REVIEW

Thermal energy dissipation and xanthophyll cycles beyond the *Arabidopsis* model

José Ignacio García-Plazaola · Raquel Esteban ·
Beatriz Fernández-Marín · Ilse Kranner ·
Albert Porcar-Castell

Abstract Thermal dissipation of excitation energy is a fundamental photoprotection mechanism in plants. Thermal energy dissipation is frequently estimated using the quenching of the chlorophyll fluorescence signal, termed non-photochemical quenching. Over the last two decades, great progress has been made in the understanding of the mechanism of thermal energy dissipation through the use of a few model plants, mainly *Arabidopsis*. Nonetheless, an emerging number of studies suggest that this model represents only one strategy among several different solutions for the environmental adjustment of thermal energy dissipation that have evolved among photosynthetic organisms in the course of evolution. In this review, a detailed analysis of three examples highlights the need to use models other than *Arabidopsis*: first, overwintering evergreens that develop a sustained form of thermal energy dissipation; second, desiccation tolerant plants that induce rapid thermal energy dissipation; and third, understorey plants in which a complementary lutein epoxide cycle modulates thermal energy dissipation. The three examples have in common a shift from a photosynthetically efficient state to a dissipative conformation, a strategy widely distributed among stress-tolerant evergreen perennials. Likewise, they show a distinct operation of the xanthophyll cycle. Expanding the list of model species beyond *Arabidopsis* will enhance our knowledge of these mechanisms and increase the synergy of the current studies now dispersed over a wide number of species.

Keywords Desiccation tolerance · Lutein epoxide cycle · Photoprotection · Thermal dissipation · Winter photoinhibition · Xanthophyll cycles

Thermal dissipation of excitation energy in *Arabidopsis*

'Model species' in biological research

Model species have helped researchers gain an in-depth understanding of complex biological processes, mainly due to the synergy created by the focus on a single species. Yet, there is a trade-off between the positive synergy and the limitations that arise when a model species fails to cover the full biological complexity of the phenomena under examination. A full comprehension of the variety of biological strategies requires not only the study of model species but also of the many other 'non model species'. For photosynthetic eukaryotic organisms, the 'chosen species' has been *Arabidopsis thaliana* (Meinke et al. 1998). Apart from this higher plant, other species have been intensively used for modelling purposes, including tobacco, rice or spinach, as well as the moss *Physcomitrella patens* and the green alga *Chlamydomonas reinhardtii*. The generation of an impressive amount of knowledge following a decade of intensive research has confirmed that *A. thaliana* is an excellent tool for biochemical, physiological and genetic studies (Somerville and Koornneef 2002). One of the characteristics that contribute to the usefulness of this

J. I. García-Plazaola (✉) · R. Esteban · B. Fernández-Marín
Department of Plant Biology and Ecology, University of the
Basque Country (UPV/EHU), Apdo 644, 48080 Bilbao, Spain
e-mail: joseignacio.garcia@ehu.es

I. Kranner
Institute of Botany, University of Innsbruck, Sternwartestraße
15, A-6020 Innsbruck, Austria

A. Porcar-Castell
Department of Forest Sciences, University of Helsinki,
Latokartanonkaari 7, P.O. Box 27, 00014 Helsinki, Finland

model plant is its massive seed production after a short growing period. This is a typical trait of temperate annual weeds and reflects a strategy of stress avoidance, whereby plants simply die when conditions become unfavourable, and survive with persistent seed banks (Grime 2002). However, annual plants represent only one lifestyle among the diverse solutions for the successful adaptation to the environment that have evolved. Besides, *Arabidopsis*-like strategies are contrary to stress tolerance strategies found in many evergreen perennials, and therefore, this species is of limited interest to those who study topics related to stress physiology. In this review, we present three examples in the context of the acclimation of photosynthetic light reactions in which the *Arabidopsis* model cannot be applied and different model-species are needed.

The mechanism of thermal energy dissipation

The fluctuating nature of light requires the existence of dynamic photoprotection mechanisms in plants. Among these, the safest and most flexible way to dissipate the excess energy absorbed by chlorophylls is via thermal energy dissipation within the photosynthetic apparatus. The operation of this mechanism results in a decrease in, or quenching of the chlorophyll fluorescence yield, the so-called non-photochemical quenching, which has been widely assessed via the chlorophyll fluorescence parameter *NPQ* (Bilger and Björkman 1990), where NPQ = $(F_{m(reference)}/F_{m(quenched)}) - 1$, with $F_{m(reference)}$ being the maximal fluorescence measured during a pulse of saturating light in the absence of NPQ, and $F_{m(quenched)}$ the maximal fluorescence measured during a pulse of saturating light and in the presence of NPQ. Because of the relative ease of measuring the quenching of the chlorophyll fluorescence signal, the parameter *NPQ* has been widely used as a proxy to study the process of thermal energy dissipation and in some instances is even used as a synonym. However, although changes in thermal energy dissipation capacity represent the main process behind the

observed reduction in $F_{m(quenched)}$ relative to $F_{m(reference)}$, other processes might also reduce $F_{m(quenched)}$ and generate NPQ. For example, the phenomena of state-transitions do not involve any thermal energy dissipation in PSII but excitation energy transfer to the less fluorescent PSI, quenching the fluorescence signal. Similarly, if $F_{m(reference)}$ and $F_{m(quenched)}$ are estimated far apart in time, factors other than thermal energy dissipation may also influence $F_{m(quenched)}$ and interact with the estimation of NPQ (see Porcar-Castell 2011 for a more detailed discussion). With these considerations in mind and following the most recent reviews on this subject (e.g.: Goss and Torsten 2010; Murchie and Niyogi 2011; Jahns and Holzwarth 2012; Nichol et al. 2012), for simplicity, the term NPQ is used hereafter to denote the non-photochemical quenching of chlorophyll fluorescence due to thermal energy dissipation, whereas *NPQ* will be used to denote the fluorescence parameter.

Kinetically, NPQ is a complex process and its biochemical, biophysical, physiological and ecological characterisation has been extensively researched over the last two decades. The use of model organisms, and specifically of mutants lacking specific steps in the generation of NPQ (De Bianchi et al. 2010), led to the development of a mechanistic model for NPQ, which has been described in several recent reviews: Demmig-Adams and Adams (2006); Goss and Torsten (2010); Horton and Ruban (2004); Jahns et al. (2009); Jahns and Holzwarth (2012); Murchie and Niyogi (2011).

Although an in-depth description of the NPQ mechanism goes beyond the scope of this review, a brief characterisation will be given (for more detailed information, see the aforementioned reviews) (Fig. 1). Basically, there are three components that contribute to the regulation of NPQ: first, the build up of a proton gradient (ΔH^+ or ΔpH) across thylakoid membranes (Horton et al. 1996), which is generated by photosynthetic proton pumping; second, the activity of the xanthophyll, or violaxanthin (V-), cycle with the corresponding formation of zeaxanthin (Z) (Demmig-Adams et al. 1990), and third, the protein PsbS, a protein

Fig. 1 Simplified model of a thylakoid membrane showing the mechanisms involved in the regulation of the qE component of NPQ in *Arabidopsis* under low and high excitation pressure. *Abbreviations*: *RC* reaction centre; *ZE* zeaxanthin epoxidase; *VDE* violaxanthin deepoxidase; *V* violaxanthin and *Z* zeaxanthin
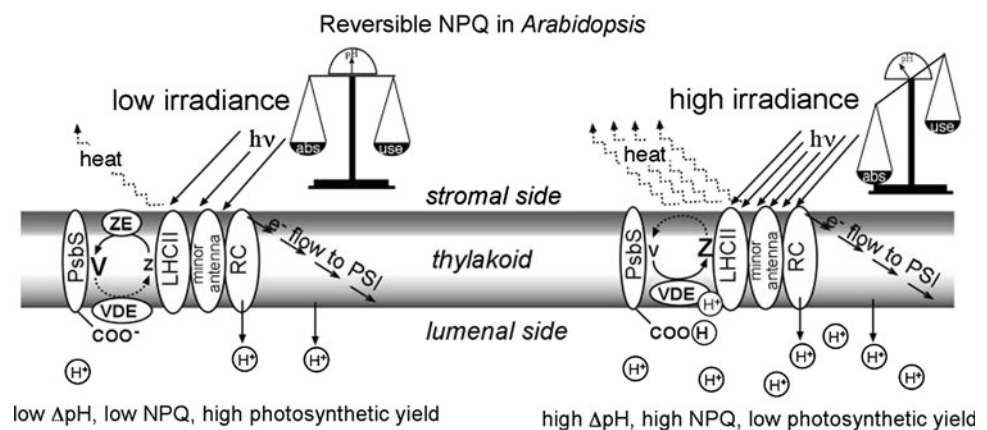
homologous to antenna components (Li et al. 2000). Both PsbS and Z act independently and have distinct regulatory functions (Bonente et al. 2008; Jahns and Holzwarth 2012). The magnitude of ΔH^+ is usually proportional to the excitation pressure, acting as a signal that activates NPQ, with PsbS and certain LHCs acting as sensors of proton concentration. This proton gradient-dependent activation and deactivation of NPQ represents its fast and ΔpH-dependent component (qE or NPQΔ_{pH}) (Krause and Weis 1991; Nichol et al. 2012), which can be turned on and off in seconds, tracking changes in light conditions (Adams et al. 1999). At the same time, low pH values activate the enzyme violaxanthin deepoxidase (VDE), forming Z from violaxanthin (V) in the peripheral sites of the LHC complexes. By means of a photophysical mechanism that is not completely understood (for more detailed information see Ruban et al. 2007; Ahn et al. 2008; Jonhson et al. 2009; Jahns and Holzwarth 2012), Z stabilizes and amplifies NPQ at different quenching sites (Jahns and Holzwarth 2012), regulating it over longer time periods than the proton gradient, ranging from minutes to hours. Besides qE, a second component is the photoinhibitory quenching 'qI', which is irreversible in the short-term (hours or days), resulting in the sustained downregulation of photochemical efficiency. A third component of NPQ, which is ΔpH-independent and entirely dependent on the Z content (Dall'Osto et al. 2005), has been recently termed 'qZ' (Nilkens et al. 2010).

Traditionally, but perhaps misleading, the mechanisms which imply a sustained loss of photochemical efficiency, have been included within the term 'photoinhibition' (Adams et al. 1995; Müller et al. 2001; Horton and Ruban 2004; Baker 2008). Photoinhibition operates at a time-scale where several processes may be involved in the reduction of the photosynthetic capacity. Thus, under some circumstances, it may be difficult to associate photoinhibition with a single process, let alone measure it. On the one hand, in the laboratory biophysicists are able to examine the dynamics of photoinhibition in the reaction centre of PSII (e.g. using different combinations of light and lincomycin). Biophysicists use the term photoinhibition to denote the sustained damage of the core PSII reaction centre D1 protein (Tyystjärvi and Aro 1996). On the other hand, ecophysiologists dealing with field data are not able to directly measure the damage to the reaction centre D1 protein. Ecophysiologists traditionally use the term photoinhibition to denote the combined effect of damage to the reaction centre D1 protein and the sustained enhancement of the capacity for thermal energy dissipation in the thylakoid membrane. Here, thermal energy dissipation is typically demonstrated through a reduction in the maximum quantum yield of photochemistry and assayed fluorometrically via the parameter F_v/F_m. Bearing these limitations in mind, the term 'photoinhibition' or (probably better) the term 'downregulation' of the light reactions of photosynthesis can be defined as the complex process involving a number of mechanisms by which the light reactions of photosynthesis shift from a fully functional state to a state where a variable fraction of the reaction centres are non-functional and the yield of thermal energy dissipation does not fully relax overnight.

The mechanism of thermal energy dissipation described above, mainly its dynamic and ΔH^+-dependent component, is capable of perceiving rapid variations in irradiance and fulfils the photoprotective requirements of *Arabidopsis*-like plants exposed to light changes related to cloudiness fluctuations or leaf movements, warranting the harmless dissipation of excitation energy under these fluctuating conditions. As thermal energy dissipation always occurs at the expense of a decrease in the quantum efficiency of energy conversion, its coupling with the metabolic requirements of energy is essential for the fitness and survival of plants (Külheim et al. 2002).

The diversity of thermal dissipation mechanisms

Thermal energy dissipation has been documented in all major groups of eukaryotic photoautotrophs. In all these groups, the common need for the fine adjustment of NPQ by environmental conditions has been one of the evolutionary drivers. This has given rise to a multiplicity of thermal energy dissipation forms as a result of different evolutionary histories of each functional group. Hence, the basic NPQ mechanism described previously varies in its regulation and components. For example the quenching site can be different in chlorophyll *c*-containing algae (Kana et al. 2012) or NPQ may be completely independent of ΔpH in brown algae (García-Mendoza and Colombo-Pallota 2007), cyanobacterial lichens (Demmig-Adams et al. 1990) or overwintering evergreens (Demmig-Adams and Adams 2006). Another remarkable difference exists in the proteins involved in sensing intra-thylakoidal pH changes. It is generally assumed that the PsbS protein operates as a sensor of the luminal pH required for the rapid induction of qE (Li et al. 2004). This assumption is valid for vascular plants. Nevertheless, a different LHC protein, called LHCSR, was recently found to be necessary for qE in the green alga *C. reinhardtii* (Peers et al. 2009). This protein is not present in higher plants, but both the PsbS and the LHCSR-dependent qE systems are present in the moss *P. patens*, where the two types of qE appear to operate independently and additively (Alboresi et al. 2010). An additional source of variability is the existence of several xanthophyll cycles, two of which are present in plants (García-Plazaola et al. 2007). Here, we will focus on this physiological diversity by describing examples in which

the regulation of NPQ goes beyond the current *Arabidopsis* model.

Thermal dissipation in winter evergreens

Requirement for photoprotection in the winter

Excess energy may appear in different temporal domains: a 'sunfleck' in a shaded understorey leaf can lead to a state of excess energy lasting only a few seconds (Adams et al. 1999; Logan et al. 1997), whereas diurnal changes in sun elevation and cloudiness largely determine the amount of excess energy to which the photosystems are exposed during the course of the day (Adams and Barker 1998). In this temporal domain (seconds to minutes), the photosystems use reversible NPQ mechanisms (explained above) to adjust the fraction of excitation energy that is being thermally dissipated, thus maintaining the energy balance between light and carbon reactions (Adams et al. 1999). In turn, evergreen species growing at high altitude or latitude face an additional, slow component of excess energy to which the reversible component is superimposed during the cold months (Demmig-Adams and Adams 2006). Low temperatures increase the levels of excess energy and the demand for photoprotection by inactivating the enzymatic carbon reactions including photorespiration, a process that is otherwise able to complement NPQ in the dissipation of excess energy (Hendrickson et al. 2004), and by impairing systems that scavenge reactive oxygen species (ROS) that rely on enzymatic steps (Adams et al. 2004). Therefore, overwintering evergreens require enhanced and robust mechanisms of thermal energy dissipation to cope with the particularly high levels of excess energy during the cold season. Although the performance of ΔpH-dependent NPQ can be modulated, a simple upregulation of this mechanism would not suffice during winter because photosystems need to be primed for excess energy dissipation from first light in the morning during cold days. At dawn, temperatures are the lowest, thereby inhibiting the generation of the necessary ΔpH or enzymatic de-epoxidation reaction, which are needed for the optimal functioning of the ΔpH-dependent NPQ (Eskling et al. 2001). In addition, the sustained form of pH-dependent NPQ, which is maintained at low temperatures (Gilmore and Björkman 1994; Gilmore 1997), does not provide sufficient robustness either, because a sudden increase in temperature during the night could disengage this type of photoprotective system, making it vulnerable to cold-induced excess light during the early morning. Therefore, overwintering evergreens require mechanisms not only with enhanced but also with sustained thermal energy dissipation capacities to keep the photosystems primed for thermal energy dissipation during

the night, or during random and short-lived warm spells in the winter.

Sustained thermal dissipation

Downregulation of the electron transport of light reactions has been observed in overwintering evergreen species, mainly boreal conifers such as *Pinus* spp. (Ottander et al. 1995; Verhoeven et al. 1996; Ensminger et al. 2004; Zarter et al. 2006b; Porcar-Castell et al. 2008a) or *Abies* spp. (Ebbert et al. 2005; Zarter et al. 2006b), in Mediterranean evergreens *Quercus* spp. (García-Plazaola et al. 1997; Ogaya and Peñuelas 2003) xeric plants as *Yucca glauca* (Adams and Barker 1998), and others. Winter downregulation has been widely characterized by a seasonal decrease in the maximum quantum yield of photochemistry or F_v/F_m (Adams et al. 1995; Adams and Barker 1998; Zarter et al. 2006a, b), where the intensity of the downregulation is largely modulated by the light environment, whereby the foliage in the top canopy is more downregulated than that in the lower canopy (García-Plazaola et al. 1997; Ogaya and Peñuelas 2003; Porcar-Castell et al. 2008b). The decrease in the maximum quantum yield of photochemistry that occurs in overwintering evergreens has both a photochemical and a non-photochemical component (Porcar-Castell et al. 2008a; Porcar-Castell 2011). In particular, total NPQ (sustained + reversible) has been found to increase manifold during winter in boreal Scots pine (Fig. 2), explaining most of the seasonal decrease in F_v/F_m (Porcar-Castell 2011), while a decrease in photochemical quenching (PQ) during the early spring (when high irradiance and low temperatures are combined) further reduces F_v/F_m during the early spring (Porcar-Castell et al. 2008a; Porcar-Castell 2011). The early spring reduction in PQ in needles of boreal Scots pine is consistent with the low levels of PSII core D1 protein found in boreal Scots pine during the same period (Ottander et al. 1995; Ensminger et al. 2004).

Sustained NPQ in overwintering evergreen foliage has been attributed to a number of processes that include the accumulation of xanthophyll-cycle pigments and especially of Z (Ottander et al. 1995; Demmig-Adams and Adams 1996; Havaux 1998; Ensminger et al. 2004), the accumulation of PsbS-related proteins, such as ELIPS (Ensminger et al. 2004; Zarter et al. 2006a, b), the thermal dissipation of excitation energy by non-functional or photoinhibited PSII reaction centres (Krause 1988; Lee et al. 2001; Ivanov et al. 2002; Ebbert et al. 2005; Sveshnikov et al. 2006), or the structural rearrangement or aggregation of LHCII complexes that promote thermal energy dissipation (Ottander et al. 1995; Gilmore et al. 2003). However, comprehensive research is still needed to unveil the role of each of these mechanisms in the observed dynamics of NPQ in
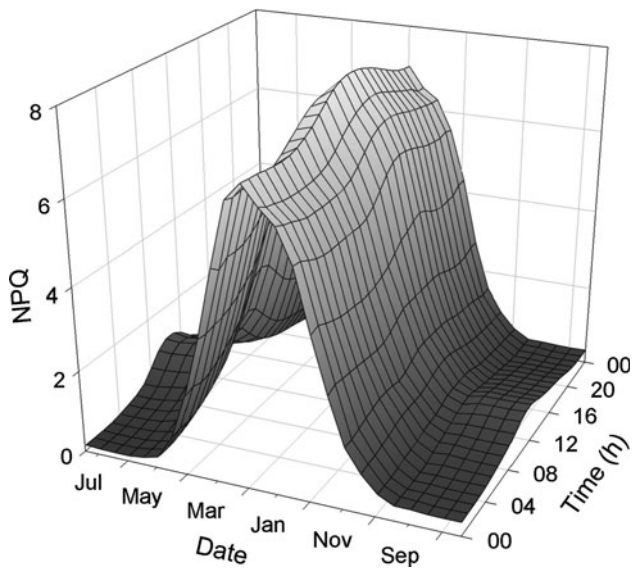
Fig. 2 Annual dynamics of total NPQ in needles of boreal Scots pine under field conditions. Note the superimposed effect of reversible NPQ, increasing in the morning and decreasing in the afternoon in response to the diurnal variation in irradiance (along the *time axis*), and of sustained NPQ, increasing drastically towards late autumn and decreasing in spring (along the *date axis*). Data were obtained with a Monitoring-PAM fluorometer (Walz, Germany) that supplied a saturating light pulse every 15–30 min. Data were previously smoothed to facilitate its 3D representation; redrawn after Porcar-Castell (2011)

overwintering evergreen foliage and the way in which these mechanisms interact with each other. Sustained NPQ in overwintering conifer needles has been found to correlate with overnight retention of the de-epoxidized fraction of the xanthophyll cycle (Adams et al. 1995; Porcar-Castell et al. 2008b; Zarter et al. 2006b). However, overnight retention of a de-epoxidized xanthophyll cycle pool alone does not necessarily explain all the sustained NPQ and depression in F_v/F_m. For example, Porcar-Castell et al. (2012) found that night retention of DEPS had relaxed to autumn levels during an early warm spell in spring in Scots pine needles, whereas F_v/F_m and sustained NPQ remained comparatively low and high, respectively, denoting that several mechanisms cooperate to generate the observed sustained NPQ in overwintering evergreen foliage.

Overall, additional studies are needed to reveal how much of the observed seasonal increase in sustained NPQ in overwintering evergreens is associated with an increase in thermal energy dissipation and how much is caused by processes such as seasonal changes in absorption cross-section areas of the photosystems or in leaf absorption (Porcar-Castell 2011). However, the available data supports that sustained NPQ enhances total thermal energy dissipation capacity beyond the levels obtained with ΔpH-dependent NPQ, a phenomenon that is also confirmed by the much lower minimum PSII operating quantum

efficiencies registered during winter compared to summer (Porcar-Castell 2011). Moreover, sustained NPQ uses mechanisms of thermal dissipation that are not simply a slow version of ΔpH-dependent NPQ but involve processes that require the regulation of gene-expression and the subsequent structural and biochemical re-organization of the photosystems (Ensminger et al. 2004; Demmig-Adams and Adams 2006; Zarter et al. 2006a, b).

Lutein-related thermal dissipation

Living in the forest understorey

Most forests worldwide with dense vegetation possess a closed canopy, in which only a small fraction of the incident solar radiation (0.5–5 %) reaches the understorey (Chazdon and Pearcy 1991). A significant proportion of this energy penetrates the canopy during brief periods of direct sunlight, the 'sunflecks', which represent one of the key factors that affect plant fitness and survival in the understorey. Hence, understorey species must be able to cope with the random variation of light in this environment, frequently involving changes of several orders of magnitude. In this scenario, leaves must be extremely efficient for light harvesting. However, highly efficient leaves, if not paired with equally efficient carbon reactions, are also predisposed to photodamage. A rapid engagement of Z and A in energy dissipation during sunfleck activity (Watling et al. 1997) and rapid disengagement upon return to low light (Adams et al. 1999) play a central role in plant response to a dynamic light environment. Plants with mechanisms for fine-tuning the light harvest and thermal dissipation have an advantage in this environment. As a consequence, a set of adaptive traits is typically displayed by shade tolerant leaves (Valladares and Niinemets 2008), generating a shade-acclimation syndrome (Lüttge 1997). Among these characteristics, pigment composition varies with respect to sun plants (Demmig-Adams 1998). One carotenoid that is found mostly in plants growing in these shady environments is the lutein epoxide (Lx), which is involved in the so-called 'Lx-cycle' (García-Plazaola et al. 2007).

The lutein epoxide cycle

Unlike the V-cycle, which is widespread in all photosynthetic organisms belonging to the green lineage of the plant kingdom, the Lx-cycle is restricted to some taxonomic groups (Esteban et al. 2009). This cycle operates through the light-driven de-epoxidation of Lx into lutein (L), a process that occurs in parallel with the de-epoxidation of V in the V-cycle, both cycles being catalyzed apparently by

the same enzymatic system (García-Plazaola et al. 2007). This de-epoxidation augments the already large pool of L in plants (L + ΔL) (Nichol et al. 2012). As will be described later, new advances were made regarding the concept of thermal dissipation since the discovery of this cycle in the parasitic plant *Cuscuta reflexa* (Bungard et al. 1999). The de-epoxidated carotenoid of the cycle, L, has been implicated with the structure and organisation of the light-harvesting complexes (Horton and Ruban 2004) but it also has a role in thermal energy dissipation. This function was demonstrated by studies on *Arabidopsis* mutants lacking L, *lutOE* plants with an extra pool of L (Pogson and Rissler 2000), *szl1NPQ1* double mutants in which a large part of the V pool was replaced by L and de-epoxidation of V-cycle was inhibited (Li et al. 2009), and *lut2* and *lut2NPQ1* mutants with altered L contents (Dall'Osto et al. 2006) and also by experiments with isolated LHCII and LHCII crystals (Pascal et al. 2005; Ruban et al. 2007).

The Lx-cycle is completed when the reversal of the epoxidation of ΔL to Lx occurs. However, this step is frequently missing or occurs at a very slow rate. The key element that marks the existence of two types of Lx-cycles is the epoxidation of L back to Lx: a 'complete' cycle, with full recovery of the Lx-pool in the dark and a 'truncated' cycle, with no overnight recovery of the initial Lx-pool (Fig. 3). The first one was described in the parasitic plant *C. reflexa* (Bungard et al. 1999) and later in *Amyema miquelii* (Matsubara et al. 2001) and in tropical and subtropical trees such as *Virola elongata* (Matsubara et al. 2009) and *Ocotea foetens* (Esteban et al. 2010). Conversely, the 'truncated Lx-cycle' was found in *Quercus*

rubra (García-Plazaola et al. 2003), *Inga sapindoides* (Matsubara et al. 2005) and avocado (*Persea americana*) (Esteban et al. 2007; Esteban et al. 2008; Förster et al. 2009; Förster et al. 2011). The same irreversible cycle seems to operate in enclosed buds of some woody plants where a conversion of Lx into ΔL following bud-burst also takes place (García-Plazaola et al. 2004). As a consequence of the lack of Lx, or the extremely slow Lx-recovery in these species, the Lx-content is typically high (with exceptions) in leaves of the innermost canopy positions (Esteban et al. 2007; Matsubara et al. 2009; Nichol et al. 2012). The most plausible explanation for this accumulation is because shaded leaves are infrequently exposed to enough light to activate the enzyme responsible for the conversion of Lx to L (García-Plazaola et al. 2007; Nichol et al. 2012). Due to the operation of the 'truncated Lx-cycle', ΔL is retained, and as mentioned above, this event attracted the attention of researchers due to the possible role of L in enhancing NPQ. It is worthy of note that the V-cycle can also show an irreversible overnight retention of antheraxanthin (A) and Z, with no overnight recovery of the V pool; however, this type of sustained de-epoxidation usually occurs in response to conditions of severe environmental stress, such as low temperature (see 'NPQ in winter evergreens' section).

The existence of both cycles (V and Lx) in some plant species suggests an ecological or physiological role for the Lx-cycle that is different or complementary to the V-cycle, which may relate to the special habitat in which this cycle operates, the deep understorey of forests. As stated above, in this environment it may be critical to balance the enhancement of light harvesting of diffuse light and protection against frequent and unpredictable sunflecks. An increasing amount of evidence suggests that the Lx-cycle may fulfil this double demand in plants living under limiting light environments. Evidence of the light-harvesting function was provided by Matsubara et al. (2007), who found a high fluorescence yield in recombinant *Lhcb5* reconstituted with Lx. Besides, a slower reduction of the photosystem II electron acceptor QA and faster formation of NPQ in the chlorophyll fluorescence induction in leaves containing reduced levels of Lx was also demonstrated. All this indicates that the presence of Lx in prolonged low-light conditions may increase light-harvesting efficiency by facilitating excitation energy transfer to chlorophyll in light limiting conditions. This role was supported by the rapid restoration of the Lx-content after a short artificial sunfleck in *O. foetens* (Esteban et al. 2010). Considering the analogy between the overnight retention of Z in sustained winter NPQ and the irreversible retention of the de-epoxidised xanthophyll ΔL, the ecophysiological studies conducted over the last decade have focused on the involvement of the cycle in the regulation of thermal dissipation. Thus, there
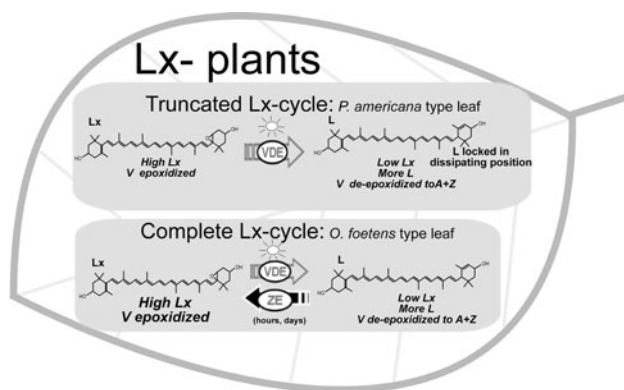

Fig. 3 Type of Lx-cycles in Lx-plants: truncated Lx-cycle (*top*) and complete Lx-cycle (*bottom*). Driven by light, Lx is de-epoxidized to L by the enzyme VDE. The complete operation of the Lx-cycle requires the epoxidation of L back to Lx. This step is a key for the operation of the two types of cycles. When there is no overnight recovery of the Lx-pool within hours or days, a truncated cycle takes place, whereas when the Lx-pool recovers overnight the cycle is completed

are several correlative pieces of evidence of a relationship between non-reversible de-epoxidation of Lx to ΔL and a decrease in F_v/F_m in response to chilling (Matsubara et al. 2002; García-Plazaola et al. 2004; Watson et al. 2004). In addition, an annual study of leaves of *Laurus nobilis* suggested the involvement of the Lx-cycle in the long-term modulation of sustained energy dissipation (Esteban et al. 2008). The same conclusion was obtained in a recent study with leaves of *P. americana* (Förster et al. 2009). Furthermore, several studies have shown the relationship between ΔL formation from Lx and the velocity of NPQ formation in *Quercus rubra* (García-Plazaola et al. 2003), *Inga* (Matsubara et al. 2008) and *Ocotea foetens* (Esteban et al. 2010). This concept has recently been confirmed by a study of leaves of *P. americana* (Matsubara et al. 2011), which concludes that the ΔL formed from Lx was able to enhance ΔpH-dependent NPQ, and therefore, the Lx-cycle contributes together with the V-cycle to the regulation of NPQ. More experiments on this species have shown that the ΔL from de-epoxidation of Lx replaces Z to sustain an enhanced capacity for NPQ (Förster et al. 2011) and that the de-epoxidation of Lx and V to ΔL and A+Z, respectively, in shade leaves increases the capacity for NPQ by 30–40 % (Nichol et al. 2012). These ecophysiological studies were supported by biochemical studies, which demonstrated a role for L in NPQ induction through the use of mutants (Pogson and Rissler 2000; Li et al. 2009). Hence, the involvement of the photo-converted ΔL in the regulation of NPQ (ΔpH-dependent interconversions) has been corroborated.

The ecophysiological meaning of the Lx-cycle

If we try to explain the behaviour of the Lx-cycle from an ecological point of view and place an Lx-species in a natural environment such as the forest understorey, the pieces of the puzzle start fitting together and all the functions explained above gain ecophysiological relevance. In a recent study in *O. foetens*, which was illuminated with artificial sunflecks in its natural environment, Lx-restoration after illumination depended on the intensity and duration of illumination, as well as the length of the subsequent dark or low-light period, opening a wide array of possibilities in which the reversible Lx-cycle facilitates photoprotection and relaxes rapidly enough to restore high efficiency in low light (Esteban et al. 2010). Therefore, in the case of plants in which the inner canopy leaves initially grow under strong light, the leaves might acclimate to progressive shading by the accumulation of Lx that enhances light-harvesting. However, when a gap forms in the forest, a 'truncated' cycle may represent an emergency mechanism of sustained energy dissipation after abrupt

changes in the light environment (García-Plazaola et al. 2003; Matsubara et al. 2005). The operation of this cycle would then facilitate the shift from highly efficient LHCs to excitation dissipating centres, stabilizing the capacity to rapidly engage these functions (García-Plazaola et al. 2007).

Thermal dissipation in desiccation-tolerant plants

Desiccation tolerance

While most photosynthetic organisms die when they dehydrate below a critical relative water content (RWC), the so-called desiccation-tolerant (DT) plants can lose more than 90 % of their water content (Rascio and La Rocca 2005) and recover normal metabolic functions upon rewatering (Vertucci and Farrant 1995; Kranner et al. 2008). This is equivalent to withstanding desiccation below absolute water contents of 0.01 g of water per g of dry mass or dropping to a water potential of −100 MPa (Alpert 2006). Desiccation tolerance is a rare but scattered strategy among photosynthetic organisms, very frequent in algae, lichens and liverworts, rare in ferns and very scarce in angiosperms (Alpert 2000; Oliver et al. 2000; Table 1). Among DT plants, a few species of monocots are able to dismantle their photosynthetic apparatus and degrade chlorophylls during desiccation (poikilochlorophyllous DT plants), but most DT plants preserve an intact photosynthetic apparatus in the dry state (homoiochlorophyllous DT plants; reviewed by Tuba et al. 1998; Proctor and Tuba 2002; Rascio and La Rocca 2005; Tuba 2008). In this section, we will refer exclusively to the latter type.

Water loss in the presence of light leads to a rapid over-excitation of chlorophylls and, consequently, oxidative stress (Heber and Shuvalov 2005). The development of a very efficient mechanism for energy dissipation allows DT plants to preserve the integrity of the photosynthetic machinery during the dry stage (Heber and Shuvalov 2005). One of the main strategies that apparently set DT-species apart from desiccation-sensitive (DS)-ones is their capability to safely regulate the activity of the photosynthetic machinery during dehydration. While PSII is switched off in DT plants (Kosugi et al. 2009; Nabe et al. 2007), it remains active in DS plants even at very low RWC when photosynthetic electron transport is totally inhibited (Nabe et al. 2007). Furthermore, although in darkness PSI remains active in the dry state in both DT and DS plants (Nabe et al. 2007; Veerman et al. 2007); under illumination it is inactivated only in DT plants (Nabe et al. 2007). This inactivation of photosystems is thought to be a well-regulated and indispensable response to dehydration in DT-species (Nabe et al. 2007).

Table 1 The taxonomic occurrence of desiccation–tolerance (DT) and the V-cycle in photosynthetic tissues of plants (modified from Alpert 2000; Jahns et al. 2009)

Group	Incidence of DT	Presence of V-cycle	Presence of Z in excess light
Cyanobacteria	Probably extremely common	/	√
Chlorolichens	Probably extremely common	√	√
Cyanolichens	Probably extremely common	/	√
Algae	Probably very common in terrestrial species; present in littoral species	√ (in Chlorophyta, Phaeophyta and some Rhodophyta)	√
		/ (in most Rhodophyta)	
Mosses	Probably very common	√	√
Liverworts	Probably common	√	√
Pteridophytes	Infrequent	√	√
Gymnosperms	Absent?	√	√
Monocots	Rare	√	√
Dicots	Very rare	√	√

The presence of the V-cycle is represented by (√) and the absence by (/)

Desiccation-induced thermal dissipation

One of the mechanisms that preserve the functionality of DT-photosynthetic organisms is the so-called desiccation-induced NPQ (NPQ$_{DT}$), which is different from that induced by light (Heber et al. 2006b; Nabe et al. 2007; Heber et al. 2010). This NPQ$_{DT}$ during dehydration-rehydration events follows a regular pattern in most DT plants (Fig. 4). NPQ$_{DT}$ increases during desiccation until it reaches a maximum value, which is usually maintained until the next rehydration (phases I–III of Fig. 4). This initial phase has been reported repeatedly for cyanobacteria (Fukuda et al. 2008), lichens (Heber 2008; Gasulla et al. 2009; Heber et al. 2011), algae (Harker et al. 1999), bryophytes (Csintalan et al. 1999; Hamerlynck et al. 2002; Beckett et al. 2005; Heber et al. 2006a; Nabe et al. 2007), pteridophytes (Eickmeier et al. 1993) and angiosperms (Xu et al. 2008; Mihailova et al. 2011). Far from representing the end of the stress, rehydration is critical for DT plants, because the sudden ingress of water together with the resumption of metabolic activity results in mechanical and oxidative stress (Kranner et al. 2005) and the photosynthetic apparatus needs to be protected while it is being reorganised (Fernández-Marin et al. 2010). Accordingly,
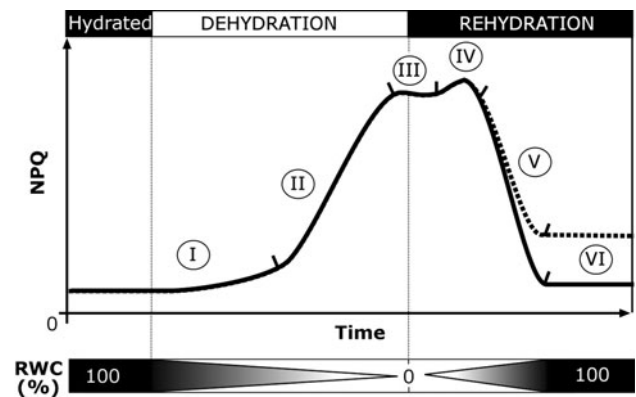

Fig. 4 Scheme summarising the NPQ response of DT plants during dehydration–rehydration events. The *Roman numerals* distinguish six different phases: phase *I* is characterised by a slow increase of NPQ at the beginning of dehydration; phase *II* represents the abrupt increase of NPQ shown by most of DT plants when RWC falls below a threshold level around 50–30 %; phase *III* shows the high level of NPQ maintained during the dry period; phase *IV* represents a slight and brief increase occurring in the very initial steps of rehydration; phase *V* is characterised by a strong decrease until the initial basal values of NPQ of phase *VI* are reached. After repeated events of dehydration, NPQ can remain at a value slightly higher (*dashed line* phase *VI*); this process has been described as hardening (see more information in the text)

on rewatering, NPQ$_{DT}$ can undergo a transient increase (Marschall and Proctor 1999; Csintalan et al. 1999; Peeva and Cornic 2009) (phase IV of Fig. 4) before decreasing to the initial basal values (phases V and VI, Fig. 4) during rehydration (Fernández-Marin et al. 2010). Nevertheless, some exceptions to this general pattern have been found among the different DT-species, for example in some chlorolichens (Calatayud et al. 1997) and angiosperms (Georgieva et al. 2007; Augusti et al. 2001; Degl'Innocenti et al. 2008; Peeva and Cornic 2009). Moreover, experimental conditions, i.e. the speed of dehydration and the light environment (Hamerlynck et al. 2002; Gasulla et al. 2009; Heber et al. 2010) affect the changes in the NPQ$_{DT}$ response even among populations of the same DT-species. Furthermore, the NPQ$_{DT}$ of rehydrated plants can increase as a result of hardening that occurs after previous dry episodes (Beckett et al. 2005; see also Fig. 4, phase VI, dashed line). Nevertheless, beyond the variability of NPQ attributable to the environmental conditions, experimental evidence shows that thermal dissipation of light energy is regulated differently and by different mechanisms in DT and DS plants during dehydration (Kopecky et al. 2005; Heber et al. 2006b; Nabe et al. 2007).

The molecular mechanism of desiccation-induced thermal dissipation

Desiccation-induced NPQ seems to be an array of mechanisms, the biochemical basis, regulatory molecules and

location of which vary among different DT organisms. One of the main differences appears to be in the participation of the V-cycle. A particularity of the formation of Z in DT organisms is its independence of light: desiccation itself triggers VDE activity (Fernández-Marín et al. 2009; Fernández-Marín et al. 2011). The presence of a Z-independent NPQ$_{DT}$ has been suggested for those groups of DT organisms that lack the xanthophyll-cycle, such as photosynthetic bacteria, cyanobacteria (Wilson et al. 2006), cyanolichens (Kopecky et al. 2005), cryptophyta and most rhodophyta (Table 1). However, even most of those groups that lack a xanthophyll cycle are able to synthesise Z and maintain high levels under light stress (Table 1); at least under these conditions, they exhibit NPQ correlated with the amount of Z (Demmig-Adams et al. 1990; Demmig-Adams and Adams 1990). The importance of Z in the NPQ$_{DT}$ of organisms with an operative V-cycle may vary between species and is controversially discussed in the literature. While some authors suggest that Z-dependent energy dissipation is not important in DT plants (Heber et al. 2007; Heber et al. 2010), most studies support that Z contributes to thermal energy dissipation both in the hydrated and desiccated state (Kranner et al. 2002; Kranner et al. 2003; Kranner et al. 2005; Kopecky et al. 2005; Fernández-Marin et al. 2010). Dehydration conditions, especially the speed of desiccation (Fernández-Marin et al. 2010), may be responsible for these apparent inconsistences. Furthermore, it has been proposed that two different components of NPQ$_{DT}$ (Z-dependent and Z-independent) may be active in the dry state (Heber et al. 2006a) and cooperate, at least when desiccation occurs in the light (Bukhov et al. 2001; Kopecky et al. 2005).

Some of the molecular differences between the NPQ$_{DT}$ and the NPQ of DS-model species such as *Arabidopsis*, are based on the cytological and biochemical characteristics of their taxonomic groups. The molecular basis of NPQ$_{DT}$ is still far from being understood and several alternatives have been proposed. On the one hand, it was suggested that NPQ$_{DT}$ takes place in the PSII reaction centres (RCs) associated either with the transformation of a P680 into a P700 without charge separation (Heber and Shuvalov 2005) or with the fast recombination of an oxidised P680 and a neighbouring reduced Chl (Heber et al. 2006b). The transformation of Chl680 into a Chl700 for energy dissipation during dehydration was proposed in chlorolichens and mosses (Heber and Shuvalov 2005), but not observed in other species of DT-bryophytes (Nabe et al. 2007). On the other hand, antennae complexes have more recently been proposed as the most plausible location for NPQ$_{DT}$ (Miyake et al. 2011). The fluorescence quenching of PSII during dehydration of DT-mosses was not thought to be induced either by state 1 to state 2 transitions, or by the detachment of LHCII from the PSII core (Nabe et al.

2007). Instead, dehydration-induced conformational changes in pigment–protein complexes (Heber 2008) and the rapid structural reorganisation of PSII (Li et al. 2010) may provide DT plants with a rapid mechanism to shift between a dissipative and a photosynthetic state during desiccation-rehydration episodes.

Overall, the switching off of the photosynthetic machinery during desiccation in DT-species is clearly a well-organised mechanism that is absent in DS-species, and NPQ$_{DT}$ in PSII is not an artefact of desiccation but an active and indispensable response to dehydration in DT-species (Nabe et al. 2007), probably associated with changes occurring in PSII antennae (Heber 2008; Li et al. 2010; Miyake et al. 2011). The NPQ$_{DT}$ is not triggered either by light or a protonation reaction, but is triggered by the dehydration process and is rapidly reversed upon rehydration.

Diversity in the *modi operandi* of xanthophyll cycles: a case of plant memory?

All of the above underlines the existence of a high level of diversity in the modi operandi of xanthophyll cycles and of NPQ forms among plants, opening up a new perspective beyond the *Arabidopsis* model (Fig. 5). In the case of Lx-species, the V-cycle is complemented with an alternative xanthophyll (Lx) cycle, which can be reversible or, more frequently, truncated (García-Plazaola et al. 2007). The same occurs when dissipation is stabilised in winter evergreens and Z formed under light is not re-epoxidised to V in darkness. Conversely, in DT plants, the desiccation-rehydration event per se is enough to engage the complete operation of the cycle without the requirement for light and darkness. This diversity in the *modi operandi* seems to have evolved with the aim of coping with the dynamics of excess light in the particular environment to which a species has adapted, but also to promediate light conditions, or, more precisely, excess irradiance over long periods of time. It has been stated in previous sections that the main component of NPQ under conditions favourable to growth is the ΔpH-dependent one, with ΔpH acting as a switch and the degree of V de-epoxidation acting as an amplifier of the response. In comparison with the rapid ΔpH development, the relatively slow enzymatic kinetics frequently result in an uncoupling of the de-epoxidation state and the irradiance at that moment, mainly in natural canopies where light is randomly distributed in both space and time. The benefit of such uncoupling is that the de-epoxidation state acts as a 'molecular memory' of the average light conditions (or more precisely of the 'excitation pressure') over the previous minutes or hours (Horton and Ruban 2004; Jahns and Holzwarth 2012). This kind of short-term biochemical memory (Table 2), lasting only a few minutes,
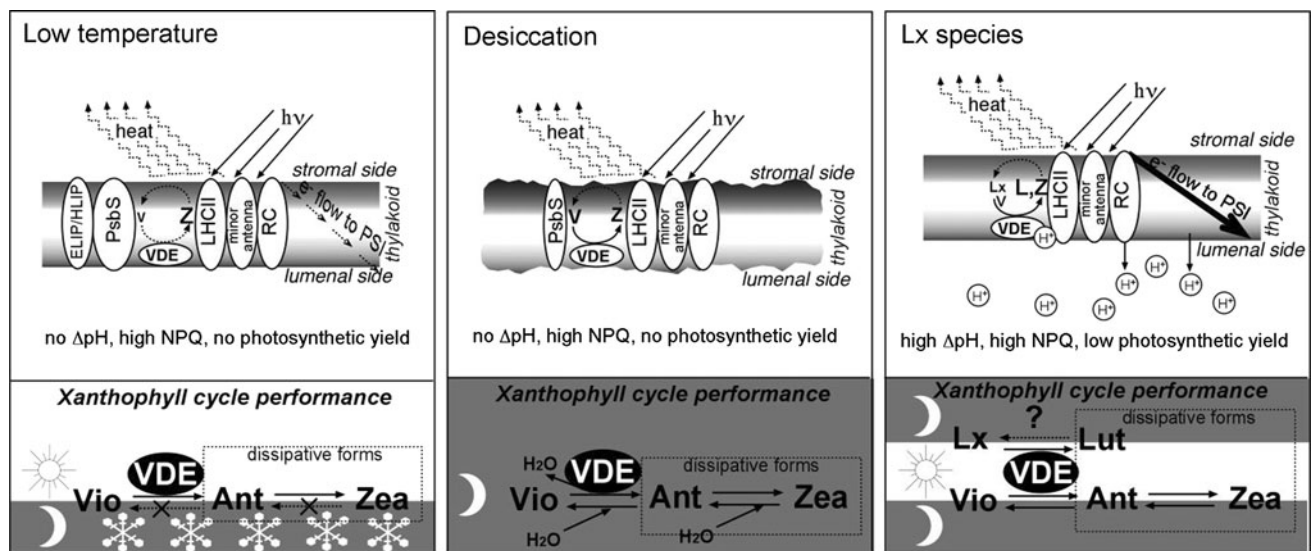
Fig. 5 Simplified models of the mechanisms involved in the regulation of sustained NPQ in the chosen examples: low temperature, desiccation and Lx-species. *Lower panels* show their respective xanthophyll cycle performances

would fulfil most requirements for a model plant in a growth chamber devoid of fluctuations in environmental stimuli. But longer-lived plants require a longer-term memory, capable of extracting the seasonal trends from the noisy, fluctuating environment. This can be achieved by modifications of the VAZ pool or the levels of certain proteins (PsbS, ELIPs, HLIPs). The magnitude of the VAZ pool is the result of the continuous light-controlled turnover rate of carotenoids (García-Plazaola et al. 2002; Beisel et al. 2010). Consequently, the VAZ pool correlates linearly with the integrated irradiance over the previous days or weeks (Niinemets et al. 2003). However, the amount of carotenoid-binding sites is limited, and the VAZ to chlorophyll ratio cannot increase forever. In experiments in which intact leaves were supplemented with extra artificial light, VAZ pool plateaued at about 200–300 mmol mol^{-1} Chl (Niinemets et al. 2003; Verhoeven et al. 1997). In the long-term, variations in the VAZ pool may be complemented by the overnight retention of de-epoxidised xanthophylls and the re-organization of the thylakoid membrane, with a significant decrease of PSII components (D1, Oxygen Evolving Complex) and a strong upregulation of ELIPs and HLIPs (Zarter et al. 2006c), as occurs under severe environmental conditions (see "Thermal dissipation in winter evergreens" section). In a scenario of more extreme conditions, such as the one suffered by DT plants, the memory response would not be enough to prevent damage, and a pre-emptive response, such as the synthesis of Z before light exposition, would be activated (Fernández-Marín et al. 2010). The operation of a parallel Lx-cycle in Lx-species adds complexity to this 'memory'. On the one hand, the reversible mode with slower recovery kinetics complements the V-cycle, thereby contributing to a finer adjustment of NPQ

Table 2 Diversity of the *Modus operandi* of xanthophyll cycles as a potential mechanism of biochemical 'memory'

Information received	Information stored	Response
Average light conditions for the last minutes	Epoxidation state of V- or Lx-cycle	Modulation of on/off responses of NPQ induced by ΔpH
Seasonally integrated excess light conditions	Variations in VAZ pool or PsbS levels	Amplification and/or stabilization of NPQ
Past illumination events of high intensity	Retention of ΔL	Stabilization of sustained NPQ
Seasonally sustained environmental stress	ELIP and HLIP levels	Stabilization of sustained NPQ
	Retention of AZ	
Future stress response required	Dark formation of Z	Amplification and/or stabilization of NPQ

(García-Plazaola et al. 2007). On the other hand, the retention of ΔL in the truncated Lx-cycle would represent the memory of a single illumination event of enough intensity to activate the mechanism. For example, in shade-acclimated leaves of avocado exposed to direct sun, the recovery of the initial Lx-pool may last more than 1 month (Förster et al. 2009), while regulating dissipative responses.

Functional diversity of thermal energy dissipation mechanisms

Throughout this review, it has been highlighted that NPQ may occur at different temporal domains and it can be

regulated by diverse mechanisms (Fig. 5). In plants with ecological niches in which severe environmental stresses (low temperature, desiccation) impair metabolism and are superimposed by irradiance, rapidly reversible ΔpH-dependent NPQ mechanisms are not enough to compensate for the excess light energy. Under these conditions, a set of ΔpH-independent NPQ mechanisms exists. Three mechanisms that could be included in the concept of downregulation have been shown in the present review: desiccation-induced NPQ, NPQ in winter evergreens and the truncated Lx-cycle with the formation of stable dissipative centres. They differ in the recovery kinetics of photochemical efficiency after the cessation of stress, lasting seconds to minutes in the first, hours to days in the second and weeks to no recovery in the last.

Overall, NPQ is the sum of a plethora of mechanisms, some of which are ΔpH-dependent, whereas others are not. Some require a long time to relax and others disengage in seconds. Some relate to the thermal deactivation of excitation energy and some may only denote an excitation energy transfer to PSI. Each plant will respond to environmental factors through the development of a different proportion of each of these components, limited by their intrinsic physiological constraints. In this sense, the *Arabidopsis* model has been extremely useful to characterise ΔpH-dependent mechanisms, but its stress avoider character restricts the possibility to transfer knowledge to other functional groups. The three examples shown here highlight these limitations. *Arabidopsis* lacks Lx, does not show sustained engagement of thermal dissipation at low temperature and dies upon desiccation. Therefore, different model species are needed in order to shed more light on the mechanisms behind sustained thermal energy dissipation, calling for an extension from the useful but highly simplified *Arabidopsis* model. For mosses, the choice could be easy: the moss *P. patens*, whose mitochondrial, chloroplastic and nuclear genomes have been fully sequenced, will provide valuable insights into the comparative physiology of the ancestral land plants (Lang et al. 2008). However, this moss lacks desiccation tolerance (Koster et al. 2010), greatly limiting its usefulness as a model for DT plants. The study of winter photoinhibition can be assessed by the use of close relatives of *A. thaliana* of a perennial nature, for which the molecular tools developed for *Arabidopsis* may be also valid. This could be the case of *Arabidopsis halleri*, frequently studied as a metal hyperaccumulator (Hanikenne et al. 2008) or *Arabis alpina*, a model used for the comparative study of the regulation of flowering time (Wang et al. 2009). An attempt to ascertain the mechanisms of winter downregulation cannot be fully accomplished without the study of evergreen woody species able to grow at high latitude or altitude. Among these, American pines such as *Pinus contorta* or

Pinus ponderosa (Demmig-Adams and Adams 2006; Zarter et al. 2006a, b) and the eurasian Scots pine (*Pinus sylvestris*) (Ottander and Öquist 1991; Ottander et al. 1995; Ivanov et al. 2002; Ensminger et al. 2004; Sveshnikov et al. 2006; Porcar-Castell et al. 2008a, b; Porcar-Castell 2011) are among the most widely studied. A model for Lx-cycle species is more elusive because most of them are trees and even in transgenic *lutOE Arabidopsis* plants, in which L replaces V (García-Plazaola et al. 2007), Lx is undetectable. Among Lx-species, the commonly cultivated avocado (*Persea americana*) has been used more frequently. Although on a much more modest scale than with *Arabidopsis*, the selection of a new generation of model species would definitely promote the understanding of the physiological mechanisms behind the complexity of NPQ and its regulation. Synergies would not only appear from the concentration of study results but probably more importantly from a substantial reduction in the time required for the development of species-specific methodologies (such as protein extractions or genetic studies). The use of a wider array of model species may lead in the near future to the development of a generic model of NPQ.

References

Adams WW III, Barker DH (1998) Seasonal changes in xanthophyll cycle-dependent energy dissipation in *Yucca glauca* Nuttall. Plant Cell Environ 21:501–512

Adams WW III, Demmig-Adams B, Verhoeven AS, Barker DH (1995) Photoinhibition during winter stress: involvement of sustained xanthophyll cycle-dependent energy dissipation. Aust J Plant Physiol 22:261–276

Adams WW III, Demmig-Adams B, Logan BA, Barker DH, Osmond CB (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 Environ 22:125–136

Adams WW III, Zarter CR, Ebbert V, Demmig-Adams B (2004) Photoprotective strategies of overwintering evergreens. Bioscience 54:41–49

Ahn TK, Avenson TJ, Ballottari M, Cheng Y-C, Niyogi KK, Bassi R, Fleming GR (2008) Architecture of a charge-tranfer state regulating light harvesting in a plant antenna protein. Science 320:794–796

Alboresi A, Gerotto C, Giacometti GM, Bassi R, Morosinotto T (2010) *Physcomitrella patens* mutants affected on heat dissipation clarify the evolution of photoprotection mechanisms upon land colonization. Proc Natl Acad Sci USA 107:11128–11133

Alpert P (2000) The discovery, scope, and puzzle of desiccation–tolerance in plants. Plant Ecol 151:5–17

Alpert P (2006) Constraints of tolerance: why are desiccation-tolerant organisms so small or rare? J Exp Biol 209:1575–1584

Augusti A, Scartazza A, Navari-Izzo F, Sgherri CLM, Stevanovic B, Brugnoli E (2001) Photosystem II photochemical efficiency, zeaxanthin and antioxidant contents in the poikilohydric *Ramonda serbica* during dehydration and rehydration. Photosynth Res 67:79–88

Baker NR (2008) Chlorophyll fluorescence: a probe of photosynthesis in vivo. Ann Rev Plant Biol 59:89–113

Beckett RP, Marschall M, Laufer Z (2005) Hardening enhances photoprotection in the moss *Atrichum androgynum* during rehydration by increasing fast- rather than slow-relaxing quenching. J Bryol 27:7–12

Beisel KG, Jahnke S, Hofmann D, Köppchen S, Schurr U, Matsubara S (2010) Continuous turnover of carotenes and chlorophyll a in mature leaves of *Arabidopsis* revealed by $^{14}CO_2$ pulse-chase labelling. Plant Physiol 152:2188–2199

Bilger W, Björkman O (1990) Role of the xanthophyll cycle in photoprotection elucidated by measurements of light-induced absorbance changes, fluorescence and photosynthesis in leaves of *Hedera canariensis*. Photosynth Res 25:173–185

Bonente G, Howes BD, Caffari S, Smulevich G, Bassi R (2008) Interactions between the photosystem II subunit PsbS and xanthophylls studied in vivo and in vitro. J Biol Chem 283:8434–8445

Bukhov NG, Kopecky J, Pfundel EE, Klughammer C, Heber U (2001) A few molecules of zeaxanthin per reaction centre of photosystem II permit effective thermal dissipation of light energy in photosystem II of a poikilohydric moss. Planta 212:739–748

Bungard RA, Ruban AV, Hibberd JM, Press MC, Horton P, Scholes JD (1999) Unusual carotenoid composition and a new type of xanthophyll cycle in plants. Proc Natl Acad Sci USA 96:1135–1139

Calatayud A, Deltoro VI, Barreno E, del Valle TS (1997) Changes in in vivo chlorophyll fluorescence quenching in lichen thalli as a function of water content and suggestion of zeaxanthin-associated associated photoprotection. Physiol Plant 101:93–102

Chazdon RL, Pearcy RW (1991) The importance of sunflecks for forest understory plants. BioScience 41:760–766

Csintalan Z, Proctor MCF, Tuba Z (1999) Chlorophyll fluorescence during drying and rehydration in the mosses *Rhytidiadelphus loreus* (Hedw.) Warnst., *Anomondon viticulosus* (Hedw.) Hook. & Tayl. And *Grimmia pulvinata* (Hedw.) Sm. Ann Bot 84:235–244

Dall'Osto L, Caffari S, Bassi R ((2005)) A mechanism of nonphotochemical energy dissipation, independent from PsbS, revealed by a conformational change in the antenna protein CP26. Plant Cell 17:1217–1232

Dall'Osto L, Lico C, Alric J, Giuliano G, Havaux M, Bassi R, 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 Biol 6:32–52

De Bianchi S, Ballottari M, Dall'Osto L, Bassi R ((2010)) Regulation of plant light harvesting by thermal dissipation of excess energy. Biochem Soc Trans 38:651–660

Degl'Innocenti E, Guidi L, Stevanovic B, Navari F (2008) CO_2 fixation and chlorophyll a fluorescence in leaves of *Ramonda serbica* during a dehydration-rehydration cycle. J Plant Physiol 165:723–733

Demmig-Adams B (1990) Carotenoids and photoprotection in plants: a role for the xanthophylls zeaxanthin. Biochim Biophys Acta 1020:1–24

Demmig-Adams B (1998) Survey of thermal energy dissipation and pigment composition in sun and shade leaves. Plant Cell Physiol 39:474–482

Demmig-Adams B, Adams WW (1996) The role of xanthophyll cycle carotenoids in the protection of photosynthesis. Trends Plant Sci 1:21–26

Demmig-Adams B, Adams WW (2006) Photoprotection in an ecological context: the remarkable complexity of thermal energy dissipation. New Phytol 172:11–21

Demmig-Adams B, Adams WW III, Czygan F-C, Schreiber U, Lange OL (1990) Differences in the capacity for radiationless energy dissipation in green and blue-green algal lichens associated with differences in carotenoid composition. Planta 180:582–589

Ebbert V, Adams WW III, Mattoo AK, Sokolenko A, Demmig-Adams B (2005) Upregulation of a PSII core protein phosphatase inhibitor and sustained D1 phosphorylation in zeaxanthin-retaining, photoinhibited needles of overwintering Douglas fir. Plant Cell Environ 28:232–240

Eickmeier WG, Casper C, Osmond CB (1993) Chlorophyll fluorescence in the resurrection plant *Selaginella lepidophylla* (Hook and Grev) Spring during high-light and desiccation stress, and evidence for zeaxanthin-associated photoprotection. Planta 189:30–38

Ensminger I, Sveshnikov D, Campbell DA, Funk C, Jansson S, Lloyd J, Shibistova O, Öquist G (2004) Intermittent low temperatures constrain spring recovery of photosynthesis in boreal Scots pine forests. Glob Change Biol 10:995–1008

Eskling M, Emanuelsson A, Åkerlund HE (2001) Enzymes and mechanisms for violaxanthin-zeaxanthin conversion. In: Aro EM, Andersson B (eds) Regulation of photosynthesis. Kluwer Academic Publishers, Dordrecht, pp 433–452

Esteban R, Jiménez ET, Jiménez MS, Morales D, Hormaetxe K, Becerril JM, García-Plazaola JI (2007) Dynamics of violaxanthin and lutein epoxide xanthophyll cycles in Lauraceae tree species under field conditions. Tree Physiol 27:1407–1414

Esteban R, Jiménez MS, Morales D, Jiménez ET, Hormaetxe K, Becerril JM, Osmond B, García-Plazaola JI (2008) Short- and long- term modulation of the lutein epoxide and violaxanthin cycles in two species of the Lauraceae: sweet bay laurel (*Laurus nobilis* L.) and avocado (*Persea Americana* Mill.). Plant Biol 10:288–297

Esteban R, Olano JM, Castresana J, Fernández-Marín B, Hernández A, Becerril JM, García-Plazaola JI (2009) Distribution and evolutionary trends of photoprotective isoprenoids (xanthophylls and tocopherols) within the plant kingdom. Physiol Plant 135:379–389

Esteban R, Matsubara S, Jiménez MS, Morales D, Brito P, Lorenzo R, Fernández-Marín B, Becerril JM, García-Plazaola JI (2010) Operation and regulation of lutein epoxide cycle in seedlings of *Ocotea foetens*. Funct Plant Biol 37:859–869

Fernández-Marín B, Balaguer L, Esteban R, Becerril JM, García-Plazaola JI (2009) Dark induction of the photoprotective xanthophyll cycle in response to dehydration. J Plant Physiol 166:1734–1744

Fernández-Marin B, Becerril JM, García-Plazaola JI (2010) Unraveling the roles of desiccation-induced xanthophyll cycle activity in darkness: a case study in *Lobaria pulmonaria*. Planta 231:1335–1342

Fernández-Marín B, Míguez F, Becerril JM, García-Plazaola JI (2011) Dehydration-mediated activation of the xanthophyll cycle in darkness: is it related to desiccation tolerance? Planta 243:579–588

Förster B, Osmond CB, Pogson BJ (2009) De novo synthesis and degradation of Lx and V cycle pigments during shade and sun acclimation in avocado leaves. Plant Physiol 149:1179–1195

Förster B, Pogson BJ, Osmond CB (2011) Lutein from deepoxidation of lutein epoxide replaces zeaxanthin to sustain an enhanced capacity for nonphoquemical chlorophyll fluorescence quenching in avocado shade leaves in the dark. Plant Physiol 156:393–402

Fukuda S, Yamakawa R, Hirai M, Kashino Y, Koike H, Satoh K (2008) Mechanisms to avoid photoinhibition in a desiccation-tolerant cyanobacterium, *Nostoc commune*. Plant Cell Physiol 49:488–492

García-Mendoza E, Colombo-Pallota MF (2007) The giant kelp *Macrocystis pyrifera* presents a different nonphotochemical quenching control than higher plants. New Phytol 173:526–536

García-Plazaola JI, Faria T, Abadía J, Abadía A, Chaves MM, Pereira JS (1997) Seasonal changes in xanthophyll composition and photosynthesis of cork oak (*Quercus suber* L.) leaves under mediterranean climate. J Exp Bot 48:1667–1674

García-Plazaola JI, Artetxe U, Hernández A, Becerril JM (2002) Regulation of xanthophyll cycle pool size in duckweed (*Lemna minor*) plants. Physiol Plant 116:121–126

García-Plazaola JI, Hernández A, Olano JM, Becerril JM (2003) The operation of the lutein epoxide cycle correlates with energy dissipation. Funct Plant Biol 30:319–324

García-Plazaola JI, Hormaetxe K, Hernández A, Olano JM, Becerril JM (2004) The lutein epoxide cycle in vegetative buds of woody plants. Funct Plant Biol 31:815–823

García-Plazaola JI, Matsubara S, Osmond B (2007) The lutein epoxide cycle in higher plants: its relationship to other xanthophyll cycles and possible functions. Funct Plant Biol 34:759–773

Gasulla F, Gómez de Nova P, Esteban-Carrasco A, Zapata JM, Barreno E, Guéra A (2009) Dehydration rate and time of desiccation affect recovery of the lichenic algae *Trebouxia erici*: alternative and classical protective mechanisms. Planta 231:195–208

Georgieva K, Szigeti Z, Savari E, Gaspar L, Maslenkova L, Peeva V, Peli E, Tuba Z (2007) Photosynthetic activity of homoiochlorophyllous desiccation tolerant plant *Haberlea rhodopensis* during dehydration and rehydration. Planta 225:955–964

Gilmore AM (1997) Mechanistic aspects of xanthophyll cycle-dependent photoprotection in higher plant chloroplasts and leaves. Physiol Plant 99:197–299

Gilmore AM, Björkman O (1994) Adenine nucleotides and the xanthophyll cycle in leaves. II. Comparison of the effects of CO_2- and temperature-limited photosynthesis on Photosystem II fluorescence quenching, the adenylate energy charge and violaxanthin deepoxidation in cotton. Planta 192:537–544

Gilmore AM, Matsubara S, Ball MC, Barker DH, Itoh S (2003) Excitation energy flow at 77 K in the photosynthetic apparatus of overwintering evergreens. Plant Cell Environ 26:1021–1034

Goss R, Torsten J (2010) Regulation and function of xanthophyll cycle-dependent photoprotection in algae. Photosynth Res 106:103–122

Grime JP (2002) Plant strategies, vegetation processes, and ecosystem properties. Willey, West Sussex

Hamerlynck EP, Csintalan Z, Nagy Z, Tuba Z, Goodin D, Henebry GM (2002) Ecophysiological consequences of contrasting microenvironments on the desiccation tolerant moss *Tortula ruralis*. Oecologia 131:498–505

Hanikenne M, Talke IN, Haydon MJ, Lanz C, Nolte A, Motte P, Kroymann J, Weigel D, Krämer U (2008) Evolution of metal hyperaccumulation required *cis*-regulatory changes and triplication of *HMA4*. Nature 453:391–396

Harker M, Berkaloff C, Lemoine Y, Britton G, Young AJ, Duval JC, Rmiki NE, Rousseau B (1999) Effects of high light and desiccation on the operation of the xanthophyll cycle in two marine brown algae. Eur J Phycol 34:35–42

Havaux M (1998) Carotenoids as membrane stabilizers in chloroplasts. Trends Plant Sci 3:147–151

Heber (2008) Photoprotection of green plants: a mechanism of ultra-fast thermal energy dissipation in desiccated lichens. Planta 228:641–650

Heber U, Shuvalov VA (2005) Photochemical reactions of chlorophyll in dehydrated photosystem II: two chlorophyll forms (680 and 700 nm). Photosynth Res 84:85–91

Heber U, Bilger W, Shuvalov VA (2006a) Thermal energy dissipation in reaction centres and in the antenna of photosystem II protects desiccated poikilohydric mosses against photo-oxidation. J Exp Bot 57:2993–3006

Heber U, Lange OL, Shuvalov VA (2006b) Conservation and dissipation of light energy as complementary processes: homoiohydric and poikilohydric autotrophs. J Exp Bot 57:1211–1223

Heber U, Azarkovich M, Shuvalov VA (2007) Activation of mechanisms of photoprotection by desiccation and by light: poikilohydric photoautotrophs. J Exp Bot 58:2745–2759

Heber U, Bilger W, Turk R, Lange OL (2010) Photoprotection of reaction centres in photosynthetic organisms: mechanisms of thermal energy dissipation in desiccated thalli of the lichen *Lobaria pulmonaria*. New Phytol 185:459–470

Heber U, Soni V, Strasser RJ (2011) Photoprotection of reaction centers: thermal dissipation of absorbed light energy vs charge separation in lichens. Physiol Plant 142:65–78

Hendrickson L, Förster B, Furbank RT, Chow WS (2004) Processes contributing to photoprotection of grapevine leaves illuminated at low temperature. Physiol Plant 121:272–281

Horton P, Ruban A (2004) Molecular design of the photosystem II light-harvesting antenna: photosynthesis and photoprotection. J Exp Bot 56:365–373

Horton P, Ruban AV, Walters RG (1996) Regulation of light harvesting in green plants. Annu Rev Plant Physiol Plant Mol Biol 47:665–684

Ivanov AG, Sane PV, Zeinalov Y, Simidjiev I, Huner NPA, Öquist G (2002) Seasonal responses of photosynthetic electron transport in Scots pine (*Pinus sylvestris* L.) studied by thermoluminescence. Planta 215:457–465

Jahns P, Holzwarth AR (2012) The role of xanthophyll cycle and of lutein in photoprotection of photosystem II. Biochim Biophys Acta 1817:182–193

Jahns P, Latowski D, Strzalka K (2009) Mechanism and regulation of the violaxanthin cycle: the role of antenna proteins and membrana lipids. Biochim Biophys Acta 1787:3–14

Kana R, Kotabová E, Sobotka R, Prásil O (2012) Non-photochemical quenching in cryptophyte alga *Rhodomonas salina* is located in chlorophyll a/c antennae. PLOS One 7:e29708

Kopecky J, Azarkovich M, Pfündel MM, Shuvalov VA, Heber U (2005) Thermal dissipation of light energy is regulated differently and by different mechanisms in lichens and higher plants. Plant Biol 7:156–167

Koster KL, Balsamo RA, Espinoza C, Oliver MJ (2010) Desiccation sensitivity and tolerance in the moss *Physcomitrella patens*: assessing limits and damage. Plant Growth Regul 62:293–302

Kosugi M, Arita M, Shizuma R, Moriyama Y, Kashino Y, Koike H, Satoh K (2009) Responses to desiccation stress in lichens are different from those in their photobionts. Plant Cell Physiol 50:879–888

Kranner I, Beckett RP, Wornik S, Zorn M, Pfeifhofer HW (2002) Revival of a resurrection plant correlates with its antioxidant status. Plant J 31:13–24

Kranner I, Zorn M, Turk B, Wornik S, Batic F (2003) Biochemical traits of lichens differing in relative desiccation tolerance. New Phytol 160:167–176

Kranner I, Cram WJ, Zorn M, Wornik S, Yoshimura I, Stabentheiner E, Pfeifhofer HW (2005) Antioxidants and photoprotection in a lichen as compared with its isolated symbiotic partners. Proc Natl Acad Sci USA 102:3141–3146

Kranner I, Beckett RP, Hochman A, Nash T III (2008) Desiccation tolerance in lichens: a review. Bryologist 111:576–593

Krause GH (1988) Photoinhibition of photosynthesis. An evaluation of damaging and protective mechanisms. Physiol Plant 74:566–574

Krause GH, Weis E (1991) Chlorophyll fluorescence and photosynthesis: The basics. Annu Rev Plant Phys 42:313–349

Külheim C, Ågren J, Jansson S (2002) Rapid regulation of light harvesting and plant fitness in the field. Science 297:91–93

Lang D, Zimmer AD, Rensing SA, Reski R (2008) Exploring plant biodiversity: the Physcomitrella genome and beyond. Trends Plant Sci 13:542–549

Lee HY, Hong YN, Chow WS (2001) Photoinactivation of Photosystem II complexes and photoprotection by non-functional neighbours in Capsicum annuum L. leaves. Planta 212:332–342

Li XP, Björkman O, Shih C, Grossman AR, Rosenquist M, Jansson S, Niyogi KK (2000) A pigment-binding protein essential for regulation of photosynthetic light harvesting. Nature 403:391–395

Li XP, Gilmore AM, Caffarri S, Bassi R, Golan T, Kramer D, Niyogi KK (2004) Regulation of photosynthetic light harvesting involves intrathylakoid lumen pH sensing by the PsbS protein. J Biol Chem 279:22866–22874

Li Z, Anh KT, Avenson TJ, Ballottari M, Cruz JA, Kramer DM, Bassi R, Fleming GR, Keasling JD, Niyogi KK (2009) Lutein accumulation in the absence of zeaxanthin restores nonphotochemical quenching in the Arabidopsis thaliana npq1 mutant. Plant Cell 21:1798–1812

Li Y, Wang ZB, Xu TH, Tu WF, Liu C, Zhang YM, Yang CH (2010) Reorganization of photosystem II is involved in the rapid photosynhtetic recovery of desert moss Syntrichia caninervis upon rehydration. J Plant Physiol 167:1390–1397

Logan BA, Barker DH, Adams WW III, Demmig-Adams B (1997) The response of xanthophyll cycle-dependent energy dissipation in Alocasia brisbanensis to sunflecks in a subtropical rainforest. Aust J Plant Physiol 24:27–33

Lüttge U (1997) Physiological ecology of tropical plants. Springer, Berlin–Heidelberg

Marschall M, Proctor MCF (1999) Desiccation tolerance and recovery of the leafy liverwort Porella platyphylla (L.) Pfeiff.: chlorophyll-fluorescence measurements. J Bryol 21:257–262

Matsubara S, Gilmore AM, Osmond CB (2001) Diurnal and acclimatory responses of violaxanthin and lutein epoxide in the Australian mistletoe Amyema miquelii. Aust J Plant Physiol 28:793–800

Matsubara S, Gilmore AM, Ball MC, Anderson JM, Osmond CB (2002) Sustained downregulation of photosystem II in mistletoes during winter depression of photosynthesis. Funct Plant Biol 29:1157–1169

Matsubara S, Naumann M, Martin R, Nichol C, Rascher U, Morosinotto T, Bassi R, Osmond B (2005) Slowly reversible de-epoxidation of lutein-epoxide in deep shade leaves of a tropical tree legume may "lock in" lutein-based photoprotection during acclimation to strong light. J Exp Bot 56:461–468

Matsubara S, Morosinotto T, Osmond B, Bassi R (2007) Short- and long-term operation of the lutein epoxide cycle in light harvesting antenna complexes. Plant Physiol 144:926–941

Matsubara S, Krause GH, Seltmann M, Virgo A, Kursar TA, Jahns P, Winter K (2008) Lutein epoxide cycle, light harvesting and photoprotection in species of the tropical tree genus Inga. Plant Cell Environ 31:548–561

Matsubara S, Krause GH, Aranda J, Virgo A, Beisel KG, Jahns P, Winter K (2009) Sun-shade patterns of leaf carotenoid composition in 86 species of neotropical forest plants. Funct Plant Biol 36:20–36

Matsubara S, Chen YC, Caliandro R, Govindjee CRM (2011) Photosystem II fluorescence lifetime imaging in avocado leaves: Contributions of the lutein epoxide and violaxanthin cycles to fluorescence quenching. J Photochem Photobiol B 104:271–284

Meinke DW, Cherry JM, Dean C, Rounsley SD, Koornneef M (1998) Arabidopsis thaliana: a model plant for genome analysis. Science 282:662–682

Mihailova G, Petkova S, Buchel C, Georgieva K (2011) Desiccation of the resurrection palnt Haberlea rhodopensis at high temperature. Photosynth Res 108:5–13

Miyake H, Komura M, Itoh S, Kosugi M, Kashino Y, Satoh K, Shibata Y (2011) Multiple dissipation components of excess light energy in dry lichen revealed by ultrafast fluorescence study at 5 K. Photosynth Res 110:39–48

Müller P, Li X-P, Niyogi KK (2001) Non-photochemical quenching. A response to excess light energy. Plant Physiol 125:1558–1566

Murchie EH, Niyogi KK (2011) Manipulation of photoprotection to improve plant photosynthesis. Plant Physiol 155:86–92

Nabe H, Funabiki R, Kashino Y, Koike H, Satoh K (2007) Responses to desiccation stress in bryophytes and important role of dithiothreitol-insensitive non-photochemical quenching against photoinhibition in dehydrated states. Plant Cell Physiol 48:1548–1557

Nichol C, Pieruschka TK, Förster B, Kolber Z, Rascher U, Grace J, Robinson SA, Pogson B, Osmond B (2012) Canopy conundrums: building on the Biosphere 2 experience to scale measurements of inner and outer canopy photoprotection from the leaf to the landscape. Funct Plant Biol 39:1–24

Niinemets U, Kollist H, García-Plazaola JI, Hernández A, Becerril JM (2003) Do the capacity and kinetics for modification of xanthophyll cycle pool size depend on growth irradiance in temperate trees? Plant Cell Environ 26:1787–1801

Nilkens M, Kress E, Lambrev P, Miloslavina Y, Müller M, Holzwarth AR, 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. Biochim Biophys Acta 1797:466–475

Ogaya R, Peñuelas J (2003) Comparative seasonal gas exchange and chlorophyll fluorescence of two dominant woody species in a Holm Oak Forest. Flora 198:132–141

Oliver MJ, Tuba Z, Mishler BD (2000) The evolution of vegetative desiccation tolerance in land plants. Plant Ecol 151:85–100

Ottander C, Öquist G (1991) Recovery of photosynthesis in winter-stressed Scots pine. Plant Cell Environ 14:345–349

Ottander C, Campbell D, Öquist G (1995) Seasonal changes in photosystem II organization and pigment composition in Pinus sylvestris. Planta 197:176–183

Pascal AA, Liu Z, Broesse K, van Oort B, van Amerongen H, Wang C, Horton P, Bassi R, Chang W, Ruban A (2005) Molecular basis of photoprotection and control of photosynthetic light-harvesting. Nature 436:134–137

Peers G, Truong TB, Ostendorf E, Busch A, Elrad D, Grossman AR, Hippler M, Niyogi KK (2009) An ancient light-harvesting protein is critical for the regulation of algal photosynthesis. Nature 462:518–521

Peeva V, Cornic G (2009) Leaf photosynthesis of Haberlea rhodopensis before and during drought. Environ Exp Bot 65:310–318

Pogson BJ, Rissler HM (2000) Genetic manipulation of carotenoid biosynthesis and photoprotection. Phil Trans R Soc London Series B, Biol Sci 355:1395–1403

Porcar-Castell A (2011) A high-resolution portrait of the annual dynamics of photochemical and non-photochemical quenching in needles of Pinus sylvestris. Physiol Plant 143:139–153

Porcar-Castell A, Juurola E, Nikinmaa E, Berninger F, Ensminger I, Hari P (2008a) Seasonal acclimation of photosystem II in Pinus sylvestris. I. Estimating the rate constants of sustained thermal energy dissipation and photochemistry. Tree Physiol 28:1475–1482

Porcar-Castell A, Juurola E, Ensminger I, Berninger F, Hari P, Nikinmaa E (2008b) Seasonal acclimation of photosystem II in

Pinus sylvestris. II. Using the rate constants of sustained thermal energy dissipation and photochemistry to study the effect of the light environment. Tree Physiol 28:1483–1491

Porcar-Castell A, García-Plazaola JI, Nichol CJ, Kolari P, Olascoaga B, Kuusinen N, Fernández-Marín B, Pulkkinen M, Juurola E, Nikinmaa E (2012) Physiology of the seasonal relationship between the photochemical reflectance index and photosynthetic light use efficiency. Oecologia. doi:10.1007/s00442-012-2317-9

Proctor MCF, Tuba Z (2002) Poikilohydry and homoihydry: antithesis or spectrum of possibilities? New Phytol 156:327–349

Rascio N, La Rocca N (2005) Resurrection plants: the puzzle of surviving extreme vegetative desiccation. Plant Sci 24:209–225

Ruban AV, Berera R, Ilioaia C, van Stokkum IHM, Kennis JTM, Pascal AA, van Amerongen H, Robert B, Horton P, van Grondelle R (2007) Identification of a mechanism of photoprotective energy dissipation in higher plants. Nature 450:575–578

Somerville C, Koornneef M (2002) A fortunate choice: the story of *Arabidopsis* as a model plant. Nature Rev Genetics 3:883–889

Sveshnikov D, Ensminger I, Ivanov AG, Campbell D, Lloyd J, Funk C, Huner NPA, Öquist G (2006) Excitation energy partitioning and quenching during cold acclimation in Scots pine. Tree Physiol 26:325–336

Tuba Z (2008) Notes on the poikilochlorophyllous desiccation-tolerant plants. Acta Biol Szegediensis 52:111–113

Tuba Z, Proctor MCF, Csintalan Z (1998) Ecophysiological responses of homoiochlorophyllous and poikilochlorophyllous desiccation-tolerant plants: a comparison and an ecological perspective. Plant Growth Reg 24:211–217

Tyystjärvi E, Aro E-M (1996) The rate constant of photoinhibition, measured in lincomycin-treated leaves, is directly proportional to light intensity. Proc Natl Acad Sci USA 93:2213–2218

Valladares F, Niinemets Ü (2008) Shade tolerance, a key plant feature of complex nature and consequences. Ann Rev Ecol Evol Syst 39:237–257

Veerman J, Vasil'ev S, Paton GD, Ramanauskas J, Bruce D (2007) Photoprotection in the lichen *Parmelia sulcata*: the origins of desiccation-induced fluorescence quenching. Plant Physiol 145:997–1005

Verhoeven AS, Adams WW III, Demmig-Adams B (1996) Close relationship between the state of the xanthophyll cycle pigments and photosystem II efficiency during recovery from winter stress. Physiol Plant 96:567–576

Verhoeven AS, Demmig-Adams B, Adams WW III (1997) Enhanced employment of the xanthophyll cycle and thermal energy dissipation in spinach exposed to high light and N stress. Plant Physiol 113:817–824

Vertucci CW, Farrant JM (1995) Acquisition and loss of desiccation tolerance. In: Galili KL (ed) Seed development and germination. Marcel Dekker Press, New York

Wang R, Farrona S, Vincent C, Joecker A, Schoof H, Turck F, Alonso-Blanco C, Coupland G, Albani MC (2009) *PEP1* regulates perennial flowering in *Arabis alpina*. Nature 459:423–427

Watling JR, Robinson SA, Woodrow IE, Osmond CB (1997) Responses of rainforest understorey plants to excess light during sunflecks. Aust J Plant Physiol 24:17–25

Watson TL, Close DC, Davidson NJ, Davies NW (2004) Pigment dynamics during cold-induced photoinhibition of *Acacia melanoxylon*. Funct Plant Biol 31:481–489

Wilson A, Ajlani G, Verbavatz JM, Vass I, Kerfeld CA, Kirilovsky D (2006) A soluble carotenoid protein involved in phycobilisome-related energy dissipation in cyanobacteria. Plant Cell 18: 992–1007

Xu DH, Li JH, Fang XW, Wang G, Su PX (2008) Photosynthetic activity of poikilochlorophyllous desiccation tolerant plant *Reaumuria soongorica* during dehydration and re-hydration. Photosynthetica 46:547–551

Zarter CR, Adams WW III, Ebbert V, Cuthbertson D, Adamska I, Demmig-Adams B (2006a) Winter downregulation of intrinsic photosynthetic capacity coupled with upregulation of Elip-like proteins and persistent energy dissipation in a subalpine forest. New Phytol 172:272–282

Zarter CR, Demmig-Adams B, Ebbert V, Adamska I, Adams WW III (2006b) Photosynthetic capacity and light harvesting efficiency during the winter-to-spring transition in subalpine conifers. New Phytol 172:283–292

Zarter CR, Adams WW III, Ebbert V, Adamska I, Jansson S, Demmig-Adams B (2006c) Winter acclimation of PsbS and related proteins in the evergreen *Arctostaphyllos uva-ursi* as influenced by altitude and light environment. Plant Cell Environ 29:869–878