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_2 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 μmol photons m^{-2} 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_{flex} 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

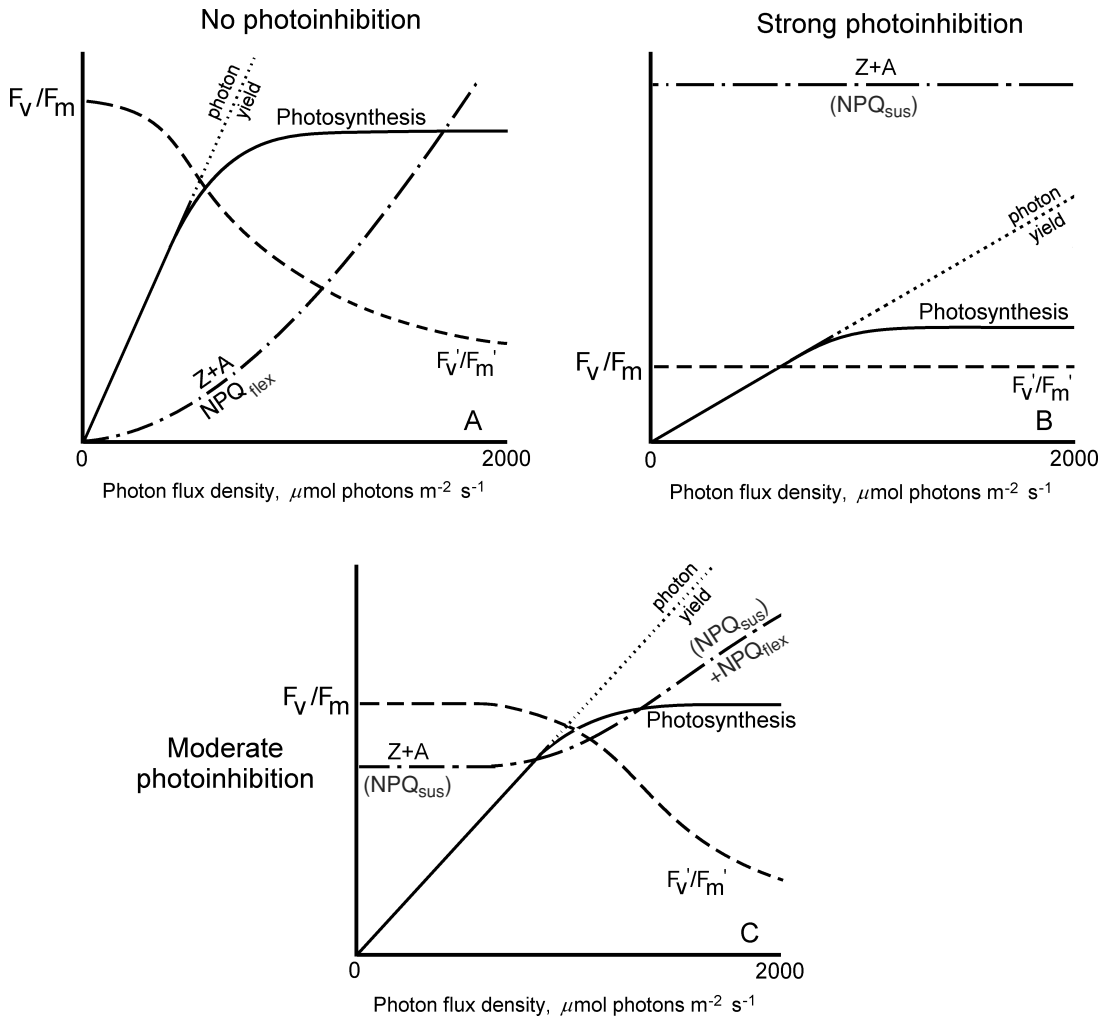

Fig. 1. Idealized light response curves of photosynthesis (solid lines), photon yield (dotted lines), PS II efficiency (F_v/F_m in darkness, F_v'/F_m' in light; dashed lines), and levels of zeaxanthin + antheraxanthin (Z + A) and of energy dissipation activity (depicted as nonphotochemical quenching of chlorophyll fluorescence, or NPQ) (mixed dashed line) in a system in which there is no photoinhibition (A), a system with strong photoinhibition (B), and one in which there is moderate photoinhibition (C). For the situation with no photoinhibition, NPQ is rapidly and completely reversible and is denoted as NPQ_{flex}. For moderate and strong photoinhibition, NPQ can be sustained and show no reversibility and is denoted as NPQ_{sus}. NPQ_{sus} is bracketed by parentheses because this value cannot, under most circumstances, be calculated correctly (see text).

was shown to be lower in the absence of such rapidly modulated thermal energy dissipation in PsbS-deficient *Arabidopsis* mutants (Külheim et al., 2002). The term "dynamic photoinhibition" (Osmond, 1994; Osmond and Grace, 1995; Osmond and Förster, this volume) has been adopted by some to describe the transient and rapidly reversible decreases in maximal PS II efficiency that result from this photoprotective energy dissipation process, even though rates of photosynthetic electron transport remain maximal (e.g. Adams et al., 1999) and photosynthesis is not inhibited.

In sun-exposed leaves under otherwise favorable conditions, the xanthophyll cycle conversion state [(Z + A)/(V + A + Z)], level of thermal energy dissipation activity (NPQ), and maximal PS II efficiency change in a very predictable manner over the course of the day, paralleling increases and decreases in PFD (Figs. 2E–L). However, the magnitude of these changes differs among species depending on the proportion of the absorbed excitation energy that is used for photosynthesis. For instance, the rapidly growing annual mesophyte sunflower has a high light- and CO_2-saturated rate of photosynthetic oxygen evolution of typically 50 to 60 μmol O_2 m^{-2} s^{-1}, whereas the evergreen shrub *Euonymus kiautschovicus* utilizes only half as much of the midday light with a photosynthetic

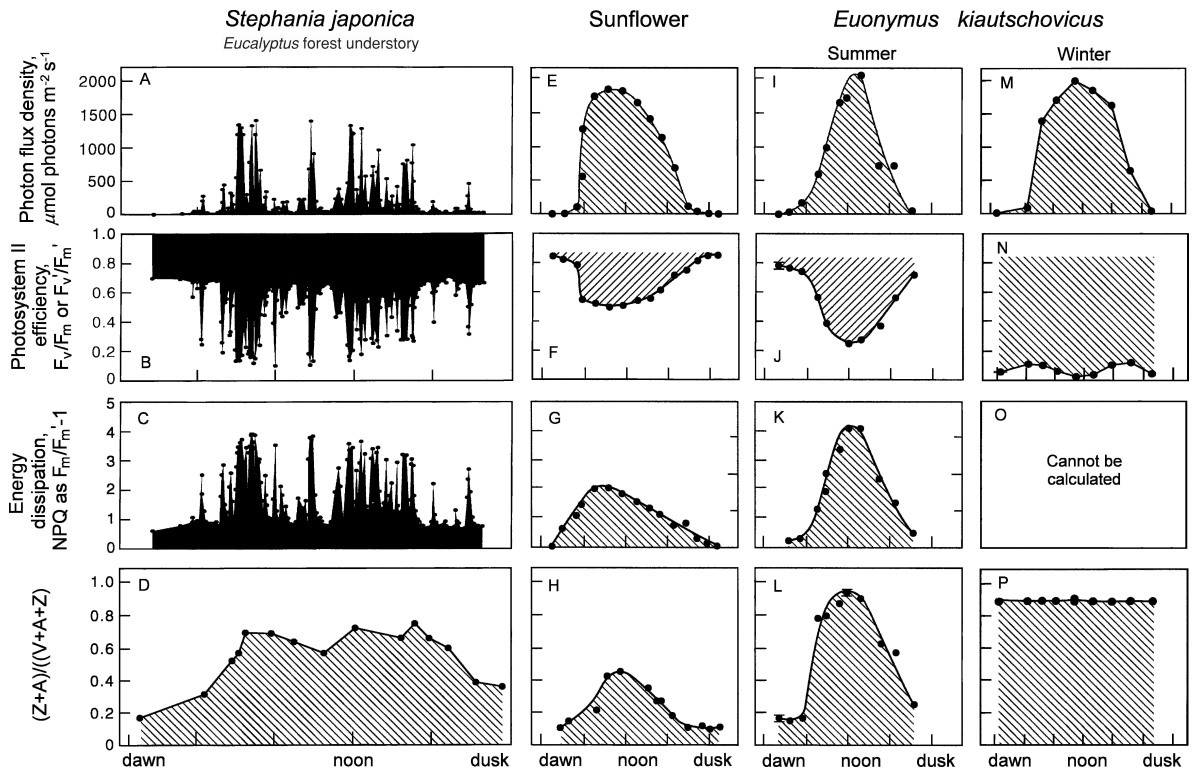

Fig. 2. Changes in photon flux density, PS II efficiency (F_v/F_m predawn and F_v'/F_m' during daylight illumination), level of photoprotective energy dissipation calculated as NPQ, and the level of zeaxanthin + antheraxanthin (depicted as a fraction of the total xanthophyll cycle carotenoids) in *Stephania japonica* growing in the understory of a forest in Australia, in sunflower growing in full sunlight, and in full-sunlight exposed *Euonymus kiautschovicus* in summer and in winter. Data are redrawn from Adams et al. (1999), Demmig-Adams et al. (1996b), and Verhoeven et al. (1998).

capacity that ranges between 20 and 30 μmol O_2 m^{-2} s^{-1} (Adams et al., 1992, 2002; Demmig-Adams et al., 1992). As a consequence of these different levels of photosynthetic utilization of absorbed light energy, *Euonymus kiautschovicus* converts a greater proportion of the xanthophyll cycle to Z + A (Fig. 2L vs. 2H) and employs higher levels of photoprotective thermal energy dissipation (Fig. 2K vs. 2G), resulting in greater midday depressions in maximal PS II efficiency (Fig. 2J vs. 2F) compared to sunflower. Or, as some prefer to view it, the more stress-tolerant evergreen species experiences a greater level of "dynamic photoinhibition".

B. Photoinhibition

Characteristics of photoinhibition include several phenomena that have been the subject of intense study for the past several decades (see Powles, 1984; Kyle et al., 1987; Barber and Andersson, 1992; Aro et al., 1993; Baker and Bowyer, 1994; Long et al., 1994; Adams et al., 1995, 2002; Barber, 1995; Osmond and Grace, 1995; Osmond et al., 1997; Melis, 1999; Telfer et al., 1999; Marshall et al., 2000; Demmig-Adams and Adams, 2003; Adir et al., 2003). Under physiologically relevant conditions, such phenomena typically arise in response to conditions of prolonged or pronounced excess light absorption; either exposure of low light-grown plants or leaves to high light, or exposure to light in the presence of one or more additional stresses. Several of these characteristics are depicted in Fig. 1B in comparison to the non-photoinhibited state shown in Fig. 1A.

The most frequently assessed parameter in this regard is the maximal efficiency of PS II, F_v/F_m. This arises not because F_v/F_m is necessarily the most relevant parameter for understanding photoinhibition, but because it is easily and rapidly determined with little perturbation to the system. In fact, decreases in F_v/F_m can arise from several different changes in the photosynthetic apparatus (Kitajima and Butler, 1975; Björkman, 1987; Adams and Demmig-Adams, 2004). Two common changes leading to decreased levels of F_v/F_m are increases in photoprotective zeaxanthin-dependent thermal dissipation and decreases in the competence of PS II reaction centers to carry out

photochemical charge separation. In intact leaves under physiologically relevant conditions, there tends to be a strong component of the former.

Strong photoinhibition is characterized by a PS II efficiency (F_v/F_m) as low as 0.1 and 0.2 in a dark-adapted, fully relaxed state, which corresponds to 12 to 24% of the F_v/F_m observed in non-photoinhibited leaves. From this low efficiency state, there is typically no or little further decrease in PS II efficiency F_v'/F_m' upon exposure to light (Fig. 1B). Another measure of the efficiency of energy conversion in photosynthesis, the photon yield (or the slope of the linear portion of the light response curve of photosynthesis), is also typically lower in photoinhibited leaves (Figs. 1B vs. 1A) (i.e. there is a strong correlation between F_v/F_m and the photon yield of photosynthesis; Björkman and Demmig, 1987; Demmig and Björkman, 1987; Adams et al., 1990). Following the light response curve of photosynthesis up to light saturation reveals that the capacity for photosynthesis is also typically lower in photoinhibited leaves compared to non-photoinhibited leaves (Figs. 1B vs. 1A). This feature is not what is expected from a simple increase in thermal dissipation. Instead, an inactivation of PS II photochemistry may contribute to this photoinhibition and likely involves inactivation and/or disassembly of PS II cores (especially the D1 protein; see Edelman and Mattoo, Häder, Huner et al., Nishiyama et al., Yokthongwattana and Melis, this volume). In addition, strongly photoinhibited leaves (Fig. 1B) have most of the pool of the xanthophyll cycle carotenoids retained as zeaxanthin, and high levels of sustained thermal energy dissipation (although calculation of NPQ in leaves that are experiencing photoinhibition over longer time periods [days to months] can be problematic in the absence of a valid control value for F_m; see Adams and Demmig-Adams 1995, 2004; Adams et al., 1995a, b). Thus strongly photoinhibited leaves are apparently in a photochemically inactive, albeit highly photoprotected state, diverting the majority of absorbed excitation energy into zeaxanthin-dependent thermal energy dissipation.

Moderate levels of photoinhibition typically involve characteristics that are intermediate between those for non-photoinhibited leaves and strongly photoinhibited leaves (Fig. 1C). Dark-adapted PS II efficiency F_v/F_m may range between 0.4 and 0.7, and PS II efficiency in the light F_v'/F_m' shows further decreases as the light becomes more excessive. Both photon yield and photosynthetic capacity may be lower than those of non-photoinhibited leaves. Furthermore, intermediate levels of Z + A are typically retained in darkness and remain engaged in a state primed for thermal energy dissipation. Thus, there is a certain level of sustained NPQ in darkness (which may be impossible to quantify; see above), and additional increases in NPQ (characterized by decreases in F_v'/F_m', but impossible to quantify as NPQ since a true F_m control cannot be obtained) occur in response to increasing levels of excess light. At midday or during exposure to light, moderately photoinhibited leaves therefore apparently rely on a combination of sustained and rapidly reversible zeaxanthin-dependent thermal energy dissipation for photoprotection.

III. Photoprotection and Photoinhibition in Winter

In the midst of winter, leaves of many evergreen species can be found in various states of photosynthetic downregulation (for reviews, see Adams et al., 2001a, 2002, 2004; Öquist and Huner, 2003). Such species typically cease growth during the autumn and may or may not exhibit decreases in the capacity for photosynthesis depending on species, light environment, and the severity of the conditions to which the plants are exposed. Most do, however, exhibit nocturnally sustained depressions in PS II efficiency that are associated with the retention of Z + A (e.g. Figs. 2N, 2P). In fact, the close association between Z + A level and PS II efficiency that is similar in leaves transiently exposed to high light under otherwise favorable conditions (experiencing "dynamic photoinhibition") and in photoinhibited leaves/needles in the winter (compare Figs. 3A and 3B), suggests that the latter are actually in the same highly protected state.

A portion of winter-induced, nocturnally sustained decreases in PS II efficiency in evergreen species is rapidly reversible upon warming (see Verhoeven et al., 1998). This portion is presumably due to maintenance of thylakoid lumen acidification at low temperature that keeps zeaxanthin in an engaged state (see Demmig-Adams et al., 1996b; Gilmore, 1997). The remaining portion of the decrease in PS II efficiency reverses only slowly over days at warmer temperatures (Adams et al., 1995; Verhoeven et al., 1996) and does not seem to involve a pH gradient across the thylakoid membrane (Verhoeven et al., 1998; Gilmore and Ball, 2000). Herbaceous annual and biennial species that maintain leaves during the winter exhibit only small nocturnally sustained decreases in PS II efficiency (see Fig. 3B, spinach), and such minor depressions reverse rapidly upon warming (Adams et al., 1995b; Verhoeven et al., 1999). In contrast to evergreen species that exhibit no change or a decrease in photosynthetic capacity in the winter compared to the summer, the herbaceous species

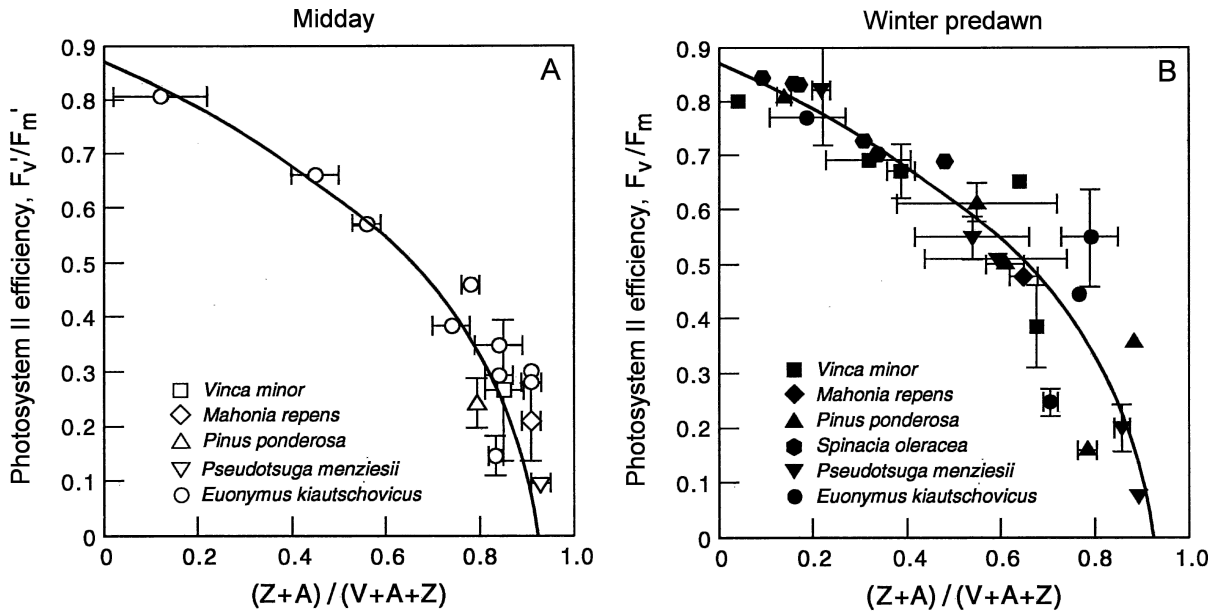

Fig. 3. Relationship between the level of zeaxanthin + antheraxanthin (depicted as a fraction of the total xanthophyll cycle carotenoids) and photosystem II efficiency as either F_v'/F_m' during exposure to light (A) or as F_v/F_m that is sustained during winter in the predawn darkness (B). The midday values for *Euonymus kiautschovicus* were determined from 10 different leaves of varying exposure to light during mild conditions in the summer (open circles), whereas all other values were determined during winter. The line fitted through the data is identical for each panel. Error bars represent standard deviations. Data redrawn from Adams et al. (1995a).

that retain their leaves typically exhibit an upregulation of photosynthetic capacity under winter conditions (see reviews of the literature in Adams et al., 2001a, 2002, 2004; Öquist and Huner, 2003; Huner et al., this volume).

In evergreen species that downregulate photosynthesis during the winter, there is a strong correlation between the capacity for photosynthesis and predawn PS II efficiency within a species both during the winter and during the period of transition from winter through spring (closed circles in Fig. 4). On the other hand, there is no correlation between the two parameters under favorable conditions during the summer. Different needles or leaves can have very different capacities for photosynthesis while all have a high PS II efficiency (open circles in Fig. 4). This is true among sun-exposed needles and leaves, between sun (high capacity) and shade (low capacity) needles/leaves of the same species, and among different species in which the capacity for photosynthesis varies greatly with differences in sink activity (utilization of the carbohydrates produced through photosynthesis for growth, storage, and respiration) but where PS II efficiency is equally high.

The strong correlation between photosynthetic capacity and PS II efficiency in evergreen species under winter conditions and during the transition from winter to spring suggests a tight link between the capacity for utilizing light energy for photosynthetic electron transport and the capacity for dissipating excess excitation energy thermally. Under favorable conditions, this involves pH modulation of (1) the activity of the enzymes responsible for converting violaxanthin to zeaxanthin and zeaxanthin to violaxanthin (see Yamamoto, this volume) and (2) PsbS, the protein facilitating chlorophyll de-excitation by zeaxanthin and antheraxanthin in energy dissipation (Li et al., 2000, 2002; see also Jung and Niyogi, this volume). Such regulation is depicted schematically in Fig. 5A, with violaxanthin present as the predominant carotenoid of the xanthophyll cycle and the PsbS "valve" closed during the night. During the winter, on the other hand, evergreen species may enter a downregulated state in which photosynthetic electron transport is greatly diminished, zeaxanthin is retained in large amounts all of the time, and Z is continuously engaged in a state that can facilitate thermal energy dissipation whenever light energy is absorbed by the light-harvesting chlorophyll (Fig. 5B). We have recently suggested that the downregulation of photosynthetic electron transport coupled with sustained engagement of zeaxanthin in energy dissipation may provide an effective means of preventing the formation of the reactive oxygen species superoxide and singlet oxygen

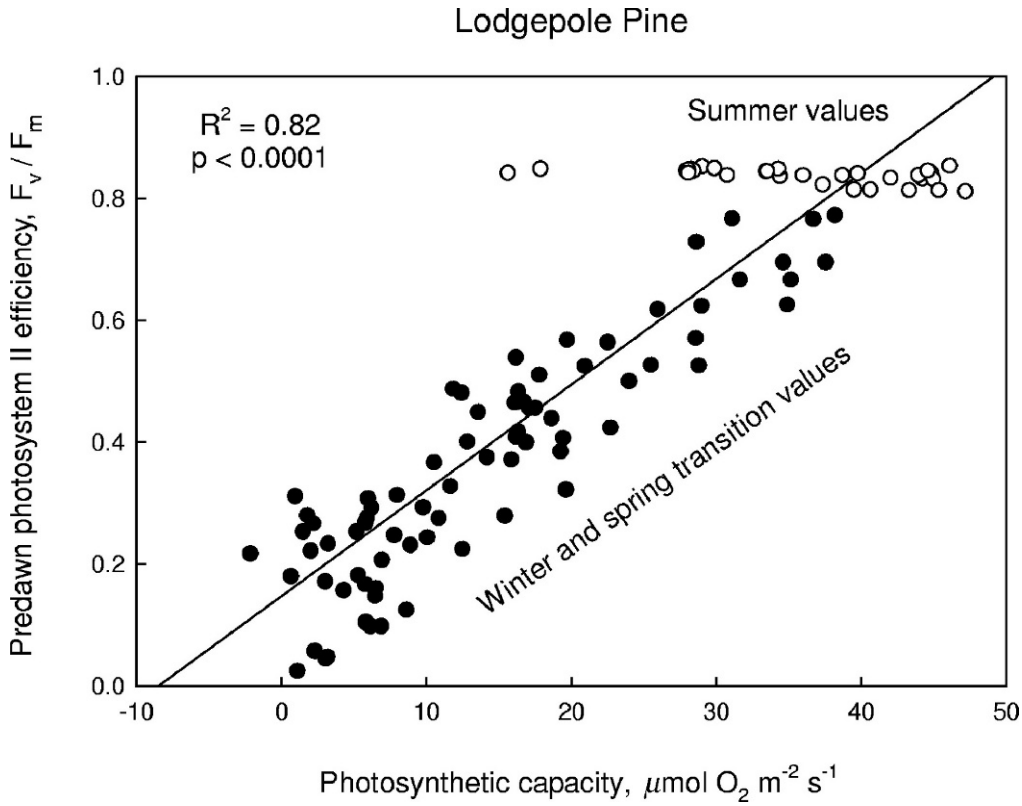

Fig. 4. Relationship between the light- and CO_2-saturated capacity for photosynthetic oxygen evolution (determined at 25°C) and photosystem II efficiency determined predawn in needles of lodgepole pine growing at approximately 3000 m in the Rocky Mountains of Colorado. Values were determined in the summers of 2001 through 2003 (open circles) or during the winter through spring transition of 2003 (closed circles). The photosynthetic capacities during the summer ranged from 15.6 to 47.2 μmol O_2 m^{-2} s^{-1}, whereas photosystem II efficiency varied little (mean summer value ± SD of $F_v/F_m = 0.836 \pm 0.013$, n = 30). Unpublished data of CR Zarter, WW Adams, and B Demmig-Adams.

(Demmig-Adams and Adams, 2003; Adams et al., 2004). Furthermore, several studies have suggested that proteins related to PsbS, such as early light-inducible proteins (ELIPs) or high light-inducible proteins (HLIPs), may play a role in xanthophyll-dependent photoprotection under more severe conditions (Norén et al., 2003; Ensminger et al., 2004; Demmig-Adams et al., this volume).

IV. Does Photoinhibition Limit the Carbon Available to the Plant?

There have been many claims that photoinhibition is likely to lead to decreases in carbon gain and reduced plant productivity, due either to photodamage or photoinactivation of the D1 protein and the attendant decrease in electron transport capacity or even to sustained photoprotective energy dissipation that continues to siphon off absorbed energy upon a return to non-excessive light conditions (e.g. Ball et al., 1991; Long et al., 1994; Melis, 1999; Werner et al., 2001; Zhu et al., 2004). This view has persisted for many years due primarily to the perspective that "damage" to D1 is "suffered" during photoinhibition (see Adir et al., 2003 for an historical review; Häder, Huner et al., Nishiyama et al., Yokthongwattana and Melis, this volume) and that this "lesion" of the photosynthetic apparatus, or "impairment" of photosynthesis, must limit the supply of carbohydrates to the rest of the plant. Thus, there is considerable support for the view that photoinhibition is something that should be protected against (e.g. Endo and Asada, this volume), when in reality photoinhibition may be a means by which plants sustain photoprotection.

While there is little doubt that D1 can be inactivated by reactive oxygen species (ROS) under strongly excessive light, this may reflect a photoprotective

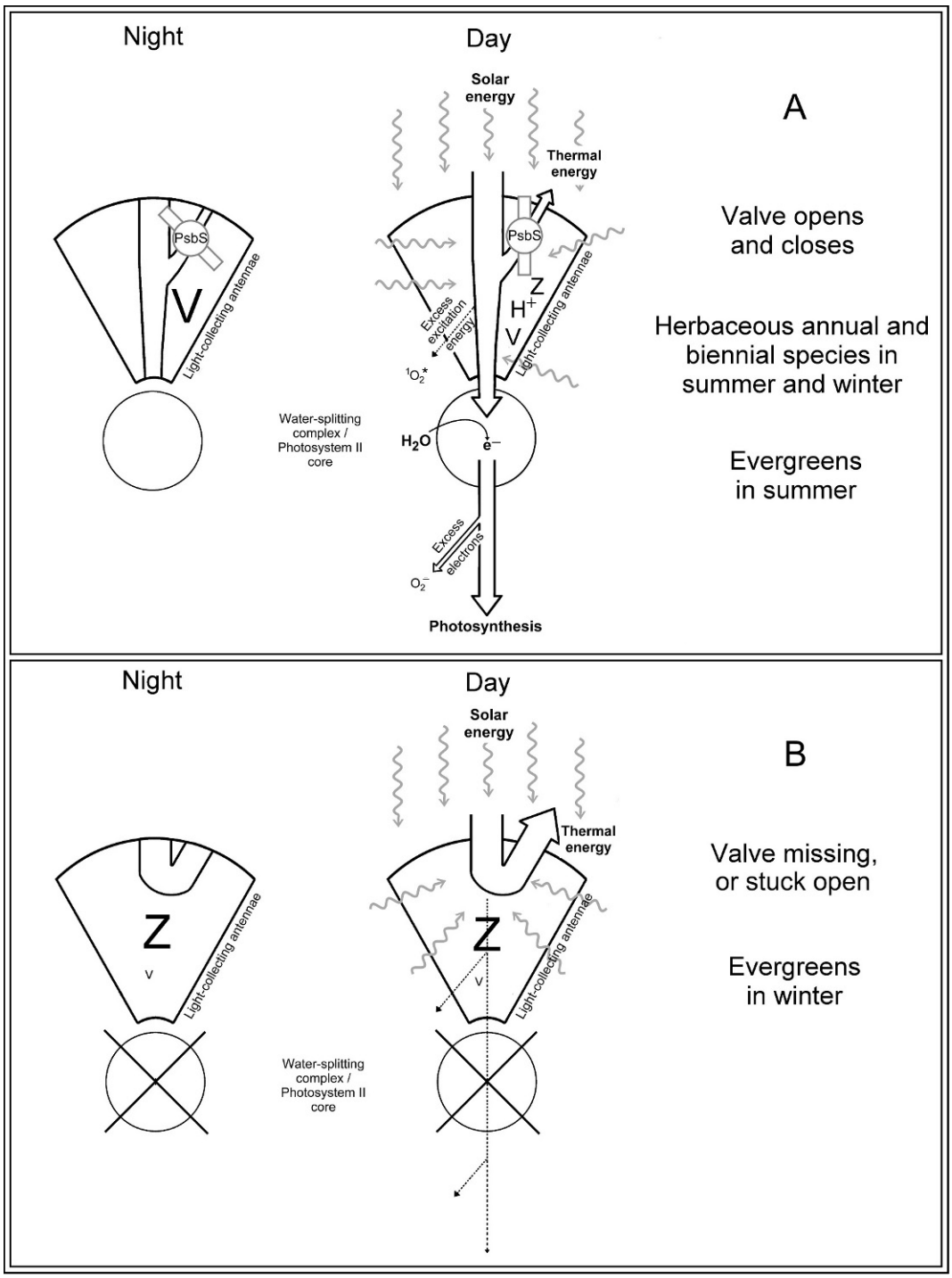

Fig. 5. Schematic depiction of (A) flexible photoprotection involving diurnal conversion of violaxanthin (V) to zeaxanthin (Z) and its engagement in energy dissipation through the protonation of the PsbS protein, thus minimizing formation of singlet excited oxygen, and (B) sustained photoprotection involving the nocturnal retention of zeaxanthin in a configuration engaged for energy dissipation and the downregulation of electron transport to minimize the formation of superoxide.

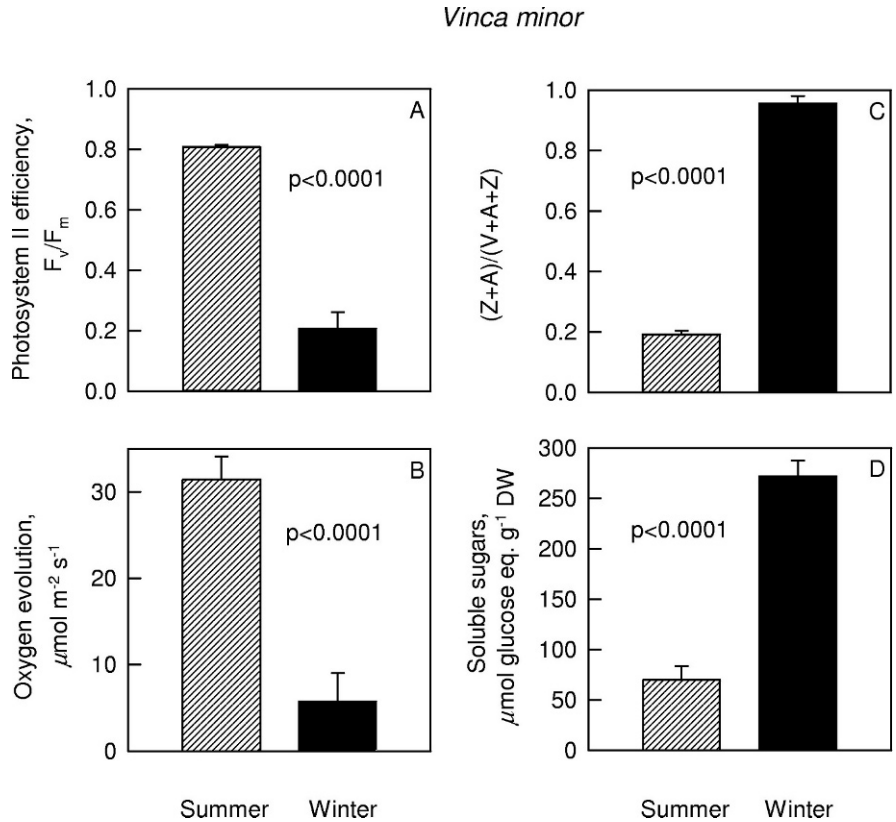

Fig. 6. Summer and winter levels of (A) predawn photosystem II efficiency, (B) light- and CO_2-saturated capacity for photosynthetic oxygen evolution (determined at 25°C), (C) predawn conversion state of the xanthophyll cycle (Z+A)/(V+A+Z), and (D) total soluble sugars in leaves of *Vinca minor* growing in full sunlight. Standard deviations are depicted, and all parameters were statistically different at the $p < 0.001$ level as determined from the Student's *t*-test. Data from Adams et al. (2001b, 2002).

downregulation of its photochemical activity via oxidative modification rather than damage (Sopory et al., 1990). In the general field of oxidative stress physiology, the classic view of protein damage by ROS and subsequent protein repair has been replaced by the realization that the proteins most susceptible to oxidation by ROS are those in the service of cellular regulation and/or signal transduction (Weindruch and Sohal, 1997; Maher and Schubert, 2000).

In addition, a number of studies purporting to show that photoinhibition involves photodamage to the D1 protein have relied on the utilization of inhibitors of chloroplast-encoded protein synthesis (see, e.g., the reviews by Melis, 1999; Nishiyama et al., this volume). However, these inhibitors can have effects beyond the simple inhibition of D1 synthesis. It is quite reasonable to assume that the photosynthetic apparatus is induced to undergo adjustments in the presence of such inhibitors that would not otherwise occur. For instance, chloramphenicol can inhibit photosynthesis directly (Okada et al., 1991), and lincomycin and streptomycin have both been found to influence calcium channels and to alter transmembrane ion gradients (Fiekers et al., 1979; Prior et al., 1990). Furthermore, some chloroplast-encoded protein synthesis inhibitors can influence the operation of the xanthophyll cycle and the engagement of zeaxanthin in energy dissipation. Lincomycin inhibits the recovery of PS II efficiency from winter photoinhibition and from high light photoinhibitory treatment, but this appears to be due to an inhibition of the disengagement of zeaxanthin from sustained photoprotective energy dissipation (Verhoeven et al., 1998; Bachmann et al., 2004) rather than to an inhibition of D1 synthesis (Bachmann et al., 2004).

The initial characterization of the impact of light on the D1 protein did not invoke the view of "damage" to the protein at all. Instead, it was simply recognized that this protein is turned over rapidly (Mattoo et al., 1984; Edelman and Mattoo, this volume). One of the

hallmarks of proteins that serve as control points in regulation is that they turn over rapidly, thus permitting rapid adjustment of their levels. There is no question that, upon exposure to excess light levels for prolonged periods, the D1 protein becomes inactivated, its levels can decrease, and the capacity for photosynthesis can decrease in turn. However, is this a response that has negative consequences for the plant, and if it could be prevented, would plant productivity actually be higher? Or is it an appropriate response of the plant to a situation where, due to a lack of opportunity for growth imposed by unfavorable environmental conditions, the demand for carbohydrates is either very low or a sufficient supply of carbohydrates to meet the maintenance and growth demands of the plant can continue to be generated while permitting photosynthesis to be downregulated in order to prevent excessive damage due to the generation of toxic reactive oxygen species (Fig. 5)?

Mesophytic species (annual and biennial crops and herbaceous species in general) exhibit little propensity for photoinhibition under high light or during winter conditions, due to high rates of utilization of the absorbed light for photosynthesis and continued growth (Adams et al., 2001a, 2002, 2004; Öquist and Huner, 2003; Huner et al., this volume). On the other hand, evergreen species, which typically cease growth in the autumn, readily experience photoinhibition in high light during the winter (Adams et al., 2001a, 2002, 2004; Öquist and Huner, 2003; Demmig-Adams et al., this volume). Furthermore, exposure of evergreen species to high levels of CO_2 throughout the winter, increasing the source to sink ratio, also result in a greater downregulation of photosynthesis (Hymus et al., 1999; Roden et al., 1999). Winter-induced photoinhibition always involves sustained decreases in PS II efficiency, and often decreases in photosynthetic capacity as well. However, overwintering leaves and needles of evergreen species also contain high levels of soluble carbohydrates (as cryoprotectants). For the example shown in Fig. 6, both photosynthetic efficiency and photosynthetic capacity were downregulated to an extreme degree in the winter, and yet the level of soluble carbohydrates was four times greater in the winter compared to the summer. Does the photoinhibition experienced by this plant limit the availability of carbohydrates? Or does the demand for carbohydrates diminish to such an extent (cessation of growth under the short, cold days of winter) that the plant can supply all of the carbohydrates that are necessary for maintenance activities and cryoprotection with a much lower rate of photosynthesis?

One might argue that, in response to low temperatures, carbohydrates are diverted and maintained in the tissues for cryoprotection and that this diversion, coupled with the lower rates of photosynthesis, does limit the supply of carbohydrates that might otherwise be available to these plants to continue growing in the freezing and subfreezing conditions of winter. However, those plants experiencing the greatest levels of photoinhibition during winter were found to exhibit the greatest rates of growth during the subsequent spring (Blennow et al., 1998; Roden et al., 1999). Furthermore, accumulation of carbohydrates also occurs in leaves of plants under photoinhibitory conditions that do not involve a particular requirement for cryoprotection or osmotic adjustment. A good correlation between the level of photoinhibition (decreases in PS II efficiency) and increased starch accumulation was found in two species of *Eucalyptus* in response to excess light under conditions of water stress and/or high temperatures (Roden and Ball, 1996). Starch also accumulates in leaves subjected to the classic photoinhibitory transfer of shade plants to high light, as illustrated in the following example.

The leaves of *Monstera deliciosa* (a neotropical evergreen hemi-epiphyte) from plants grown under low light (10 μmol photons m^{-2} s^{-1}) and then transferred to high light (700 μmol photons m^{-2} s^{-1} for 10 h per day) experienced photoinhibition as determined from a 50% decrease in light-saturated electron transport during the first day (not shown) and nocturnally-sustained depressions in PS II efficiency to below 0.6 (Fig. 7A). Nonetheless, leaf carbohydrate content increased fourfold over the next five days (Fig. 7B), the majority of which accumulated as starch in the chloroplasts. It does not seem unreasonable to conclude that, faced with the sudden wealth of available light following transfer from low to high light, PS II and photosynthesis can be downregulated (or experience photoinhibition) and still provide a greater income of carbohydrates than was possible during the low light growth conditions. The persistent photoinhibition in such transferred shade leaves may be related to a carbon export capacity that cannot be increased to the level of that typically found in a high light acclimated leaf. For instance, vein density of *Monstera deliciosa* leaves was significantly different between those grown in low light (2.8 ± 0.3) versus those grown in a sunlight-exposed glasshouse (4.9 ± 0.5), and vein density cannot be increased in fully expanded leaves (not shown). Upon transfer from low to high light, growth rates will increase in response to the appropriate signals in the elevated light environment, new leaves will be produced with higher rates of photosynthesis, and carbon supply is unlikely to be a limiting factor.

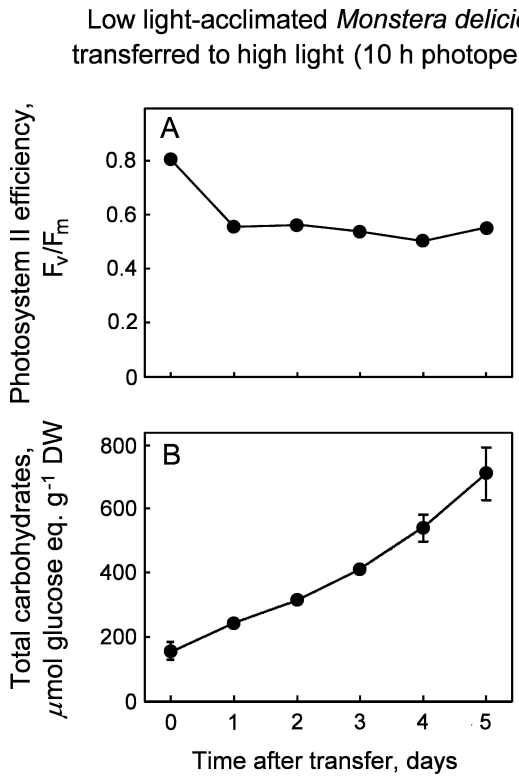

Fig. 7. Predawn determinations of photosystem II efficiency (A) and total non-structural carbohydrates (B) in low-light grown (10 μmol photons m^{-2} s^{-1}) leaves of *Monstera deliciosa* determined prior to (0 day) and daily upon transfer to high light (700 μmol photons m^{-2} s^{-1} for 10 h per day). Starch represented the greatest fraction of carbohydrates. Error bars represent standard deviations. Unpublished data of B Demmig-Adams, BA Logan, TR Rosenstiel, V Ebbert and WW Adams.

V. An Integrated View of Photoprotection

Zeaxanthin-dependent thermal energy dissipation thus spans many scales, providing photoprotection under the most benign conditions (e.g. understory of a rainforest; Logan et al., 1997) to the most severe that plants experience. This photoprotective process is modulated through several means to provide the level of thermal dissipation required 1) for flexible engagement and disengagement whenever the level of excess absorbed excitation energy varies rapidly (e.g. Figs. 1A and 2A–D) or 2) when photoprotection must be engaged in a sustained manner under long-term photoinhibitory conditions (e.g. Figs. 1B and 2M–P). The latter appears to occur readily in evergreen species during winter stress (e.g. Adams et al., 2001a, 2002, 2004; Öquist and Huner, 2003; Demmig-Adams et al., this volume) and upon exposure of shade-acclimated plants to high light (e.g. Demmig-Adams et al., 1998, this volume). For both of these scenarios, the capacity for detoxification of reactive oxygen species and other radicals is likely to be limited due to either low levels of antioxidants (shade-acclimated leaves) or an inhibition of the activity of enzymatic antioxidants by the low temperatures. On the other hand, under conditions of limiting nutrients (Verhoeven et al., 1997; Logan et al., 1999; Morales et al., this volume), and low water availability and/or high temperatures (Barker et al., 2002), photosynthesis can be downregulated, and zeaxanthin retained nocturnally, but without being maintained in an engaged state primed for thermal energy dissipation. Instead, the retained zeaxanthin remains poised for engagement (presumably upon protonation of the PsbS protein) and can thus respond more rapidly than if violaxanthin had to first be enzymatically converted to zeaxanthin, yet the system maintains complete flexibility in terms of engagement and disengagement. These three possible scenarios are depicted schematically in the context of whole plant source sink relationships in Figure 8.

Downregulation (or repression) of photosynthesis is a well-characterized response to conditions in which the supply of carbohydrates by source leaves exceeds the export and utilization of those sugars (Krapp and Stitt, 1995; Koch, 1996; Paul and Foyer, 2001). No one has ever suggested that rubisco or any of the other enzymes involved in the fixation and reduction of CO_2 to sugars are damaged when their levels decrease under sink-limiting conditions. In addition, some components of photosynthetic electron transport and ATP synthesis are downregulated in response to sugar repression or sink-limiting conditions (Krapp and Stitt, 1995; Dijkwel et al., 1996). Furthermore, levels of the D1 protein decrease dramatically under low light when spinach leaves are fed glucose (Kilb et al., 1996). It seems only logical that, in a situation where carbohydrates are in abundance and the biochemistry of photosynthesis is downregulated, primary photochemistry and photosynthetic electron transport should also be downregulated to reduce the likelihood of electrons being passed on to oxygen to form toxic superoxide (Fig. 5). This downregulation should be most easily achieved through the D1 protein that is turned over more rapidly than any other protein in the thylakoid membranes (Mattoo et al., 1984; Edelman and Mattoo, this volume). Is this one of the functions of light-mediated D1 turnover?

Some have been puzzled by the fact that a transgenically altered tobacco line with reduced levels of the cytochrome b_6f complex (and thus impaired

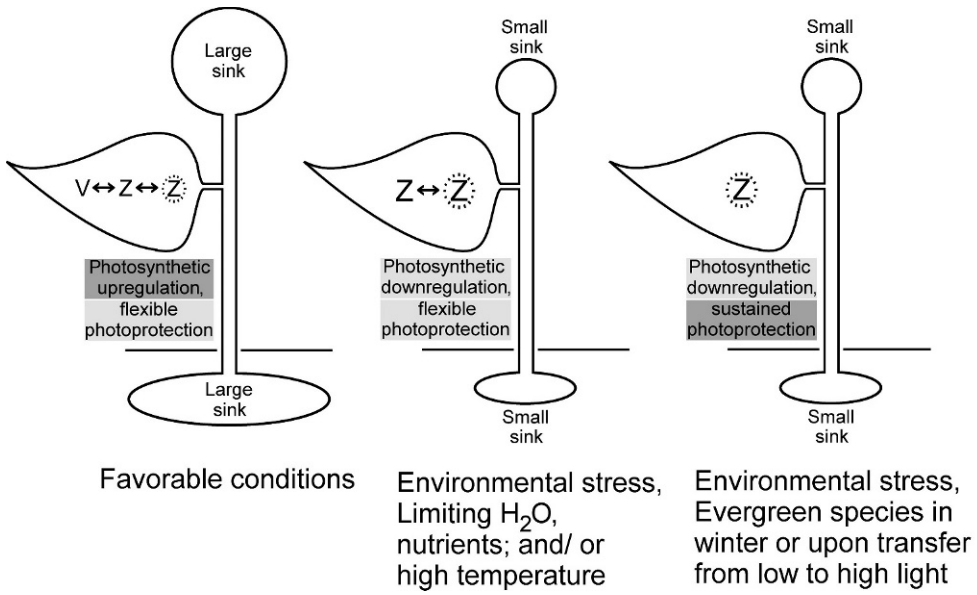

Fig. 8. Schematic depiction of photosynthetic upregulation versus downregulation and the engagement of flexible versus sustained zeaxanthin-dependent energy dissipation to effect photoprotection under different environmental conditions. Z surrounded by lines represents its engagement in energy dissipation. Under favorable conditions, growth and utilization of the products of photosynthesis is maximal (large sinks for carbohydrates), photosynthesis is upregulated or maintained at a high level for maximal utilization of the absorbed energy, and violaxanthin is converted to zeaxanthin and zeaxanthin and is engaged in energy dissipation as needed to siphon off excess absorbed excitation energy that is released harmlessly as heat. Under the less favorable conditions of reduced water availability, limiting nutrients, or high temperatures, growth is reduced (smaller sinks for carbohydrates), photosynthesis is often downregulated, and zeaxanthin may be retained nocturnally and engaged as required in energy dissipation only when absorbed excitation energy exceeds that which can be utilized by photosynthesis. In evergreen species that experience winter conditions or that are acclimated to low light and then suddenly exposed to high light, growth and utilization of carbohydrates is low (small sinks), photosynthesis is downregulated, and large amounts of zeaxanthin are retained in a state engaged for energy dissipation.

electron transport) experienced less photoinhibition (based upon decreases in PS II efficiency) compared to the wild type (Hurry et al., 1996; Yokthongwattana and Melis, this volume). If sustained decreases in PS II efficiency are interpreted to reflect sustained engagement of zeaxanthin in photoprotective energy dissipation, then such findings are entirely predictable. Any impairment in electron transport should be expected to limit the conversion of violaxanthin to zeaxanthin and the latter's engagement in energy dissipation due to an inability to acidify the thylakoid lumen to the same extent as the wild type tobacco.

What about photoprotection and photoinhibition in cyanobacteria and algae that do not export carbon to distant sinks? All algae employ xanthophylls in photoprotective energy dissipation, e.g. either zeaxanthin as part of the xanthophyll cycle in green, brown, and some red algae (Demmig-Adams et al., 1990; Uhrmacher et al., 1995; Gevaert et al., 2003; Ursi et al., 2003), diatoxanthin in diatoms and dinoflagellates as part of the diadinoxanthin-diatoxanthin cycle (Evens et al., 2001; Lavaud et al., 2004), or zeaxanthin that accumulates constitutively under high light in cyanobacteria and some red algae (Demmig-Adams et al., 1990; Cunningham et al., 1989). It has been suggested that zeaxanthin protects photodamaged PS II centers of algae exposed to photoinhibitory conditions (Jin et al., 2003). Is it not also possible that PS II centers are inactivated and/or disassembled under high light in response to signals exchanged among algae/bacteria when their densities are high and thus resources for growth and division are potentially limited? It is well known that bacteria decrease their rate of growth in response to signals from neighbors in close proximity, and it has now been established that both cyanobacteria and green algae produce signaling compounds that bacteria respond to in such quorum sensing (Braun and Bachofen, 2004; Teplitski et al., 2004). Whenever light is in excess, there are two possible responses at either end of a spectrum of potential adjustments: upregulate photosynthesis to utilize the additional light energy, or downregulate photosynthesis to minimize the possibility of forming reactive oxygen species (Figs. 1, 5, and 8; Demmig-Adams and Adams, 2003; Adams et al., 2004).

Photoprotection of photosynthesis over different time scales and in response to many different environmental conditions thus involves finely tuned adjustments in the capacity to utilize the absorbed excitation energy through photosynthetic electron transport and modulation of zeaxanthin-dependent energy dissipation. The adjustments vary from the highly flexible regulation of the xanthophyll cycle enzymes and PsbS protein protonation to the retention of zeaxanthin and its sustained configuration in a dissipative state under more severe stress. Although each of these has been categorized as being distinct from one another based upon the kinetics of engagement (qE or energy dependent quenching for that which is flexible versus qI or inhibitory quenching for that which is sustained), they truly represent extremes of a continuum of zeaxanthin-dependent photoprotection that is critical to the maintenance of the photosynthetic apparatus under conditions of excess light.

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