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Photoprotective, excited-state quenching mechanisms in diverse photosynthetic organisms

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Light-harvesting complexes (LHCs) serve a dual role in photosynthesis, depending on the prevailing light conditions. In low light, they ensure photosynthetic efficiency by maximizing the light absorption cross-section and subsequent energy storage. Under excess light conditions, LHCs perform photoprotective quenching functions to prevent harmful chemical species such as triplet chlorophyll and singlet oxygen from forming and damaging the photosynthetic apparatus. In this Minireview, various photoprotective quenching mechanisms that have been identified in different photosynthetic organisms are surveyed and summarized, and implications for improving photosynthetic productivity are briefly discussed.

Photosynthesis is the process by which photosynthetic organisms transform light energy into chemical energy, which powers essentially all life on Earth (1). Light is absorbed by (bacterio)chlorophylls ((B)Chls),[2] bilins, and carotenoids (Cars) in antenna pigment–protein complexes and transferred to the reaction center (RC), the site of primary charge separation (2). Although the overall features of the RC are similar in various organisms, the antenna complexes for light harvesting are extremely diverse and highly dependent on where the organism lives (3, 4). This is because organisms can adapt to the quality and amount of light available to them. However, under conditions that limit RC productivity, such as high light or other stress conditions, light harvesting must be modulated to prevent excess excitation from reaching the RC. The most rapid mechanisms involve the safe dissipation of excess energy as heat, also observed as a reduction in fluorescence, in the process collectively known as non-photochemical quenching (NPQ) (5). NPQ is a general term that includes mechanistically distinct processes that almost certainly have independent evolutionary origins. The molecular mechanisms of antenna fluorescence quenching are still not completely understood, partly because they differ depending on the antenna system and the organism from which they originate (6, 7). Some of these mechanisms overlap in certain organisms, which has evolutionary implications (8). The overall concept of photoprotective quenching is illustrated in Fig. 1. In this Minireview, protective quenching components and mechanisms in various photosynthetic organisms are discussed.

Green bacteria

The green photosynthetic bacteria are composed of the distantly related green sulfur Chlorobiaceae and green filamentous anoxygenic Chloroflexaceae (9). The green bacteria and an aerobic *Acidobacterium*, *Chloracidobacterium* (*Cab.*) *thermophilum* (10), have a light-harvesting antenna called the chlorosome. Chlorosomes consist of a large number of aggregated BChls (*c*, *d*, or *e*) enveloped by a lipid monolayer with some proteins and a Bchl *a*-containing CsmA protein called the baseplate in addition to carotenoids, lipids, and quinones (11, 12). Chlorosomes are remarkable in that the BChl aggregates self-assemble without a protein scaffold. The energy absorbed by the chlorosomes is transferred to the reaction center (a type I iron–sulfur cluster for Chlorobi and *Cab. thermophilum*; type II for Chloroflexi), which in Chlorobi and *Cab. thermophilum* is mediated by the molecular wire known as the Fenna-Matthews-Olson (FMO) complex (13). The FMO complex is trimeric in structure, with each monomer enclosing seven BChl *a* molecules in mostly β-pleated sheet polypeptides and an eighth BChl *a* located between the monomer interfaces (14, 15).

Under oxidizing conditions, green sulfur bacteria have a redox-regulated fluorescence quenching at the level of the light-harvesting complexes that inhibits energy transfer to the reaction center (9, 16). Quinones mediate this fluorescence quenching (17), which was observed to be much stronger in the chlorosomes from *Chlorobaculum tepidum* than in *Chloroflexus aurantiacus* (17, 18), presumably due to the chlorobium quinone that is present only in Chlorobi. It may be that the quenching mechanism is attenuated in Chloroflexi because they are found in oxic habitats, compared with the strictly anaerobic Chlorobi. However, addition of exogenous quinones to whole cells of *Cfx. aurantiacus* showed specific quenching of BChl *c*, and the effect is similar to that observed in the green sulfur bacteria (19). Subsequently, the quenching effect of chlo-

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[2] The abbreviations used are: BChl, bacteriochlorophyll; LHC, light-harvesting complex; Car, carotenoid; RC, reaction center; Chl, chlorophyll; NPQ, non-photochemical quenching; OCP, orange carotenoid protein; PB, phycobilisome; NTD, N-terminal domain; CTD, C-terminal domain; OCP^{o}, inactive orange form; OCP^{r}, orange carotenoid protein, red form; FRP, fluorescence recovery protein; APC, allophycocyanin; PC, phycocyanin; Hli, high-light–inducible; VDE, violaxanthin de-epoxidase; FMO, Fenna-Matthews-Olson; LHCSR, light-harvesting complex stress-related.

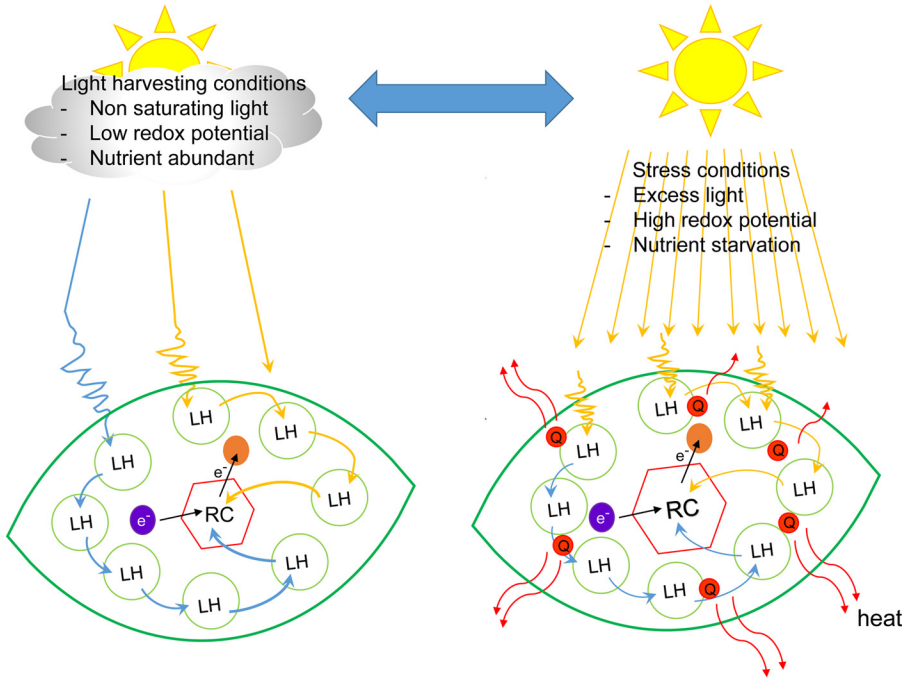

Figure 1. Generalized diagram of light-harvesting regulation under normal and stress conditions. Quenching centers (Q) are formed in the light-harvesting antenna to dissipate excess excitation safely as heat (*red wiggly arrows*) during stress conditions. *LH,* light-harvesting antenna; *RC,* reaction center; *e,* electron; *violet circle,* electron donor; *orange circle,* electron acceptor.

robium quinone was suggested to be associated with the 1′-oxo group in the molecule (20). Chlorosomes from *Cab. thermophilum*, which has menaquinone-8, also exhibit fluorescence quenching under oxic conditions (21), despite being in aerobic environments.

BChl *c* radicals have also been detected in oxidized chlorosomes and implicated in the quenching process (22). However, it was suggested that BChl *c* radicals are possibly artifacts of the extraction process, when considering that the fluorescence quenching effect is larger in the isolated chlorosomes than in whole cells (23). Another proposed mechanism of photoprotection in chlorosomes involves BChl triplet state quenching, because BChl triplets are able to sensitize the formation of harmful singlet oxygen species (12). In this regard, carotenoids are important molecules that either directly quench BChl triplets or scavenge any singlet oxygen produced. In chlorosomes, however, the photoprotection function of carotenoids was found necessary for the baseplate BChl *a* rather than the BChl aggregates (24). Another mechanism that may protect chlorosomes is the formation of triplet excitons that arise from the interactions among the closely packed BChl pigments (25).

Similar to the chlorosomes, the FMO complex also exhibits redox-dependent quenching, although the mechanism of action is different. Spectroscopic experiments have shown that the fluorescence lifetime of the protein shortens to ~60 ps under oxidizing conditions as opposed to the ~2-ns lifetime observed under reducing conditions (26). The quenching mechanism is different from that in the chlorosomes as it is proposed to be mediated by cysteine residues located near the lowest energy BChl *a* molecules (BChls 2 and 3) (27). The proposed mechanism is such that under oxidizing conditions, the cysteine thiol is converted to a thiyl radical that abstracts an electron from the excited BChl *a* to safely dissipate excess excitation: $R^{\bullet} - BChl\ a^{*} \rightarrow R^{-} - BChl\ a^{+} \rightarrow R^{\bullet} - BChl\ a$ + heat. These findings point to a simple yet elegant approach of regulating excitation energy in a photosynthetic light-harvesting antenna. Fig. 2*A* illustrates the quenching mechanisms in green bacteria.

Cyanobacteria and red algae

Cyanobacteria are oxygenic prokaryotes that have water-soluble extramembrane light-harvesting antenna complexes called phycobilisomes (PBs). Phycobilisomes are composed of phycobiliproteins that covalently bind linear tetrapyrrole pigments called bilins, as well as linker proteins (28). Phycobilisomes have a core made up of allophycocyanin (APC), from which phycocyanin (PC) rods project. In some organisms, the rods also contain phycoerythrin (PE), in addition to PC.

Blue-green light-induced quenching of PB fluorescence in cyanobacteria is mediated by the orange carotenoid protein (OCP) (29), as shown schematically in Fig. 2*B*. OCP contains a non-covalently bound ketocarotenoid, which in the inactive orange form (OCP^{o}) traverses both the N- and C-terminal domains (NTD and CTD) (30). Photoactivation converts OCP^{o} into the red form (OCP^{r}), with the protein undergoing substantial conformational changes and domain rearrangements (31–33) that may lead to a ~12-Å pigment translocation into the NTD (34). The OCP^{r} then binds to the phycobilisome and quenches excitations of the bilins before they are transferred to chlorophylls. The overall process of OCP regulation has been intensely studied (35, 36), although the physical mechanism of excited-state quenching of bilins is still not certain. Recent dynamic crystallography data provide a glimpse into the initial events of OCP photoactivation (37). It is proposed that there is a transient keto-enol shift upon photoactivation that disrupts the interactions between the conjugated carbonyl group of the

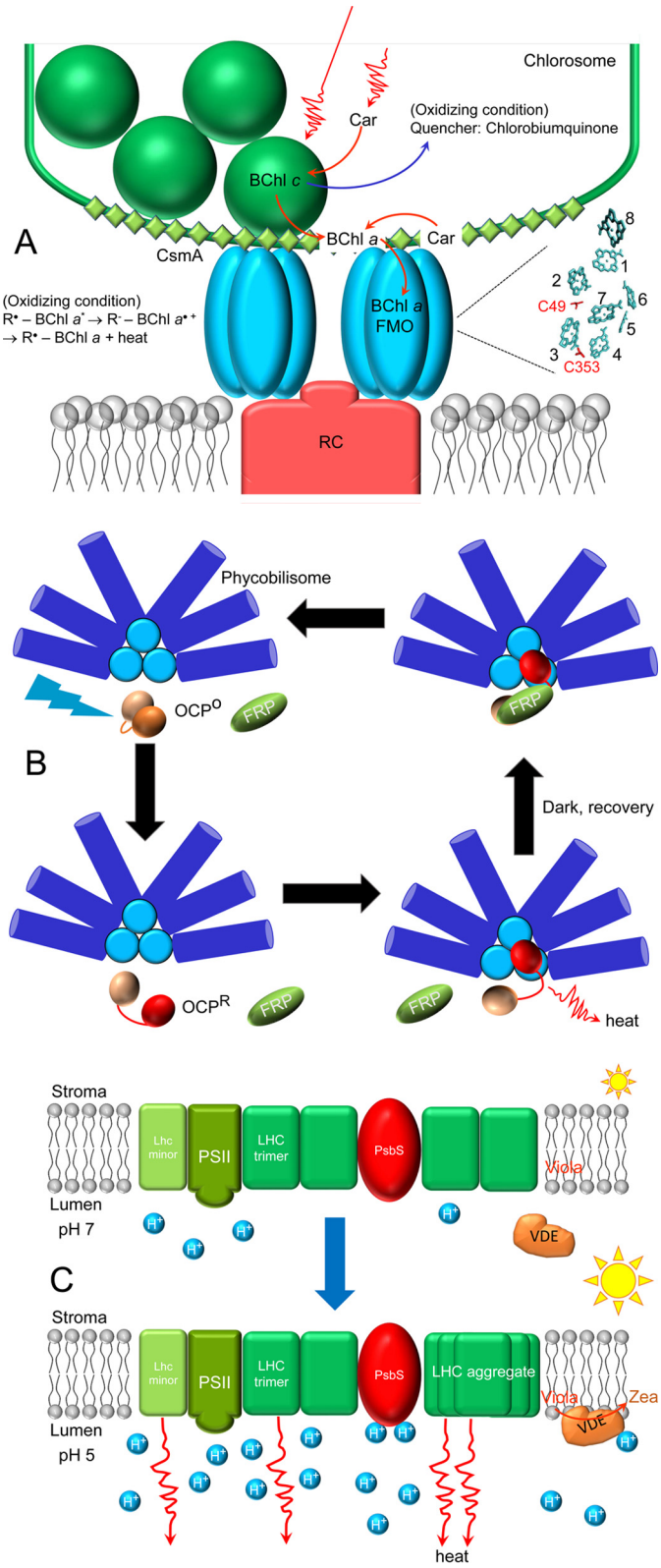

Figure 2. Schematic illustration of quenching mechanisms in selected organisms. *A,* quenching in green bacteria located in chlorosomes and FMO complex under oxidizing conditions. For clarity, only the macrocyclic rings (*cyan*) of the various BChl *a* molecules of FMO are shown numbered *1–8*, with the Cys residues (*C49* and *C353*) involved in the redox-regulated quenching. *BChl,* bacteriochlorophyll; *Car,* carotenoid; *RC,* reaction center. *B,* cyanobacterial orange carotenoid protein (*OCP*)-mediated quenching of phycobilisome fluorescence after activation by blue-green light. OCP^O, *orange form*; OCP^R, *red form*; FRP is fluorescence recovery protein. *C,* components of NPQ in higher plants upon acidification of the lumen, including PsbS protonation, violaxanthin (*Viola*) to zeaxanthin (*Zea*) conversion by VDE, and subsequent formation of quenching centers that dissipate excess excitation energy as heat.

carotenoid β1 ring and the protein, which in turn drives the separation of the N- and C-terminal domains. Previously, it was suggested that the rotation of the β-ionylidene ring drives the structural rearrangement (38), but what exactly leads to the global structural rearrangement remains to be determined. OCP was shown to burrow into the APC core of the PB, bringing the carotenoid in close proximity to the excited bilin for quenching (39). OCP-PB binding is reversible with OCP detachment from the PB aided by the fluorescence recovery protein (FRP) (40). Although FRP was previously found to bind to the CTD of OCP^r, the latest mass spectrometry results suggest that FRP also interacts with the NTD after CTD binding (41) and that facilitates the bridging of the two domains to recover the compact OCP^o. Although OCP has been widely studied, there are still unresolved questions, such as the site and the mechanism of quenching by the carotenoid. The site has been narrowed down to the APC core (29, 42) with either APC 660 or 680 as the quenching site (43–45). Several hypotheses have been proposed for the carotenoid-mediated quenching: charge transfer (46, 47) and energy transfer from the APC-excited bilin to Car followed by internal conversion to the ground state (42, 48), yet there is no experimental evidence to confirm the involvement of any of these mechanisms. In addition to PB fluorescence quenching, OCP has also been shown to quench damaging singlet oxygen in the thylakoid membranes under strong orange-red light when OCP is not activated (49).

A non-OCP-related PB quenching was recently reported (50) using single molecule spectroscopy. Results from this study suggest a novel strategy for cyanobacterial photoprotection that is light-controlled. Fluorescence data show that PBs have multiple intrinsic channels in its subunits and that quenching can occur in any of them, although the core is the frequent target. This is a unique mechanism that provides rapid photoprotection before the OCP mechanism is activated.

Other photoprotective mechanisms operating in cyanobacteria involve high-light–inducible (Hli) and iron starvation-inducible (IsiA) proteins. Cyanobacterial Hlips, or small Cab-like proteins, are single helix proteins that bind Chl *a*, which are ancestors of the LHC superfamily (51). Hlips are not involved in light harvesting but are necessary for cyanobacterial survival under high light illumination and other stress conditions (52–54). In particular, Hlips are suggested to have a photoprotective role related to Chl biosynthesis and PSII assembly (55). Energy dissipation in Hlips occurs via direct energy transfer from the Chl *a* Q_y excited-state to the carotenoid (β-carotene) S_1 state based on transient absorption data (56). This study provided the first direct experimental evidence for such a mechanism. Subsequently, transient absorption studies on purified FLAG-tagged chlorophyll synthase (f.ChlG) with high-light–inducible proteins HliD/C also confirmed the Chl *a* to Car energy transfer at room and cryogenic temperatures (57). Resonance Raman spectroscopy identified two forms of β-carotene in Hlips, one

of which has a twisted conformation that lowers its S_1 energy and may act as the quencher (58).

During iron starvation conditions, cyanobacteria produce the IsiA protein (59), which forms a ring around photosystem I trimers (60). IsiA is a pigment–protein complex with high sequence similarity to CP43, a core antenna of PSII, containing Chl *a* and carotenoids (61). IsiA uncoupled to PSI exhibits quenching of Chl *a* fluorescence, with carotenoids previously identified as energy dissipators via transfer of Chl *a* Q_y to the carotenoid S_1 state (62, 63). In these studies, however, no spectral signature from the carotenoid was observed in the transient absorption data but otherwise incorporated in the fitting models, by assuming that the quencher cannot be sufficiently populated due to a slow rate of Car–Chl *a* transfer. More recently, results from Chen *et al.* (64) have shown that the quenching mechanism does not involve the carotenoids and is instead regulated through Chl *a*–protein interactions by cysteine residues in the IsiA protein. This is analogous to the redox-dependent quenching mechanism first observed in the FMO complex (27) from green sulfur bacteria and now appears to be present in an oxygenic photosynthetic organism as well. It remains to be determined how prevalent Cys-regulated quenching mechanisms are in nature.

Red algae have two light-harvesting antennas, phycobilisomes and LHCI complex that are connected to the RCs of PSII and PSI, respectively (65). Red algae do not have OCP, however, and little is known about their photoprotection mechanisms. Decoupling of PE from the PB core was proposed as a strategy in *Porphyridium cruentum*, according to single molecule fluorescence data (66). State transitions involving PB mobility remain a matter of debate in cyanobacteria (67) but were shown to be important for the mesophilic red algae *P. cruentum* and *Rhodella violacea* (68). In the thermophilic red algae (*Cyanidium caldarium* and *Cyanidioschyzon merolae*), NPQ is the main mechanism for excess energy dissipation, but it is located in the PSII reaction center and not the antenna (68, 69).

Green algae, moss, and diatoms

In higher plants, NPQ is constitutive, whereas in green algae it is inducible and takes effect after a few hours of high-light exposure or decreased CO_2 supply (70, 71). NPQ in eukaryotic algae is regulated by the light-harvesting complex stress-related (LHCSR) protein (72), an ancient member of the LHC family that binds Chls (*a* and *b*) and xanthophylls (73). In *Chlamydomonas reinhardtii*, two types are expressed: constitutive LHCSR1 and high-light–induced LHCSR3 (72, 74). In addition to LHCSR, *C. reinhardtii* has nine LHCBM (1–9) genes that code for LHCII, each with distinct roles and a different involvement in NPQ (75–77), which will not be detailed here. The VAZ xanthophyll cycle involving the enzymatic conversion of violaxanthin → antheraxanthin → zeaxanthin by violaxanthin de-epoxidase also plays a role in green algae NPQ. However, zeaxanthin-dependent NPQ in green algae is highly variable depending on the organism (78).

A proposed model (70) for NPQ activation in *C. reinhardtii* begins with light-harvesting complex stress-related 3 expression under high light, followed by association with PSII-LHCII to form the PSII–LHCII–LHCSR3 supercomplex. LHCSR3 protonation occurs upon acidification of the lumen that leads to the formation of the quenching center. The quenching mechanism was proposed to be due to charge transfer from Chl to Car (73).

In a recent study, it was determined that LHCSR3 production is induced by the blue light phototropin receptor (79). Using a mutagenesis approach, the pH-sensing region was localized to the C terminus of LHCSR3, as it is particularly rich in acidic residues that can be protonated (80). More recently, this has been narrowed down to three (Asp-177, Glu-221, and Glu-224) residues (81). Although LHCSR associates with PSII, it can also move to PSI as shown by Allorent *et al.* (82). After heterologous overexpression in *Nicotiana* sp., LHCSR1 was shown to bind Chl *a* only and that it is involved in NPQ (83). *In vivo* studies in *C. reinhardtii* were conducted using a "minimal NPQ cell" lacking PSI and PSII to demonstrate that LHCSR1 was also pH-sensitive and that it induces LHCII quenching (84), which supports the previous observation of NPQ in an LHCSR3-lacking mutant (85). Results from single molecule spectroscopy revealed the presence of two dissipative states in LHCSR1, controlled by pH and carotenoid composition (86).

Although *C. reinhardtii* has the gene for the photosystem II subunit S (PsbS), it does not express the protein (71). PsbS was expressed in *C. reinhardtii*, and it was determined that PsbS affects the induction of the LHCSR3 mechanism in green algae (87). However, PsbS alone is not enough to carry out LHCSR-regulated NPQ.

LHCSR genes are also present in moss and diatoms, but not in higher plants. The moss *Physcomitrella patens* utilizes both LHCSR and PsbS proteins in NPQ, in addition to the xanthophyll cycle (88). LHCSR-dependent quenching was shown to be enhanced by zeaxanthin binding to LHCSR (89), which is not the case for green algae (73). Because mosses are evolutionary intermediates between algae and higher plants, the presence of both LHCSR and PsbS-mediated NPQ mechanisms provides some insight into the evolution of photosynthesis from aquatic to land environments (6).

The diatom *Phaeodactylum tricornutum* has an LHCSR ortholog denoted LHCX1 protein that controls NPQ (51), but with a few differences. Unlike LHCSR3, it is expressed constitutively and is most likely not a pH sensor because there are no lumenal residues that can be protonated (90). The presence of flexible and rapid quenching mechanisms is essential for diatoms because they are found in highly fluctuating light environments. In addition to LHCX, NPQ in diatoms is dependent on a variant of the xanthophyll cycle activated by light-driven ΔpH, involving the de-epoxidation of diadinoxanthin to diatoxanthin (DT). DT binds to LHCX to induce the aggregation and formation of quenching centers (6, 91). Based on time-resolved fluorescence data, the following two quenching centers were proposed: Q1 found in detached LHC oligomers and Q2 located in LHCX–DT–PSII (92). Exactly how DT is involved in the quenching is still not clear (6, 91). LHCX1 involvement in antenna aggregation and altered pigment interactions was recently shown in *Cyclotella meneghiniana* (93).

Higher plants

The requirements for the energy-dependent component of NPQ called qE in higher plants include ΔpH, PsbS protein, and the VAZ xanthophyll cycle. Activation of qE depends on PsbS (94, 95), a member of the LHC superfamily but with four instead of three transmembrane α-helices (51), which is the evolutionary counterpart of LHCSR from green algae (8). The availability of the PsbS crystal structure (96) has clarified some of the questions regarding PsbS. For instance, it was initially thought that PsbS was a pigment-binding protein (94), but the compact PsbS structure appears to preclude the formation of pigment-binding sites (96). This supports the observation that PsbS in reconstituted liposomes is stable without pigments (97). PsbS was also determined to be dimeric in both inactive and active forms (96), in contrast to the previous suggestion that monomerization of PsbS happens upon NPQ activation. Still, PsbS remains enigmatic, and among the issues that are still being debated involve PsbS localization and its interaction with other photosynthetic complexes (95). Recent cross-linking data from dark- and light-adapted thylakoids show that in the dark unquenched state, PsbS associates with the PSII supercomplex, whereas in the quenched state, it predominantly interacts with LHCII trimers (98). More recently, pulldown experiments have revealed that ΔpH and zeaxanthin affects PsbS–antenna interactions (99).

Activation of NPQ that occurs upon the generation of ΔpH leads to the protonation of PsbS (Glu-122 and Glu-226) (100) and the activation of the xanthophyll (VAZ) cycle (5, 6). At low pH, the enzyme violaxanthin de-epoxidase (VDE) is protonated, undergoes conformational rearrangement, and associates with the MGDG-rich region of the thylakoid membrane, where VDE uses ascorbate as a co-substrate to convert violaxanthin to antheraxanthin and to zeaxanthin (101, 102). Together, PsbS and the VAZ cycle facilitate the structural rearrangement of PSII antenna complexes to generate quenching centers (78, 95). The molecular mechanisms and nature of these quenching centers remain a subject of intense investigation and discussion, however, and are detailed elsewhere (4, 5, 7, 78).

Concluding remarks/future directions

Over the years, extensive research on non-photochemical quenching has led to a better understanding of the machineries and mechanisms driving this process, although questions still remain. In particular, the location and molecular mechanism of quenching in the various antenna complexes still need to be determined. How and where the different protein complexes involved in NPQ interact remain open questions. The availability of increasingly advanced techniques in spectroscopy, molecular biology and biochemistry, and computational modeling are very important tools in tackling these unknowns (5, 103–105).

Photosynthesis is a dynamic and complex process that requires several strategies for improvement of yield and efficiency, among which involve light harvesting optimization and non-photochemical quenching manipulations (103, 104, 106). For instance, new results indicate that NPQ can be exploited for improving photosynthetic productivity as shown in the work of Kromdijk *et al.* (107). By increasing the rate of xanthophyll cycle conversion and the amount of PsbS, an increase in the biomass yield of tobacco was achieved. In green algae, NPQ was also down-regulated to increase biomass production (85). Knowledge obtained about regulation of antennas can also be used for designing bioreactors to improve cyanobacterial biomass or metabolite production (108).

Although efficient light harvesting ensures photosynthetic efficiency, exposure to excess light and other stress conditions render the organisms susceptible to photooxidative damage. Therefore, mechanisms to balance between light harvesting and photoprotection must be in place to ensure the protection of the photosynthetic apparatus and survival of the organism. Photosynthetic organisms have evolved different light-harvesting capabilities to adapt to the varying environments in which they are found. Although light-harvesting antennas are structurally diverse, they are basically variations on a theme. Ultimately, antenna complexes function to maximize as well as regulate light absorption for the reaction center. Moreover, molecules such as carotenoids and quinones, together with the tuning effect of protein amino acid residues, are key players in the regulation of light harvesting in the antenna systems described herein. The diverse mechanisms of regulating excess excitation provide clues from which to borrow and may be used to improve photosynthetic efficiency, particularly in crop plants.

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