

The role of xanthophyll cycle carotenoids in the protection of photosynthesis

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The use of solar energy in photosynthesis depends on the ability to safely dissipate excess energy. The key dissipation process employed by plants in their natural environment is mediated by a particular group of carotenoids. Multiple levels of control allow adjustments in energy dissipation activity in response to changing levels of light stress in the natural environment. Recent advances in the understanding of the photophysics, biochemical regulation and ecophysiology of this essential photo-protective process are reviewed.

Although global food chains depend on the use of solar energy by photosynthetic organisms, the absorption of sunlight in excess of what can be used for photosynthesis poses a serious threat. Excess energy can result in photo-oxidative damage to the photosynthetic apparatus as well as to a range of other essential cell components. Recent research has made rapid progress in the identification and characterization of a ubiquitous process that safely dissipates the potentially destructive excess energy.

Research development over the past decade

Early research identified a dissipation process that was proposed to protect the photosynthetic apparatus (reviewed in Ref. 1). This process could be induced by lowering the pH within the photosynthetic membrane, a condition triggered by excess light. Since the process was characterized indirectly from changes in chlorophyll fluorescence emission, it was termed high energy-dependent or pH-dependent fluorescence quenching.

A connection was subsequently made between energy dissipation and the carotenoids of the xanthophyll cycle (Fig. 1)^{2,3}. Under excess light, violaxanthin is converted rapidly via the intermediate antheraxanthin to zeaxanthin, and this reaction is reversed under low light levels (reviewed in Refs 4–7). This reversible sequence of two independent reactions is termed the xanthophyll cycle and is present throughout the plant kingdom^{5,8}. The carotenoids participating in this cycle are the only carotenoids present in the photosynthetic membrane that undergo very rapid, light-triggered concentration changes. Although the brilliant work of Yamamoto⁴ and Hager⁸ had characterized how the biochemistry of the xanthophyll cycle is regulated by excess or limiting light (see below), the functional role of the cycle had remained elusive until recently.

Numerous correlations were shown subsequently between increases in the level of zeaxanthin and increases in energy dissipation as estimated from chlorophyll fluorescence quenching^{2,9} (reviewed in Refs 3 and 10), leading to the proposal that zeaxanthin mediates the harmless dissipation of excess energy as heat (Fig. 2). Zeaxanthin was proposed to catalyze the removal of the same energized form of chlorophyll (excited singlet chlorophyll) that gives rise to chlorophyll fluorescence, which is the same form of chlorophyll that is used for photosynthesis (Fig. 2)³. The xanthophyll cycle seemed to be ideally suited to interfere at this sensitive step, allowing efficient use of energy under low light followed by a rapid switch to dissipation under excess light.

Resistance to this proposal of a causal link between zeaxanthin and energy dissipation arose from the lack of a mechanism allowing a simple energy transfer from the light-harnessing chlorophyll to zeaxanthin. Contemporary theory¹¹ assumed that a transfer of energy from excited singlet chlorophyll to zeaxanthin was thermodynamically impossible. Subsequently, the question of an

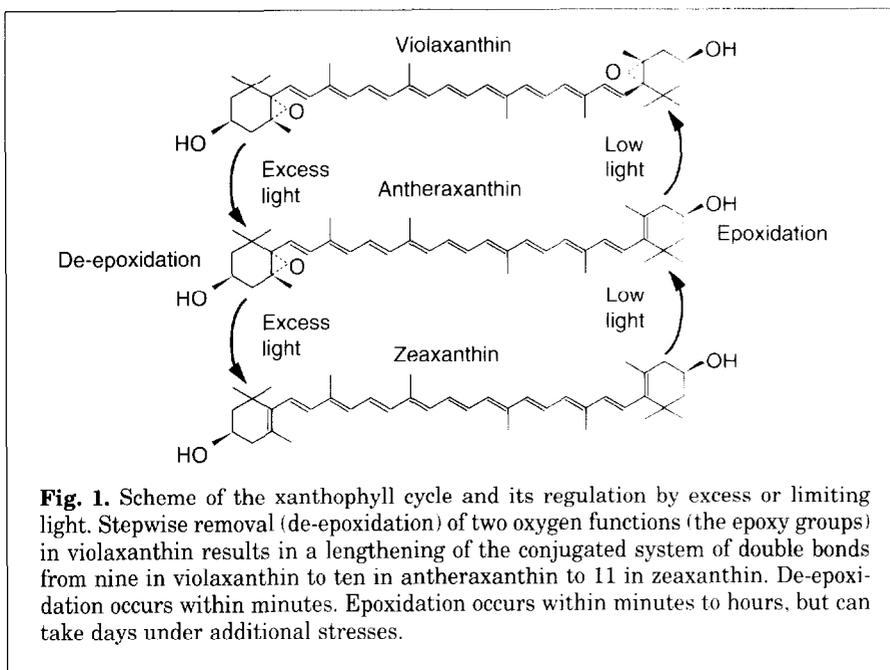


Fig. 1. Scheme of the xanthophyll cycle and its regulation by excess or limiting light. Stepwise removal (de-epoxidation) of two oxygen functions (the epoxy groups) in violaxanthin results in a lengthening of the conjugated system of double bonds from nine in violaxanthin to ten in antheraxanthin to 11 in zeaxanthin. De-epoxidation occurs within minutes. Epoxidation occurs within minutes to hours, but can take days under additional stresses.

involvement of the xanthophyll cycle in energy dissipation, as well as the photophysics of these carotenoids, received intense interest resulting in new insights into the mechanism, regulation, ubiquity and environmental response of this essential energy dissipation process.

Advances over the past eight years include the confirmation of a causal link between the combined presence of zeaxanthin (and antheraxanthin) and a low pH within the photosynthetic membrane on one hand and photoprotective energy dissipation on the other. These findings revealed that high energy-dependent/pH-dependent and xanthophyll cycle-dependent dissipation are one and the same process *in vivo* (Figs 2 and 3)^{7,10,12-15}. Recently, strong evidence has been provided demonstrating the essential involvement of the xanthophyll cycle in energy dissipation in the chloroplast under physiological conditions¹⁶⁻¹⁸. In addition, new developments in the photophysics of carotenoids have revealed that a simple and direct downhill energy transfer from excited singlet chlorophyll to zeaxanthin is thermodynamically possible (Fig. 4a)^{13,19}. Consequently, this area of research is attracting very strong and expanding interest.

Role of the xanthophyll cycle in energy dissipation

Much recent debate has centered on whether energy dissipation can be induced by low pH alone or whether the presence of zeaxanthin (and antheraxanthin⁹) is obligatory for dissipation to occur^{6,12-15,20}. It has been speculated recently⁷ that these differing views might be explained by the development of alternative forms of dissipation when xanthophyll cycle-dependent dissipation is prevented. A series of important experiments has now clearly established that under physiological conditions, the key energy dissipation process is obligatorily and stoichiometrically dependent on the presence of zeaxanthin and antheraxanthin^{9,16-18,21}. For example, energy dissipation was shown to be inducible in darkness by protonation of zeaxanthin-containing chloroplast membranes but not in zeaxanthin-free chloroplasts¹⁶. In addition, an elegant experiment where zeaxanthin was allowed to be reconverted to violaxanthin under excess light led to a loss of energy dissipation activity in spite of the continued presence of a low pH¹⁷. Furthermore, a survey of energy dissipation in leaves of a wide variety of plant species in the field concluded that excess absorbed light is invariably dissipated via xanthophyll cycle-dependent energy dissipation²². It is thus concluded that zeaxanthin and pH act synergistically and are both required for energy dissipation *in vivo*.

Site of energy dissipation within the photochemical apparatus

Proposed energy-dissipation sites within the photochemical system initially included the photochemical reaction centers as well as the light-collecting, chlorophyll- and carotenoid-binding antenna complexes of photosystem II (discussed recently in Refs 12 and 15). The antenna system is increasingly thought to be the key site of energy dissipation under physiological conditions^{12,14,15,20}. Dissipation of excess energy in the antennae would thus protect the photochemical reaction centers from overexcitation. The antennae are layered around the photosystem II centers with chlorophyll a-binding core antennae being most closely associated with the centers, followed by the inner, minor components and the outer, major components of the chlorophyll a- and b-binding, light-harvesting antennae (see Refs 7, 15 and 20). Whereas the major, peripheral complexes bind

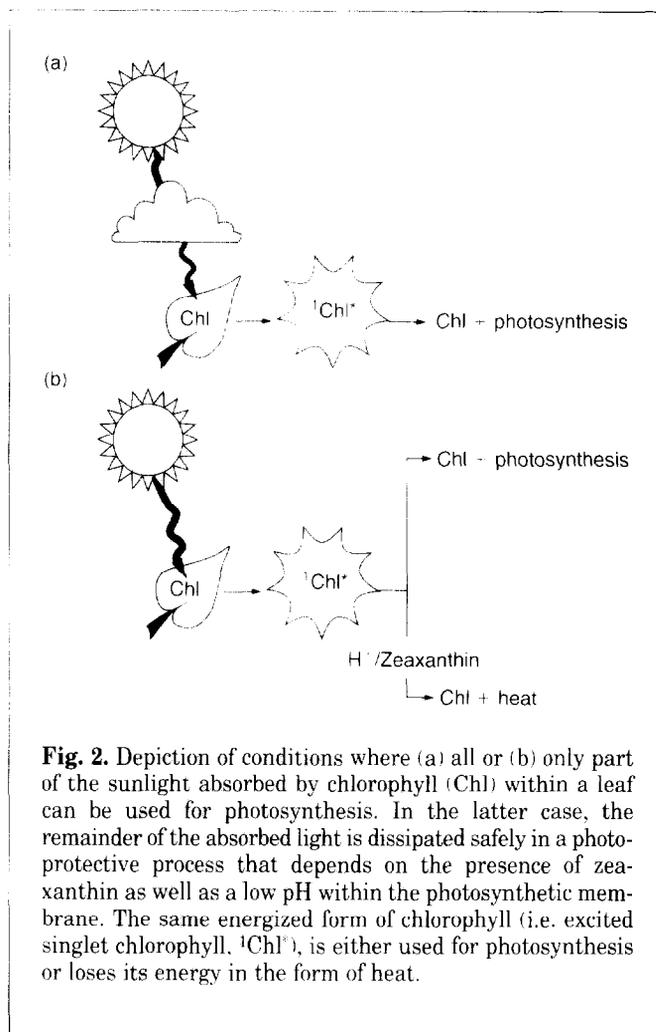


Fig. 2. Depiction of conditions where (a) all or (b) only part of the sunlight absorbed by chlorophyll (Chl) within a leaf can be used for photosynthesis. In the latter case, the remainder of the absorbed light is dissipated safely in a photoprotective process that depends on the presence of zeaxanthin as well as a low pH within the photosynthetic membrane. The same energized form of chlorophyll (i.e. excited singlet chlorophyll, ¹Chl^{*}), is either used for photosynthesis or loses its energy in the form of heat.

the majority of the chlorophyll molecules, the minor, proximal antennae bind only a small fraction of the total chlorophyll but are enriched with the xanthophyll cycle components⁷ – these particular components of the antenna system of photosystem II, the minor, proximal antennae, are emerging as key sites of dissipation^{7,12,20,23}. This view is also supported by several recent studies²⁴⁻²⁷ of the response of photosynthetic systems in which the levels of these various antenna proteins are altered (i.e. chlorophyll b-deficient mutants and plants grown under intermittent light). Härtel and Lokstein²⁵ reported recently that the lack of the minor, proximal antennae in plants grown under intermittent light inhibits a key component of energy dissipation.

It has also been shown that plants deficient in the major, peripheral light-harvesting complexes exhibited a drastically slowed reversion of antheraxanthin and zeaxanthin to violaxanthin subsequent to high light exposures²⁴. Based on such observations, the proposal was made that the major, peripheral light-harvesting complex may actually carry the epoxidase function²⁸. However, several alternative possibilities for a maintenance of high levels of antheraxanthin and zeaxanthin subsequent to light stress have also been proposed (cf. 'combinations of environmental stresses').

Regulation of energy dissipation in the antennae by the proton gradient

The pH within the photosynthetic membrane exerts a dual function in regulating energy dissipation (Fig. 3). First,

pH-decreases in the lumen of the membrane induce the biochemical conversion of violaxanthin to antheraxanthin and zeaxanthin under excess light, as was so elegantly characterized more than two decades ago by Yamamoto¹ and Hager⁸. In addition, a low pH within certain membrane domains²¹ (see below) is necessary to facilitate the xanthophyll cycle-dependent energy dissipation process itself¹².

Involvement of structural changes in antenna proteins

The protonation of proteins of the antenna system has been proposed to cause structural changes of these proteins necessary to induce energy dissipation (Fig. 3). Initially, this proposal involved the peripheral or bulk light-harvesting complexes¹¹. More recently, protonation of the minor, proximal antenna proteins has been proposed to be a key step in the induction of energy dissipation^{7,12,14,15,20,23}. The role of these protonation-induced structural changes may be to bring chlorophyll and zeaxanthin (or antheraxanthin) molecules into the close proximity required for an efficient energy transfer between these two molecules (Fig. 4a)^{12,18,19}. Alternatively, zeaxanthin (and antheraxanthin) may induce structural changes necessary for a protonation-induced loss of energy directly from chlorophyll in the form of heat (Fig. 4b)^{6,7,12-15,20}.

New insights into the photophysics of the xanthophyll cycle carotenoids

Major advances have been made recently in the photophysics of carotenoids, opening up the possibility of a simple downhill transfer of energy from excited singlet chlorophyll to zeaxanthin (Fig. 4a)^{12,15,19}. In essence, zeaxanthin could act much like a lightning rod, receiving the excess energy from chlorophyll and then dissipating it harmlessly. Carotenoids are known to be able to lose excitation energy relatively rapidly in the form of heat. In contrast, chlorophyll has a high probability of passing energy on to the ever-present oxygen (O₂) leading to the potential for photo-oxidative damage. Energy transfer to zeaxanthin would thus prevent this dangerous transfer of energy to O₂. However, direct experimental evidence for this attractive possibility is needed in order to identify the molecular mechanism of xanthophyll cycle-dependent energy dissipation *in vivo*.

The important work of Frank¹⁹ and Owens¹⁵ has shown that the properties of most higher plant carotenoids are distinctly different from those of lower photosynthetic organisms. In bacteria and certain algal groups, carotenoids that are structurally different from those of higher plants have been shown to act as accessory light-harvesting pigments that pass excitation energy down to chlorophylls¹¹ (see also Refs 12 and 15). In contrast, most higher plant carotenoids (those with ten or more conjugated carbon-carbon double bonds) have now been shown to possess a previously poorly characterized, low-lying energy level that can instead accept energy from the excited singlet state of chlorophyll. This analysis has led to

the proposal of a novel model¹⁹ (see also Ref. 15) in which the xanthophyll cycle conversions constitute a 'molecular gear shift' from violaxanthin (with nine conjugated carbon-carbon double bonds) to antheraxanthin and zeaxanthin (with ten and 11 carbon-carbon double bonds, respectively; see Fig. 1), which could potentially accept energy from chlorophyll and then dissipate this energy as heat (Fig. 4a).

Environmental responses

Diurnal responses to changes in the light environment

In nature, changes in the level of excess light, pH, and the levels of antheraxanthin and zeaxanthin often occur in parallel, such as in sun-exposed sites where diurnal increases and decreases in excess light over hours are closely tracked by increases and decreases in the levels of antheraxanthin and zeaxanthin in leaves as well as their levels of energy dissipation (cf. Fig. 6)^{10,12,29,30}. In contrast, extremely rapid and pronounced fluctuations in excess light can be experienced by leaves in the understory of a forest during a series of sunflecks³⁰. Such fluctuations on a timescale of seconds are matched by equally rapid changes in the level of energy dissipation. Under these conditions, high levels of antheraxanthin and zeaxanthin are maintained subsequent to the first sunfleck. In this case, rapid fluctuations in pH are likely to modulate energy dissipation against a background of continuously high levels of antheraxanthin and zeaxanthin.

The biochemical conversions among the xanthophyll cycle components as well as the control of their engagement in energy dissipation via pH provide an elegant control mechanism for regulating a plant's energy balance in response to how much excess light is absorbed. This regulation insures that, when light is low and limiting to photosynthesis, no competing dissipation of energy occurs. On the other hand, it allows a rapid switch to effective energy dissipation whenever excess light is absorbed.

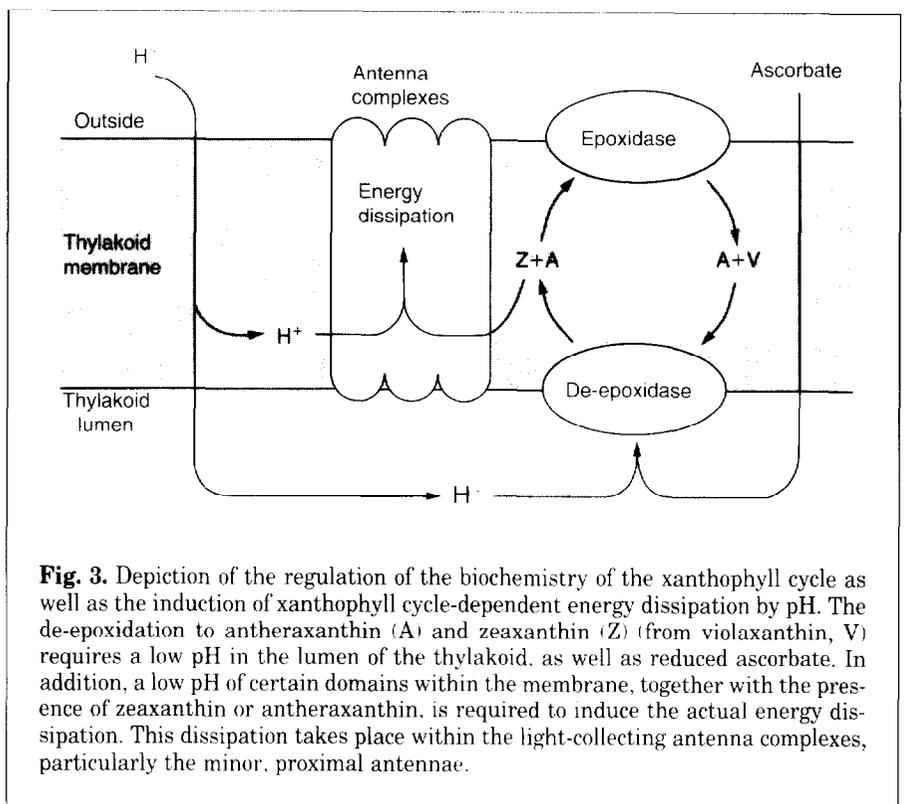
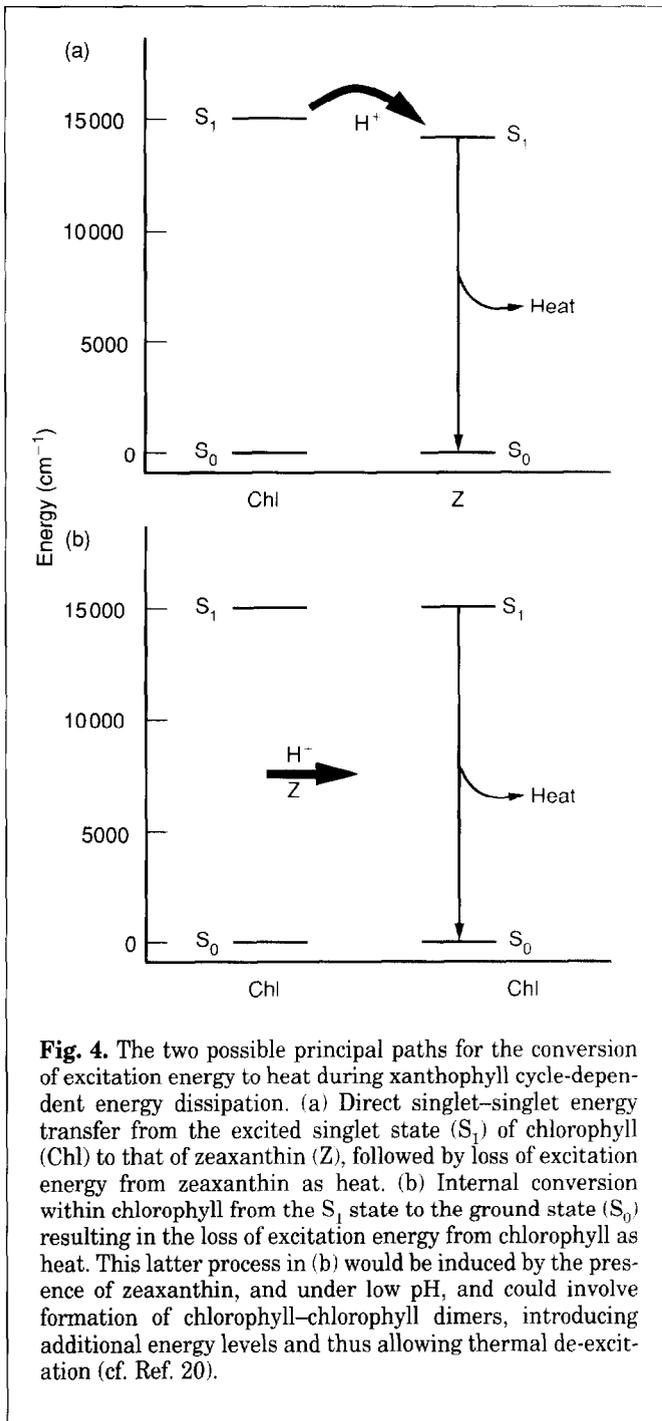


Fig. 3. Depiction of the regulation of the biochemistry of the xanthophyll cycle as well as the induction of xanthophyll cycle-dependent energy dissipation by pH. The de-epoxidation to antheraxanthin (A) and zeaxanthin (Z) (from violaxanthin, V) requires a low pH in the lumen of the thylakoid, as well as reduced ascorbate. In addition, a low pH of certain domains within the membrane, together with the presence of zeaxanthin or antheraxanthin, is required to induce the actual energy dissipation. This dissipation takes place within the light-collecting antenna complexes, particularly the minor, proximal antennae.

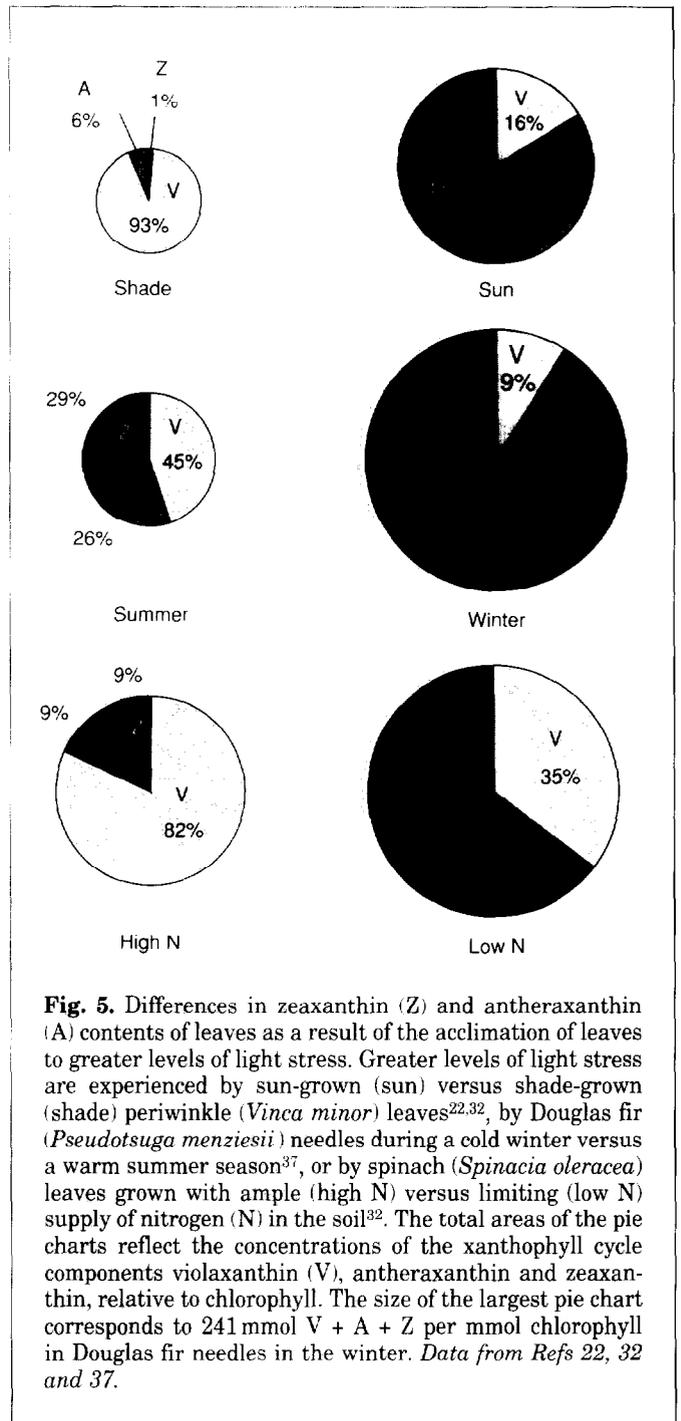


Acclimation to sun and shade

Compared to shade-grown leaves, sun-acclimated leaves possess not only a higher capacity for the use of light in photosynthesis but also for rapid increases in xanthophyll cycle-dependent energy dissipation^{10,31,32}. Sun-grown leaves typically exhibit a larger total pool size of the xanthophyll cycle components^{33,34} as well as a greater ability to convert this pool to antheraxanthin and zeaxanthin rapidly under high light (Fig. 5)^{31,32}.

Combinations of environmental stresses

All additional environmental stresses that lower a plant's photosynthetic rate, such as water stress, nutrient stress, or temperature stress, increase the degree to which absorbed



light can be excessive, increasing the need for energy dissipation³⁴. A wide variety of environmental stresses has now been shown to induce increases in the levels of xanthophyll cycle-dependent energy dissipation^{12,30,34}. As is the case for shade-sun acclimation, increases in the ratio of the total pool of the xanthophyll cycle carotenoids to chlorophyll, as well as the maximal degree of conversion to zeaxanthin and antheraxanthin, are also observed under combinations of stress factors (Fig. 5). In addition to these adjustments in the levels of zeaxanthin and antheraxanthin, changes in how the necessary pH gradient is generated under stress conditions have also been reported recently³⁵. Under low-temperature stress, a larger pH gradient can be generated by a combination of changes in the proton permeability of

the photosynthetic membrane, as well as in the ATPase activity³⁵. This leads to an increased pH gradient and thus enhanced xanthophyll cycle-dependent energy dissipation for a given light intensity at low temperatures³⁵⁻³⁷, and compensates for the low rates of photosynthetic use of absorbed light.

Exposure to combinations of stresses in the field can also lead to a maintenance of high levels of zeaxanthin and antheraxanthin throughout the day and night (Fig. 6)³⁷. For example, the diurnal transient changes in the levels of antheraxanthin and zeaxanthin under favorable conditions in the summer are in stark contrast to the high zeaxanthin and antheraxanthin levels persisting throughout cold days during the winter in many species (Fig. 6). It has also been proposed that the maintenance of high levels of xanthophyll cycle-dependent energy dissipation may be responsible for the lasting depressions in the efficiency of energy conversion in photosystem II that can be observed in overwintering plants on cold days in the field (Fig. 6)³⁷. The overall efficiency of energy conversion in photosystem II would be expected to remain low as long as high levels of energy dissipation persist in the antennae, since less of the absorbed light is delivered to the photochemical reaction centers. The same proposal had been previously made for the effects of combined high light intensity and either water stress³⁸ or salinity stress^{34,39}.

From these studies, it is clear that the kinetics of the re-conversion of zeaxanthin or antheraxanthin to violaxanthin are extremely dynamic and can be slowed considerably by additional environmental stresses. As a consequence, xanthophyll cycle-dependent energy dissipation can be the underlying mechanism not only of rapidly reversible components of energy dissipation but also of slowly reversible ones.

The means by which removal of zeaxanthin and antheraxanthin is delayed under these conditions is still unknown. Gilmore and Björkman³⁵ demonstrated that a low pH within the photosynthetic membrane can be maintained in low light or complete darkness, at low temperatures, allowing zeaxanthin and antheraxanthin to remain engaged for energy dissipation. However, there have also been reports that the synthesis of proteins is required for the return to a high photon efficiency of photosystem II after winter stress⁴⁰. Several studies^{41,42} now suggest that maintenance of a highly de-epoxidized xanthophyll cycle is related to changes in the protein composition of photosystem II, maximizing energy dissipation by virtue of a major reorganization of the light-harvesting complexes⁴¹ (see also Ref. 15).

Ubiquity of xanthophyll cycle-dependent energy dissipation among higher plant species, and its implications

All higher plant species examined to date possess the xanthophyll cycle. Without the built-in ability for photoprotective energy dissipation, photosynthesis could probably not proceed in nature in the presence of O₂. Genetic differences in the ability of plants to increase the capacity for xanthophyll cycle-dependent energy dissipation have not yet been identified. Rather, a surprising degree of uniformity in the response of a wide diversity of higher-plant species to excess light has been demonstrated²². The ability to show high levels of xanthophyll cycle-dependent energy dissipation may be a highly conserved trait because (1) it arose early during evolution, (2) it probably does not involve a large metabolic cost, and (3) excess light is experienced by almost all leaves at certain times, even in the deeply shaded understory of a forest when sunflecks hit the leaves^{30,32}. Future studies will have to determine whether or not over-

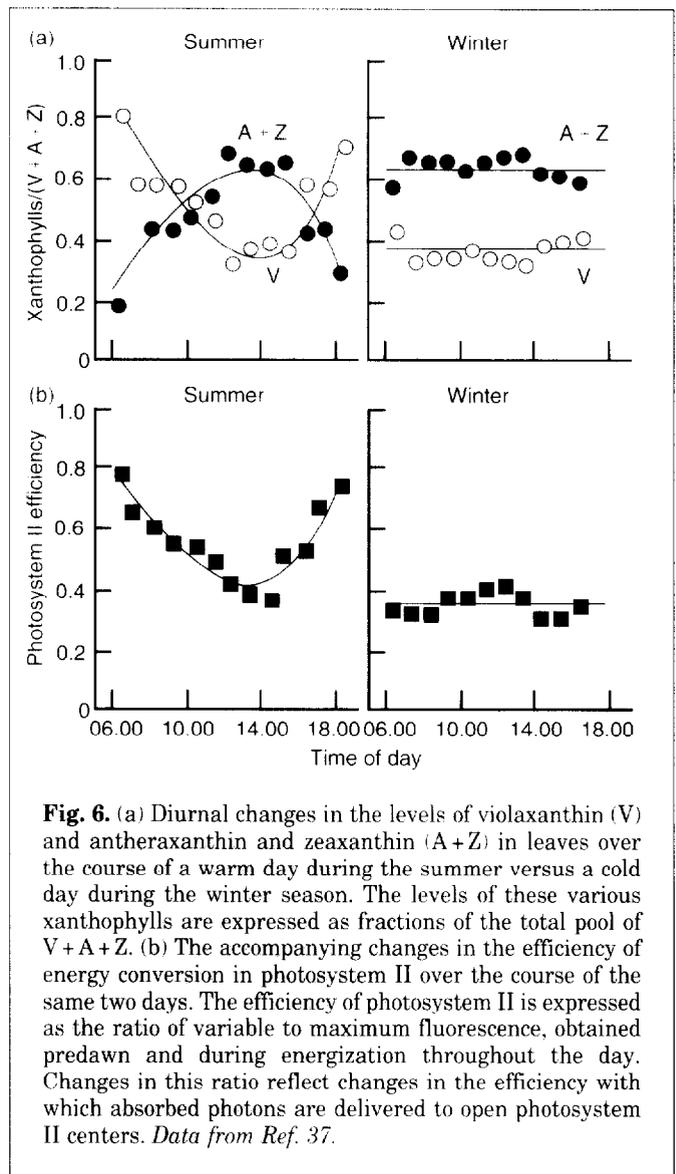


Fig. 6. (a) Diurnal changes in the levels of violaxanthin (V) and antheraxanthin and zeaxanthin (A + Z) in leaves over the course of a warm day during the summer versus a cold day during the winter season. The levels of these various xanthophylls are expressed as fractions of the total pool of V + A + Z. (b) The accompanying changes in the efficiency of energy conversion in photosystem II over the course of the same two days. The efficiency of photosystem II is expressed as the ratio of variable to maximum fluorescence, obtained predawn and during energization throughout the day. Changes in this ratio reflect changes in the efficiency with which absorbed photons are delivered to open photosystem II centers. Data from Ref. 37.

expression of the enzymes of the xanthophyll cycle can improve the stress tolerance of certain species.

Future research directions

In the immediate future, research on the xanthophyll cycle in plants is likely to focus on several important areas:

- The molecular mechanism of xanthophyll cycle-dependent dissipation *in vivo* – does dissipation *in vivo* occur via a direct singlet energy transfer from chlorophyll to zeaxanthin (and antheraxanthin) or is it mediated by zeaxanthin (and antheraxanthin) in a stoichiometric and obligatory but indirect function?
- The mechanism(s) through which zeaxanthin and antheraxanthin can be retained – engaged for energy dissipation – in leaves under environmental stresses.
- The generation of plant lines in which expression of the enzymes of the xanthophyll cycle is suppressed or enhanced, to examine the role of the xanthophyll cycle for the survival and productivity of plants.

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