5A, 17A, NW12A/2008G035, 2010G019

Crystal structure of minor light-harvesting complex CP29 from spinach

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Introduction

CP29 is one of the minor light-harvesting complexes of higher-plant photosystem II (PSII). It is located between the major light-harvesting complex LHCII and the core complex. CP29 is necessary for PSII organization and a key component for the stability of the PSII-LHCII supercomplex. Beside the efficient light-harvesting and energy transfer functions, CP29 plays a bridging-type role in transferring the excitation energy from the outmost antenna LHCII to the reaction center. In recent years, there has been increasing evidence that CP29 is important for photoprotection, through which excess energy can be dissipated safely and plants can be protected from photodamage. Structural information of CP29 is indispensable for an improved understanding of the energy transfer process and the regulatory mechanism. Here, we report the first crystal structure of minor light-harvesting complex CP29 from *Spinacia oleracia* at 2.80-Å resolution.

Results and discussion

Overall structure of CP29

The structure of CP29 was solved by single isomorphous replacement with anomalous scattering (SIRAS) and separately by molecular replacement. Each crystallographic asymmetric unit contains one CP29 monomer. The apoprotein of spinach CP29 has two long, intertwined transmembrane α-helices A and B, forming a left-handed supercoil. A shorter helix C lies nearly perpendicular to the membrane plane. Two short amphipathic helices D and E are located on the lumenal surface (Fig. 1A).

The crystal structure of CP29 contains 13 chlorophyll-binding sites, which are assigned as eight Chls *a*, four Chls *b* and one possible mixture of Chl *a* and Chl *b* at the 610 site. Each CP29 monomer contains three carotenoid molecules: lutein (Lut), violaxanthin (Vio) and neoxanthin (Neo), occupying a separate site in CP29 (Fig. 1A). Based on the present X-ray structure, an integrated pigment network in CP29 is constructed.

Potential quenching centers in CP29

In the present structure, two important pigment clusters are observed. Chlorophyll molecules *a*615 and *a*611 share one central ligand (phosphate group of G3P), forming a typical sandwich structure. The homodimer *a*615-*a*611 is the closest associated couple of Chl molecules in CP29 and has strong interactions with Chl *a*612 and Lut, yielding a strongly coupled cluster *a*615-*a*611-*a*612-Lut, which may serve as a potential non-photochemical quenching center in CP29. A second pigment cluster, namely Vio-a603-a609 is thought to be another potential quenching center in CP29 structure. The violaxanthin could be converted to zeaxanthin through the xanthophyll cycle, which plays a key role in stimulating energy dissipation under high light conditions. In addition, the converted Zea, together with the Chl *a* dimer *a*603-*a*609, forming a strongly coupled pigment cluster, may function as the quenching site via charge transfer mechanism.

Moreover, these two pigment clusters are located at the periphery of CP29 monomer and distributed on both sides (Fig. 1B). Based on the structural features, it was speculated that the two pigment clusters are function as potential quenching centers under high light conditions, while the strongly interacting Chl *a* pairs (*a*611-*a*615 and *a*603-*a*609) likely serve as the exit and/or entrance in energy transfer pathways under normal light conditions.

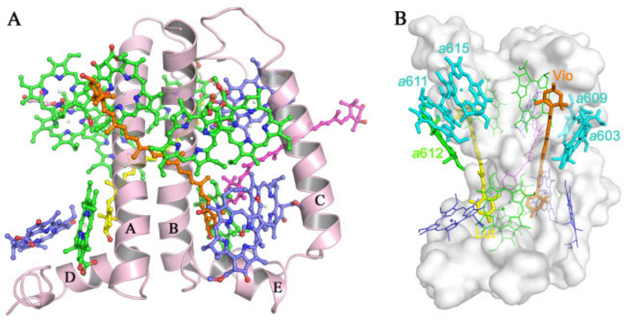

Fig. 1. (A) Overall structure of CP29. View in parallel with the membrane plane. Helices A-E are labeled. For clarity, the Chl phytyl chains are not shown. Green, Chl *a*; blue, Chl *b*; yellow, Lut; orange, Vio; magenta, Neo; light pink, G3P. **(B)** Two important pigment clusters in CP29. View along the membrane plane. Pigment clusters *a*615-*a*611-*a*612-Lut and Vio-*a*603-*a*609 are shown as sticks. Other pigments are shown as lines with the same color designation as in Figure A.

References

[1] X.W. Pan et al., *Nat Struct Mol Biol* **18**, 309-315 (2011).

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