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## The Cytochrome $b_6 f$ Complex as a Perpetual Mobile for Adaptive Structural Reorganizations of the Photosynthetic Membranes in Chloroplasts and Cyanobacteria

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Abstract. The cytochrome bc-complexes in bacteria, plants and animals are essential for the energy transduction systems of the fundamental life processes photosynthesis and respiration. In the oxygen-evolving photosynthetic species (cyanobacteria, algae and plants), the cytochrome  $b_6 f$  complex (cyt  $b_6 f$ ) is also known to trigger the short-term (in the minute range) adaptive mechanism state-transitions. State transitions balance the distribution of the excitation light energy to photosystem II and photosystem I in response to changes in the redox state of the plastoquinone (PQ) pool. The changes in the redox state of the PQ pool are the fastest indicator for a change in the environmental conditions. In addition to having many other benefits, a detailed understanding of the ability of cvt  $b_6 f$  to regulate photosynthetic electron transport and to sustain its optimal efficiency is also a versatile and power tool for governing the stability and function of future artificial photosynthetic systems under variable environmental conditions. However, until recently, it was unclear how the cyt  $b_6 f$  plays the role of redox sensor for the PO pool redox changes, how this signal is transduced across the membrane and how it leads to activation of structural reorganizations, which accompany state transitions.

In this presentation, we will present examples from our recent work [Vladkova (2016) J Biomol Struct Dyn] illustrating the benefits from both the analyses of the diversity of cyt bc crystal structures and the application of the hydrophobic mismatch concept for answering the above questions. The available bacterial and mitochondrial cyt  $bc_1$  and cyanobacterial and algal cyt  $b_6 f$  X-ray crystal structures in the Protein Data Bank were used for analysis. The molecular volume of the single chlorophyll a molecule in the cyt  $b_6 f$  was found different in the variety of the cyt  $b_6 f$  crystal structures. It correlated with conformational changes at both the positive and the negative membrane sides of cyt  $b_6 f$ . These correlations were accompanied by changes in the hydrophobic thickness of cyt  $b_6 f$ . No such changes were observed in the analyzed cyt  $bc_1$  crystal structures. It was concluded that the cyt  $b_6 f$  governs the state transitions via

its chlorophyll *a* molecule, which plays the roles of the crucial redox sensor and of the transmembrane signal transmitter for the changes in the redox state of the PQ pool. The driving force for membrane reorganization during the induction and progression of state transitions is the hydrophobic mismatch induced by the changed hydrophobic thickness of the cyt  $b_6 f$  upon the change in the redox state of the PQ pool. Therefore, the cyt  $b_6 f$  can be envisioned as a perpetual mobile for adaptive structural reorganizations of the oxygenic photosynthetic membranes upon changes in the redox state of the PQ pool.

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