Chapter 11

Photoprotection of Photosystem II: Reaction Center Quenching Versus Antenna Quenching

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Summary

Understanding the role of the xanthophyll cycle and elucidating the mechanisms of antenna quenching through the non-photochemical dissipation of excess absorbed energy in the photoprotection of the photochemical apparatus continues to be a major focus of photosynthetic research. In addition to antenna quenching, there is evidence for the non-photochemical dissipation of excess energy through the PS II reaction center. Hence, this photoprotective mechanism is called reaction center quenching. One technique to assess reaction center quenching is photosynthetic thermoluminescence. This technique represents a simple but powerful probe of PS II photochemistry that measures the light emitted due to the reversal of PS II charge separation through the thermally-dependent recombination of the negative charges stabilized on Q_A^- and Q_B^- on the acceptor side of PS II with the positive charges accumulated in the S_2- and S_3-states of the oxygen evolving complex. Changes in the temperature maxima for photosynthetic thermoluminescence may reflect changes in redox potentials of recombining species within PS II reaction centers. Exposure of *Synechococcus* sp. PCC 7942, *Pinus sylvestris* L., *Arabidopsis thaliana*, and *Chlamydomonas reinhardtii* to either low temperatures or to high light induces a significant downshift in the temperature maxima for $S_2Q_B^-$

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and $S_3Q_B^-$ recombinations relative to $S_2Q_A^-$ and $S_3Q_A^-$ recombinations. These shifts in recombination temperatures are indicative of lower activation energy for the $S_2Q_B^-$ redox pair recombination and a narrowing of the free energy gap between Q_A and Q_B electron acceptors. This, in turn, is associated with a decrease in the overall thermoluminescence emission. We propose that environmental factors such as high light and low temperature result in an increased population of reduced Q_A (Q_A^-), that is, increased excitation pressure, facilitating non-radiative $P680^+Q_A^-$ radical pair recombination within the PS II reaction center. The underlying molecular mechanisms regulating reaction center quenching appear to be species dependent. We conclude that reaction center quenching and antenna quenching are complementary mechanisms that may function to photoprotect PS II to different extents in vivo depending on the species as well as the environmental conditions to which the organism is exposed.

I. Introduction

Changes in irradiance, temperature, nutrient, and water availability result in imbalances between the light energy absorbed through photochemistry and energy utilization through photosynthetic electron transport coupled to carbon, nitrogen, and sulphur reduction. This leads to photoinhibition of photosynthesis under controlled laboratory conditions as well as natural field conditions (Powles, 1984; Krause, 1988; Aro et al., 1993; Long et al., 1994; Keren and Ohad, 1998). Recovery from photoinhibition in plants, green algae, and cyanobacteria is thought to involve a PS II repair cycle in which photodamaged D1 is degraded and the resynthesized D1 is re-inserted to form a functional PS II reaction center (Aro et al., 1993; Keren and Ohad, 1998; Melis, 1999). It has been shown in some chilling-sensitive plant species, green algae, and cyanobacteria that protection against photoinhibition may be accounted for, in part, by the rate of repair relative to the rate of photodamage to D1 (Nishida and Murata, 1996; Keren and Ohad, 1998; Melis, 1999). Alternatively, certain cold tolerant plant species such as winter wheat (*Triticum aestivum* L), rye (*Secale cereale* L), and *Arabidopsis thaliana*, exhibit a minimal dependence on D1 repair but exhibit increased photosynthetic capacity and reprogramming of photosynthetic carbon metabolism in response to cold acclimation (Huner et al., 1993; Hurry et al., 1995; Strand et al., 1997; Demmig-Adams et al., 1999; Adams et al., 2001; Stitt and Hurry, 2002; A. Strand et al., 2003). Although the Mehler reaction appears to contribute to photoprotection in cold tolerant cereals, cold acclimation of Monopol wheat results in the repression of photorespiration (Savitch et al., 2000). This reprogramming of metabolism results in an increased capacity to keep Q_A oxidized and PS II reaction centers open under high excitation pressure induced by either excessive irradiance or low temperatures (Huner et al., 1998; Huner et al., 2003; Öquist and Huner, 2003). Thus, photoprotection in these species is accomplished, in part, through an increase in photochemical quenching (q_P) (Krause and Jahns, 2003).

In contrast to the D1 repair cycle and photochemical quenching, the concept of radiationless dissipation of excess energy through antenna quenching was originally developed on the basis of the Butler model for energy transfer and used to account for Chl fluorescence quenching (Butler, 1978). Non-photochemical quenching (NPQ) of excess excitation energy in the antenna pigment bed of PS II is considered to be the major PS II photoprotective mechanism (Demmig-Adams and Adams, 1992; Horton et al., 1999; Demmig-Adams et al., 1999; Gilmore, 2000; Gilmore and Ball, 2000; Ort, 2001; Demmig-Adams and Adams, 2002). Recently, the term, feedback de-excitation, has been

Abbreviations: A-band – thermoluminescence band between −15° and −10°C; A – antheraxanthin; B_1-band – thermoluminescence band between +20°C and +30°C in the absence of DCMU; B_2-band – thermoluminescence band between +35° and +40°C in the absence of DCMU; C-band – thermoluminescence band between +50° and +60°C; CHB – cold hard band; Cyt b_{559} – cytochrome b_{559}; D1 – photosystem II reaction center polypeptide; D2 – photosystem II reaction center polypeptide; ELIPs – early light inducible proteins; F_o – minimum yield of chlorophyll fluorescence at open PS II centers in dark-adapted leaves; F_m – maximum yield of fluorescence at closed PS II reaction centers in dark adapted leaves; F_v – variable yield of fluorescence in dark adapted leaves; F_v/F_m – maximum PS II photochemical efficiency in dark adapted leaves; LHCII – the major Chl a/b pigment-protein complex associated with PSII; NPQ – non-photochemical quenching; OEC – oxygen evolving complex; Pheo – pheophytin; PI – photoinhibition; PS I – photosystem I; PS II – photosystem II; PS IIα – photosystem IIα centers; PS IIβ – photosystem II β centers; PsbS – PS II subunit and gene product of the *PsbS* gene; PsbZ – PS II subunit and gene product of *ycf9*; PQ – plastoquinone; Q-band – thermoluminescence band between 0° and +10°C in the presence of DCMU; Q_A – primary electron-accepting quinone in PS II reaction centers; Q_B – secondary electron-accepting quinone in PS II reaction centers; q_E – ΔpH-dependent high energy quenching; q_N – non-photochemical quenching coefficient; q_O – quenching coefficient for basal fluorescence; q_P – photochemical quenching coefficient; Q_y – chlorophyll a absorption band; TL – thermoluminescence; T_M – temperature of maximum thermoluminescence emission; V – violaxanthin; Z – zeaxanthin; Zv – thermoluminescence band between −80° and −30°C