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PHOTOPROTECTION AND OTHER RESPONSES OF PLANTS TO HIGH LIGHT STRESS

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INTRODUCTION

This review deals with the responses of the photosynthetic organs of plants to high light, with an emphasis on a recently recognized mechanism that protects

the photosynthetic apparatus against damage under conditions frequently encountered by plants. As Powles (123) did before us, we restrict our discussion to light absorbed by chlorophyll—i.e. visible light. Light stress results not from high light per se, but rather from an excess of absorbed light beyond that utilized in photosynthesis. An excess of light can arise when the ratio of photon flux density (PFD) to photosynthesis is high. This ratio can increase through increases in PFD or through decreases in photosynthesis at a constant PFD, such as might occur under chilling conditions or in response to water stress.

Plants exhibit an entire spectrum of responses to increasing PFD (Figure 1). Over a range of PFDs, an increase in the absorption of light by chlorophyll will result in an increase in photosynthetic CO₂ fixation. Above a certain PFD, however, photosynthesis will be incapable of utilizing all the energy absorbed by chlorophyll. In this range of PFDs various mechanisms operate that protect the photosynthetic apparatus against damage from the accumulation of excessive energy. However, whenever the utilization and dissipation of energy through photosynthesis, in combination with the photoprotective processes, are insufficient for dealing with the absorbed light, the photosynthetic apparatus may be damaged. Whereas the interpretation of photooxidative reactions as damage is unequivocal, the interpretation of the effects related to PS II inactivation and turnover is not, as discussed below. Shade-acclimated leaves or organisms have low capacities not only for photosynthetic electron transport but also for photoprotective responses such as thermal energy dissipation (see below). They therefore experience sustained inactivations of the photosynthetic process at much lower levels of PFD than do sun-acclimated leaves or organisms. In contrast, in the absence of other stress factors sun leaves may be able to dissipate full sunlight entirely, through the combination of high rates of photosynthetic electron transport and high rates of thermal energy dissipation. We also examine several examples of increased photoprotective energy dissipation in sun leaves exposed to a combination of high light and other environmental stress factors.

Several reviews on the responses of plants to high light have appeared previously, each emphasizing the aspects of this response that were currently receiving the most attention. Björkman (23; see also 12–15) reviewed the acclimation of the photosynthetic apparatus to different PFDs—an acclimation that allows a greater capacity for the utilization of high light levels by leaves that develop under higher PFD than by leaves that develop under lower PFD. Interest has also focused on the set of conditions under which damage can occur (36, 96, 115, 123). Although damage to the photosynthetic apparatus was widely considered to be the primary response of leaves to excessive light, some photoprotective responses were considered in the review of photoinhibition in this series eight years ago (123); Krause (92) and Baker

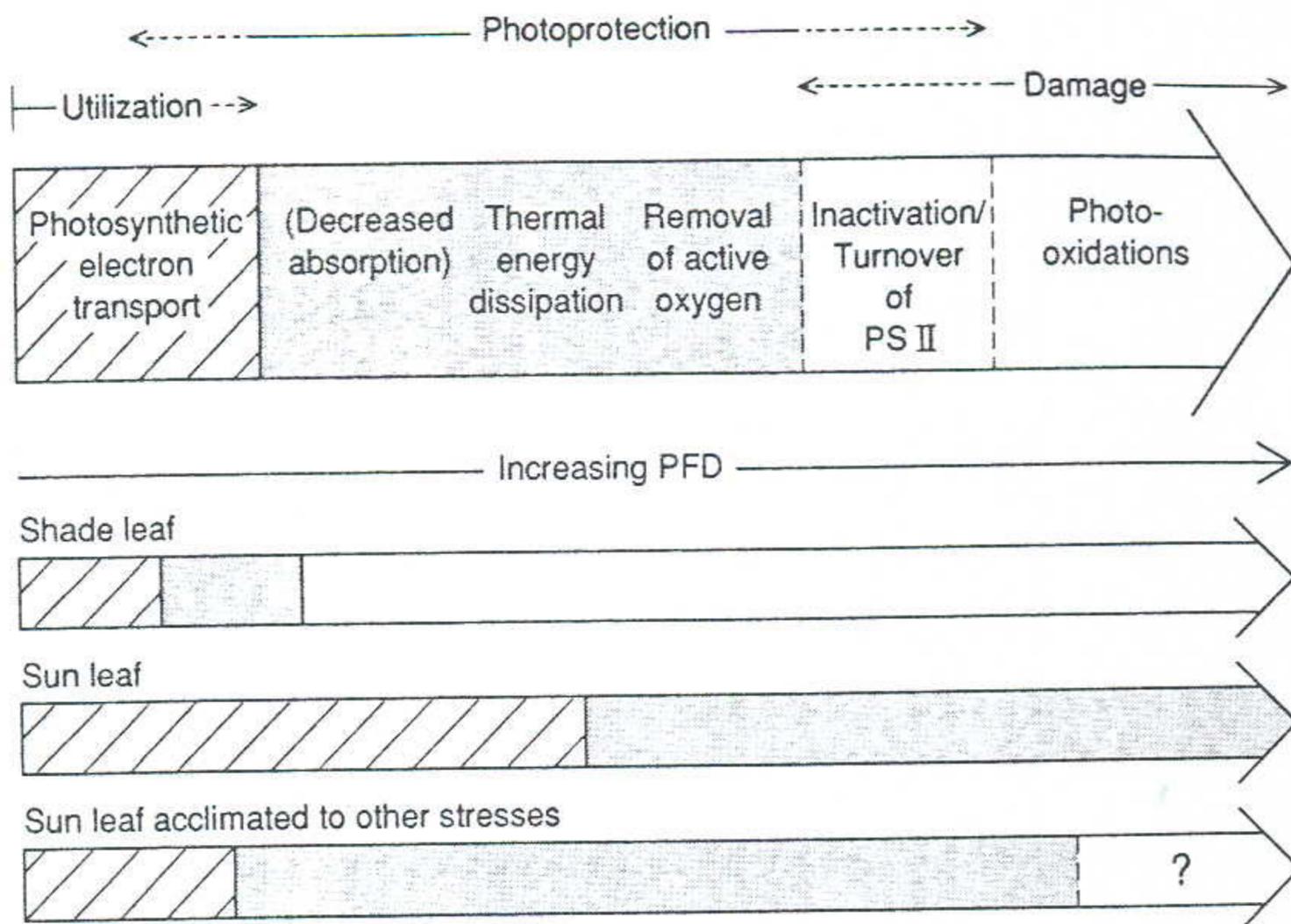


Figure 1 Schematic representation of the responses of the photosynthetic apparatus of plants to the absorption of increasing levels of PFD, including the utilization of light through photosynthesis, various photoprotective responses, and potential damage. The regions of overlap represent areas where the interpretation of the response is controversial, or where the response could be viewed as both utilization and photoprotection, or photoprotection and damage. The relative magnitude of the different responses is generally illustrated in the lower three boxes for a shade leaf, a sun leaf, and a sun leaf that experiences one or more additional stresses. It is not known to what degree inactivation/turnover of PS II (and possible photooxidation) occurs in sun leaves acclimated to additional stresses.

(17) attended to both types of responses as well. The role of thermal energy dissipation in photoprotection and photoinhibition was examined recently (42; see also 24–26, 44, 46, 52, 94), whereas other aspects of photoprotection (scavenging of active oxygen species) have been reviewed by Asada & Takahashi (16; see also 63).

Prior to the occurrence of any photooxidative processes, another phenomenon takes place: "Photoinhibition" of photosynthesis had originally been defined as a decrease in the rate of photosynthesis, particularly in the efficiency of photosynthetic energy conversion. During the previous decade the term photoinhibition was used almost synonymously with damage to PS II. However, it has now been demonstrated that a decrease in the efficiency of photosynthetic energy conversion (i.e. photoinhibition) can result not only from some form of "damage" to PS II but also from an increase in thermal energy dissipation, which is a photoprotective process and does not represent

damage (Figure 1). While measurements of photosynthesis rates and of chlorophyll fluorescence (of the ratio of variable to maximum fluorescence from PS II, F_v/F_m ; 4, 27, 39, 94) have allowed the identification of decreases in photochemical efficiency under a wide range of conditions (including high-light exposures of shade-grown organisms and the exposure of sun leaves to high light in combination with other environmental stresses), these measurements have not allowed an unequivocal separation between decreases in photochemical efficiency resulting from an increase in thermal energy dissipation and decreases that may be associated with some form of "damage." It has been shown that increases in thermal energy dissipation can, under some conditions, be sustained upon return to low (or non-excessive) light such that the kinetics of the recovery process cannot be used to distinguish between protective responses to, and adverse effects of, high light.

One model has been used (90; but see also 94) in which the particular chlorophyll fluorescence characteristics were interpreted to indicate, on the one hand, thermal energy dissipation presumably in the chlorophyll pigment bed (decrease in the instantaneous and maximum fluorescence yield, F_o and F_m ; see 5-8, 20, 24, 25, 28, 39, 40, 42, 49, 50, 53, 127, 149) and, on the other, an inactivation of the photochemical reaction center of PS II or a decreased transfer of excitation energy to PS II (increase in the instantaneous fluorescence yield; see 6, 8, 24, 25, 39, 48, 59, 64, 77, 139). The controversy between "damage" to the photosynthetic apparatus and photoprotective energy dissipation in response to high light has persisted for some time and is further complicated by the fact that different investigators examine widely differing plant materials under treatment conditions that are also disparate. In most studies, shade-grown leaves or algae have been exposed to several times the growth PFD (and often higher than full sunlight), and in other studies isolated systems (such as thylakoids), which apparently lack some of the photoprotective responses, have been exposed to highly excessive PFDs. There is now reason to believe that the responses of such systems to an excess of light are qualitatively different from the responses of plants growing in natural sunlight (cf Figure 1).

In this review we emphasize a major photoprotective process, involving the xanthophyll cycle, that facilitates the dissipation of excessive energy directly within the chlorophyll pigment bed under conditions normally encountered by plants in the field. Not only can the xanthophyll cycle respond rapidly to changes in absorbed light to provide protection during peak PFD each day, but the content of the xanthophyll cycle components themselves exhibits pronounced acclimation such that the leaves of plants found in high light habitats have larger pool sizes of the xanthophyll cycle components and thus presumably a much greater capacity for photoprotective energy dissipation than do the leaves of plants in shaded habitats. This factor makes a major

contribution to the difference between the responses of shade and sun leaves or organisms to high light.

UTILIZATION OF LIGHT THROUGH PHOTOSYNTHETIC ELECTRON TRANSPORT

The primary function of the chloroplast can be considered to be the utilization of the products of photosynthetic electron flow for the fixation of CO_2 by Rubisco. Up to a certain level of PFD, increases in PFD result in further increases in photosynthetic CO_2 fixation, and increases in the PFD the plant experiences every day result in increases in their maximal photosynthetic capacity. This acclimation of the photosynthetic apparatus to high PFD includes an increase in the levels of most of the photosynthetic electron transport carriers, as well as an increase in the capacity of the biochemistry of photosynthesis, particularly in the level of the enzyme responsible for fixing CO_2 (and O_2), Rubisco (12–14). Therefore sun plants (or leaves) have a greater capacity to “dissipate” high levels of PFD by utilizing the captured energy through photosynthesis than can shade plants (Figure 1). This acclimation may thus also result in a higher capacity of electron transport reactions leading to acceptors other than CO_2 .

Both for short-term increases in incident PFD and for longer-term increases in growth PFD, other reactions in addition to CO_2 fixation can contribute to supporting photosynthetic electron flow. These reactions would include the fixation of O_2 by Rubisco, leading to the formation of phosphoglycolic acid as the initial step in photorespiration (17; see also 83). It has been shown that in water-stressed cotton the ratio of oxygenation to carboxylation increases while the absolute rates of both decrease (30). There is also the potential for the direct reduction of O_2 by PS I in the Mehler reaction, leading to the formation of O_2^- and then H_2O_2 (82). Whereas these products of the Mehler reaction are potentially damaging species (16; see also 152, 153), it has been pointed out that the Mehler reaction nonetheless does represent a dissipative pathway (125), particularly when coupled to the ascorbate peroxidase reaction (see below; 63, 135). Further studies are necessary to determine under what conditions direct O_2 reduction in the Mehler reaction occurs *in vivo*, and what the potential for these reactions in the dissipation of excitation energy might be. The reduction of other compounds [e.g. nitrogen (33) or, possibly, sulfur (10)] by electrons from photosynthetic electron transport also occurs, but not necessarily at a high rate. All of the above reactions that can sustain some level of electron flow may, however, have an important role—e.g. when photosynthetic rates are low—in the build-up of a transthylakoid pH gradient, which is in turn the prerequisite for the major thermal energy dissipation process in the photochemical system (see below).

PHOTOPROTECTION

Prevention of Excessive Light Absorption

Whereas photoprotection afforded through the removal of excess excitation energy (thermal dissipation) within the photochemical apparatus and removal of active oxygen (discussed in the following two sections) appear to be ubiquitous in higher plants, the mechanisms whereby the absorption of light by chlorophyll is decreased are varied and species specific. Such responses include the movement of chloroplasts and whole leaves. Some plants can alter leaf angle over short time intervals (minutes), an action that can decrease the absorption of light when the leaf blade is positioned parallel to the incident light (29, 91, 124). Such movements may become persistent under conditions of heat or drought stress (62, 67, 99).

Over longer time intervals leaves may develop with leaf angles that minimize light absorption where growth occurs in excessive light (57). Likewise, leaves may develop greater surface reflectance (due to pubescence, a waxy cuticle, or the accumulation of salt on the epidermis) under conditions where light is excessive (58, 107). Absorption of (excess) light within the leaf by screening compounds (pigments) other than chlorophyll may also reduce the amount of light absorbed by chlorophyll, but whether the accumulation of such compounds is photoprotective is not yet known.

Removal of Excess Excitation Energy Directly within the Light-Capturing System

Upon the absorption of more light than can be utilized through photosynthetic electron transport, several photoprotective mechanisms can prevent the potentially damaging accumulation of excitation energy in the photochemical apparatus. One of the most recently discovered of these is the harmless and controlled thermal dissipation of excessive energy directly within the photochemical system, presumably in the chlorophyll pigment bed (20, 39, 42, 53, 68, 75, 127). This dissipation process, the main focus of our review, involves the xanthophyll cycle, or rather the de-epoxidized state of the xanthophyll cycle (especially the xanthophyll zeaxanthin; 42). We discuss primarily thermal energy dissipation as determined from changes in chlorophyll fluorescence from PS II. However, there is evidence that the same process occurs in PS I as well (39, 69, 136; S. S. Thayer, H. Y. Yamamoto, and O. Björkman, personal communication). Other suggested dissipative mechanisms within the photochemical apparatus (see 94) include a charge-recombination process within the reaction centers (149), as well as a dissipative electron cycle around the reaction center of PS II (60, 126, 134).

To date there has been only one study (30) on the crop plant cotton, in which it was shown that even in a well-watered plant with high rates of photosynthesis only 25% of the absorbed light at peak PFD in the field was

used for CO₂ fixation, 19% for photorespiration (i.e. 44% used in photosynthetic electron transport), and the remaining 56% was completely accounted for by thermal energy dissipation as quantified from a decrease in the yield of chlorophyll fluorescence. In such sun leaves there is no evidence of any damage, nor indeed of any sustained reductions in the efficiency of photosynthetic energy conversion—despite the fact that they do experience an excess of light, absorbing more than twice as much energy as is utilized in electron transport. Leaves such as these do experience transient decreases in the efficiency of photosynthetic energy conversion, resulting from the increased thermal dissipation at midday—decreases that are fully reversible.

When sun-exposed leaves experience other environmental stress factors in addition to high light, the fraction of light experienced by these leaves as excessive can increase strongly. Such conditions can result in sustained reductions in the efficiency of photosynthetic energy conversion that were thought to indicate some form of damage (123). However, in several recent studies a combination of light with other environmental stress factors under field conditions induced a pronounced and sustained increase in thermal energy dissipation that could largely account for the change in photochemical efficiency (5, 25, 30; cf Figure 1). These examples are discussed in further detail below.

Removal of Active Oxygen Formed in the Photochemical Apparatus

Two main forms of active oxygen are apparently involved in the initiation of photooxidative damage, the superoxide anion radical, O₂⁻, and its products and singlet oxygen, ¹O₂. It has been suggested that both the superoxide anion radical and singlet oxygen are involved—e.g. in chilling-enhanced photooxidations (in chilling-sensitive leaves; 85, 152, 153). Various antioxidants, most importantly reduced ascorbate and reduced glutathione, can be involved in the de-activation of these species in multiple ways (for a review see 16).

As mentioned above, the direct reduction of O₂ by PS I (the Mehler reaction) results in the formation of the superoxide anion radical, O₂⁻. The enzyme superoxide dismutase converts O₂⁻ to hydrogen peroxide, H₂O₂, and the latter can subsequently react with ascorbate via ascorbate peroxidase to form water and oxygen. Ascorbate can be oxidized in two steps; first to the monodehydroascorbate radical, which is re-reduced directly by NADPH (via monodehydroascorbate reductase) and, second, potentially further to dehydroascorbate, which is re-reduced (via dehydroascorbate reductase) by reduced glutathione, which is in turn also reduced by NADPH (via glutathione reductase; see 16, 63). Various components of this ascorbate (and glutathione) metabolism have been found in increased amounts under excess light in leaves acclimated to such conditions, particularly at chilling tempera-

tures (e.g. 38, 80, 86, 132, 133) but also under water stress (65). Furthermore, the chloroplasts of leaves that develop in high light environments possess greater quantities both of ascorbate and of various enzymes involved in ascorbate metabolism than do leaves that develop in the shade (63, 70).

Ascorbate serves not only to reduce hydrogen peroxide but also to reduce violaxanthin to antheraxanthin and zeaxanthin in the xanthophyll cycle (137, 154). Thus in addition to supporting some rate of linear electron flow via its consumption of NADPH and H_2O_2 , ascorbate facilitates the formation of zeaxanthin and thereby the development of thermal energy dissipation. It has furthermore recently been suggested that the former reaction may also be involved in thermal energy dissipation. It has been hypothesized that the Mehler peroxidase reaction induces the development of a large transthylakoid pH gradient (since it supports linear electron flow without ATP consumption) that in turn promotes significant zeaxanthin formation (111; see also 135). The extent to which this reaction occurs *in vivo* remains to be explored further.

Another species of oxygen that can be formed in the thylakoid membranes is the highly reactive (and damaging) singlet excited state of oxygen (1O_2), which can be formed through interaction with the excited triplet state of chlorophyll. Upon absorption of a photon, chlorophyll enters the excited singlet state, which normally leads to photochemistry. However, under an excess of light, accumulating chlorophyll molecules in the excited singlet state can enter the excited triplet state. The interaction of such chlorophyll molecules in the excited triplet state with oxygen leads to the generation of 1O_2 . The photoprotective function of carotenoids in photosynthesis has been thought to be limited to this area: De-excitation of 1O_2 or of the triplet excited state of chlorophyll directly (95, 138). Leaves that have developed in high light possess larger total carotenoid pools than do leaves that have developed in the shade (see below). We suggest below that carotenoids have another function, namely a process involving the xanthophyll cycle (zeaxanthin) leading to the de-excitation of chlorophyll molecules in the singlet excited state through zeaxanthin.

INACTIVATION/TURNOVER OF PS II

With regard to the phenomenon of photoinhibition, more attention has probably been focused on the PS II reaction center proteins (particularly D_1) than on any other single factor. The D_1 protein (also referred to as the 32-kDa herbicide-binding or Q_B protein) carries several of the primary components of the photochemical reaction sequence that are affected during the inactivation of PS II through extremely excessive PFDs and considerably prior to removal

of D_1 (32, 34, 35, 143, 147). Light also stimulates D_1 protein turnover (104, 150). This turnover consists of the assembly of complexes, which takes place within the stromal lamellae, followed by migration of these complexes into the granal lamellae and a degradation process involving the translocation of PS II components from granal to stromal lamellae (11, 86, 103; see also 15). Several investigators (see 96, 115) have suggested that the D_1 protein is damaged by high light and subsequently replaced, and studies using inhibitors of protein synthesis have shown that recovery from photoinhibition can be dependent on protein synthesis (64, 77, 78, 130, 148). It was therefore suggested that the migration of PS II complexes (carrying D_1) between stromal and granal thylakoids represents a "PS II repair cycle" involving migration of "damaged" PS II centers [without their light harvesting complex II (LHC-II) peripheral complex] out of the granal thylakoids and migration of undamaged (but inactive) PS II centers (also without peripheral LHC-II) into the stromal lamellae (11, 86, 105, 110). A model was proposed suggesting that the extent of photoinhibition is determined by the relative rates of such "damage" and "repair" during exposure to excessive light in leaves (77, 78) and algae (98, 129, 130).

Further responses involving reversible movements of various components of PS II from granal to stromal thylakoids have also been described: A disconnection of PS II from the LHC-II peripheral complex followed by migration of PS II from granal to stromal thylakoids was observed at elevated (144, 145) and at chilling (102) temperatures. However, these responses were suggested to be of a photoprotective nature, decreasing the antenna size of PS II under excess light and possibly leading to other changes that make the PS II centers without LHC-II less susceptible to damage (101; see also 35). It is unclear which other aspects of PS II heterogeneity (for reviews see 76, 94) are involved in this response.

How are the various forms of modification and translocation of PS II components related, on one hand, to each other and, on the other hand, to normal turnover, any destruction by excessive light, and photoprotective responses? The observations discussed above may represent different aspects of the same phenomenon. This phenomenon might consist of a photoinhibitory inactivation of PS II that depends on protein synthesis for its reversal but that, nevertheless, has a photoprotective quality involving some form of increased energy dissipation within the PS II center (see discussions in 94, 117, 119, 139, 140). Alternatively, these could be two distinct phenomena, a reversible conversion of PS II centers into an inactivated but dissipating form (see also 126, 134, 149), and a removal and replacement of PS II components. In either case, consideration must be given to the possibility that reductions in photochemical efficiency (F_v/F_m) may be associated with some form of energy dissipation not only when they result from increased thermal

energy dissipation in the chlorophyll pigment bed, but also when caused by an inactivation of the PS II centers.

Apart from the current controversy over the nature of the inactivation of the PS II centers, however, the question whether this phenomenon occurs in plants acclimated to conditions of excess light remains to be investigated. Studies that have identified the reaction center complexes as the site of photoinhibition have generally used organisms grown under low PFD (or isolated chloroplasts or thylakoids) and then experimentally exposed to high PFDs. Preliminary experiments with sun leaves exposed to PFDs equivalent to full sunlight under otherwise favorable conditions suggest that their response does not involve an equilibrium between inactivating and protein synthesis-dependent recovery processes, as long as thermal energy dissipation occurs (B. Demmig-Adams and W. W. Adams III, unpublished data). In such leaves only the inhibition of thermal energy dissipation (with dithiothreitol, DTT; see below) resulted in a sensitivity of the recovery process to the protein synthesis inhibitor chloramphenicol. Furthermore, the reversible photoinhibition, possibly involving the PS II reaction center, that is observed in nonhardened spinach leaves at chilling temperatures in the light is avoided in leaves acclimated to such temperatures in the field (142; see also 139, 140), possibly through an increased scavenger activity and an increase in thermal energy dissipation via zeaxanthin (133).

THE XANTHOPHYLL CYCLE AND THERMAL ENERGY DISSIPATION: A PHOTOPROTECTIVE RESPONSE

Characteristics of the Xanthophyll Cycle

The xanthophyll cycle consists of light-dependent conversions of three xanthophylls (oxygenated carotenoids) in a cyclic reaction involving a de-epoxidation sequence from the diepoxide violaxanthin via the monoepoxide antheraxanthin to the epoxide-free form zeaxanthin, and an epoxidation sequence in the reverse direction (for reviews see 81, 137, 154). These two reaction sequences are catalyzed by two different enzymes and can occur simultaneously in the light. This xanthophyll cycle is present in the thylakoid membranes of all higher plants, ferns, mosses, and several algal groups (46, 81, 131, 146). The formation of zeaxanthin is not restricted to those organisms that possess the xanthophyll cycle, and zeaxanthin can be found in most aerobic photosynthetic organisms that have developed under conditions of excessive PFD (42, 46).

The dependence of the reactions of the xanthophyll cycle on light is the consequence of the regulation, and not the biochemistry, of the cycle (for reviews see 81, 137, 154). This regulation is exercised by several factors associated with photosynthetic electron transport (see below); it results in the

accumulation of zeaxanthin under an excess of light and the reconversion of zeaxanthin to violaxanthin upon return to non-excessive light levels. As PFD increases (see Figure 1) there is no de-epoxidation of violaxanthin as long as all of the absorbed light is utilized through photosynthetic electron transport (in the linear portion of a PFD response curve of photosynthesis—i.e. in the photon yield region). Violaxanthin begins to be converted to antheraxanthin and zeaxanthin at the PFD at which photosynthesis can not use all of the excitation energy. The content of zeaxanthin in leaves has been shown to increase with increasing degrees of excess PFD from there on (20, 53; for reviews see 42, 44, 46).

Several regulatory factors (81, 137, 154) allow the fine-tuning of the formation of zeaxanthin to the amount of excess PFD absorbed. The de-epoxidation of violaxanthin to zeaxanthin requires a low (acidic) thylakoid lumen pH (see also 122) and reduced ascorbate (which is re-reduced by NADPH); the availability of violaxanthin to the de-epoxidase may also be regulated, although this latter possibility has not been fully clarified. The epoxidation of zeaxanthin to violaxanthin requires O_2 and NADPH and has a higher pH optimum than the de-epoxidation reactions. The xanthophyll cycle also operates in both PS II and PS I, and it is regulated by the same parameters in both photosystems (S. S. Thayer, H. Y. Yamamoto, and O. Björkman, unpublished data; see also 136).

Recent progress in the investigation of the xanthophyll cycle has been stimulated by methodological progress—e.g. much-improved techniques for HPLC separation of zeaxanthin and lutein (74, 146), as well as the use of absorbance change measurements from whole leaves (20-22).

Association among the De-epoxidized State of the Xanthophyll Cycle, Thermal Energy Dissipation, and Photoprotection

Another parameter that typically increases along with an increasing excess of light absorbed by chlorophyll is thermal energy dissipation, presumably in the chlorophyll pigment bed. This dissipation activity can be quantified from changes in the yield of chlorophyll fluorescence, and several approaches that give similar results have been used (20, 42, 43, 46). Linear relationships between the amount of zeaxanthin (or the de-epoxidation state of the xanthophyll cycle) and thermal energy dissipation have been observed in leaves under a wide range of conditions, including situations in which energy dissipation is rapidly reversible (20, 43, 49, 53, 54, 75) upon termination of the treatment with excessive light (a type of change in the yield of fluorescence that has been referred to as “energy-dependent” or “pH-dependent quenching”; 92-94) as well as those in which both thermal energy dissipation and the level of zeaxanthin decrease slowly upon return to non-excessive light (41). There are, however, situations in which zeaxanthin is present and there

is no thermal dissipation of energy, although only in the absence of excessive light (22, 52, 54, 75).

The strongest evidence to date in support of a causal relationship between zeaxanthin and thermal energy dissipation has been obtained using an inhibitor of the de-epoxidation of violaxanthin to zeaxanthin, DTT (155), in intact leaves (3, 20–22, 49, 75, 151) and lichens (42, 43, 47). In systems in which zeaxanthin formation has been prevented by the presence of DTT, exposure to excessive light produces no rapidly reversible decrease in the yield of chlorophyll fluorescence—i.e. no increase in thermal energy dissipation. Leaves that contained and retained zeaxanthin and were subsequently treated with DTT exhibited no inhibition of thermal energy dissipation (O. Björkman and W. Bilger, personal communication), and thus the inhibition of thermal energy dissipation by DTT is through the inhibition of zeaxanthin formation. The inhibition of thermal energy dissipation (in DTT-treated systems) is accompanied by an increased reduction state of PS II centers—i.e. by an accumulation of excitation energy in PS II—which is thought to result in adverse effects. A sustained decrease in the efficiency of photosynthetic energy conversion can be detected in DTT-treated systems after treatment with high light.

Similar results with regard to the development of thermal energy dissipation, the reduction state of the PS II centers, and sustained decreases in the efficiency of photosynthetic energy conversion have been obtained in other studies comparing systems in which zeaxanthin formation did not occur with systems in which zeaxanthin could form rapidly. These have included treatment of leaves under chilling conditions (which inhibits the enzymatic conversion of violaxanthin to zeaxanthin; 55) and comparisons of lichens both with green algal phycobionts (which possess the xanthophyll cycle) and with blue-green algal phycobionts (which do not possess the xanthophyll cycle and thus cannot form zeaxanthin rapidly; 47, 48, 51). Blue-green algal lichens that did possess zeaxanthin (synthesized slowly over days) exhibited responses similar to those of green algal lichens (47).

With regard to the situation in which zeaxanthin can be present in the absence of thermal energy dissipation, it has been suggested that the thylakoid membrane must be in the energized state (i.e. that light must be excessive) in order for zeaxanthin to be active in thermal energy dissipation (42, 46). The factors responsible for inducing this activity apparently involve the presence of a pH gradient across the thylakoid membrane (a low lumen pH; 72) as well as another, unidentified condition that may in fact be induced by a low lumen pH (71, 73, 75). Thus similar factors (those that respond to an excess of absorbed light) regulate both the formation of zeaxanthin (biochemical control) and its activity in thermally dissipating excessive excitation energy (biophysical control).

Several hypotheses have been offered about the nature of the involvement of zeaxanthin in energy dissipation. Investigators have obtained results that they interpret to indicate that there is one energy dissipation process (characterized by a decrease in the yield of both F_o and F_m) that is dependent on zeaxanthin, and that there may be another process that also causes a decrease in the yield of chlorophyll fluorescence and can also be rapidly reversible (3, 49, 72, 75). We have suggested that zeaxanthin may in some (direct or indirect) manner facilitate the de-excitation of accumulated chlorophyll singlet excited states (42, 44, 52). In contrast, Horton and coworkers (112, 127) have suggested that zeaxanthin modifies the pH response of a thermal energy dissipation process (the only one in their interpretation) to allow this process to occur at pH values presumably normally found in vivo. As mentioned above, it has furthermore now been suggested that the effect of the Mehler peroxidase reaction also occurs via an increased formation/activation of zeaxanthin (111). All of these investigators seem to agree that zeaxanthin is involved in thermal energy dissipation and that this is the major photoprotective dissipation process that occurs in leaves over a range of conditions normally encountered by plants.

Operation of the Xanthophyll Cycle in the Field

DIURNAL DE-EPOXIDATION AND EPOXIDATION. In this section we describe the response of the xanthophyll cycle to daily changes in incident PFD in leaves of plants growing in full sunlight but not subject to any other environmental stress. In such plants there are pronounced changes in the (de-)epoxidation state of the xanthophyll cycle over the course of a day. As incident PFD increases, de-epoxidation of violaxanthin occurs and zeaxanthin levels increase along with PFD, and as PFD levels decline in the afternoon zeaxanthin is reconverted to violaxanthin (Figure 2). This is a typical response and has been observed in a wide range of plant species growing in natural sunlight (2). Thus the xanthophyll cycle operates in the field even in photosynthetically highly active plants, as has been shown for a variety of annual crop species, as well as in other species with lower rates of photosynthesis (2, 44, 46, 50). A close relationship between the absorption of excess light and the de-epoxidation of violaxanthin and thus formation of zeaxanthin has also been demonstrated using leaves with different orientations that receive peak PFD at different times during the day. In such leaves the peak levels of zeaxanthin are found in each leaf during the period of maximum incident PFD, either during the morning, at midday, or during the afternoon, depending upon the particular exposure (9; see also 50).

Similar responses of changes in the yield of chlorophyll fluorescence to incident PFD have been obtained from a variety of plants growing in the field (1, 5, 7, 8, 50), which indicates that pronounced diurnal changes in thermal

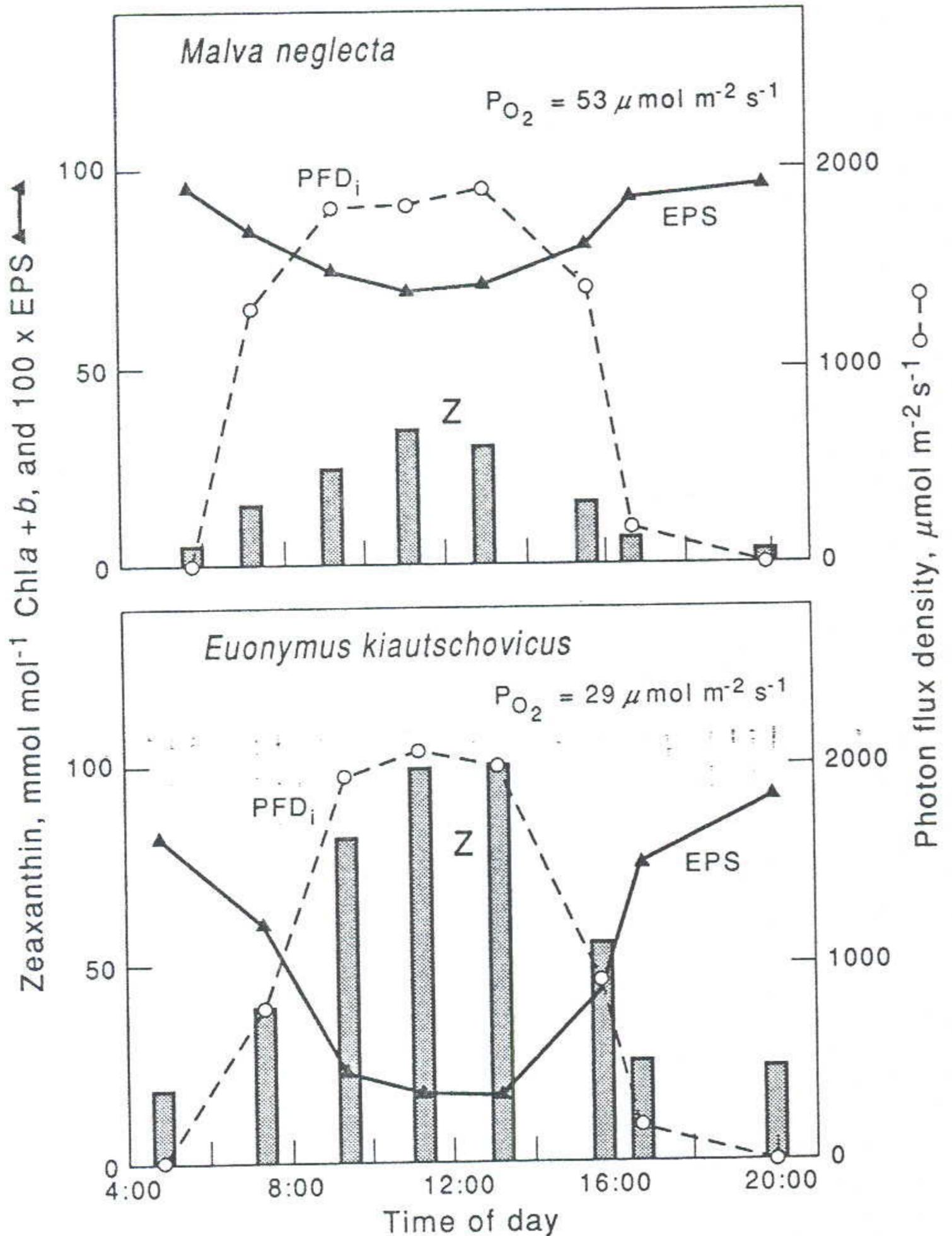


Figure 2 Diurnal changes in the photon flux density incident upon the upper leaf surface, the level of zeaxanthin, and the epoxidation state of the xanthophyll cycle (EPS = [violaxanthin + 0.5 antheraxanthin]/[violaxanthin + antheraxanthin + zeaxanthin]) in leaves of the mesophyte *Malva neglecta* and the xerophytic shrub *Euonymus kiautschovicus* on 15 September 1990 in Boulder, Colorado. The CO₂-saturated rates of photosynthetic O₂ evolution (P_{O₂}) determined at 1950 μmol photons m⁻² s⁻¹ and 25°C are also given for similar leaves from the same plants. The pool size of the xanthophyll cycle was 114.8 ± 6.5 (n = 8) mmol violaxanthin + antheraxanthin + zeaxanthin per mol chlorophyll a + b in *E. kiautschovicus* and 157.4 ± 10.1 (n = 8) in *M. neglecta*. Data from Ref. 2.

energy dissipation of the type associated with zeaxanthin (quenching of F_o and F_m) occur in the field. More concomitant measurements of zeaxanthin content and thermal energy dissipation activity are needed. Nonetheless, it does appear that zeaxanthin is associated with the major thermal energy dissipation process in plants in the field, at least under favorable conditions.

An increase in thermal energy dissipation is associated with some decrease in the photochemical efficiency of PS II (F_v/F_m) and in the photon yield of photosynthesis (5, 50; see also 24, 39). Other reported changes in F_v/F_m in response to incident PFD in the field may also involve increases in thermal energy dissipation associated with zeaxanthin (1, 7, 8, 50, 79, 114, 119).

The degree to which the xanthophyll cycle is de-epoxidized at midday can vary considerably among leaves of different species (or even the same species) depending on their capacity for photosynthetic electron transport (see Figure 2; 2, 45, 146). Leaves with the higher rates of photosynthesis exhibited less de-epoxidation (they formed less zeaxanthin at peak PFD—i.e. they had a higher epoxidation state, EPS); leaves with lower rates of photosynthesis exhibited more de-epoxidation (they formed more zeaxanthin—i.e. had a lower EPS). From the observation that cotton dissipated (probably via zeaxanthin) all of the energy in excess of that utilized through photosynthetic electron transport (see earlier; 30) it can be concluded that the percentage of (thermally) dissipated excitation energy and thus the degree of de-epoxidation of the xanthophyll cycle should in turn indicate what fraction of the absorbed light is utilized. A linear relationship between the epoxidation state of the xanthophyll cycle and ratio of photosynthesis/PFD (multiplied by the pool size of the xanthophyll cycle) has recently been reported for a variety of species with different rates of photosynthesis (146). The potential of this relationship for the remote sensing of photosynthetic performance of plants from the status of the xanthophyll cycle is currently being explored (66).

SHADE-SUN ACCLIMATION OF THE XANTHOPHYLL CYCLE POOL The size of the xanthophyll cycle pool (violaxanthin + antheraxanthin + zeaxanthin) undergoes a marked acclimation to the light environment (45, 56, 146). In leaves that have developed in low light, the xanthophyll cycle pool is relatively small, whereas in leaves that have developed in high (sun) light the xanthophyll cycle pool can represent more than 30% of the total carotenoids present in the photosynthetic apparatus (Figure 3). This holds for species typically found either only in the shade or only in full sunlight, and for leaves of the same species that develop in different light environments. β -carotene also exhibits similar changes in response to PFD during development, and this is consistent with a specific stimulation of β,β -carotenoid synthesis (β -carotene and the three xanthophylls of the xanthophyll cycle are all β,β -carotenoids; see also 88) in response to high (or excessive) PFD. In contrast, α -carotene appears to accumulate in larger amounts in the shade, and the

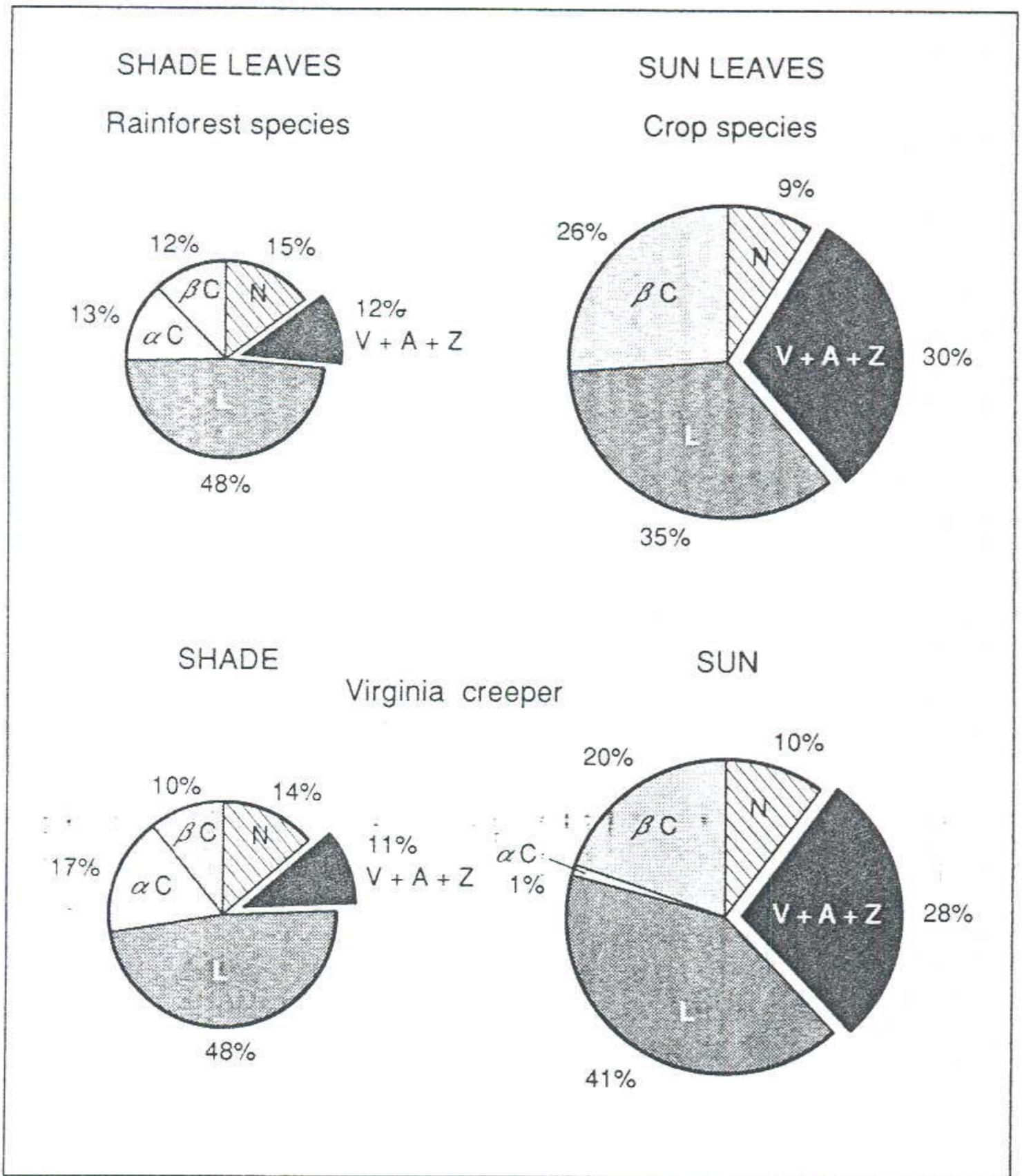


Figure 3 Comparisons of the carotenoid composition of seven deep-shade-grown rainforest species with seven annual crop species grown in full sunlight, and two leaves of Virginia creeper (*Parthenocissus quinquefolia*), one of which developed in deep shade and one of which developed in full sunlight. V + A + Z = violaxanthin + antheraxanthin + zeaxanthin = total components of the xanthophyll cycle; L = lutein; β C = β -carotene; α C = α -carotene; N = neoxanthin. The relative sizes of the pie diagrams reflect the difference in the total carotenoid content on a chlorophyll basis between the sun and shade leaves. Data from Ref. 45.

accumulation of neoxanthin and lutein does not appear to be influenced by PFD in a consistent pattern. This shade-sun acclimation of the xanthophyll cycle pool size is a general response and has been found in similar magnitudes in a total of 36 different species of higher plants in two surveys (45, 146), in a moss (131), a marine macroalga (64, 84), and in a variety of green algal

lichen species when these experience high light in the moistened state (W. W. Adams III, B. Demmig-Adams, and O. L. Lange, unpublished data). Even in organisms that do not possess a xanthophyll cycle, the content of zeaxanthin (per chlorophyll) was higher in high-light than in low-light environments, as reported for a red alga (37) and for blue-green algae (106, 120). An increased zeaxanthin content or an increase in the xanthophyll cycle pool size (allowing for a greater potential for the formation of zeaxanthin) is presumably related to a greater capacity to dissipate excess excitation energy thermally. Therefore the shade-sun acclimation of the photosynthetic apparatus involves an increased capacity not only for the utilization of light in photosynthesis, but also for photoprotective thermal energy dissipation.

It has been suggested that the stimulation of the synthesis of the xanthophyll cycle components occurs in response to the degree of excessive PFD. However, it may also be the case that a large xanthophyll cycle pool (particularly on a leaf area basis) is associated with a high rate of photosynthesis/high metabolic rate (which in turn can support high rates of carotenoid biosynthesis). This interpretation is suggested by a report that among species growing in full sunlight those with the higher photosynthesis rates (mostly annual crop species) also had the largest xanthophyll cycle pools, in spite of the fact that they experienced lesser degrees of excessive light than a variety of perennial shrubs and vines with xanthophyll cycle pools equal to or smaller than those in the annual crop species (45). These differences are illustrated by the two species shown in Figure 2. *Malva neglecta* (a mesophyte), with a high rate of photosynthesis, exhibited a relatively high epoxidation state at midday owing to a lesser degree of zeaxanthin formation as well as a large total xanthophyll cycle pool. *Euonymus kiautschovicus* (a xerophytic shrub), with a lower rate of photosynthesis, exhibited a low epoxidation state at midday owing to the formation of a high level of zeaxanthin coupled with a xanthophyll cycle pool smaller than that found in *M. neglecta*. It thus seems clear that rapidly growing, mesophytic species, for example, have the potential to form zeaxanthin far in excess of that required for thermal energy dissipation in full sunlight under otherwise favorable conditions. It is not known, however, to what degree more xerophytic shrubs and vines maintain the level of the xanthophyll cycle pool at an amount just sufficient for thermal energy dissipation, or if they may also rely on other means of photoprotection.

RESPONSE OF THE XANTHOPHYLL CYCLE TO THE INTERACTION OF LIGHT AND ENVIRONMENTAL STRESS FACTORS A variety of environmental stress factors can influence the operation of the xanthophyll cycle. This influence is probably not direct but rather acts through effects on the capacity for photosynthetic electron transport. Any environmental stress factor that causes a decrease in photosynthesis rates (as many do) will have the effect of

increasing the ratio of PFD/photosynthesis, even if PFD remains constant. Under such circumstances continued absorption of light by chlorophyll leads to an increased level of excess excitation energy, and any increase in the amount of energy dissipated thermally should provide greater photoprotection. This topic still requires considerable investigation, but the evidence to date indicates that zeaxanthin is important in the dissipation of additional excessive energy when plants are subjected to some environmental stress factor in the presence of light. In some cases (see below) this response involves a slow reversal of the increase in zeaxanthin-associated energy dissipation upon return to favorable conditions. However, stress does not necessarily cause sustained effects on photochemical efficiency (100).

Water stress Upon cessation of watering, leaves of *Nerium oleander* (which does not perform osmotic adjustment) exhibited sustained decreases in the yield of chlorophyll fluorescence indicative of increased thermal energy dissipation (25, 41), as well as sustained increases in the level of zeaxanthin (41), when such leaves remained at the growth PFD throughout the period of desiccation. The xanthophyll cycle pool also increased in size as water stress developed over a number of days (41). In this case the phenomenon of "photoinhibition," i.e. the sustained decrease in the efficiency of photosynthetic energy conversion, is apparently largely caused by a photoprotective response (25, 41).

In cotton (which does exhibit osmotic adjustment), water stress also resulted in an increase in thermal energy dissipation (30). The percentage of the absorbed light dissipated thermally increased from 56% under well-watered conditions (water potential = -1.1 MPa) to perhaps as much as 75% under severe water stress (water potential = -2.8 MPa). Decreases in the yield of chlorophyll fluorescence indicative of increased thermal energy dissipation of up to 98% of the absorbed light have also been observed in several other species experiencing water stress under natural conditions in the field (5, 7).

Salinity Sustained decreases in the efficiency of photosynthetic energy conversion were observed in the leaves of mangroves exposed to full sunlight on the eastern coast of Queensland, Australia. These decreases in photochemical efficiency could be fully accounted for by increases in thermal energy dissipation (25, 28), probably associated with zeaxanthin (see 56). Further concomitant assessments of thermal energy dissipation and zeaxanthin content should be performed on both halophytes and nonhalophytes exposed to saline conditions in the field. With respect to energy dissipation there are indications that cotton, a halotolerant nonhalophyte, exhibits a response to growth under high salinity different from that of mangroves (E. Brugnoli and O. Björkman, personal communication).

Nutrient stress In maize seedlings, nitrogen limitation results in a reduction in both shoot growth and the capacity for photosynthesis; it also resulted in an increase in leaf zeaxanthin content (89). Under excessive PFD, nitrogen-deficient plants increased their thermal energy dissipation (as quantified from decreases in chlorophyll fluorescence yield). Another interesting study on the effect of nitrogen availability found that the dominant carotenoid in plankton in nitrate-rich surface waters was fucoxanthin, whereas the major carotenoid present in plankton from nitrate-poor surface waters was zeaxanthin (116). Thus, when the nitrogen supply is sufficient, light capture appears to be emphasized (fucoxanthin is a carotenoid involved in the transfer of captured energy to chlorophyll); when nitrogen is limiting (presumably to the construction of the photosynthetic apparatus), photoprotection appears to be emphasized as a means of dissipating the absorbed energy.

Iron deficiency in sugar beet leaves caused a loss of chlorophyll and a smaller decrease in the xanthophyll cycle pool size, resulting in an increase in the size of the pool per chlorophyll (108). In spite of the fact that these plants were growing at only ~20% of full sunlight, the de-epoxidation state of the xanthophyll cycle increased strongly (almost to complete de-epoxidation) with increasing iron deficiency. This finding is consistent with the relationship between the degree of excess light and the epoxidation state of the xanthophyll cycle.

High temperature The rate of de-epoxidation of violaxanthin to zeaxanthin increases with increasing leaf temperature (21), as would be expected of an enzymatic reaction. A similar temperature response has been obtained for the development of thermal energy dissipation as assessed from measurements of the change in chlorophyll fluorescence yield in intact leaves (3, 21). Whether elevated temperatures affect not only the formation of zeaxanthin but also the activation of zeaxanthin through membrane energization remains to be investigated.

Low temperature De-epoxidation of violaxanthin to zeaxanthin occurs slowly at low temperatures in plants that are not acclimated to chilling temperatures (55), as well as in some plants that have acclimated to chilling temperatures (B. Demmig-Adams and W. W. Adams III, unpublished data). In contrast, a greater rate of de-epoxidation at all temperatures was reported in leaves of *Malva parviflora* during the spring than during the summer (21). Although de-epoxidation can be slow at chilling temperatures, the final extent of de-epoxidation can be pronounced once steady-state conditions have been reached, since a given level of PFD can represent highly excessive excitation energy due to the inhibition of photosynthesis by such temperatures (3, 21).

In addition, we (W. W. Adams III and B. Demmig-Adams, unpublished

data) have observed that, in exposed habitats in the field, a number of evergreen species contained large amounts of zeaxanthin prior to sunrise during cold periods in the winter. Apparently the epoxidation of zeaxanthin to violaxanthin is inhibited on cold nights; the predawn levels of zeaxanthin can be as high as those found at midday. The leaves therefore contain zeaxanthin and are presumably able to dissipate excessive energy (the excess of excitation energy may be substantial given the inhibition of photosynthesis by low temperature) as soon as light is absorbed by chlorophyll following sunrise. Thus the acclimation of xanthophyll cycle reactions to chilling conditions in these plants may occur through the retention of zeaxanthin throughout cold periods (see also 108) rather than through any adjustment in the rapidity of zeaxanthin formation. The retention of zeaxanthin was also accompanied by sustained reductions in photochemical efficiency (W. W. Adams III and B. Demmig-Adams, unpublished data; see also 113, 133). Sustained reductions in photochemical efficiency have likewise been observed in response to high light under chilling conditions in the field in a number of other studies (62, 119, 141, 142). The underlying mechanism of these changes remains to be determined.

General response to high light + stress To summarize, sustained reductions in the efficiency of photosynthetic energy conversion can be observed in plants from sun-exposed habitats that are also subjected to an additional stress factor such as reduced water or nutrient availability, high salinity, or low temperature. In several examples examined to date, these sustained reductions were associated with both sustained increases in thermal energy dissipation (of the type associated with zeaxanthin) and sustained increases in zeaxanthin content. Thus there are cases in which the phenomenon of photoinhibition in the field can be accounted for by increased employment of a photoprotective response. It is not known to what extent (if indeed at all) a slow reversal of zeaxanthin-associated energy dissipation upon return to more favorable conditions lowers the productivity of plants in the field.

CONCLUSIONS

There is now considerable evidence for an involvement of zeaxanthin in photoprotective energy dissipation within the photochemical apparatus under excess light. The exact nature of this involvement remains to be identified. Furthermore, the potential for zeaxanthin formation (through increases in the total pool of the xanthophyll cycle components under higher PFD) changes as part of a plant's shade-sun acclimation, and de-epoxidation/epoxidation occurs routinely during the course of the day in the field in sun-exposed habitats. Thus the response of sun leaves to excessive light is qualitatively

very different from that of shade leaves. In sun leaves that do not experience any environmental stress, the combination of a high capacity for photosynthetic electron transport (utilization of the absorbed energy) coupled with a high capacity for photoprotective thermal energy dissipation (involving zeaxanthin) can apparently account for the complete removal of all of the energy absorbed by chlorophyll under full sunlight.

Sun leaves that experience additional stress, such as low water availability or low temperatures, often exhibit photoinhibition in the form of sustained reductions in the efficiency of photosynthetic energy conversion (much as do shade leaves exposed to high light). However, in several cases in which this phenomenon has been more fully characterized, such a response was largely the consequence of sustained increases in photoprotective thermal energy dissipation associated with zeaxanthin rather than of other causes. Additional studies are needed to explore further the role of zeaxanthin-associated thermal energy dissipation, as well as other photoprotective mechanisms, in permitting the photosynthetic apparatus to function under high light—both in otherwise favorable conditions and in combination with other stresses.

In contrast to sun leaves, shade leaves have a low capacity not only for photosynthetic electron transport but also for the dissipation of excess excitation energy associated with zeaxanthin. Under high light, shade leaves experience an inactivation of PS II reaction centers; recovery from this inactivation can depend on a synthesis of components of these centers. The nature of this response of shade leaves requires further elucidation. It also remains to be determined whether a similar phenomenon can be involved in the response of sun leaves to a combination of light and additional environmental stress factors.

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