Chapter 11
Photoprotective Mechanisms in the Genus *Quercus* in Response to Winter Cold and Summer Drought

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Abstract The photosynthetic apparatus must cope with the excess energy when light exceeds what plant can use. Under these conditions, plants, including oaks, can activate an array of "photoprotection mechanisms", which are crucial to understand the relationships between plants and their environment. First, this chapter gives a general description of the different photoprotection mechanisms that operate at several levels: (i) the reduction of light collection by chlorophylls, (ii) the enhancement of the metabolic use of light energy absorbed, (iii) the enhancement of the dissipation of the absorbed energy as heat, and (iv) the mechanisms for preventing and repairing oxidative damage (Sect. 11.1). These photoprotection mechanisms are subsequently analyzed in detail for evergreen oaks exposed to winter stress (Sect. 11.2) and for both deciduous and evergreen oaks under drought-stress conditions (Sect. 11.3), with particular emphasis on the role of free and enzymatic antioxidants, xanthophyll cycles and sustained engagement of dissipation. Afterwards, the chapter addresses with the need of photoprotection in deciduous oaks during autumn senescence associated to the risks of chlorophyll degradation and reactive oxygen species (ROS) generation (Sect. 11.4).

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E. Gil-Pelegrín et al. (eds.), *Oaks Physiological Ecology. Exploring the Functional Diversity of Genus* Quercus *L.*, Tree Physiology 7,
https://doi.org/10.1007/978-3-319-69099-5_11

11.1 Photoprotection in Leaves, the Basics

Whenever light exceeds what plants can use, the photosynthetic apparatus has the unavoidable need to get rid of the excess energy by activating an array of "photoprotection mechanisms". Photoprotection is foundational to understand the relationships between plants and their environment and it has been recently reviewed by several authors (e.g. Goss and Lepetit 2015; Ruban 2016; Wobbe et al. 2015). Basically, photoprotection mechanisms operate at several hierarchic levels that first, reduce light collection by chlorophylls (Sect. 11.1.2); second, enhance the metabolic use of light energy absorbed (Sect. 11.1.3); third, enhance the dissipation of the absorbed energy as heat (Sect. 11.1.4); and fourth, prevent and repair oxidative damage (Sect. 11.1.5).

11.1.1 Dealing with Light Excess in Quercus Canopies

Applying a shade tolerance index that ranges from 0-untolerant to 5-maximum tolerance, Niinemets and Valladares (2006) classified 57 oak species as intermediate shade-tolerant or shade-intolerant species (index 1–3.5), reaching scores lower than those of the traditionally considered shade-tolerant genus, such as *Abies*, *Picea*, *Acer* or *Fagus* (index 4–5) (Fig. 11.1). As a consequence of this limited shade-tolerance, *Quercus* seedlings usually regenerate in the understory of relatively open canopies, but cannot compete under deep shade with seedlings of more shade-tolerant species, such as beech (Hansen et al. 2002). To survive in such open understories, oak seedlings have to be able to dynamically adjust photosynthetic activity and photoprotection mechanisms to changes in light environment, such as those generated by canopy opening, while maintaining a high photosynthetic gain (Hansen et al. 2002; Naidu and De Lucia 1997). However, even among *Quercus* species, the degree of such plasticity differs, with the more shade-tolerant being less plastic and more susceptible to high light (Rodríguez-Calcerrada et al. 2007).

11.1.2 Decreasing Light Absorption: Morphological and Biochemical Adjustments

When light interception by photosynthetic cells is in excess of what plants can use, it can be reduced efficiently through the development of plastic morphological modifications. Most of them are slowly reversible in the short-term and they can be grouped in two main categories: (1) changes in leaf anatomy and morphology (leaf and petiole angle, lamina size, leaf rolling, chloroplast movements) and (2) changes in leaf reflectance (pubescence, wax deposition, accumulation of red pigments) and/or regulation of antenna size. A comparative examination of the leaves developed in

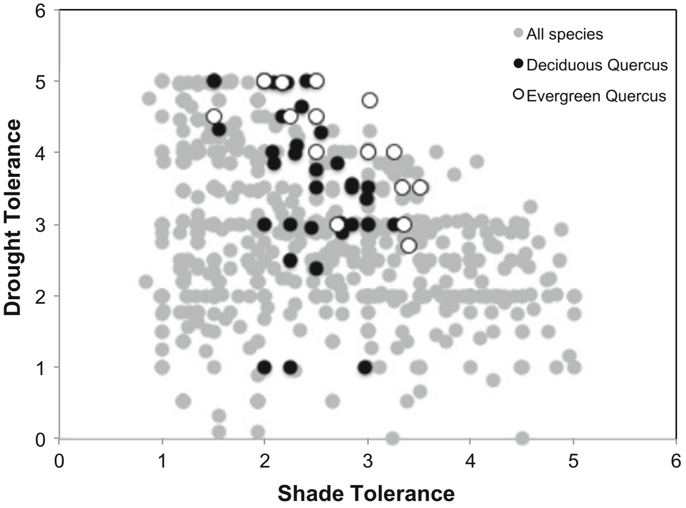


Fig. 11.1 Relationship between shade tolerance and drought tolerance indexes in *Quercus* species in the context of northern hemisphere trees and shrubs. Database published by Niinemets and Valladares (2006), (see the original publication for details on index calculation). Light grey symbols show data from all species included in the database, black symbols correspond to deciduous *Quercus* species, and white symbols to evergreen species

the outer (sun) and inner (shade) crown of a well-developed *Quercus* tree immediately reveals most of these characters, particularly in the more plastic species such as *Q. velutina* or *Q. coccifera*. Thus, when developed in a sunny position, leaves are thicker, with more layers of palisade parenchyma and higher epidermal cell thickness (Ashton and Berlyn 1994). Leaf angle also responds to canopy position and, for example in *Q. coccifera,* there is considerable variation in this character, with steeper leaves in the upper canopy and more horizontal shade leaves (Rubio de Casas et al. 2007). Leaf rolling is also common among Mediterranean *Quercus* species and it increases with irradiance within the canopy, reducing the effective light-interception area (Niinemets 2007). At the biochemical level, irradiance acclimation within *Quercus* canopies is reflected by a shift to higher values of chlorophyll (Chl) *a/b* and Carotenoid/Chl ratios in more exposed positions (Hansen et al. 2002). As Chl *b* is only present in light harvesting complexes (LHCs) and carotenoids are mostly involved in photoprotection, these trends are indicative of a change from efficient light harvesting under low irradiance to high capacity for energy dissipation in sunny positions.

Other foliar traits that greatly affect leaf interaction with the environment are pubescence (presence of hairs) and glaucescence (presence of waxes). The presence of a hairy epidermis increases both the thickness of the boundary layer (Bacelar et al. 2004) and the leaf hydrophobicity (Brewer et al. 1991) and reduces the susceptibility to herbivory (Karioti et al. 2011). In *Q. ilex*, adaxial trichomes can also contribute to water absorption thanks to their high hydrophilicity (Fernández et al. 2014). However, the exact selective pressure that makes a plant species pubescent is difficult to demonstrate. Independently of what is the main function of trichomes, pubescence always generates a change in the spectral properties of leaves (Holmes and Keiller 2002) increasing light reflectance at all wavelengths of the spectrum and consequently, reducing leaf absorptance up to 50% in some species (Ehleringer 1982).

In the case of *Quercus* species, trichomes are mainly present in the abaxial leaf surface, but some species (i.e.: *Q. ilex*, *Q. pyrenaica*, *Q. pubescens*, *Q. macranthera*) have trichomes in the adaxial side of their leaves, at least during the early stages of their development (Bussotti and Grossoni 1997; Hardin 1979). An unavoidable consequence of the presence of leaf trichomes is that the uniform photon scattering at all wavelengths caused by the hairy surface reduces light reaching the mesophyll (Karabourniotis and Bornman 1999). For example, when trichomes were mechanically removed from *Q. ilex* leaves, reflectance decreased by 5% (Morales et al. 2002). Furthermore, this treatment also enhanced susceptibility to photoinhibition, demonstrating the photoprotective role of leaf pubescence for this species (Morales et al. 2002). Similarly, reflectance from hairless species such as *Q. coccifera* is on average 5% lower than in *Q. ilex* (Morales et al. 2002). In agreement with a protective role, it has been shown that in *Q. ilex* pubescence is higher in xeric ecotypes compared to mesic ones (Camarero et al. 2012). Apart from their role in protection against excessive radiation, trichomes also contribute in *Q. ilex* to attenuate UVA and UVB protection thanks to the presence of flavonoids (Karabourniotis and Bornman 1999). However, this is probably not the main factor determining pubescence, as shown by the decrease in leaf hair density with increasing elevation (and consequently UV exposure) in *Q. ilex* (Filella and Peñuelas 1999).

In some *Quercus* species, leaf reddening is conspicuous at certain developmental stages. The question of the functional role of leaf reddening (caused by the accumulation of anthocyanins, carotenoids or betacyanins) has been tackled by a surprisingly high number of studies (reviewed in Chalker-Scott 1999; Hughes 2011; Steyn et al. 2002). Two main hypotheses have been tested in those studies: red pigments act as light filters reducing the irradiance reaching the photosynthetic cell layers, or alternatively, red molecules act as antioxidants. An alternative hypothesis, not related to photoprotection is that red colouration in leaves represents a type of communication signal between plants and insects (Archetti et al. 2008). This hypothesis has been experimentally tested in *Q. coccifera* by Karageorgou and Manetas (2006). These authors showed that green leaves were more damaged by herbivore insects with little differences on photoinhibition between both phenotypes. Despite the role in bio-communication, the photoprotective hypothesis is also supported in *Quercus* species by the fact that anthocyanins appear during critical phenological periods such as leaf expansion in *Q. coccifera* (Manetas et al. 2003) or *Q. ilex* (Brossa et al. 2009) and autumn senescence in *Q. rubra* (Lee et al. 2003) or *Q. palustris* (Boyer et al. 1988) (see also Sect. 11.4.2); but also in response to low temperature stress in evergreen *Quercus* species (Ramírez-Valiente et al. 2015) (see Sect. 11.2.1). Such anthocyanin accumulation is triggered by light, and consequently is not observed when senescing leaves are artificially shaded (Lee et al. 2003). Furthermore, when comparing young leaves from red and green phenotypes of *Q. coccifera*, the higher photochemical efficiency of first, together with their shade-like phenotype (Manetas et al. 2003), support that shading generated by the accumulation of such pigments enhances photoprotection during leaf expansion.

11.1.3 Metabolic Dissipation

Another mechanism that can reduce over-excitation of the photosynthetic machinery is to enhance the metabolic use of the light energy absorbed by processes as photorespiration, the cyclic electron transport,the water-water cycle or/and the chlororespiration. All these processes act as alternative electron sinks, thus preventing damage to the photosynthetic apparatus (Ort and Baker 2002).

Photorespiration results in a light-driven loss of CO_2 from cells that are simultaneously fixing CO_2 by the Calvin cycle. Photorespiratory reactions can dissipate the energy excess either directly (by ATP, NAD(P)H and reduced ferredoxin) or indirectly (*e.g.*, via alternative oxidase and providing an internal CO_2 pool) (Voss et al. 2013). This process has been described also for species of the genus *Quercus* in response to different stress factors (see Sect. 11.3.1) as: (i) water stress in *Q. ilex* (Tsonev et al. 2014), (ii) drought stress in *Q. suber*, *Q. ilex* and *Q. coccifera* (Peguero-Pina et al. 2009), (iii) low temperature in *Q. guyavifolia* (Huang et al. 2016a), (iv) high temperature in *Q. ilex* (Peñuelas and Llusia 2002) and (v) high temperature combined with high CO_2 in resprouts from *Q. ilex* (Pintó-Marijuan et al. 2013). In the latter, photorespiration was showed to be dependent on CO_2 concentration (Pintó-Marijuan et al. 2013). These data suggest that photorespiration provides a “safety-valve” for excess energy to avoid photochemical damage when CO_2 assimilation is inhibited (Peñuelas and Llusia 2002), thus preventing accumulation of reactive oxygen species (ROS) (Voss et al. 2013). The leaf internal CO_2 pool provided by photorespiration supports the Calvin cycle and isoprenoid biosynthesis (Peñuelas and Llusia 2002).

Chlororespiration also might play a role in the regulation of photosynthesis by modulating the activity of cyclic electron flow around photosystem (PS) I (Peltier and Cournac 2002). Besides, it has been described as a protective mechanism based on the induction of chloroplast NAD(P)H dehydrogenase by stressful treatments (e.g. Öquist and Huner 2003; Streb et al. 2005). This protective role was studied in winter-acclimated *Q. ilex* and *Q. suber,* whose leaves produced zeaxanthin (Z) in darkness (possibly by creation of a chlororespiratory pH-gradient), contributing to winter hardening. (Brüggemann et al. 2009). Cyclic electron flow around PSI and water-water cycle have been found to be involved in winter photoprotection of evergreen Asian oaks *Q. douglasii* and *Q. guyavifolia* (Huang et al. 2016b).

The Mehler reaction, that reduces oxygen to superoxide anion (O_2^-), and subsequently to water by the ascorbate-glutathione pathway (described in Sect. 11.1.5.) is other major sink for the electrons from the photosynthetic electron transport chain.

11.1.4 Enhancing Dissipation

Once light has been absorbed, the first site of photoprotection is within the LHCs themselves. If light is excessive and excited Chl is unable to drive photochemistry, then the lifetime of the singlet state is extended, resulting in a higher yield of triplet state formation. This is undesirable because energy transfer from triplet Chl to oxygen generates singlet oxygen ($^1O_2$), a highly reactive type of ROS. However, in addition to driving photochemistry, excited Chl can return to the ground state by the emission of light (chlorophyll fluorescence) or by the harmless emission of heat (safe thermal dissipation of excess absorbed light energy), a process that is modulated by the xanthophyll cycles. The latter route is a major component of photoprotection, also termed non-photochemical quenching (NPQ) as it results in an easily measurable quenching of chlorophyll fluorescence (Müller et al. 2001; Murchie and Niyogi 2011). Two xanthophyll cycles associated to the thermal energy dissipation have been described in higher plants so far: the ubiquitous violaxanthin-zeaxanthin cycle (VAZ-cycle) and the taxonomically restricted lutein epoxide-lutein cycle (LxL-cycle) (Esteban and García-Plazaola 2014).

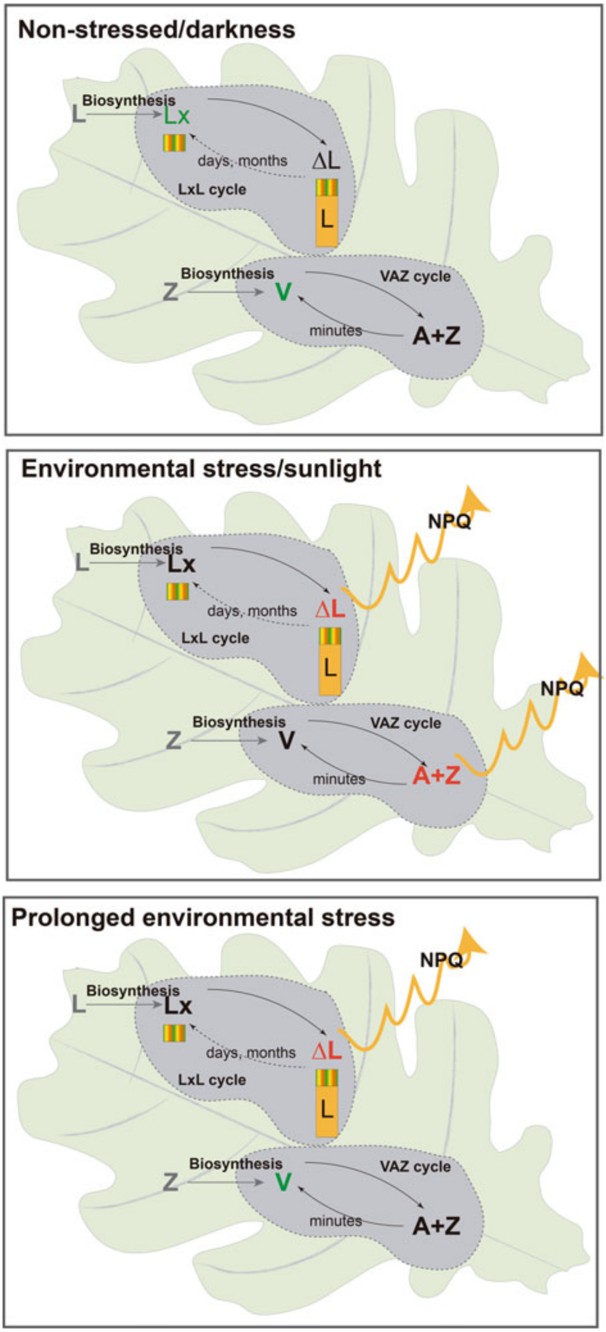
The regulation of energy dissipation through NPQ associated to the VAZ-cycle is one of the main photoprotective mechanisms described in higher plants (Niyogi 1999). The cycle involves inter-conversions between three carotenoids in the thylakoid membrane: violaxanthin (V), antheraxanthin (A) and zeaxanthin (Z). Under excess light, the efficient PSII light-harvesting antenna is switched into a photoprotected state in which the potentially harmful excess of absorbed energy is thermally dissipated. Changes occur rapidly and reversibly, enhanced by the de-epoxidation of V to Z via A. This mechanism has been described in many *Quercus* species in response to different stress factors (see Sects. 11.2.2 and 11.3.2 for a more detailed description of the regulation of NPQ by these stresses): (i) the excess of light (e.g. *Q. suber*, García-Plazaola et al. 1997; *Q. ilex*, Corcuera et al. 2005a; *Q. alba*, Wang and Bauerle 2006; *Q. petraea*, Rodríguez-Calcerrada et al. 2007; *Q. coccifera*, Peguero-Pina et al. 2013); (ii) summer drought (e.g. *Q. coccifera*, Peguero-Pina et al. 2008; *Q. ilex* and *Q. suber*, Peguero-Pina et al. 2009), and (iii) winter stress due to low temperatures (e.g. *Q. ilex*, Corcuera et al. 2005b; Camarero et al. 2012; *Q. myrsinaefolia*, Yamazaki et al. 2011).

The light-driven inter-conversions between lutein epoxide (Lx) and lutein (L) in the thylakoid membrane, constitutes the LxL-cycle (Fig. 11.2). This cycle operates concurrently with the VAZ-cycle (Esteban and García-Plazaola 2014). Lutein epoxide de-epoxidation enhances the already large pool of L in leaves, giving rise to newly formed L molecules (ΔL) (Nichol et al. 2012). In darkness, the epoxidation back from ΔL to Lx operates at two modes: one "completed", in which the initial Lx pool is restored in minutes or hours, and one "truncated", in which ΔL remains for a longer period (days or weeks). The latter, has been widely described in leaves of the genus *Quercus*: *Q. ilex*, (Llorens et al. 2002); *Q. ilex*, *Q. coccifera*, *Q. robur*, *Q. faginea* and *Q. suber*, (García-Plazaola et al. 2002); *Q. rubra* (García-Plazaola et al. 2003a). In addition, the "truncated" LxL-cycle has been also described in the enclosed buds of some woody plants, as *Q. robur*, when bud-burst takes place (García-Plazaola et al. 2004). The regulation of energy dissipation through NPQ is, as in the case for the VAZ-cycle, associated to the operation of LxL-cycle (Esteban and García-Plazaola 2014). Indeed, faster engagement of NPQ in leaves with ΔL not containing A + Z prior to light exposure was described in *Q. rubra* under light stress (García-Plazaola et al. 2003a). The ecophysiological significance of this "truncated" LxL-cycle in species of the genus *Quercus* relies on the fact that Lx de-epoxidation may represent an emergency mechanism of special relevance for long-term downregulation of photosynthetic efficiency, supplementing retention of Z + A and their sustained engagement in energy dissipation in response to prolonged environmental stress, in cases of winter or summer acclimation (Llorens et al. 2002; García-Plazaola et al. 2002) or sudden exposure to high light, as the generation of forest gaps or budbreak (Esteban and García-Plazaola 2014). Thus, the combination of both cycles increases the plasticity of photoprotective responses in *Quercus* species.

11.1.5 Antioxidant and Repair Mechanisms (Free and Enzymatic Antioxidants)

Environmental stress conditions that result in restricted CO_2 fixation rates can induce an imbalance between the generation and utilization of photosynthetic electrons. Thus, whenever excess excitation energy is not safely removed, photo-oxidative damage can occur due to an enhanced formation of ROS in the chloroplasts (Hernández et al. 2012). Besides the oxidation of different molecules (i.e. lipids, proteins, sugars, nucleic acids), ROS may also impair the PSII repair process through the inhibition of the de novo synthesis of PSII proteins (primarily the D1 protein) (Takahashi and Badger 2011). To cope with this situation, chloroplasts possess non-enzymatic and enzymatic antioxidant defense mechanisms. These mechanisms detoxify ROS and maintain an adequate cellular redox balance (Mittler 2002), alleviating the inhibition of PSII repair (Takahashi and Badger 2011).

The general operating mechanism of non-enzymatic, low molecular weight, antioxidants consists in the donation of electrons or hydrogen atoms to the oxidizing agent. For example, carotenoids as xanthophylls and carotenes can act as direct scavengers of ROS and stabilize the light-harvesting complexes within the thylakoid membranes (Bassi and Caffarri 2000). Tocopherols (Toc) are also


Non-stressed/darkness
L
Biosynthesis
Lx
days, months
ΔL
LxL cycle
L
Z
Biosynthesis
V
VAZ cycle
minutes
A+Z
Environmental stress/sunlight
NPQ
L
Biosynthesis
Lx
days, months
ΔL
LxL cycle
L
NPQ
Z
Biosynthesis
V
VAZ cycle
minutes
A+Z
Prolonged environmental stress
NPQ
L
Biosynthesis
Lx
days, months
ΔL
LxL cycle
L
Z
Biosynthesis
V
VAZ cycle
minutes
A+Z

◂**Fig. 11.2** Concurrent operation of LxL- and VAZ-cycles in *Quercus*. In non-stressed leaves, the LxL- and VAZ-cycles remained in the epoxidated forms, Lx and V shown (shown in green). These carotenoids can be synthesized by *novo* from L and Z respectively (shown in grey). Under environmental stress or sunlight, the light harvesting antenna is switched into a photoprotected state, in which Lx and V are de-epoxidated to the de-epoxidated forms (L and A + Z respectively; shown in orange). In the case of LxL-cycle, Lx enhances the already large pool of L in leaves, giving rise to newly formed L molecules (ΔL). The potentially harmful excess of absorbed energy can be then dissipated thermally (NPQ). When the leaf is again without stress or in darkness, A + Z is epoxidated-back to V, restoring the initial V pool (minutes or hours). However, in the LxL-cycle, ΔL remains for a longer period (days, months), giving rise to the “truncated” LxL-cycle (dashed arrow). If the stress is sustained for a long time, a faster engagement of NPQ occurs then in leaves, activated by the truncated LxL-cycle (ΔL) and without any dissipation through A + Z. The combination of both cycles, with different mode and kinetics of operation increases the plasticity of NPQ in *Quercus* species

lipophilic antioxidants, and are able to donate single electrons to lipid peroxyl radicals, preventing the propagation of lipid peroxidation chains in thylakoids (Munné-Bosch 2005). Other plant molecules such as lipoic acid, anthocyanins, (poly)phenols, melatonine and tocotrienols have also been described to have antioxidant activity, but their relevance in vivo has not been fully determined. Ascorbate is the most abundant antioxidant in *Quercus* leaves (García-Plazaola et al. 1999a, b, 2000) and a substrate for ascorbate peroxidase (APX) that detoxifies H_2O_2. It is also involved in the regeneration of (oxidized) tocopheryl radical to Toc, and is a co-substrate for V de-epoxidase in the VAZ-cycle.

Enzymatic antioxidants are proteins that use electron donors, mainly antioxidants and NAD(P)H, either to eliminate ROS or to regenerate “burned” (oxidized) antioxidants (Hernández et al. 2012). Among others, antioxidative enzymes include glutathione reductase (GR), monodehydroascorbate reductase (MDAR), catalase (CAT), APX and other peroxidases. The interaction with non-enzymatic antioxidants such as ascorbate (Asc) and glutathione (GSH) plays a central role in the chemical and metabolic destruction of ROS. Ascorbate is considered as the key compound of O_2^- and H_2O_2 removal in the chloroplast, and the ascorbate-glutathione cycle constitutes a powerful pathway to maintain Asc in its reduced form by using GSH as an electron donor (Noctor and Foyer 1998). Another large group of non-enzymatic antioxidants are the superoxide dismutases (SODs), which constitute the first line of defense against ROS, catalyzing the decomposition of O_2^- in chloroplasts and other organelles (Alscher et al. 2002).

Several studies have dealt with the role of non-enzymatic and enzymatic antioxidants in different *Quercus* species. In particular, the changes in antioxidant concentration under several stress factors have been analyzed, such as drought in deciduous (e.g. *Q. robur*, Schwanz and Polle 2001; *Q. pubescens*, Gallé et al. 2007) and evergreen species (e.g. *Q. coccifera* and *Q. ilex*, Baquedano and Castillo 2006) (see also Sect. 11.3.3), winter stress in evergreens (e.g. *Q. ilex*, Corcuera et al. 2005a; *Cyclobalanopsis helferiana*, Zhu et al. 2009) (see also Sect. 11.2.3), and other factors such as pollutants (e.g. *Q. ilex*, Munné-Bosch et al. 2004). In general positive responses of antioxidant pools to those stress factors confirm the important role of this strategy in the battery of photoprotective defense mechanisms in *Quercus*.

11.2 Photoprotection in Evergreen Oaks During Winter

11.2.1 When and Where Evergreen Oaks Are Exposed to Winter Stress?

Many oak species are evergreen, sub-evergreen or brevideciduous, meaning that they maintain leaf function for most or all of the year. Evergreen species occur in all of the major lineages and across all the continents of their distribution in the Northern Hemisphere, including in Asia, Europe, North Africa and North and Meso America. In the Americas, in the southeastern United States, California and in northern, high elevation regions of Mexico, in some areas of the Mediterranean basin, and in high mountains in Asia, numerous oaks are exposed to chilling and freezing temperatures. While these different regions experience contrasting climatic regimes, they are similar in having thermal seasonality marked by warm summers and relatively cold winters. Plants with evergreen leaves, which are not programmed to senesce and abscise in response to cold temperatures, require mechanisms to protect the photosynthetic apparatus during freezing. This allows them to benefit in terms of carbon gain by maintaining function under mild freezing stress. Mediterranean oaks have been the subject of considerable study in the Mediterranean basin and California; these regions experience cold wet winters and hot dry summers, in contrast to the southeastern US and northeastern Mexico, where summers are hot and wet and winters are cold and dry. Nights in the Mediterranean region of southern Europe and North Africa frequently reach freezing temperatures during winter months (December, January and February) but only rarely extend below −10 °C. Leaf photochemistry is known to be impaired by night-time freezing temperatures as a result of impairment of enzymatic processes involved in photosynthesis. Acclimation to cold temperatures in overwintering evergreen oaks species has been linked to increases in antioxidants and xanthophyll pigments (García-Plazaola et al. 1997, 1999a, b; Brüggemann et al. 2009) (see Sect. 11.2.2), as well as changes in the composition of PS II antenna and increases in cyclic electron transport that allow increased quenching of absorbed light (Öquist and Huner 2003). In a common garden in the Mediterranean region of France, where two evergreen (*Q. ilex* and *Q. suber*) and two deciduous (*Q. afares* and *Q. faginea*) were grown for almost two decades, evergreen species showed important differences in cold acclimation ability and protection of the photosynthetic apparatus (Cavender-Bares et al. 2005). In the two evergreen species, photosynthetic function in leaves showed a strong acclimation response during winter, which protected the leaves even at −15 °C. This did not occur in the deciduous species.

Starch and lipid content increased in the evergreen species, and sugar content increased in *Q. ilex*, the most freezing tolerant species, consistent with changes associated with cold acclimation to stabilize membrane structure and function. These changes appeared to be coordinated with hydraulic function, such that species with long-lived leaves had greater protection of both the photosynthetic apparatus and xylem transport.

In general, species responses to chilling and freezing were predicted by their climates of origin. Thus for example, in another common garden experiments with the American live oaks, which maintain green leaves throughout the year, divergences in response to cold were tested for by examining PS II photosynthetic yield ($\Delta F/F_M'$) and NPQ under chilling or warm growing conditions after short-term exposure to three temperatures (6, 15 and 30 °C) and under moderate light (400 μmol m^{-2} s^{-1}). Without cold acclimation (tropical treatment), the most northern population of the species occurring in areas with cold winters, *Q. virginiana*, showed the highest photosynthetic yield in response to chilling temperatures (6 °C). With cold acclimation, *Q. virginiana* populations showed greater NPQ under chilling temperatures than the tropical *Q. oleoides* populations, suggesting enhanced mechanisms of photoprotective energy dissipation in the species adapted to cold winters. In a subsequent experiment that included more species from this lineage, species from climates with cold winters again showed greater leaf-level freezing tolerance than the tropical species, *Q. oleoides*, as indicated by changes in maximal photochemical efficiency of PSII (F_V/F_M) under continuous dark environments after freezing at −10 °C (Koehler et al. 2012; Cavender-Bares et al. 2011). At the population level, the degree of their loss of photosynthetic function depended on the mean minimum temperature of their climate of origin. Interestingly, seedlings originating from warmer climates had higher anthocyanin concentration in leaves when grown under cold winter conditions but did not exhibit a higher de-epoxidation state (Ramírez-Valiente et al. 2015).

Photoprotection mechanisms against chilling in Asian oaks have only been studied in a couple of species native to savanna-valleys and high elevations (above 3000 m.a.s.l.) of Southwest China: *C. helferiana* and *Q. guyavifolia* (Zhu et al. 2009; Huang et al. 2016a, b). These species are exposed to below zero temperatures during winter (mostly at night). When freezing night temperatures reduce or inhibit photosynthesis, energy dissipation, photorespiration and alternative electron flow acquire a key role in the photoprotection of photosynthetic apparatus (Huang et al. 2016a). All together, these mechanisms allow an efficient performance and protection of PSII of Asian oaks during winter.

In summary, the presence of a cold season in their habitat of origin together with a proper period of acclimation represent the two main factors explaining when and where *Quercus* evergreen species are able to successfully deal with winter stress.

11.2.2 Sustained Energy Dissipation Under Winter Stress

Evergreen oaks growing in areas where temperatures drop below freezing have been shown to employ sustained thermal energy dissipation during the winter months (García-Plazaola et al. 1999b, 2003b; Martínez-Ferri et al. 2004). Sustained thermal energy dissipation is characterized by reductions in maximal photochemical efficiency that correlates with overnight retention of the de-epoxidized forms of the VAZ and LxL-cycles: Z, A and ΔL (García-Plazaola et al. 2002). It is thought that this mechanism represents a sustained form (or forms) of thermal energy dissipation that protects the photosynthetic apparatus from excess excitation pressure during conditions of high light and low temperatures that occur during winter (Adams et al. 2004; Verhoeven 2014). This type of sustained dissipation has been widely observed in other evergreens acclimated to winter conditions. The mechanism(s) of sustained thermal dissipation are not fully understood, however dark retention of A and Z, as well as reorganization of photosynthetic proteins including increases in early light induced proteins (ELIP) are likely involved (Verhoeven 2014).

Studies on Mediterranean evergreen oak species have reported winter values of F_V/F_M ranging from 0.4 to 0.7, correlating with retention of A + Z, such that values for AZ/VAZ range from 0.3 to 0.7 (García-Plazaola et al. 1999a, 2003b; Martínez-Ferri et al. 2004), while in alpine Asian oaks winter values of F_V/F_M can be even lower (around 0.1) (Zhu et al. 2009; Huang et al. 2016b). This pattern is consistent with winter induced sustained thermal dissipation occurring in these species. In fact, dramatic increases in sustained dissipation were demonstrated to occur upon exposure to sudden drops in temperature (García-Plazaola et al. 2003b). However, observations that during winter, F_V/F_M values continued to decrease while AZ/VAZ remained the same, suggest that processes other than sustained thermal dissipation are likely also causing winter declines in F_V/F_M, possibly including some sustained photo-damage (Martínez-Ferri et al. 2004). Additionally, pool sizes of xanthophyll cycle pigments as well as L and β-carotene (β-Car) have also been shown to increase during winter in Mediterranean oak species, suggesting an increased capacity for photoprotection (García-Plazaola et al. 1999a, 2003b; Martínez-Ferri et al. 2004).

In a study comparing co-occurring deciduous and evergreen oaks in northern Florida, a region with cold but mild winters, short-term chilling stress (without prior cold acclimation) resulted in greater than 50% reduction in maximum photosynthesis, 60–70% reduction in electron transport rate and irreversible quenching of PSII fluorescence in both species (Cavender-Bares et al. 1999). However, the kinetics of recovery after combined high light exposure and chilling showed that the evergreen species exhibited greater photoprotective quenching (qE) and less irreversible quenching (qI) than the deciduous species. Higher photoprotective capacity may be inherent in evergreen oaks compared to deciduous oaks even without cold acclimation.

11.2.3 Antioxidants: Responses of Free and Enzymatic Antioxidants to Winter Stress

Studies examining the antioxidant responses of cold tolerant *Quercus* species to low temperatures have demonstrated that responses vary considerably depending upon both species and the particular environmental conditions encountered (García-Plazaola et al. 1999a, 2000, 2003b; Corcuera et al. 2005a). In a study comparing winter to spring antioxidant content in *Q. ilex*, a high synthesis of Asc (without significant effects on α-Toc and GSH) occurred in winter (2–3 fold over spring on a leaf area basis, García-Plazaola et al. 1999a). However, in another study comparing a cold with a mild winter, the most highly induced antioxidant in the coldest winter was α-Toc, being 400 and 60% higher (on an area basis) than the mild winter in *Q. coccifera* and *Q. ilex* respectively (García-Plazaola et al. 2003b). In this study, a decrease in Asc content was observed in both species in the coldest winter relative to the mild one.

A study examining enzymatic antioxidants in *Q. ilex* dealing with winter stress reported an induction in GR and MDAR activity in winter, but a weak response of other antioxidant enzymes (CAT, SOD, APX, García-Plazaola et al. 1999a). Interestingly, both GR and MDAR use NADPH as electron donor, which is a sink for photosynthetic electrons, minimizing overexcited photosynthetic electron chain and ROS production. The authors concluded that MDAR activity plays a central role in the Asc regeneration. A weak response of APX, GR, SOD and guaiacol peroxidase has been also reported for *Q. ilex* in its upper altitudinal extreme in the Iberian Peninsula (Corcuera et al. 2005a), which could mean that the constitutive activity of these enzymes is enough to cope with oxidative stress at low temperatures. Similarly, enhanced activity of GR, SOD and particularly of MDAR have also been described in Asian oak *C. helferiana* during chilling period (Zhu et al. 2009).

Antioxidant contents in response to winter stress can change, not only depending on chilling severity, but also on internal (ecotype, leaf ontogeny) and external factors (time of the day, irradiance). In this sense, García-Plazaola et al. (1999b) reported that the antioxidant content in *Q. ilex* (Asc, GSH, α-Toc) was constitutively higher in sun than in shade leaves during winter. Besides, it decreased sensitively along a sunny day, showing antioxidant content is dynamic and it changes depending on consumption and regeneration. Furthermore, an age-dependent tocopherol accumulation has been observed in woody plants including oaks (Hansen et al. 2002), but its physiological meaning is unknown.

Additionally, provenances of ecotypes also condition antioxidant content, and commonly, ecotypes adapted to colder climates evolve higher antioxidant content. In a common garden study with *Q. ilex* from three contrasting Mediterranean climatic provenances (semiarid, cold and oceanic), Camarero et al. (2012) observed that the highest content of α-Toc occurred in *Q. ilex* seedlings from the coldest provenance, which supports the role of this antioxidant in cold adaptation. García-Plazaola et al. (2000) also reported an increase in VAZ and β-Car (in a Chl ratio) in Mediterranean *Q. ilex* growing in an altitudinal gradient in winter, but the response in other antioxidants was not so evident.

Overall, studies suggest that climate has been a key factor in shaping species and population differences in winter stress antioxidant response in *Quercus*. Despite the remarkable diversity in the antioxidant strategies followed by different species, generally, enhanced hydrophilic antioxidants (particularly MDAR) together with increased Z (and α-Toc in some cases) could summarize oak antioxidant response to winter stress.

11.3 Photoprotection in Drought-Stressed *Quercus*

Drought leads to water deficit in the leaf tissue, which affects many physiological processes such as photosynthesis. Stomatal closure is a common response to drought stress in *Quercus* species (e.g. Mediavilla and Escudero 2003; Peguero-Pina et al. 2009), as a way of minimizing water loss at the expense of reducing net CO_2 assimilation. Under this situation, when light incident on the leaf surface exceeds largely the amount that can be used for photosynthesis, different mechanisms allow the protection of the photosynthetic apparatus both dissipating excess of light as heat (Demmig-Adams and Adams 2006) or decreasing ROS formation. Photoprotective mechanisms have been described for both evergreen and deciduous *Quercus* species in response to moderate or severe drought stress conditions, although with some differences among them.

11.3.1 Functional Differences Between Deciduous and Evergreen Species Under Drought

The photoprotective mechanisms of deciduous *Quercus* species under drought stress have been analyzed since the 1990s. Thus, several studies have dealt with this topic in *Q. robur* and *Q. petraea*, two of the most representative oaks widely distributed in Europe under temperate-nemoral climate (www.euforgen.org). Both *Q. robur* and *Q. petraea* have developed effective photoprotective mechanisms to withstand mild water deficit (Epron et al. 1992; Schwanz et al. 1996), although both species seem unable to effectively cope with severe drought stress in terms of photoprotection (Epron and Dreyer 1992; Schwanz and Polle 2001). Nevertheless, deciduous oak species are not exclusive of the humid climates, but they are also present in more xeric habitats with summer drought, i.e. the so-called "nemoro-Mediterranean oaks" (Corcuera et al. 2002). Among them, *Q. pubescens*, which has a wide distribution range including most of central and southern Europe (www.euforgen.org), is able to withstand and survive extreme summer droughts (Damesin and Rambal 1995). The tolerance of this species to water stress has been related to the existence of efficient photoprotective mechanisms, as showed by Marabottini et al. (2001), Gallé et al. (2007), Contran et al. (2013) and Hu et al. (2013). Other "nemoro-Mediterranean oaks" such as *Q. cerris* and *Q. frainetto* also exhibited efficient photoprotective mechanisms in response to drought stress (ca. −3 MPa, Wolkerstorfer et al. 2011).

The photoprotection mechanisms have also been studied in drought-stressed evergreen oaks, mainly in those species occurring under Mediterranean-type climates (i.e. the so-called "Mediterranean oaks", Corcuera et al. 2002). Although photoprotective mechanisms are strong enough in these species, the performance of their photosynthetic machinery in response to an intense summer stress period varied markedly among them, as showed by Peguero-Pina et al. (2009) for *Q. coccifera*, *Q. ilex* and *Q. suber*. Apart from the "Mediterranean oaks", few studies have dealt with photoprotective mechanisms in other evergreen oaks. Zhu et al. (2009) reported that *Cyclobalanopsis helferiana*—a resilient species that can survive in the savannas in the hot-dry valleys in SW China—was highly tolerant to severe drought stress (ca. −4 MPa at predawn) due to the existence of photoprotective mechanisms that resembled the performance of "Mediterranean oaks" explained below (see Sects. 11.3.2 and 11.3.3 for details). Recently, Ramírez-Valiente et al. (2015) found that four evergreen oaks (*Q. virginiana*, *Q. geminata*, *Q. fusiformis* and *Q. oleoides*) included in a group of species called *Quercus* series *Virentes* from southern USA, Mexico and Central America, living under contrasting climatic conditions, developed photoprotective mechanisms when exposed to drought stress.

In conclusion, both deciduous and evergreen *Quercus* species occurring under contrasting climates implement different photoprotective mechanisms under drought stress. Regardless of this common performance, some evergreen (e.g. *Q. coccifera* and *Q. ilex*) and deciduous (e.g. *Q. pubescens*) oaks living under Mediterranean-type climates seem to be better adapted for withstanding severe drought periods. By contrast, deciduous oaks from temperate-nemoral climates have developed effective photoprotective mechanisms only to withstand mild water deficit, being unable to effectively cope with the severe water scarcity experienced by evergreen species. This differential physiological performance under water stress might play an important role in tree mortality and landscape formation in the context of future climate projections, which suggest that the proportion of land surface under extreme drought can be dramatically increased by the end of the present century (Xu et al. 2013).

11.3.2 Energy Dissipation and Xanthophyll Cycles Under Drought

During a drought episode, the dissipation as heat (thermal dissipation) of part of the absorbed energy acquires a crucial role in the photoprotection of the photosynthetic apparatus preventing the accumulation of ROS. Independent of the leaf strategy, both deciduous and evergreen oaks use thermal dissipation as an important alleviation mechanism under water limitation conditions. The vast majority of works, where thermal energy dissipation was studied in drought-stressed oaks, has been conducted in Europe but a few examples from North America are found in the bibliography. Despite the existence of two xanthophyll cycles (VAZ and LxL-cycles) in *Quercus* species (García-Plazaola et al. 2002), very little knowledge is available regarding the relevance of LxL-cycle and thermal dissipation during drought in oaks (Llorens et al. 2002).

Deciduous oaks normally display lower values of NPQ under drought conditions than evergreen species do. An example is provided by Mahall et al. (2009) when comparing two Mediterranean oak species under field conditions in southern California: seedlings of *Q. agrifolia* (evergreen) showed NPQ of 3.09 at the end of summer 2002, while co-occurring *Q. lobata* (deciduous) seedlings showed values of 1.91. Similar examples can be found in the Mediterranean Basin: i.e. compare *Q. ilex* NPQ values of 3.8 against values of the deciduous *Q. humilis* (NPQ = 3.0) under severe drought (Gulías et al. 2002). Compared to Mediterranean oaks, "nemoro-Mediterranean species" generally show lower NPQ values under moderate water stress. In this regard, *Q. pubescens* increased NPQ only from 0.7 (when well watered) to 1.7 under imposed drought during summer 2004 (Gallé et al. 2007). NPQ values, however, can be enhanced after previous drought events as it is shown in the same work: a drought episode during the next summer (2005) in the same trees induced an increase of NPQ that reached values of up to 5 (Gallé et al. 2007). Also in *Q. petraea,* a reversible decrease of photochemical efficiency (probably related to an enhanced AZ/VAZ) was shown to prevent photoihnnhibitory damage under moderate water stress with a predawn water potential below −2 MPa (Epron et al. 1992).

In evergreen *Quercus* species, sustained de-epoxidation of xanthophylls can be induced during a prolonged drought event: i.e. 3 weeks without irrigation during the summer led to very high AZ/VAZ morning-levels c.a. 0.8 in *Q. coccifera* seedlings (Peguero-Pina et al. 2008). This photoprotective mechanism could be related to a low intra-thylakoid lumenal pH and efficiently prevented photoinhibitory damage. Both dynamic and chronic photoinhibition have been observed during water stress in *Q. coccifera* and *Q. ilex* (Baquedano and Castillo 2006). And although the responsiveness of photoprotective mechanisms will partly depend on the climate of origin, heterogeneity of responses can also be found within evergreen oaks of the same climatic region (i.e. Mediterranean). Thus, *Q. ilex* and *Q. coccifera* tended to sustain a chronic photoinhibition evidenced by a decrease in predawn F_V/F_M values to 0.3–0.4 and an overnight retention of A + Z at water potentials below −6 MPa (Peguero-Pina et al. 2009). This was interpreted by these authors as an additional photoprotective mechanism that preserved the photosynthetic pigment machinery after a long summer stress period. By contrast, F_V/F_M in *Q. suber* remains at high values around 0.7 and most of the midday A + Z were converted into V during the night, irrespective of the degree of water stress (Peguero-Pina et al. 2009). In line with this, García-Plazaola et al. (1997) did not find changes in predawn F_V/F_M and the VAZ pool was maintained in a highly epoxidated state at predawn under drought stress in *Q. suber*. A similar performance was found by Zhu et al. (2009) for the evergreen *C. helferiana* in response to severe drought stress, i.e. a down-regulation of PSII activity characterized by gradually NPQ increases with an overnight retention of A + Z.

In summary, drought generally triggers an increase of NPQ in oaks when leaf predawn water potential falls below −2 to −3 MPa. Commonly, this rise in NPQ is mainly, although not completely, related to the de-epoxidation of xanthophylls: i.e. A + Z and NPQ correlate well in sun leaves (García-Plazaola et al. 1997). The highest NPQ values have been recorded for Mediterranean evergreen oaks: i.e. NPQ of up to 10 was measured in adult *Q. suber* trees subjected to three consecutive years of severe drought (ca. −4 MPa at predawn) (Grant et al. 2010). Also acclimation, due to either provenance (i.e. xericity of the site) or seasonal acclimation (i.e. end of dry season) and hardening after repeated periods of drought, are able to induce a progressive increase in VAZ pool, de-epoxidation state of xanthophylls (i.e. AZ/VAZ values) and NPQ (Grant et al. 2010; Camarero et al. 2012; Ramírez-Valiente et al. 2015). All these mechanisms efficiently reduce the risks of photodamage under drought conditions in oaks.

11.3.3 Role of Free and Enzymatic Antioxidants Against Drought

Non-enzymatic and enzymatic antioxidant defense mechanisms detoxify ROS and maintain an adequate cellular redox balance under drought stress conditions in order to avoid photo-oxidative damage (Hernández et al. 2012). The role of antioxidants in drought-stressed *Quercus* has been studied mainly in conjunction with other photoprotective mechanisms, such as VAZ and LxL-cycle, both in deciduous and evergreen species. Specifically, several studies have dealt with interspecific variations in the concentration and/or activity of different antioxidants and its influence on the differential physiological performance of oak species under water stress.

The first studies about this topic were published during the 1990s, in which *Q. robur* experienced a reduction in SOD and catalase activities when subjected to mild drought stress (ca. −1 MPa) (Schwanz et al. 1996). Furthermore, even under severe drought (ca. −3 MPa at predawn), Schwanz and Polle (2001) did not find a photoprotective response of antioxidants in *Q. robur* because the key enzymes involved in antioxidant protection (i.e. SOD) declined and oxidation of Asc and GSH increased under these conditions. Contrary to these findings, Hu et al. (2013) stated that, under similar conditions, this species enhanced its leaf Asc and thiol levels as the most drought-sensitive species in response to an increase in ROS production when compared with *Q. petraea* and, specially, *Q. pubescens*. The latter species maintained high amounts of antioxidants (mainly Asc and α-Toc), minimizing oxidative stress and irreversible damage in leaves under severe drought conditions (ca. −4 MPa at predawn) (Gallé et al. 2007). Similar results were found by Contran et al. (2013), who stated that *Q. pubescens* reacted to water deficit by increasing antioxidant enzyme activity, avoiding ROS toxic effects. The tolerance of this species to water shortage in terms of foliar antioxidant status has also been evidenced by Marabottini et al. (2001) and Hu et al. (2013). For these reasons, *Q. pubescens* is considered as a drought-tolerant species when compared with *Q. robur* and *Q. petraea*. In this regard, *Q. cerris* and *Q. frainetto*—two deciduous oaks that co-occur with *Q. pubescens*—increased three times the α-Toc content during summer in response to drought stress (ca. −3 MPa, Wolkerstorfer et al. 2011). However, these authors could not explain whether the observed accumulation of α-Toc contributed to the protection against the photo-oxidation.

Evergreen oaks, specially those species occurring under Mediterranean-type climates, show efficient antioxidant defenses against drought stress. Faria et al. (1996) found that SOD and APX activities in *Q. suber* were high enough to cope with the increase in ROS under reversible stressful conditions of midday, providing an additional mechanism for energy dissipation. Baquedano and Castillo (2006) found midday dynamic photoinhibition in water-stressed *Q. coccifera* and *Q. ilex* plants (ca. −1.5 MPa at predawn) coupled with a significantly increase in the total antioxidant activity and in the Asc pool. In an additional study on *Q. ilex*, Nogués et al. (2014) found a sustained increase in non-enzymatic (total Asc and phenolic compounds) and enzymatic antioxidants (APX and GR) in response to drought stress (ca. −2.5 MPa at midday). According to these authors, this may indicate the activation of defense responses for scavenging ROS produced under increasing limitations of primary metabolism, and to ultimately avoid stronger oxidative damage in the photosynthetic apparatus of *Q. ilex*. Besides Mediterranean oaks, Zhu et al. (2009) found that SOD and glutathione peroxidase showed a sustained high activity during the driest period of the year (ca. −4 MPa at predawn) for

C. helferiana, a drought-resistant evergreen oak occurring in SW China. This high activity of antioxidant system could efficiently scavenge ROS and protect the photosynthetic apparatus from oxidative injury.

In conclusion, both free and enzymatic antioxidants play an important role in photoprotection against drought in *Quercus* species. However, although some evergreen species seem to display higher antioxidant protection, more comparative studies are needed to elucidate the role of environmental factors in antioxidant activity in oaks.

11.3.4 Synergic Effect of Drought and Heat Waves

Climatic observation of the last century reveals a trend to a higher frequency and intensity of "extreme climatic events" such as severe drought episodes, intense rainfall events or heat waves (IPCC 2014). The term "extreme climatic event" is debatable and its meaning may depend on the organism, the issue or the scale of analysis (see Smith 2011 for an ecological revision). From a meteorological point of view, a heat wave could be defined as an extraordinary event of abnormally high temperatures above the 90th percentile (for a location and season), persisting for at least 3 days (based on the definition from Pezza et al. 2012). Heat waves can have a high impact in ecosystems, particularly when co-occurring with a period of drought, due to their potential to directly or indirectly trigger irreversible changes in them. One of the most severe heat waves in the last century (see "list of heat waves, 2016" for a complete list of most significant heat waves over the last century) was the summer heat wave of 2003, which affected western and central Europe. This was the hottest episode in the last 180 years, reaching temperatures up to 6 °C above the long-term average and, additionally occurred on a year of considerable drought, with annual precipitation 50% below the average (Luterbarcher et al. 2004; Stott et al. 2004). Besides its extremity in magnitude, the European heat wave of 2003 affected different "Temperate-Nemoral" and Mediterranean ecosystems dominated by *Quercus* species. Thus, many of the works available in the literature correspond to this scenario. Nevertheless, the unpredictability of heat waves, limits the availability of field data to those obtained during the course of studies that were already in course when a heat wave event occurred (referred to as "opportunistic studies" in Smith 2011). Hence, in this section, manipulative experiments dealing with the interaction of heat and drought and their effects on photoprotective responses of *Quercus* species have also been included to build up a complete overview of the synergistic effects of heat waves and drought over *Quercus* photoprotection strategies.

Water availability is the main factor determining the effects of a heat wave over a population of *Quercus*. This statement could be expected from a merely physical point of view since transpirative cooling alleviates heating, preventing leaves to reach lethal temperatures. This premise is reinforced by field works: i.e. even extraordinary hot episodes as the European heat wave of 2003 did not affect the growth of *Q. robur* if water supply from the soil was available (Wilkinson et al. 2012). Similarly, *Q. rubra* seedlings are able to increase their biomass under imposed artificial heat waves of up to +6 °C above control whenever water supply is assured, while low soil moisture content itself induces a decrease of biomass (Ameye et al. 2012; Bauweraerts et al. 2013). In that sense, biogeographical and topological location (type of substrate and its capability for water retention, elevation, orography and its interaction with fog or cloud retention, wind, etc.) as well as species-dependent tolerance to drought, determine the consequences of extremely hot and dry episodes (Bertini et al. 2011; Contran et al. 2013). Thus, higher mortality and reduced growth experienced by *Q. petraea* changed oak forests towards a new stand composition where the more drought-tolerant Turkey oak *Q. cerris* has became dominant after the summer of 2003 in Italy (Bertini et al. 2011).

In addition to a proper water supply, some other factors can buffer or mitigate the effect of episodes of simultaneous heat and drought in oaks. This is the case of canopy buffering-effect over the understory plants and seedlings. As an example, during August 2003, maximum temperatures were on average up to 3 °C cooler under the oak forest canopy of the Southern Swiss Alps than in open areas. When compared to other forest types, only the beech forests produced a greater cooling effect (Renaud and Rebetez 2009). Also elevated CO_2 (i.e. 700 ppm) seems to mitigate the effect of heat waves and drought stress in *Quercus* in a supposed scenario of future atmospheric conditions (Ameye et al. 2012).

In a broad sense, *Quercus* species could be generally considered as tolerant to the combined effect of heat waves and drought (Gallé et al. 2007; García-Plazaola et al. 2008; Haldimann et al. 2008; Ameye et al. 2012; Bauweraerts et al. 2013; Contran et al. 2013). Photoprotective barriers of many *Quercus* species start with structural passive-protection of leaves: i.e. many species are covered by a more or less dense hairy surface which reduces light absorption by photosynthetic cell layers (see Sect. 11.1.2 for details). Leaves of *Q. ilex*, which is typically considered as a plastic species, show higher density of adaxial trichomes in xeric habitats than when growing on continental sites or in mesic sites (Camarero et al. 2012). As a constitutive and less dynamic leaf property, density and structure of foliar hairs could have its main meaning in terms of long-term acclimation and ecological stress memory, more than in the immediate response to an acute and quick event such as a heat wave. Nevertheless, morphological acclimation to a more xeric and/or hot environment may provide advantages against a sudden episode of extreme temperature (such as heat wave).

At the chloroplast level, most species down-regulate the photochemical efficiency to prevent photo-oxidative damage. Thus, $\Delta F/F_M'$ decreased 88% at midday: i.e. $\Delta F/F_M'$ values fell from 0.8 at sunrise to 0.1 at midday during the heat wave 2003 in *Q. pubescens* (Haldimann et al. 2008). The decrease is more acute if trees were previously exposed to a heat wave as it has been shown in controlled heat wave experiments of consecutive +12 °C episodes with *Q. rubra* (Bauweraerts et al. 2014). Also predawn F_V/F_M can experience a progressive decrease when trees are exposed for several days to unusually high temperatures combined with low water availability (Gallé et al. 2007). This down-regulation of photochemistry can be attributed, at least in part, to enhanced de-epoxidation and higher pools of VAZ and LxL-cycles during the stress (García-Plazaola et al. 2008; Haldimann et al. 2008) and it seems to be related to reorganization of thylakoid membranes but not to changes in the amount of LHC II proteins, at least in *Q. pubescens* (Haldimann et al. 2008). Under these conditions, heat dissipation is enhanced and high NPQ kept during stress. Additionally, excitation pressure can decrease by a combined Chl loss and Chl a/b increase (García-Plazaola et al. 2008; Haldimann et al. 2008; Contran et al. 2013), although these effects are species-dependent and related to the severity and extent of the heat wave. The antioxidant system can also enhance, in particular α-Toc, for which a dramatic enhancement has been described in response to extreme heat (García-Plazaola et al. 2008). In some species as is the case of *Q. ilex*, some monoterpenes as α-pinene, seem to be involved in the thermotolerance of the leaves through the antioxidative protection of membranes (Copolovici et al. 2005) while other volatiles, such as isoprene, can confer thermotolerance through mechanisms independent of the antioxidant response (Peñuelas et al. 2005).

In sum, an efficient down regulation of photochemical efficiency together with an up regulation of NPQ, and an enhanced antioxidative response, allow most *Quercus* species to effectively protect their photosynthetic apparatus against the combined effects of heat and drought, although the effect of drought superimposed with a severe heat wave can kill many *Quercus* trees within a population in a short time-lapse of days or weeks (Haldimann et al. 2008; Bertini et al. 2011). The additional die-back of further individuals in the following years due to weakness and predisposition to succumb to biotic or abiotic menace must be also considered, and both immediate and delayed effects of heat waves plus drought are able to strongly affect the composition of the ecosystem (Breda and Badeau 2008; Bertini et al. 2011).

11.4 Photoprotection During Autumn Senescence

11.4.1 The Risks of Chlorophyll Degradation and Leaf Senescence

In winter-deciduous oak species, leaf senescence involves a highly coordinated process of remobilization of nutrients that is triggered by the shortening photoperiod and decreasing temperatures characteristic of autumn conditions (Rosenthal and Camm 1996; Hoch et al. 2001; Keskitalo et al. 2005; Fracheboud et al. 2009).

The most visible sign of autumn is the dramatic change in leaf pigment content resulting from chlorophyll degradation, while carotenoids are retained longer, and in some species anthocyanins are produced. Pigment changes are accompanied by decreases in photosynthesis, however, maximal photochemical efficiencies are retained at high levels until very late in autumn when chlorophyll contents are quite low, suggesting that the chlorophyll that is retained during senescence resides in functional photosynthetic centers (Adams et al. 1990; Keskitalo et al. 2005; Moy et al. 2015). In contrast to photosynthesis, respiration is maintained later into autumn in order to provide energy needed for remobilization of leaf nutrients prior to leaf abscission (Adams et al. 1990; Collier and Thibodeau 1995; Hoch et al. 2001; Keskitalo et al. 2005). The process of disassembly and degradation of the photosynthetic apparatus must occur in a manner that prevents the accumulation of damaging reactive oxygen species that might preclude optimal nutrient resorption (Matile et al. 1999; Lee et al. 2003). Therefore, photoprotective strategies are an important component of the process of leaf senescence.

11.4.2 Why Leaves Turn Red?: Anthocyanic and Acyanic Oaks

Much of the beauty of autumn resides in the immense variation in color of leaf foliage among species, with colors varying from reds to yellows. According to Hoch et al. (2001) among oaks there are 9 species that produce high amounts of anthocyanins during autumn (all in North America) and 10 species in which anthocyanin production is nonexistent, low or infrequent (split between North America and Europe). The synthesis of anthocyanins during autumn occurs after chlorophyll degradation has begun and the pigments accumulate in the vacuoles of upper palisade cells (Hoch et al. 2001; Lee et al. 2003). The anthocyanins are hypothesized to serve as a light screen during autumn senescence (see Sect. 11.1.2.), which protects the photosynthetic apparatus during the period of nutrient resorption (Hoch et al. 2001, 2003; Lee and Gould 2002; Lee et al. 2003).

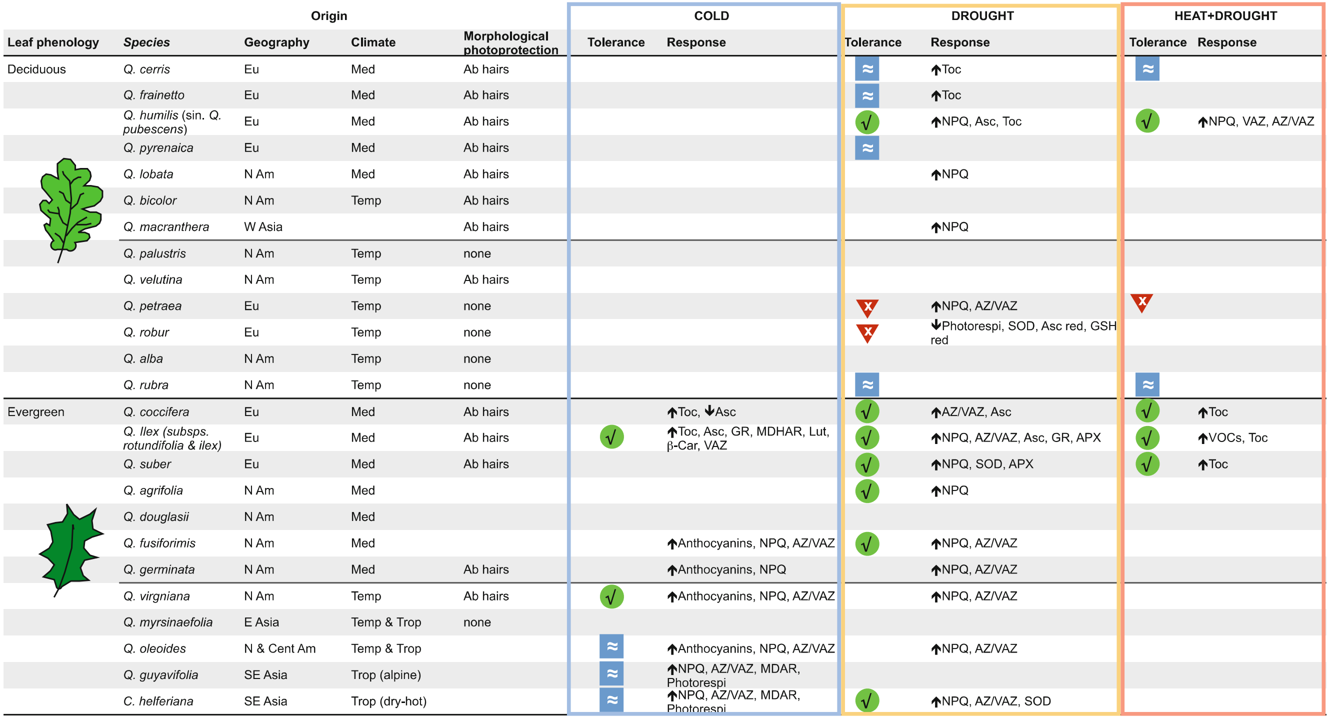
11.4.3 Coordinate Operation of Photoprotection Mechanisms in Senescing Leaves

The mechanisms of photoprotection during autumn senescence have not been particularly well studied. Pigment studies have demonstrated that carotenoids are degraded more slowly than chlorophylls affecting in a photoprotective capacity during the degradation process (Adams et al. 1990; Lee et al. 2003; Keskitalo et al.

2005). Additionally, the accumulation of anthocyanins, discussed above, likely serves a photoprotective role. A study monitoring both carotenoids and anthocyanins found no difference in the rate of degradation of carotenoids in anthocyanic and acyanic species (Lee et al. 2003), suggesting that carotenoid based photoprotection likely functions in all species. Few studies have been conducted using methods that differentiate individual carotenoids. The available data show that in aspen and sugar maple, the VAZ-cycle pigments were retained in higher abundance than other carotenoids, while in an oak species (*Q. bicolor*) the VAZ-cycle pigments were retained at relatively high levels only in early stages of autumn senescence, while L was retained in higher abundance than other carotenoids in late autumn (Keskitalo et al. 2005; Moy et al. 2015). Additionally, the oak species was shown to accumulate the PsbS protein in early autumn, which did not occur in the maple, suggesting a role for increased xanthophyll associated energy dissipation in early autumn in the oak (Moy et al. 2015). These studies suggest that there is variation among species in the strategies used for photoprotection during autumn senescence.

11.5 Concluding Remarks

This chapter has outlined that oaks are remarkably plastic and diverse (both inter- and intra-specifically) in terms of morphological and biochemical photoprotective mechanisms (Fig. 11.3), providing tolerance to winter cold and summer drought. These unfavourable climatic conditions are indeed, the key factor in shaping *Quercus* distribution and stress responses, being particularly Mediterranean evergreen oaks more resilient to them. Future climate change scenarios predict warmer and dryer environmental conditions in most of the distribution range of *Quercus*, detailed physiological studies are, therefore, essential to anticipate to the ecological responses. However, most of the information available nowadays comes from a few Mediterranean species, being holm oak (*Q. ilex*) the one most intensively studied. We conclude then that several knowledge gaps should be filled into get a more complete and global perspective of the group in all its distribution range: (i) photoprotective mechanisms and their ecological significance in Asian oaks are understudied, (ii) the role of L (considering the LxL-cycle) in the development of NPQ has received little attention in species of the genus and (iii) few is still known regarding thylakoid proteins and energy dissipation mechanisms in *Quercus*.



		Origin			COLD		DROUGHT		HEAT+DROUGHT	
Leaf phenology	*Species*	Geography	Climate	Morphological photoprotection	Tolerance	Response	Tolerance	Response	Tolerance	Response
Deciduous	*Q. cerris*	Eu	Med	Ab hairs			≈	↑Toc	≈	
	Q. frainetto	Eu	Med	Ab hairs			≈	↑Toc		
	Q. humilis (sin. *Q. pubescens*)	Eu	Med	Ab hairs			√	↑NPQ, Asc, Toc	√	↑NPQ, VAZ, AZ/VAZ
	Q. pyrenaica	Eu	Med	Ab hairs			≈			
	Q. lobata	N Am	Med	Ab hairs				↑NPQ		
	Q. bicolor	N Am	Temp	Ab hairs						
	Q. macranthera	W Asia		Ab hairs				↑NPQ		
	Q. palustris	N Am	Temp	none						
	Q. velutina	N Am	Temp	Ab hairs						
	Q. petraea	Eu	Temp	none			X	↑NPQ, AZ/VAZ	X	
	Q. robur	Eu	Temp	none			X	↓Photorespi, SOD, Asc red, GSH red		
	Q. alba	N Am	Temp	none						
	Q. rubra	N Am	Temp	none			≈		≈	
Evergreen	*Q. coccifera*	Eu	Med	Ab hairs		↑Toc, ↓Asc	√	↑AZ/VAZ, Asc	√	↑Toc
	Q. Ilex (subsps. rotundifolia & ilex)	Eu	Med	Ab hairs	√	↑Toc, Asc, GR, MDHAR, Lut, β-Car, VAZ	√	↑NPQ, AZ/VAZ, Asc, GR, APX	√	↑VOCs, Toc
	Q. suber	Eu	Med	Ab hairs			√	↑NPQ, SOD, APX	√	↑Toc
	Q. agrifolia	N Am	Med				√	↑NPQ		
	Q. douglasii	N Am	Med							
	Q. fusiforimis	N Am	Med			↑Anthocyanins, NPQ, AZ/VAZ	√	↑NPQ, AZ/VAZ		
	Q. germinata	N Am	Med	Ab hairs		↑Anthocyanins, NPQ		↑NPQ, AZ/VAZ		
	Q. virgniana	N Am	Temp	Ab hairs	√	↑Anthocyanins, NPQ, AZ/VAZ		↑NPQ, AZ/VAZ		
	Q. myrsinaefolia	E Asia	Temp & Trop	none						
	Q. oleoides	N & Cent Am	Temp & Trop		≈	↑Anthocyanins, NPQ, AZ/VAZ		↑NPQ, AZ/VAZ		
	Q. guyavifolia	SE Asia	Trop (alpine)		≈	↑NPQ, AZ/VAZ, MDAR, Photorespi				
	C. helferiana	SE Asia	Trop (dry-hot)		≈	↑NPQ, AZ/VAZ, MDAR, Photorespi	√	↑NPQ, AZ/VAZ, SOD		

Fig. 11.3 Summary of the oak species mentioned in the present chapter, their geographic origin, main functional traits, degree of tolerance to abiotic stressors and main photoprotective mechanisms employed by each species. Abbreviations: *Am* America, *Cent* central, Eu: Europe, *Med* Mediterranean, Temp: temperate, *Trop* tropical

Acknowledgements R.E. and B.F.M received a "Juan de la Cierva-Incorporación" grant (IJCI-2014-21452 and IJCI-2014-22489, respectively). This research was supported by projects CTM2014-53902-C2-2-P from the Ministry of Education and Science of Spain and the ERDF (FEDER), RTA2015-00054-C02-01 from the Spanish National Institute for Agriculture and Food Research and Technology (INIA) and research project UPV/EHU IT-1018-16.

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