Trends in Photochemistry & Photobiology
Vol. 16, 2014

Review

Retrograde operational sensing and signalling pathways maintain photostasis in green algae, cyanobacteria and terrestrial plants

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ABSTRACT

The balance in cellular energy flow between the energy source and metabolic sinks is termed photostasis. An imbalance in energy flow may be a consequence of the cumulative impact of changes in either, or both, light and temperature and is sensed by photoautotrophs as a change in excitation pressure, a measure of the relative redox state of quinone A of photosystem II reaction centres which reflects the reduction state of the intersystem electron transport chain. Changes in excitation pressure constitute an 'operational' retrograde redox signal which mediates changes in nuclear and plastid gene expression required to optimize photosynthesis and avoid the oxidative damage associated with excessive light energy absorption during abiotic stress. Restructuring of the photosynthetic apparatus in response to environmental change is accomplished by the coordination of retrograde operational signalling pathways with the photoreceptor-mediated sensing and signalling pathways which regulate chloroplast biogenesis and photomorphogenesis. Phenotypic and photosynthetic responses to abiotic stresses in green algae, cyanobacteria and terrestrial plants are compared with respect to acclimation to excitation pressure.

KEYWORDS: photostasis, operational signals, redox regulation, photosynthesis, green algae, cyanobacteria, terrestrial plants

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ABBREVIATIONS

β-CC, β-cycloitral; σ_{PSII}, effective absorptive cross section photosystem II; τ^{-1}, turnover metabolic sinks; ALA, aminolevulinic; ATP, adenosine triphosphate; CAO, chlorophyllide a oxygenase; CBF, c-repeat/dehydration-responsive binding factor; Chl, chlorophyll; CHLH, Mg-chelatase; CO_2, carbon dioxide; COP1, constitutive photomorphogenic 1; Cyt b_6/f, cytochrome b_6/f; DBMIB, 2,5-dibromo-3-methyl-6-isoprophylbenzoquinone DCMU, 3-(3'-4'-dichlorophenyl)-1,1-dimethylurea; E_K, irradiance at which photosysthetic quantum yield balances photosynthetic capacity; EX_1/EX_2, executer 1/executer 2; fd, ferredoxin; GLK, golden2-like; GUN, genomes uncoupled; H_2O_2, hydrogen peroxide; HEP, high excitation pressure; HFR1, long hypocotyl in far red 1; HL, high light; HY5, long hypocotyl 5; I, irradiance; LAF1, long after far red light 1; LEP, low excitation pressure; LT, low temperature; MEcPP, methylerythritol cyclophosphate; NADPH, reduced nicotinamide adenine dinucleotide phosphate; NPQ, nonphotochemical quenching; $^1O_2$, singlet oxygen; $OH^{\bullet}$, hydroxyl radicals; O_2, oxygen; O_2^-, superoxide; P680, specialized photosystem II chlorophyll a; P700, specialized photosystem I chlorophyll a; PAP, 3'-phosphoadenosine 5'-phosphate; PCR, photosynthetic carbon reduction; PET, photosynthetic electron transport; PC, plastocyanin; PGE, plastid gene expression; PIF, phytochrome interacting factors; POR, protochlorophyllide oxidoreductase; PSI, photosystem I; PSII, photosystem II;

PQ, plastoquinone; PQH_2, plastoquinol; Q_A, quinone A; Q_B, quinone B; ROS, reactive oxygen species; Yz, tyrosine.

INTRODUCTION

Photosynthesis is the process by which photoautotrophic organisms convert the energy available in light into biologically useful reducing power in the form of NADPH (reduced nicotinamide adenine dinucleotide phosphate) and chemical energy in the form of ATP (adenosine triphosphate). The energy available as sunlight is absorbed by the light-harvesting pigment-protein complexes associated with photosystem II (PSII) and photosystem I (PSI) in eukaryotic photoautotrophs and subsequently trapped as electrons through photo-oxidation of P680 and P700 in PSII and PSI respectively. The flow of electrons between these two photosystems is facilitated by the step-wise reduction and oxidation of the structural components of intersystem photosynthetic electron transport (PET) which consists of the plastoquinone (PQ) pool, cytochrome b_6/f complex (Cyt b_6/f) and plastocyanin (PC). Photosynthetically derived reductants are consumed through carbon, nitrogen and sulphur metabolism, cellular respiration and ultimately growth (Figure 1).

In eukaryotic photoautotrophs photosynthesis occurs within the chloroplasts. Chloroplasts are descendent from a free-living photoautotrophic ancestor similar to extant cyanobacteria which entered the eukaryotic lineage through an endosymbiotic event over a billion years ago [1-3]. Following this event the genome of the endosymbiont underwent significant reduction with the majority of the genes having been lost or transferred to the host nucleus [4-6]. As a consequence, the chloroplast genome encodes less than 10% of the proteins required for plastid function and development [4-6]. The remainder of the chloroplast-localized proteins are encoded by the nuclear genome and synthesized in the cytoplasm before import into the plastid. Such genetic heterogeneity means that many plastid localized protein complexes are molecular mosaics of plastid and nuclear-encoded genes [7].

Establishment of photoautotrophic metabolism therefore requires considerable coordination between these two spatially separated genomes to ensure proper chloroplast biogenesis and development, while maintenance of photoautotrophic metabolism requires coordinated adjustments in nuclear and plastid gene expression necessary to optimize photosynthesis and avoid the photo-oxidative damage associated with excessive light energy absorption during abiotic stress. Developmental cues and environmental stimuli including light, temperature and nutrient availability are integrated to ensure proper chloroplast development and the modulation of photosynthetic efficiency and capacity in mature chloroplasts. Coordinated regulation is achieved through the exchange of information between the nucleus and plastids. Anterograde signals arise in the nucleus and regulate the expression of plastid localized genes [8]. The reverse mechanism, retrograde signalling, transmits information communicating the developmental and functional state of the plastid to the nucleus to induce appropriate changes in the expression of nuclear-encoded genes involved in chloroplast function and development.

The aim of this review is to provide an overview contrasting the relative roles of light quality in the regulation of chloroplast biogenesis and photoautotrophic architecture versus the role of light intensity in the regulation of the structure and functionality of the photosynthetic apparatus. The former is associated with 'biogenic signals' whereas the latter are referred to as 'operational signals'. The reader is referred to excellent reviews on this subject by Pogson and co-workers [9-11] and Jarvis and Lopez-Juez [12].

1. Biogenic signals

1.1. Photoreceptor-mediated light quality signalling during chloroplast biogenesis

In the context of biogenic control, perception of light is mediated by blue light sensitive photoreceptors (crytochromes, phototropins and zeitlupe) and red light sensitive photoreceptors (phytochromes) [13, 14]. Photoreceptors are activated by absorption of specific wavelengths enabling detection of specific changes in light quality and are responsible for activating signalling cascades regulating light-dependent events including photomorphogensis and photoperiodic responses [10, 12, 14-17].

Chloroplast biogenesis is the developmental differentiation of a proplastid, the plastid progenitor, to a mature chloroplast either directly or through the dark-grown etioplast as an intermediate and ultimately leads to the establishment of photoautotrophic metabolism. In darkness photomorphogensis is repressed by two nuclear repressors, phytochrome-interacting factors (PIFs) and constitutive photomorphogenic 1 (COP1), which prevent the accumulation of positive regulators of light-activated gene expression [10, 12, 13]. Following illumination, phytochromes and cryptochromes facilitate the removal of PIFs and COP1 from the nucleus thereby allowing the accumulation of positive transcription factors including golden2 like(s) (GLKs), long hypocotyl in far red 1 (HFR1), long hypocotyl 5 (HY5) and long after far red light 1 (LAF1) [10, 12, 13]. These positive transcription factors promote the expression of nuclear-encoded genes involved in photomorphogenesis and photosynthesis though cis-acting promoter elements [13, 17, 18]. These light signalling components are closely related to chloroplast biogenesis; PIF3 is negative regulator of chloroplast development [19] whereas HY5 and GLK are positive regulators of chloroplast development [20, 21].

1.2. Developmental retrograde plastid signals

1.2.1. Plastid gene expression (PGE)-dependent retrograde signals

In addition to perception of light signals by phytochromes, the chloroplast itself mediates signals during biogenesis. When chloroplast biogenesis is blocked either by use of specific genetic backgrounds [22], site specific inhibition of plastid transcription or translation by chemical inhibitors [23-25], or by oxidative damage caused by carotenoid deficiency following norflurazon treatment [26], the expression of nuclear-encoded genes involved in photosynthesis and chloroplast biogenesis are reduced. It has been postulated that signals derived from the plastid, which are dependent on PGE, control the expression of nuclear-encoded genes. These signals are believed to function to coordinate the expression of nuclear-encoded genes required for the proper biogenesis and assembly of the photosynthetic apparatus [8, 27].

Significant insight into the mechanism of these PGE-dependent signalling pathways has been gained from a series of *Arabidopsis thaliana* mutants that accumulate nuclear-encoded photosynthetic genes despite photobleaching caused by norflurazon treatment [28]; since these mutants fail to repress nuclear gene expression they were designated *genomes uncoupled* (*gun*) mutants due to the apparent lesions in the plastid-to-nucleus signalling pathways. One of the mutants, *gun1*, showed de-repression of nuclear gene expression in plants treated with an inhibitor of PGE indicating a role for GUN1 in PGE-dependent retrograde signalling pathways [29]. GUN1 was identified as a pentatricopeptide-repeat protein suggesting a potential role for it as a regulator of plastid-localized gene expression in a manner that influences retrograde signalling [30].

Of the *gun* mutants isolated, four of the mutants (*gun2, gun3, gun4* and *gun5*) were demonstrated to have mutations in genes encoding enzymes in the tetrapyrrole pathway that culminates in chlorophyll (Chl), heme and chromophore synthesis (Figure 2) [31]. Although the Chl biosynthesis intermediate, Mg-protoporhyrin IX, was subsequently identified as a potential retrograde signal (Figure 2) [32], the role of this intermediate remains equivocal [33, 34]. Recently, it has been reported that a specific heme pool may be a primary retrograde signal for chloroplast biogenesis (Figure 2) [30, 35].

Research suggests GUN1 may function downstream of tetrapyrrole-dependent signals and act as a convergent point for tetrapyrrole and PGE-dependent signals [8, 29]. Convergence between multiple retrograde pathways would allow the chloroplast to integrate disparate signalling conduits that regulate similar nuclear-encoded genes [8]. Once perceived by the nucleus, ABI4 binds cis-acting promoter elements and may play a role in the inhibition of light-dependent transcription factors [29]; ABI4 has been postulated to act downstream of GUN1 in plastidic retrograde signalling [29, 36]. GUN1 has also been identified as a component of additional signalling pathways including those derived from the circadian clock [37] and de-etiolation [38], as well as sugar and redox signals [29] suggesting GUN1 acts as a hub within the chloroplast coordinating multiple signalling pathways. However, GUN1-dependent plastid

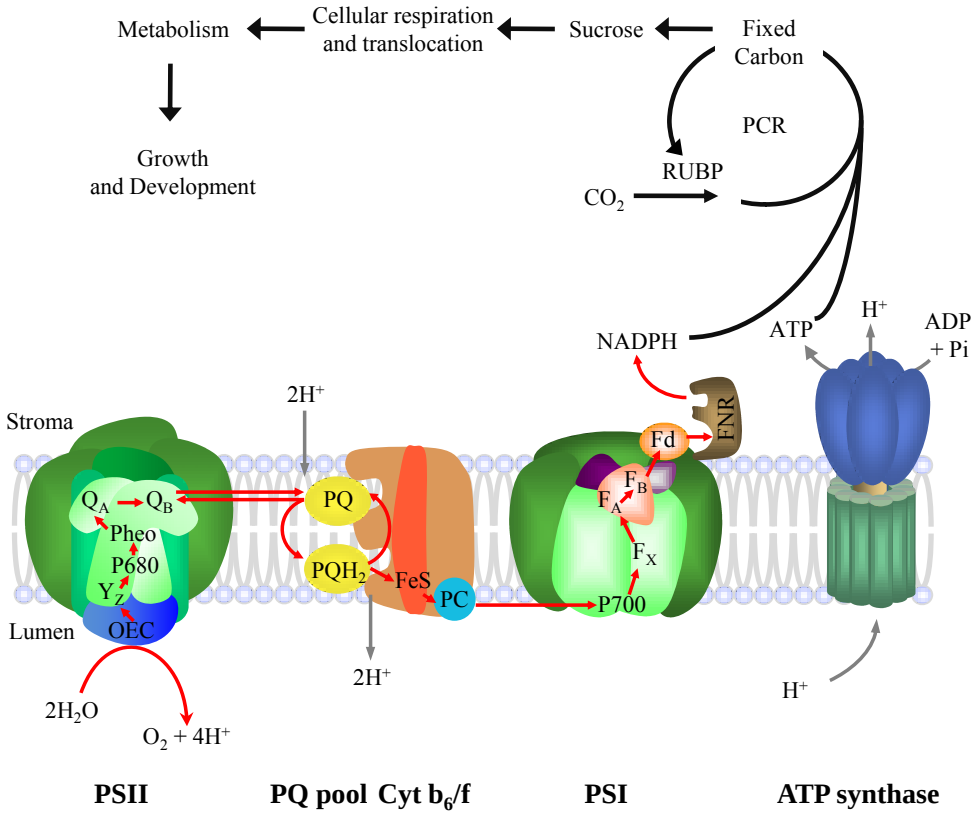

Figure 1

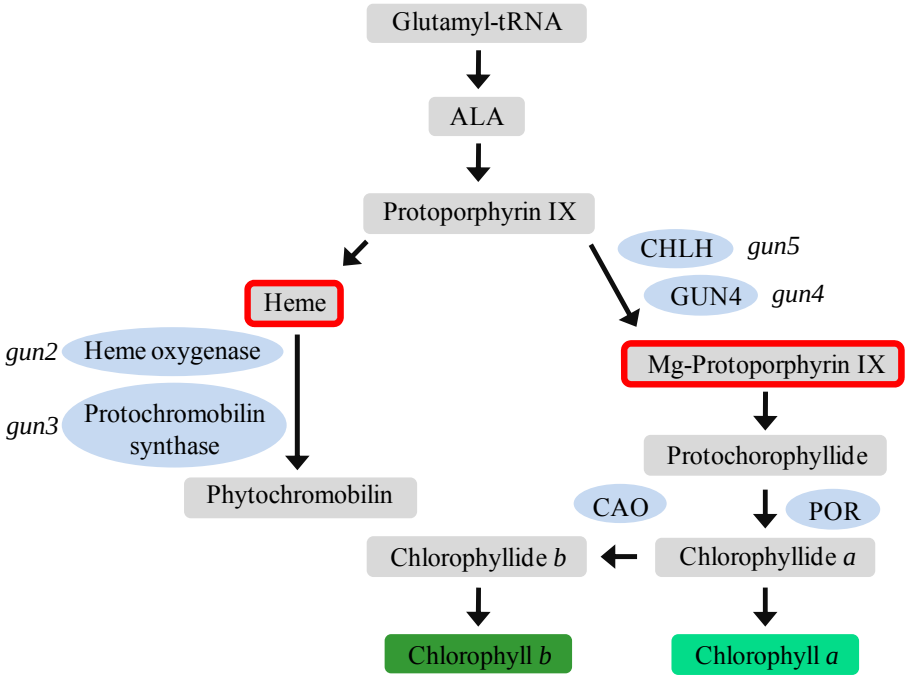

Figure 2

retrograde signalling may only function during the early stages of chloroplast development [39, 40].

Plastid biogenesis requires a balance between positive signals derived from phytochrome-mediated light quality sensing and negative signals derived from the functional state of the plastid itself [3]. A genetic screen identified four mutants with a *gun* phenotype but with mutations in *cry1* alleles [27]. Since cry1 is a strong inducer of light-harvesting gene expression, it appears that cry1 can be converted from a positive to a negative regulator of nuclear-encoded light-harvesting gene expression when chloroplast biogenesis is blocked. It was postulated that the functional state of the plastid can 'remodel' biogenic light signals crucial for chloroplast biogenesis [27, 41, 42].

1.2.2. Interactions between light and temperature during plant development

Light and temperature are two of the most critical environmental cues regulating photoautotrophic development. During development light quality signals are perceived by specialized photoreceptors. Five phytochrome genes (*PHYA*, *PHYB*, *PHYC*, *PHYD* and *PHYE*) have been identified in *A. thaliana* [43]. Regulatory roles for phytochromes have been identified in all aspects of plant growth and development from seed germination, in regulation of mature plant architecture, to control of the onset of reproductive development [44]. However, photoreceptor-mediated sensing and signalling pathways have been shown to act in a temperature-dependent manner [45, 46]. For example, *phyB* mutants display early flowering at 22 °C, while this phenotype was abolished when temperature was decreased to 16 °C. The use of multiple mutants indicates a predominant role for *phyE* in suppression of flowering at lower temperatures [46, 47]. Similar functional hierarchies in phytochrome dominance have been demonstrated for the regulation of germination, internode elongation and rosette habit, flowering time and

Legend to Figure 1. Simplified model illustrating intersystem photosynthetic electron transport and carbon assimilation. Linear electron flow from water to nicatindamide adenine dinucleotide ($NADP^+$) is shown in red. Light energy is simultaneously absorbed by the pigment-binding light-harvesting complex polypeptides associated with photosystem II (PSII) and photosystem I (PSI; shown in dark green). Absorbed energy is transferred to specialized chlorophyll *a* molecules, P680 and P700, in the reactions centres of PSII and PSI, respectively (shown in light green). Photo-excited P680 (P680*) is the primary electron donor in the PSII reaction centre and pheophytin (Pheo) is the primary electron acceptor; P680* is photo-oxidized to $P680^+$. Yz is a tyrosine molecule facilitating electron transfer from water to $P680^+$ via the oxygen evolving complex (OEC). Pheo passes the electron to quinone A (Q_A), the first stable electron acceptor of PSII. The electron then passes to the mobile electron carrier quinone B (Q_B) which detaches from the PSII reaction centre and gains two protons to become plastoquinol (PQH_2) before becoming a part of the PQ pool present within the hydrophobic thylakoid membrane. The electron then passes to the Rieske iron-sulfur protein (FeS) of the Cytochrome b_6/f (Cyt b_6/f) complex and the mobile copper-binding protein plastocyanin (PC) on the lumenal side of Cyt b_6/f. Within the PSI reaction centre, P700 is excited to P700* and then photo-oxidized to $P700^+$ becoming the primary electron donor within PSI. The electron is then passed through three iron-sulfur proteins (F_A, F_B and F_X) to ferredoxin (Fd), a mobile protein on the stromal side of PSI, which facilitates the reduction of $NADP^+$ to NADPH (reduced $NADP^+$) through electron transfer to the enzyme ferredoxin-NADP oxioreductase (FNR). $P700^+$ gains an electron from reduced PC. Intersystem electron transport concentrates protons on the lumenal side of the thyalkoid membrane providing the proton motive force used to produce ATP from ADP and inorganic phosphate (Pi) via ATP synthase. ATP and NADPH are consumed during carbon assimilation in the photosynthetic carbon reduction (PCR) cycle; CO_2 is combined with the acceptor molecule ribulose-1,5-bisphosphate (RuBP) to generate fixed carbon in the form of triose phosphates which are transported to the cytosol for sucrose biosynthesis. In terrestrial plants, sucrose is either translocated to distant sink tissue or consumed through cellular respiration and ultimately growth.

Legend to Figure 2. Tetrapyrrole pathway in plastids. Key intermediates in the pathway culminating in chlorophyll and phytochromoblin are shown in grey with key enzymes shown in blue. Molecules highlighted in red are suspected 'biogenic' plastid retrograde signals (discussed in text). Location of *gun* mutations are noted. ALA, aminolevulinic acid; CAO, chlorophyllide a oxygenase; CHLH, Mg-chelatase; POR, protochlorophyllide oxioreductase. Tetrapyrrole pathway adapted from Larkin [118].

freezing tolerance [44]. Integration of light quality and temperature signals is suggested to provide plants with more reliable information on seasonal progression allowing for controlled regulation of plant development and architecture [44, 45, 48].

2. Operational signals

Using phytochrome mutants, Walters *et al.* [49] demonstrated that light-dependent adjustments to the structure and function of the fully developed photosynthetic apparatus of *A. thaliana*, in response to changing irradiance can occur independently of photoreceptors. However, the defective photoacclimation responses in the *det1* signal transduction mutant in *A. thaliana* does support some degree of cross-talk between photoreceptor-regulated responses and other regulators of photosynthetic acclimation [49]. Furthermore, Fey *et al.* [50] demonstrated redox signals from the photosynthetic apparatus are capable of inducing changes in nuclear-encoded gene expression independently of photoreceptor-mediated signalling.

Photoautotrophs must balance the energy trapped through the extremely fast (femtosecond to picosecond timescale), temperature-independent photophysical light absorption, energy transfer and photochemistry within the photosystems, with energy utilization through much slower, temperature-sensitive metabolic sinks consisting of biochemical reactions (second to minute timescale) and subsequently growth (hours to days to weeks timescale). This energetically balanced cellular state between energy source and sink is referred to as photostasis [51]. Photostasis can be represented by the equation $\sigma_{PSII} \bullet E_K = \tau^{-1}$ where σ_{PSII} is the effective absorption cross section of PSII, E_K is the irradiance (I) at which photosynthetic quantum yield matches sink turnover (τ^{-1}) [52]. Since the maintenance of photostasis integrates temperature-insensitive photophysical and photochemical processes with temperature-dependent processes, PSII can be exposed to excessive excitation energy whenever the light energy absorbed exceeds either the turnover rate of the metabolic sinks that consume this energy through biochemistry and metabolism and/or the capacity to dissipate the excess energy as heat through non-photochemical quenching (NPQ; Figure 3) [53, 54]. Such an imbalance in cellular energy is termed high excitation pressure (HEP) and can be represented by the inequality, $\sigma_{PSII} \bullet E_K > \tau^{-1}$ [51, 55, 56]. Thus, an imbalance of cellular energy flow may be a consequence of the cumulative impact of changes in either, or both, light and temperature [57]. High light (HL) would satisfy this condition directly by increasing the product $\sigma_{PSII} \bullet E_K$ with minimal effects on τ^{-1} whereas low temperature (LT) satisfies the same condition by exerting minimal effects on $\sigma_{PSII} \bullet E_K$ but decreasing τ^{-1}. Since diffusion of plastoquinol (PQH_2) within the plane of the thylakoid membrane and its subsequent oxidation by the Cyt b_6/f complex is the rate limiting step of PET [58], HEP results in the reduction of the components of the PET which culminates in the accumulation of closed PSII reaction centres (Figure 4). This can be measured non-invasively *in vivo* by the Chl *a* fluorescence parameter 1-qP [57, 59] or 1-qL [60-62]. While light-absorption and photochemistry are also associated with PSI, it is not considered to be limiting during steady state photosynthesis as its photochemical turnover rate exceeds that of PSII [63] and is therefore excluded from the equation for photostasis.

Changes in either growth irradiance or temperature will modulate excitation pressure generated within the chloroplast. The resulting reduction of the components of the PET chain represents an 'operational redox signal' that can be used to re-establish photostasis and a new homeostatic cellular energy state associated with acclimation to the new environment. Thus, acclimation to HL should mimic acclimation to LT. Furthermore, since nutrient limitations and water availability will also induce HEP by lowering τ^{-1} [64], we suggest that, because of the nature of photoautotrophic growth, all photosynthetic organisms acclimate to changes in their environment by sensing and responding to excitation pressure, an important "operational signal".

Operational signals can also regulate chloroplast biogenesis as reported by Rosso *et al.* [65]. The extent and the patterns of leaf variegation in the *Arabidopsis thaliana* mutant, *immutans*, is regulated by excitation pressure [65]. IMMUTANS is a nuclear encoded, plastid terminal oxidase (PTOX) [66, 67] essential for the catalysis of chlororespiration and functions to oxidize the PQH_2 pool and reduce O_2 to water in the chloroplast [68, 69].

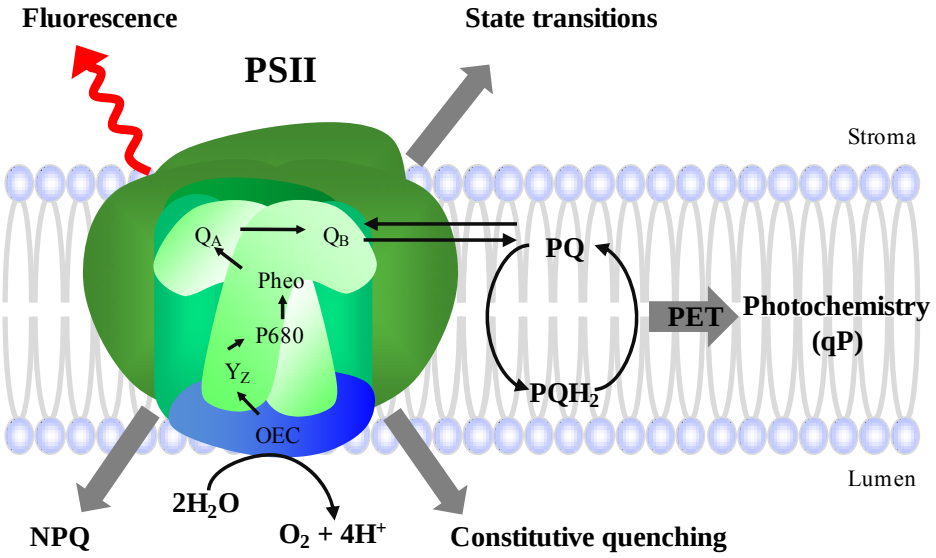

Figure 3. Fates of light energy absorbed by photosystem II (PSII). Light energy absorbed by the PSII antenna can either be released as fluorescence, dissipated as heat through non-photochemical quenching (NPQ), dissipated as heat through constitutive quenching, or used to drive photochemistry (qP) and intersystem photosynthetic electron transport (PET). OEC, oxygen evolving complex; P680, reaction centre chlorophyll *a*; Pheo, pheophytin; PQ, plastoquinone; PQH_2, reduced plastoquinone; Q_A, quinone A; Q_B, quinone B, Y_Z, tyrosine.

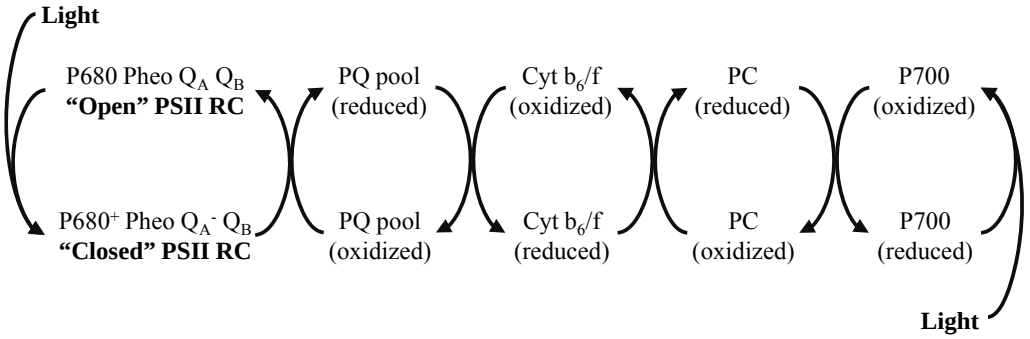

Figure 4. Light-dependent closure of photosystem II reaction centre (PSII RC). The PSII RC consists of P680, the reaction centre chlorophyll *a*, Pheophytin (Pheo) and quinone A (Q_A) which are bound to the PSII reaction centre polypeptides. Excitation energy is used to excite P680 which is photo-oxidized to $P680^+$ following electron transfer to Pheo and finally Q_A reducing Q_A to Q_A^-; this results in stable charge separation and closure of the PSII RC ($P680^+$ Pheo Q_A^-) as $P680^+$ cannot undergo further photo-oxidation. Conversion of the "closed" PSII RC to an "open" PSII RC requires reduction of $P680^+$ via oxidation of water and concomitant transfer of the electron from Q_A^- to the plastoquinone (PQ) pool via Q_B. Following complete reduction, PQ is protonated to form plastoquinol (PQH_2) which leads to the step-wise reduction of the cytochrome b_6/f complex (Cyt b_6/f), plactocynanin (PC) and ultimately $P700^+$, the photo-oxidized photosystem I (PSI) reaction centre chlorophyll *a*. The proportion of closed PSII RC is measured *in vivo* as 1-qP which is an estimate of the relative redox state of Q_A as $(Q_A^-) / ((Q_A^-) + (Q_A^+))$. Since reduced Q_B is in rapid equilibrium with the PQ pool, 1-qP also reflects the redox state of the photosynthetic electron transport chain.

Rosso *et al.* [65] reported that PTOX was essential to reduce excitation pressure during the early stages of chloroplast biogenesis in Arabidopsis before the establishment of complete photosynthetic competence. In wild type Arabidopsis, the modulation of excitation pressure by PTOX during the first 6 h of greening results in the assembly of a functional photosynthetic apparatus

and normal green leaf sectors. In *immutans*, the absence of PTOX results in excessively high excitation pressure during early greening and photo-oxidative damage to the photosynthetic apparatus which results in white sectors, the typical phenotype observed for *immutans*. Thus, expression of *IMMUTANS*, and thus the variegated phenotype appears to be governed by chloroplast redox retrograde regulation.

2.1. Green algae

Growth and development of the green algae *Chlorella vulgaris* and *Dunaliella* sp. under HL results in a typical yellow to yellow-green pigmentation relative to the dark green pigmentation typical of growth and development at low light (LL). This yellow to yellow-green phenotype is characterized, in part, by a relatively lower Chl content per cell and higher Chl a/b ratios with concomitant decreases in the level of the major PSII light-harvesting (LHCII) pigment-binding polypeptides relative to the darker green phenotype [57, 70-76]. The xanthophyll cycle is also activated during growth under HL. Functionally this results in a significant decrease in the apparent quantum yield for oxygen (O_2) evolution when measured on a per cell basis [70, 77]. These results are consistent with the notion that these green algae respond to HL by decreasing σ_{PSII} through reductions in the physical size of LHCII, as well as an increased capacity to dissipate excess energy as heat through NPQ [70, 72-74, 76, 77]. As predicted, phenotype as well as photosynthetic performance during growth at HL is mimicked by growth at LT in *C. vulgaris*. This change in σ_{PSII} induced by growth at HEP imparts enhanced photoprotection and increased resistance to photoinhibition compared to LL control cells [57, 70, 77].

The phenotypic and photosynthetic similarity between cells grown at either HL or LT is attributed to the observation that *C. vulgaris* is limited in its capacity to adjust either carbon metabolism [71] or growth rates [74] in response to HEP. Thus, *C. vulgaris* is limited in its capacity to up-regulate τ^{-1}. Consequently, *C. vulgaris* survives under HEP by altering the structure and function of the photosynthetic apparatus and up-regulates NPQ to reduce the capacity to absorb and trap available light energy through a decrease in σ_{PSII}. Thus, *C. vulgaris* survives and re-establishes photostasis under HEP by decreasing its photosynthetic efficiency ($\sigma_{PSII} \bullet E_K$) to match its sink capacity (τ^{-1}). This increases the quantum requirement for the closure of PSII reaction centres, measured as the number of photons required to close PSII reaction centres, which accounts for its increased resistance to photoinhibition.

The yellow-green HEP phenotype in *C. vulgaris* can revert to the normal, green LEP phenotype following a shift from LT to moderate temperature at a constant irradiance [75]. This temperature-induced greening is associated with an increase in Chl per cell and accumulation of Lhcb2 polypeptides [75] which is very similar to the greening observed when the green algae *C. pyrenoidosa* [78] and *D. terticolectra* [79] were transferred from high to low light. Temperature-induced greening in *C. vulgaris* without a change in light intensity precludes the contribution of sensors involved in light sensing *per se*.

Furthermore, acclimation to HEP in *C. vulgaris* and *D. tertiolecta* is mimicked by use of chemical inhibitors of PET that regulate the redox state of the PQ pool. This is accomplished through application of either 3-(3'-4'-dichlorophenyl)-1,1-dimethylurea (DCMU) or 2,5-dibromo-3-methyl-6-isoprophylbenzoquinone (DBMIB) [73-75]. Since DCMU blocks the transfer of electrons from PSII to the PQ pool, the PQ pool remains oxidized in the light [80]. DCMU mimics the effects of low light or moderate temperature on the redox state of the PQ pool and generates the dark-green LEP phenotype characterized by relatively high Chl per cell, low Chl a/b ratio (approximately 3.0 to 4.0) and high levels of *Lhcb2* transcript and Lhcb2 polypeptide abundance [66-68]. In contrast, DBMIB prevents the oxidation of PQH_2 by PSI in the light [80]. Treatment with DBMIB therefore mimics the effects of HEP on the redox state of the PQ pool and generates the yellow-green HEP phenotype characterized by relatively lower Chl per cell, high Chl a/b ratio (approximately 10) and reduced *Lhcb2* expression and Lhcb2 polypeptide abundance [73-75]. Since the phenotypic and photosynthetic adjustments in *C. vulgaris* can be modulated chemically with DMBIB and DCMU and with temperature with no change in irradiance, the attainment of photostasis is a response to

'operational signals' from the chloroplast to the nucleus and does not require 'biogenic signals' typically involved in photomorphogenesis. Furthermore, since PSII reaction centres are completely closed in the presence of either DCMU or DBMIB, the redox state of Q_A can not be the sensor. Thus, it appears that the redox state of the PQ pool is an important sensor within PET and source of redox signals regulating photostasis [51, 56, 57].

2.2. Cyanobacteria

Although cyanobacteria are oxygenic, they do not exhibit a xanthophyll cycle characteristic of terrestrial plants and green algae [81]. Furthermore, cyanobacteria are characterized by the presence of pigment-protein complexes extrinsic to their thylakoid membranes called phycobilisomes. These phycobilisomes function to harvest light energy and transfer the energy to PSII and PSI reaction centres analogous to the major LHCII and LHCI associated with eukaryotic photoautotrophs. Do prokaryotic photosynthetic microbes respond in a similar manner to HEP as observed for green algae? This question was addressed by examining the response of the filamentous cyanobacterium, *Plectonema boryanum*, to HEP generated by growth at either HL or LT [82, 83]. Similar to *C. vulgaris, P. boryanum* also exhibited minimal plasticity in the ability to adjust growth rates (τ^{-1}) in response to irradiance. Consequently, this cyanobacterium alters the structure and composition of its phycobilisomes to minimize the absorption of light energy which results in a decrease in the efficiency of photosynthetic O_2 evolution [82, 83]. This results in a change in phenotype from the typical blue-green for control cells grown under LEP to a red-brown phenotype for cells grown at HEP. Similar to *C. vulgaris*, the HEP phenotype in *Plectonema boryanum* is completely reversible upon a shift from low growth temperature (15 °C) to warm temperatures (29 °C) with no change in irradiance [82, 83]. However, unlike *C. vulgaris*, the operational signal appears to emanate downstream of the PQ pool in this cyanobacterium based on its phenotypic responses to DCMU and DBMIB [82]. The precise source of the redox signal remains unclear but is probably associated with PSI.

2.3. Terrestrial plants

In contrast to green algae and cyanobacteria which respond to growth and development under HEP through reductions in σ_{PSII} due to limited capacity to adjust τ^{-1}, overwintering cultivars of wheat and rye respond to HEP through a stimulation of τ^{-1} through up-regulation of photosynthetic capacity [57, 84, 85] and biomass accumulation with minimal dependence on NPQ and minimal changes in the structure and function of PSII and PSI. Consequently, in contrast to *C. vulgaris* and *P. boryanum*, the dwarf growth habit associated with cold acclimation in winter wheat and rye occurs with minimal changes in pigmentation and structure and function of PET [64, 86]. Rather, cold acclimated plants display a dwarf phenotype and exhibit increased cytoplasmic volume with concomitant increases in sucrose and structural carbohydrate content, as well as an increase in leaf thickness such that the total biomass of the dwarf plants matches or exceeds that of those displaying the typical elongated growth habit [64, 86-90]. The cold-acclimated dwarf phenotype reflects underlying changes at the molecular and biochemical level consistent with a stimulation in carbon metabolism through increased expression and activities of the carbon-fixing enzyme Rubisco (Ribulose-1,5-bisphosphate carboxylase/oxygenease) [64, 86, 88, 91] and the sucrose biosynthesis enzymes, cFBPase (cytosolic fructose-1,6-bisphosphatease) and SPS (sucrose-phosphate synthase) [64, 86, 88, 91, 92]. Cold-acclimation is further associated with increased sucrose export to sink tissues and the capacity for increased carbohydrate storage in crown tissue [93-96].

However, a comparable dwarf phenotype and enhanced photosynthetic capacity is generated by growth and development of winter cereals under HL. Consequently, the dwarf phenotype and enhanced photosynthetic performance is governed by excitation pressure rather than by LT *per se* [57, 85]. Comparable responses to HEP with respect to dwarf phenotype and enhanced photosynthetic performance have been reported for *A. thaliana* [97] and *Brassica napus* [64, 86]. Thus, although winter cereals, like green algae and cyanobacteria, maintain photostasis in

response to excitation pressure, the mechanism by which they do so is quite distinct; winter hardy terrestrial plants adjust sink capacity (τ^{-1}) whereas *C. vulgaris* and *P. boryanum* adjust σ_{PSII}. Recently, it was reported that both the dwarf phenotype and enhanced photosynthetic performance normally induced by cold acclimation in *B. napus* can be induced at warm growth temperatures simply by overexpressing the *B. napus* CBF (C-repeat/dehydration-responsive binding factor) nuclear transcription factor (*BnCBF*17) [86, 98]. It has been suggested that the family of CBFs may represent important integrators of chloroplast redox, phytochrome and phytohormones signalling in terrestrial plants [80].

3. Sensing and retrograde operational signalling

Photosynthetic organisms constantly monitor changes in light quality through photoreceptor-mediated sensing and signalling pathways (biogenic signals) as well as change in light energy availability through the redox state of the photosynthetic apparatus (operational signals). However, the nature of the redox sensor remains equivocal. In green algae and cyanobacteria, the ability to mimic photoacclimation and a yellow-green HL phenotype with HL, LT or inhibitors of PET has originally indicated the involvement of the redox state of the PQ pool as the primary sensor governing gene expression and phenotype [70, 73, 74, 99, 100]. However, experiments with *P. boryanum* [82, 83], *A. thaliana* [101] and tobacco [102] indicate that the PQ pool is not the primary source of redox signals in all species. In addition to the redox state of the PQ pool, ferredoxin, thioredoxins and peroxioredoxins on the acceptor side of PSI [103], as well as the reducing side of PSI [101] have been postulated to function as components of the retrograde redox sensing and signalling network [29, 104].

Recently, much research has focussed on elucidation of retrograde operational signalling pathways between the chloroplast and the nucleus. Metabolically active chloroplasts, mitochondria and peroxisomes produce reactive oxygen species (ROS) including singlet oxygen ($^1O_2$), the hydroxyl radicals radical ($OH^{\bullet}$), superoxide (O_2^-) and hydrogen peroxide (H_2O_2) under normal conditions. Photoautotrophs are able to maintain relatively low ROS levels due to the action of ROS scavengers such as ascorbate peroxidase and carotenoids. However, when energy absorption exceeds the capacity for utilization under abiotic stresses including temperatures extremes, drought and HL, ROS production increases [105, 106]. The *A. thaliana fluorescent* (*flu*) mutant over-accumulates the Chl precursor protochlorophyllide leading to specific increases in $^1O_2$ production without increased accumulation of other ROS types (Figure 2) [107, 108]; illumination of the *flu* mutant causes a rise in $^1O_2$ levels and increased expression of a suite of nuclear genes. Components of ROS signalling required for $^1O_2$-dependent changes in nuclear gene expression have been identified including EXECUTER 1 (EX1) and EXECUTER 2 (EX2) [109]. EX1 and EX2 were identified in a suppressor screen of *flu* mutants and were identified as chloroplast-localized proteins [109].

H_2O_2 produced by the chloroplast is also postulated to induce the expression of nuclear-encoded genes. Since H_2O_2 has a longer half-life relative to $^1O_2$ and a lower toxicity it may be better suited as a long distance retrograde signal [105]. H_2O_2 generated by HL treatment has been demonstrated to increase the expression of the nuclear-encoded *APX2* in *A. thaliana* [110]. Although H_2O_2 can be generated in different compartments under varying stresses, a specific role for chloroplast-generated H_2O_2 has been demonstrated in tobacco plants [111] indicating a role of H_2O_2 in retrograde redox signalling.

More recently metabolites have been identified as potential sources of retrograde plastid signals during environmental stresses. Products derived from secondary metabolism including 3'-phosphoadenosine 5'-phosphate (PAP) [112, 113] and methylerythritol cyclophosphate (MEcPP) [114], and carotenoid oxidation products such as β-cycloitral (β-CC) [115] have been identified as plastid signals generated during HL and drought stress. These products function to induce changes in gene expression involved in stress responses including ROS scavenging, photoacclimation and drought tolerance [11]. Signalling associated with these metabolites is consistent with the thesis that the chloroplast itself acts as a universal

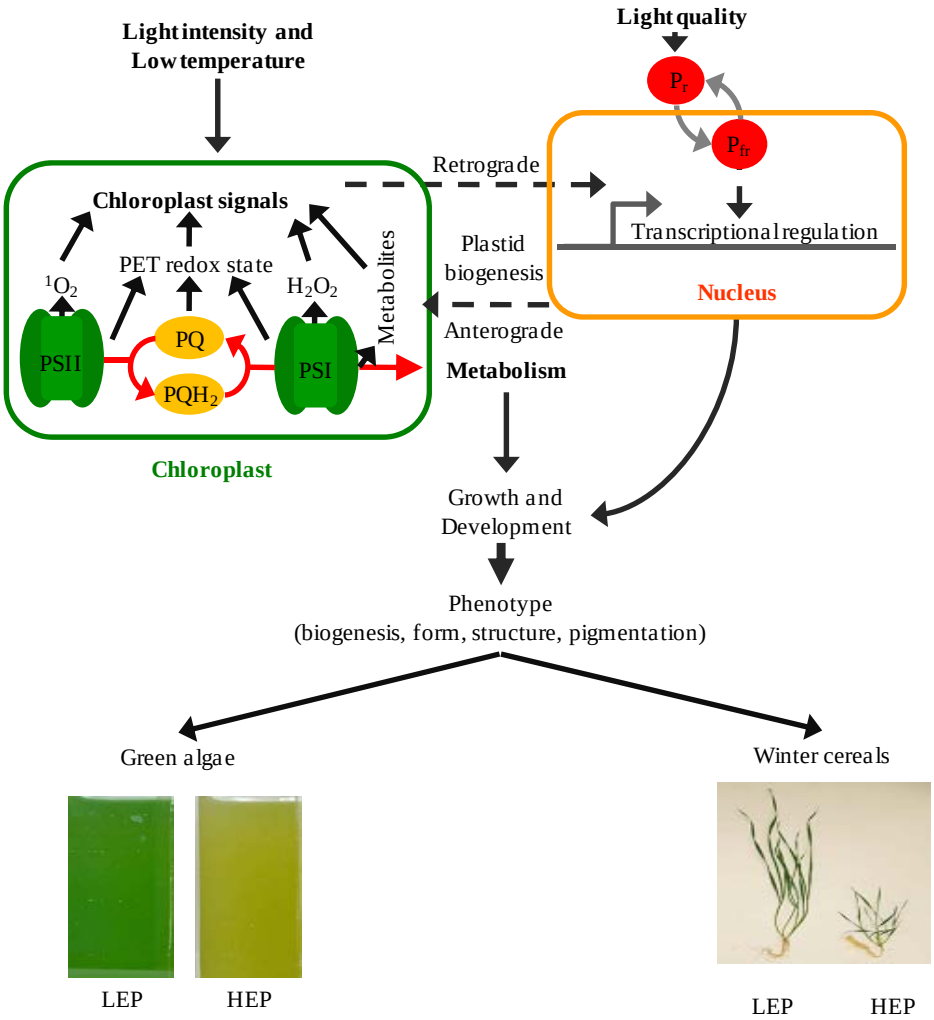

Figure 5. Model illustrating the roles of 'biogenic' and 'operational' signals in the regulation of photoautotroph phenotype. Light quality is sensed by photoreceptors which mediate the proper biosynthesis and assembly of thylakoid membranes and associated protein complexes during chloroplast biogenesis and photomorphogenesis; the anterograde phytochrome-mediated sensing and signalling pathways that enable responses to change in light quality are defined as 'biogenic' signals. By contrast, light intensity and temperature are sensed by mature chloroplasts as changes in the redox status of photosynthetic electron transport (PET) with contributions from photosystem II (PSII), the plastoquinone (PQ) pool and photosystem I (PSI). An imbalance in cellular energy flow may be a consequence of the cumulative impact of changes in either, or both, light and temperature. Changes in the redox state of PET are communicated to the nucleus through retrograde signalling pathways potentially involving reaction oxygen species ($^1O_2$, singlet oxygen and H_2O_2, hydrogen peroxide) and products of secondary metabolism (metabolites) to regulate the structure and efficiency of the photosynthetic apparatus to re-establish photostasis; retrograde signals derived from the functional state of the chloroplast are defined as 'operational signals'. Remodelling of the photosynthetic apparatus is reflected in green algae and cyanobacteria as a change in pigmentation. The yellow-green pigmentation obtained by growth and development under high excitation pressure (HEP) versus the dark green pigmentation at low excitation pressure (LEP) in green algae reflects a decrease in photosynthetic efficiency through reductions in light-harvesting complex abundance and chlorophyll per cell. In terrestrial plants, long-distance signals communicating changes in the redox state of PET induce changes in plant growth and development and are reflected as changes in mature plant architecture. The dwarf habit of winter cereals following growth and development under HEP versus the elongated habit at LEP reflects underlying structural, molecular and biochemical changes consistent with up-regulation of carbon metabolism. Therefore, we suggest the phenotype in photoautotrophs is likely reflective of cross-talk between phytochrome-mediated photomorphogenesis as well as chloroplast-mediated photosynthetic events.

environmental sensor and as a mediator of operational signals during acclimation to environmental change. However, these chloroplast-derived metabolites may be involved in the initiation of stress response as opposed to coordination of the plastid and nuclear genomes necessary to achieve energy homeostasis *per se*.

CONCLUSIONS

The elucidation of the sensors as well as the complex, myriad retrograde signal transduction pathways involved in the 'operational' control of photostasis remains a major challenge for future research. However, a clear consensus has emerged that photoautotrophs utilize 'operational' signals to modify and reorganize the photosynthetic apparatus in response to changes in their abiotic environment. Clearly, multiple components may contribute to regulation of gene expression and phenotype by excitation pressure while the extent of this contribution to phenotypic plasticity may be species-dependent, developmental stage and degree of energy imbalance. The elucidation of cross-talk between 'biogenic' and 'operational' sensing and signalling pathways (Figure 5) [116, 117] and the extent to which cross-talk alters photosynthetic performance and phenotype remains another important challenge for future research.

ACKNOWLEDGEMENTS

NPAH acknowledges the financial support of the NSERC Discovery Grants programme, the Canadian Foundation for Innovation and the Canada Research Chairs programme.

CONFLICT OF INTEREST STATEMENT

No conflict of interest to declare.

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