Plant Physiol. Rep.
https://doi.org/10.1007/s40502-022-00689-2

REVIEW ARTICLE

History of excess-light exposure modulates extent and kinetics of fast-acting non-photochemical energy dissipation

Barbara Demmig-Adams[1] · **Stephanie K. Polutchko**[1] · **Jared J. Stewart**[1] · **William W. Adams III**[1]

Received: 5 August 2022 / Accepted: 22 September 2022

Abstract Many challenging environmental conditions create a scenario where plants must respond to excess excitation energy. This review addresses the role of plant memory for prior excess-light exposure in shaping plant response with an emphasis on photoprotective non-photochemical energy dissipation and on evergreen species that have a particular propensity for this process. A summary of possible causes for variation in this latter process is presented, with attention to (i) genetic differences among photosynthetic organisms, (ii) different growth light environments during the organism's development, and (iii) the immediate exposure history of a leaf. Specific features of non-photochemical energy dissipation subject to such variation are considered, including (i) the maximal extent of non-photochemical energy dissipation (along with the size of the pool of interconvertible xanthophylls violaxanthin, antheraxanthin, and zeaxanthin and the extent of their interconversion over a timeframe of minutes) and (ii) the onset and relaxation kinetics of non-photochemical energy dissipation. This review focuses specifically on the modifiable features of rapidly relaxing, pH-dependent non-photochemical fluorescence quenching (NPQ) and emphasizes the effect of recent light-exposure history on both leaf zeaxanthin content and the onset kinetics of fast-acting NPQ. It is concluded that responses to excess light are a common feature of plant response to a host of environmental challenges not only in sun-exposed, open locations but also when plants are subject to shading by over-hanging canopies, and that the study of plant response to various environmental stresses should thus include attention to excess excitation energy. Studies under controlled conditions should mimic natural light environments and be conducted with plants acclimated to such light conditions.

Keywords Kinetics · Fluctuating light environment · pH-dependent NPQ · Zeaxanthin · Xanthophyll

Abbreviations

A	Antheraxanthin
Chl	Chlorophyll
F	Steady-state fluorescence
F_m	Maximal fluorescence in darkened leaves
F_m'	Maximal fluorescence under actinic light
F_v	Variable fluorescence in darkened leaves
F_v'	Variable fluorescence under actinic light
NPQ	Non-photochemical fluorescence quenching
PFD	Photon flux density
PSII	Photosystem II
V	Violaxanthin
Z	Zeaxanthin
VAZ	Xanthophyll cycle pool (V + A + Z)

Introduction and overview

Many challenging environmental conditions create a scenario where the plant must respond to excess excitation energy (see, e.g., Logan et al., 1999; Demmig-Adams and Adams, 2018). We herein address the role of plant memory for prior excess-light exposure in shaping plant response and discuss implications for the study of plant response to the environment. While light energy fuels photosynthesis, it simultaneously presents a challenge to the operation of photosynthesis. Absorption of more light than can be utilized through the photochemical pathway leads to one or more

✉ Barbara Demmig-Adams
barbara.demmig-adams@colorado.edu

[1] Department of Ecology and Evolutionary Biology, University of Colorado, Boulder, CO 80309, USA

Published online: 21 October 2022

evasive responses (Logan et al., 1999). For example, when excitation energy exceeds the capacity for photosynthesis/photochemical utilization, an alternative, photoprotective pathway is activated that dissipates excess energy non-photochemically as heat (see relevant chapters in Demmig-Adams et al., 2014). This latter process, and its modulation in response to the external light environment, is the topic of this review. When the rate of alternative, non-photochemical dissipation of excitation energy does not increase enough, or does not increase fast enough, excitation transfer to oxygen leads to formation of reactive oxygen species (ROS). These ROS can act as gene regulators that can suppress expression of photosynthetic genes (Foyer, 2018), directly attack photosynthetic and other cell structures, and even trigger programmed cell death (Wagner et al., 2004). While activated, non-photochemical energy dissipation does not simply dispose of unusable energy, but routes a given fraction of excitation energy away from photochemistry – not only under excessive light but also upon return to limiting light levels. For that reason, fast-acting non-photochemical energy dissipation is engaged under excess light and typically disengaged upon return to limiting light (Adams et al., 1999). Fast-acting non-photochemical dissipation is carefully regulated through (1) pH-dependent formation and removal of a xanthophyll-based quencher and (2) a pH-sensing protein that activates non-photochemical dissipation (see chapters in Demmig-Adams et al., 2014). This was demonstrated for the model plant *Arabidopsis thaliana* and the model green alga *Chlamydomonas reinhardtii* by showing that fast-acting non-photochemical energy dissipation was inhibited in mutants deficient in either the pH-sensing protein (Li et al., 2000, 2004) or the pH-controlled enzyme that produces the xanthophyll zeaxanthin (Z) from the corresponding di-epoxide violaxanthin (V) via the mono-epoxide antheraxanthin (A) (Niyogi et al., 1997, 1998).

In this review, we show that variation in non-photochemical energy dissipation can have several causes, including (i) genetic differences among photosynthetic organisms, (ii) growth light environment during the organism's development over days and weeks, and (iii) immediate exposure history over minutes and hours. We also review specific features of non-photochemical energy dissipation that are subject to variation, including (i) the maximal extent of non-photochemical energy dissipation (along with the size of the pool of interconvertible xanthophylls and the extent of their conversion over a few minutes) and (ii) the onset and relaxation kinetics of non-photochemical energy dissipation.

Recently, a simple, elegant mechanistic model was developed to predict how the onset kinetics of non-photochemical energy dissipation (assessed from non-photochemical quenching of chlorophyll fluorescence, NPQ) will vary over a series of light exposures from interaction of only the pH-sensing protein and zeaxanthin in the microalga *Nannochloropsis* (that possesses no lutein and exhibits no state shifts; Short et al., 2022). Different proteins and xanthophylls, with corresponding functions, facilitate non-photochemical energy dissipation in different species and/or genotypes of photosynthetic organisms (see chapters in Demmig-Adams et al., 2014). During rapid fluctuations in the external light environment, these other proteins and xanthophyll cycles are likewise controlled by changes in intra-thylakoid pH as an indicator for whether excitation is limiting or in excess (see chapters in Demmig-Adams et al., 2014).

In addition to these above pH-dependent components, non-photochemical energy dissipation can have pH-independent components that are characterized by gradual onset under excess light and slow reversal under limiting light or darkness. There is a large body of work comparing fast-acting, pH-dependent NPQ with slowly reversible, pH-independent non-photochemical energy dissipation in different species and/or different growth environments (for reviews, see chapters in Demmig-Adams et al., 2014; see also Demmig-Adams & Adams, 2006; Demmig-Adams et al., 2022). Notably, even pH-dependent NPQ can persist for extended periods of time in darkness when temperature is low enough to maintain trans-thylakoid pH gradient in darkness (Gilmore & Björkman, 1994a, 1994b, 1995; Demmig-Adams et al., 1996b; Verhoeven et al., 1998; Demmig-Adams et al., 2006).

However, the present review focuses specifically on modifiable features of rapidly relaxing, pH-dependent NPQ. We highlight adjustments in the maximal capacity of fast-acting NPQ, as driven by growth light environment during plant development over days and weeks, and superimposed adjustments to NPQ onset kinetics driven by recent history of exposure to excess light over time frames from minutes to hours. We discuss that the modifiable kinetic and other features of fast-acting NPQ make it inadvisable to classify NPQ types solely by their kinetics. In acknowledgment of this complexity, we here use a descriptive terminology of "fast-acting, pH-dependent" NPQ, rather than implying an association between NPQ kinetics and particular quenchers (Nilkens et al., 2010). We here emphasize the effect of recent light-exposure history on both leaf zeaxanthin content and on the onset kinetics of fast-acting NPQ. To compare NPQ onset kinetics and extent with leaf carotenoid composition, we present NPQ features alongside concomitant adjustments in xanthophyll cycle (VAZ) pool as well as the fraction of this pool that is converted to Z (or Z + A) over short periods (10–15 min) of exposure to excess light.

We relate these findings to preservation of an excess-light-responsive state of the photochemical system in leaves returned to low light or darkness. Our focus here is on leaf preloading with some zeaxanthin and on an apparent enhanced accessibility of violaxanthin for conversion to

additional zeaxanthin. Specifically, we address leaves' ability for an exceptionally rapid onset of pH-dependent NPQ, as opposed to earlier work focusing on the variable recovery kinetics and the slow return to high photochemical efficiency (and long-term retention of zeaxanthin) under environmental stress that lowers plant growth rate (and limits plant sink activity; Adams et al., 2013, 2014).

Sunflecks in shaded environments provide a much-needed energy boost

Experience of excess light is an extremely common occurrence for photosynthetic organisms in natural settings; excess light is a rather continuous condition in open locations with daylong sunlight exposure as well as a common intermittent condition underneath canopies of vegetation or on days with partial cloud cover. In fact, it's challenging to locate any leaf in natural settings that does not experience excess light at one time or another over the course of every single day (Demmig-Adams et al., 2020). In natural settings, changes in non-photochemical energy dissipation intimately track the patterns of incident light (photon fluence density, PFD), such as often-bell-shaped PFD curves in fully exposed locations over the course of a day, or the rapid PFD fluctuations found in variable light environments (Fig. 1a–d).

Fast-growing plants with high photosynthetic capacity (e.g., herbaceous annual or biennial crops and weeds) are unable to grow in deep shade and typically occur either in open locations, fully sunlight-exposed gaps in forests, or under canopies that allow ample light penetration. In contrast, shade-tolerant species can grow under denser canopies with a more minimal light supply. However, even on the deeply shaded floor of a multi-layered rainforest, where vegetation is remarkably sparse, leaves of rainforest species (e.g., *Alocasia*) occur specifically in locations where they experience at least some shafts of higher light intensity (termed sunflecks) that represent excess light and are associated with rapid increases and decreases in non-photochemical energy dissipation (Logan et al., 1997).

The sought-after supply of sufficient light for photosynthesis, growth, and reproduction in variably shaded environments thus typically includes exposure to excess light (Demmig-Adams et al., 2020). Sunflecks represent both a boost to the plant's carbon budget (Chazdon & Pearcy, 1986, 1991; Pearcy, 1990) and a need for increased photoprotection (Adams et al., 1999). When leaves are occasionally found in the deepest shade without exposure to sunflecks, these leaves are typically older leaves overgrown by other leaves (that provide a high level of shading) or they belong to a vine (example of *Smilax australis,* Table 1), where only some leaves extend into continuous deep shade while another part of the plant is growing in a higher-light environment with better light supply (e.g., Adams et al., 1988). The vine may supplement such deeply shaded leaves with carbon from the leaves that receive more light.

Wide range of growth light environments for the vine *Smilax australis*

Figure 1 depicts diurnal changes in light incident on leaves of the vine *Smilax australis* growing either in unfiltered sunlight (Fig. 1a) or under a eucalypt canopy that allowed passage of many sunflecks of rather high intensity over the course of the day (Fig. 1b). These PFD distribution patterns were mirrored by diurnal changes in the estimated rates of photosystem II (PSII) photochemistry (rate of photochemical utilization of absorbed light, P, through PSII) and of the alternative non-photochemical pathway of energy dissipation as heat (D rate) (Fig. 1c,d). PSII photochemistry rate was estimated from the chlorophyll fluorescence parameter $(F_m' - F)/F_m' \times PFD$, i.e., the fraction of light utilized for photochemistry multiplied by PFD, as described by Genty et al. (1990), and non-photochemical dissipation rate was correspondingly estimated from $(1 - F_v'/F_m') \times PFD$ (for further detail, see Adams et al., 1999; see also Demmig-Adams et al., 1996a).

For leaves experiencing continuous sun exposure, the estimated PSII photochemistry rate increased during midday but much less so than the incident PFD (Fig. 1a,c). As expected, the rate of non-photochemical energy dissipation was low during the morning and afternoon, but much higher over midday (Fig. 1c). Even in fast-growing annual and biennial crops or weeds with very high rates of photosynthesis/photochemistry, only about 40–50% of full sunlight at midday can be used for photosynthesis/photochemistry (Demmig-Adams et al., 1996a).

In the fluctuating light environment, estimated PSII photochemistry rate of *Smilax australis* exhibited modest increases during sunflecks, and decreases during intermittent low-light periods throughout the day (Fig. 1b,d), while the estimated rate of non-photochemical dissipation exhibited corresponding but much more pronounced increases and decreases (Fig. 1d). It should be noted that the few data points for estimated non-photochemical dissipation rate do not fully capture the speed of return to low D rates between sunflecks. Data points taken closer together during a sunfleck and a subsequent low-light period (see just before 14:00 h) suggest that D rate dropped quickly (Fig. 1d). Changes in the photochemical system upon transition from sunfleck to a low post-sunfleck PFD occur rapidly as indicated by more continuous measurements of incident PFD, PSII efficiency $[(F_m' - F)/F_m']$, and NPQ $(F_m/F_m' - 1)$ in another vine (*Stephania japonica*) growing in the same habitat (Adams et al., 1999).

In the open, sun-exposed environment, xanthophyll cycle conversions in *Smilax australis* (Fig. 1e) followed the

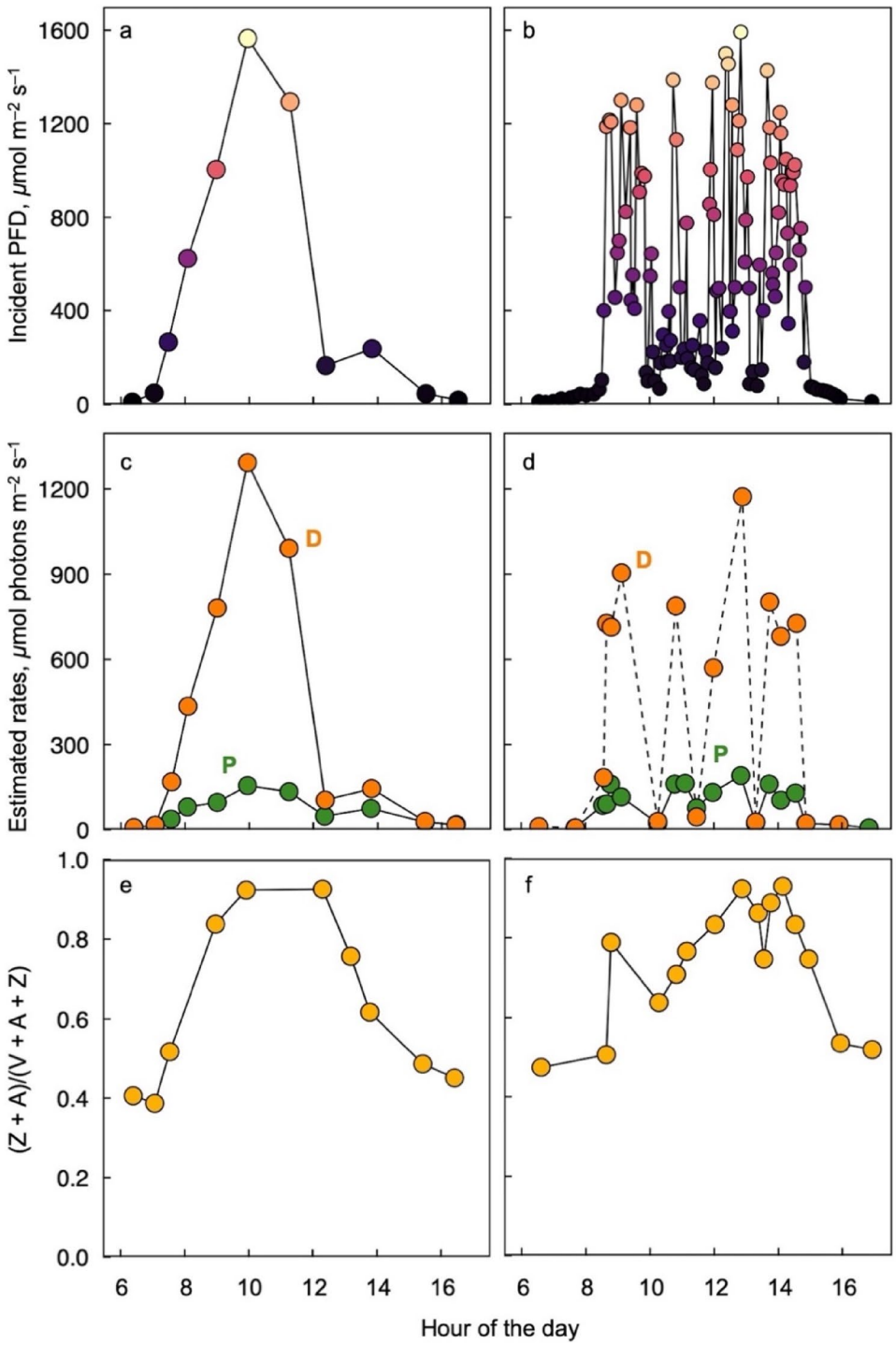

Fig. 1 Diurnal changes in PFD incident on leaves of the evergreen vine *Smilax australis* exposed to full sunlight (**a**) or growing in the understory of a *Eucalyptus* forest (**b**) and associated changes in (**c**,**d**) the estimated flux of photons utilized in photochemistry (P; green symbols) or dissipated as heat (D; orange symbols) and (**e**,**f**) the xanthophyll cycle conversion state. A dashed line is used in (**d**) because changes in D were likely faster than represented by the sampling frequency. Data re-graphed from Adams et al. (1999). A, antheraxanthin; V, violaxanthin; Z, zeaxanthin

general pattern displayed by the rate of non-photochemical dissipation (Fig. 1c). In other words, in the open, sun-exposed environment, incident PFD (Fig. 1a), the estimated rate of non-photochemical energy dissipation (Fig. 1c), and xanthophyll pool (VAZ) conversion state (Fig. 1e) all changed gradually over the course of the day. In contrast, in the environment with multiple sunflecks of high intensity, incident PFD (Fig. 1b) and the estimated rate of non-photochemical energy dissipation (Fig. 1d) changed much more rapidly than VAZ pool conversion state (Fig. 1f). In other words, VAZ pool conversion state did not track the multiple rapid increases and decreases in incident PFD and in the estimated rate of non-photochemical dissipation and instead remained elevated throughout the day (Fig. 1f). These findings are consistent with a particularly important role of the pH-sensing PsbS protein in rapid engagement and

Table 1 Carotenoid content on a chlorophyll (Chl) basis and chlorophyll *a/b* ratio of leaves of the evergreen vine *Smilax australis* leaves growing in deep shade (excess-light-naïve; $n=2$), in the understory below an *Eucalyptus* forest with an open canopy (canopy organization allows sunlit areas; Sunflecks; $n=16$), and in full sunlight ($n=8$ to 11)

Compounds	Deep shade / Excess-light-naïve	Sunflecks	Full sunlight
mmol (V + A + Z) mol^{-1} Chl	42	96 ± 6	140 ± 15
mmol β-carotene mol^{-1} Chl	74	83 ± 7	108 ± 5
mmol lutein mol^{-1} Chl	96	126 ± 7	153 ± 3
mmol neoxanthin mol^{-1} Chl	43	40 ± 2	42 ± 1
mmol α-carotene mol^{-1} Chl	41	12 ± 2	6 ± 1
Chl *a/b*	3.38	3.60 ± 0.09	3.58 ± 0.13

Values represent means for each leaf ± standard deviation where available. Data from Adams et al. (1999). A, antheraxanthin; V, violaxanthin; Z, zeaxanthin

disengagement of non-photochemical energy dissipation in these rapidly fluctuating light environments. Külheim et al. (2002) demonstrated such a role in rapidly fluctuating natural environments, where the PsbS-deficient *npq4* mutant of *Arabidopsis thaliana* exhibited significantly reduced reproductive fitness (reduced seed production), whereas *npq4* exhibited no adverse effects under constant high PFD in controlled conditions (Niyogi et al., 1998).

Moreover, under both continuous unfiltered sun exposure and in the sunfleck-rich environment, the xanthophyll cycle started out with partial conversion to Z + A at predawn and then rose to near 100% conversion either over midday in full-sun exposure or for most of the day in the sunfleck-rich environment (Fig. 1e,f). These findings suggest that presence of pre-existing zeaxanthin speeds up onset of fast-acting NPQ, which may be of particular importance in rapidly fluctuating light environments. Further experimental evidence in support of this interpretation is summarized in the section below on *Recent light-exposure history affects onset kinetics of pH-dependent NPQ.*

Table 1 compares an additional feature of the light environment as well as leaf ascorbate and carotenoid contents for *Smilax australis* plants growing in deep shade without sunflecks (excess-light-naïve leaves) with the leaves growing either in continuous unfiltered sun exposure or with frequent sunflecks (as depicted in Fig. 1). Total daily light supply (mol photons per day) was extremely low in deep shade, much higher in the environment with frequent sunflecks, and further increased by another 28% in continuous unfiltered sun (Table 1). The trends exhibited by the estimated rates of PSII photochemistry and non-photochemical dissipation (Fig. 1c,d) suggest that much of this additional light supply exceeded what the plant was able to use for carbon gain. Similarly, whereas ascorbate levels were non-detectable in deep shade, they were high in the environment with multiple sunflecks and strongly further increased (by another 160%) in continuous full sun (Table 1). Ascorbate plays a dual role in photoprotection against excess light through (i) its role in the xanthophyll cycle as well as (ii) a supporting role in the Mehler process where oxygen acts as an electron acceptor and resulting hydrogen peroxide is detoxified by ascorbate-dependent peroxidase (Grace & Logan, 1996).

Some, but not all, leaf carotenoids occur at greater levels in response to excess light in the growth environment (Logan et al., 1996). The only carotenoid that exhibited decreased levels relative to chlorophyll in response to greater light supply was α-carotene (Table 1), which is consistent with an exclusive role of α-carotene in shade-grown leaves (Demmig-Adams & Adams, 2018; Verhoeven et al., 1999). The carotenoid neoxanthin exhibited no differences in concentration relative to chlorophyll across the entire range of light environments (Table 1). Compared to their levels in excess-light-naïve leaves, the other ubiquitous leaf carotenoids were present at higher levels relative to chlorophyll, with β-carotene exhibiting modestly higher levels (12% & 46%), lutein showing a more pronounced enhancement (31% & 59%), and the xanthophyll cycle pool (VAZ) exhibiting the greatest enhancement (128% & 233%) in environments with multiple sunflecks or continuous unfiltered sun, respectively (Table 1). These trends are consistent with the binding of β-carotene to core antennae, the latter of which comprise a greater fraction of chlorophyll in high-light environments (Krause et al., 2001), as well as roles of β-carotene (see, e.g., Telfer, 2014), lutein (see, e.g., Dall'Osto et al., 2006; Avenson et al., 2008; Esteban & García-Plazaola, 2014; Agostini et al., 2021), and VAZ in photoprotection, with a particular role of the xanthophyll cycle pigments under highly excessive light (see, e.g., Demmig-Adams et al., 2020).

Chlorophyll *a/b* ratio is indicative of the ratio of Chl *b*-containing light-harvesting complexes (Green & Durnford, 1996) to Chl *b*-less core antennae and is inversely related to PSII antenna size as well as typically higher in sun versus shade leaves (Krause et al., 2001; Logan et al., 1996). This ratio was the same in the environments with multiple sunflecks and continuous full sun and was lower only in deep shade (excess-light-naïve leaves; Table 1). In natural settings, PSII antenna size of species able to occupy a wide range of light environments can thus be

the same between continuous full sun exposure versus a fluctuating light environment with sunflecks under a canopy (Adams et al., 1999; see also Schumann et al., 2017). Substantial amounts of excess light in the latter light environments can apparently be addressed to a large extent by non-photochemical energy dissipation. Maintenance of a relatively high PSII antenna size paired with a high capacity for rapidly modulated non-photochemical energy dissipation presumably allows leaves under a canopy to optimize both carbon gain and photoprotection during continuous rapid alternation between limiting and excess light.

Response to growth light environment typical for evergreen plant species

Plant species vary in how strongly their maximal capacity for fast-acting, pH-dependent NPQ responds to growth light intensity. Figure 2 illustrates that a long-lived, slow-growing evergreen (example of *Monstera deliciosa*; Fig. 2a,c,e), capable of growing in deep shade as well as in full sunlight, had a limited ability to increase its maximal photosynthetic capacity (Fig. 2a) and thus a limited associated capacity for utilization of excitation energy through the photochemical pathway. Conversely, this evergreen species exhibited tremendous variation in the capacity for alternative removal of excitation via pH-dependent non-photochemical dissipation (assessed as NPQ capacity; Fig. 2c) as well as in the accumulation of the de-epoxidized components (zeaxanthin and antheraxanthin; Fig. 2e) of the xanthophyll cycle.

In contrast to rapidly growing, short-lived species (example spinach; Fig. 2b,d,f), shade-tolerant evergreen species like *Monstera deliciosa* are able to slow their metabolism enough to meet their energy demands and thrive in deep shade with extremely limited energy supply. However, because such species do not increase their photosynthetic capacity with increasing growth light supply as much as annual species (Fig. 2a,b), they instead increase the capacity for non-photochemical energy dissipation and production of the de-epoxidized components of the xanthophyll cycle between intermediate and high light supply (Fig. 2c,e).

In other words, evergreen species do not channel increasing light supply into increasing additional productivity as much as annual species. Conversely, modulation of the capacity for non-photochemical energy dissipation plays a particularly prominent role in slow-growing species when these develop under conditions of highly excessive light (Logan et al., 1998; Demmig-Adams et al., 2006). The pronounced upregulation of the pool size of xanthophyll cycle pigments (here VAZ) in this scenario can be considered part of plant memory for prior excess-light exposure. To test for adjustments in maximal capacity for non-photochemical energy dissipation, plants should be grown under PFDs that cover the entire range of PFDs tolerated by a given species,

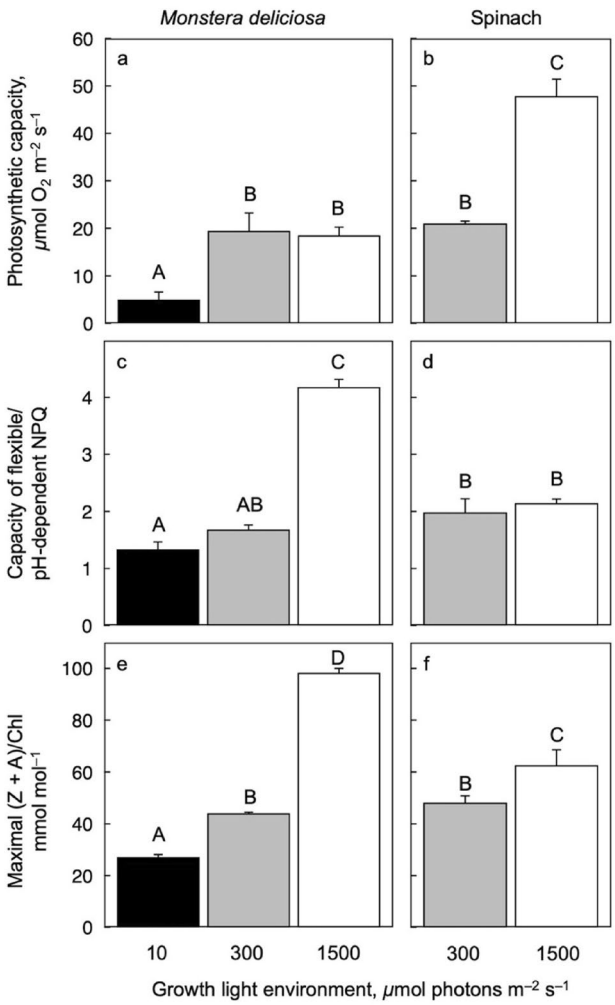

Fig. 2 Effect of growth light environment (PFD) on light- and CO_2-saturated photosynthetic capacity (**a**,**b**), the maximal capacity of pH-dependent NPQ (**c**,**d**), and maximal zeaxanthin (Z) and antheraxanthin (A) level relative to chlorophyll (Chl; **e**,**f**) in the slow-growing evergreen species *Monstera deliciosa* (**a**,**c**,**e**) as compared to the fast growing annual spinach (**b**,**d**,**f**). Significant differences among means are indicated by different upper-case letters ($n=3$; $p<0.01$). Data re-graphed from Demmig-Adams et al., (2006a, 2006b). The capacity of pH-dependent NPQ was determined as the fraction of NPQ after rapid vacuum-infiltration of leaves with the uncoupler nigericin in 0.01% TWEEN during continuous exposure to highly excessive light (for details, see methods in Demmig-Adams et al., 2006a, 2006b). The maximal capacity of photosynthetic electron transport was determined as is customary from the light- and CO_2-saturated rate of oxygen evolution. Maximal NPQ capacity was determined as is customary under conditions (an atmosphere of 2% O_2, 0% CO_2) that allow full development of the trans-thylakoid pH required for NPQ induction but only a minimal rate of photochemical energy dissipation in all leaves (despite different electron transport capacities in different species)

and it should be noted whether a given species responds more like spinach or more like *M. deliciosa*.

Recent light-exposure history affects onset kinetics of pH-dependent NPQ

In addition to adjustments in the maximal capacity of fast-acting NPQ in response to growth PFD, both sun-grown and deep-shade-grown, excess-light-naïve plants accelerate the onset kinetics of fast-acting NPQ upon repeat exposure to experimental excess light as shown here for the example of the evergreen groundcover *Vinca minor* grown either outdoors in full sunlight (Fig. 3a) or in deep shade (Fig. 3b). Overall, Fig. 3 shows that sun-grown leaves of *Vinca minor* had a greater capacity for fast-onset NPQ than shade-grown leaves and that both sets of leaves exhibited much slower

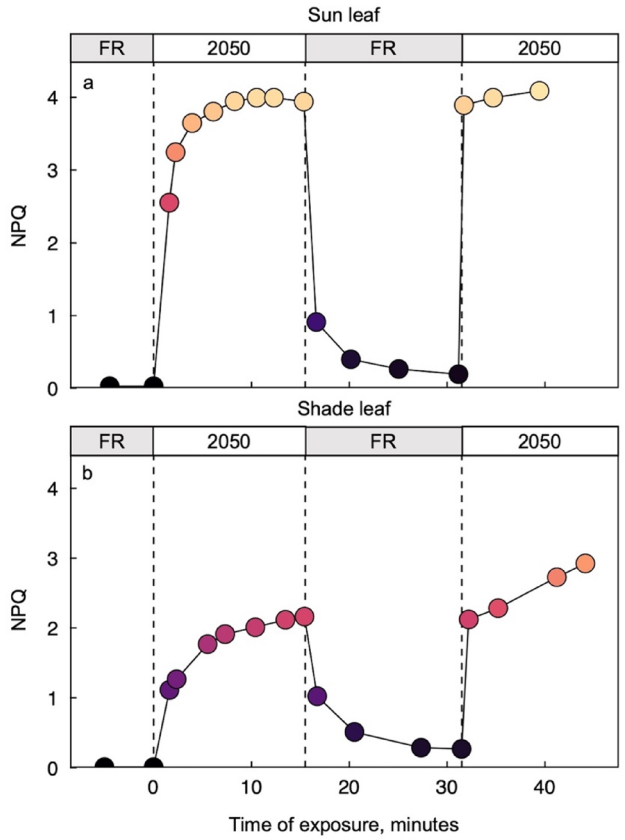

Fig. 3 Time course of NPQ development in leaves of the evergreen groundcover *Vinca minor* grown in either full sun (**a**) or deep shade (**b**) upon experimental exposure to high PFD (2,050 µmol m^{-2} s^{-1}). Leaves were collected from their outside growth environment predawn. Measurements were conducted on leaf discs kept under a stream of humidified air in a measurement chamber; prior to the first high-light exposure, leaf discs were kept in darkness with a very low level of far-red (FR) light for 15 min. This was followed by a first exposure to high light for 15 min, a subsequent dark period (with FR) of another 15 min, and a second exposure to high light for 15 min. Re-graphed from Demmig-Adams (1998)

onset of NPQ during a first exposure to excess (very high) light after an extended dark period compared to subsequent exposures to excess light (Demmig-Adams, 1998). A similar response to repeated experimental exposure to excess light had been reported previously, with a less rapid onset of fast-acting NPQ in zeaxanthin-free leaves (Fig. 4a) and a much faster onset of fast-acting NPQ in zeaxanthin-preloaded leaves (Fig. 4b) in a subsequent exposure (Demmig-Adams et al., 1989).

Similar responses to repeated exposure to excess light as those reported for leaves (Figs. 3,4) were also reported for the alga *Nannochloropsis* (Short et al., 2022). As in plants, subsequent exposures to excess light led to faster onset of NPQ than the first exposure after an extended dark period. The above-mentioned model put forth by these authors (Short et al., 2022), based on interaction of a pH-responding protein and a pH-controlled xanthophyll (zeaxanthin), was able to predict this variability in the onset kinetics of NPQ. These findings further indicate that pH-dependent NPQ, involving the same protein and xanthophyll, can have variable kinetics. Conversely, different NPQ onset kinetics per se do not mean that different molecular players must be involved. Rather, these findings indicate that the most rapid onset of pH-dependent NPQ requires a state of the photochemical system that maintains a memory of excess-light exposure, which here includes a retention of some zeaxanthin resulting in leaves preloaded with zeaxanthin prior to another exposure to excess light (see also Matuszyńska et al., 2016).

Yet another feature that characterizes the photochemical system's readiness for dealing with highly excessive light is the extent to which the available VAZ pool can be converted to its de-epoxidized forms (zeaxanthin and antheraxanthin) over a time frame of 10 to 15 min. Excess-light-naïve leaves of *Vinca minor* grown in deep shade converted merely 34% of their smaller VAZ pools (28 mmol V + A + Z per mol Chl) to zeaxanthin (or a corresponding 44% to zeaxanthin + antheraxanthin) compared to sun-grown leaves that converted 66% of their larger pools (100 mmol V + A + Z per mol Chl) to zeaxanthin (or a corresponding 81% to zeaxanthin + antheraxanthin) over 10 to 15 min of experimental exposure to very high light (Demmig-Adams, 1998). Similar differences were seen in other species (Demmig-Adams, 1998). These findings suggest that deep-shade-grown leaves without a history of daily excess-light exposure do not have the organization of the photochemical system necessary to reach full conversion of their VAZ pools. This may mean that violaxanthin and/or violaxanthin de-epoxidase in excess-light-naïve leaves are not in the correct position to support rapid VAZ pool conversion and engagement of the resulting epoxidized forms in non-photochemical dissipation. Such a limitation likely involves various aspects of thylakoid organization (see, e.g., Szilágyi et al., 2007;

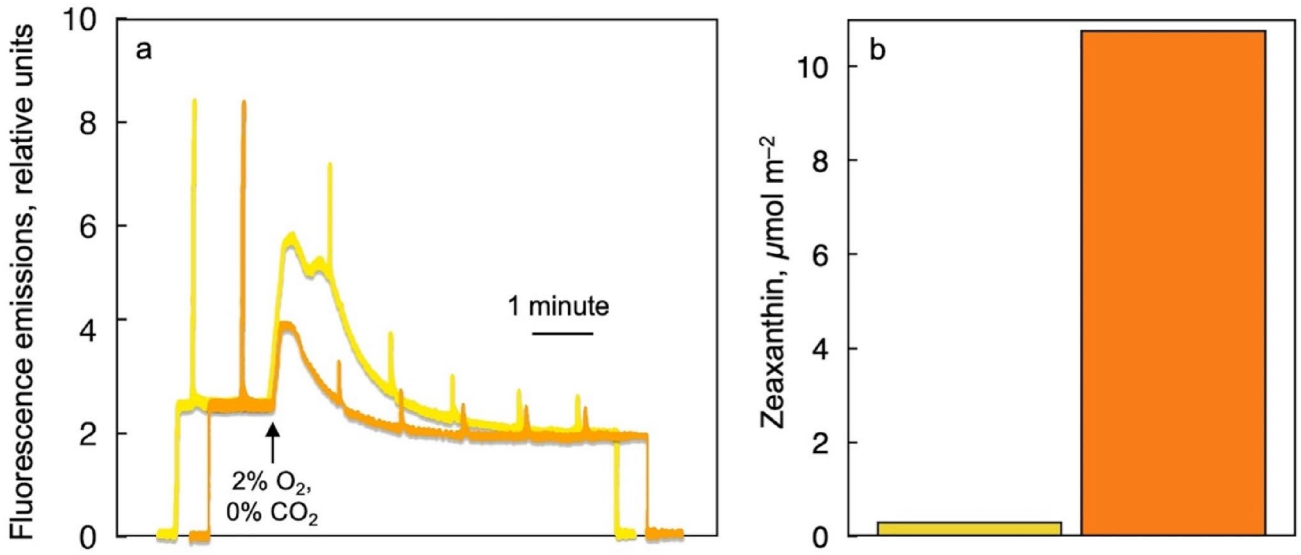

Fig. 4 (**a**) Time course of changes in chlorophyll fluorescence recorded from leaf discs of the evergreen vine *Hedera helix* maintained in a measuring chamber under a low light level of 100 µmol photons m^{-2} s^{-1} in humidified air and suddenly switched to a stream of humidified 2% O_2 and 0% CO_2 (making even the low PFD highly excessive) in a first treatment (yellow line), followed by return to air for 60 min and a subsequent second excessive-light exposure in 2% O_2 and 0% CO_2, and (**b**) corresponding zeaxanthin content of leaves determined immediately prior to the first and second treatments, respectively. Data re-graphed from Demmig-Adams et al. (1989)

Kirchhoff, 2014). The xanthophyll features described above, i.e., VAZ pool size, the fraction of this pool available for de-epoxidation over a timeframe of minutes, and retention of its de-epoxidized forms, can all be considered part of plant memory for excess-light exposure. In other words, plant memory for excess light apparently involves maintenance of a thylakoid organization with a large VAZ pool fully accessible to conversion (or remaining partly converted) for some time upon return to low light or darkness following an exposure to excess light.

Growth light environment modulates multiple molecular players that respond to excess light

Antioxidant metabolites and antioxidant enzymes

Vinca major plants growing in controlled environments under 12-h photoperiods of either 20, 100, or 1200 µmol photons m^{-2} s^{-1} exhibited increasing levels of NPQ (0.08 ± 0.39, 0.28 ± 0.05, 0.84 ± 0.08, respectively) with increasing growth PFD (Grace & Logan, 1996), consistent with the greater NPQ capacities of plants grown in natural settings with different light supply (Fig. 3). Furthermore, both VAZ pool size (Fig. 5a) and conversion state, (Z + A)/(V + A + Z), exhibited concomitant increases (from 0 ± 0 to 0.07 ± 0.02 and 0.58 ± 0.05 for the conversion state under 20, 100, and 1200 µmol photons m^{-2} s^{-1}, respectively; Grace & Logan, 1996). Both 20 and 100 µmol photons m^{-2} s^{-1} can be assumed to represent non-excessive light, with the possible caveat that onset of 100 µmol photons m^{-2} s^{-1} after a 12-h dark period could represent a brief transition period where absorbed light may not be fully utilized.

Moreover, acclimatory adjustments, especially in the leaves grown under 1200 µmol photons m^{-2} s^{-1}, were also seen in other photoprotective systems, such as antioxidant metabolites (here, ascorbate and glutathione; Fig. 5b,c) and antioxidant enzymes (here, ascorbate peroxidase, glutathione reductase, and superoxide dismutase; Fig. 5d,e,f) that are concentrated in the chloroplasts of leaves but are also found in other compartments. This finding is relevant here because it indicates that numerous systems are adjusted in concert in response to growth PFD.

Thylakoid organization and composition

The findings summarized here concerning modulation of non-photochemical energy dissipation suggest that the same xanthophyll quenchers can interact with a host of molecular modulators in causing pronounced variation in kinetics and extent of xanthophyll cycle conversion state as well as non-photochemical dissipation activity (see also Demmig-Adams et al., 2012, 2020; Adams et al., 2013; Demmig-Adams & Adams, 2018).

Plant memory of excess-light exposure under pronounced environmental stress can involve components of non-photochemical energy dissipation with slow kinetics of onset and relaxation and typically includes lasting preservation of the VAZ pool in a highly converted (de-epoxidized) state

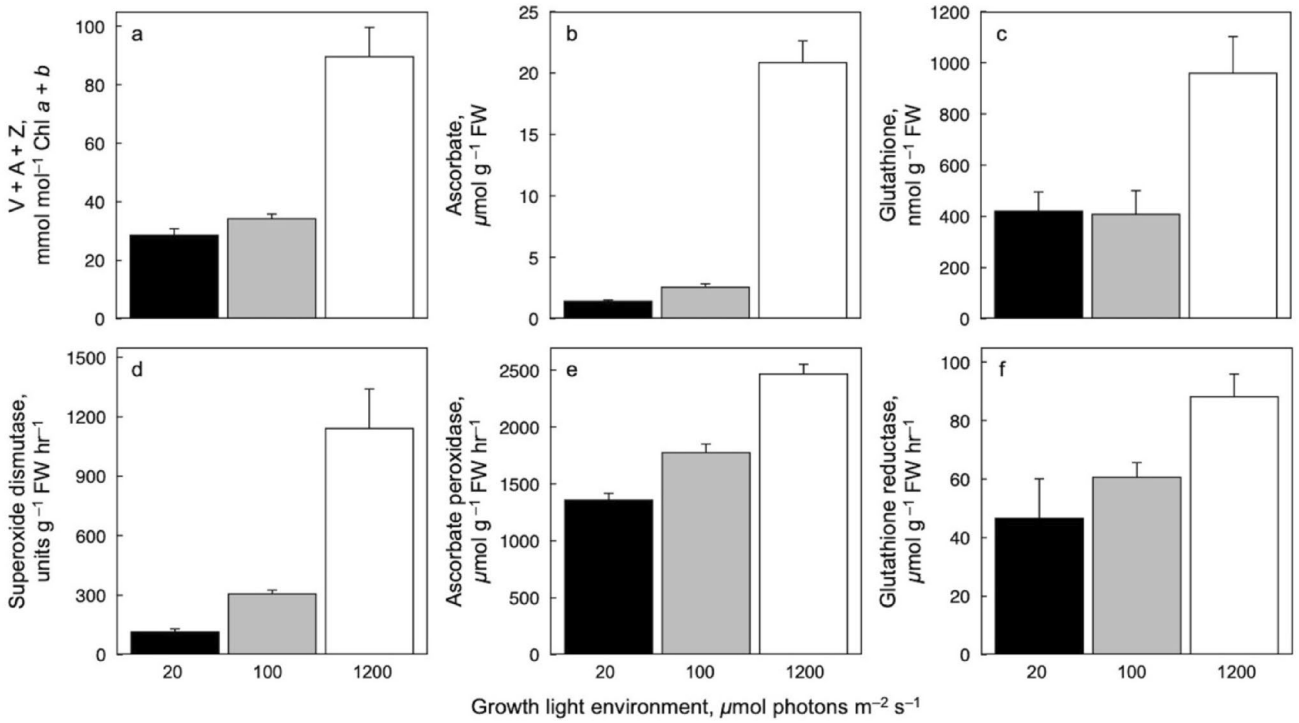

Fig. 5 Foliar levels of (**a**) the xanthophyll cycle pool, (**b**) ascorbate, and (**c**) glutathione as well as enzyme activities of (**d**) superoxide dismutase, (**e**) ascorbate peroxidase, and (**f**) glutathione reductase in leaves of the evergreen groundcover *Vinca major* grown under 20, 100, and 1200 μmol photons m^{-2} s^{-1}; $n = 3$ leaves; FW, fresh weight. Data from Grace and Logan (1996). No statistical analyses were provided in the latter report. A, antheraxanthin; V, violaxanthin; Z, zeaxanthin; FW, fresh weight; hr, hour

(Adams et al., 1995, 2006; Kress & Jahns, 2017; Demmig-Adams et al., 2020; see also Ruban & Johnson, 2010; Jahns & Holzwarth, 2012). However, we here emphasize preservation of an elevated de-epoxidation state in darkness *without* appreciable depression of PSII photochemical efficiency. Such preservation ranges from retention of small pool fractions in the de-epoxidized state in fluctuating or open environments (Demmig-Adams et al., 2020) to retention of high fractions in environments with additional environmental stress (Barker et al., 2002). As documented above (Figs. 3,4), leaves preloaded with zeaxanthin in initial experimental exposure to excess light exhibit an accelerated onset of fast-acting NPQ during a subsequent exposure. Plant memory evidently also supports fast-acting NPQ in variable natural light environments, with sunflecks (Fig. 1) that may seem irregular when observed on any given day but do repeat themselves predictably from day to day under the same canopy and with the same arc of the sun across the sky (Adams et al., 1999). Larger shifts in the sunfleck pattern under a given canopy typically occur only as the sun's path changes during the year, as the canopy drops leaves, or as the result of an occasional permanent break in the canopy.

Growth light intensity and dynamics affect various aspects of thylakoid organization, including localization, conformation, and composition of thylakoid proteins and pigments, and involve pH-, redox-, and phosphorylation-related events (see, e.g., Kirchhoff, 2014; Suorsa et al., 2015; Schumann et al., 2017; Kim et al., 2019; Hommel et al., 2022). The memory of excess-light exposure presumably involves some, or all, of these same factors. The following paragraphs describe concomitant modulation of concentration and/or activity of (i) the zeaxanthin-removing xanthophyll cycle enzyme zeaxanthin epoxidase and (ii) the photosystem II core protein D1 and examples for associated events.

Plant memory of excess-light exposure causes preservation of an excess-light-responsive state of the photochemical system upon return to low light or darkness that can last either for minutes, overnight, or even longer. Whereas the focus of this review is on plant memory for excess light without the concomitant presence of other environmental stresses, such as unfavorable temperature and/or drought (see, e.g., Demmig-Adams et al., 1988; Barker et al., 2002; Demmig-Adams & Adams, 2006; Putzler et al., 2022), the latter factors induce particularly pronounced alterations that persist upon return to low light or darkness. For example, correlations between zeaxanthin retention and modulation of the PSII core protein D1 and the zeaxanthin-removing enzyme (zeaxanthin epoxidase) of the VAZ cycle have been noted. Long-term retention of de-epoxidized xanthophylls

was associated with concomitant degradation of both zeaxanthin epoxidase and D1 (Bethmann et al., 2019). A shorter-term, reversible inactivation of zeaxanthin epoxidase was associated with sustained D1 phosphorylation (Hoang et al., 2020). Comparable phenomena have been reported for extended excess-light exposure either after transfer of deep-shade-grown, excess-light-naïve plants to high light or by overwintering conifers during winter. A multi-day exposure of deep-shade-grown *Monstera deliciosa* to highly excessive light induced waves of intensifying zeaxanthin retention. This started with retention of some zeaxanthin and prolonged D1 phosphorylation (without D1 degradation) throughout the first night and was followed by a further increase in nocturnally retained zeaxanthin and strong D1 degradation after additional days of exposure to highly excessive light (Demmig-Adams et al., 2006). Similarly, moderate nocturnal zeaxanthin retention was associated with nocturnally sustained D1 phosphorylation (without D1 degradation) in conifers overwintering at a moderately high elevation of 1730 m (Ebbert et al., 2005), whereas strong D1 degradation associated with more pronounced nocturnal zeaxanthin retention occurred in conifers overwintering at extreme elevations of 2930 m (Zarter et al., 2006). Modulation of D1 phosphorylation and turnover as well as modulation of zeaxanthin epoxidase activity and turnover thus also appear to be part of the suite of mechanisms involved in plant memory for excess-light exposure.

Summary and conclusions (with an emphasis on evergreen species)

- Excess-light-naïve leaves take longer to adopt the excess-light-responsive state of the photochemical system and have limited readiness to convert the VAZ pool to zeaxanthin.
- The kinetics of fast-acting, pH-dependent NPQ are variable and respond to the leaf's memory of excess-light exposure.
- Over short time frames, this memory includes residual zeaxanthin, and possible associated changes, and further speeds up the onset of fast-acting NPQ.
- Both sun-grown and deep-shade-grown (excess-light-naïve) leaves exhibit such a memory of recent excess-light exposure with faster onset kinetics of fast-acting NPQ in zeaxanthin-preloaded leaves.
- Multiple features of the xanthophyll cycle (here VAZ), including pool size, degree of rapidly attainable de-epoxidation, and retention of de-epoxidized forms for various times in darkness, form part of plant memory for prior excess-light exposure.
- NPQ kinetics are not suitable to attribute different components of non-photochemical energy dissipation to different quenchers, but likely indicate involvement of different modulators of quencher concentration, localization, and action. A range of characterizations, beyond onset and relaxation kinetics, is needed to help assess underlying mechanisms of non-photochemical energy dissipation.
- Plant life form impacts the maximal capacity for non-photochemical energy dissipation. In response to increasing growth light supply up to full sunlight, slow-growing evergreens exhibit limited increases in maximal photosynthetic capacity paired with dramatic increases in maximal NPQ capacity.
- Growth of study plants in well-defined light environments, including those that mimic specific natural light environments, should be helpful in future studies of the dynamics of non-photochemical energy dissipation, including NPQ kinetics and capacity. Conversely, growth of plants under continuous non-excessive light, which prevents acclimation processes, is unlikely to reveal the full range of possible non-photochemical energy dissipation responses.

Broader implications

Responses to excess light are a common feature of plant response to a host of environmental challenges, and not only in sun-exposed, open locations but also when plants are subject to shading by over-hanging canopies. The study of plant response to various environmental stresses should thus include attention to excess excitation energy. Any studies under controlled conditions should mimic natural light environments and be conducted with plants acclimated to such light conditions.

Acknowledgements This work was supported by the University of Colorado and the National Science Foundation (IOS-1907338).

Author contributions B.D.-A. and W.W.A. conceived the manuscript. B.D.-A. wrote the manuscript with contributions from W.W.A., S.K.P., and J.J.S. Figures were envisioned by B.D.-A. and rendered by S.K.P. and J.J.S. with input from W.W.A. All authors read and approved the final manuscript.

Declarations

Conflict of interest The authors declare no conflict of interest.

References

Adams, W. W., III, Zarter, C. R., Mueh, K. E., Amiard, V., & Demmig-Adams, B. (2006). Energy dissipation and photoinhibition: A continuum of photoprotection. In B. Demmig-Adams, W. W. Adams III, & A. K. Mattoo (Eds.), *Photoprotection, Photoinhibition,*

Gene Regulation, and Environment (pp. 49–64). Springer. https://doi.org/10.1007/1-4020-3579-9_5

Adams, W. W., III, Muller, O., Cohu, C. M., & Demmig-Adams, B. (2014). Photosystem II efficiency and non-photochemical fluorescence quenching in the context of source-sink balance. In B. Demmig-Adams, G. Garab, W. W. Adams III, & Govindjee (Eds.), *Non-Photochemical Quenching and Energy Dissipation in Plants, Algae and Cyanobacteria* (pp. 503–529). Springer. https://doi.org/10.1007/978-94-017-9032-1_23

Adams, W. W., III., Demmig-Adams, B., Logan, B. A., Barker, D. H., & Osmond, C. B. (1999). Rapid changes in xanthophyll cycle-dependent energy dissipation and photosystem II efficiency in two vines, *Stephania japonica* and *Smilax australis*, growing in the understory of an open *Eucalyptus* forest. *Plant, Cell & Environment, 22*(2), 125–136. https://doi.org/10.1046/j.1365-3040.1999.00369.x

Adams, W. W., III., Demmig-Adams, B., Verhoeven, A., & Barker, D. (1995). 'Photoinhibition' during winter stress: Involvement of sustained xanthophyll cycle-dependent energy dissipation. *Functional Plant Biology, 22*(2), 261. https://doi.org/10.1071/PP9950261

Adams, W. W., III., Muller, O., Cohu, C. M., & Demmig-Adams, B. (2013). May photoinhibition be a consequence, rather than a cause, of limited plant productivity? *Photosynthesis Research, 117*(1), 31–44. https://doi.org/10.1007/s11120-013-9849-7

Adams, W. W., III., Terashima, I., Brugnoli, E., & Demmig, B. (1988). Comparisons of photosynthesis and photoinhibition in the CAM vine *Hoya australis* and several C3 vines growing on the coast of eastern Australia. *Plant, Cell & Environment, 11*(3), 173–181. https://doi.org/10.1111/j.1365-3040.1988.tb01134.x

Agostini, A., Nicol, L., Da Roit, N., Bortolus, M., Croce, R., & Carbonera, D. (2021). Altering the exciton landscape by removal of specific chlorophylls in monomeric LHCII provides information on the sites of triplet formation and quenching by means of ODMR and EPR spectroscopies. *Biochimica Et Biophysica Acta (BBA) Bioenergetics, 1862*, 148481. https://doi.org/10.1016/j.bbabio.2021.148481

Avenson, T. J., Ahn, T. K., Niyogi, K. K., Ballottari, M., Bassi, R., & Fleming, G. R. (2008). Lutein can act as a switchable charge transfer quencher in the CP26 light-harvesting complex. *Journal of Biological Chemistry, 284*(5), 2830–2835. https://doi.org/10.1074/jbc.M807192200

Barker, D. H., Adams, W. W., III., Demmig-Adams, B., Logan, B. A., Verhoeven, A. S., & Smith, S. D. (2002). Nocturnally retained zeaxanthin does not remain engaged in a state primed for energy dissipation during the summer in two Yucca species growing in the Mojave Desert. *Plant, Cell & Environment, 25*(1), 95–103. https://doi.org/10.1046/j.0016-8025.2001.00803.x

Bethmann, S., Melzer, M., Schwarz, N., & Jahns, P. (2019). The zeaxanthin epoxidase is degraded along with the D1 protein during photoinhibition of photosystem II. *Plant Direct, 3*(11), e00185. https://doi.org/10.1002/pld3.185

Chazdon, R. L., & Pearcy, R. W. (1986). Photosynthetic responses to light variation in rainforest species. *Oecologia, 69*(4), 524–531. https://doi.org/10.1007/BF00410358

Chazdon, R. L., & Pearcy, R. W. (1991). The importance of sunflecks for forest understory plants. *BioScience, 41*(11), 760–766. https://doi.org/10.2307/1311725

Dall'Osto, L., Lico, C., Alric, J., Giuliano, G., Havaux, M., & Bassi, R. (2006). Lutein is needed for efficient chlorophyll triplet quenching in the major LHCII antenna complex of higher plants and effective photoprotection *in vivo* under strong light. *BMC Plant Biology, 6*(1), 1–32. https://doi.org/10.1186/1471-2229-6-32

Demmig, B., Winter, K., Krüger, A., & Czygan, F.-C. (1988). Zeaxanthin and the heat dissipation of excess light energy in *Nerium oleander* exposed to a combination of high light and water stress. *Plant Physiology, 87*(1), 17–24. https://doi.org/10.1104/pp.87.1.17

Demmig-Adams, B., Garab, G., Adams, W. W., III, & Govindjee (2014). *Non-Photochemical Quenching and Thermal Energy Dissipation in Plants, Algae and Cyanobacteria. Advances in Photosynthesis and Respiration*. Springer. https://doi.org/10.1007/978-94-017-9032-1

Demmig-Adams, B. (1998). Survey of thermal energy dissipation and pigment composition in sun and shade leaves. *Plant & Cell Physiology, 39*(5), 474–482. https://doi.org/10.1093/oxfordjournals.pcp.a029394

Demmig-Adams, B., & Adams, W. W., III. (1996a). Chlorophyll and carotenoid composition in leaves of *Euonymus kiautschovicus* acclimated to different degrees of light stress in the field. *Functional Plant Biology, 23*(5), 649–659. https://doi.org/10.1071/PP9960649

Demmig-Adams, B., & Adams, W. W., III. (2006a). Photoprotection in an ecological context: The remarkable complexity of thermal energy dissipation. *New Phytologist, 172*(1), 11–21. https://doi.org/10.1111/j.1469-8137.2006.01835.x

Demmig-Adams, B., & Adams, W. W., III. (2018). An integrative approach to photoinhibition and photoprotection of photosynthesis. *Environmental and Experimental Botany, 154*, 1–3. https://doi.org/10.1016/j.envexpbot.2018.05.006

Demmig-Adams, B., Adams, W. W., III., Barker, D. H., Logan, B. A., Bowling, D. R., & Verhoeven, A. S. (1996b). Using chlorophyll fluorescence to assess the fraction of absorbed light allocated to thermal dissipation of excess excitation. *Physiologia Plantarum, 98*(2), 253–264. https://doi.org/10.1034/j.1399-3054.1996.980206.x

Demmig-Adams, B., Cohu, C. M., Muller, O., & Adams, W. W., III. (2012). Modulation of photosynthetic energy conversion efficiency in nature: From seconds to seasons. *Photosynthesis Research, 113*(1–3), 75–88. https://doi.org/10.1007/s11120-012-9761-6

Demmig-Adams, B., Ebbert, V., Mellman, D. L., Mueh, K. E., Schaffer, L., Funk, C., Zarter, C. R., Adamska, I., Jansson, S., & Adams, W. W., III. (2006b). Modulation of PsbS and flexible vs sustained energy dissipation by light environment in different species. *Physiologia Plantarum, 127*(4), 670–680. https://doi.org/10.1111/j.1399-3054.2006.00698.x

Demmig-Adams, B., Gilmore, A. M., & Adams, W. W., III. (1996c). In vivo functions of carotenoids in higher plants. *The FASEB Journal, 10*(4), 403–412. https://doi.org/10.1096/fasebj.10.4.8647339

Demmig-Adams, B., Polutchko, S. K., & Adams, W. W., III. (2022). Structure-function-environment relationship of the isomers zeaxanthin and lutein. *Photochem, 2*(2), 308–325. https://doi.org/10.3390/photochem2020022

Demmig-Adams, B., Stewart, J. J., López-Pozo, M., Polutchko, S. K., & Adams, W. W., III. (2020). Zeaxanthin, a molecule for photoprotection in many different environments. *Molecules, 25*(24), 5825. https://doi.org/10.3390/molecules25245825

Demmig-Adams, B., Winter, K., Krüger, A., & Czygan, F.-C. (1989). Zeaxanthin and the induction and relaxation kinetics of the dissipation of excess excitation energy in leaves in 2% O_2, 0% CO_2. *Plant Physiology, 90*(3), 887–893. https://doi.org/10.1104/pp.90.3.887

DemmigAdamsAdams, B. W. W., III. (1992). Photoprotection and other responses of plants to high light stress. *Annual Review of Plant Physiology and Plant Molecular Biology, 43*(1), 599–626.

Ebbert, V., Adams, W. W., III., Mattoo, A. K., Sokolenko, A., & Demmig-Adams, B. (2005). Up-regulation of a photosystem II core protein phosphatase inhibitor and sustained D1 phosphorylation in zeaxanthin-retaining, photoinhibited needles of overwintering Douglas fir. *Plant, Cell & Environment, 28*(2), 232–240. https://doi.org/10.1111/j.1365-3040.2004.01267.x

Esteban, R., & García-Plazaola, J. I. (2014). Involvement of a second xanthophyll cycle in non-photochemical quenching of chlorophyll fluorescence: the lutein epoxide story. In B. Demmig-Adams, G. Garab, W. W. Adams III, & Govindjee (Eds.), *Non-Photochemical Quenching and Energy Dissipation in Plants, Algae and Cyanobacteria* (pp. 277–295). Springer. https://doi.org/10.1007/978-94-017-9032-1_12

Foyer, C. H. (2018). Reactive oxygen species, oxidative signaling and the regulation of photosynthesis. *Environmental and Experimental Botany, 154*, 134–142. https://doi.org/10.1016/j.envexpbot.2018.05.003

Genty, B., Harbinson, J., Briantais, J.-M., & Baker, N. R. (1990). The relationship between non-photochemical quenching of chlorophyll fluorescence and the rate of photosystem 2 photochemistry in leaves. *Photosynthesis Research, 25*(3), 249–257. https://doi.org/10.1007/BF00033166

Gilmore, A. M., & Björkman, O. (1994a). Adenine nucleotides and the xanthophyll cycle in leaves: I. Effects of CO_2- and temperature-limited photosynthesis on adenylate energy charge and violaxanthin de-epoxidation. *Planta*, *192*(4), 526–536. https://doi.org/10.1007/BF00203591

Gilmore, A. M., & Björkman, O. (1994b). Adenine nucleotides and the xanthophyll cycle in leaves: II. Comparison of the effects of CO2- and temperature-limited photosynthesis on photosystem II fluorescence quenching, the adenylate energy charge and violaxanthin de-epoxidation in cotton. *Planta, 192*(4), 537–544. https://doi.org/10.1007/BF00203592

Gilmore, A. M., & Björkman, O. (1995). Temperature-sensitive coupling and uncoupling of ATPase-mediated, nonradiative energy dissipation: Similarities between chloroplasts and leaves. *Planta, 197*(4), 646–654. https://doi.org/10.1007/BF00191573

Grace, S. C., & Logan, B. A. (1996). Acclimation of foliar antioxidant systems to growth irradiance in three broad-leaved evergreen species. *Plant Physiology, 112*(4), 1631–1640.

Green, B. R., & Durnford, D. G. (1996). The chlorophyll-carotenoid proteins of oxygenic photosynthesis. *Annual Review of Plant Biology, 47*(1), 685–714. https://doi.org/10.1104/pp.112.4.1631

Hoang, M. H., Kim, H.-S., Zulfugarov, I. S., & Lee, C.-H. (2020). Down-regulation of zeaxanthin epoxidation in vascular plant leaves under normal and photooxidative stress conditions. *Journal of Plant Biology, 63*(5), 331–336. https://doi.org/10.1007/s12374-020-09260-8

Hommel, E., Liebers, M., Offermann, S., & Pfannschmidt, T. (2022). Effectiveness of light-quality and dark-white growth light shifts in short-term light acclimation of photosynthesis in *Arabidopsis*. *Frontiers in Plant Science, 12*, 615253. https://doi.org/10.3389/fpls.2021.615253

Jahns, P., & Holzwarth, A. R. (2012). The role of the xanthophyll cycle and of lutein in photoprotection of photosystem II. *Biochimica Et Biophysica Acta (BBA)-Bioenergetics, 1817*(1), 182–193. https://doi.org/10.1016/j.bbabio.2011.04.012

Kim, E., Watanabe, A., Sato, R., Okajima, K., & Minagawa, J. (2019). pH-responsive binding properties of light-harvesting complexes in a photosystem II supercomplex investigated by thermodynamic dissociation kinetics analysis. *The Journal of Physical Chemistry Letters, 10*(13), 3615–3620. https://doi.org/10.1021/acs.jpclett.9b01208

Kirchhoff, H. (2014). Diffusion of molecules and macromolecules in thylakoid membranes. *Biochimica Et Biophysica Acta (BBA)-Bioenergetics, 1837*(4), 495–502. https://doi.org/10.1016/j.bbabio.2013.11.003

Krause, G. H., Koroleva, O. Y., Dalling, J. W., & Winter, K. (2001). Acclimation of tropical tree seedlings to excessive light in simulated tree-fall gaps. *Plant, Cell & Environment, 24*(12), 1345–1352. https://doi.org/10.1046/j.0016-8025.2001.00786.x

Kress, E., & Jahns, P. (2017). The dynamics of energy dissipation and xanthophyll conversion in Arabidopsis indicate an indirect photoprotective role of zeaxanthin in slowly inducible and relaxing components of non-photochemical quenching of excitation energy. *Frontiers in Plant Science, 8*, 2094. https://doi.org/10.3389/fpls.2017.02094

Külheim, C., Ågren, J., & Jansson, S. (2002). Rapid regulation of light harvesting and plant fitness in the field. *Science, 297*(5578), 91–93. https://doi.org/10.1126/science.1072359

Li, X.-P., Björkman, O., Shih, C., Grossman, A. R., Rosenquist, M., Jansson, S., & Niyogi, K. K. (2000). A pigment-binding protein essential for regulation of photosynthetic light harvesting. *Nature, 403*(6768), 391–395. https://doi.org/10.1038/35000131

Li, X.-P., Gilmore, A. M., Caffarri, S., Bassi, R., Golan, T., Kramer, D., & Niyogi, K. K. (2004). Regulation of photosynthetic light harvesting involves intrathylakoid lumen pH sensing by the PsbS protein. *Journal of Biological Chemistry, 279*(22), 22866–22874. https://doi.org/10.1074/jbc.M402461200

Logan, B. A., Demmig-Adams, B., & Adams, W. W., III. (1999). Acclimation of photosynthesis to the environment. In G. S. Singhal, G. Renger, S. K. Sopory, K.-D. Irrgang, & Govindjee (Eds.), *Concepts in Plant Photobiology: Photosynthesis and Photomorphogenesis* (pp. 477–512). Narosa Publishing House

Logan, B. A., Barker, D. H., Adams, W. W., III., & Demmig-Adams, B. (1997). The response of xanthophyll cycle-dependent energy dissipation in *Alocasia brisbanensis* to sunflecks in a subtropical rainforest. *Functional Plant Biology, 24*(1), 27–33. https://doi.org/10.1071/PP96059

Logan, B. A., Barker, D. H., Demmig-Adams, B., & Adams, W. W., III. (1996). Acclimation of leaf carotenoid composition and ascorbate levels to gradients in the light environment within an Australian rainforest. *Plant, Cell & Environment, 19*(9), 1083–1090. https://doi.org/10.1111/j.1365-3040.1996.tb00215.x

Logan, B. A., Demmig-Adams, B., Adams, W. W., III., & Grace, S. C. (1998). Antioxidants and xanthophyll cycle-dependent energy dissipation in *Cucurbita pepo* L. and *Vinca major* L. acclimated to four growth PPFDs in the field. *Journal of Experimental Botany, 49*(328), 1869–1879. https://doi.org/10.1093/jxb/49.328.1869

Matuszyńska, A., Heidari, S., Jahns, P., & Ebenhoeh, O. (2016). A mathematical model of non-photochemical quenching to study short-term light memory in plants. *Biochimica Et Biophysica Acta (BBA)-Bioenergetics, 1857*(12), 1860–1869. https://doi.org/10.1016/j.bbabio.2016.09.003

Nilkens, M., Kress, E., Lambrev, P., Miloslavina, Y., Müller, M., Holzwarth, A. R., & Jahns, P. (2010). Identification of a slowly inducible zeaxanthin-dependent component of non-photochemical quenching of chlorophyll fluorescence generated under steady-state conditions in *Arabidopsis*. *Biochimica Et Biophysica Acta (BBA)-Bioenergetics, 1797*(4), 466–475. https://doi.org/10.1016/j.bbabio.2010.01.001

Niyogi, K. K., Björkman, O., & Grossman, A. R. (1997). Chlamydomonas xanthophyll cycle mutants identified by video imaging of chlorophyll fluorescence quenching. *The Plant Cell, 9*(8), 1369–1380. https://doi.org/10.1105/tpc.9.8.1369

Niyogi, K. K., Grossman, A. R., & Björkman, O. (1998). Arabidopsis mutants define a central role for the xanthophyll cycle in the regulation of photosynthetic energy conversion. *The Plant Cell, 10*(7), 1121–1134. https://doi.org/10.1105/tpc.10.7.1121

Pearcy, R. W. (1990). Sunflecks and photosynthesis in plant canopies. *Annual Review of Plant Physiology and Plant Molecular Biology, 41*, 421–453. https://doi.org/10.1146/annurev.pp.41.060190.002225

Putzler, C. C., Polich, S. B., & Verhoeven S, M. (2022). Sustained zeaxanthin-dependent thermal dissipation is induced by desiccation and low temperature in the fern *Polypodium virginianum*. *Physiologia Plantarum, 174*(4), e12743.

Ruban, A. V., & Johnson, M. P. (2010). Xanthophylls as modulators of medbrane protein function. *Archives of Biochemistry and Biophysics, 504*(1), 78–85. https://doi.org/10.1016/j.abb.2010.06.034

Schumann, T., Paul, S., Melzer, M., Dörmann, P., & Jahns, P. (2017). Plant growth under natural light conditions provides highly flexible short-term acclimation properties toward high light stress. *Frontiers in Plant Science, 8*, 681. https://doi.org/10.3389/fpls.2017.00681

Short, A. H., Fay, T. P., Crisanto, T., Hall, J., Steen, C. J., Niyogi, K. K., Limmer, D. T., & Fleming, G. R. (2022). Xanthophyll-cycle based model of the rapid photoprotection of *Nannochloropsis* in response to regular and irregular light/dark sequences. *The Journal of Chemical Physics, 156*(20), 205102. https://doi.org/10.1063/5.0089335

Suorsa, M., Rantala, M., Mamedov, F., Lespinasse, M., Trotta, A., Grieco, M., Vuorio, E., Tikkanen, M., Järvi, S., & Aro, E. M. (2015). Light acclimation involves dynamic re-organization of the pigment–protein megacomplexes in non-appressed thylakoid domains. *The Plant Journal, 84*(2), 360–373. https://doi.org/10.1111/tpj.13004

Szilágyi, A., Sommarin, M., & Åkerlund, H.-E. (2007). Membrane curvature stress controls the maximal conversion of violaxanthin to zeaxanthin in the violaxanthin cycle—influence of α-tocopherol, cetylethers, linolenic acid, and temperature. *Biochimica Et Biophysica Acta (BBA) - Biomembranes, 1768*(9), 2310–2318. https://doi.org/10.1016/j.bbamem.2007.06.001

Telfer, A. (2014). Singlet oxygen production by PSII under light stress: Mechanism, detection and the protective role of β-carotene. *Plant & Cell Physiology, 55*(7), 1216–1223. https://doi.org/10.1093/pcp/pcu040

Verhoeven, A. S., Adams, W. W., III., & Demmig-Adams, B. (1998). Two forms of sustained xanthophyll cycle-dependent energy dissipation in overwintering. *Euonymus kiautschovicus Plant, Cell & Environment, 21*(9), 893–903. https://doi.org/10.1046/j.1365-3040.1998.00338.x

Verhoeven, A. S., Adams, W. W., III., & Demmig-Adams, B. (1999). The xanthophyll cycle and acclimation of *Pinus ponderosa* and *Malva neglecta* to winter stress. *Oecologia, 118*(3), 277–287. https://doi.org/10.1007/s004420050728

Wagner, D., Przybyla, D., op den Camp, R., Kim, C., Landgraf, F., Lee, K. P., Wursch, M., Laloi, C., Nater, M., Hideg, E., & Apel, K. (2004). The genetic basis of singlet oxygen induced stress responses of *Arabidopsis thaliana*. *Science*, *306*(5699), 1183–1185. https://doi.org/10.1126/science.1103178

Zarter, C. R., Adams, W. W., III., Ebbert, V., Cuthbertson, D. J., Adamska, I., & Demmig-Adams, B. (2006). Winter down-regulation of intrinsic photosynthetic capacity coupled with up-regulation of Elip-like proteins and persistent energy dissipation in a subalpine forest. *New Phytologist, 172*(2), 272–282. https://doi.org/10.1111/j.1469-8137.2006.01815.x