CellPress

Review

Multi-Level Light Capture Control in Plants and Green Algae

Lutz Wobbe,[1] Roberto Bassi,[2] and Olaf Kruse[1,*]

Life on Earth relies on photosynthesis, and the ongoing depletion of fossil carbon fuels has renewed interest in phototrophic light-energy conversion processes as a blueprint for the conversion of atmospheric CO_2 into various organic compounds. Light-harvesting systems have evolved in plants and green algae, which are adapted to the light intensity and spectral composition encountered in their habitats. These organisms are constantly challenged by a fluctuating light supply and other environmental cues affecting photosynthetic performance. Excess light can be especially harmful, but plants and microalgae are equipped with different acclimation mechanisms to control the processing of sunlight absorbed at both photosystems. We summarize the current knowledge and discuss the potential for optimization of phototrophic light-energy conversion.

Improving Green Cell Factories for Light Conversion

Among the current societal challenges is the depletion of photosynthesis-derived fossil carbon stores. This calls for sustainable alternatives based on the ability of particular photosynthetic organisms to convert CO_2 into organic products using light energy [1]. In phototrophs, light-harvesting and energy-dissipation processes are primary key events for the efficient formation of ATP and the reducing equivalents necessary for CO_2 fixation. Understanding the molecular details of light-conversion processes is therefore crucial for their (bio)-technological exploitation. Recently, major progress was made on the characterization of short- and long-term acclimation mechanisms which adjust the light-harvesting capacity in plants and microalgae to ever-changing environmental conditions [2–5]. A tight control of light capture is vital because of the janus-faced nature of light: it drives photosynthesis but is harmful when provided in excess. In this review we try to depict the complex regulatory network underlying the adjustment of photosynthetic light harvesting in plants and green microalgae, which operates on distinct time-scale and implicates different cellular compartments.

Light-Harvesting Proteins

While photosystem **reaction center** (see Glossary) proteins exhibit strong conservation in their primary sequence and their general supercomplex architecture (Figure 1A) and mechanisms [6], antenna systems have undergone a far higher level of diversification, particularly in aquatic systems [7–9]. However, only organisms equipped with light-harvesting complex (LHC)-like antenna proteins, which first appeared in green algae as an evolution from a cyanobacterial ancestor [10], managed to survive in the subaerial environment characterized by high oxygen, low moisture, and strong irradiances, making life highly stressful for sessile photosynthetic organisms. Phylogenetic analysis of the LHC protein family identified as many as 30 proteins [11], only a third of which are conserved through the chlorophyta as subunits of photosystems (PS) I and II. Many have as yet undefined functions likely related to photoprotection, pigment

Trends

Light capture at both photosystems needs to be tightly adjusted to the prevailing light supply to prevent an over-excitation of photosystems, causing photodamage.

Control mechanisms preferred by plants and microalgae reveal numerous differences: *A. thaliana*, a sessile organism, possesses constitutive mechanisms for energy-dependent quenching (qE) that can be activated rapidly. By contrast, the mobile organism *C. reinhardtii* uses a combination of state transitions (qT) and an inducible qE mechanism.

While qE and qT protect the photosynthetic apparatus without changing light-harvesting antenna composition, long-term acclimation fine-tunes antenna stoichiometry.

Cytosolic translation control, in particular, is emerging as a key process in fine-tuning antenna size and composition.

Antenna engineering in green algae improves the efficiency of light-to-biomass conversion.

[1]Bielefeld University, Faculty of Biology, Center for Biotechnology (CeBiTec), Universitätsstrasse 27, 33615, Bielefeld, Germany
[2]Universita degli Studi di Verona, Department of Biotechnology, Strada Le Grazie 15, 37134 Verona, Italy

*Correspondence:
olaf.kruse@uni-bielefeld.de (O. Kruse).

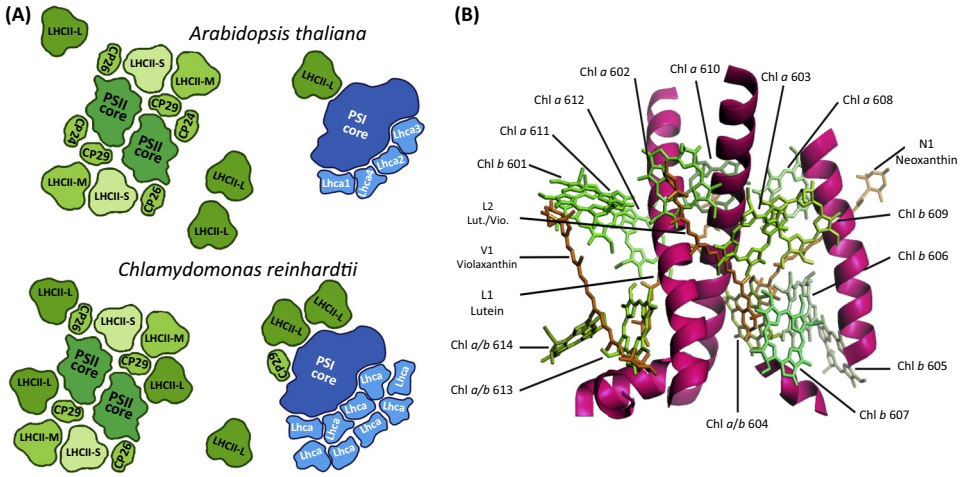

Figure 1. Organization and Structure of Key Photosynthetic Components. (A) Supramolecular organization of photosystems (PS)I and PSII with their light-harvesting complex (LHC) antenna proteins in higher plants (upper panel) and the green algae model system *Chlamydomonas reinhardtii*. Based on data from [112–114] for plants and [115–117] for *Chlamydomonas*. The core components and the antenna system of photosystem II are shown in green and components of the PSI–LHCI supercomplex in blue. Upon phosphorylation part of the PSII antenna can connect to PSI. (B) Structure of monomeric LHCII according to crystallographic data [15]. Four binding sites for xanthophylls and 14 binding sites for chlorophylls are indicated. In other members of the LHC family the number of binding sites for chromophores can vary. Abbreviations: CP, chlorophyll-binding protein; Lut., lutein; Vio., violaxanthin.

metabolism, and biogenesis as assessed for early light-induced proteins (ELIPs) [12], light-harvesting complex stress-related (LHCSR) [13], and photosystem II chlorophyll-binding protein S (PSBS) [14]. The most conserved and widespread LHC proteins include the subunits of the PSII antenna moiety, the trimeric LHCII-M, monomeric chlorophyll-binding proteins (CP)29 and CP26, and the dimeric LHCI subunits of PSI (Figure 1A and Table 1).

LHCs have a common architecture, as shown by available protein structures and homology [15–17]. Their major functional traits are associated to bound chromophores, which are as many as 14 chlorophylls (Chl) and four xanthophylls for each ~22 kDa polypeptide, and diverse, including two types of Chls and 4 xanthophyll species (Figure 1B). Chl *b* occupies more peripheral binding sites and transfers excitation energy to an excitonically tightly connected central Chl *a* cluster [18] which delocalizes **excitons** for further transfer towards reaction centers (Figure 1A, PSII core; 2A, D1/D2). Each Chl is in tight contact with one of the xanthophylls (Figure 1B) which are essential for **triplet chlorophyll** quenching (lutein; Figure 2B,C) and **singlet oxygen**/superoxide scavenging (violaxanthin/neoxanthin; Figure 2D). By contrast, enhanced quenching/scavenging can be obtained by exchanging violaxanthin bound to site L2 (Figure 1B) by zeaxanthin, which is produced under excess light conditions only.

Recent findings highlight that LHCII isoforms have additional photoprotective functions besides their primary role as efficient light-harvesting devices, and that isoforms differ in this regard (Table 1).

Short-Term Light-Acclimation Mechanisms

Light intensity and spectral quality undergo rapid variations depending on external factors such as the time of day, weather, and shading from other cells in a dense algal culture or within the canopy of land plants. Light capture and photochemistry must be optimized to cope with light limitation. Instead, photon capture is minimized, energy dissipation activated, and protection against **reactive oxygen species (ROS)** enhanced when light is in excess.

Glossary

Cyclic electron transfer (CET): mode of photosynthetic electron transport. Electrons are recycled from reduced ferredoxin or NADPH to PQ. This generates a proton gradient across the thylakoid membrane, enabling the exclusive production of ATP without simultaneous production of NADPH. By contrast, linear electron transport involves water-splitting at PSII and the generation of NADPH.

Exciton: view that electron excitation generates a quasi-particle capable of migrating.

Non-photochemical quenching (NPQ): excited singlet chlorophyll (^{1}Chl*) can have different fates in the photosynthetic apparatus. Its excitation can be used to trigger photochemical processes (qP; charge separation and photosynthetic electron transport) or relax back to the ground state by emitting fluorescence. It can also de-excite by dissipating heat (NPQ). NPQ is a collective term including several quenching mechanisms (qE, qT, qI, qZ, and qM; see Box 1).

Photosynthetic control: feedback control mechanism that restrains photosynthetic electron flow when ATP accumulation results from a high proton motive force (PMF). Photosynthetic electron transport is connected to the translocation of protons from the stromal to the luminal side of the thylakoid membrane, which acidifies the thylakoid lumen (ΔpH) and leads to the accumulation of positive charges ($\Delta\Psi$), both contributing to a rise in the proton motive force. Lumen acidification slows down PQ oxidation by the cytochrome *b6f* complex, thus restricting electron flow and a further acidification of the lumen.

Plastoquinone (PQ): lipid-soluble and diffusible electron carrier, which connects PSII and PSI via the cytochrome *b6f* complex as a component of the photosynthetic electron transport chain.

Reaction centers: core complexes of PSI and PSII which harbor so-called 'special pair' chlorophyll *a* molecules. Excitation energy is transferred from the light-harvesting antenna to these chlorophyll molecules, causing charge separation as an initial event of photosynthetic electron transport.