Photoprotective Strategies of Overwintering Evergreens

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High levels of solar radiation (direct and reflected off snow) can be absorbed by green leaves in the winter. However, the energy that is absorbed by these leaves often cannot be used through photosynthesis under winter conditions. Most colored objects would simply bleach if faced with the same conditions, because light-absorbing pigments pass energy on to oxygen, forming reactive oxygen species that destroy the pigments. Two key means by which overwintering leaves prevent reactive oxygen-mediated damage have been identified. One, used by all leaves in the winter, involves the employment of xanthophyll carotenoids in a photoprotective process whereby the light energy absorbed by chlorophyll is converted to heat and dissipated harmlessly. The other, found in some evergreen species but not in overwintering annual or biennial mesophytes, involves the degradation of proteins responsible for generating high-energy electrons, thereby suppressing transfer of these electrons to oxygen.

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Absorption of a photon by chlorophyll lifts an electron to a higher-energy orbital, resulting in an excited molecule referred to as the singlet excited state of chlorophyll ($^1\text{Chl}^*$; figure 1a). The excitation energy is typically passed on from one chlorophyll molecule to another, eventually reaching a photochemical reaction center where the energy is used to generate high-energy electrons for photosynthetic electron transport. However, when $^1\text{Chl}^*$ is not used for photochemistry, chlorophyll may enter a triplet excited state ($^3\text{Chl}^*$) that can pass the excitation energy on to oxygen, resulting in the formation of singlet excited oxygen ($^1\text{O}_2^*$; figure 1a). Furthermore, the electrons that would normally go toward the formation of NADPH for reduction of CO$_2$ to sugars have the potential to be passed on to oxygen instead, leading to the formation of superoxide (O$_2^-$; figure 1a). Although (or perhaps because) they are rooted in one place, plants do not allow either of these reactive oxygen species to accumulate to levels that could result in significant damage or programmed cell death in the leaves until their life cycle is completed or until extreme conditions no longer allow maintenance of green tissues.

**Photoprotection in the absence of additional stress**

Fortunately, plants have protective mechanisms to counteract the formation of reactive oxygen species within the chloroplast. As the first line of defense, the energy-rich electron in the chlorophyll molecule can be returned from $^1\text{Chl}^*$ to the ground state through a process (Niyogi 2000, Demmig-Adams and Adams 2002) that is facilitated by a protein acting as a sensor of excess light (photosystem II [PSII] PsbS protein; Li et al. 2000) and by the carotenoids zeaxanthin and antheraxanthin of the xanthophyll cycle (zeaxanthin-dependent energy dissipation; figures 1, 2; Demmig-Adams and Adams 1996). The central role of this thermal dissipation process is demonstrated by its importance to the fitness of a species. Stefan Jansson’s group has recently shown that, under fluctuating light and otherwise favorable conditions, the reproductive success of PsbS-deficient mutants is significantly reduced (Külheim et al. 2002).

In darkness or low light and in the absence of additional stress, the carotenoid violaxanthin is normally the predominant component of the xanthophyll cycle. As light levels increase over the course of the day and exceed the level that can be used for photosynthesis, violaxanthin is converted to zeaxanthin (through the intermediate antheraxanthin), and the PsbS protein presumably signals that the latter two carotenoids should become engaged in facilitating the thermal dissipation of the excess absorbed excitation energy (figures 1a, 2). Protons that accumulate in the lumen of the thylakoid membranes play a crucial role in this rapidly modulated process; the enzyme responsible for converting violaxanthin to zeaxanthin is stimulated by the lowered pH (Hager 1980, Eskling et al. 1997), and these protons are also sensed by the PsbS protein (Li X-P et al. 2002) to trigger the
energy dissipation process. As light levels diminish in the afternoon, zeaxanthin becomes disengaged from energy dissipation and is reconverted to violaxanthin. Not surprisingly, those species with higher rates of photosynthesis employ relatively lower levels of zeaxanthin-dependent energy dissipation, and those with lower rates of photosynthesis employ higher levels of zeaxanthin-dependent energy dissipation (Demmig-Adams et al. 1999).

This photoprotective process also exhibits considerable potential for acclimation. For instance, the PsbS protein is probably subject to sun and shade acclimation (Li et al. 2000); the total pool of xanthophyll cycle carotenoids can be up to four or five times greater in fully exposed leaves than in deeply shaded leaves of some evergreens; and the capacity for thermal energy dissipation can likewise be several times higher in sun-exposed than in shaded leaves of evergreens (Demmig-Adams 1998). Whereas the acclimative extremes of the xanthophyll cycle response have been well documented, the critical role of thermal energy dissipation in fluctuating light environments was shown more recently (Adams et al. 1999, Demmig-Adams and Adams 2002, Külheim et al. 2002). During intermittent high light exposure in the sunfleck-punctuated understory of a forest, a pool of zeaxanthin can be formed and maintained throughout the day. Zeaxanthin-dependent energy dissipation kicks in rapidly for photoprotective diversion of the excess excitation energy and, perhaps just as important, becomes rapidly disengaged when direct sunlight is intercepted by the forest canopy and the light levels drop to those limiting to photosynthesis. The ability to rapidly optimize both light utilization and photoprotection is undoubtedly critical to the impact of zeaxanthin on plant fitness (Külheim et al. 2002). If the dissipation process remained engaged under low light subsequent to a sunfleck, it might compete with photosynthesis and diminish the already low level of photosynthetic CO₂ fixation, which is crucial to the productivity of understory plants when they receive only diffuse radiation (which is most of the time; Chazdon and Pearcy 1991).

On the other hand, the photoprotection afforded through zeaxanthin-dependent energy dissipation plays a crucial role in the success of plants, even in relatively shady habitats where the only stress encountered may be brief periods of moderately excessive light.

Photoprotective energy dissipation thus exhibits extreme flexibility in its response to the environment, both through acclimation to different light environments and through rapid modulation in its engagement and disengagement in response to rapid changes in the level of excess light. It should therefore come as no surprise that photoprotection may be employed to an even greater extent by plants that maintain green leaves in winter, under environmental stress that results in a decreased ability to utilize absorbed sunlight through photosynthesis.

### Staying green during the winter

Many plants retain green leaves during the winter. However, the fact that green leaves are present does not mean that the same level of photosynthetic competency is maintained throughout the year. The level of photosynthetic activity varies from day to day as temperature varies, and all plant species probably cease to take up CO₂ on days when temperatures are significantly below freezing. However, different species may also exhibit adjustments in the maximal intrinsic capacity for photosynthesis in response to the progression of seasons. Almost every conceivable type of response has been observed, depending on the species of plant and on the light levels and other conditions to which it is exposed (e.g., Adams et al. 2002).

The extremes of this spectrum of responses can be illustrated using two plant species that have been characterized
in fully sun-exposed sites in Colorado (figure 3). *Malva neglecta* (a biennial herb known as mallow, common mallow, or cheeseweed) exhibits very high intrinsic photosynthetic capacities during the winter and spring but lower rates in the summer (Verhoeven et al. 1999, Adams et al. 2002). This type of response is consistent with a number of other studies showing that winter-active annual (e.g., winter cereals) and biennial mesophytes upregulate photosynthetic capacity in response to low temperatures and winter conditions, including an increase in enzymes involved in carbohydrate synthesis (e.g., Strand et al. 1999, Adams et al. 2002, Öquist and Huner 2003). The association between the intrinsic capacity of electron transport and net photosynthetic CO₂ uptake in the field has not been established, but the fact that leaves of *M. neglecta* can accumulate starch diurnally on winter days with temperatures above freezing (Adams et al. 2001a) is strong evidence that the latter occurs. On the other hand, a number of evergreens, both coniferous and broad-leaved species, have been shown to downregulate photosynthetic capacity during the winter season to varying degrees in high light (Adams et al. 2002, Öquist and Huner 2003). For instance, Douglas fir (*Pseudotsuga menziesii*) exhibits an extreme response in this regard, with the highest intrinsic capacity for photosynthesis in the spring (25 micromoles of oxygen per square meter per second), a lower capacity in summer, and capacities approaching zero in the winter (figure 3).

The leaf- and chloroplast-level processes that are the focus of this article are connected to whole-plant processes such as water and carbohydrate transport. In the winter, water flow in the xylem of hardy evergreens can be diminished by air embolisms that form during freeze–thaw cycles (Sperry and Sullivan 1992, Mayr et al. 2002). Entering a state of reduced photosynthetic activity and stomatal closure may be instrumental to survival in evergreens that occupy harsher environments than those of overwintering herbaceous mesophytes.

One well-characterized factor influencing the capacity for photosynthesis is the level of carbon utilization within the whole plant (Koch 1996, Paul and Foyer 2001). When carbon is utilized at a higher rate (for growth, metabolism, or storage), photosynthetic capacity is typically upregulated, whereas when carbon is utilized at a lower rate, the capacity for photosynthesis is typically lower. This adjustment of photosynthetic capacity occurs via transcriptional modulation of the levels of proteins involved in light harvesting, electron transport, and carbohydrate metabolism. These response patterns are consistent with the behavior of the herbaceous annual and biennial species that upregulate photosynthetic capacity in the summer, and capacities approaching zero in the winter

Figure 3. Summer versus winter comparison of (a) the maximal intrinsic capacity for photosynthesis (light- and carbon dioxide–saturated rates of oxygen evolution per foliar area, in micromoles [µmol] oxygen per square meter [m²] per second [s], assessed at 25°C); (b) the total foliar pool of xanthophyll cycle carotenoids (millimoles of violaxanthin, antheraxanthin, and zeaxanthin [V + A + Z] per mole chlorophylls a + b); (c) the sustained conversion of the xanthophyll cycle to zeaxanthin and antheraxanthin (as a percentage of the total xanthophyll cycle pool: [Z + A]/[V + A + Z]); and (d) maximal photosystem II (PSII) photochemical efficiency as a percentage of light absorbed in the PSII antenna (from the chlorophyll fluorescence parameter F₆₇₃/F₅₃₅ [variable fluorescence divided by maximum fluorescence], where 100% efficiency would be represented by F₆₇₃/F₅₃₅ = 1) in leaves or needles of Malva neglecta (mallow, common mallow, or cheeseweed) and *Pseudotsuga menziesii* (Douglas fir) growing in full sunlight. Leaves or needles were removed from the field before sunrise and maintained in petri plates on moist filter paper at room temperature under approximately 8 µmol photons per m² per second until assessment. Thus, the determined photochemical efficiency of PSII during winter represents a sustained depression that is not rapidly reversible through an increase in the pH in the thylakoid lumen upon warming. The same is true for the elevated xanthophyll cycle conversion state. *Malva neglecta* was assessed on 15 August 2000 and 10 January 2001; *P. menziesii* was assessed on 9 August 2000 and 14 January 2001. Data depict mean ± standard deviation, with n = 6 for photosynthetic capacity and PSII efficiency and n = 3 for pigment parameters. Significant differences were determined from a student’s t-test (***, p < 0.0001; **, p < 0.01). Data from Adams and colleagues (2002).
winter and the evergreen species that downregulate photosynthesis in the winter. The herbaceous species grow in winter during the intermittent periods when temperatures rise above freezing and liquid water is available, whereas the evergreen species cease their visible growth during the autumn and do not resume it again until the new year’s flush of emerging leaves (or needles) and branches appears in the spring.

This persistent downregulation of photosynthesis in evergreen species is manifest at higher levels of organization as well. For example, the subalpine ecosystem in the Rocky Mountains of Colorado exhibits only respiratory loss of CO$_2$ for several months during the winter, even on days that are sunny and warmer (Monson et al. 2002). The dominant evergreen species in this ecosystem include three conifers and one broad-leaved evergreen ground cover, all of which exhibit strong downregulation of intrinsic photosynthetic capacity during the winter. Similarly strong downregulation of intrinsic photosynthetic capacity was observed in two conifers growing near the tree line in the Alps (Stecher et al. 1999) and in the CO$_2$ uptake of an evergreen boreal forest in Siberia (Lloyd et al. 2002).

The key to preserving chlorophyll and remaining evergreen under such conditions may be to suppress the formation of the reactive oxygen species (figure 1) as high levels of photons continue to be absorbed by the light-harvesting system. This is achieved by coordinating a selective degradation of a few key proteins involved in the generation of high-energy electrons (while preserving most of the proteins in the photosynthetic membrane) and by arresting the xanthophyll cycle and the sustained engagement of zeaxanthin in a photoprotective configuration (figures 1b, 2). Species that downregulate photosynthetic capacity exhibit degradation of PSII core proteins (most notably the D1 protein, the site of photoinhibition; Ottander et al. 1995, Adams et al. 2001a) and the oxygen-evolving complex (responsible for the splitting of water and the donation of electrons for transport through the photosynthetic electron transport chain), whereas the light-harvesting proteins are largely preserved (figure 1b).

The inactivation and degradation of the D1 protein (and associated photoinhibition of photosynthesis) under stress conditions is frequently referred to as photodamage and viewed as an undesirable phenomenon that is thought to result in reduced plant growth and productivity (Long et al. 1994, Melis 1999, Adir et al. 2003). However, a cause-and-effect relationship has not been established between D1 degradation and reduced growth under natural conditions. Environmental factors that limit growth decrease the demand for carbohydrate and trigger a downregulation of photosynthesis. It has been argued that downsizing of the D1 pool is part of this downregulation of photosynthesis and upregulation of photoprotection (Adams et al. 2001b, 2002). If decreases in D1 (and development of photoinhibition) were responsible for decreased growth and productivity, this would be expected to occur through an insufficient supply of carbohydrate. However, the opposite has been observed for plants experiencing photoinhibition (Roden and Ball 1996, Adams et al. 2001a). Furthermore, decreases in the level of the D1 protein and oxygen-evolving complex may actually decrease the likelihood of photooxidative damage.

Degradation of the proteins involved in the generation of high-energy electrons presumably suppresses the formation of superoxide within the chloroplast (figure 1). However, cutting off the utilization of absorbed excitation energy through electron transport increases the potential to form $^{1}O_2$* in the preserved light-harvesting complexes. The latter is prevented by elevated levels of zeaxanthin-dependent energy dissipation, a process that remains engaged 24 hours a day (figures 1b, 2; Adams et al. 1995, 2001a, 2001b, 2002, Ottander et al. 1995, Verhoeven et al. 1996, 1998, 1999, Adams and Barker 1998, Stecher et al. 1999, Gilmore and Ball 2000, Matsubara et al. 2002, Close et al. 2003, Öquist and Huner 2003). The pool of xanthophyll cycle carotenoids is elevated in the winter needles of Douglas fir (compared with levels in the summer). Most of this pool is retained as zeaxanthin and antheraxanthin throughout the day and night during the winter, and PSII remains in a state that is highly efficient at dissipating excess excitation energy, as reflected by the low predawn photochemical efficiency in January even when temperatures rise (figure 3).

These coupled changes in the light-processing system counteract the generation of two potentially dangerous reactive oxygen species in the chloroplast (figure 1a): O$_2^-$ (suppressed by diminished water splitting and electron flow through D1) and $^{1}O_2$* (suppressed by thermal energy dissipation in the PSII antennae). Suppressing the formation of reactive oxygen species may be more effective than scavenging them once they have been formed. The latter process occurs through antioxidation systems (e.g., Niyogi 1999), some of which depend on enzymatic reactions (e.g., superoxide detoxification via superoxide dismutase and ascorbate peroxidase) limited by low temperatures on the coldest days of winter. On the other hand, complete suppression of reactive oxygen species may not occur, nor may it be desirable, as these species function in signaling and may contribute to the upregulation of photoprotection (see Demmig-Adams and Adams 2002).

One might conclude that there is simply no point in maintaining a functional electron transport chain when growth and the demand for photosynthetic ceases and when its continued functioning has the potential to generate large amounts of superoxide. By selectively degrading just a few key proteins, plants presumably keep the cost of reactivating photosynthesis to a minimum when whole-plant activity resumes during the spring. This minimal cost is likely to be far less than the cost of constructing entire new leaves, and it may maximize carbon return over the lifetime of leaves in evergreen species with considerably lower maximal rates of photosynthesis than the shorter-lived leaves of annual, biennial, and seasonally deciduous species (figures 3, 4; see also Mooney and Dunn 1970, Kikuzawa 1995, Durand and Goldstein 2001).

The winter response of Douglas fir and other evergreen species in full sunlight is in contrast to that of herbaceous
species such as *M. neglecta* (figure 3). *Malva neglecta* exhibits
no increase in the total xanthophyll cycle pool relative to
chlorophyll (although all pigments may increase in the win-
ter compared with the summer) and retains zeaxanthin and
highly dissipative PSII units only under actual freezing tem-
peratures (figure 3). On subfreezing nights, the leaves of *M.
neglecta* can retain some zeaxanthin and thus maintain the
light-harvesting system in a photoprotected state that can dis-
sipate excess excitation energy with dawn’s first light (Adams
et al. 1995, 2001b). This condition, however, is rapidly
reversible on warming (Verhoeven et al. 1996, 1999), probab-
elike to that observed during spring and summer.

**A continuum of strategies**

The two different strategies we have described for dealing with
excess light in winter represent the opposite ends of a con-
tinuum. The sun-exposed needles of most conifers have been
found to exhibit some level of photosynthetic downregu-
lation during the winter, although not necessarily to near-zero
levels of photosynthesis as shown for Douglas fir (figure 3).
For instance, in sun-exposed needles of Ponderosa pine, the
capacity for photosynthesis in winter may still be more than
half that observed in summer (figure 4; see also Verhoeven
et al. 1999). Some broad-leaved evergreen species have been
found to exhibit relatively strong winter downregulation of
photosynthesis in sun-exposed sites (e.g., *Vinca minor*),
whereas others have shown no downregulation of photo-
synthesis in winter (e.g., *Euonymus kiautschovicus* and *Ma-
nonia repens*; Adams et al. 2002). These differences do not neces-
sarily reflect genetic differences, since the response of a
given species depends on the severity of the environmental
conditions. The broad-leaved evergreen species *Arctostaphy-
los uva-ursi* (bearberry or kinnikinnick) exhibits complete
downregulation of photosynthesis during winter at an ele-
vation of 3000 meters in the Rocky Mountains, whereas un-
der the less severe winter conditions at 2000 meters in the Front
Range, its capacity for photosynthesis during winter is sim-
ilar to that observed during spring and summer.

Regardless of the extent to which evergreen species down-
regulate photosynthesis in sun-exposed sites during the
winter, all evergreens have been found to upregulate photo-
protection to some extent. This includes some or all of the
features shown for sun-exposed needles of Ponderosa pine
(figure 4), such as an increase in the pool of xanthophyll
cycle carotenoids, the retention of zeaxanthin and anthera-
xanthin when temperatures rise, and the sustained engage-
ment of zeaxanthin and antheraxanthin in a state primed for
photoprotection, as indicated by the persistently reduced ef-
ficiency of solar energy conversion to photochemistry.

In less sun-exposed sites, the response of evergreen species
to winter conditions can be different from that of the same
species in the sun. Most species examined thus far showed no
downregulation of photosynthesis in the shade (e.g., Pon-
derosa pine in figure 4), and some even exhibited an upreg-
ulation of photosynthetic capacity in winter (Adams et al.
2001b, 2002, Matsubara et al. 2002). However, the response
depends on species and conditions; downregulation of photo-
synthesis has been found in shaded needles of Douglas fir at
lower elevations in the foothills of the Rocky Mountains
(Adams et al. 2002), in shaded needles of *Picea abies* and
*Pinus cembra* in the Alps (Stecher et al. 1999), and in shaded
subalpine fir (*Abies lasiocarpa*) and *Ar. uva-ursi* at 3000
meters (but not at 2000 meters for the latter, as described
above). Upregulation of photoprotection in the winter does
occur in the shade (as assessed from xanthophyll cycle
parameters and PSII efficiency), but generally to a lesser
extent than observed in sun-exposed needles or leaves
(figure 4; Stecher et al. 1999, Adams et al. 2001b, 2002,
Matsubara et al. 2002). During periods when temperatures are
substantially below freezing, much greater amounts of zea-
xanthin can be retained and engaged in the photoprotective
state in shaded leaves, as indicated by PSII efficiencies that can
approach zero in the predawn darkness (Verhoeven et al.
1998). Like the lowered PSII efficiencies in herbaceous *M.
neglecta*, the depressions in PSII efficiency that are sustained
at low temperatures in evergreen shade leaves tend to
reverse quickly when the temperature rises (Verhoeven et al.
1998).

Depressions in PSII efficiency that reverse rapidly on
warming are thought to result from the nocturnal mainte-
nance of protons in the lumen of the thylakoid membranes
(Gilmore and Björkman 1995, Demmig-Adams et al. 1996,
Gilmore 1997). This may also be true of the portion of the low-
ered PSII efficiency in sun-exposed leaves or needles of ever-
green species that occurs under subfreezing temperatures
and reverses rapidly on warming (see Verhoeven et al. 1998,
Adams et al. 2001b). But what is responsible for the sus-
tained thermal dissipation activity in evergreens that does not
reverse rapidly when temperatures rise? It is apparently not
dependent on pH (Verhoeven et al. 1998, Gilmore and Ball
2000), which is perhaps to be expected, given that water split-
ting and electron transport are severely downregulated in
some evergreens, and the generation of a low pH within the
thylakoid lumen might thus be difficult. The PsbS protein
might still be associated with this phenomenon, as was suggested by an increase in PsbS level during the transfer of Scots pine from warm conditions to lower temperatures (all in relatively low light; Savitch et al. 2002). However, studies involving conifers exposed to full sunlight in summer and winter did not reveal marked changes in the level of the PsbS protein with the change of season. It is tempting to speculate that other proteins related to PsbS—but not dependent on low pH—may be involved (cf. figure 1; see Norén et al. 2003).

In addition to upregulating either the capacity for photosynthesis or the capacity for photoprotective thermal dissipation in winter, there is yet another adjustment that can be made to diminish the impact of excess light experienced by species that maintain leaves during the winter. By decreasing chlorophyll content, plants can lower the light-harvesting capacity of their leaves, thus diminishing the absorption of light. Although the majority of leaves in the canopy of most species do not exhibit this response, decreases of 40% or more in foliar chlorophyll content have been observed in the most sun-exposed leaves of some evergreen species (e.g., in *P. menziesii*, *V. minor*, *E. kiautschovicus*, and *Yucca glauca*; Adams and Barker 1998, Adams et al. 2002). Although the decreased light-harvesting capacity is likely to be a contributing factor in the response of these leaves to the increased level of excess light experienced during winter stress, the species showing this response nevertheless exhibit a strong upregulation of photoprotection.

### Future elucidation of mechanisms and integration of signals

This overview illustrates that different evergreen species employ somewhat different photoprotective responses. This will be important for researchers in further elucidating the molecular mechanisms of photoprotection and identifying genes that may be critical for plant survival and fitness. For example, we have shown that herbaceous mesophytes rely predominantly on pH-dependent sustained thermal dissipation, whereas longer-lived evergreen species employ a pH-independent form of sustained dissipation. The pH-dependent form of thermal dissipation is catalyzed by the PsbS protein, which is crucial for fitness (Külheim et al. 2002). However, this protein may not be involved in the pH-independent form of dissipation. Which other genes may be involved is a question for future research.

Furthermore, the interaction of photoprotective mechanisms with other aspects of plant growth and physiology among the diverse species that maintain leaves through the winter is poorly understood. The nature and integration of signal transduction between the chloroplast and other cellular sites, and between the chloroplast and the rest of the plant, and the response of the signals to seasonal change remain to be explored. These signals may include redox balance signals (Huner et al. 1998, Pfannschmidt et al. 2001, Mullineaux and Karpinski 2002) and hormone signals (e.g., jasmonic acid; see, e.g., Reinbothe et al. 1997, Wierstra and Mullineaux 2001) and signal transduction between the chloroplast and other cellular sites, and between the chloroplast and other cellular sites, and between the chloroplast and the rest of the plant, and the response of the signals to seasonal change.

Figure 4. Summer versus winter comparison of (a) the maximal intrinsic capacity for photosynthesis (in micromoles oxygen per square meter per second); (b) the total foliar pool of xanthophyll cycle carotenoids (millimoles combined violaxanthin, antheraxanthin, and zeaxanthin [V + A + Z] per mole chlorophyll a + b); (c) the sustained conversion of the xanthophyll cycle to zeaxanthin and antheraxanthin (Z + A); and (d) maximal photosystem II (PSII) photochemical efficiency as a percentage of light absorbed in the PSII antenna in sun and shade needles of Ponderosa pine. Sun-exposed needles were assessed on 5 June 2000 and on 13 and 14 January 2001; shaded needles were assessed on 16 June 2000 and 13 January 2001. Data depict the mean ± standard deviation, with *n* = 6 for photosynthetic capacity and PSII efficiency and *n* = 3 to 4 for pigment parameters. Significant differences were determined from a student’s t-test (****, *p* < 0.0001; ***, *p* < 0.001; **, *p* < 0.01). Data from Adams and colleagues (2002).
factors are likely to be involved in seasonal responses, such as low nutrient availability (Close et al. 2003), the temporal unavailability of water during subfreezing temperatures, and the impact of freeze–thaw induced cavitation and its reversal in the spring (Sperry and Sullivan 1992, Mayr et al. 2002). Although some of these possibilities will be difficult to address, and the integration of these diverse factors is a challenging feat, this information is needed to gain a complete understanding of plant responses—photosynthesis and photoprotection, in particular—to the seasonal challenge of winter.

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