

How a Tiny ATP Synthase Hairpin Loop Affects Dark Adaption in Plants and Algae

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Cysteine redox modulation in proteins is a reversible adaptation to changing environments. For example, activity adjustment of the chloroplast ATP synthase (CF1FO) ensure full activity in the light and deactivation during night. The latter is believed to prevent ATP hydrolysis and build-up of excessive proton motive force (pmf). The adjustment is realised by a cysteine couple in the central CF1FO stalk, the γ -subunit. While being oxidised in the dark, the disulphide is cleaved enzymatically upon illumination which decreases the activation threshold of ATP synthesis/hydrolysis in vascular plants. Although molecular details are known, the general role of CF1FO redox regulation is not understood; it is not vital and absent in non-green chloroplasts.

To revisit potential functions of the redox tuning, we performed reciprocal γ -subunit domain exchanges between *Chlamydomonas reinhardtii* and *Arabidopsis thaliana*. We did not swap the cysteines but the adjacent γ -hairpin loop that shows sequence variations between terrestrial and aquatic phototrophs. (i) The *Chlamydomonas* wild type enzyme remains active despite its disulphide, leading to an elevated dark-pmf. Introducing the plant-like hairpin loop restored the redox fine-tuning mechanism known from plants and the modified algal enzyme maintained a significantly lower dark-pmf. Photosynthesis was not changed in contrast to bioenergetics under heterotrophic dark conditions where various processes, such as chlororespiration, were more active. Only in wild type the photosystem II quantum yields remained stable in darkness for several days. The energetic coupling between mitochondria and the algal chloroplast is influenced by the circadian clock, and misregulated during extended dark when CF1FO is inactive. Consequently, the plant-like mutants had a more reduced plastoquinone pool. (ii) The dark-pmf and CF1FO activity are also important in vascular plants. Preventing CF1FO redox regulation in *Arabidopsis* increases ATPase activity and thus the dark-pmf. It also sustains high photosynthetic capacities, whereas wild type plants displayed dark-induced senescence.

Our findings link the CF1FO redox regulation to a genetic versatility of the γ -hairpin loop and reveal that the ATP saving mechanism in the dark upon CF1FO inactivation is an oversimplification: While switching off CF1FO activity has developmental implications in plants, this strategy restricts bioenergetics unicellular algae.

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