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Energy transfer and distribution in photosystem super/megacomplexes of plants

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Traditionally, two types of photosystem reaction centers (PSI and PSII) are thought to be spatially dispersed in the plant thylakoid membrane. In this model, PSI and PSII independently accept excitation energy from their own peripheral light-harvesting complexes, LHCI and LHCII, respectively, and form supercomplexes (PSI–LHCI and PSII–LHCII). However, recent studies using a combination of mild detergent treatment and spectroscopic analysis have revealed the existence of various megacomplexes such as a PSI–PSII megacomplex and a PSII megacomplex. Flexibility in the formation of supercomplexes and megacomplexes is important for land plants to regulate excitation energy to survive under strong and fluctuating sunlight on land.

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Introduction

Plants utilize two types of photosystem reaction centers, PSI and PSII, which are both driven by excitation energy generated from visible light absorption [1]. PSII extracts an electron from water. PSI accepts the electron (linear electron flow) and accumulates reducing power to perform carbon dioxide fixation [2]. The ancestors of plants lived under a deep water layer, where the light intensity is weak, and evolved to increase the efficiency of PSII and PSI, so both PSII and PSI can operate under dim light.

Later, plants advanced into land, where direct sunlight hits the leaves and both PSII and PSI work actively. However, the electron is transferred via a physical diffusion process and is therefore easily stacked. The availability of CO_2 is the rate-limiting factor [3]. When excess excitation energy is accumulated, it causes harmful effects. To avoid this scenario, plants try to transfer excess excitation energy from PSII to PSI (slow the upstream PSII and accelerate the downstream PSI) or quench the energy (reduce linear electron flow to protect PSI).

Excitation energy, as we call it here, is the singlet excited state of the π-electron in chlorophylls (Chls). Chl *a* can maintain the excited state for ~5000 picoseconds (ps: 10^{-12} s), so energy transfer or dissipation mechanisms must be faster than this. If not, the singlet excited state is converted to the triplet excited state, and eventually produces harmful singlet oxygen species.

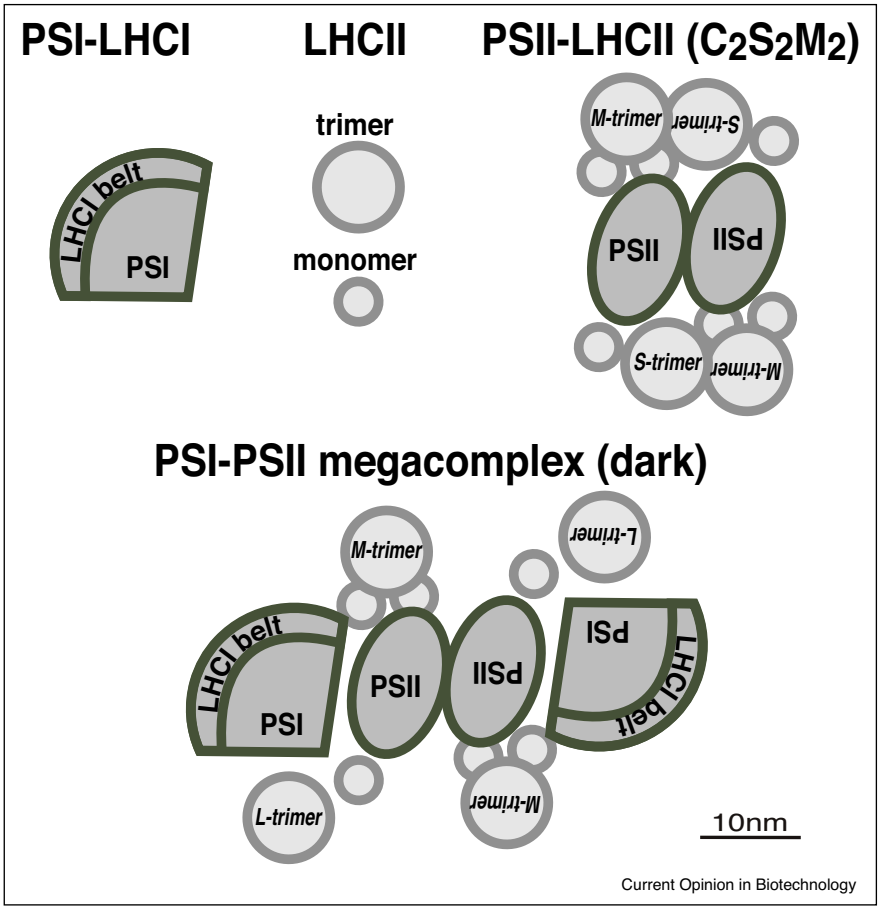
The energy transfer speed depends on the distance between the energy donor and acceptor. Thus, all Chl-binding proteins associated with energy-transfer pathways should form complexes to reduce this distance. For example, PSII–LHCII is a complex of PSII and its light-harvesting antenna (LHCII) (Figure 1, upper), and comprises ~28 protein subunits [4•]. PSI also forms a complex with its antenna (LHCI) (Figure 1, upper), and the PSI–LHCI complex comprises ~16 subunits [5••]. When plants regulate their energy-transfer pathways, the composition and formation of photosystem complexes are altered. Here, we summarize recent discoveries of variation in photosystem complexes, and discuss plant strategies to survive the strong and fluctuating sunlight conditions on land.

Grana margin and stroma lamella regions

In total, ~50% of Chls, ~60% of PSIIs, and all PSIs are found in grana margin and stroma lamemma regions in dark-adapted spinach [6••]. The PSI–PSII megacomplex (>2.4 megadaltons: MDa) was found in these regions by large-pore blue native-PAGE in *Arabidopsis thaliana* (*A. thaliana*) [7]. PSI, LHCI, PSII, and LHCII coexisted in a single gel band. In this method, pigment–protein complexes are solubilized by digitonin, negatively charged by Coomassie Brilliant Blue, and separated by electrophoresis. This method gives high resolution and reproducibility, but it is difficult to discriminate the possible co-migration of PSI–LHCI and PSII–LHCII [8].

Two years later, the direct measurement of energy transfer between PSI and PSII proved the existence of the PSI–PSII megacomplex in *A. thaliana* [9••]. The PSI–PSII megacomplex was isolated from dark-adapted leaves by large-pore clear native-PAGE, because Coomassie Brilliant Blue disturbs the excited state in LHCII. In the PSI–PSII megacomplex, excitation energy is

Figure 1



Proposed structure of photosynthesis reaction center complexes: PSI–LHCI [5••], LHCII, PSII–LHCII [4•], and PSI–PSII megacomplex [9••].

transferred from PSII to PSI very fast (~20 ps), suggesting a direct association between PSI and PSII. In the megacomplex, the ratio of PSI:PSII = 1:1. PSI and PSII possess LHCII L-trimers and M-trimers, respectively. Minor LHCII monomers (Lhcb4–6) are also detected. According to the dimeric structure of PSII, we assume that 1 PSI–PSII megacomplex is composed of 1 PSII dimer, 2 PSI–LHCI complexes, 6 LHCII monomers, and 4 LHCII trimers (Figure 1, lower). Additionally, the relative amount of PSI–PSII megacomplexes increases under high light in *A. thaliana* and *Selaginella martensii* [9••,10], suggesting a photoprotective role for the megacomplex in plants. All excitation energy in the megacomplex is trapped by PSI when PSII becomes closed-state. Therefore, measurements of variable fluorescence to maximum fluorescence (Fv/Fm) may have low sensitivity to PSII in the PSI–PSII megacomplex.

Plants transfer excess excitation energy in the megacomplex from PSII to PSI [9••]. Recent findings suggest that PSI efficiently dissipates the excess excitation energy in *A. thaliana* [11]. Two mechanisms have been proposed for this: zeaxanthin-dependent charge transfer quenching around low-energy Chls in LHCI [12], and energy transfer from low-energy Chls to $P700^+$ [13,14]. The former may be enhanced by violaxanthin de-epoxidase as part of the xanthophyll cycle. The latter is caused by enhanced energy transfer to PSI by PSI–PSII megacomplex formation [9••], and the P700 oxidation system [15,16]. In plants, both mechanisms require low-energy Chls in LHCI. The latest crystal structure of the PSI–LHCI complex revealed the positions of the low-energy Chls and zeaxanthin-binding sites in LHCI [5••].

The other role of LHCI is to provide binding sites for LHCII to bind PSI in *A. thaliana* (Figure 2) [17••]. LHCI is the major binding site for LHCII, and LHCI mutation decreases LHCII binding to PSI by up to 69% [18]. This binding site is close to the quenching sites in LHCI; therefore, the excitation energy of bound-LHCII could be preferentially dissipated. However, PsaH/K, the binding site for the LHCII L-trimer, exists on the opposite side to LHCI [19], so the excitation energy can easily reach P700 in PSI. Multiple LHCIIs can transfer energy