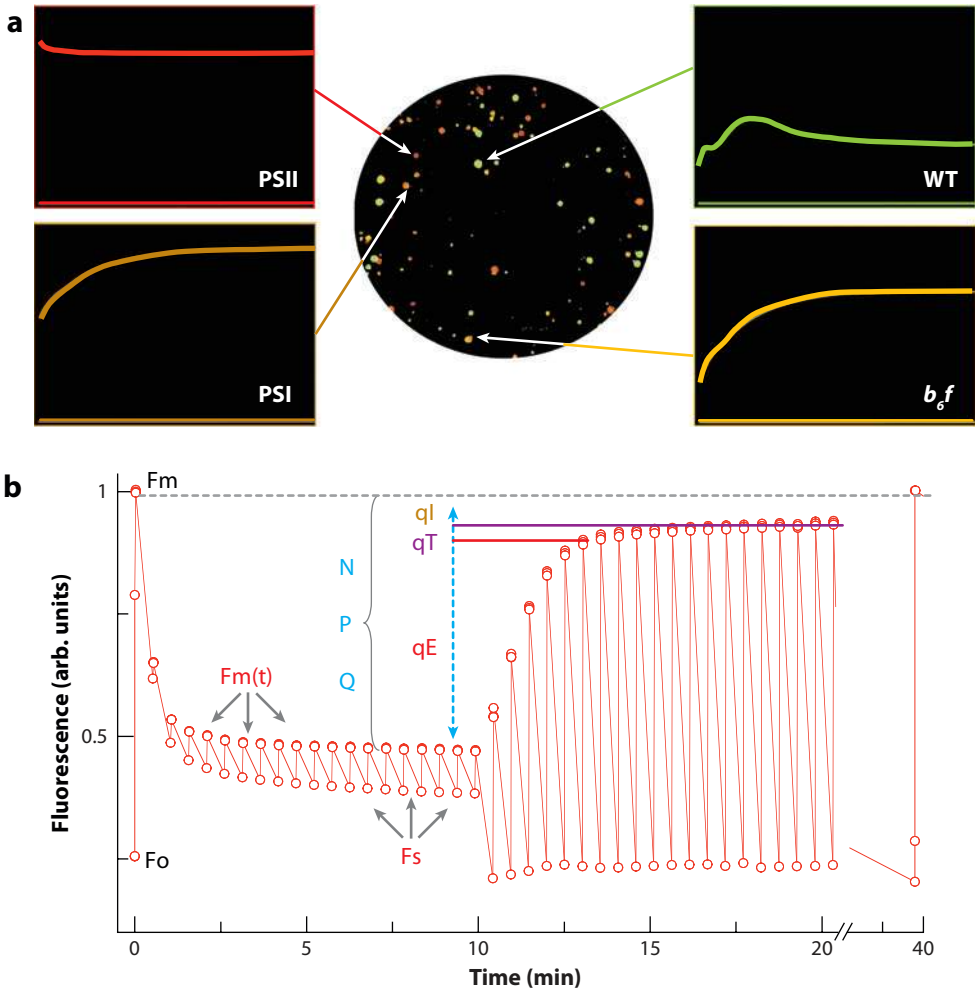


Figure 2

Chlorophyll fluorescence characteristics used for genetic screens of photosynthesis mutants. (*a*) Digital imaging of *Chlamydomonas* fluorescence from dark adapted wild-type and mutant colonies subjected to transient illumination. Cells were transformed with antibiotic resistance cassettes and grown four weeks on selectable medium on Petri dishes. Plates were exposed to a 1.5-sec illumination with moderate actinic light (50 μE m^{-2} s^{-1}) and 50 images were recorded. A false color imaging system allows the ratio of two captured images best suited for the rapid identification of mutant phenotypes to be presented. Fluorescence kinetics from different clones are reproducible, and typical signatures of the various mutant strains (courtesy of Xenie Johnson). (*b*) Kinetics of changes in fluorescence yield in a leaf subjected to continuous illumination saturating for photosynthesis (~500 μE m^{-2} s^{-1}, of red light). Illumination results in a sustained decrease in fluorescence yield, Fm from the "closed" PSII RC (i.e., with primary quinone acceptors fully reduced). This decrease is quantified by the NPQ parameter (Fm-Fm(t)/Fm(t) (40). Upon dark adaptation, NPQ relaxes with multiphasic kinetics, which allows the identification of three kinetic components (reviewed in Reference 112): qE, which is ΔpH sensitive, qT, associated with state transitions, and qI, which mainly reflects photoinhibition. qE and qT are considered as short-term acclimation responses (see text). Mutants altered in NPQ can be screened from the distinct behavior of their Fm parameter. Another essential photosynthetic parameter that can be calculated based on this measurement is the quantum yield of PSII (ΦPSII), which is given by (Fm(t)-F(s)/Fm(t) (90). F_0, minimum PSII fluorescence yield at open centers (i.e., with primary quinone acceptor Q_A fully oxidized). Fm, maximum PSII fluorescence yield at closed centers (Q_A reduced). Fs, steady-state fluorescence yield. Data were obtained using a JTS-10 spectrofluorimeter (Biologic, France).

Alternative electron flow: a process involving the rerouting of electrons away from the major photosynthetic electron transfer pathway involving the activity in series of PSI and PSII. Electrons can be diverted to oxygen at the PSI or PSII acceptor side, recycled around PSI or, in some cases, can be directly or indirectly shunted into the respiratory chain

ΔpH: transthylakoid proton gradient

CEF: cyclic electron flow

redirection toward alternative electron sinks.

(*i*) *Metabolic flexibility*. The assimilation of CO_2 in the Benson-Calvin cycle requires ATP and NADPH in a 3:2 ratio (see 5). This ratio cannot be completely satisfied by LEF, which generates a pH gradient insufficient for the required ATP generation. Based on the "rotational hypothesis" for ATP synthesis by the cp CFo-CFi complex (46), proton efflux through a proton channel in the membrane induces rotation of the transmembrane CFo-ring of ATP synthase, which acts as an electric motor that provokes rotation of the central γ stalk. The rotation of γ against CFi induces conformational changes of the β subunits, the site of catalysis. A 360° rotation of the CFo-ring corresponds to full rotation of the central stalk, leading to the synthesis of three ATPs. It follows that **n**, the H^+/ATP ratio, is determined by the stoichiometry of CFo monomers in the transmembrane ring, i.e., $14/3 = 4.7$ in photosynthetic eukaryotes (268), and $13/3 = 4.3$ in the chlorophyte *Chlamydomonas* (183). Combined with the number of three H^+ transferred to the lumen per electron transfer from water to $NADP^+$ (i.e., 12 H^+ per 2 NADPH), this figure yields the number of ATP synthesized per NADPH of $3 \times 6/14 \approx 1.29$ (or $3 \times 6/13 \approx 1.38$) (but see 296). Diverting electrons from the reducing side of PSI (or PSII, see below and **Figure 3*a***) back to the PQ pool creates an alternative electron flow that could contribute to the generation of an extra ΔpH without net production of reducing equivalents. Thus, branched pathways for electron flow may significantly contribute to balancing the ATP/NADPH stoichiometry to allow for continued carbon fixation by the Benson-Calvin cycle. Besides electron diversion among alternative sinks, differential utilization of ATP and reducing power to fuel various metabolic pathways may significantly contribute to modify the ATP/NADPH ratio, and, as a consequence, in vivo carbon fixation. This additional level of flexibility contributes to generating a correct balance between light absorption and carbon assimilation (see 146).

(*ii*) *Photoprotection*. Absorption of light in excess of the capacity of PET may cause photodamage (reviewed in References 105, 112). However, the capacity for electron transport is variable and depends on several parameters including temperature, CO_2 availability or hygrometry, which modulate the efficiency of CO_2 assimilation. The Benson-Calvin Cycle is activated upon a transition from darkness to light, which helps balance the generation of ATP and reductant with their utilization. Hence, at a given low light condition, full activation of carbon fixation would lead to depletion of Benson-Calvin cycle intermediates. Conversely, under conditions of deactivation, low light might lead to full reduction of the photosynthetic electron carriers (see 111), which would be actively counterbalanced by the existence of alternative sinks.

(*iii*) *Fueling other metabolic pathways and/or signaling networks*. Besides providing electrons to the Benson-Calvin Cycle, reduced NADP feeds other metabolic pathways (reviewed in Reference 88) and triggers regulatory networks controlled by the thioredoxin/peroxyredoxin systems (reviewed in Reference 50) (**Figure 3**). The overall flow of electrons into these pathways is probably limited, although nitrite reduction can draw as much as 10% of the electrons generated on the acceptor side of PSI (74). The acceptor side of PSI is nonetheless a unique site for sensing overall carbon and nitrogen metabolism, allowing for direct adjustment of electron utilization by CEF (cylic electron flow) or the Mehler reaction (see below), or indirect adjustment through feedback processes associated with the Fd-thioredoxin regulatory system.

Photorespiration. In C3 plants, oxygenation of ribulose-1,5-bisphosphate by RuBisCo may represent a major alternative sink for electrons (**Figure 3*a***) (reviewed in Reference 316). Greater than 20% of total electron flux through RuBisCo may fuel O_2 reduction (219). Since this process competes with CO_2 assimilation, modulation of the relative rate of O_2 and CO_2 reduction may contribute to maintaining a

redox homeostasis with respect to electron transport and ATP synthesis, especially when CO_2 availability is restricted. Therefore, oxygenase activity of RuBisCo is no longer viewed as a wasteful side product of carbon assimilation. In accord with this idea, it has been proposed that the dual role of RuBisCo may represent a major factor in constraining the evolution of the enzyme toward efficient CO_2 assimilatory capacity (219). This may also explain why genetic engineering of RuBisCo to reduce its oxygenase activity has not been successful (reviewed in References 127, 136, 238).

The Mehler reaction. Reduced Fd or one of the Fe-S clusters bound to PSI (**Figure 3*a***) can be directly oxidized by O_2. The reaction leads to the production of $O_2^{\cdot-}$, which are rapidly converted to H_2O_2 by a cp-associated Cu-Zn superoxide dismutase (SOD). Efficient dismutation of superoxides is critical for reducing photodamage. *Arabidopsis* mutants in which the cp Cu/ZN-SOD activity was eliminated exhibited pronounced photosensitivity (197). These mutants exhibit patterns of expression for nuclear-encoded photosynthetic genes associated with oxidative stress under conditions that would not normally elicit a stress response. These results suggest an essential role of ROS in retrograde signaling from the cp to the nucleus (see below).

In principle, H_2O_2 produced by SOD may be converted to O_2 and H_2O by the activity of catalase. This occurs in peroxisomes where H_2O_2 is generated as a consequence of the oxidation of glycolate. Chloroplasts do not have catalase, but $O_2^{\cdot-}$ generated by the Mehler reaction is rapidly consumed by cp ascorbate peroxidase, which synthesizes a monodehydroascorbate radical (MDA) from ascorbate and H_2O_2 (188). MDA is extremely reactive and can be reduced directly by photosynthetic electrons at a rate comparable to that of NADP reduction (83). Alternatively, MDA can be reduced by MDA reductase, which can use NADPH generated by PET as a substrate, or by an indirect pathway involving the gluthatione/NADPH system (reviewed in Reference 17).

Like other alternative electron flow pathways, the Mehler reaction may perform two physiological functions. It has a photoprotective role and helps balance the ratio of reductant to ATP. Consistent with these functions, antisense *Arabidopsis* plants with a reduced cp ascorbate peroxidase exhibit increased photosensitivity (290). There are conflicting estimates of the contribution of the Mehler reaction as a terminal acceptor for photosynthetic electrons. Based on isotope discrimination, probably the most reliable approach, it has been proposed that up to 30% of PSI high light-generated electrons are consumed by the Mehler reaction in watermelon leaves (189). However, studies with transgenic tobacco mutants with reduced levels of RuBisCo did not show the expected increase in Mehler reaction (reviewed in Reference 20).

Recently, an additional role for the Mehler reaction has been proposed (82). While oxidation of the PQ pool was observed upon addition of low levels of O_2 to anaerobic *Chlamydomonas* cells in the dark, much stronger oxidation was observed when O_2 was added during exposure to limiting light (82). This reflects a high capacity of the Mehler reaction to catalyze reoxidation of the PQ pool relative to respiration. Thus, the Mehler reaction may participate in modulating state transitions, a process controlled by the redox state of the PQ pool (see **Figure 3**), at least at the onset of illumination.

Metabolic interactions between organelles: the malate shuttle. NADPH generated by PET can be reoxidized by the mitochondrial respiratory chain (**Figure 3**), through the exchange of reducing power between the two organelles. This exchange is catalyzed by the malate-oxaloacetate shuttle (264). Although metabolic interactions between cp and mitochondria have multiple physiological consequences (reviewed in Reference 212), the role of the mitochondria as a sink for photosynthetic electrons in vivo is still not clear. Based on studies with transgenic potato plants with reduced levels of the malate dehydrogenase (MDH), Laisk et al. (153) propose that the malate shuttle can contribute up to 10% of total PSII-driven

Retrograde signaling: a signal generated within organelles (chloroplast and mitochondria) that is transduced to the nucleus, eliciting changes in gene expression

MDA: monodehydroascorbate

NDH: NAD(P)H plastoquinone reductase

FQR: ferredoxin quinone reductase

electron flow. This value is close to the theoretical value required to achieve the proper ATP/NADPH stoichiometry for carbon fixation in plants.

Several *Chlamydomonas dum* (dark uniparental minus) mutants affected at different steps in mitochondrial electron transfer are available (244). Their comparative analysis led to a consensus phenotype; they exhibit enhanced reduction of the PQ pool in the dark and a reduced rate of electron flow at the onset of illumination (51, 53, 241). These features were interpreted as resulting from a "Pasteur effect," i.e., activation of glycolysis due to lower cp ATP levels in the dark because of the absence of mitochondrial ATP input. These *dum* mutations did not affect PET rates under steady-state, CO_2 saturating conditions (53), suggesting that only a minor fraction of photosynthetic electrons are diverted to respiration when photosynthesis is fully active. In addition to the *Chlamydomonas dum* mutants, the *cms2* mutant of tobacco is probably the best-studied respiratory mutant in plants (212). Its extensive analysis confirms the role of respiration in "supporting" photosynthesis at the onset of illumination (73) and suggests functions with respect to the control of redox state homeostasis (reviewed in Reference 211).

A direct role of respiration in providing ATP to the Calvin-Benson Cycle is supported by the analysis of a second site suppressor mutant of a cp ATP synthase mutant of *Chlamydomonas*. In contrast to the original mutant, this suppressor strain (still devoid of cp ATP synthase) can grow photoautotrophically, suggesting that in this new genetic context, the energetic coupling between mitochondria and chloroplasts is tight enough to provide ATP for high rates of CO_2 assimilation in vivo (162). These results clearly demonstrate the potential of the malate shuttle as a source of ATP for photosynthesis.

Cyclic electron flow around PSI. Electrons generated on the reducing side of PSI can be reinjected at its donor side (**Figure 3**). First discovered by Arnon (14), this CEF may be very important in counteracting hyperreduction of PSI (129). First observed in vitro, there has been a long debate as to whether CEF exists under physiological conditions and if so, what its function might be. There is growing evidence that it can be a constitutive activity, increasing under stress conditions such as low temperature and drought (reviewed in References 129, 132, 256, 271; see also 146).

Despite the large number of studies devoted to CEF, the actual pathway by which electrons are transferred from the acceptor back the donor side of PSI is still under debate. At least two major routes for CEF have been identified. The first involves the activity of a cp NDH (NAD(P)H plastoquinone reductase) complex, analogous to Complex I of the mitochondrial respiratory chain, which would catalyze electron transfer from NADPH (or NADH) to the PQ pool (**Figure 3**). A cp-localized protein complex similar to that of the mitochondrial enzyme was inferred from analyses of cp and nuclear genomes of vascular plants (reviewed in Reference 256). The subunit composition of the tobacco NDH complex was determined, and the role of each subunit defined by phenotypic analysis of *Arabidopsis* mutants (255). A genetic screen based on fluorescence transients following illumination led to identification of several nuclear factors required for the proper assembly of the NDH complex (144, 273). However, these studies have not yet clearly defined the contribution of the NDH complex in CEF; *ndh* mutants are not specifically altered with respect to maximal CEF rates (202).

A second CEF pathway is dependent on an as-yet unidentified activity called FQR (ferredoxin-quinone reductase), which catalyzes direct oxidation of reduced Fd by the PQ pool (**Figure 3*a***). The contribution of FQR to CEF was deduced by treating cells with antimycin A, a specific inhibitor of CEF in vitro (reviewed in Reference 32). However, no biochemical or in vivo studies have been reported that confirm a role for FQR in CEF. Recent characterization of the *pgr5* and *pgrl1* mutants (197), along with genomic analyses (see below) suggest that CEF may be modulated by a novel

complex that contains PGR5 and PGRL1 proteins; the latter provides a membrane anchor for the complex (66). It is tempting to suggest that the PGR5/PGRL1 complex is part of the FQR enzyme, as suggested by Shikanai et al. (271), as mutant strains have a reduced efficiency in reducing the pool of PQ in vitro (197). However, in vivo experiments tend to suggest a regulatory role for PGR5/PGRL1 rather than a direct involvment of this complex in CEF (66, 202). Alternatively, FQR has been linked to the cyt b_6f complex, and in particular to the c′ heme (282), which has been proposed to be a cofactor responsible for reduction of the PQ pool by stromal reductant (see 130). Understanding the coordinate control of CEF relative to LEF and the different pathways for electron flow is a critical step for further understanding of CEF. Several models have been proposed in the past (105).

(*i*) *Restricted diffusion model*. Photosynthetic protein complexes show heterogeneous lateral distribution in thylakoid membranes. PSII is mostly in appressed grana stacks, whereas PSI is concentrated in the nonappressed stroma lamellae, grana margin and end membranes. In contrast, the cyt b_6f complex is homogeneously distributed (reviewed in Reference 3). Because of restricted diffusion of soluble electron carriers (see 157), it has been proposed that PSII transfers electrons only to those cyt b_6f complexes located in the grana. This would elicit LEF involving PSI complexes located at the periphery of grana stacks. Ultimately, NADPH would be generated at the grana margins and/or ends and then, with ATP, be used to fuel the Benson-Calvin cycle. PSI in the stroma lamellae would also reduce Fd, but the latter would only have access to cyt b_6f for driving CEF (3). This model suggests that there is little competition between LEF and CEF because the processes are spatially separated. The small amount of PSII in the stroma lamellae, in the "cyclic compartment," would correspond to those undergoing repair after photodamage (see below; 15) and/or providing a light-induced source of reductant that contributes to redox homeostasis when PSI of the stroma lamella become too oxidized. The NDH complex in the stroma lamellae may also participate in this process via a redox-dependent injection of electrons into the PQ pool. Additionally, a PQ terminal oxidase (PTOX) (227) in the thylakoid membranes may serve as a safety valve, withdrawing electrons upon hyperreduction.

Finally, limiting the access of CEF-reduced Fd molecules to the space between neighboring, appressed membrane stacks would shield the cyt b_6f complex in the grana from CEF-generated electrons, which could potentially over-reduce this complex and interrupt LEF.

(*ii*) *The supercomplex model*. Based on differences in the lateral distribution of PSI and PSII, the notion that LEF and CEF need to operate within two distinct thermodynamic compartments has been expanded into the supercomplex model, where CEF in plants occurs within tightly bound PSI-cyt b_6f supercomplexes that contain stoichiometric amounts of PC and Fd (131). This model accounts for the finding that electrons generated on the PSI acceptor side by CEF are not shared with the soluble acceptor pool; they appear to be thermodynamically isolated from the stroma (131). Although no such supercomplexes with altered CEF efficiency have been isolated (47), a recent analysis of *Arabidopsis* has shown that some Fd molecules are bound to thylakoid membranes in an amount that varies in mutants with different CEF capacities (66). Because no NADP reduction occurs unless exogenous Fd is added to these isolated thylakoids, it is tempting to speculate that the bound Fd is trapped within a PSI-cyt b_6f supercomplex and not accessible to NADP-mediated electron transport.

(*iii*) *FNR model*. FNR partitions between the stroma and thylakoid membranes, where it is bound to either PSI or cyt. b_6f (see 328). It has been proposed that a PSI-FNR complex fosters efficient LEF (i.e., NADP reduction) within a PSI-Fd-FNR ternary complex (132). Conversely, PSI complexes free of FNR would only reduce Fd, which would then freely diffuse in the stroma stimulating CEF, via interactions with cyt b_6f. Although attractive, this model has not been experimentally verified. Experimentation using RNAi lines of tobacco

PTOX: plastoquinone terminal oxidase

FNR: ferredoxin NADP reductase

P700: primary electron donor to PSI

with reduced amounts of FNR (100) should provide a valuable resource for evaluating this hypothesis.

(*iv*) *Competition model.* A more dynamic view of CEF has been proposed to account for increased CEF efficiency upon reduction of the PSI electron acceptors by a short preillumination of dark-adapted leaves (47). This view envisions competition between CEF and LEF for reducing equivalents. Under steady-state illumination, this competition would favor LEF, possibly because of a higher efficiency of Fd reduction. CEF would dominate as the redox state of PET components increases. This hypothesis is supported by studies in which dark-adapted leaves, or leaves subjected to limiting CO_2 levels showed high rates of CEF upon illumination (94). In such material, the Benson-Calvin cycle is largely inactive and illumination causes rapid reduction of PSI electron acceptors, a prerequisite for CEF (reviewed in Reference 129). Based on this simple regulatory mechanism, changes in CEF relative to LEF rates would reflect a change in the level of reducing equivalents stored in the PSI donor pool, providing a flexible system to achieve efficient CO_2 assimilation without wasting absorbed excitation energy (see 132).

Downregulation of the Rate of PET

Numerous processes in addition to the engagement of alternative electrons sinks downstream of PSI modulate PET activity. The two main products of PET, reducing equivalents (e.g., NADPH) and a *trans*-thylakoid ΔpH that drives ATP generation, participate in feedback mechanisms that control the overall photosynthesis rate (**Figure 3*a***). The light-generated ΔpH plays a major role in modulating light-harvesting efficiency, which participates in electron transport control at low light (NPQ 112; see below). However, the ΔpH also affects photosynthetic electron flow directly, by modulating the rate of PQ oxidation at the lumenal site of the cyt b_6f complex. This kinetic effect, known as "photosynthetic control," is the consequence of the tight coupling between electron and proton transfer during oxidation of PQH_2 (reviewed in Reference 110) (**Figure 3*a***). Lumen acidification typically decreases the rate of PQH_2 oxidation by three-to fourfold, strongly suggesting that this kinetic step is a bottleneck in the overall process of photosynthesis. At variance with conditions in which photosynthesis is limited by CO_2 assimilation, where all electron donors upstream of PSI should be reduced, the onset of photosynthetic control should lead to the oxidation of the electron carriers located downstream of the cyt b_6f (i.e. PC and P700), and to the concomitant reduction of electron carriers located upstream of this complex (i.e., the PQ pool).

Experiments demonstrating that increasing light intensity leads to a progressive accumulation of $P700^+$ and PQH_2 have provided strong evidence that photosynthetic control causes the limiting step of photosynthesis to move from the PSI acceptor side to the cyt b_6f complex. However, other processes may affect the limiting step in PET. Recent data from tobacco WT plants of increasing leaf age, and mutant plants with abnormal sugar export from mesophyll cells, have shown that the rate of light-saturated electron flow becomes sensitive to the amount of PC in the lumen (266).

What is the rationale for moving the limiting step of photosynthesis as light intensity increases? Hyperreduction of photosynthetic electron carriers causes photodamage, mainly mediated by the generation of reduced O_2 species. It is likely that sustained oxidation of P700 resulting from a kinetic limitation at the level of the cyt b_6f complex efficiently protects PSI from oxidative damage. It is generally assumed that PSII is the primary target of photoinhibition (see below; 15). However, PSI can also be photodamaged, when the cells experience stress conditions [e.g., low temperature (277)] that impair electron flow (248). The mechanism of PSI photoinhibition likely involves overreduction of electron carriers on the acceptor side of the PSI complex (FX and FA/FB) and their interaction with $O_2^{\cdot-}$, which triggers the production of hydroxyl radicals. Therefore, limiting the rate of electron

flow upstream of PSI by photosynthetic control should decrease the photosensitivity of the PSI complex.

Steps in regulating PET have also been inferred from studies of various mutant strains. For example, extensive PSI photoinhibition is observed in both *pgr5* and *pgrl1* mutants (197; G. Finazzi & P. Joliot, unpublished), which lack one of the two components of the PGR5-PGRL1 complex. The phenotype is consistent with inhibition of CEF, resulting in decreased ATP availability and overreduction of PSI acceptors (197). Alternatively, these mutants may experience a change in the coupling of electron flow to photophosphorylation, due to a change in the phosphate potential (ATP/ADP x Pi), as suggested by Kramer and colleagues (64, 146) This condition may also cause hyperreduction of PET (19). However, analysis of the *pgr5* mutant is not consistent with both of these hypotheses; CEF and ΔpH are only slightly reduced in the mutant under conditions in which PSI inhibition is sustained (202). It was then hypothesized that increased PSI photosensitivity of the *pgr5* mutant stems from a deficiency in redox-mediated regulation of PET. Indeed, both *pgr5* and *pgrl1* display chronic hyperreduction of P700 in continuous light under conditions in which sustained P700 oxidation is observed in WT cells.

A redox-based control of PET was previously proposed (128, 152). Recent work (101) provides an experimental rationale for this hypothesis. Light-induced redox changes of P700 in WT and transgenic lines of tobacco in which photosynthesis was inhibited by antisense suppression of either FNR or GAPDH (glyceraldehyde 3-phosphate dehydrogenase), which should result in rapid accumulation of reduced Fd or NADPH, were compared. Photosynthesis was similarly reduced in both transgenic lines, with P700 more oxidized in as-GAPDH plants than in the WT, although no oxidation of P700 was observed in as-FNR plants. Because the rates of photosynthesis and the extent of the ΔpH (evaluated indirectly through the onset of NPQ, see below) were similar in the different lines, changes in photosynthetic control were excluded as a possible cause for the different redox states of P700. Instead it was proposed that redox poise of the $NADP^+$/NADPH pool may control electron flow at the level of the cyt b_6f complex by a direct negative feedback loop. Based on the similarity between the phenotypes of as-FNR and *pgr* mutants, it has been proposed that the PGR5-PGRL1 complex may participate in redox regulation of cyt b_6f activity, through a still unknown mechanism (101).

Adaptation: a process of natural selection by which the genetic information in an organism changes through accumulation of mutations or lateral gene transfer

Alternative Mechanisms for a Regulation of PET

Whereas electron diversion at the acceptor side of PSI and downregulation of the catalytic efficiency of the cyt b_6f complex by acidification of the lumen represent the major modes of adjusting the rate of PET with the rate of CO_2 assimilation in plants and freshwater algae, recent findings suggest that other regulatory processes may dominate in other photosynthetic environments. The recent analysis of photosynthesis in both the prokaryotic and eukaryotic marine phytoplankton has revealed a novel mechanism of adaptation of photosynthesis. Photosynthesis in the oligotrophic regions of the oceans is usually limited by nutrient availability, which results in a strong reshaping of the photosynthetic apparatus. Typically, Fe levels impose a strong constraint on the amount of this element that can be incorporated into the photosynthetic complexes (see below), which may result in an imbalance between the amount of PSII and of PSI synthesized; the latter is dramatically reduced owing to its high Fe requirement for stable assembly (reviewed in Reference 181). Instead of experiencing sustained photoinhibition because of overreduction of PSII, these marine photoautotrophs undergo rerouting of PSII-generated electrons into a water-to-water cycle, catalyzed by a PQ terminal oxidase (PTOX) (**Figure 3*a***). In both cyanobacteria and the picoeukaryote *Ostreococcus*, this alternate electron flow to O_2 is prominent, with ~50% of the electrons generated from H_2O oxidation routed to the reduction of O_2 at the cost of CO_2 fixation (21, 52). When photosynthesis is

limited by PSI availability, as in the case of Fe deficiency, this PTOX-catalyzed water-to-water cycle has a major advantage relative to electron flow to other sinks. It still allows the development of a ΔpH-mediated NPQ response, which should contribute to photoprotection, and fuel ATP synthesis for housekeeping purposes, despite the limited PSI capacity. Similar to CEF in plants experiencing high light and CO_2 limitation, the water-to-water cycle around PSII may increase the ATP synthesized per PSI turnover and help sustaining cell survival during nutrient deprivation or other conditions leading to a significant drop in the PSI levels.

A similar phenomenon was reported in the high mountain plant *Ranunculus glacialis* (360). This species counteracts photodamage under high light and low temperature conditions by reversibly increasing the levels of PTOX in the thylakoid membranes. The conditions experienced by photosynthetic organisms in the open ocean and in the high mountain environment share some common features, i.e., a stress situation that combines exposure to highly fluctuating light intensities and reduced photosynthetic performance. Under both conditions, rerouting electrons through a kinetic competition between PTOX and the cyt b_6f complex modifies the overall rate of LEF almost instantaneously, providing a very strong advantage under light fluctuating conditions relative to the NPQ response, which has an onset/relaxation time of several minutes (owing to the slow process of zeaxhanthin to violaxanthin epoxidation) (**Figure 4, 5**).

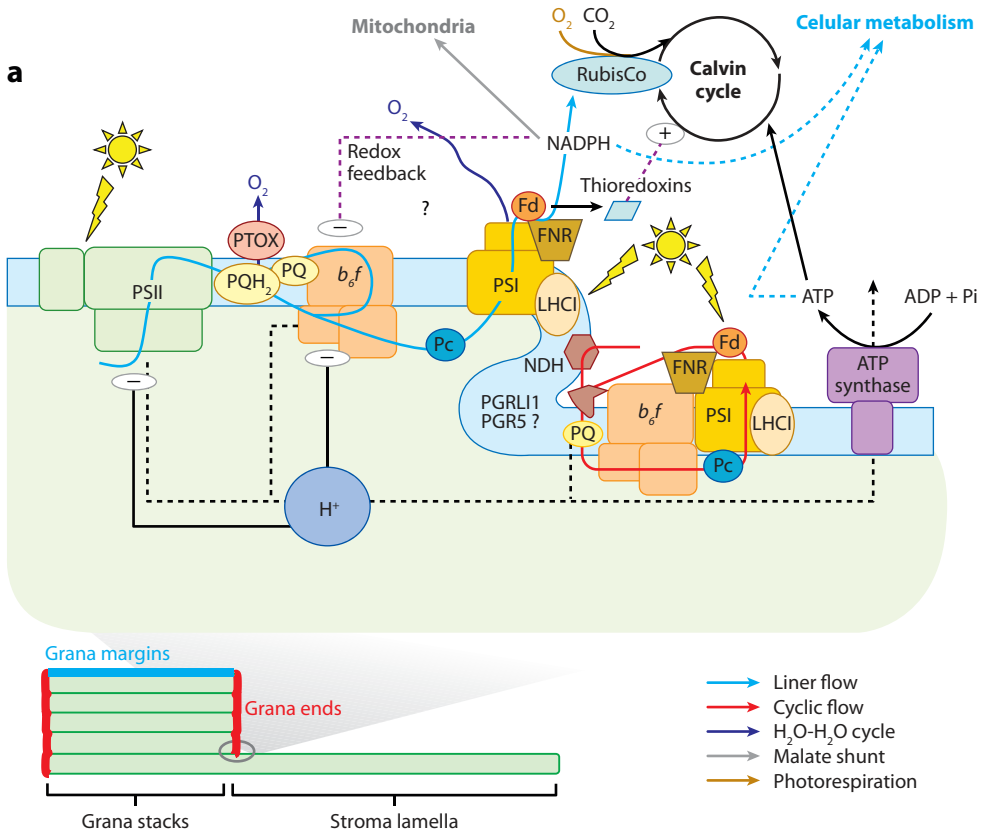


Figure 3

(*Continued*)

Competition Between Alternative Electron Transfer Pathways?

In summarizing the contributions of the various alternative pathways for PET, a somewhat paradoxical picture emerges: in plants O_2 reduction by PET can account for up to 60% of the electrons generated by photosynthetic H_2O oxidation through photorespiration [20%, (219)], the Mehler reaction [30%, (17)], and respiration [10%, malate shuttle, (153)]. In marine organisms, this process can reach 40%–50% of overall PSII-driven electron flux based on PTOX activity alone (21, 52). In addition, 25% of the PSI acceptor side electrons may fuel CEF (132), while another ~15%–20% can be directed toward metabolic and regulatory pathways. Together, these data suggest that the quantum yield of photosynthesis should be extremely low because LEF from H_2O to CO_2 should represent a limited fraction of overall electron flow.

This seeming paradox likely reflects the difficulty in quantifying alternative pathways in vivo. Measurements of photosynthesis under fluctuating environmental conditions can result in multiple, overlapping feedback loops that modulate both electron flow and light-harvesting efficiency. In addition, acclimation processes that develop as environmental conditions fluctuate, or adaptation processes that have evolved in distinct environmental niches, would affect concentrations and/or activity of components that influence the various PET activities. Future advances in understanding the physiology of photosynthesis will require the analysis of acclimation in organisms well chosen for their contrasting ecological niches (e.g., 208, 271).

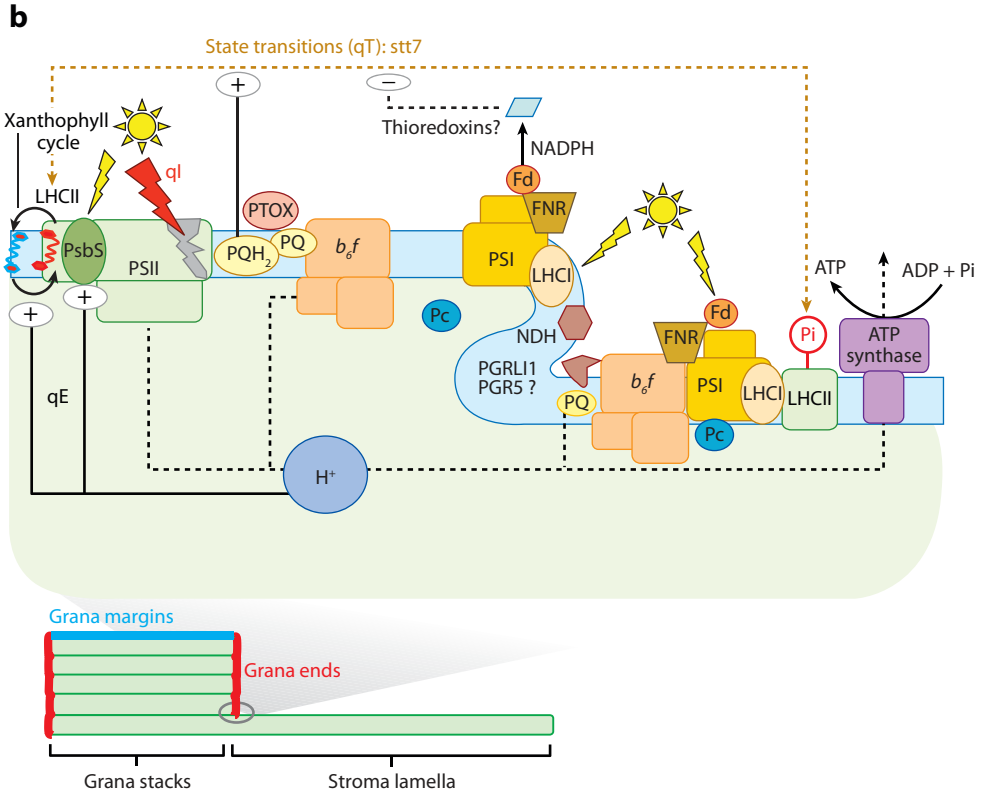


Figure 3

(*Continued*)

Q_A: primary quinone acceptor of Photosystem II

qI: photoinhibition component of NPQ

qT: State transitions component of NPQ

LHC: light-harvesting complex

qE: energy dependent component of NPQ

Regulation of Light-Harvesting Capacity

Photosynthesis is regulated by mechanisms that affect the rate of excitation of the two photosystems. These mechanisms mainly act at the level of PSII and are collectively referred to as nonphotochemical quenching (NPQ) because they decrease the fluorescence yield of PSII centers when the Q_A quinone is reduced (see Reference 112 for a review). According to a definition based on NPQ relaxation kinetics (112), there are three distinct components (**Figure 2*b***): (*i*) qI, mainly related to photoinhibition, or a slowly reversible damage to PSII RC (16); (*ii*) qT, state transitions, a change in the relative size of the antenna associated with PSII and PSI; this involves movement of the LHCII (light-harvesting complex) antenna between reactions centers, a process triggered by reversible phosphorylation of specific LHCII polypeptides (4); and (*iii*) qE or "high energy state quenching," which is associated with the development of a low pH in the thylakoid lumen (e.g., 320).

ΔpH dependent quenching (qE). This process is reflected by a decrease in the fluorescence quantum yield through generation of a light-dependent pH gradient across the thylakoid membranes (48, 320). The onset of qE is largely enhanced by deepoxidation of violaxanthin to zeaxanthin (254), a process catalyzed by a thylakoid-bound deepoxidase that is activated by a low lumenal pH (233) (**Figure 3*b***).

Figure 3

The complex picture of photosynthesis: branched pathways in photosynthetic electron flow, superimposed on highly regulated light excitation processes. Thylakoid membranes display a heterogeneous distribution of photosynthetic proteins, with PSII enriched in stacked membranes in the grana regions and PSI enriched in unstacked membranes in the stroma lamellae regions (*lower panel*). Photosynthesis activity results from the balance between light absorption and its utilization for CO_2 assimilation. (*a*) Electron flow can be redirected to alternative pathways, which depends on changes in compartmentalization or in interaction between photosynthetic proteins. This modulates the efficiency of LEF (*blue*) and CEF (*red*). As shown here, compartmentalization may occur within supercomplexes, including all required electron carriers, or it may depend on a kinetic competition between the cyclic and linear pathway in a freely diffusing system. Red arrows point either to a direct reinjection of electrons from the PSI acceptor side to the plastoquinone pool or to an activity of the chlororespiratory enzyme NDH. Electron diversion at the PSI acceptor side also occurs via the water-water cycle catalyzed by the Mehler reaction (*dark blue*), or the export of reducing equivalents for a diversity of metabolic pathways (e.g., to the mitochondrion via the malate shuttle, *gray*). Electrons generated in PSII can be rerouted toward oxygen at the level of the plastoquinone pool, before reaching cyt b_6f and PSI, via the catalytic activity of the chlororespiratory enzyme PTOX (*dark blue*). *Gold line*: photorespiratory activity of RuBisCo. Photosynthetic electron transfer generates an electrochemical proton gradient across the thylakoid membranes ($\Delta\mu H^+$), which is used for ATP synthesis. Steady-state $\Delta\mu H^+$ results from proton pumping by photosynthetic electron flow and proton consumption for ATP synthesis. The size of $\Delta\mu H^+$ is modulated by the overall metabolic state through ATP/ADPxPi ratio. $\Delta\mu H^+$ controls the rate of electron flow at the level of cyt b_6f and PSII complexes. The redox state of PSI electron acceptors, particularly the NADP/NADPH ratio, may also control cyt b_6f complex activity. (*b*) Thermal dissipation in outer antenna of PSII within LHCII (qE) is modulated by the xanthophyll cycle and the PSII minor subunit PsbS (PSII-S). Both processes are triggered by acidification of lumenal pH, which activates violaxanthin deepoxydase, and triggers protonation of two conserved glutamic residues on PsbS. A regulatory kinase (STT7), activated by reduction of intersystem electron carriers, produces reversible protein phosphorylation that induces changes in association of a fraction of antenna proteins between PSII and PSI in a process known as State Transitions (qT). The kinase may be downregulated by reduced thioredoxins. This double control system provides an efficient feedback signaling, which matches light absorption capacity of each photosystem to the redox state of the electron transfer chain. Photoinhibition (qI) is observed upon overexcitation of the photosystems with respect to the capacity for photo-induced electron transfer. Fd, ferredoxin; FNR, Fd: $NADP^+$ reductase; Pc, plastocyanin; PQ, plastoquinone; PTOX, plastoquinone terminal oxidase; NDH, NADP plastoquinone reductase.

This process is reversed by the epoxydation of zeaxanthin to violaxanthin, which is a relatively slow process. More specifically, qE is defined as the shortening of a specific chl fluorescence lifetime [e.g., from ~2 to 0.3 ns in land plants (93) under conditions in which PSII centers are fully reduced]. It results from the onset of a nonradiative, nondamaging deactivation of singlet excited chlorophyll. Since qE is easily detectable (see **Figure 2*b***), it is a convenient measure of the condition of both WT and mutant plants under different environments conditions (reviewed in References 108, 111, 154, 208, 218, 236, 287).

The site and mechanism(s) of qE have been long debated, until an elegant genetic approach developed in *Chlamydomonas* and *Arabidopsis* led to the isolation of mutants with modified NPQ responses. This screen was based on the identification of strains unable to decrease their Fm upon exposure to high light (see **Figure 2**). Since most of these mutants were deficient in the xanthophyll cycle (208), there is now a consensus that the major form of qE occurs within the PSII antenna and involves xanthophylls. Fluorescence quenching may be induced by direct energy transfer from chl to carotenoids. It has been proposed that the S1 energy level of violaxanthin would lie above the Qy transition of chl, whereas the opposite would be true of zeaxanthin (reviewed in Reference 84). Thus, violaxanthin deepoxidation would represent a source-sink transition with respect to the directionality of energy transfer between chl and carotenoids. Although extremely appealing, this hypothesis has been challenged by Polivka and colleagues, who found that the (forbidden) S1 levels of antheraxanthin and zeaxanthin were both probably below the Qy transition of chl (237). Alternatively, conformational changes that influence qE may occur upon binding of carotenoids to the antenna complexes (111). Consistent with this hypothesis are recent Raman resonance and ultrafast optical spectroscopy data (226, 254), which suggest that aggregation of LHCII molecules results in quenching amplification by a mechanism involving one of the luteins bridging the first and third helices of LHCII, as well as xanthophyll cycle carotenoids. Finally, quenching may occur via a charge transfer within a chl-carotenoid dimer, i.e., a species in which there is a strong overlap of the π-electrons of carotenoid and chl. A recent analysis of NPQ mutants of *Arabidopsis* by ultrafast spectroscopy supports this hypothesis; qE may proceed through the generation of a chl-zeaxanthin excited state that is capable of quenching bulk chl fluorescence, and then relaxing through the generation of a $chl^{-\cdot}$ and $zeaxanthin^{+\cdot}$ charge-separated state that quickly back-reacts to the ground state (109).

A genetic approach has also revealed the existence of previously unknown components of the NPQ machinery. These include the minor PSII subunit PSII-S (PsbS) (164), see **Figure 3*b***) and the recently identified LHCSR2 and 3 in *Chlamydomonas* (G. Peers & K.K. Niyogi, personal communication). A null mutation in PSII-S, a polypeptide of apparent molecular mass of 22 kDa, in the *npq4* mutant of *Arabidopsis* results in a substantial qE reduction, while PSII-S overexpression amplifies the quenching response (166). Furthermore, lumenal-exposed glutamates in PSII-S appear to be involved in sensing the pH of the lumen. However, although these results demonstrate that PSII-S is required for qE development in plants, its exact role in the process remains unclear (210). A major issue with respect to qE is whether PSII-S binds the qE quenching pigment(s), and/or if it acts as an allosteric regulator. Clearly, PSII-S modulates the pH-dependence of qE, as removal of specific, stromal exposed glutamic acid residues completely abolishes qE in *Arabidopsis* (165). Furthermore, transcriptomic (138, 151, 199) and proteomic studies (92) reveal an upregulation of PSII-S upon exposure of *Arabidopsis* and rice to excess illumination (see below).

LHCSR proteins of *Chlamydomonas* belong to the LHCII family, but do not share features with PSII-S, except that the transcripts encoding these proteins also significantly increase when the organism experiences stress (see below). LHCSRs are absent in land plants, but present in a variety of photosynthetic

organisms, like diatoms (13), that show an extremely high NPQ capacity.

It is tempting to propose that several mechanisms are used by photosynthetic organisms to achieve a pH-dependent downregulation of PSII excitation under conditions that lead to hyperreduction of the photosynthetic electron transport chain. In this sense, there is parallel between the regulation of light harvesting and of electron flow. These different strategies have probably converged during evolution to control the redox state of electron transfer components. The physiological relevance of qE is suggested by the observation that it is present in most, if not all, photosynthetic organisms, and that mutants with an impaired xanthophyll cycle show a reduced fitness when exposed to naturally fluctuating conditions (149). However, the role of qE in photoprotection has been questioned on an experimental basis (261).

State transitions (qT). Since the light-harvesting antenna of the two photosystems have distinct absorption spectra, changes in the spectral composition of the incident light affects the relative excitation of the two photosystems. State transitions were first described in unicellular photosynthetic organisms (45, 198) as a mechanism for balancing the absorption capacity of the photosystems in an environment in which the light quality was changing. This phenomenon involves a reversible association of the major LHCII antenna with PSII in state 1 or PSI in state 2 (reviewed in References 4, 318), and depends on phosphorylation of LHCII by a membrane-bound protein kinase, which in turn causes association of LHCII with PSI in the stroma lamellae, grana ends, and grana margins (**Figure 3*b***). Two hypotheses have been proposed to explain this phenomenon. It may be triggered by conformational changes within LHCII proteins upon phosphorylation (207), leading to docking of P_i-LHCII to PSI. This process is likely mediated by the PSI-H subunit; an *Arabidopsis* null mutant for this protein undergoes no state transition (171). Additionally, lateral displacement of LHCII may be favored by electrostatic repulsion due to increases in negative charges at the thylakoid surface upon LHCII phosphorylation (reviewed in Reference 4).

qT is a slower process than qE (**Figure 4**). Moreover, while qE is related to electron flow via the formation of an electrochemical proton gradient across the thylakoid membranes, state transitions are directly triggered by changes in the redox state of the electron transfer chain. The kinase responsible for LHCII phosphorylation is activated upon reduction of intersystem electron carriers (**Figure 3*b***). The kinase may be deactivated upon subsequent reoxidation of the intersystem electron carriers. In vitro studies suggest that state transition may also involve suppression of LHCII kinase activity by reduced thioredoxin (246) (**Figure 3*b***). The redox state of the thioredoxins would fine tune photosynthetic performance by coordinating the light absorption charactistics of the photosystems to redox regulation of key enzyme activities of the Benson-Calvin cycle (reviewed in Reference 50).

Dissecting the molecular mechanism underlying state transitions and the physiological consequences of the process has been challenging. The absence of state transitions in *Chlamydomonas* and plant mutants lacking the cyt b_6f complex first suggested a role for this complex in transducing redox signals from intersystem electron carriers to the kinase that triggers a state transition (reviewed in Reference 318). The control of state transitions was further explored using genetic and biochemical approaches (305, 332). The kinase involved in state transitions was identified in *Chlamydomonas* using a fluorescence-based screening procedure which took advantage of the distinct fluorescence features associated with states 1 and 2 (68). A mutant locked in state 1, *stt7*, fails to phosphorylate LHCII proteins under conditions that favor state 2. The *STT7* gene encodes a thylakoid-associated ser-thr protein kinase required for LHCII phosphorylation, but it is not yet known whether it is a part of a kinase cascade or whether LHCII serves directly as a substrate (e.g., 250 for a further discussion). Two STT7 homologs exist in land plants, STN7 and STN8

(31), which phosphorylate different substrates (44, 299).

Several thylakoid membrane proteins of PSII and LHCII undergo light- and redox-dependent phosphorylation. In *Chlamydomonas*, 15 thylakoid proteins, mostly PSII core subunits and LHCII polypeptides, are differentially phosphorylated when the cells are in state 1 relative to state 2 (297). Of particular interest is the finding that a minor PSII antenna component, CP29, undergoes sequential, multiple phosphorylations. Two sites are phosphorylated under state 1 conditions, two additional sites under state 2 conditions, and three additional sites under high light. The differential phosphorylation of CP29 likely introduces an additional level of flexibility to LHC function, and may be modulated by redox activating (reduction of intersystem electron carriers) and deactivating (reduction of thioredoxins) signals (reviewed in References 250, 304). Owing to the tight interplay between changes in the redox state of photosynthetic electron carriers and the occurrence of state transitions, this kinase-mediated process may well serve a dual function in metabolic control and signal transduction.

(*i*) *Metabolic implications of state transitions.* In plants, state transitions balance the absorption properties of the two photosystems in low light. This process does not seem essential for plant survival, as suggested by the limited phenotypical change associated with *Arabidopsis* mutants unable to perform state transitions as a consequence of a loss of PSI-H or STN7 (85, 172). State transitions in *Chlamydomonas* are larger than in plants: 85% of the LHCII of *Chlamydomonas* is implicated in this process, whereas only 20%–25% of the LHCII complexes are involved in plant state transitions (discussed in Reference 318). Because of this large LHCII redistribution, state transitions in *Chlamydomonas* may not simply fulfill the role of balancing light absorption between the photosystems, as in plants. Instead, they may increase the performances of PSI at the expenses of PSII, potentially representing a switching mechanism that converts the organism from predominantly LEF to predominantly CEF (discussed in References 80, 318).

(*ii*) *State transitions in intracellular signaling.* In addition to short-term acclimation processes, longer-term changes can cause an overall change in the amount of PSII and PSI antenna proteins and lead to readjustment of photosystem stoichiometry (**Figure 4**) (e.g., 8). Such responses may involve signaling networks that coordinate nuclear and cp gene expression (reviewed in Reference 232). It is not clear if STT7, or its plant homologue STN7 (31), are involved in this long-term acclimation. In land plants, illumination for several days with PSI-enriched light increased PSII antenna size. The opposite was observed when plants were illuminated with PSII-enriched light. This long-term acclimation no longer occurs in the *stn7* mutant (44), sugggesting that this kinase may function in both short- and long-term acclimation responses. However, this possibility is not consistent with plant transcription patterns (see below; 44, 292), and no such long-term responses have been noted in *Chlamydomonas* cells (250).

Photoinhibition (qI). PSII and water oxidation are extremely susceptible to ROS-mediated photoinactivation (e.g., 16, 220). This process is counterbalanced by a repair process that involves partial disassembly of inactive PSII, proteolytic degradation of the photodamaged reaction center protein D1, and cotranslational insertion of newly synthesized D1 into PSII (reviewed in Reference 16, 23).

The repair cycle in plants requires a lateral migration of PSII complexes between grana and stroma membranes, as recently confirmed by a proteomic analysis of *Arabidopsis* (15). The process is modulated by phosphorylation of PSII, which leads to the dissociation of the RC into monomers and migration of the monomers from the grana to the stroma lamellae. The degradation of damaged D1 proceeds from its stromal-exposed N terminus. N-terminal phosphorylation of D1 in plant may protect it from degradation. D1 degradation requires the activity of the DEG-P2 and FTS-H proteases (reviewed in Reference 2). There are other

CP: chlorophyll protein

ROS: reactive oxygen species

cp proteases that participate in a range of repair and housekeeping functions and that likely contribute to the dynamics of photosynthetic function (1, 6, 10).

PHOTOSYNTHESIS DYNAMICS AND SIGNALING PROCESSES

The functional flexibility of the photosynthetic apparatus described above allows photoautotrophs to rapidly cope with fluctuating environmental conditions. These rapid responses are essentially autonomous from longer-term acclimation responses that require changes in gene expression. In the face of sustained changes in light intensity or nutrient availability, which can depend on habitat, seasonal differences and diurnal rhythm, acclimation responses can take hours to days and depend on de novo transcription and translation (**Figure 4**). Such acclimation processes may involve changes in the antenna/RC and/or PSI/PSII ratios (8). Such responses may also require communication among the different subcellular compartments. Modifying photosynthetic performance in response to environmental change involves changes in the nucleocytoplasmic contribution to the physiological functions of the cp. The critical nature of this contribution reflects the fact that the two compartments share the genetic information required to construct the individual complexes of the photosynthetic apparatus. Over the past decade experimental evidence has accumulated to support intercompartmental control. We refer to forward signals as those involving nuclear control of cp gene expression (24, 30, 59, 176, 249, 317), while retrograde signaling

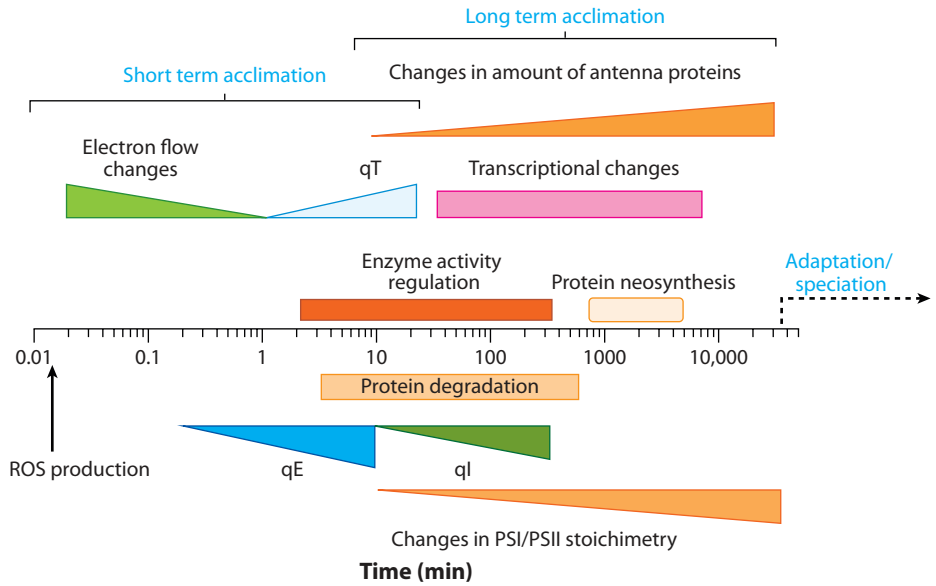


Figure 4

Time scale of major short-term and long-term acclimation processes in vascular plants. The diagram represent "consensus" time scales for regulation of light-harvesting capacity (the qE, qT, and qI components of NPQ) as well as rates of electron flow. Short-term acclimation processes also include regulation of enzymatic activities e.g., via kinase-dependent phosphorylation cascades, as well as protein-degradation mechanisms involved, for example, in acclimation to nutrient stress or for housekeeping purposes. On longer time scales, changes in gene expression and net protein synthesis processes are induced, which contribute to acclimation to both biotic and abiotic stimuli. Eventually, adaptation processes develop, which involve genetic changes leading to irreversible acclimation to specific environments, opening the way to speciation process.

describes potential cp factors that control the expression of nuclear genes (28, 86, 155, 161, 213, 229). Here we briefly describe major characteristics of these pathways with an emphasis on the most recent results and their relevance to acclimation.

Nuclear Factors Controlling Posttranscriptional Processes in the Chloroplast

The nucleus controls cp gene expression through a number of nucleus-encoded factors that act posttranscriptionally on specific, or a limited number of, cp target(s) transcript(s). They mainly act on the maturation and stability (M factors) and/or translation (T factors) of cp transcripts. Most such factors were identified using genetic approaches that identified nuclear mutants in *Chlamydomonas* or *Arabidopsis* with altered expression of one or of a small group of cp gene(s) (reviewed in Reference 24). These studies focused either on identification of the various sequence motifs on the cp mRNA targets that were recognized by these factors, the potential activity of the factor, whether they are part of a larger complexes, and where in the cp they are localized. The potential regulatory role of these factors has not been seriously considered, and there are still very few studies that address this issue. A light- and/or redox-dependent regulatory role that might link to transcript stability, splicing, and translation (reviewed in Reference 26) has been proposed for some of these nuclear-encoded elements. Based on in vitro experiments, Kim & Mayfield (137) proposed that a multimeric complex of nuclear-encoded polypeptides control D1 translation in *Chlamydomonas* in a redox- and light-dependent manner. However, it is not clear that all of these potential regulatory factors are specific for D1 translation. In fact, recently, one has been found to also be associated with the D2 and not with the D1 transcript in vivo (267).

Recently, the expression of several *trans*-acting, cp control factors was shown to be modulated in vivo by environmental conditions. The expression of ATAB2, an *Arabidopsis* nuclear factor controlling translation of the D2 subunit of PSII, and PSI-B of PSI was shown to be light-sensitive and under the control of the blue light photoreceptor cryptochromes (see below; 25). In *Chlamydomonas*, the nuclear-encoded factors, TCA1 and MCA1, which act posttranscriptionally on expression of the cp gene *petA* (encoding cyt *f*), vary markedly depending on environmental conditions. For example, MCA1, a protein with a half-life of ~2 h, is rapidly lost when *Chlamydomonas* is deprived of nitrogen; such conditions result in a decline in the level of the cyt b_6f complex (240).

Retrogade Signaling Pathways

Retrograde signaling refers to signaling systems that inform the nucleus of both cp metabolism and gene expression. Current studies suggest that at least four pathways in the cp may generate signals that modulate the expression of nuclear genes. Most of these pathways have not been characterized in detail and they may overlap more extensively than thought originally.

Tretrapyrrole intermediates signaling. Chl precursors had been early suspected to influence light-induced expression of *LHCB* and *RBCS* genes in *Chlamydomonas*: cells treated with inhibitors of the later steps in chl biosynthesis no longer exhibited light-dependent gene expression (125, 126). These observations were confirmed and extended upon by Beck and coworkers (147, 148), who emphasized a specific role of Mg-protoporphyrin IX (Mg-ProtoIX), Mg-protoporphyrin IX-monomethylester (Mg-ProtoIXMe), and possibly of subunit H of the Mg-chelatase complex in retrograde signaling (56). Remarkably, light-induced transcription of the *HSP70 Chlamydomonas* nuclear gene, which is mediated by the tetrapyrrole signaling pathway, can be mimicked in darkness by the addition of exogenous Mg-ProtoIX, but not by the addition of its precursor ProtoIX, although the latter is converted to Mg-ProtoIX and Mg-ProtoIXMe within the cp (148). The authors speculated that light caused release

Mg-ProtoIX: Mg-protoporphyrin IX

Mg-ProtoIXMe: Mg-protoporphyrin IX monomethylester

of an envelope-located Mg-ProtoIX and Mg-ProtoIXMe to the nucleo-cytosol.

Independent work with *Arabidopsis* implicated Mg-ProtoIX, Mg-ProtoIXMe and Mg-chelatase in retrograde signaling (reviewed in Reference 213). A genetic strategy was developed based on findings that carotenoid-deficient plants showed decreased accumulation of several photosynthesis-related transcripts, including that of *LHCB*, most likely as a response to photooxidative damage resulting from the formation of triplet chl that is no longer quenched by carotenoids (reviewed in References 96, 285). Five mutants were isolated that exhibited high-level expression of a reporter gene driven by an *LHCB* promoter in plants exposed to norfluorazon, an inhibitor of carotenoid synthesis. In these mutants *LHCB* transcript accumulation was uncoupled from depressed carotenoid synthesis; the strains were designated genome-uncoupled (gun) mutants. Four mutants (*gun 2–5*) were altered in tetrapyrrole biosynthesis, leading to decreased Mg-ProtoIX and Mg-ProtoIXMe production. Thus, accumulation of Mg-ProtoIX and/or Mg-ProtoIXMe was proposed to inhibit expression of *LHCB* genes. As described below, the fifth mutant, *gun1*, is downstream in the signaling pathway (145). Because biosynthesis intermediates in the tetrapyrrole pathway promote the production of ROS production upon illumination, it is still not clear whether the changes in gene expression relate directly or indirectly to changes in the levels of chl intermediates (see below).

ROS signaling. Three types of ROS are produced in the course of photosynthetic electron flow: $^1O_2$ mainly at PSII and $O_2^{\cdot-}$ and H_2O_2 mainly on the acceptor side of PSI. Shapira and colleagues reported specific ROS control of RuBisCo production in *Chlamydomonas* and tobacco (61, 118). These authors demonstrated that the control was a direct effect on cp translation of the large subunit (LS); translation was inhibited upon a shift from low to high light. This regulation has been ascribed to an oxidative response based on the protective effect of the addition of exogenous ascorbate to the system prior to shifting the organism to high light. In addition, translational arrest could be observed in low light when the $O_2^{\cdot-}$-producer methylviologen was used as a PSI terminal electron acceptor.

Production of ROS in cp dramatically affects nuclear gene expression (87, reviewed in References 11, 155, 187, 190). In *Arabidopsis* the levels of up to 8000 out of 26000 transcripts were affected by ROS generation (87). Although it is difficult to assess the specific contribution of each ROS to retrograde signaling, a $^1O_2$-specific signaling pathway was identified in *Arabidopsis*. The *Arabidopsis flu* mutant accumulates the chl precursor protochlorophyllide in the dark; this does not occur in WT cells owing to a negative feed-back loop of tetrapyrrole intermediates on their precursor conversion (182). When the dark-maintained *flu* mutant is exposed to light, the photosensitized protochlorophyllide elicits the production of $^1O_2$, which causes bleaching of young seedlings or growth arrest in mature leaves. Based on selection and characterization of second-site suppressors of these responses, the genes encoding the thylakoid proteins EXECUTER 1 and 2 were identified (160, 306). A comparative global analysis of transcript changes upon light exposure of dark-adapted *Arabidopsis* WT, *flu*, *ex1flu*, *ex2flu*, and *ex1ex2flu* mutants showed that the flu-controlled $^1O_2$ response was similar to a general stress response that can be induced by pathogen attack, wounding, or light and drought stress. This led the authors to conclude that cp $^1O_2$ production was not primarily part of a photosynthesis acclimation process. However, a definite conclusion awaits a molecular identification of the function of each of the 30 cp-targeted gene products whose transcription is upregulated in the *flu* mutant in an Executer 1-/Executer 2-sensitive manner.

H_2O_2 and $O_2^{\cdot-}$ may have a more direct effect on the regulation of photosynthetic genes. H_2O_2 stimulates the accumulation of some nuclear transcripts encoding PSI and PSII subunits in *Arabidopsis* (69). *Arabidopsis*

"knockdown" plants with reduced expression of the thylakoid superoxide dismutase (247) did not show a net increase in superoxide anions when compared to the WT, probably because of the development of compensatory pathways in the knockdown line. However, the knockdown line may still show a transient increase in $O_2^{\cdot-}$ production in the vicinity of PSI, which may participate in signaling. Indeed, this line had smaller cp, lower chl levels, and decreased photosynthetic rates relative to the parental plants. The knockdown plants also exhibited significant reduction in the accumulation of transcripts encoding antenna proteins, OEEs and FNR. In contrast, transcripts encoding polypeptides of PSII, PSI, the cyt b_6f complex, NADH dehydrogenase, RuBisCo, ribosome and anthocyanin biosynthesis increased, which may reflect a compensatory mechanism for the enhanced degradation of their protein products (247).

Redox signaling. The level of reductants accumulated at the acceptor side of PSI in the stromal compartment (thioredoxins, Fd, NADPH), as well as the redox state of the intersystem electron carriers (PQ, cyt b_6f complex) have been implicated in numerous changes in nuclear transcript levels. Their contributions have been assessed using site-specific inhibitors and mutants of PET. Following the work of Escoubas et al. (75), who demonstrated that the redox state of intersystem electron carriers affects *LHCB* expression in *Dunalliela*, many other reported redox control of expression, both transcriptional and post-transcriptional, of genes encoding photosynthesis-related proteins (e.g., 234; see 79, 319 for a review). The cyt b_6f complex itself has been implicated in the control of the light-induced expression of several genes in *Chlamydomonas* involved in chl biosynthesis: these transcripts no longer accumulate upon illumination of cyt b_6f mutants lacking either the whole complex or having an inactive complex due to an impaired Qo site (269). However, no evidence was found that redox changes were responsible for the altered gene expression.

Little is known about the intermediates that relay cp redox signals to the nucleus. Redox signals from the PQ pool are likely to be transduced through quinol binding to the cyt b_6f complex, eliciting changes in interaction of the ser-thr kinases required with state transitions (see above). The protein kinases associated with cyt b_6f were identified genetically as the *STT*7 gene product in *Chlamydomonas* and the *STN*7 gene product in *Arabidopsis* (31, 68, 250). These kinases have two neighboring, surface-exposed cysteines near their N terminus that are required for kinase activity (250). A thiol/disulfide redox regulation of the kinase raises the possibility of a thioredoxin-mediated, envelope directed, retrograde signaling from the lumen side of the thylakoid memebranes, where kinase activation occurs upon plastoquinol binding to the b_6f complex (332). The STT7/STN7 kinase system could also have targets other than the LHCB proteins and be involved in remodeling of the photosynthetic apparatus during long-term acclimation responses. A paralog *Arabidopsis* gene *STN*8 (*STL1* in *Chlamydomonas*) encodes another thylakoid-bound kinase that participates in the phosphorylation of PSII subunits and may also be part of a signal transduction chain (299). The possible involvement of STN7 and STN8 in retrograde regulation of nuclear photosynthetic transcripts has been investigated in two independent transcriptomic studies. Both studies show that the *stn*7 mutant does not display major differences in photosynthetic transcript accumulation when compared to WT (44, 292). However, the two studies differ in that only one (292) reports a modified thylakoid composition in the *stn*7 mutant when compared to the WT, with upregulation of LHCA1 and LHCA2 and downregulation of LHCB1 at the protein level. Furthermore, the *stn8* mutant displayed moderate to high downregulation of transcripts encoding most subunits of the photosynthetic complexes (44). These results suggest that STN8 either induces expression of photosynthetic genes, or that STN7 in the absence of STN8 has an inhibitory effect on gene expression. That no significant changes

in photosynthesis-related transcripts were observed in the *stn7/stn8* double mutant suggests the second interpretation.

Plastid gene expression signaling. Treatment of plant seedlings with chloramphenicol or lyncomycin, inhibitors of cp translation, causes decreased expression of a set of nuclear genes encoding cp-targeted proteins (reviewed in Reference 96). Thus, it was suggested that a protein synthesized in the cp is involved in retrograde signaling and activates gene expression in the nucleus. This hypothesis has been challenged based on characterization of *Arabidopsis* mutants altered in translation in mitochondria, cp, or in both organelles (228). Downregulation of nuclear expression of photosynthesis-related genes was markedly increased when translation was impaired in both organelles. Based on these findings, the authors conclude that a double signal originating from both organelles was required for efficient retrograde signaling. In such circumstances, it is particularly difficult to rule out a contribution of the energy balance of the plants to the observed changes in transcript abundance. Still the specificity of the changes for nuclear-derived transcripts encoding photosynthesis-related polypeptides supports retrograde regulation rather than a nonspecific ATP effect.

Antenna remodelling: a process in which the light-harvesting capacity is modified by changing the subunit composition and/or organization of the antenna proteins

Supplemental Material

PHOTOPROTECTION OF RC BY ANTENNA REMODELING

Many fluctuations in environmental conditions cause large changes in expression of a diversity of photosynthesis-related genes. These changes are often measured at the transcript level, with no direct evidence for a change in protein content. However, there are several instances in which environmental cues elicit significant modifications in protein composition. Long-term acclimation responses to light have been placed into two categories by Falkowski & Owens (77): the chlorophyte *Dunaliella tertiolecta* copes with changes in growth irradiance by modulating the number of RC, a strategy termed n-type photoacclimation, the diatom *Skeletonema costatum* responds to decreasing growth irradiance by increasing the antenna absorption cross-section, a strategy termed σ-type photoacclimation. Changes in transcripts and polypeptides associated with antenna complexes have been dominant subjects of study since photosynthetic antennae are abundant cellular constituents and undergo marked changes when organisms are shifted between extreme environmental conditions (see **Supplemental Table 3**). Furthermore, antenna remodeling may represent a major strategy used by photosynthetic organisms to protect RC against photodamage. For photosynthetic eukaryotes, antenna complexes are exclusively composed of nuclear-encoded subunits that share the same biosynthetic pathway in the nucleo-cytosol before they are imported into cp. By contrast, the other major thylakoid-embedded complexes involved in photosynthesis are composed of both nuclear and cp-encoded subunits, and complex formation requires coordinated synthesis/assembly that involves distinct genetic compartments. As described below, two environmental changes that primarily affect PSII, upon changes in light intensity, or PSI, upon changes in Fe availability, share as a common feature the remodeling of antenna complexes as a first response to the environmental signal; subsequent responses may involve modification of RC content.

Remodeling PSII Antenna in Response to Light Intensity

In addition to the short-term responses already discussed (qE and qT, see above), acclimation to changes in light intensity can develop on a time scale of hours and be accompanied by altered protein accumulation (**Figure 4**). Perhaps the most dramatic change in photosynthesis during exposure of plants and algae to high light is photoinhibition; a process in which the quantum yield of photosynthesis declines. Photoinhibition, a phenomenon that usually occurs when the rate of light energy conversion is lower than the rate of light energy absorption, primarily affects PSII RC, which are highly

susceptible to photodamage. As discussed above, charge recombination between the PSII primary electron acceptor in its semiquinone state and the oxidized chl donor lead to accumulation of excited triplet chl. These chl molecules can react with O_2, generating $O_2^{\cdot-}$, which can damage PSII and other cell constituents. A repair cycle for PSII exists at all light intensities since even at low light photodamage occurs, although at a low rate (134). However, when repair rate of photodamaged PSII no longer matches its rate of degradation, a net inhibition of photosynthesis (photoinhibition) is observed and the number of PSII RC decreases (16).

Before photoinhibition becomes significant at elevated light intensities, there is a striking change in the complement of light-harvesting proteins. Plants and green algae transferred from low to high light downsize their PSII antenna within a few hours of the transfer (see Reference 180 for a review). These changes suggest a dynamic process that controls PSII light-harvesting capacity. There are six major gene products that contribute to PSII antenna in vascular plants (121). Light-dependent regulation of antenna size was shown to mainly affect LHCB1-2-3-6 proteins, whereas the levels of LHCB4-5 remain unaltered in barley (86) and *Arabidopsis* (22). It is of note that remodeling of light-harvesting antenna is mostly restricted to the *LHCB* gene family, which is mostly associated with PSII, with little, if any, change in LHCA protein content, which harvests light energy almost exclusively for PSI (22, 70). As discussed below, this contrasts to the situation in which PSI antennae are remodeled in iron-starved cells.

Several distinct processes have been implicated in light-driven changes in antenna size. An increased degradation of pre-existing antenna proteins with increasing light intensity occurs in spinach (120, 323), *Arabidopsis* (326), and barley (86). However, decreased translation of antenna proteins and dilution by cell division is key in the overall decrease in antenna content in *Chlamydomonas* (72, 179). Translational repression of LHCB proteins in *Chlamydomonas* is supported by analyses of a dark green mutant that led to the identification of a nuclear factor that binds *LHCBM* transcripts. This factor, designated NAB1, stabilizes the *LHCBM* mRNA and represses its translation by sequestering it in a preinitiation complex (200). A similar decrease in *LHCB* translation was observed upon increased illumination in tobacco (230). All (post)translational changes in LHCII expression in *Chlamydomonas* (72) or *Dunaliella* (58, 177) develop after a transient decrease in *LHCB* mRNAs that could be a consequence of increased turnover or repressed transcription. In summary, the decrease in PSII antenna size upon exposure of plants/algae to increasing light intensity results from a series of regulation processes that include active degradation of pre-existing LHCII antenna proteins and changes in both the rate of transcript accumulation and mRNA translation.

The signal that triggers changes in *LHCB* expression has been controversial. Several researchers have favored ROS signaling since ROS would be produced during absorption of excess excitation and was previously shown to cause decreased *LHCB* expression (214). Intermediates in the tetrapyrrole biosynthesis may also participate (reviewed in Reference 213), although the effect may be indirect. Additionally, a redox signal originating from the PQ pool or from the cyt b_6f complex itself has been implicated in *LHCB* control algae based on site specific inhibitors of PET (58, 75, 230). Consistent with this, the signal operates in low light, in a photosynthesis mutant of barley that was unable to reoxidized intersystem electron carriers upon illumination (86). These authors considered it unlikely that the signaling was through ROS since ROS accumulation is not likely to occur in low light (but see 134).

The existence of complex kinetics associated with changes in LHCB transcript levels argues for a plurality of sensing mechanisms (58). The electrochemical proton gradient established across thylakoid membranes was shown to contribute to the early phase of LHCB control, before being overridden by redox signals generated from intersystem electron carriers. Furthermore, Koussevitsky et al. (145)

demonstrated that three major types of cp retrograde signals (redox signals, cp gene expression signals, and chl biosynthetic intermediates) converge to regulate *LHCBM* expression. Using an *LHCBM* promoter fused to the luciferase reporter gene in *Arabidopsis*, several *gun1* alleles were identified that exhibited altered responses to the three potential regulatory signals. It was thus suggested that the pentatrico peptide repeats protein GUN1 (see above) acts as a common effector in three distinct retrograde signaling pathways, leading to the mobilization of the ABI4 product, a transcription factor that binds to the *LHCBM* promoters contiguous to the light responsive element.

Remodeling PSI Antenna Upon Changes in Iron Availability

Iron is of primary importance in biological systems because it is a central constituent of hemes and iron-sulfur clusters. The activities of many enzymes rely on these redox centers, particularly for those enzymes active in energy conversion processes. It is thus not surprising that sophisticated systems for iron acquisition and distribution have evolved to insure maintenance of iron homeostasis in plants and algae (see References 49, 65 for reviews). Iron mobilization is particularly critical for microalgae in the open ocean, where iron can be severely limiting, and for terrestrial plants where the dominant form of iron in oxygenated soils is Fe^{3+}, which has limited solubility in H_2O at neutral and alkaline pH. In photosynthesis, PSI has the highest iron content (12 Fe per RC), and is particularly vulnerable to iron deficiency. This is illustrated by the marked drop in PSI content when diatoms (283), *Chlamydomonas* (192), plants (270), and possibly *Ostreococcus* (52), are deprived of iron; PSII and cyt b_6f complexes are also affected to some extent. In cyanobacteria the reduction in the amount of PSI RC relative to other molecular constituents of the photosynthesis apparatus is particularly severe, leading in some instances to a fourfold decrease in the PSI/PSII ratio (57, 98, 259). In marine cyanobacteria and green algae, the reduced PSI content is counterbalanced by an enhanced activity of a water-to-water cycle, mediated by the chlororespiratory enzyme PTOX (see above).

Studies concerning the ways in which antenna complexes change upon Fe-deprivation in cyanobacteria have contributed significantly to our understanding of antenna remodeling around PSI. Cyanobacteria lose their phycobilisome when deprived of Fe (97), in large part because of an arrest in the synthesis of phycobiliproteins. The starved cells also synthesize a limited number of new proteins including IdiA, which acts on the acceptor side of PSII offering some protection against PSII degradation (158, 184), and IsiB, a flavodoxin that can substitute for the iron-containing Fd, which acts on the acceptor side of PSI (163). Flavodoxin was recently shown to confer increased tobacco plants tolerance to iron starvation (294, 295). However, the most spectacular change upon iron starvation of some cyanobacteria is the synthesis of IsiA. IsiA is a chl a binding protein similar to CP43, a core antenna protein of PSII. The IsiA that is synthesized during iron deprivation forms a ring, consisting of 18 IsiA polypeptides, surrounding the PSI cores (see 276). The original concept concerning changes in the photosynthetic apparatus upon Fe deprivation was that of a reduction in the number of PSI centers and that each center would associate with a larger, newly synthesized antenna (38, 42). However, this view has been challenged based on the observation that the new antenna system could not only make the individual PSI centers more efficient in utilizing excitation energy by increasing the absorption cross section, it may also serve to quench excess absorbed excitation energy (113), which would afford the cells photoprotection by lowering the potential for ROS formation. However, this point is still debated (119). In particular, Wilson and coworkers recently showed that energy dissipation in Fe-starved cyanobacteria (315) does not involve IsiA but rather the orange carotenoid protein (OCP).

Remodeling of the PSI antenna upon Fe deprivation also occurs in photosynthetic eukaryotes. In the halotolerant eukaryotic alga, *Dunaliella salina*, Fe deprivation results in a decrease in the number of PSI RC and elevated synthesis of a major chl a/b binding protein of the LHC family called TIDI (thylakoid iron deficiency-induced protein). TIDI is associated with the remaining PSI cores as part of a large supercomplex (303). Changes in PSI antenna were also suggested to be a means of minimizing photooxidative damage when *Chlamydomonas* becomes Fe starved (192). When grown in the presence of 1 μM Fe, i.e., conditions in which no chlorosis is observed, *Chlamydomonas* undergoes a remodeling of the PSI peripheral antenna, LHCI. LHCI, is comprised of 9 subunits encoded by *LHCA* genes (279). Early responses to Fe deprivation include a disconnection of LHC1 from PSI cores and a change in the composition and stoichiometric content of LHC1 subunits, with a downregulation of LHCA-5 and -3 and upregulation of LHCA-4 and -9 (204). These gross changes are mediated by a specific degradation of PSI-K subunit (192) and a specific N-terminal processing of the LHCA3 (204), which is in stromal contact with PSI-K (35, 36). The protective effect of decreased PSI sensitization by LHC1 has been demonstrated elegantly using a genetic approach. First, a light-sensitive mutant lacking PSI-F (*psaf* mutant) showed improved phototrophic growth in iron-limiting conditions, indicating that a partially defective PSI strain could be rescued by reorganization of the PSI antenna during iron deprivation. Second, crossing this mutant to the *crd1* mutant, which shows constitutive uncoupling of the PSI peripheral antenna because of the absence of PSI-K, further enhanced growth at 150 μE $m^{-2}s^{-1}$ independent of the Fe concentration in the medium, and largely relieved the light sensitivity of the original *psaF* mutation (192, 194).

Despite the spectacular chlorosis developed by Fe-deprived plants, and the wealth of data available on the sophisticated circuitry for Fe transport and distribution, fewer than a handful of studies characterize the photosynthesis properties of Fe-deprived plants: a general drop in chl content and reduced electron transport capacity have been reported (see 156, 270 and references therein). Recently, a proteomic study with Fe-deficient spinach leaves (293) suggested a remodeling of the LHCII antenna, including a transient change in their state of oligomerization, with no significant change in the PSI antenna composition. These results are widely different from those obtained with *Chlamydomonas*, including a recent proteomic analysis indicating little effect on levels of LHCII proteins upon Fe deprivation (203). The reasons for these discrepancies are presently unclear. They could originate from the photoautotrophic conditions used for growing spinach, which are markedly different from the photoheterotrophic conditions used to grow *Chlamydomonas*.

GENE EXPRESSION RESPONSES WITH RESPECT TO ENVIRONMENTAL CHANGE

As discussed above, the flexibility of PET and light harvesting in photosynthetic eukaryotes is controlled by multiple signaling pathways that integrate processes in the cp and nucleo-cytosol and that are extremely sensitive to a diversity of environmental cues (**Figure 5**). The recent application of transcriptomic proteomic and metabolomic analyses to a number of photosynthetic systems affords researchers opportunities to use multiple global approaches to develop a system biology perspective. Time has come to evaluate many of the "omic" studies to better understand the molecular flexibility of the photosynthetic apparatus, even if many of the studies were not initially oriented in that way. We have therefore generated tables that summarize data concerning changes in expression of genes encoding proteins associated with photosynthetic function under various environmental conditons. **Supplementary Table 1** lists various microarray platforms used in the studies discussed below, while references detailing the technical aspects of the various omics plateforms are given in

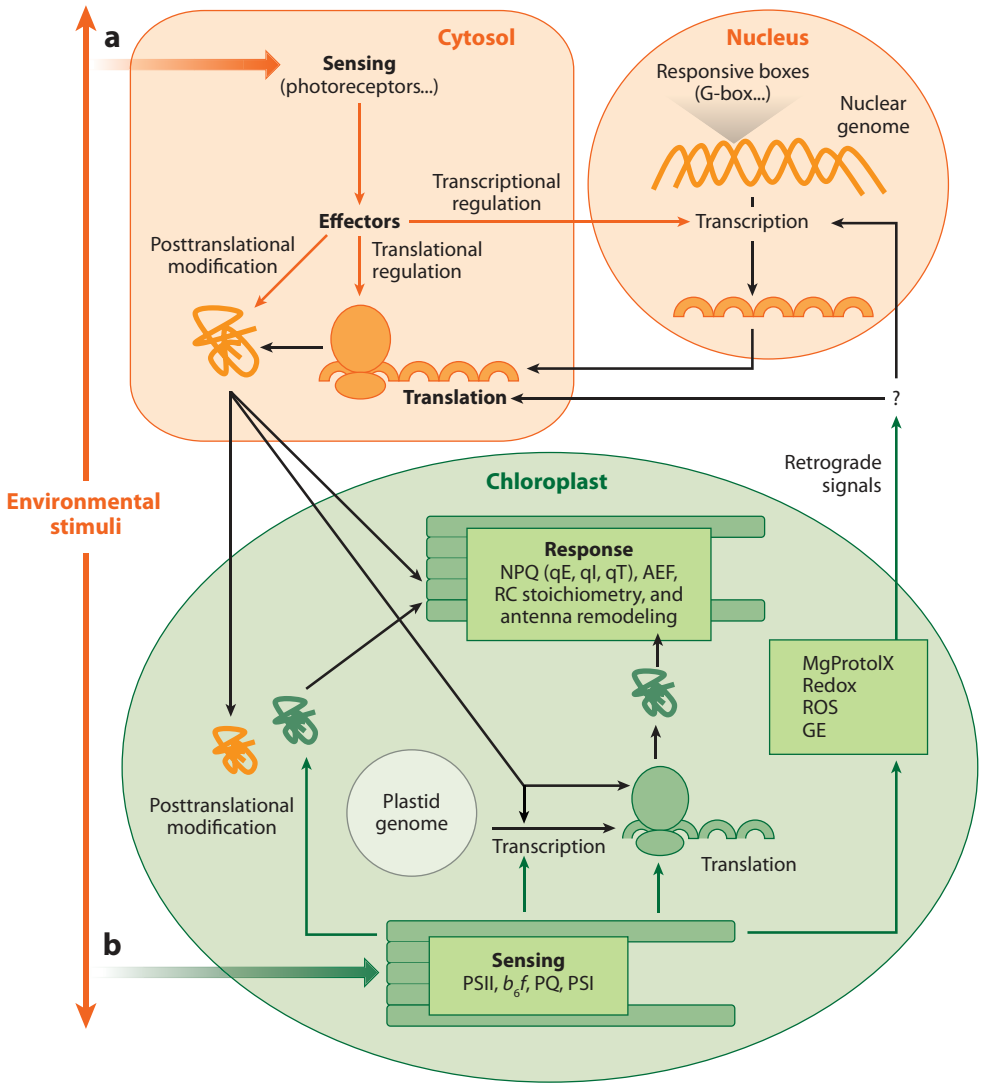
Supplemental Material

Supplemental Material

Supplementary Table 2. Supplementary Table 3 (follow the Supplemental Material link from the Annual Reviews home page at http://www.annualreviews.org) summarizes the regulatory characteristics (upregulated or downregulated) associated with the photosynthesis-related transcripts and/or proteins reported in various studies. We chose to keep the nomenclature for genes and proteins used in the original publications, even though different authors may have used different names for the same gene or protein.

Influence of Light on Expression of Photosynthetic-Related Genes

The importance of acclimation of photosynthetic eukaryotes to changing light conditions is exemplified by the finding that ~32% of the genes represented on a 9.2 K *Arabidopsis* microarray respond when seedlings are transferred form the dark to 152 μE m^{-2} s^{-1} white light (175). The transcripts from half of the light-responsive genes increase while those of the other half decrease. The proteins encoded by the target genes participate to a range of



putative functions, many not directly related to photosynthesis. Many of the responses were similar when dark-grown seedlings were transferred to far-red, red, or blue irradiances (175), suggesting cross-talk between specific photoreceptors. In a more recent comparative study, using arrays representing ~27,400 genes in rice and 15,500 genes in *Arabidopsis*, about 20% of the transcripts showed significant change in abundance when dark grown seedlings were transferred to 220 μE m^{-2} s^{-1} (rice) or 160 μE m^{-2} s^{-1} (*Arabidopsis*) of white light (123). Again, in both cases, for about half of the light-responsive genes the transcripts increased while the other half the transcripts decreased, and individual far-red, red, and blue light irradiances triggered similar changes.

Response to low photon flux: the role of photoreceptors. When transferred from the dark to very low-fluence white light (0.01 μE m^{-2} s^{-1}: VLFL) *Chlamydomonas* exhibits increased transcript accumulation for a number of photosynthesis-related genes. Using quantitative RT-qPCR (116, 169) and cDNA arrays (114), it was shown that VLFL light triggers the accumulation of transcripts encoding proteins involved in pigment synthesis, light-harvesting, and other activities associated with the photosynthetic apparatus (see **Supplementary Table 3**). The coordinated increase in the levels of transcripts for photosynthetic proteins in such a low light suggests the action of specific photoreceptors in modulating gene expression rather than mechanisms that depend on net photosynthetic electron flow.

VLFL: very low fluence

PHY: phytochrome

Three main classes of photoreceptors have been implicated in light-dependent signal transduction. Blue light-responses are triggered by cryptochromes (reviewed in 168) and phototropins (reviewed in 60), while phytochromes (reviewed in 201, 251) are involved in sensing red-light. Ma et al. (175) used null-mutants for phytochrome (PHY) A and B to study their role in far-red light-triggered response in *Arabidopsis*. These phy mutants typically show elongated hypocotyls and a number of abnormal morphological features (175, 243, 312). At the transcript level, as only general responses were described in the study of Ma et al. (175), it is difficult to assess the specific behavior of photosynthesis-related genes in the various mutant contexts. Nevertheless, PHYA and PHYB play major, but distinct roles in triggering far-red light responses. The PHYA null mutant abolishes most changes observed in the far-red light responses. The PHYB null mutant significantly influences the abundance of only a small subset of far-red light-responsive transcripts. Further analysis of signaling

Supplemental Material

Figure 5

Integration of environmental stimuli in the nucleocytosol and the chloroplast in photosynthetic acclimation processes. Sensing: Environmental stimuli are sensed in the cytosol (pathway *a*) by a variety of sensors (e.g., photoreceptors). Subsequent signal transduction leads to transcriptional and/or to translational regulation of nuclear genes, and/or to posttranslational protein modifications. Nucleo-cytosolic target genes and proteins (*orange*) include subunits of the photosynthetic complexes, regulatory proteins (e.g., STT7 or PGR5) as well as proteins involved in plastid gene expression (e.g., M and T factors). The chloroplast is also a sensor of environmental stimuli (pathway *b*), leading to ROS production, changes in redox poise of the plastoquinol pool and terminal electron acceptors Fd, Thx, and NADP. Integration of these signals affects expression of chloroplast-encoded proteins (*green*) at the transcriptional and/or translational level. Posttranslational modifications also affect nuclear-encoded (*orange*; e.g., phosphorylation of LHCII complexes) or plastid-encoded proteins (*green*, e.g., D1 turnover during photoinhibition or RuBisCo carbamylation). Finally, retrograde signaling triggered by ROS, redox signaling, chl intermediates (e.g., Mg-protochlorophyllide IX), and plastid gene expression (GE) modulates transcription and/or translation of nuclear-encoded photosynthetic transcripts. Responses: The global process of sensing triggers a variety of photosynthetic responses. Regulation of light absorption (NPQ -qE, -qI, and/or -qT) or of alternative electron flow (AEF) pathways (e.g., PTOX) takes place to optimize energy absorption and utilization. Remodeling of membrane and soluble protein complexes optimizes their activity in response to a changing environment.

CRY: cryptochrome
PHOT: phototropins

pathways involved in PHYA-mediated far-red light-responses on a genome-wide scale have highlighted the potential existence of a complex network of different paths that control expression of distinct sets of genes (308). Six proteins have been linked to this response network. FHY1, FAR1, and FHY3 act upstream of PHYA in the far-red light response, while FIN219, SPA1, and REP1 act downstream in this pathway. Ghassemian et al. (91) reported a major PHYA-coordinated increase in the levels of transcripts encoding photosynthesis-related proteins during red-light photomorphogenesis of etiolated seedlings (see below). Together, these results suggest a critical role of PHYA with regard to expression of photosynthesis genes. Finally, phytochrome-mediated signaling triggers expression of distinct transcription factors, suggesting distinct mechanisms for controlling downstream gene expression (291).

Based on analyses of a mutant defective for both cryptochromes (CRY) 1 and 2, these photoreceptors appear to be responsible for the majority of the blue-light–dependent changes in transcript levels in *Arabidopsis* (175). This was confirmed by Ohgishi and colleagues (215), who monitored transcript levels in *Arabidopsis* in response to blue irradiation using combinations of mutants of cryptochromes and phototropins. CRY1 and CRY2 act as key regulators for an early blue-light–induced gene expression, whereas the phototropins (PHOT), PHOT1 and PHOT2, play only a subsidiary role. Some of the target transcripts encode cp-targeted proteins like SIG3, a sigma factor responsible for blue-light induction of cp *psbD* transcription, or enzymes involved in the Benson-Calvin cycle.

While blue light-triggered gene expression is mainly controlled by CRY and not PHOT in *Arabidopsis*, PHOT appears to control the levels of many photosynthesis-related transcripts in *Chlamydomonas*: Most of the VLFL response is lost in a mutant strain in which the level of PHOT1 was dramatically reduced by RNAi (114). Some genes induced in a WT strain of *Chlamydomonas* by blue VLFL are also induced by red VLFL in a PHOT1-dependent manner, suggesting the existence of a cross-talk between blue- and red-light responses (114).

Finally, overexpression of photoreceptors in *Arabidopsis* produced an antagonistic effect on the expression of some photosynthesis-related genes: indeed overexpression of CRY1 repressed expression of *LHC* genes which are normally induced by blue light. Furthermore, overexpression of PHYA triggered downregulation of *RBCS*, which is normally induced by far-red light. These unexpected results suggest a high-light stress response in which a number of photosynthesis-related genes are repressed, due to the enhanced perception of light by the overaccumulated photoreceptors (175).

Blue light and red light regulate expression of many transcription factors (124). Among these transcription factors, HY5, an effector of light-dependent photomorphogenesis in *Arabidopsis*, has been studied most extensively. This bZIP transcription factor acts downstream of PHYA and B, CRY1 and 2, and the UV-B photoreceptor, highlighting its role in most light-dependent responses that have been examined in *Arabidopsis* (9, 143, 224, 298; see 122 for a review). HY5 binds in vitro to the promoters of light-inducible genes such as those encoding chalcone synthase and the small subunit of RuBisCo (9, 55). However, indentification of HY5 binding sites had not been extended to many of the potential targets genes, nor, importantly, had it been tested by in vivo studies. Using an approach that couples chromatin immunoprecipitation with immunological identification of an HA-tagged HY5 (ChIP-chip), Lee et al. (159) reported a genome-wide in vivo analysis of HY5 binding sites. Of the approximately 30,000 genes represented on the 193 K microarray (an array of oligonucleotides positioned at intervals of 500 bp along the genome), there were 3894 genes, dispersed across all five chromosomes, that exhibited binding to HY5. The HY5 target genes showed significant enrichments for three upstream motifs; the motif present at the highest frequency was the well-known G-box (CACGTG), which was identified in previous studies of light-dependent

transcription. Other potential HY5-binding motifs include G-box like CG hybrids (GACGTG) and a CA hybrid (GACGTA) (159), also known to be consensus HY5 binding sequences, as well as the light-responsive Z-box (322). Of the 3103 transcripts that were reported in a previous study as displaying statistically significant light-dependent accumulation (173), 24% have HY5 binding sites (159). Photosynthesis-related genes showed the highest statistically significant enrichment in the population of HY5-target genes. Studies using a *hy5* mutant demonstrated that a subset of photosynthesis-related genes involved in chl synthesis (CHS), light harvesting (LHC), and the Benson-Calvin cycle (RBCS1A), were strictly dependent on binding of HY5 for their light-induced upregulation. As HY5 is involved in far-red, red, blue, and UV-B signaling, it may de facto be involved in expression of many photosynthetic genes under numerous light conditions. However, note that binding of HY5 to its target sequences is not sufficient for transcriptional responses. Binding of HY5 to its target sequences is observed in plants grown either in the dark, in the light, or harvested at dawn or dusk; these conditions result in vastly different expression levels from the same HY5 target genes. Additional cofactors and/or upstream modifications of the HY5 protein itself are likely to play an important role in modulating HY5 activity (159). Furthermore, the HY5 protein accumulates to higher levels in the light than in the dark as a consequence of differential degradation rates (221, 222). The COP1 protein has been proposed to play a key role in targeting degradation of multiple photomorphogenic transcription factors, including HY5 (107, 221, 222). This explains a repressor role of COP1 with respect to *Arabidopsis* in light-driven responses. To study the effect of COP1 at the a genome-wide level, Ma et al. (174) have used mutant strains with decreased accumulation of COP1. The levels of many light-responsive transcripts were increased in the *cop1* mutant strains in the dark to levels comparable to those observed in WT seedlings in the light. In addition, these mutants show an exaggerated light response. The effect of COP1 on light-regulated transcript accumulation is extremely widespread; the levels of more than 1300 transcripts (about 20% of those assayed) are influenced by COP1 levels. Numerous transcripts encoding proteins for photosynthetic light reactions, carbon metabolism, starch synthesis, and photorespiration are increased in mutants with reduced COP1. Furthermore, the levels of 53 transcripts encoding transcription factors were affected in *cop1* mutants, which reinforces the view that the effect of COP1 on gene expression is largely due to its influence on the accumulation of transcription factors associated with light-responsive gene expression.

Expression of photosynthetic genes during photomorphogenesis. Although photomorphogenesis is a distinct process from the acclimation of plants to low light described above, they have similar features because they rely on similar signal transduction pathways. Ghassemian et al. (91) studied photomorphogenesis in *Arabidopsis* by monitoring changes in transcript levels in etiolated seedlings subjected for 24 h to red-light. Greening of the etiolated seedlings occurred rapidly under red-light illumination and correlated with a massive upregulation of more than 60 transcripts encoding photosynthesis-related proteins, including 8 PSI subunits, 5 PSII subunits, 6 LHCAs, 3 LHCBs, the minor antenna proteins CP24, CP26 and CP29, 3 LILs, 3 ATPase subunits, Fd, Fd-NADP reductase, proteins involved in chl synthesis, and enzymes involved in the Benson-Calvin cycle including RuBisCo (see **Supplementary Table 3**). Such extensive coordination of the levels of photosynthesis-related transcripts had not been previously described. The authors report that the red-light driven induction of these transcripts depends largely on actions of PHYA. The fact that the induction of different photosynthesis-related transcripts occurs at different times following the initiation of greening led the authors to suggest that this integrated response is triggered by several independent actions of the

Supplemental Material

PHYA over the time course of greening rather than by a single action.

Differentiation of plastids in etiolated rice seedlings transferred from the dark to the light for a period of 8 h was examined at the proteome level by Kleffmann et al. (141). Proteins involved in photosynthesis were already present at low levels in the dark, with RuBisCo and proteins involved in chl biosynthesis among the most abundant proteins in etioplasts. Fd-NADP oxidoreductase and enzymes involved in the Benson-Calvin cycle were the first to accumulate following the light exposure. These observations support earlier biochemical studies performed with *Chlamydomonas* in which activation of photosynthesis was monitored during the greening of the Y-1 mutant (see 27 for a review). The upregulation of photosynthetic proteins reported by Kleffmann et al. (141) correlates with reported increases in photosynthetic transcript abundance, suggesting an integrated light-driven response at the transcript and protein levels. This increased abundance of transcripts seems to be mainly due to a light-driven increase in their stability rather than to transcriptional regulation (140, 280). In line with this conclusion, Kleffman et al. report on a light-driven phosphorylation of a cp RNA-binding protein, RNP29, a process known to influence stability of plastid-encoded mRNAs (43, 194, 170). Photosynthesis-related transcripts also accumulate during shoot genesis of somatic embryos in rice; 11 photosystem-related transcripts and 10 chl biosynthesis-related transcripts increased during shoot development (284) (see **Supplementary Table 3**).

Response to moderate light intensities. At variance with acclimation to VLFL and/or photomorphogenesis, which clearly involve the building and/or the remodeling of the photosynthetic apparatus, acclimation to moderate light favors optimization of photosynthetic efficiency. Therefore, it can stimulate short-term acclimation processes such as state transitions (see above) that may also contribute a retrograde signaling through altered protein phosphorylation (see above).

Kurth et al. (151) used cp-specific gene sequence tags (GST) on nylon membrane to assess the light response of 1800 genes encoding nuclear-encoded, cp-targeted proteins, for *Arabidopsis* seedlings transferred from the dark to moderate-intensity white light. The light-induced transcripts related to photosynthesis include those for LHCs, PSI and PSII subunits, PC, Fd, and genes involved in CO_2 fixation, such as those encoding RuBisCo and RuBisCo activase (see **Supplementary Table 3**). *Arabidopsis* seedlings subjected to a change from dark to moderate (152 $\mu E\ m^{-2}\ s^{-1}$) white light showed massive accumulation of photosynthesis-related transcripts including those encoding LHC proteins, subunits of PSI and PSII, chl and heme biosynthesis proteins, the fixation of CO_2 and starch synthesis (see **Supplementary Table 3**) (175). Transcripts encoding components of the photosynthetic light reactions showed the strongest activation. Transcripts such as those encoding components of the photosynthetic light reactions (17 LHC proteins, 15 PSI proteins, 14 PSII proteins, and 10 proteins involved in electron transport and ATP synthesis) and photosynthetic carbon metabolism and starch synthesis (28 proteins including RuBisCo and Fd) were more sensitive to red and blue-light than to far-red light, whereas genes involved in chl and heme biosynthesis were more sensitive to far-red than to red or blue light. Photosynthesis-related transcripts involved in chl synthesis and LHCs were among those showing the most comparable behavior between *Arabidopsis* and rice (123).

Responses to high light intensity and drought. As described above, light has a deleterious effect on photosynthesis when absorbed in excess. Acclimation to high light triggers changes in the absorption capacity as well as in the capacity to redirect electrons toward alternative sinks. This trend, deduced from functional studies, is supported by three transcriptomic studies focused on longer acclimation processes (**Supplementary Table 3**). Numerous mRNAs encoding LHCs markedly declined upon exposure of *Arabidopsis* (138),

barley (18), and rice (199) to high light, which should contribute, together with NPQ, to further downregulate light sensitization of the photosynthetic apparatus. In addition, there was a significant reduction in the level of transcripts for other photosynthesis-related polypeptides, including subunits of PS-I, PS-II, and the cyt b_6f complex. In contrast, a transcript for NAD-MDH was upregulated in rice transferred from 200 $\mu E.m^{-2}.s^{-1}$ to 1000 $\mu E.m^{-2}.s^{-1}$ illumination (199); the NAD-MDH may participate in rerouting photosynthetic electrons, thus contributing to the capacity of redox homeostasis under the different conditions of illumination. Currently, there is no systematic analysis of patterns of light-dependent expression for *PGR5* and *PGRL1* because they have only been recently implicated in FQR-mediated CEF (see above). Among the other transcripts that accumulate in high light in both *Arabidopsis* and rice are the PSII-S and ELIP2, i.e., proteins implicated in efficient photoprotection strategies.

Using proteomic approaches for studies of *Arabidopsis* plants subjected to high-light (1000 $\mu E\ m^{-2}\ s^{-1}$) for 1–5 days, Giacomelli et al. (92) also showed an increased abundance of PSII-S, which is consistent with the increased capacity of plants exposed to high light to develop an efficient NPQ response. An intriguing response was that of the accumulation of the tetratricopeptide repeat YCF37 protein, whose *Synechocystis* homolog is a thylakoid-associated protein involved in PSI assembly or oligomerization (71, 314). The accumulation of YCF37 in high light–exposed *Arabidopsis* plants suggests a potential role in the protection of PSI from high-light damage or its repair once damage occurs. While some subunits of PSII (O and P), PC and FNR decreased in abundance under the same conditions, 14 other proteins of the photosynthetic apparatus showed no significant change in accumulation. According to the authors, this suggests that one should be cautious when trying to extrapolate changes in transcript abundance to that of protein accumulation. Furthermore, comparisons among separate studies can be misleading because of differences in the experimental protocols used, which often include differences in the duration of light exposure and the exact quality of the illumination.

In *Chlamydomonas*, two genome-wide studies have shown the combined effects of CO_2 and light on transcript levels (81, 116). In an early study, Im et al. (115) used RFDD (restriction fragment differential display) to identify high light–responsive transcripts that were either regulated solely by high light or that were also responsive to CO_2 levels. Later, a more extensive analysis (116) identified a number of photosynthesis-related transcripts that accumulated when the cells were exposed to both elevated light (1000 $\mu E\ m^{-2}\ s^{-1}$) and CO_2 concentrations. RuBisCo activase, LIl3, and LI818r-3 (renamed LHCSR3) transcripts increased under both high and low CO_2 conditions. The three protein products of those transcripts may contribute electron sinks (through activation of RuBisCo) or photoprotective mechanisms (for LIL3 and LHCSR3) that are independent of CO_2 availability. Transcripts encoding CHLI, LHCA4, PSAE and D, OEE3, and a CP-26-like protein accumulated in high light, but only under high-CO_2 conditions. This elevated transcript abundance in high light contrasts with the massive repression of photosynthesis-related transcripts upon transfer of vascular plants to a similar light regime, as discussed above. The difference suggests that exposure of *Chlamydomonas* to 1000 $\mu E\ m^{-2}\ s^{-1}$ may not produce significant photooxidative damage or ROS if CO_2 is not limiting for photosynthesis.

Fischer et al. (81) used a newer 10 K oligonucleotide array to examine high light-dependent transcript accumulation in *Chlamydomonas* (2500 $\mu E\ m^{-2}\ s^{-1}$ for 1 h). The pattern of downregulated transcripts in high light remained roughly similar in mixotrophic [TAP (tris acetate phosphate) medium] and phototrophic conditions [HSM (high salt medium)] whether maintained at high or low CO_2 concentration, whereas the number of transcripts showing increased accumulation and the extent of that accumulation were significantly lower in the presence of acetate TAP (medium) or in

TAP: tris acetate phosphate medium

HSM: high salt medium

cultures supplemented with high CO_2 (HSM-CO_2 medium). Furthermore, only about half of the responding genes overlapped between the TAP and HSM-CO_2 conditions. These observation indicate that major differences in transcript accumulation observed upon transfer of cells from low to high light are modulated by other aspects of the growth conditions. Regarding photosynthesis-related transcripts, a number of mRNAs including *PSID* and *-E*, *PSIIW*, *OEE2* and *3*, and many *LHCs* (4 *LHCAs* and 2 *LHCBs*) showed a significant decrease under high light in all conditions, but there was a more pronounced effect with cells grown in TAP or HSM-CO_2 when compared to cells grown in HSM. Note that *PSIE* and *-D* and *OEE3* behave in opposite ways under high light and high CO_2 concentrations in the study of Fisher et al. (81) and Im et al. (116). This comparison clearly underlines the difficulties encountered when trying to compare studies that were performed under different conditions. Nevertheless, these studies clearly confirm the integration between light absorption capacity, PET, and the efficiency of CO_2 assimilation, which are generally reflected by level of gene expression.

Growth conditions also affect global nuclear gene expression when *Arabidopsis* plants are switched to high light. When low light–grown plants under a short-day photoperiod (7.5 h photoperiod) were transferred to high light, both the level of transcript and protein for NADP-malate-dehydrogenase increased (29). This was not observed when low light-grown plants under a long photoperiod (16 h) were switched to high light. This could reflect increased light stress in high light for plants previously grown in low light under a short photoperiod when compared to those grown under a long photoperiod, providing a photoprotective mechanism by inducing the malate shuttle to eliminate excessive PET.

In *Arabidopsis* 70% of the high light–induced genes were also induced by drought, revealing a major overlap between these two stress responses that could reflect a similar strategy for minimizing photooxidative damage (138). These findings again parallel the physiological information, which suggests a strong similarity in the short-term acclimation features of plants to either high light or drought with respect to both CEF and NPQ. Salt and drought stress signal transduction in plants has been reviewed (323, 331). *Arabidopsis* plants subjected to a 2-h period of dehydration showed a decreased abundance in photosynthesis-related transcripts encoding LHB1B2, OEE3, RBCS, and geranylgeranyl reductase. The same transcripts increase when dehydrated plants are rehydrated (217). A likely sequence target for specific transcription factors involved in this response is ACTCAT, which is found between about –40 and –1000 upstream of 58 rehydration-inducible genes, including two photosynthesis-related genes (217). Some transcripts encoding proteins associated with photosynthesis that decrease encode PETC, PETE, CP29, LHCs, phytoene desaturase and RuBisCo subunits; these same responses have been observed in barley subjected to drought stress (18, 225, 289). In *Xerophyta viscosa*, proteomic analyses show that three subunits of PSII, the PSII stability factor HCF136 (235), and LHCB2 are reduced (at the protein level) upon dehydration (117). Transcripts encoding three subunits of PSI, two subunits of PSII, PC, and a protein annotated as a chl a/b binding protein are induced in rice during a 48-h rehydration period following a drought stress (330). Although it is difficult to draw definitive conclusions from the limited set of photosynthesis-related transcripts examined in these studies, the results are consistent with a downregulation of photosynthetic transcripts upon dehydration and their induction upon rehydration. In contrast, RuBisCo in sugar beet leaves (99) and RuBisCo activase in rice (258) were shown to be upregulated at the protein level under drought stress. The RuBisCo may serve as an alternative electron valve for drought-stressed plants.

No major changes in photosynthesis-related transcript abundances were reported for plants subjected to high-salinity stress of *Arabidopsis* (288), barley (with the exception of a

transcript encoding a purported 10-kDa PSII subunit) (225) and rice (133) (with the exception of the CP26 transcript) (54). These results are surprising since salt stress has been reported to affect photosynthetic activity (see 133).

Effect of Nutrients and Temperature on Photosynthesis-Related Genes

Changes upon deprivation in elemental sulfur, nitrogen, and phosphate are part of a general stress response. While the light responses of photosynthetic genes essentially allow for optimization of photosynthetic activity under different external conditions, exposure to a prolonged nutrient stress results in the progressive disassembly of photosynthetic activity. Nutrient deprivation causes a massive reduction in the levels of both transcripts and proteins associated with photosynthetic function, which may follow a complex regulatory path. Nutrient sensing and signaling in plants have recently been reviewed (see 262).

Acclimation to iron starvation shows specific traits that were presented above. *Chlamydomonas* deprived of sulfur, nitrogen, and phosphorus exhibit a marked change in photosynthesis, including upregulation of cyclic electron flow, and photoprotective responses. There is also a reduction in the level of photosynthesis-related transcripts, which leads to a decrease in overall photosynthetic capacity. For *Chlamydomonas*, changes in photosynthetic transcript levels have been documented in the cases of both sulfur or phosphorus deprivation (183, 329), while phosphorus and nitrogen deprivation have been examined in *Arabidopsis* (195, 265, 321) and nitrogen deprivation in rice (167). The response to sulfur starvation in *Chlamydomonas* develops in two phases in the wild type (329). During the first eight hours of starvation, many photosynthetic transcripts coding for LHCs, subunits of PSI, OEEs, and ATP synthase remain stable or increase slightly. On the other hand, the transcripts encoding the subunits of the cyt b_6f complex diminish. Between 8 and 24 h of sulfur starvation, there is a massive decrease in the level of transcripts encoding polypeptides associated with all of the photosynthetic complexes (see **Supplemental Table 3**). The hypothesis that global decline in transcripts encoding proteins of the photosynthetic apparatus constitutes a general stress response to conditions that compromise photosynthetic growth is supported by the use of mutants defective for genes specific for acclimation to a particular nutrient deprivation condition. In *Chlamydomonas*, for instance, the *sac1* and *psr1* mutants, which are affected in sulfur and phosphorus deprivation responses, respectively, still show a massive reduction in transcripts for photosynthesis proteins when starved for sulfur and phosphorus, respectively (193, 329). The downregulation of photosynthesis-related transcripts is detected even earlier in the *sac1* mutant than in WT; this probably reflects the inability of the mutant to develop an appropriate acclimation response, leading to an increased stress response. In marked contrast to this downregulation response, increased expression of a few new photosynthesis-related genes occurs in the absence of sulfur or phosphorus in the WT strain of *Chlamydomonas*, as well as in mutants defective for proper regulation of the specific acclimation processes (193, 329). These genes encode LHCSR-type antenna proteins, some of which may promote an NPQ response, or be required for protection against photooxidative damage. Furthermore, a transcriptomic study of *Arabidopsis* revealed upregulation of malate dehydrogenase, FNR and Fd under low nitrate conditions (309).

Temperature. Several studies suggest a remodeling of the photosynthetic apparatus when plants are exposed to heat or cold. Transcriptional networks that control cellular responses during cold stress in plants have been reviewed (323). In *Arabidopsis*, exposure to prolonged cold (5° to 10°C for up to 40 days) leads to a differential accumulation of photosynthetic proteins, as monitored by proteomic studies. Some proteins display increased accumulation (7, 95), while the abundance of others decline (95). In one study (95), 43 photosynthesis-related proteins showed altered accumulation levels when

exposed to the cold. Apart from the RuBisCo subunits (see below), enzymes of the Benson-Calvin cycle were largely downregulated in the cold. These authors also identified increased levels of ATPase CF1 subunits, PSI-E1, and PSII-Q2 in the cp stroma; these polypeptides are usually found on the lumen side of PSII. Also increased in the stroma was the iron-sulfur subunit of the cyt b_6f complex, which is a transmembrane polypeptide of the cyt b_6f complex. The results suggest that stable assembly of the major photosynthetic complexes is cold sensitive. In particular, the surprising stromal location of two lumenal TAT substrate proteins, the Rieske protein and PSII-Q2, strongly suggests a cold sensitivity of the TAT pathway, whose function requires a $\Delta\mu$H-dependent assembly-disassembly cycle (191). The other PSII subunits associated with the oxygen evolving site were either elevated or reduced, suggesting a reorganization of those multimeric protein complexes in response to temperature decrease. While PSII-O2 and PSII-P1 decreased in abundance, PSII-O1 and PSII-P2 showed increased accumulation under the same condition. The opposite behavior of different proteins encoded by paralogous genes (such as PSII-O1 and O2 and PSII-P1 and P2) argues for contrasting structural and/or functional characteristics that might optimize their action with respect to temperature. Also RuBisCo-related proteins showed a heterogeneous accumulation pattern in the cold, with apparent changes in their molecular mass. Some structural rearrangement in RuBisCo complexes, triggered by differences in subunit composition and/or posttranslational modifications in the cold, may help fine-tune the enzymatic activity.

Cold stress also causes a reduction in a number of photosynthesis-related transcripts in barley (286). This transcriptomic response is not observed in pigment mutants impaired in cp development, probably because of a pre-existing downregulation that is controlled by retrograde signaling (see above). Besides a global downregulation of photosynthetic genes, some reorganization of LHC antenna complexes in the cold might also occur as two transcripts encoding LHCII type I proteins showed decreased accumulation in the cold, while an LHCII type III-encoding transcript was induced under the same conditions in barley (18).

A temperature-dependent reorganization of the photosynthetic machinery is exemplified in a proteomic study of *Populus* during a period of moderate heat stress: the abundance of PSII proteins decreased while PSI and ATP synthase CF1 proteins increased (78). This contrasting behavior of photosynthetic complexes may reflect a switch to predominantly CEF when temperatures rise. Furthermore, phosphorylation of PSII antenna subunit CP29 (e.g., 37) following exposure to low temperatures may enhance the resistance of the light-harvesting complex to the cold. Finally, a long-term cold-acclimation (as in alpine plants, e.g., 281) results in the synthesis of specific proteins (e.g., PTOX) that are normally poorly expressed, and that may largely remodel PET.

Sugar and expression of photosynthesis-related genes. CO_2 assimilation by photosynthetic organisms leads to sugar and starch biosynthesis. Photosynthetic sugars can be used as a direct energy source in respiration or the stored starch can be used in fermentation metabolism. The intracellular concentration of sugars, which exquisitely reflects the metabolic state of photosynthetic cell, can serve to feedback control the rate of photosynthetic carbon fixation (see References 252, 253 for reviews). These feedback mechanisms lead to marked changes in gene expression, which includes downregulation of a large set of photosynthesis-related transcripts. Osuna et al. (223) observed a significant decline in transcripts encoding subunits of all photosynthetic complexes, LHCs, and enzymes of the Benson-Calvin cycle upon addition of sucrose or glucose to carbon-depleted *Arabidopsis* seedlings (see **Supplementary Table 3**). Thus, sugar-mediated regulation of gene expression resembles that upon nutrient starvation, although the physiological rationale is different. During nutrient deprivation the growth is arrested and the levels of photosynthetic proteins decline,

although the cells maintain a low-level capacity for photosynthetic electron flow and ATP synthesis for housekeeping purposes. Remodelling of photosynthesis induced by high sugar content minimizes the deleterious effects of light absorption under conditions in which no net photosynthesis is required. It resembles the fruit ripening process where photosynthetic competence is lost in the tissue; discussion of the ripening process is beyond the scope of this review, although some information about it is presented in **Supplementary Table 3.**

Sugar control of photosynthetic activity occurs over the diurnal cycle, where alternating dark and light periods have a major effect on the metabolism of photosynthetic organisms. There is a large variation in sugar content of a plant during night/day cycles, which have a major effect on the abundance and cycling of many transcripts (41; see 252, 313 for reviews). Three independent transcriptomic studies with *Arabidopsis* have shown that an impressively large number of photosynthesis-related transcripts depend on circadian rhythms (41, 102, 263). In these studies, many transcripts encoding LHCA and LHCB proteins, subunits of PSI, PSII, the b_6f complex, ATP synthase, and enzymes involved in chl synthesis and the Benson-Calvin cycle display a clock-dependent cycling with respect to abundance (see **Supplementary Table 3**). By studying the WT and starchless *pgm* mutant plants, Blasing et al. (41) reported that the sugar content affects 25%–50% of transcripts that show diurnal changes. Photosynthesis-related transcripts display their lowest abundance during the dark period, and while one study suggests that their accumulation levels peak at subjective (see below) midday (102), another reports their peak at the end of the night/onset of the light period (41). This discrepancy has been tentatively explained by Blasing et al. (41) by a free-running circadian rhythm (i.e., under continuous light) in the study by Harmer et al. (102), whereas their own study focused on cycling in dark/light periods. Notably, a free-running experiment under continuous light will increase sugar content of plants, which in turn could lead to changes in the cycling period. Several transcript of unknown function show the same temporal patterns as those of known photosynthetic transcripts, raising the possibility that they represent novel photosynthetic genes (263).

That varying sugar contents might affect circadian rhythm through retrograde signaling from the cp to the nucleus has been proposed in a recent study of *Arabidopsis* by Hassidim et al. (103). The authors report on the identification of a cp RNA binding (CRB) protein, whose inactivation dramatically affects cp morphology and photosynthetic performance. *crb* mutants are also affected in the circadian rhythm, with significant alterations in the expression of oscillator as well as output genes, suggesting a direct signaling role of the cp in the circadian clock. The *stn7* and *gun1* mutants (described above) also show alterations in circadian clock–dependent transcriptional regulations in contrast to the *gun5* mutant, which was not affected (103). These results strongly suggest that the cp plays a prominent role in regulation of the circadian rhythm in *Arabidopsis*, through signaling pathways that are dependent on the regulated activity of the thylakoid kinase STN7 and the GUN1 (but not GUN5) retrograde signaling pathway.

In Search of Regulons

Environmental changes trigger large-scale reprogramming of nuclear gene expression (**Figure 5**). At a genome-wide scale, the new frontier lies in the identification of response-effectors, such as signal sensors, transcription factors, and their corresponding genomic binding sites, which may lead to the characterization of genome-wide regulons. Ideally, at the transcript level, each regulon would include signal-sensors, transcription factors whose binding to specific promoter elements could be modulated, and a set of corresponding target genes that would be functionally related.

To identify potential regulons, several studies combined the analysis of genome-wide transcript responses triggered in a multitude of different stresses, in order to cluster genes that

Regulon: a group of genes that are coexpressed, usually because they share a subset of promoter elements that respond to environmental or developmental signals

TFBS: transcription factor-binding site(s)

show a similar behavior in all responses. Richly et al. (245) analyzed the differential expression of 3292 cp-related transcripts in 35 different environmental and genetic conditions in *Arabidopsis*. The authors conclude there are three main classes of responses for nuclear-encoded—but cp-related—transcripts: a systematic downregulation, a systematic upregulation, or a mixed response. As discussed above, these categories would be illustrated by the overall inhibition of photosynthetic transcripts upon nutrient stress as part of a general stress response, or the induction of cp-related transcripts in switches from the dark to low or moderate light. Responses that would comprise transcripts that are either up- or downregulated would be triggered when combining these two types of environmental changes. That a particular gene may belong to different classes, depending on the condition tested, is apparent from a detailed analysis of the data presented by Richly et al. (245), where the same photosynthesis-related gene responds differently—as might be expected—in different genetic or environmental conditions. In another study by the same authors using the same microarray built mainly with cp-related transcripts in *Arabidopsis*, Biehl et al. (39) analyzed 101 different nuclear transcriptomes obtained in various conditions and described 23 distinct "regulons" that would behave similarly in different stress situations. Although a large proportion of the same genes were either up- or downregulated for 28 treatments, they did not behave in the same way in the 73 remaining conditions. This result points to the complex and sometimes antagonistic regulatory networks that are triggered by distinct conditions. Photosynthesis-related transcripts all group in regulon 1, whereas regulon 2 groups mainly transcripts encoding proteins involved in cp gene expression, such as plastid ribosomal proteins, but also the PGRL1 protein, potentially involved in the modulation of CEF. These two regulons, which behave very similarly, support a coordinated expression pattern between nuclear- and cp-encoded photosynthetic transcripts, which is required for a functional response in overall photosynthesis. Regulons 1 and 2 are different from all the other regulons described in this study in that they contain a majority of functionally related genes. Most other regulons identified by Biehl et al. (39) did not group genes that encode products acting in a specific subcellular compartment or in the same biochemical pathway. While showing a coordinated expression pattern, regulons 1 and 2 exhibit markedly different regulations than all other regulons. The gene content of these other regulons differed markedly from a random chromosome localization, in sharp contrast to regulons 1 and 2 whose gene content is dispersed across all chromosomes. Thus genes required for dynamics changes in photosynthesis may respond through specific promoter elements, which enable a coordinated response for functionally related genes dispersed in the genome. This is reminiscent of the in vivo HY5-binding sites that are widespread across the genome, as discussed earlier (159).

Further evidence for a coordinated response of photosynthetic-related genes through upstream *cis*-acting elements came with the study of Vandepoele et al. (301). These authors analyzed expression data from 1168 different *Arabidopsis* Affymetrix ATH1 microarray experiments. Clusters of coexpressed transcripts may be subjected to common regulatory networks. For each of these clusters, the authors analyzed the 1000-bp promoter regions in order to find potential transcription factor-binding sites (TFBS), which would play a regulatory role. They uncovered 80 TFBSs and 139 potential regulatory modules, a number of which were hitherto unknown. They authors identified 695 regulons containing coexpressed genes with at least one common regulatory motif, covering a total of 4100 genes. In addition to the identification of the well-known light-responsive G-Box promoter-element, which is involved in light-dependent induction of plant gene transcription (310, 311), the authors found additional regulatory modules that could be implicated in the coordinated expression of photosynthesis-related genes. First, enrichment in a particular module, containing

G-box- and I-box-like sequences, was preferentially found upstream of genes encoding various chlorophyll-binding proteins, PSI and PSII subunits, as well as ferredoxin. Additional modules showed a preferential overrepresentation among photosynthesis genes (301). The presence of multiple independent modules acting as multiple switches and able to be combined together upstream of photosynthesis-related genes suggests that multiple different regulatory networks affect the expression of subsets of photosynthetic genes, rather than a simple "all-on" or "all-off" model that would act as a master switch. The combination of those various modules likely plays a key role in regulating transcription of photosynthetic genes in different ways, in regard to the physiological condition encountered by the organism.

A coregulated response of photosynthetic transcripts has also been proposed in barley (76). Analysis of EST (expressed sequence tag) data in 69 cDNA libraries for different tissues or at different developmental stages revealed potential coordinate expression of functionally related ESTs from plants exposed to different conditions. Photosynthesis-related transcripts of both the light and dark reactions exhibited coordinate expression patterns.

Taken together, these studies strongly suggest a coregulation of photosynthesis-related transcripts in *Arabidopsis* and barley (39, 76, 301). Their expression additionally seems to be coordinated to the response of genes involved in plastid gene expression in *Arabidopsis* (39).

CONCLUSION

Several decades of photosynthesis research have demonstrated that eukaryotes performing oxygenic photosynthesis have developed acclimation and adaptation strategies for modifying specific features of light energy conversion. We have provided an overview of the plurality of electron transfer pathways potentially used following light-induced charge separation within the RC, and described how the sensitization of RC by absorbed light energy is under the control of regulation processes that mold photosynthetic activities as environmental conditions change. This flexibility depends on key proteins currently being identified, generally as a result of genetic screens based on changes in chl fluorescence. **Table 1** lists tentatively the proteins that appear to contribute to the dynamics of the photosynthetic machinery. The list encompasses subunits of light-harvesting and electron-transfer complexes whose conditional expression may contribute to a remodeling of the photosynthetic apparatus, enzymes that control branching pathways for electron transfer or that contribute to posttranslational modification of photosynthetic targets and signaling proteins. Not included are several additional proteins that participate in biogenesis and assembly of photosynthetic complexes because they have not been identified in available acclimation studies.

Although many of the regulatory proteins do not share specific biochemical and/or structural features, their function converges at the physiological level. Short-term acclimation processes that regulate light harvesting and PET facilitate the formation of remodeled photosynthetic complexes with distinct properties. The effectors that elicit these changes are most often sensitized by pH and/or redox conditions, while the new structural/functional components may also be sensitive to redox conditions. This is illustrated by PSII-S and possibly LHCSR, which enhance the sensitivity of the NPQ in response to pH (165, but see also 139) and for PGR5/PGRL1, whose function modifies redox properties of PET downstream of the cyt b_6f complex (66, 196, 197) by an as-yet unknown mechanism (see also 101).

Acclimation processes also rely on changes in stoichiometry between photosynthetic proteins, which may be achieved by controlling the relative amount and/or activities of a limited number of regulatory proteins of nuclear origin that control cp gene expression. This concept has grown from extensive studies of *Chlamydomonas* and vascular plants that demonstrated concerted accumulation of subunits of individual complexes of the photosynthetic apparatus through a series of assembly-dependent

Table 1 Proteins potentially playing a prominent role in the dynamics of photosynthesis, as revealed by functional, genetic, proteomic, and genomic studies, discussed in this review

Gene (families)	Protein	Role
APX, PTOX, NDH	Chloroplast ascorbate peroxidase, plastid terminal oxidase, NADPH dehydrogenase	Alternative electron sinks for the light reactions of photosynthesis
ELIP2	Early light-induced protein	Dissipation of excess light energy
HCF136	Lumen of stroma lamellae	PSII stability/assembly factor
LHCSR2 & LHCSR3	Chloroplast proteins of the light-harvesting complexes	Dissipation of excess light energy
PETE & FED	Plastocyanin and ferredoxin	Linear and cyclic electron flow
PGR5 & PGRL1	Chloroplast proteins	Cyclic electron flow
PSBO1&2/PSBP1&2	Subunits of the oxygen evolving complex	Dynamic changes of subunit composition of the oxygen evolving complex involving paralog gene products
PSII-S	Photosystem II subunit	Dissipation of excess light energy
RBCS & RBCL	Subunits of RuBisCo	Photosynthetic carbon fixation
		Alternative electron sink (through oxygenase activity)
STT7/ STN7&STN8	Chloroplast protein kinases	State transition. Chloroplast to nucleus retrograde signaling
YCF37	Thylakoid bound in Synechocystis	Potentially implicated in PSI assembly
Nuclear genes acting on chloroplast gene expression	Sigma factors involved in plastid transcription. M (plastid mRNA maturation and stability) and T factors (plastid mRNA translation)	Control of plastid gene expression

translational regulation events, defined as CES cascades [control by epistasy of synthesis (59)]. Here, changes in expression of a single nuclear factor controlling translation of a "dominant" subunit may cause increased or decreased accumulation of the whole protein complex by modulating negative feedback of translation of the other subunits.

Because acclimation of photosynthetic processes is largely regulated at the (post)-translational level, most of the transcriptomic studies performed to date provide only a limited contribution to our understanding of acclimation processes in photosynthesis organisms. Nevertheless, three trends were observed. Very low to moderate light fluences induce photosynthetic gene expression whatever their spectral quality. In contrast, most photosynthetic genes are downregulated in a multitude of stress conditions, highlighting that downregulation is part of the general stress response. In a few cases specific responses of a subset of photosynthesis genes were observed. For example, abundantly and rarely expressed *LHC* genes exhibit distinct regulation patterns in different plant tissues and under variable conditions (144). Furthermore, downregulation in expression of a subset of *LHC* genes, which should minimize photooxidative damage, is often accompanied by an upregulation of genes encoding proteins that may have a photo-protective function such as PSII-S, LHCSR2, and LHCSR3 (see **Supplementary Table 3**). Transcriptomic studies, when combined with promoter-motif analysis, chromatin immunoprecipitation experiments, and functional characterization of transcription factors—as described for HY5 and COP1—offer a great opportunity to dissect, at the molecular level, transcriptional networks involved in the light response of photosynthetic genes. Proteomic studies have also contributed interesting concepts, such as the alternative expression of paralogous proteins that result in changes in the subunit composition of photsynthetic complexes, as discussed above. Thus, both transcriptomic studies and

CES: control by epistasy of synthesis

proteomic approaches should lead to the identification of new genes and protein products that are key players in photosynthetic acclimation and adaptation, as is illustrated by the numerous "unknowns" that have been found in those studies, and that share behavior similar to that of known photosynthetic genes.

Currently, transcriptomic, proteomic, and metabolomic techniques are rarely combined in integrated studies. A tighter integration of these techniques, with an emphasis on the behavior of photosynthesis-related genes and proteins, coupled with a detailed analysis of the functional properties of the photosynthetic apparatus, represents the new frontier in photosynthesis research. Such studies should provide a more global view of photosynthetic cells in an ever-changing environment.

SUMMARY POINTS

1. When excitation pressure exceeds the capacity of the cells for CO_2 assimilation, photosynthetic electrons are diverted away from carbon assimilation.
2. Overexcitation also causes downregulation of the absorption capacity of the photosynthetic apparatus, mainly at the level of photosystem II.
3. Acclimation to environmental stimuli is achieved by remodeling photosystem I and II antenna complexes.
4. Sensing of environmental stimuli by the chloroplast leads to retrograde signaling, affecting nuclear gene expression.
5. Acclimation to environmental stimuli is triggered by coordinated genetic responses, as revealed by transcriptomic and proteomic studies.
6. All of these responses are integrated into a global response at the cellular level, which highlights the extreme flexibility of the photosynthetic machinery.

DISCLOSURE STATEMENT

The authors are not aware of any biases that might be perceived as affecting the objectivity of this review.

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Annual Review of Genetics

Volume 42, 2008

Contents

Mid-Century Controversies in Population Genetics
James F. Crow 1

Joshua Lederberg: The Stanford Years (1958–1978)
Leonore Herzenberg, Thomas Rindfleisch, and Leonard Herzenberg 19

How *Saccharomyces* Responds to Nutrients
Shadia Zaman, Soyeon Im Lippman, Xin Zhao, and James R. Broach 27

Diatoms—From Cell Wall Biogenesis to Nanotechnology
Nils Kroeger and Nicole Poulsen 83

Myxococcus—From Single-Cell Polarity to Complex Multicellular Patterns
Dale Kaiser 109

The Future of QTL Mapping to Diagnose Disease in Mice in the Age of Whole-Genome Association Studies
Kent W. Hunter and Nigel P.S. Crawford 131

Host Restriction Factors Blocking Retroviral Replication
Daniel Wolf and Stephen P. Goff 143

Genomics and Evolution of Heritable Bacterial Symbionts
Nancy A. Moran, John P. McCutcheon, and Atsushi Nakabachi 165

Rhomboid Proteases and Their Biological Functions
Matthew Freeman 191

The Organization of the Bacterial Genome
Eduardo P.C. Rocha 211

The Origins of Multicellularity and the Early History of the Genetic Toolkit for Animal Development
Antonis Rokas 235

Individuality in Bacteria
Carla J. Davidson and Michael G. Surette 253

Transposon Tn5
William S. Reznikoff 269

Selection on Codon Bias
Ruth Hershberg and Dmitri A. Petrov 287

How Shelterin Protects Mammalian Telomeres
Wilhelm Palm and Titia de Lange 301

Design Features of a Mitotic Spindle: Balancing Tension and Compression at a Single Microtubule Kinetochore Interface in Budding Yeast
David C. Bouck, Ajit P. Joglekar, and Kerry S. Bloom 335

Genetics of Sleep
Rozi Andretic, Paul Franken, and Mehdi Tafti 361

Determination of the Cleavage Plane in Early *C. elegans* Embryos
Matilde Galli and Sander van den Heuvel 389

Molecular Determinants of a Symbiotic Chronic Infection
Kattherine E. Gibson, Hajime Kobayashi, and Graham C. Walker 413

Evolutionary Genetics of Genome Merger and Doubling in Plants
Jeff J. Doyle, Lex E. Flagel, Andrew H. Paterson, Ryan A. Rapp, Douglas E. Soltis, Pamela S. Soltis, and Jonathan F. Wendel 443

The Dynamics of Photosynthesis
Stephan Eberhard, Giovanni Finazzi, and Francis-André Wollman 463

Planar Cell Polarity Signaling: From Fly Development to Human Disease
Matias Simons and Marek Mlodzik 517

Quorum Sensing in Staphylococci
Richard P. Novick and Edward Geisinger 541

Weird Animal Genomes and the Evolution of Vertebrate Sex and Sex Chromosomes
Jennifer A. Marshall Graves 565

The Take and Give Between Retrotransposable Elements and Their Hosts
Arthur Beauregard, M. Joan Curcio, and Marlene Belfort 587

Genomic Insights into Marine Microalgae
Micaela S. Parker, Thomas Mock, and E. Virginia Armbrust 619

The Bacteriophage DNA Packaging Motor
Venigalla B. Rao and Michael Feiss 647

The Genetic and Cell Biology of Wolbachia-Host Interactions
Laura R. Serbus, Catharina Casper-Lindley, Frédéric Landmann, and William Sullivan 683

Effects of Retroviruses on Host Genome Function
Patric Jern and John M. Coffin 709

X Chromosome Dosage Compensation: How Mammals Keep the Balance
Bernhard Payer and Jeannie T. Lee 733

Errata

An online log of corrections to *Annual Review of Genetics* articles may be found at http://genet.annualreviews.org/errata.shtml