Photoprotective, excited-state quenching mechanisms in diverse photosynthetic organisms
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Abstract
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.

Introduction
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), bilins and carotenoids (Cars) in antenna pigment-protein complexes, and transferred to the reaction center (RC), the site of primary charge separation (2). While 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 in order 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 nonphotochemical 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 Figure 1. In this minireview, protective quenching components and mechanisms in various photosynthetic organisms are discussed.

Green Bacteria
The green photosynthetic bacteria are comprised 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 in mostly beta-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 *Cfx. aurantiacus* (17,18), presumably due to the chlorobiumquinone that is present only in *Chlorobi*. It may be that the quenching mechanism is attenuated in *Chloroflexi* since they are found in oxic habitats, compared to 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 chlorobiumquinone 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, since 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 thyl radical that abstracts an electron from the excited BChl a to safely dissipate excess excitation: $R^* - BChl \; a^* \rightarrow R^- - BChl \; a^{* -} \rightarrow R^* - BChl$.
$a + \text{heat}$. These findings point to a simple yet elegant approach of regulating excitation energy in a photosynthetic light-harvesting antenna. Figure 2A illustrates the quenching mechanisms in green bacteria.

**Cyanobacteria and red algae**

Cyanobacteria are oxygenic prokaryotes that have a water-soluble extramembrane light-harvesting antenna complexes called phycobilisomes (PBs). Phycobilisomes are comprised 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 Figure 2B. OCP contains a noncovalently bound ketocarotenoid, which in the inactive orange form (OCP$^o$) traverses both the N- and C-terminal domains (NTD, 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 $\sim 12 \, \text{Å}$ 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 carotenoid $\beta 1$ 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 $\beta$-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). While FRP was previously found to bind to the CTD of OCP$^r$, 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 (SCPs), 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 (52,53) (54). Particularly, Hlips are suggested to have a photoprotective role related to Chl biosynthesis and PS II assembly (55). Energy dissipation in Hlips occurs via direct energy transfer from the Chl a Qy excited state to the carotenoid (β-carotene) S1 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 S1 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 Qy to the carotenoid S1 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. 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 (64). This is analogous to the redox-dependent quenching mechanism first observed in the FMO complex (27) from green sulfur bacteria and which 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 phycocerythrin (PE) from the PB core was proposed as a strategy in Porphyridium (P.) 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, 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, 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 CO2 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 \((a \text{ and } b)\) and xanthophylls (73). In *Chlamydomonas (C.) 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 different involvement in NPQ (75-77), which will not be detailed here. The VAZ xanthophyll cycle involving the enzymatic conversion of violaxanthin \((V) \rightarrow \text{antheraxanthin (A)} \rightarrow \text{zeaxanthin (Z)}\) 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 LHCSR3 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 (PHOT) receptor (79). Using a mutagenesis approach, the pH sensing region was localized to the C-terminal 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, Glu 224) residues (81). Although LHCSR associates with PSII, it can also move to PSI as shown by Allorent and co-workers (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 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 LH CX1 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 luminal residues that can be protonated (90). The presence of flexible and rapid quenching mechanisms is essential for diatoms since 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 \(\Delta pH\), involving the de-epoxidation of diadinoxanthin (DD) to diatoxanthin (DT). DT binds to LHCX to
induce the aggregation and formation of quenching centers (6,91). Based on time-resolved fluorescence data, 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 LHCXR 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 with 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 its localization and 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, pull-down 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 (95) (78). The molecular mechanisms and nature of these quenching centers remain a subject of intense investigation and discussion, however, and are detailed elsewhere (4,5,7,8).

Concluding remarks/future directions

Over the years, extensive research on nonphotochemical 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 an open question. The availability of increasingly advanced techniques in spectroscopy, molecular biology and biochemistry, and computational modelling 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 nonphotochemical quenching manipulations
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 downregulated 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).

While 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 in order 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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Conflict of Interest

The authors declare that they have no conflicts of interest with the contents of this article.

References

1. Blankenship, R. E. (2014) Molecular Mechanisms of Photosynthesis, Second ed., Wiley
2. Mirkovic, T., Ostromov, E. E., Anna, J. M., van Grondelle, R., Govindjee, and Scholes, G. D. (2017) Light absorption and energy transfer in the antenna complexes of photosynthetic organisms. Chem. Rev. 117, 249–293
3. Croce, R., and van Amerongen, H. (2014) Natural strategies for photosynthetic light harvesting. Nat. Chem. Biol. 10, 492–501
4. Büchel, C. (2015) Evolution and function of light harvesting proteins. Journal of Plant Physiology 172, 62–75
5. (2014) Non-photochemical quenching and energy dissipation in plants, algae and cyanobacteria Springer, Dodrecht, Dordrecht, the Netherlands
6. Goss, R., and Lepetit, B. (2015) Biodiversity of NPQ. Journal of Plant Physiology 172, 13–32
7. Ruban, A. V. (2016) Nonphotochemical chlorophyll fluorescence quenching: mechanism and effectiveness in protecting plants

(103,104,106)
from photodamage. *Plant. Physiol.* **170**, 1903–1916

8. Niyogi, K. K., and Truong, T. B. (2013) Evolution of flexible non-photochemical quenching mechanisms that regulate light harvesting in oxygenic photosynthesis. *Current Opinion in Plant Biology* **16**, 307–314

9. Blankenship, R. E., and Matsuura, K. (2003) Antenna complexes from green photosynthetic bacteria. in *Light-Harvesting Antennas in Photosynthesis* (Green, B. R., and Parson, W. W. eds.), Springer Netherlands, Dordrecht. pp 195–217

10. Bryant, D. A., Costas, A. M. G., Maresca, J. A., Chew, A. G. M., Klatt, C. G., Bateson, M. M., Tallon, L. J., Hostetler, J., Nelson, W. C., Heidelberg, J. F., and Ward, D. M. (2007) *Candidatus Chloracidobacterium* thermophilum: An Aerobic Phototrophic Acidobacterium. *Science* **317**, 523–526

11. Orf, G. S., and Blankenship, R. E. (2013) Chlorosome antenna complexes from green photosynthetic bacteria. *Photosynth. Res.* **116**, 315–331

12. Pšenčík, J., Butcher, S. J., and Tuma, R. (2014) Chlorosomes: Structure, function and assembly. in *The structural basis of biological energy generation* (Hohmann-Marriott, M. F. ed.), Springer Science and Business, Dordrecht. pp 77–109

13. Olson, J. M. (2004) The FMO protein. *Photosynth. Res.* **80**, 181–187

14. Tronrud, D. E., Wen, J., Gay, L., and Blankenship, R. E. (2009) The structural basis for the difference in absorbance spectra for the FMO antenna protein from various green sulfur bacteria. *Photosynth. Res.* **100**, 79–87

15. Wen, J., Zhang, H., Gross, M. L., and Blankenship, R. E. (2011) Native electrospray mass spectrometry reveals the nature and stoichiometry of pigments in the FMO photosynthetic antenna protein. *Biochemistry* **50**, 3502–3511

16. Hohmann-Marriott, M. F., and Blankenship, R. E. (2007) Variable fluorescence in green sulfur bacteria. *BBA-Bioenergetics* **1767**, 106–113

17. Frigaard, N.-U., Takaichi, S., Hirota, M., Shimada, K., and Matsuura, K. (1997) Quinones in chlorosomes of green sulfur bacteria and their role in the redox-dependent fluorescence studied in chlorosome-like bacteriochlorophyll c aggregates. *Arch. Microbiol.* **167**, 343–349

18. Frigaard, N.-U., Matsuura, K., Hirota, M., Miller, M., and Cox, R. P. (1998) Studies of the location and function of isoprenoid quinones in chlorosomes from green sulfur bacteria. *Photosynth. Res.* **58**, 81–90

19. Frigaard, N., Tokita, S., and Matsuura, K. (1999) Exogenous quinones inhibit photosynthetic electron transfer in *Chloroflexus aurantiacus* by specific quenching of the excited bacteriochlorophyll c antenna. *Biochim. Biophys. Acta* **1413**, 108–116

20. Tokita, S., Frigaard, N.-U., Hirota, M., Shimada, K., and Matsuura, K. (2000) Quenching of bacteriochlorophyll fluorescence in chlorosomes from *Chloroflexus aurantiacus* by exogenous quinones. *Photochem. Photobiol.* **72**, 345–350

21. Garcia Costas, A. M., Tsukatani, Y., Romberger, S. P., Oostergetel, G. T., Boekema, E. J., Golbeck, J. H., and Bryant, D. A. (2011) Ultrastructural
analysis and identification of envelope proteins of “Candidatus Chloracidobacterium thermophilum” chlorosomes. *J. Bacteriol.* 193, 6701–6711

22. van Noort, P. I., Zhu, Y., LoBrutto, R., and Blankenship, R. E. (1997) Redox effects on the excited-state lifetime in chlorosomes and bacteriochlorophyll c oligomers. *Biophys. J.* 72, 316–325

23. Melø, T. B., Frigaard, N. U., Matsuura, K., and Razi Naqvi, K. (2000) Electronic energy transfer involving carotenoid pigments in chlorosomes of two green bacteria: *Chlorobium tepidum* and *Chloroflexus aurantiacus*. *Spectrochim. Acta A Mol. Biomol. Spectrosc.* 56, 2001–2010

24. Arellano, J. B., Bernt Melø, T., Borrego, C. M., García-Gil, J., and Naqvi, K. R. (2000) Nanosecond laser photolysis studies of chlorosomes and artificial aggregates containing bacteriochlorophyll e: evidence for the proximity of carotenoids and bacteriochlorophyll a in chlorosomes from *Chlorobium phaeobacteroides* strain CL1401. *Photochem. Photobiol.* 72, 669–675

25. Kim, H., Li, H., Maresca, J. A., Bryant, D. A., and Savikhin, S. (2007) Triplet exciton formation as a novel photoprotection mechanism in chlorosomes of *Chlorobium tepidum*. *Biophys. J.* 93, 192–201

26. Zhou, W., LoBrutto, R., Lin, S., and Blankenship, R. E. (1994) Redox effects on the bacteriochlorophyll a-containing Fenna-Matthews-Olson protein from *Chlorobium tepidum*. *Photosynth. Res.* 41, 89–96

27. Orf, G. S., Saer, R. G., Niedzwiedzki, D. M., Zhang, H., McIntosh, C. L., Schultz, J. W., Mirica, L. M., and Blankenship, R. E. (2016) Evidence for a cysteine-mediated mechanism of excitation energy regulation in a photosynthetic antenna complex. *Proc. Natl. Acad. Sci. U.S.A.* 113, E4486–E4493

28. Adir, N. (2005) Elucidation of the molecular structures of components of the phycobilisome: reconstructing a giant. *Photosynth. Res.* 85, 15–32

29. Wilson, A., Ajlani, G., Verbavatz, J.-M., Vass, I., Kerfeld, C. A., and Kirilovsky, D. (2006) A soluble carotenoid protein involved in phycobilisome-related energy dissipation in cyanobacteria. *Plant Cell* 18, 992–1007

30. Kerfeld, C. A., Sawaya, M. R., Brahmandam, V., Cascio, D., Ho, K. K., Trevithick-Sutton, C. C., Krogmann, D. W., and Yeates, T. O. (2003) The crystal structure of a cyanobacterial water-soluble carotenoid binding protein. *Structure* 11, 55–65

31. Gupta, S., Guttmann, M., Leverenz, R. L., Zhumadilova, K., Pawlowski, E. G., Petzold, C. J., Lee, K. K., Ralston, C. Y., and Kerfeld, C. A. (2015) Local and global structural drivers for the photoactivation of the orange carotenoid protein. *Proc. Natl. Acad. Sci. U.S.A.* 112, E5567–E5574

32. Liu, H., Zhang, H., Orf, G. S., Lu, Y., Jiang, J., King, J. D., Wolf, N. R., Gross, M. L., and Blankenship, R. E. (2016) Dramatic domain rearrangements of the cyanobacterial orange carotenoid protein upon photoactivation. *Biochemistry* 55, 1003–1009

33. Maksimov, E. G., Sluchanko, N. N., Mironov, K. S., Shirshin, E. A., Klementiev, K. E., Tsoraev, G. V., Moldenhauer, M., Friedrich, T., Los,
D. A., Allakhverdiev, S. I., Paschenko, V. Z., and Rubin, A. B. (2017) Fluorescent labeling preserving OCP photoactivity reveals its reorganization during the photocycle. *Biophys. J.* **112**, 46–56

34. Leverenz, R. L., Sutter, M., Wilson, A., Gupta, S., Thurotte, A., Bourcier de Carbon, C., Petzold, C. J., Ralston, C., Perreau, F., Kirilovsky, D., and Kerfeld, C. A. (2015) A 12 Å carotenoid translocation in a photoswitch associated with cyanobacterial photoprotection. *Science* **348**, 1463–1466

35. Kirilovsky, D., and Kerfeld, C. A. (2012) The orange carotenoid protein in photoprotection of photosystem II in cyanobacteria. *BBA-Bioenergetics* **1817**, 158–166

36. Kirilovsky, D., and Kerfeld, C. A. (2016) Cyanobacterial photoprotection by the orange carotenoid protein. *Nature Plants* **2**, 16180

37. Bandara, S., Ren, Z., Lu, L., Zeng, X., Shin, H., Zhao, K.-H., and Yang, X. (2017) Photoactivation mechanism of a carotenoid-based photoreceptor. *Proc. Natl. Acad. Sci. U.S.A.* **114**, 6286–6291

38. Maksimov, Eugene G., Shirshin, Evgeny A., Sluchanko, Nikolai N., Zlenko, Dmitry V., Parshina, Evgeniya Y., Tsaraev, Georgy V., Klementiev, Konstantin E., Budylin, Gleb S., Schmitt, F.-J., Friedrich, T., Fadeev, Victor V., Paschenko, Vladimir Z., and Rubin, Andrew B. (2015) The signaling state of orange carotenoid protein. *Biophys. J.* **109**, 595–607

39. Harris, D., Tal, O., Jallet, D., Wilson, A., Kirilovsky, D., and Adir, N. (2016) Orange carotenoid protein burrows into the phycobilisome to provide photoprotection. *Proc. Natl. Acad. Sci. U.S.A.* **113**, E1655–E1662

40. Sutter, M., Wilson, A., Leverenz, R. L., Lopez-Igual, R., Thurotte, A., Salmeen, A. E., Kirilovsky, D., and Kerfeld, C. A. (2013) Crystal structure of the FRP and identification of the active site for modulation of OCP-mediated photoprotection in cyanobacteria. *Proc. Natl. Acad. Sci. U.S.A.* **110**, 10022–10027

41. Lu, Y., Liu, H., Saer, R., Li, V. L., Zhang, H., Shi, L., Goodson, C., Gross, M. L., and Blankenship, R. E. (2017) A molecular mechanism for nonphotochemical quenching in cyanobacteria. *Biochemistry* **56**, 2812–2823

42. Scott, M., McCollum, C., Vasil’ev, S., Crozier, C., Espie, G. S., Krol, M., Huner, N. P. A., and Bruce, D. (2006) Mechanism of the down regulation of photosynthesis by blue light in the cyanobacterium *Synechocystis* sp. PCC 6803. *Biochemistry* **45**, 8952–8958

43. Gwizdala, M., Wilson, A., and Kirilovsky, D. (2011) *In vitro* reconstitution of the cyanobacterial photoprotective mechanism mediated by the orange carotenoid protein in *Synechocystis* PCC 6803. *Plant Cell* **23**, 2631–2643

44. Kuzminov, F. I., Karapetyan, N. V., Rakhimberdieva, M. G., Elanskaya, I. V., Gorbunov, M. Y., and Fadeev, V. V. (2012) Investigation of OCP-triggered dissipation of excitation energy in PSI/PSII-less *Synechocystis* sp. PCC 6803 mutant using non-linear laser fluorimetry. *BBA-Bioenergetics* **1817**, 1012–1021

45. Zhang, H., Liu, H. J., Niedzwiedzki, D. M., Prado, M., Jiang, J., Gross, M. L., and Blankenship, R. E. (2014)
Molecular mechanism of photoactivation and structural location of the cyanobacterial orange carotenoid protein. *Biochemistry* **53**, 13–19

46. Tian, L. J., van Stokkum, I. H. M., Koehorst, R. B. M., Jongerius, A., Kirilovsky, D., and van Amerongen, H. (2011) Site, Rate, and Mechanism of Photoprotective Quenching in Cyanobacteria. *J. Am. Chem. Soc.* **133**, 18304–18311

47. Berera, R., van Stokkum, I. H. M., Gwizdala, M., Wilson, A., Kirilovsky, D., and van Grondelle, R. (2012) The photophysics of the orange carotenoid protein, a light-powered molecular switch. *J. Phys. Chem. B* **116**, 2568–2574

48. Maksimov, E. G., Schmitt, F. J., Shirshin, E. A., Svirin, M. D., Elanskaya, I. V., Friedrich, T., Fadeev, V. V., Paschenko, V. Z., and Rubin, A. B. (2014) The time course of non-photochemical quenching in phycobilisomes of *Synechocystis* sp. PCC 6803 as revealed by picosecond time-resolved fluorimetry. *BBA-Bioenergetics* **1837**, 1540–1547

49. Sedoud, A., López-Igual, R., ur Rehman, A., Wilson, A., Perreau, F., Boulay, C., Vass, I., Krieger-Liszka, A., and Kirilovsky, D. (2014) The cyanobacterial photoactive orange carotenoid protein is an excellent singlet oxygen quencher. *Plant Cell* **26**, 1781–1791

50. Gwizdala, M., Berera, R., Kirilovsky, D., van Grondelle, R., and Krüger, T. P. J. (2016) Controlling light harvesting with light. *J. Am. Chem. Soc.* **138**, 11616–11622

51. Engelken, J., Funk, C., and Adamska, I. (2012) The extended light-harvesting complex (LHC) protein superfamily: Classification and evolutionary dynamics. in *Functional Genomics and Evolution of Photosynthetic Systems* (Burnap, R., and Vermaas, W. eds.), Springer Netherlands, Dordrecht. pp 265–284

52. He, Q., Dolganov, N., Björkman, O., and Grossman, A. R. (2001) The high light-inducible polypeptides in *Synechocystis* PCC 6803: EXPRESSION AND FUNCTION IN HIGH LIGHT. *J. Biol. Chem.* **276**, 306–314

53. Bhaya, D., Dufresne, A., Vaulot, D., and Grossman, A. (2002) Analysis of the hli gene family in marine and freshwater cyanobacteria. *FEMS Microbiology Letters* **215**, 209–219

54. Komenda, J., and Sobotka, R. (2016) Cyanobacterial high-light-inducible proteins — Protectors of chlorophyll–protein synthesis and assembly. *BBA-Bioenergetics* **1857**, 288–295

55. Knoppová, J., Sobotka, R., Tichý, M., Yu, J., Konik, P., Halada, P., Nixon, P. J., and Komenda, J. (2014) Discovery of a chlorophyll binding protein complex involved in the early steps of Photosystem II assembly in *Synechocystis*. *Plant Cell* **26**, 1200–1212

56. Staleva, H., Komenda, J., Shukla, M. K., Slouf, V., Kana, R., Polivka, T., and Sobotka, R. (2015) Mechanism of photoprotection in the cyanobacterial ancestor of plant antenna proteins. *Nat. Chem. Biol.* **11**, 287–291

57. Niedzwiedzki, D. M., Tronina, T., Liu, H., Staleva, H., Komenda, J., Sobotka, R., Blankenship, R. E., and Polívka, T. (2016) Carotenoid-induced non-photochemical quenching in the cyanobacterial chlorophyll synthase–HliC/D
58. Llansola-Portoles, M. J., Sobotka, R., Kish, E., Shukla, M. K., Pascal, A. A., Polívka, T., and Robert, B. (2017) Twisting a β-carotene, an adaptive trick from nature for dissipating energy during photoprotection. *J. Biol. Chem.* **292**, 1396–1403

59. Wilson, A., Boulay, C., Wilde, A., Kerfeld, C. A., and Kirilovsky, D. (2007) Light-induced energy dissipation in iron-starved cyanobacteria: roles of OCP and IsiA proteins. *Plant Cell* **19**, 656–672

60. Wang, Q., Hall, C. L., Al-Adami, M. Z., and He, Q. (2010) IsiA is required for the formation of Photosystem I supercomplexes and for efficient state transition in *Synechocystis* PCC 6803. *PLoS ONE* **5**, e10432

61. Murray, J. W., Duncan, J., and Barber, J. (2006) CP43-like chlorophyll binding proteins: structural and evolutionary implications. *Trends Plant Sci* **11**, 152–158

62. Berera, R., van Stokkum, I. H. M., d'Haene, S., Kennis, J. T. M., van Grondelle, R., and Dekker, J. P. (2009) A mechanism of energy dissipation in cyanobacteria. *Biophys. J.* **96**, 2261–2267

63. Berera, R., van Stokkum, I. H. M., Kennis, J. T. M., van Grondelle, R., and Dekker, J. P. (2010) The light-harvesting function of carotenoids in the cyanobacterial stress-inducible IsiA complex. *Chem. Phys.* **373**, 65–70

64. Chen, H.-Y. S., Liberton, M., Pakrasi, H. B., and Niedzwiedzki, D. M. (2017) Reevaluating the mechanism of excitation energy regulation in iron-starved cyanobacteria. *BBA-Bioenergetics* **1858**, 249–258

65. Neilson, J. A. D., and Durnford, D. G. (2010) Structural and functional diversification of the light-harvesting complexes in photosynthetic eukaryotes. *Photosynth. Res.* **106**, 57–71

66. Liu, L.-N., Elmalk, A. T., Aartsma, T. J., Thomas, J.-C., Lamers, G. E. M., Zhou, B.-C., and Zhang, Y.-Z. (2008) Light-induced energetic decoupling as a mechanism for phycobilisome-related energy dissipation in red algae: a single molecule study. *PLoS ONE* **3**, e3134

67. Kirilovsky, D. (2015) Modulating energy arriving at photochemical reaction centers: orange carotenoid protein-related photoprotection and state transitions. *Photosynth. Res.* **126**, 3–17

68. Kaňa, R., Kotabová, E., Lukeš, M., Papáček, Š., Matonoha, C., Liu, L.-N., Prášil, O., and Mullineaux, C. W. (2014) Phycobilisome mobility and its role in the regulation of light harvesting in red algae. *Plant. Physiol.* **165**, 1618–1631

69. Krupnik, T., Kotabová, E., van Bezouwen, L. S., Mazur, R., Garstka, M., Nixon, P. J., Barber, J., Kaňa, R., Boekema, E. J., and Kargul, J. (2013) A reaction center-dependent photoprotection mechanism in a highly robust Photosystem II from an extremophilic red alga, *Cyanidioschyzon merolae*. *J. Biol. Chem.* **288**, 23529–23542

70. Tokutsu, R., and Minagawa, J. (2013) Energy-dissipative supercomplex of photosystem II associated with LHCSR3 in *Chlamydomonas reinhardtii*. *Proc.
71. Minagawa, J., and Tokutsu, R. (2015) Dynamic regulation of photosynthesis in Chlamydomonas reinhardtii. The Plant Journal 82, 413–428

72. Peers, G., Truong, T. B., Ostendorf, E., Busch, A., Elrad, D., Grossman, A. R., Hippler, M., and Niyogi, K. K. (2009) An ancient light-harvesting protein is critical for the regulation of algal photosynthesis. Nature 462, 518–521

73. Bonente, G., Ballottari, M., Truong, T. B., Morosinotto, T., Ahn, T. K., Fleming, G. R., Niyogi, K. K., and Bassi, R. (2011) Analysis of LhcSR3, a protein essential for feedback de-excitation in the green alga Chlamydomonas reinhardtii. PLOS Biology 9, e1000577

74. Xue, H., Bergner, S. V., Scholz, M., and Hippler, M. (2015) Novel insights into the function of LHCSR3 in Chlamydomonas reinhardtii. Plant Signaling & Behavior 10, e1058462

75. Ferrante, P., Ballottari, M., Bonente, G., Giuliano, G., and Bassi, R. (2012) LHCBM1 and LHCBM2/7 polypeptides, components of major LHCCI complex, have distinct functional roles in photosynthetic antenna system of Chlamydomonas reinhardtii. J. Biol. Chem. 287, 16276-16288

76. Natali, A., and Croce, R. (2015) Characterization of the major light-harvesting complexes (LHCBM) of the green alga Chlamydomonas reinhardtii. PLoS ONE 10, e0119211

77. Girolomoni, L., Ferrante, P., Berteotti, S., Giuliano, G., Bassi, R., and Ballottari, M. (2017) The function of LHCBM4/6/8 antenna proteins in Chlamydomonas reinhardtii. J. Exp. Bot. 68, 627–641

78. Derks, A., Schaven, K., and Bruce, D. (2015) Diverse mechanisms for photoprotection in photosynthesis. Dynamic regulation of photosystem II excitation in response to rapid environmental change. BBA-Bioenergetics 1847, 468–485

79. Petroutsos, D., Tokutsu, R., Maruyama, S., Flori, S., Greiner, A., Magneschi, L., Cusant, L., Kottke, T., Mittag, M., Hegemann, P., Finazzi, G., and Minagawa, J. (2016) A blue-light photoreceptor mediates the feedback regulation of photosynthesis. Nature 537, 563–566

80. Liguori, N., Roy, L. M., Opacic, M., Durand, G., and Croce, R. (2013) Regulation of light harvesting in the green alga Chlamydomonas reinhardtii: The C-terminus of LHCSR Is the knob of a dimmer switch. J. Am. Chem. Soc. 135, 18339–18342

81. Ballottari, M., Truong, T. B., De Re, E., Erickson, E., Stella, G. R., Fleming, G. R., Bassi, R., and Niyogi, K. K. (2016) Identification of pH-sensing sites in the light harvesting complex stress-related 3 protein essential for triggering non-photochemical quenching in Chlamydomonas reinhardtii. J. Biol. Chem. 291, 7334–7346

82. Allorent, G., Tokutsu, R., Roach, T., Peers, G., Cardol, P., Girard-Bascou, J., Seigneurin-Berny, D., Petroutsos, D., Kuntz, M., Breyton, C., Franck, F., Wollman, F.-A., Niyogi, K. K., Krieger-Liszkay, A., Minagawa, J., and Finazzi, G. (2013) A dual strategy to cope with high light in Chlamydomonas reinhardtii. Plant Cell 25, 545–557
83. Pinnola, A., Ghin, L., Gecchele, E., Merlin, M., Alboresi, A., Avesani, L., Pezzotti, M., Capaldi, S., Cazzaniga, S., and Bassi, R. (2015) Heterologous expression of moss LHCSR1: the Chlorophyll a-xanthophyll pigment-protein complex catalyzing non-photochemical quenching, in Nicotiana sp. J. Biol. Chem. 290, 24340–24354

84. Dinc, E., Tian, L., Roy, L. M., Roth, R., Goodenough, U., and Croce, R. (2016) LHCSR1 induces a fast and reversible pH-dependent fluorescence quenching in LHCII in Chlamydomonas reinhardtii cells. Proc. Natl. Acad. Sci. U.S.A. 113, 7673–7678

85. Berteotti, S., Ballottari, M., and Bassi, R. (2016) Increased biomass productivity in green algae by tuning non-photochemical quenching. Sci. Rep. 6, 21339

86. Kondo, T., Pinnola, A., Chen, W. J., Dall'Osto, L., Bassi, R., and Schlau-Cohen, G. S. (2017) Single-molecule spectroscopy of LHCSR1 protein dynamics identifies two distinct states responsible for multi-timescale photosynthetic photoprotection. Nat. Chem. 9, 772–778

87. Correa-Galvis, V., Redekop, P., Guan, K., Griess, A., Truong, T. B., Wakao, S., Niyogi, K. K., and Jahns, P. (2016) Photosystem II subunit PshS is involved in the induction of LHCSR protein-dependent energy dissipation in Chlamydomonas reinhardtii. J. Biol. Chem. 291, 17478–17487

88. Alboresi, A., Gerotto, C., Giacometti, G. M., Bassi, R., and Morosinotto, T. (2010) Physcomitrella patens mutants affected on heat dissipation clarify the evolution of photoprotection mechanisms upon land colonization. Proc. Natl. Acad. Sci. U.S.A. 107, 11128–11133

89. Pinnola, A., Dall’Osto, L., Gerotto, C., Morosinotto, T., Bassi, R., and Alboresi, A. (2013) Zeaxanthin binds to light-harvesting complex stress-related protein to enhance nonphotochemical quenching in Physcomitrella patens. Plant Cell 25, 3519–3534

90. Bailleul, B., Rogato, A., de Martino, A., Coesel, S., Cardol, P., Bowler, C., Falciaatore, A., and Finazzi, G. (2010) An atypical member of the light-harvesting complex stress-related protein family modulates diatom responses to light. Proc. Natl. Acad. Sci. U.S.A. 107, 18214–18219

91. Lavaud, J., and Goss, R. (2014) The peculiar features of non-photochemical fluorescence quenching in diatoms and brown algae. in Non-photochemical quenching and energy dissipation in plants, algae and cyanobacteria (Demmig-Adams, B., Garab, G., Adams, W., and Govindjee eds.), Springer, Dordrecht, the Netherlands. pp 421–443

92. Miloslavina, Y., Grouneva, I., Lambrev, P. H., Lepetit, B., Goss, R., Wilhelm, C., and Holzwarth, A. R. (2009) Ultrafast fluorescence study on the location and mechanism of non-photochemical quenching in diatoms. BBA-Bioenergetics 1787, 1189–1197

93. Ghazaryan, A., Akhtar, P., Garab, G., Lambrev, P. H., and Büchel, C. (2016) Involvement of the Lhcx protein Fcp6 of the diatom Cyclotella meneghiniana in the macro-organisation and structural
flexibility of thylakoid membranes. *BBA-Bioenergetics* **1857**, 1373–1379

94. Li, X.-P., Bjorkman, O., Shih, C., Grossman, A. R., Rosenquist, M., Jansson, S., and Niyogi, K. K. (2000) A pigment-binding protein essential for regulation of photosynthetic light harvesting. *Nature* **403**, 391–395

95. Brooks, M. D., Jansson, S., and Niyogi, K. K. (2014) PsbS dependent non-photochemical quenching. in *Non-photochemical quenching and energy dissipation in plants, algae and cyanobacteria* (Demmig-Adams, B., Adams, W., and Garab, G. eds.), Springer, Dordrecht, the Netherlands. pp 297–314

96. Fan, M., Li, M., Liu, Z., Cao, P., Pan, X., Zhang, H., Zhao, X., Zhang, J., and Chang, W. (2015) Crystal structures of the PsbS protein essential for photoprotection in plants. *Nature Structural and Molecular Biology* **22**, 729–735

97. Wilk, L., Grunwald, M., Liao, P.-N., Walla, P. J., and Kühlbrandt, W. (2013) Direct interaction of the major light-harvesting complex II and PsbS in nonphotochemical quenching. *Proc. Natl. Acad. Sci. U.S.A.* **110**, 5452–5456

98. Correa-Galvis, V., Poschmann, G., Melzer, M., Stühler, K., and Jahns, P. (2016) PsbS interactions involved in the activation of energy dissipation in *Arabidopsis*. **2**, 15225

99. Sacharz, J., Giovagnetti, V., Ungerer, P., Mastroianni, G., and Ruban, A. V. (2017) The xanthophyll cycle affects reversible interactions between PsbS and light-harvesting complex II to control non-photochemical quenching. **3**, 16225

100. Li, X.-P., Gilmore, A. M., Caffarri, S., Bassi, R., Golan, T., Kramer, D., and Niyogi, K. K. (2004) Regulation of photosynthetic light harvesting involves intrathylakoid lumen pH sensing by the PsbS protein. *J. Biol. Chem.* **279**, 22866–22874

101. Müller, P., Li, X.-P., and Niyogi, K. K. (2001) Non-photochemical quenching. A response to excess light energy. *Plant. Physiol.* **125**, 1558–1566

102. Jahns, P., Latowski, D., and Strzalka, K. (2009) Mechanism and regulation of the violaxanthin cycle: The role of antenna proteins and membrane lipids. *BBA-Bioenergetics* **1787**, 3–14

103. Murchie, E. H., and Niyogi, K. K. (2011) Manipulation of photoprotection to improve plant photosynthesis. *Plant. Physiol.* **155**, 86–92

104. Ort, D. R., Merchant, S. S., Alric, J., Barkan, A., Blankenship, R. E., Bock, R., Croce, R., Hanson, M. R., Hibberd, J. M., Long, S. P., Moore, T. A., Moroney, J., Niyogi, K. K., Parry, M. A. J., Peralta-Yahya, P. P., Prince, R. C., Redding, K. E., Spalding, M. H., van Wijk, K. J., Vermaas, W. F. J., von Caemmerer, S., Weber, A. P. M., Yeates, T. O., Yuan, J. S., and Zhu, X. G. (2015) Redesigning photosynthesis to sustainably meet global food and bioenergy demand. *Proc. Natl. Acad. Sci. U.S.A.* **112**, 8529–8536

105. Tietz, S., Hall, C. C., Cruz, J. A., and Kramer, D. M. (2017) NPQ(T): a chlorophyll fluorescence parameter for rapid estimation and imaging of non-photochemical quenching of excitons in photosystem-II-associated antenna complexes. *Plant, Cell & Environment* **40**, 1243–1255

106. Long, Stephen P., Marshall-Colon, A., and Zhu, X.-G. (2015) Meeting the global food demand of the future
by engineering crop photosynthesis and yield potential. *Cell* **161**, 56–66

107. Kromdijk, J., Głowacka, K., Leonelli, L., Gabilly, S. T., Iwai, M., Niyogi, K. K., and Long, S. P. (2016) Improving photosynthesis and crop productivity by accelerating recovery from photoprotection. *Science* **354**, 857–861

108. Lea-Smith, D. J., Bombelli, P., Dennis, J. S., Scott, S. A., Smith, A. G., and Howe, C. J. (2014) Phycobilisome-deficient strains of *Synechocystis* sp. PCC 6803 have reduced size and require carbon-limiting conditions to exhibit enhanced productivity. *Plant. Physiol.* **165**, 705–714
FIGURE LEGENDS

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.

Figure 2. Schematic illustration of quenching mechanisms in selected organisms. (A) Quenching in green bacteria located in chlorosomes and Fenna-Matthews-Olson (FMO) complex under oxidizing conditions. For clarity, only the macrocyclic rings (cyan) of the various BChls a 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. OCPO (orange form), OCPR (red form), FRP (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 violaxanthin de-epoxidase (VDE) and subsequent formation of quenching centers that dissipate excess excitation energy as heat.
Figure 1

Light harvesting conditions
- Non saturating light
- Low redox potential
- Nutrient abundant
Figure 2
Photoprotective, excited-state quenching mechanisms in diverse photosynthetic organisms
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