



A security network in PSI photoprotection: regulation of photosynthetic control, NPQ and O₂ photoreduction by cyclic electron flow

Frédéric Chaux, G. Peltier, Xenie Johnson

► To cite this version:

Frédéric Chaux, G. Peltier, Xenie Johnson. A security network in PSI photoprotection: regulation of photosynthetic control, NPQ and O₂ photoreduction by cyclic electron flow. *Frontiers in Plant Science*, 2015, 6, pp.875. 10.3389/fpls.2015.00875 . cea-02049530

HAL Id: cea-02049530

<https://cea.hal.science/cea-02049530>

Submitted on 10 Jan 2024

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



A security network in PSI photoprotection: regulation of photosynthetic control, NPQ and O₂ photoreduction by cyclic electron flow

Frédéric Chaux^{1,2,3}, Gilles Peltier^{1,2,3} and Xenie Johnson^{1,2,3*}

¹ CEA, Direction des Sciences du Vivant, Institut de Biologie Environnementale et de Biotechnologie, Laboratoire de Bioénergétique et Biotechnologie des Bactéries et Microalgues, CEA Cadarache, Saint-Paul-lez-Durance, France, ² UMR Biologie Végétale et Microbiologie Environnementale, Centre National de la Recherche Scientifique, Saint-Paul-lez-Durance, France, ³ Laboratoire de Bioénergétique et Biotechnologie des Bactéries et Microalgues, Aix Marseille Université, Saint-Paul-lez-Durance, France

OPEN ACCESS

Edited by:

Wei Huang,
Kunming Institute of Botany, China

Reviewed by:

Eva-Mari Aro,
University of Turku, Finland
Stefano Santabarbara,
Consiglio Nazionale delle Ricerche,
Italy

*Correspondence:

Xenie Johnson
xenie.johnson@cea.fr

Specialty section:

This article was submitted to
Plant Physiology,
a section of the journal
Frontiers in Plant Science

Received: 31 July 2015

Accepted: 02 October 2015

Published: 15 October 2015

Citation:

Chaux F, Peltier G and Johnson X
(2015) A security network in PSI
photoprotection: regulation
of photosynthetic control, NPQ
and O₂ photoreduction by cyclic
electron flow.
Front. Plant Sci. 6:875.
doi: 10.3389/fpls.2015.00875

Cyclic electron flow (CEF) around PSI regulates acceptor-side limitations and has multiple functions in the green alga, *Chlamydomonas reinhardtii*. Here we draw on recent and historic literature and concentrate on its role in Photosystem I (PSI) photoprotection, outlining causes and consequences of damage to PSI and CEF's role as an avoidance mechanism. We outline two functions of CEF in PSI photoprotection that are both linked to luminal acidification: firstly, its action on Photosystem II with non-photochemical quenching and photosynthetic control and secondly, its action in poisoning the stroma to overcome acceptor-side limitation by rebalancing NADPH and ATP ratios for carbon fixation.

Keywords: cyclic electron flow, PSI photoinhibition, non-photochemical quenching, oxygen photoreduction, luminal acidification, photosynthetic control, ATP, malate valve

In the early years of photosynthesis research, a cyclic photophosphorylation was described that required ferredoxin (Fd), did not evolve oxygen (O₂) and resulted in the accumulation of ATP (Arnon et al., 1954). From this observation, experiments performed in a variety of organisms from cyanobacteria to higher plants using a combined pharmacological and *in vitro* approach created a robust model for what is now referred to as cyclic electron flow (CEF; thoroughly reviewed, in Bendall and Manasse, 1995). More recently, *Arabidopsis thaliana* lines altered in CEF have been identified and have enriched the ways we have to study these pathways (Joet et al., 2001; Munekage et al., 2002, 2004; DalCorso et al., 2008). Biochemical approaches have shown that the Proton-Gradient Regulator5 (PGR5) and PGR5-Like1 (PGRL1) proteins form an interaction that results in a ferredoxin-plastoquinone reductase (FQR) activity (Hertle et al., 2013). In the unicellular, green alga, *Chlamydomonas reinhardtii*, this pathway and the function of these proteins is conserved (Petroutsos et al., 2009; Tolleter et al., 2011; Johnson et al., 2014). In *Chlamydomonas* a second type of CEF is also in operation where the mediator at the level of the PQ pool is a type-2 NADPH dehydrogenase (Desplats et al., 2009), with the *nda2* mutant shown to have a phenotype in CEF (Jans et al., 2008). Here, we focus on the PGR5 pathway and work done on the *Chlamydomonas* mutants *pgr5* and *pgrl1* mutants, that both demonstrate no PGR5/PGRL1-dependent CEF (Alric, 2014). Our focus is on *Chlamydomonas* but due to the conservation of this pathway we also make reference to work done in other photosynthetic organisms.

Cyclic electron flow is a generator of proton motive force that (i) can produce supplementary ATP to meet ATP:NADPH requirements for the Calvin Benson Bassham (CBB) cycle and the CO₂ concentrating mechanism (CCM; reviewed by Alric, 2010), and (ii) triggers regulatory mechanisms, namely non-photochemical quenching (NPQ) and cytochrome *b₆f* complex (*cytb₆f*) “photosynthetic control” (Joliot and Johnson, 2011). Its rate is highest under conditions where the stromal poise is reduced, thus PGR5-CEF has been considered as a regulator of redox homeostasis for the photosynthetic chain (Nishikawa et al., 2012). Among the phenotypes observed in CEF-altered strains of both *Arabidopsis* and *Chlamydomonas*, Photosystem I (PSI) photoinhibition arose in conditions of high light or limiting CO₂ (Munekage et al., 2002; Dang et al., 2014; Johnson et al., 2014) and fluctuating light (Suorsa et al., 2012) leading to the assignment of yet another role for PGR5-CEF. While Photosystem II (PSII) photoinhibition is frequently observed and has complex models that describe the mechanism (Murata et al., 2012), PSI photoinhibition remains poorly understood. In this work, we review the potential causes of photoinhibition that occur at the acceptor-side of PSI and the processes triggered by CEF that can contain it. For the sake of comprehensive reviewing of mechanisms involved in PSI photoprotection, other connected pathways are also introduced.

ACCEPTOR-SIDE LIMITATION IS THE CAUSE OF PSI PHOTOINHIBITION

PSI photoinhibition was first reported in isolated chloroplasts submitted to strong light (Jones and Kok, 1966). Satoh was able to differentiate two types of damage that corresponded to damage to the two photosystems using fragmented chloroplasts. Artificial donors were used to measure the capacity of PSI to transfer electrons to terminal acceptor, NADPH. These experiments showed that the addition of the PSII inhibitor, DCMU specifically but incompletely prevented photo-inactivation of PSI (Satoh, 1970a,b). Photo-inactivation of PSI was avoided by addition of excess Fd showing that PSI photoinhibition is an acceptor-side limited phenomenon. The observation that the same group of co-factors that could enhance CEF (including Fd) were also involved in the avoidance of photoinactivation of PSI led to the discussion of CEF as a photoprotectant for PSI (Satoh, 1970c). Further studies demonstrated the destruction of PSI-bound iron-sulfur centers (F_X , $F_{A/B}$) by oxidative species primarily superoxide anion radical ($O_2^{\bullet-}$) (Sonoike et al., 1995). Production of $O_2^{\bullet-}$ can occur within: the iron-sulfur centers of PSI, reduced Fd and stromal flavodehydrogenases (NADP⁺ ferredoxin dehydrogenase, glutathione reductase and monohydrate ascorbate reductase) in plant chloroplasts (discussed, in Asada, 2000). In permissive conditions, radicals are enzymatically neutralized into water, resulting in the net uptake of O₂ reported by Mehler (1951), establishing a pseudo-cyclic pathway for electrons known as the water-water cycle. When radical production exceeds detoxifying capacity, $O_2^{\bullet-}$ irreversibly damages PSI primary acceptors (F_X , $F_{A/B}$) and prevents stable accumulation of P700⁺ in high light (Figure 1). This is because of fast charge recombination at the level of intermediary acceptors $A_{0/1}$ (Setif and Brettel, 1990). The

resultant decrease in the quantity of oxidizable P700 is thus a common measurement for probing the photoinhibition of PSI.

Interestingly, no singlet oxygen (1O_2) is produced in overexcited PSI (triplet excited state, 3P700) because P700 is sterically screened from O₂ (Setif et al., 1981). Hence, P700⁺ and 3P700 are most probably efficient quenchers of excess excitation of plant PSI as observed for cyanobacterial PSI (Schlodder et al., 2005; Shubin et al., 2008). Contrarily, 1O_2 is the main photo-damaging species produced in acceptor-side limited PSII (3P680) (Durrant et al., 1990). It is remarkable that O₂ can be sensitized in PSII and not in PSI (Hideg and Vass, 1995), in other words that 1O_2 production within PSII was not evolutionarily eliminated. Over time this may be why a signaling role has developed for 1O_2 (Telfer, 2014) resulting in some selectivity in the degradation of PSII protein under photoinhibitory conditions. As compared to the “monolithic” architecture of PSI, the modular architecture of PSII allows for a unique degradation of damaged D1 and re-use of other subunits (extensively reviewed, in Caffarri et al., 2014) and may be another reason why PSII damage-and-repair cycle has been a target of selective pressure. On the contrary, PSI has no known molecular mechanism *per se* to set its turnover in tune with light intensity. The protection of PSI from photoinhibition would appear to require a set of distinctly different properties than that of PSII (Allahverdiyeva et al., 2015) which includes buffering acceptor side limitations in the stroma. Selective, irreversible photoinhibition of PSI in *Chlamydomonas* is observed to occur both in CEF-altered strains (Dang et al., 2014; Johnson et al., 2014; Kukuczka et al., 2014; Bergner et al., 2015) and in strains with severe acceptor side limitations such as those lacking RuBisCO (Johnson et al., 2010). *Crpgr5* and *Crpgrl1* strains demonstrate decreased amounts of oxidizable P700 and PSI protein measured by western hybridization after exposition to high light (Johnson et al., 2014; Kukuczka et al., 2014) and after transition from high (2%) to atmospheric concentrations of CO₂ (Dang et al., 2014). In the following sections we present CEF’s role in triggering several mechanisms avoiding long-lasting limitations at the acceptor-side of PSI.

CEF TRIGGERS FAST QUENCHING, PHOTOSYNTHETIC CONTROL AND PSII PHOTOINHIBITION RESULTING IN PSI PHOTOPROTECTION

As already suggested (Sonoike, 2011), non-photochemical quenching (NPQ) of PSII avoids excessive electron flow to PSI *via* linear electron flow (LEF) to prevent photoinhibition. CEF limits electrons entering the thylakoid chain because it prompts both excitation-dependent quenching (qE) and indirectly PSII photoinhibition (qI), thus avoiding overflow to PSI. Acidification of the lumen triggers qE (Briantais et al., 1979) and occurs during CEF due to coupling of electron transfer and proton translocation in the *cytb₆f*. Since both LEF and CEF pass through *cytb₆f*, the exact contribution of CEF to the formation of a qE is hard to determine but an altered ability to develop qE is observed in *Crpgr5* and *Crpgrl1* strains (Tolte et al., 2011; Dang et al., 2014; Johnson et al., 2014; Kukuczka et al., 2014) concomitantly with PSI photoinhibition (Dang et al., 2014; Johnson et al., 2014). This

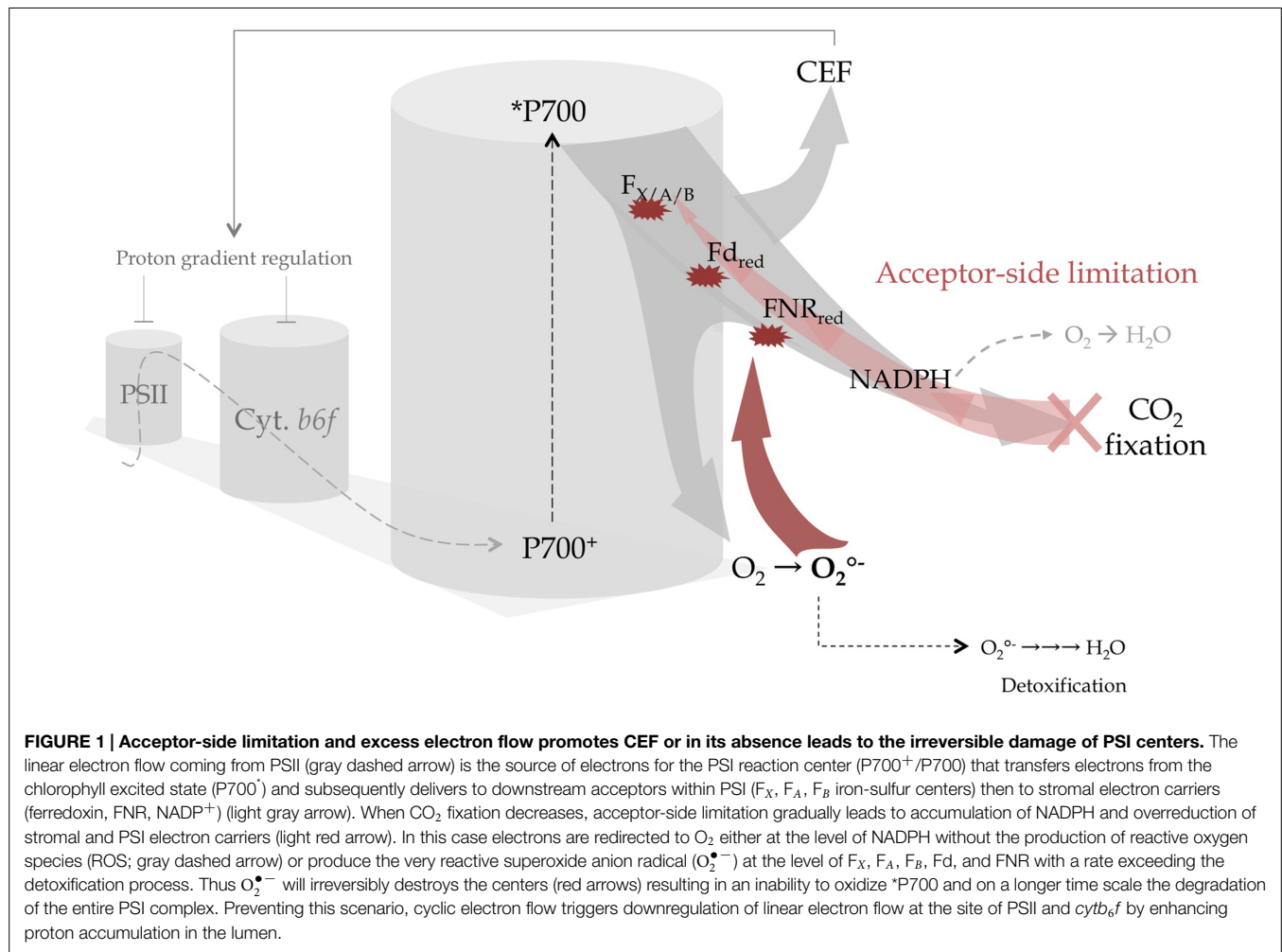
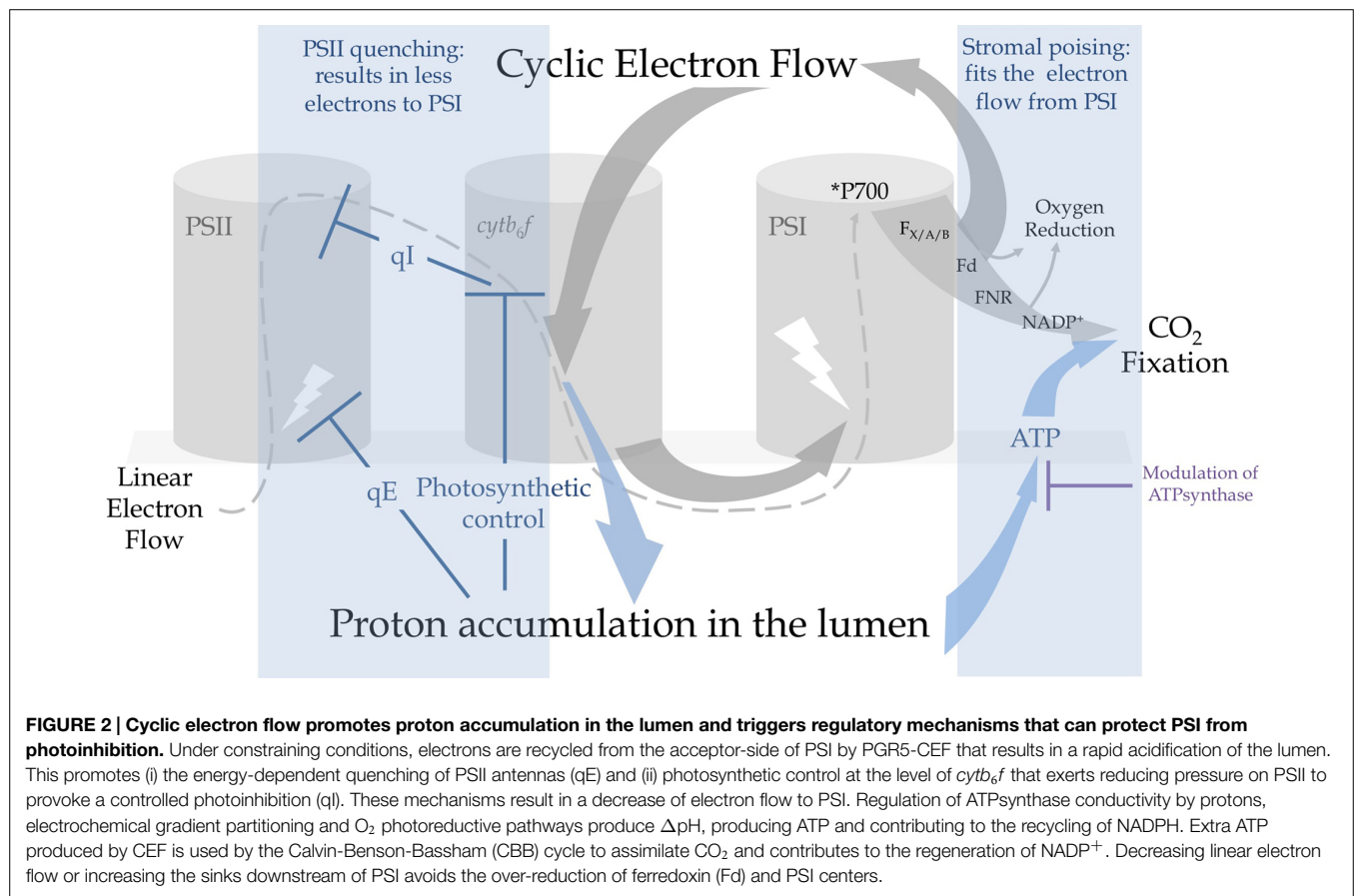


FIGURE 1 | Acceptor-side limitation and excess electron flow promotes CEF or in its absence leads to the irreversible damage of PSI centers. The linear electron flow coming from PSII (gray dashed arrow) is the source of electrons for the PSI reaction center (P700⁺/P700) that transfers electrons from the chlorophyll excited state (P700^{*}) and subsequently delivers to downstream acceptors within PSI (F_X, F_A, F_B iron-sulfur centers) then to stromal electron carriers (ferredoxin, FNR, NADP⁺) (light gray arrow). When CO₂ fixation decreases, acceptor-side limitation gradually leads to accumulation of NADPH and overreduction of stromal and PSI electron carriers (light red arrow). In this case electrons are redirected to O₂ either at the level of NADPH without the production of reactive oxygen species (ROS; gray dashed arrow) or produce the very reactive superoxide anion radical (O₂^{•-}) at the level of F_X, F_A, F_B, Fd, and FNR with a rate exceeding the detoxification process. Thus O₂^{•-} will irreversibly destroys the centers (red arrows) resulting in an inability to oxidize *P700 and on a longer time scale the degradation of the entire PSI complex. Preventing this scenario, cyclic electron flow triggers downregulation of linear electron flow at the site of PSII and *cytb₆f* by enhancing proton accumulation in the lumen.

is also consistent both with the failure to acidify the lumen under short saturating illumination in *Atpgr5* plants (Suorsa et al., 2012) and reduced growth of *Crpgrl1* strains in fluctuating light (Dang et al., 2014). A recent report challenging the effects of rapid quenching of PSII in PSI photoprotection showed that an absence of qE (in *Atnpq4* mutants lacking the PsbS protein that induces qE in higher plants, Li et al., 2000) does not have a dramatic effect on P700 oxidation kinetics at any light regime as opposed to *Atpgr5* mutants where steady state oxidation of P700 is abolished (Tikkanen et al., 2015). Partial compensatory mechanisms may, however, act between CEF and qE as double mutant strain *Crpgrl1npq4*, (lacking both CEF and the LHCSR3 protein that acts as the activator for qE in *Chlamydomonas*, Peers et al., 2009), are particularly susceptible to PSI photoinhibition in comparison to the simple *Crpgrl1* mutant (Kukuczka et al., 2014; Bergner et al., 2015). This may coincide with a PSI-photoprotective role recently proposed for LHCSR3 via its association with the PSI antenna system under “state 2 conditions” (Allorent et al., 2013; Bergner et al., 2015) but here LHCSR3-dependent quenching of LHCI and/or PSI-bound LHCII has not been strictly established. The argument against would be that the quenching of PSI antenna is irrelevant given the harmlessness of *P700 and furthermore photo-oxidation events at PSI (measured on isolated complexes *in vitro*) have been shown to take place

after photoinhibition is completed, chlorophyll oxidation being preceded by irreversible carotenoid oxidation (Santabarbara, 2006). For now, the literature would suggest that qE is a first level of photoprotection in photoinhibitory conditions and rapidly protects not only PSII but also PSI by reducing electron flow (Figure 2).

Aside from ATP production and qE, high pmf downregulates LEF (Rumberg et al., 1968) at the site of PQH₂ oxidation: originally called “back pressure,” (Stiehl and Witt, 1969), and now known as “photosynthetic control.” Comparison of the *CrΔrbcL* mutant against the double mutant *CrΔrbcL pgr5* or wildtype (WT) clearly shows the effects of photosynthetic control imposed by CEF witnessed by a strong increase in chlorophyll fluorescence in the single mutant indicative of a gradually decreasing electron flow, while the double mutant has fluorescence kinetics that resemble the WT (Johnson et al., 2014). The mutant lacking RuBisCO is an important genetic tool to observe the effects of an absence of CO₂ fixation on CEF because it is difficult to modulate CO₂ much below atmospheric concentrations in *Chlamydomonas* due to the efficiency of the carbon concentrating mechanism (CCM): thus this double mutant gives us a window on the mechanisms of CEF as if the WT were under strong CO₂-limited conditions. As important as qE in fluctuating light, photosynthetic control is established when a rapid response to



severe acceptor side limiting conditions is required to buffer a sudden burst of electron flow toward PSI (Suorsa et al., 2012). Moreover, while qE is not constitutive but inducible in *Chlamydomonas*, on the contrary to plants (Peers et al., 2009), photosynthetic control is likely to be crucial in the very first hours of exposition to drastic conditions. As a secondary consequence of photosynthetic control, reducing pressure increases on the Q_B site of PSII so that PSII centers remain in a closed state longer. Overexcited chlorophyll (³P680) activates O₂ into ¹O₂ triggering photoinhibition of PSII (reviewed, in Sonoike, 2011; Murata et al., 2012). Highlighting the key role of pmf in control of linear electron transfer, PSI was shown more susceptible to photoinhibition than PSII in nigericin-infiltrated leaves where control at the level of *cytb₆f* could not develop (Joliot and Johnson, 2011). Moreover, photoinhibition of PSI in *Atpgr5* could be avoided by modulating PSII turnover with the addition of the protein translation inhibitor lincomycin (Tikkanen et al., 2014). Thus, PSII photoinhibition mediated by photosynthetic control is a secondary level of photoprotection in drastic photoinhibitory conditions that exceed qE dissipation capacity: it indirectly but effectively acts as a shunt to avoid sustained PSI acceptor-side limitations (Figure 2).

In *Chlamydomonas*, the *pgr5* mutation combined with an absence of chloroplast ATPsynthase results in a less photosensitive phenotype than the ATPase mutant alone, where light sensitivity has been attributed to luminal over-acidification (Johnson et al., 2014). This observation shows that photosynthetic control relying

on CEF actively contributes to decreasing the luminal pH and supports previous work (Rott et al., 2011). In higher plants, triggering of low luminal pH has also been correlated with changes in conductivity of the ATPsynthase to protons (Kanazawa and Kramer, 2002) and also to partitioning of the proton motive force between its osmotic (or concentration gradient, ΔpH) and electrical (ΔΨ) component (Avenson et al., 2005). ATPsynthase conductivity to protons is increased in *Atpgr5* (Avenson et al., 2005; Wang et al., 2015) with similar observations seen in knocked-down *PGR5* rice lines (Nishikawa et al., 2012). This may be ruled by the concentration of substrate for ATP production, i.e., ADP and phosphate (P_i): in spinach thylakoids, artificially decreasing P_i levels resulted in lower ATPase conductivity and a lower luminal pH, thus promoting qE (Takizawa et al., 2008). These observations show the metabolic interconnections between ATP, CEF and ATPsynthase. As already suggested (Shikanai, 2014), further studies should be done to explain the acceptor-side limitation occurring in strains affected in *PGR5*-CEF in the light of the scenario proposed by Kramer and coworkers for qE regulation.

O₂ REDUCTION WORKS WITH CEF IN DISSIPATING EXCESSIVE ELECTRON FLOW

A number of recent observations have shown the direct interaction of CEF with chloroplast metabolism because CEF

regulates acceptor-side limitation in the absence of reactions for consumption of NADPH. Rubisco-less mutants but also CBB cycle mutants and those affected in starch metabolism show a strong increase in CEF or in CEF-dependent photosynthetic control that results in a repressed rate of LEF (Livingston et al., 2010; Johnson and Alric, 2012; Johnson et al., 2014; Krishnan et al., 2015). When the CBB cycle is an insufficient sink for reducing power, O₂ photoreduction pathways may work in conjunction with CEF to protect PSI. On the other hand, under non-acceptor side limited conditions (steady state high light and/or high CO₂) an absence of CEF in *Crpgr1* did not result in photoinhibition to PSI and this capacity to acclimate was shown to be due to a sustained dependence on O₂ photoreduction pathways (Dang et al., 2014). While photorespiration is a minimal process in green algae due to the CCM, other important sinks exist for reducing equivalents downstream of PSI that terminate on O₂. These include: (i) export of reducing power to the respiratory chain to stimulate oxidative phosphorylation in the mitochondria, (ii) ROS-producing (“Mehler”) reactions with a concomitant increase in detoxifying enzymes and (iii) ROS-independent (“Mehler-like”) NADPH:O₂ oxidoreduction probably by flavodiiron proteins (FLV; Peltier et al., 2010). Mechanisms (ii) and (iii) dually generate proton gradient and thus ATP (Forti and Elli, 1995, 1996) and regenerate NADP⁺ thus avoiding PSI acceptor-side limitations, and over-expression of FLV proteins 1 and 3 in cyanobacteria have been observed to stabilize PSI under fluctuating light (Allahverdiyeva et al., 2013). Mechanism (i) mitochondrial cooperation, also generates ATP but the ATP is probably not reshuttled back into the chloroplast, its major role would be thus to regenerate oxidized NADP⁺ (Figure 2).

Radmer and Kok (1976) first observed the potential for O₂ to replace CO₂ fixation during a light-to-dark transition or in the presence of CBB cycle inhibitors. The role of such an acceptor side activity within the chloroplast such as Mehler (O₂ reduction) or hydrogenase (H⁺ reduction) would enable *Chlamydomonas* cells to reoxidise the electron transport chain in the light, convincingly shown after anaerobic incubation (Forti et al., 2005; Ghysels et al., 2013). In the *Crpgr5 ΔrbcL*, lacking both CO₂ fixation and CEF, O₂ photoreduction rates can completely compensate for CO₂ fixation resulting in WT O₂ evolution levels (Johnson et al., 2014). Similarly, in a detached leaf assay addition of antimycin A provokes both production of H₂O₂ and a strong sustained malate

dehydrogenase activity resulting in high rates of mitochondrial O₂ uptake (Fridlyand et al., 1998). While very removed from the steady-state metabolic flow observed in WT strains under standard conditions, these experimental observations provide us with the maximal rates for the different pathways, and suggest possible compensatory reactions. It would appear that CEF down regulates ATP-independent O₂ reducing pathways and up regulates ATP-dependent CO₂ reduction by CBB cycle. Therefore, CEF can be seen as limiting ROS production under acceptor side limitations. Furthermore, it has been suggested that an interplay between CEF and O₂ photoreduction acts as a buffer to poise electron flow toward carbon fixation (Backhausen et al., 2000). The action of H₂O₂ as an activator of NDH CEF in *Arabidopsis* provides further evidence that O₂ photoreduction pathways and CEF are working in tandem (Strand et al., 2015). The model that emerges is that regulation of temporary excesses of reductant at the acceptor side of PSI is controlled by an interplay between CEF, the Mehler reaction, FLV proteins and the malate valve with another level of control exerted by redox regulators such as thioredoxins (Scheibe and Dietz, 2012). These pathways likely form a set of communicating reactions that can rebalance NADPH/NADP⁺ ratios and avoid PSI photoinhibition.

CONCLUDING REMARKS

While the study of mutants reveals to us the limitations of a system, the complete photosynthetic apparatus is perfectly able to acclimate to both light and changing redox conditions with CEF and its protective role over PSI placed centrally as a regulator of this flexibility. Further understanding of PSI photoinhibition, proposed to be a major determinant in crop productivity (Tikkanen et al., 2014), may allow the rational modification of photosynthesis to improve the efficiency of plant crops and the production of renewable algal biomass.

ACKNOWLEDGMENTS

This work was supported by grants from the Agence Nationale de la Recherche (ChloroPaths: ANR-14-CE05-0041-01) and the CEA Tech Department of Commissariat des Energies Atomiques et Energies Alternatives (CEA) for FC grant. We thank Jean Alric for constructive discussions.

REFERENCES

- Allahverdiyeva, Y., Mustila, H., Ermakova, M., Bersanini, L., Richaud, P., Ajlani, G., et al. (2013). Flavodiiron proteins Flv1 and Flv3 enable cyanobacterial growth and photosynthesis under fluctuating light. *Proc. Natl. Acad. Sci. U.S.A.* 110, 4111–4116. doi: 10.1073/pnas.1221194110
- Allahverdiyeva, Y., Suorsa, M., Tikkanen, M., and Aro, E. M. (2015). Photoprotection of photosystems in fluctuating light intensities. *J. Exp. Bot.* 66, 2427–2436. doi: 10.1093/jxb/eru463
- Allorent, G., Tokutsu, R., Roach, T., Peers, G., Cardol, P., Girard-Bascou, J., et al. (2013). A dual strategy to cope with high light in *Chlamydomonas reinhardtii*. *Plant Cell* 25, 545–557. doi: 10.1105/tpc.112.108274
- Alric, J. (2010). Cyclic electron flow around photosystem I in unicellular green algae. *Photosynth. Res.* 106, 47–56. doi: 10.1007/s1120-010-9566-4
- Alric, J. (2014). Redox and ATP control of photosynthetic cyclic electron flow in *Chlamydomonas reinhardtii*: (II) involvement of the PGR5-PGRL1 pathway under anaerobic conditions. *Biochim. Biophys. Acta* 1837, 825–834. doi: 10.1016/j.bbabi.2014.01.024
- Arnon, D. I., Allen, M. B., and Whatley, F. R. (1954). Photosynthesis by isolated chloroplasts. *Nature* 174, 394–396. doi: 10.1038/174394a0
- Asada, K. (2000). The water-water cycle as alternative photon and electron sinks. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 355, 1419–1431. doi: 10.1098/rstb.2000.0703
- Avenson, T. J., Cruz, J. A., Kanazawa, A., and Kramer, D. M. (2005). Regulating the proton budget of higher plant photosynthesis. *Proc. Natl. Acad. Sci. U.S.A.* 102, 9709–9713. doi: 10.1073/pnas.0503952102
- Backhausen, J. E., Kitzmann, C., Horton, P., and Scheibe, R. (2000). Electron acceptors in isolated intact spinach chloroplasts act hierarchically to prevent

- over-reduction and competition for electrons. *Photosynth. Res.* 64, 1–13. doi: 10.1023/A:1026523809147
- Bendall, D. S., and Manasse, R. S. (1995). Cyclic Photophosphorylation and Electron Transport. *Biochim. Biophys. Acta* 1229, 23–38. doi: 10.1016/0005-2728(94)00195-B
- Bergner, S. V., Scholz, M., Trompelt, K., Barth, J., Gabelein, P., Steinbeck, J., et al. (2015). STATE TRANSITION7-dependent phosphorylation is modulated by changing environmental conditions, and its absence triggers remodeling of photosynthetic protein complexes. *Plant Physiol.* 168, 615–634. doi: 10.1104/pp.15.00072
- Briantais, J. M., Vernotte, C., Picaud, M., and Krause, G. H. (1979). A quantitative study of the slow decline of chlorophyll a fluorescence in isolated chloroplasts. *Biochim. Biophys. Acta* 548, 128–138. doi: 10.1016/0005-2728(79)90193-2
- Caffarri, S., Tibiletti, T., Jennings, R. C., and Santabarbara, S. (2014). A comparison between plant photosystem I and photosystem II architecture and functioning. *Curr. Peptide Sci.* 15, 296–331. doi: 10.2174/1389203715666140327102218
- DalCorso, G., Pesaresi, P., Masiero, S., Aseeva, E., Schunemann, D., Finazzi, G., et al. (2008). A complex containing PGR1 and PGR5 is involved in the switch between linear and cyclic electron flow in *Arabidopsis*. *Cell* 132, 273–285. doi: 10.1016/j.cell.2007.12.028
- Dang, K. V., Plet, J., Tolleter, D., Jokel, M., Cuine, S., Carrier, P., et al. (2014). Combined increases in mitochondrial cooperation and oxygen photoreduction compensate for deficiency in cyclic electron flow in *Chlamydomonas reinhardtii*. *Plant Cell* 26, 3036–3050. doi: 10.1105/tpc.114.126375
- Desplats, C., Mus, F., Cuine, S., Billon, E., Cournac, L., and Peltier, G. (2009). Characterization of Nda2, a plastoquinone-reducing type II NAD(P)H dehydrogenase in *Chlamydomonas* chloroplasts. *J. Biol. Chem.* 284, 4148–4157. doi: 10.1074/jbc.M804546200
- Durrant, J. R., Giorgi, L. B., Barber, J., Klug, D. R., and Porter, G. (1990). Characterization of triplet states in isolated photosystem II reaction centers—oxygen quenching as a mechanism for photodamage. *Biochim. Biophys. Acta* 42, 9205–9213.
- Forti, G., and Caldiroli, G. (2005). State transitions in *Chlamydomonas reinhardtii*. The role of the Mehler reaction in state 2-to-state 1 transition. *Plant Physiol.* 137, 492–499.
- Forti, G., and Elli, G. (1995). The function of ascorbic acid in photosynthetic phosphorylation. *Plant Physiol.* 109, 1207–1211. doi: 10.1007/978-94-009-0173-5_431
- Forti, G., and Elli, G. (1996). Stimulation of photophosphorylation by ascorbate as a function of light intensity. *Plant Physiol.* 112, 1509–1511.
- Fridlyand, L. E., Backhausen, J. E., and Scheibe, R. (1998). Flux control of the malate valve in leaf cells. *Arch. Biochem. Biophys.* 349, 290–298. doi: 10.1006/abbi.1997.0482
- Ghysels, B., Godaux, D., Matagne, R. F., Cardol, P., and Franck, F. (2013). Function of the chloroplast hydrogenase in the microalga *Chlamydomonas*: the role of hydrogenase and state transitions during photosynthetic activation in anaerobiosis. *PLoS ONE* 8:e64161.
- Hertle, A. P., Blunder, T., Wunder, T., Pesaresi, P., Pribil, M., Armbruster, U., et al. (2013). PGR1 is the elusive ferredoxin-plastoquinone reductase in photosynthetic cyclic electron flow. *Mol. Cell.* 49, 511–523. doi: 10.1016/j.molcel.2012.11.030
- Hideg, E., and Vass, I. (1995). Singlet oxygen is not produced in photosystem-I under photoinhibitory conditions. *Photochem. Photobiol.* 62, 949–952. doi: 10.1111/j.1751-1097.1995.tb09162.x
- Jans, F., Mignolet, E., Houyoux, P. A., Cardol, P., Ghysels, B., Cuine, S., et al. (2008). A type II NAD(P)H dehydrogenase mediates light-independent plastoquinone reduction in the chloroplast of *Chlamydomonas*. *Proc. Natl. Acad. Sci. U.S.A.* 105, 20546–20551. doi: 10.1073/pnas.0806896105
- Joet, T., Cournac, L., Horvath, E. M., Medgyesy, P., and Peltier, G. (2001). Increased sensitivity of photosynthesis to antimycin A induced by inactivation of the chloroplast ndhB gene. Evidence for a participation of the NADH-dehydrogenase complex to cyclic electron flow around photosystem I. *Plant Physiol.* 125, 1919–1929. doi: 10.1104/pp.125.4.1919
- Johnson, X., and Alric, J. (2012). Interaction between starch breakdown, acetate assimilation, and photosynthetic cyclic electron flow in *Chlamydomonas reinhardtii*. *J. Biol. Chem.* 287, 26445–26452. doi: 10.1074/jbc.M112.370205
- Johnson, X., Steinbeck, J., Dent, R. M., Takahashi, H., Richaud, P., Ozawa, S., et al. (2014). Proton gradient regulation 5-mediated cyclic electron flow under ATP- or redox-limited conditions: a study of DeltaATPase pgr5 and DeltarbcL pgr5 mutants in the green alga *Chlamydomonas reinhardtii*. *Plant Physiol.* 165, 438–452. doi: 10.1104/pp.113.233593
- Johnson, X., Wostrikoff, K., Finazzi, G., Kuras, R., Schwarz, C., Bujaldon, S., et al. (2010). MRL1, a conserved Pentatricopeptide repeat protein, is required for stabilization of rbcL mRNA in *Chlamydomonas* and *Arabidopsis*. *Plant Cell* 22, 234–248. doi: 10.1105/tpc.109.066266
- Joliot, P., and Johnson, G. N. (2011). Regulation of cyclic and linear electron flow in higher plants. *Proc. Natl. Acad. Sci. U.S.A.* 108, 13317–13322. doi: 10.1073/pnas.1110189108
- Jones, L. W., and Kok, B. (1966). Photoinhibition of chloroplast reactions. II. Multiple Effects. *Plant Physiol.* 41, 1044–1049. doi: 10.1104/pp.41.6.1044
- Kanazawa, A., and Kramer, D. M. (2002). *In vivo* modulation of nonphotochemical exciton quenching (NPQ) by regulation of the chloroplast ATP synthase. *Proc. Natl. Acad. Sci. U.S.A.* 99, 12789–12794. doi: 10.1073/pnas.182427999
- Krishnan, A., Kumaraswamy, G. K., Vinyard, D. J., Gu, H., Ananyev, G., Posewitz, M. C., et al. (2015). Metabolic and photosynthetic consequences of blocking starch biosynthesis in the green alga *Chlamydomonas reinhardtii* sta6 mutant. *Plant J.* 81, 947–960. doi: 10.1111/tj.12783
- Kukuczka, B., Magneschi, L., Petroustos, D., Steinbeck, J., Bald, T., Powikrowska, M., et al. (2014). Proton gradient regulation5-like1-mediated cyclic electron flow is crucial for acclimation to anoxia and complementary to nonphotochemical quenching in stress adaptation. *Plant Physiol.* 165, 1604–1617. doi: 10.1104/pp.114.240648
- Li, X. P., Bjorkman, O., Shih, C., Grossman, A. R., Rosenquist, M., Jansson, S., et al. (2000). A pigment-binding protein essential for regulation of photosynthetic light harvesting. *Nature* 403, 391–395. doi: 10.1038/35000131
- Livingston, A. K., Kanazawa, A., Cruz, J. A., and Kramer, D. M. (2010). Regulation of cyclic electron flow in C(3) plants: differential effects of limiting photosynthesis at ribulose-1,5-bisphosphate carboxylase/oxygenase and glyceraldehyde-3-phosphate dehydrogenase. *Plant Cell Environ.* 33, 1779–1788. doi: 10.1111/j.1365-3040.2010.02183.x
- Mehler, A. H. (1951). Studies on reactions of illuminated chloroplasts. II. Stimulation and inhibition of the reaction with molecular oxygen. *Arch. Biochem. Biophys.* 34, 339–351. doi: 10.1016/0003-9861(51)90012-4
- Munekage, Y., Hashimoto, M., Miyake, C., Tomizawa, K., Endo, T., Tasaka, M., et al. (2004). Cyclic electron flow around photosystem I is essential for photosynthesis. *Nature* 429, 579–582. doi: 10.1038/nature02598
- Munekage, Y., Hojo, M., Meurer, J., Endo, T., Tasaka, M., and Shikanai, T. (2002). PGR5 is involved in cyclic electron flow around photosystem I and is essential for photoprotection in *Arabidopsis*. *Cell* 110, 361–371. doi: 10.1016/S0092-8674(02)00867-X
- Murata, N., Allakhverdiev, S. I., and Nishiyama, Y. (2012). The mechanism of photoinhibition *in vivo*: re-evaluation of the roles of catalase, alpha-tocopherol, non-photochemical quenching, and electron transport. *Biochim. Biophys. Acta* 1817, 1127–1133. doi: 10.1016/j.bbabi.2012.02.020
- Nishikawa, Y., Yamamoto, H., Okegawa, Y., Wada, S., Sato, N., Taira, Y., et al. (2012). PGR5-dependent cyclic electron transport around PSI contributes to the redox homeostasis in chloroplasts rather than CO(2) fixation and biomass production in rice. *Plant Cell Physiol.* 53, 2117–2126. doi: 10.1093/pcp/pcs153
- Peers, G., Truong, T. B., Ostendorf, E., Busch, A., Elrad, D., Grossman, A. R., et al. (2009). An ancient light-harvesting protein is critical for the regulation of algal photosynthesis. *Nature* 462, 518–521. doi: 10.1038/nature08587
- Peltier, G., Tolleter, D., Billon, E., and Cournac, L. (2010). Auxiliary electron transport pathways in chloroplasts of microalgae. *Photosynth. Res.* 106, 19–31. doi: 10.1007/s11120-010-9575-3
- Petroustos, D., Terauchi, A. M., Busch, A., Hirschmann, I., Merchant, S. S., Finazzi, G., et al. (2009). PGR1 participates in iron-induced remodeling of the photosynthetic apparatus and in energy metabolism in *Chlamydomonas reinhardtii*. *J. Biol. Chem.* 284, 32770–32781. doi: 10.1074/jbc.M109.050468
- Radmer, R. J., and Kok, B. (1976). Photoreduction of O(2) Primes and Replaces CO(2) Assimilation. *Plant Physiol.* 58, 336–340. doi: 10.1104/pp.58.3.336
- Rott, M., Martins, N. F., Thiele, W., Lein, W., Bock, R., Kramer, D. M., et al. (2011). ATP synthase repression in tobacco restricts photosynthetic electron transport, CO₂ assimilation, and plant growth by overacidification of the thylakoid lumen. *Plant Cell* 23, 304–321. doi: 10.1105/tpc.110.079111
- Rumberg, B., Reinwald, E., Schroder, H., and Siggel, U. (1968). Correlation between electron flow, proton translocation and phosphorylation in chloroplasts. *Naturwissenschaften* 55, 77–79. doi: 10.1007/BF00599483

- Santabarbara, S. (2006). Limited sensitivity of pigment photo-oxidation in isolated thylakoids to singlet excited state quenching in photosystem II antenna. *Arch. Biochem. Biophys.* 455, 77–88. doi: 10.1016/j.abb.2006.08.017
- Satoh, K. (1970a). Mechanism of photoinactivation in photosynthetic systems.1. dark reaction in photoinactivation. *Plant Cell Physiol.* 11, 15–27.
- Satoh, K. (1970b). Mechanism of photoinactivation in photosynthetic systems.2. occurrence and properties of 2 different types of photoinactivation. *Plant Cell Physiol.* 11, 29–38.
- Satoh, K. (1970c). Mechanism of photoinactivation in photosynthetic systems.3. site and mode of photoinactivation in photosystem.1. *Plant Cell Physiol.* 11, 187–197.
- Scheibe, R., and Dietz, K. J. (2012). Reduction-oxidation network for flexible adjustment of cellular metabolism in photoautotrophic cells. *Plant Cell Environ.* 35, 202–216. doi: 10.1111/j.1365-3040.2011.02319.x
- Schlodder, E., Cetin, M., Byrdin, M., Terekhova, I. V., and Karapetyan, N. V. (2005). P700+ and 3P700-induced quenching of the fluorescence at 760 nm in trimeric Photosystem I complexes from the cyanobacterium *Arthrospira platensis*. *Biochim. Biophys. Acta* 1706, 53–67. doi: 10.1016/j.bbabi.2004.08.009
- Setif, P., and Brettel, K. (1990). Photosystem-I photochemistry under highly reducing conditions—study of the P700 triplet-state formation from the secondary radical pair (P700+–A1–). *Biochim. Biophys. Acta* 1020, 232–238. doi: 10.1016/0005-2728(90)90152-T
- Setif, P., Hervé, G., and Mathis, H. (1981). Flash-induced absorption changes in photosystem I. Radical Pair or Triplet Formation? *Biochim. Biophys. Acta* 638, 257–267. doi: 10.1016/0005-2728(81)90235-8
- Shikanai, T. (2014). Central role of cyclic electron transport around photosystem I in the regulation of photosynthesis. *Curr. Opin. Biotechnol.* 26, 25–30. doi: 10.1016/j.copbio.2013.08.012
- Shubin, V. V., Terekhova, I. N., Kirillov, B. A., and Karapetyan, N. V. (2008). Quantum yield of P700+ photodestruction in isolated photosystem I complexes of the cyanobacterium *Arthrospira platensis*. *Photochem. Photobiol. Sci.* 7, 956–962. doi: 10.1039/b719122g
- Sonoike, K. (2011). Photoinhibition of photosystem I. *Physiol. Plant.* 142, 56–64. doi: 10.1111/j.1399-3054.2010.01437.x
- Sonoike, K., Terashima, I., Iwaki, M., and Itoh, S. (1995). Destruction of photosystem I iron-sulfur centers in leaves of *Cucumis sativus* L. by weak illumination at chilling temperatures. *FEBS Lett.* 362, 235–238. doi: 10.1016/0014-5793(95)00254-7
- Stiehl, H. H., and Witt, H. T. (1969). Quantitative treatment of the function of plastoquinone in photosynthesis. *Z. Naturforsch. B* 24, 1588–1598. doi: 10.1515/znb-1969-1219
- Strand, D. D., Livingston, A. K., Satoh-Cruz, M., Froehlich, J. E., Maurino, V. G., and Kramer, D. M. (2015). Activation of cyclic electron flow by hydrogen peroxide *in vivo*. *Proc. Natl. Acad. Sci. U.S.A.* 112, 5539–5544. doi: 10.1073/pnas.1418223112
- Suorsa, M., Jarvi, S., Grieco, M., Nurmi, M., Pietrzykowska, M., Rantala, M., et al. (2012). PROTON GRADIENT REGULATION5 is essential for proper acclimation of *Arabidopsis* photosystem I to naturally and artificially fluctuating light conditions. *Plant Cell* 24, 2934–2948. doi: 10.1105/tpc.112.097162
- Takizawa, K., Kanazawa, A., and Kramer, D. M. (2008). Depletion of stromal P(i) induces high 'energy-dependent' antenna exciton quenching (q(E)) by decreasing proton conductivity at CF(O)–CF(1) ATP synthase. *Plant Cell Environ.* 31, 235–243. doi: 10.1111/j.1365-3040.2007.01753.x
- Telfer, A. (2014). Singlet oxygen production by PSII under light stress: mechanism, detection and the protective role of beta-carotene. *Plant Cell Physiol.* 55, 1216–1223. doi: 10.1093/pcp/pcu040
- Tikkanen, M., Mekala, N. R., and Aro, E. M. (2014). Photosystem II photoinhibition-repair cycle protects Photosystem I from irreversible damage. *Biochim. Biophys. Acta* 1837, 210–215. doi: 10.1016/j.bbabi.2013.10.001
- Tikkanen, M., Rantala, S., and Aro, E. M. (2015). Electron flow from PSII to PSI under high light is controlled by PGR5 but not by PSBS. *Front. Plant Sci.* 6:521. doi: 10.3389/fpls.2015.00521
- Tolter, D., Ghysels, B., Alric, J., Petroustos, D., Tolstygina, I., Krawietz, D., et al. (2011). Control of hydrogen photoproduction by the proton gradient generated by cyclic electron flow in *Chlamydomonas reinhardtii*. *Plant Cell* 23, 2619–2630. doi: 10.1105/tpc.111.086876
- Wang, C., Yamamoto, H., and Shikanai, T. (2015). Role of cyclic electron transport around photosystem I in regulating proton motive force. *Biochim. Biophys. Acta* 1847, 931–938. doi: 10.1016/j.bbabi.2014.11.013

Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Copyright © 2015 Chaux, Peltier and Johnson. This is an open-access article distributed under the terms of the Creative Commons Attribution License (CC BY). The use, distribution or reproduction in other forums is permitted, provided the original author(s) or licensor are credited and that the original publication in this journal is cited, in accordance with accepted academic practice. No use, distribution or reproduction is permitted which does not comply with these terms.