

# Chapter 5

## Energy Dissipation and Photoinhibition: A Continuum of Photoprotection

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### Summary

The photosynthetic apparatus is exquisitely adapted to capture light energy and convert it into reduced carbon compounds while also protecting against the potential deleterious effects of excessive excitation energy. The latter is achieved through fine regulation of thermal energy dissipation over multiple time scales and in response to many different environmental stresses. Over short time scales in the absence of additional stress, control is exerted through pH regulation of the enzymatic conversion of violaxanthin to zeaxanthin (and its return to violaxanthin) and engagement of zeaxanthin in thermal energy dissipation. Under more extreme exposure to excess light (transfer of shade leaves to high light or the imposition of additional stresses in the presence of high light), greater levels of zeaxanthin are retained and may also be maintained in a dissipative configuration even in darkness. Engagement of zeaxanthin in thermal energy dissipation lowers the maximal efficiency of photosystem II (PS II) as the excess excitation energy is diverted away from the reaction centers and harmlessly released as heat. Thus, maximal PS II efficiency exhibits decreases and increases with varying degrees of light absorption. Under prolonged and/or pronounced exposure to excess light, maximal PS II efficiency can furthermore exhibit nocturnally sustained decreases as the potential for photoprotective zeaxanthin-dependent energy dissipation is maintained. Zeaxanthin-dependent energy dissipation that is sustained at moderate temperatures is also typically accompanied by downregulation of photosynthesis, including photosynthetic electron transport. Decreases in photosynthetic electron transport presumably lower the likelihood of electrons reducing molecular oxygen to superoxide, and sustained zeaxanthin-dependent energy dissipation mitigates the formation of singlet excited oxygen. Thus, while sustained decreases in maximal PS II efficiency and photosynthetic capacity are key characteristics of photoinhibition, they are also the features that provide powerful photoprotection against the formation of toxic reactive oxygen species.

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## I. Introduction

The photosynthetic portions of all plants exposed to sunlight regularly face the potential problem of excess excitation energy. Although a decrease in photosynthesis was recognized as one response to excess light more than a century ago (see Osmond and Förster, this volume) and subsequently termed photoinhibition fifty years ago (Kok, 1956), the more ubiquitous occurrence of photoprotective energy dissipation as a common response to even moderately excessive light has only been recognized for the past decade-and-a-half. In this Chapter, we summarize information about how the two phenomena are inextricably linked, and represent photoprotective responses along a continuum of adjustments in response to excess light.

## II. Characteristics of Energy Dissipation and Photoinhibition

### A. Flexible Energy Dissipation

Under physiologically normal conditions, dark adaptation (e.g. a night of darkness) returns the photosynthetic apparatus to its most oxidized and relaxed state in leaves. If the interval of darkness is relatively short, progression into the oxidized state can be facilitated with far-red radiation (Schreiber et al., 1984; Adams and Demmig-Adams, 2004). In such a state, the efficiency of excitation energy transfer within PS II light-harvesting antennae and of photochemical charge separation within PS II reaction centers is maximal. This state is reflected in an elevated ratio of variable to maximal chlorophyll fluorescence  $F_v/F_m$  (typically 0.78–0.87 in C3 and CAM plants, but lower in C4 plants) that is emitted primarily from photosystem II (PS II), and a photon yield of photosynthesis that is also maximal (0.106 O<sub>2</sub> evolved per absorbed photon, but lower in C4 plants) (Kitajima and Butler, 1975; Björkman and Demmig, 1987; Adams et al., 1990; Adams and Demmig-Adams, 2004). This situation is illustrated by the light response curve depicted in Fig. 1A, where PS II efficiency  $F_v/F_m$  is maximal at 0  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ , and the slope of the light response curve of photosynthesis in the light-limited region (= photon yield) is steep (Björkman and Demmig, 1987).

Increasing light levels lead to a number of responses within the leaf (Fig. 1A). Photosynthesis increases proportionally to the increases in PFD until its rate begins to saturate. As saturation is approached, the concentration of protons in the thylakoid lumen increases, activating the enzyme violaxanthin de-epoxidase that

converts violaxanthin (V, not shown) into antheraxanthin (A) and zeaxanthin (Z) (Yamamoto, 1979, this volume; Hager, 1980; Demmig-Adams et al., 1989a). There is also a concurrent protonation of specific sites on the PsbS protein, resulting in a conformational change that presumably facilitates the engagement of zeaxanthin (and antheraxanthin) in photoprotective thermal energy dissipation (Li et al., 2000, 2002; Ma et al., 2003; Jung and Niyogi, this volume). The latter can be assessed through changes in nonphotochemical quenching (NPQ) of chlorophyll fluorescence calculated as  $F_m/F_m' - 1$  (Bilger and Björkman, 1990). A strong linear correlation has been demonstrated between the foliar content of Z + A and the total level of NPQ during active engagement (Bilger and Björkman, 1991, 1994; Demmig-Adams and Adams, 1994a,b, 1996). Thus, as a proportionally greater fraction of the absorbed light cannot be utilized in photosynthesis at higher light levels, there is a compensatory increase in the level of Z + A, which is then engaged in dissipation of the excess excitation energy as heat. There is furthermore a concomitant decrease in maximal PS II efficiency as the level of energy dissipation increases (Adams et al., 1989, 1995, 1999; Björkman and Demmig-Adams, 1994; Demmig-Adams et al., 1995, 1996a; Demmig-Adams and Adams, 1996; Demmig-Adams et al., this volume), as predicted from the analysis by Kitajima and Butler (1975), reflecting a diversion of the excess excitation energy away from PS II reaction centers.

For a high light-grown leaf, such increases in thermal energy dissipation and decreases in maximal PS II efficiency are flexible; they are rapidly reversible upon transition to non-excessive light or darkness as the deprotonation of PsbS presumably leads to a rapid disengagement of Z + A from their thermal dissipating function and a return to high PS II efficiency in limiting light. Hence NPQ is designated as NPQ<sub>flex</sub> in Fig. 1A. Upon such transitions, however, Z + A are converted much more slowly to V by zeaxanthin epoxidase, and under these conditions the linear correlation between the amount of Z + A and the level of thermal energy dissipation no longer exists. On the other hand, retention of Z + A under such conditions permits a more rapid engagement of energy dissipation upon a subsequent exposure to excessive light (Demmig-Adams et al., 1989b; Barker et al., 2002), since it only requires the rapid protonation of PsbS without the (slower) enzymatic conversion of V to Z + A. This rapid modulation of thermal energy dissipation is particularly physiologically relevant e.g. under conditions of intermittent cloud cover or in the understory of a forest (Fig. 2A–D; Adams et al., 1999). In fact, reproductive fitness