4B. Effects of Radiation and Temperature

1. Introduction

In Chapter 4A on the plant's energy balance, we discussed traits that reflect radiation or otherwise avoid high radiation loads in high-light environments. Many plants lack these adaptations and absorb potentially damaging levels of radiation. In this chapter, we discuss some of the negative effects of excess radiation and the physiological mechanisms by which some plants avoid damage (Sect. 2.1). Effects of ultraviolet radiation and plant mechanisms to avoid or repair damage are treated in Sect. 2.2. Finally, some effects of both high and low temperatures are addressed in Sect. 3.

2. Radiation

2.1 Effects of Excess Irradiance

Species that are adapted to shade often have a restricted capacity to acclimate to a high irradiance. Unacclimated plants have a low capacity to use the products of the light reactions for carbon fixation, and tend to be damaged by high irradiance levels, because the energy absorbed by the photosystems exceeds the energy that can be used by carbon-fixation reactions. The excess energy can give rise to the production of reactive oxygen species (ROS) (i.e., toxic, reactive oxygen-containing molecules that rapidly lose an electron) and radicals (molecules with unpaired electrons) that break down membranes and chlorophyll (**photodamage**) (Sect. 3.3 of Chapter 2A on photosynthesis). Acclimated plants have protective mechanisms that avoid this photodamage. For example, the energy absorbed by the light-harvesting complex may be lost as heat through reactions associated with the **xanthophyll cycle**. When the cycle converts violaxanthin to zeaxanthin or antheraxanthin, nonradiative mechanisms dissipate energy by a mechanism that is not yet fully known (Sect. 3.3.1 of Chapter 2A on photosynthesis). This mechanism is induced by acidification of the thylakoid lumen that results from the formation of a proton-motive force. The strong acidification of the lumen induces an enzymatic conversion of the carotenoid violaxanthin into zeaxanthin. When both zeaxanthin is present and the thylakoid lumen is acidic, excess light energy is lost as heat by a mechanism not yet fully known. **Chlorophyll fluorescence** analysis can detect this nonphotochemical quenching of excess light energy (Box 2A.4 and Sect. 3.1 of Chapter 2A on photosynthesis).

2.2 Effects of Ultraviolet Radiation

Effects of ultraviolet (UV) radiation on plants have been studied for more than a century. The finding that the stratospheric UV-screening

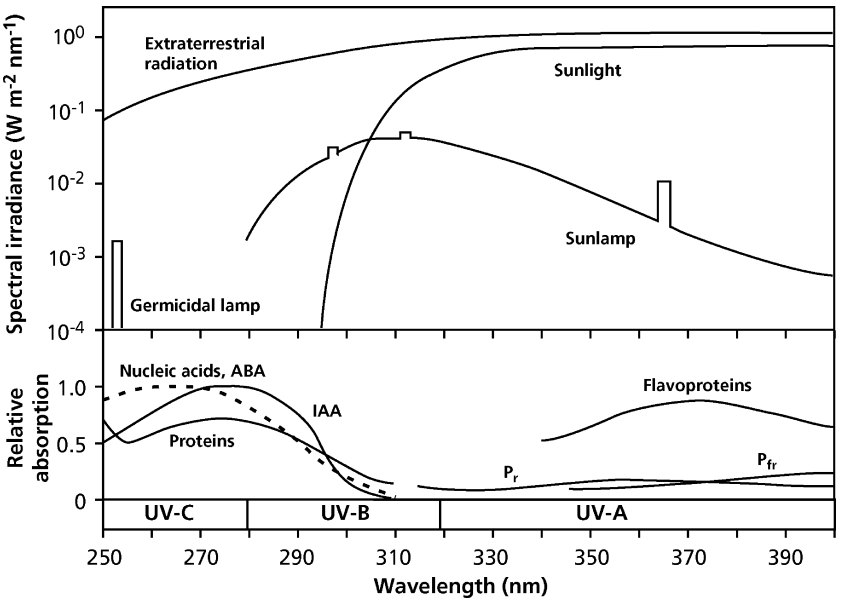

FIGURE 1. Spectral irradiance at 30 cm from common UV lamps, solar spectral irradiance before attenuation by the Earth's atmosphere (extraterrestrial), and as would be received at sea level at midday in summer at temperate latitudes. The absorption spectra of a number of plant compounds are also shown; ABA (abscisic acid) and nucleic acids are represented by the same curve; IAA (indole acetic acid) and the two forms of phytochrome (P_r and P_{fr}) are represented by the same curve as protein. Major subdivisions of the UV spectrum are indicated at the bottom; UV-B is ultraviolet light in the region 280–320 nm (Caldwell 1981).

ozone layer has been substantially depleted due to human activities, however, has increased interest in this topic. Ozone in the Earth's atmosphere prevents all of the UV-C (< 280 nm) and most of the UV-B (280–320 nm) radiation from reaching the Earth's surface (Fig. 1). Due to differences in optical density of the atmosphere, the UV radiation reaching the Earth is least at sea level in polar regions and greatest at high altitude and low latitude (e.g., the Andes). Cloud cover greatly reduces solar UV irradiance.

2.2.1 Damage by UV

Many compounds in plant cells absorb photons in the ultraviolet region (Fig. 1); the most destructive actions of UV include effects on nucleic acids. **DNA** is by far the most sensitive nucleic acid. Upon absorption of UV radiation, polymers of pyrimidine bases, termed **cyclobutane-pyrimidine dimers**, are formed which leads to loss of biological activity. Although RNA and proteins also absorb UV radiation, much higher doses are required for inactivation to occur, possibly due to their higher concentration in the cell compared with DNA. **ROS** play a role in mediating effects of UV-B: membranes are damaged, due to lipid peroxidation (Jansen et al. 1998).

Algae and bacteria are considerably more sensitive to UV-B radiation than are leaves of higher plants, due to less shielding of their DNA. Higher plants that are sensitive to solar UV show a reduction in photosynthetic capacity, leaf expansion, and height; they tend to have thicker leaves, which are often curled, and increased axillary branching. Although part of the reduced leaf expansion may be the result of reduced photosynthesis, it also involves direct effects on cell division (Fig. 2), with both effects leading to reductions in plant growth and productivity. There may be additional effects on plant development, e.g., on leaf epidermal cell size and leaf elongation in *Deschampsia antarctica* (Antarctic hair-grass) (Ruhland & Day 2000).

2.2.2 Protection Against UV: Repair or Prevention

Damage incurred by nucleic acids due to UV absorption can be repaired at the molecular level by splitting the **pyrimidine dimers**. Identification, followed by excision of the lesions from a DNA molecule and replacement by an undamaged patch

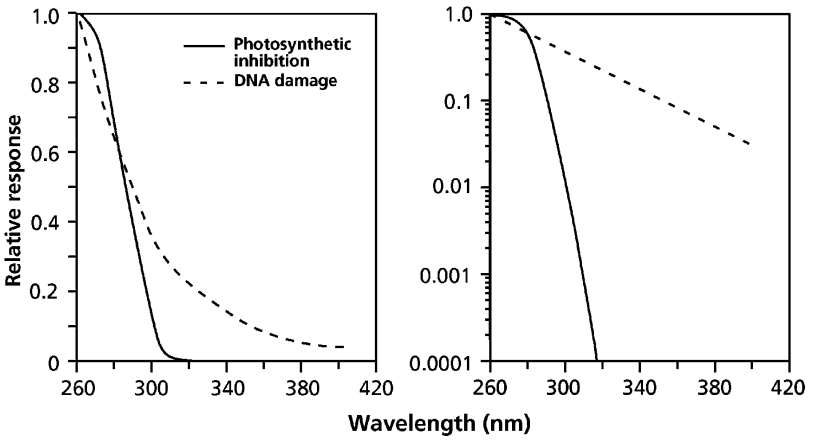

FIGURE 2. The damaging effect of UV on the dichlorophenol-indophenol reduction of chloroplasts isolated from *Spinacia oleracea* (spinach) ("photosynthetic inhibition") and on DNA in microorganisms ("DNA damage"). The same data are plotted on a linear (*left*) and an exponential (*right*) scale, showing that DNA is very sensitive to UV radiation, compared with photosynthesis (Jones & Kok 1966, as cited in Caldwell 1981, and Sewtlow 1974).

using the other strand as a template, has also been demonstrated. Genotypes of *Oryza sativa* (rice) that lack the capacity to repair damaged DNA show a high sensitivity to UV (Hidema et al. 1997). Plants have effective mechanisms to repair damage in all cells and organelles that contain DNA (Stapleton et al. 1997). Scavenging of ROS can also alleviate UV-B stress; levels of key anti-oxidants (glutathione and ascorbate) and of enzymes that detoxify ROS [e.g., superoxide dismutase (SOD) and ascorbate peroxidase] are up-regulated in response to UV-B (Jansen et al. 1998).

Plants can minimize UV exposure by having **steeply inclined leaves**, especially at lower latitudes, and by **reflecting** or **absorbing UV** in the **epidermis**. Epidermal cells may selectively absorb UV because of the presence of **phenolic compounds** (specific flavonoids) (Stapleton & Walbot 1994 Martz et al. 2007). Next to flavonoids, sinapate esters of phenolics provide some protection against UV in Brassicaceae [e.g., *Arabidopsis thaliana* (thale cress)] (Sheahan 1996). The phenolic compounds sometimes occur in leaf hairs (Karabourniotis et al. 1992, 1998). Both adaptation and acclimation to UV occur via the production of phenolic compounds (Burchard et al. 2000, Mazza et al. 2000). The most effective location for phenolics to screen UV is in the cell walls of epidermal cells, rather than in their vacuoles, where phenolics may also accumulate. The epidermis of evergreens transmits, on average, approximately 4% of the incident UV, and it does not allow penetration beyond 32 μm, as opposed to, on average, 28% and 75 μm, respectively, for leaves of deciduous plants (Day 1993). Conifer needles screen UV-B far more effectively because the absorbing compounds are located in the cell walls as well as inside their epidermal cells. The epidermis of herbaceous species is relatively ineffective at UV-B screening because UV-B may still penetrate through the epidermal cell walls, even if their vacuoles contain large amounts of UV-absorbing phenolics (Fig. 3; Day et al. 1994).

Polyamines, **waxes**, and specific **alkaloids** may also contribute to UV tolerance, either because they absorb UV or because they act as scavengers of ROS (Frohnmeyer & Staiger 2003).

3. Effects of Extreme Temperatures

3.1 How Do Plants Avoid Damage by Free Radicals at Low Temperature?

Variation in growth potential at different temperatures may reflect the rate of photosynthesis per unit leaf area, as discussed in Sect. 7 of Chapter 2A on photosynthesis. A frequently observed effect of chilling is **photooxidation**, which occurs because the biophysical reactions of photosynthesis are far less temperature sensitive than are the biochemical ones. Chlorophyll continues to absorb light at low temperatures, but the energy cannot be transferred to the normal electron-accepting components with sufficient speed to avoid **photoinhibition**. One mechanism by which cold-acclimated plants avoid photooxidation is to increase the components of the **xanthophyll cycle** (Williams et al. 2003), just as observed at excess radiation (Sect. 3.3.1 of Chapter 2A on photosynthesis). This prevents the formation of **ROS**; radicals may form when oxygen is reduced to superoxide (Apel & Hirt 2004). The xanthophyll cycle is widespread among plants, however, and other mechanisms probably also protect the photosynthetic apparatus of cold-adapted species,

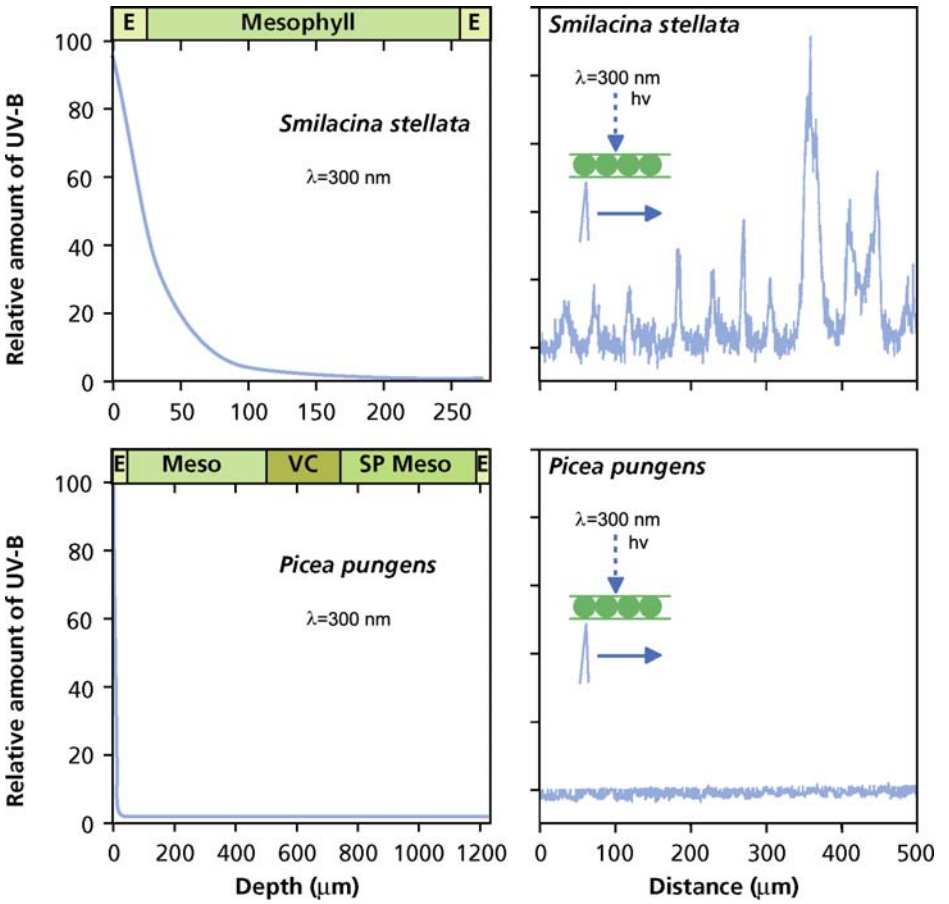

FIGURE 3. (*Left*) Relative amount of UV-B (300 nm) as a function of depth in intact foliage of an herbaceous species [*Smilacina stellata* (false Solomon's seal)] and a conifer [*Picea pungens* (Colorado spruce)]. Measurements were made with a fiberoptic microprobe. E, epidermis; Meso, mesophyll; VC, vascular cylinder; SP Meso, spongy mesophyll. Note that UV-B penetrates into the mesophyll of the herbaceous leaf, whereas it is quickly attenuated in the epidermis of the conifer needle. (*Right*) Pattern of UV-B transmission under an epidermal peel, removed from the rest of the leaf, of *Smilacina stellata* (false Solomon's seal) and *Picea pungens* (Colorado spruce). Measurements were made by running a microscopic fiberoptic sensor along the underside of irradiated peels, parallel to the leaf axis, as illustrated by the image in the figures. UV-B penetrates (the spikes) through cell walls between cells of the epidermis in the herbaceous species, where UV-absorbing compounds are located in the vacuole. In the conifer species, minimal transmission occurs, because UV-absorbing compounds are present in the cell wall (after Day et al. 1993).

especially if low temperatures coincide with high levels of irradiance, such as at high altitude.

Once ROS are formed, they must be scavenged to avoid their damaging effect. Upon exposure to oxidative stress some ROS are produced in nonacclimated plants which induce the expression of genes coding for enzymes like chalcone synthase, which is involved in the synthesis of phenolic anti-oxidants (Henkov et al. 1996). High-alpine species contain higher concentrations of a range of **anti-oxidants**, such as ascorbic acid (vitamin C), α-tocopherol (vitamin E), and the tripeptide glutathione. Their concentrations increase with increasing altitude (Fig. 4). The alpine site and the lowland environments from which the plants shown in Fig. 4 were collected receive a similar daily quantum input (Körner & Diemer 1987). The higher level of anti-oxidants in the high-altitude plants enables them to cope with multiple stresses, including lower, early-morning temperature, higher level of irradiance at peak times, or higher levels of UV-B. The concentrations of anti-oxidants also show a diurnal pattern,

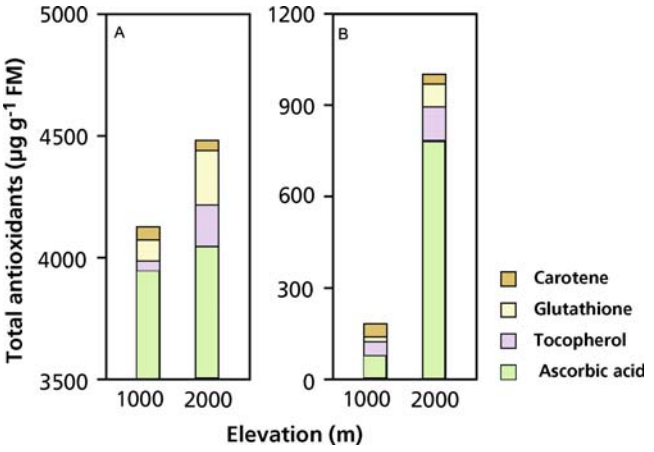

FIGURE 4. The concentration of various antioxidants in leaves of (a) *Homogyne alpina* (alpine coltsfoot) and (b) *Soldanella pusilla* (alpine snowbell) measured in plants growing at 1000 m (Wank) and at 2000 m (Obergurgl). Note the different scales on the *y*-axis (after Wildi & Lütz 1996).

with highest values at midday and lower ones at night (Wildi & Lütz 1996). **Superoxide dismutase** (SOD) and **catalase** are major enzymes that are involved in avoiding damage by ROS. SOD catalyzes the conversion of superoxide to hydrogen peroxide (H_2O_2), and catalase converts H_2O_2 to water and oxygen.

Acclimation to low temperature in *Zea mays* (corn) is enhanced by exposure to a low soil water potential (Irigoyen et al. 1996). Both stresses enhance the level of the phytohormone ABA (Box 7.1), which is involved in acclimation to both a low soil water potential and a low temperature, although through separate signal-transduction pathways. In addition, there are ABA-independent stress-signaling pathways that "cross-talk" with the ABA-dependent pathways (Ishitani et al. 1997).

3.2 Heat-Shock Proteins

A sudden rise in temperature, close to the lethal temperature, induces the formation of mRNAs coding for **heat-shock proteins** (Parcellier et al. 2003). Some of the genes coding for heat-shock proteins are homologous with those from animals; in fact, heat-shock proteins were first discovered in *Drosophila*. Although the precise role of heat-shock proteins is not yet known, they do increase the plant's heat tolerance. Some of these proteins are only produced after exposure to high temperatures; others are also found after exposure to other extreme environmental conditions (e.g., low temperature, water stress, high light, and drought). There is some evidence that an increase in **membrane fluidity** specifically enhances the expression of genes encoding heat-shock proteins; however, the mechanisms of the perception of changes in membrane fluidity are unknown (Xiong et al. 2002).

Heat-shock proteins may be involved in the protection of the photosynthetic apparatus and prevent photooxidation. Other heat-shock proteins belong to the class of the **chaperones,** which also occur in plant cells that are not exposed to high temperatures, but in smaller quantities. Chaperones are involved in arranging the tertiary structure of proteins. Heat-shock proteins are formed both after a sudden increase in temperature and upon a more gradual and moderate rise in temperature, although not to the same extent. This class of proteins is, therefore, probably also involved in the tolerance of milder degrees of heat stress (Parcellier et al. 2003).

3.3 Are Isoprene and Monoterpene Emissions an Adaptation to High Temperatures?

There is increasing evidence that plants, especially some tree species and ferns, can cope with rapidly changing leaf temperatures through the production of the low-molecular-mass hydrocarbon: **isoprene** and **monoterpenes** (Peñuelas & Munné-Bosch 2005). Around Sydney in Australia, these hydrocarbons account for the haze in the Blue Mountains. Isoprene (2-methyl-1,3-butadiene) is the single most abundant biogenic, nonmethane hydrocarbon entering the atmosphere due to emission by plants in both temperate and tropical ecosystems, and the reason for these high emission rates has puzzled scientists for a long time (Sharkey & Yeh 2001). Many isoprene-emitting species lose about 15% of fixed carbon as isoprene emissions, with extreme values up to 50%. Global isoprene emissions from

plants to the atmosphere amount to 180–450 $\times$ 10^{12}g carbon per year, more than any other volatile organic carbon lost from plants (Lichtenthaler 2007). There should be sufficient evolutionary pressure to eliminate this process, if it serves no function. The finding that emissions increase at high temperature and under water stress has stimulated research into a role in coping with high leaf temperatures. The change in **isoprene emission** capacity through the canopy is similar to the change in **xanthophyll cycle** intermediates, which suggests that isoprene and monoterpene emission may be the plant's protection against excess heat, just as the xanthophyll cycle protects against excess light (Loreto et al. 1998, Loreto & Velikova 2001) (Sect.3.3.1 of Chapter 2A on photosynthesis). In the presence of realistic concentrations of isoprene or monoterpenes, leaves are, indeed, protected against high-temperature damage of photosynthesis (Fig. 5; Sharkey et al. 2008).

How hot do leaves normally get? Leaf temperatures of *Quercus alba* (white oak) at the top of the canopy can increase by as much as 14°C above air temperature, and the leaf temperature may drop by 8°C within minutes (Singsaas & Sharkey 1998). Using isoprene may be an effective way of changing membrane properties rapidly enough to track leaf temperature. In plants that are not subject to such high temperatures or changes in leaf temperature, slower and less wasteful methods may be more effective.

3.4 Chilling Injury and Chilling Tolerance

Many (sub)tropical plants grow poorly at or are damaged by temperatures between 10 and 20°C. This type of damage is quite different from frost damage, which occurs at subzero temperatures, and is generally described as **chilling injury**. Different parts of the plant may well differ in their sensitivity to low temperatures, and this sensitivity may vary with age. For example, germinating seeds and young seedlings of *Gossypium herbaceum* (Levant cotton) and *Glycine max* (soybean) are far more chilling sensitive than are mature plants. For *Oryza sativa* (rice) and *Sorghum bicolor* (millet), processes that occur in the phase just prior to flower initiation are most sensitive. Low temperatures may disturb the formation of pollen mother cells, and thus cause sterility. Ripening fruits of (sub)tropical crops are also rapidly damaged by low temperatures.

The physiological cause of low-temperature damage varies among species and plant organs. The following factors play a role:

1. Changes in membrane fluidity
2. Changes in the activity of membrane-bound enzymes and processes, such as electron transport in chloroplasts and mitochondria, and in compartmentation
3. Loss of activity of low-temperature-sensitive enzymes

Chilling resistance may involve **membrane properties**, which are affected by the composition of the membranes. Both the proteins and the lipids in the membrane may play a role. When plants are exposed to low temperatures, the desaturation of fatty acids occurs mainly from 18:2 to 18:3. **Chilling tolerance** correlates with a high proportion of *cis*-unsaturated fatty acids in the phosphatidylglycerol molecules of chloroplast membranes. Evidence for this comes from work with *Nicotiana tabacum* (tobacco) plants transformed with glycerol-3-phosphate acyltransferase from either a cold- tolerant species or a cold-sensitive one. Overexpression of the enzyme from the cold-tolerant species increases cold tolerance, whereas the tobacco plants become more sensitive to cold stress

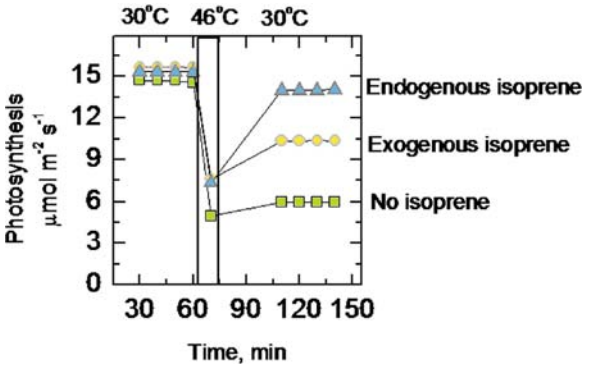

FIGURE 5. Thermoprotection of photosynthetic capacity by isoprene. Photosynthesis of detached leaves of *Pureria lobata* (kudzu) was measured at the indicated temperatures. One leaf was fed water, and so made isoprene from endogenous sources. Two other leaves were fed 4 µM fosmidomycin, and inhibitor of the pathway leading to isoprene, and isoprene emission was monitored until >90% of the isoprene emission capacity was lost. One of these leaves was then provided with 2 µL L^{-1} isoprene in the air stream (exogenous isoprene treatment). Modified after Sharkey et al. (2008).

when over-expressing the enzyme from cold-sensitive plants. Cold sensitivity of the transgenic tobacco plants correlates with the extent of fatty acid unsaturation in phosphatidyl-glycerol which is due to different selectivities for the saturated and *cis*-unsaturated fatty acids of the enzyme from contrasting sources (Bartels & Nelson 1994, Murata & Los 1997).

The degree of saturation of the fatty acid affects the **membrane's fluidity**, as shown for mitochondria: the ratio between unsaturated and saturated fatty acids is about 2 for chilling-sensitive species and about 4 for resistant species. It is likely that the mitochondrial membranes of sensitive species tend to "solidify" at a relatively high temperature, hampering membrane-associated processes and causing "leakage" of solutes out of various compartments or out of the cells.

Heat-shock proteins are expressed at low temperatures (Sabehat et al. 1998), and these probably function in much the same way as discussed in Sect. 3.2.

There is some evidence that the low temperature is **perceived** through changes in **fluidity** of the plasma membrane, which then activates cold-inducible genes. For example, partial desaturation of membrane lipids in vivo, by using a water-soluble palladium complex as a catalyst, enhances the level of transcript of a gene that is also up-regulated at low temperature (Xiong et al. 2002).

3.5 Carbohydrates and Proteins Conferring Frost Tolerance

As outlined in Sect. 9 of Chapter 3 on plant water relations, frost damage only occurs at subzero temperatures, when the formation of **ice crystals** within cells causes damage to membranes and organelles and dehydration of cells; ice crystals that form outside of cells (e.g., in cell walls) generally cause little damage. Cold tolerance is correlated with the concentration of **soluble carbohydrates** in the cells (Fig. 6; Sakai & Larcher 1987). These carbohydrates play a role in **cryoprotection** (Crowe et al. 1990). Differences in cold tolerance between *Picea abies* (Norway spruce), *Pinus contorta* (lodgepole pine), and *Pinus sylvestris* (Scots pine), following exposure of hardened needles to 5.5°C, are closely correlated with their carbohydrate concentration. *Picea abies* maintains high sugar concentrations by having larger reserves to start with and lower rates of respiration, which decline more rapidly when sugars are depleted (Ögren et al. 1997).

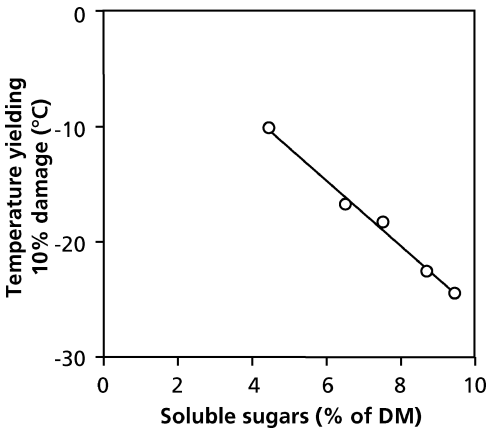

FIGURE 6. Temperature causing 10% damage of the needles of *Pinus sylvestris* (Scots pine) as dependent on the concentration of soluble carbohydrates in the needles. Variation in sugar concentration was obtained by exposure of intact plants to temperatures ranging from –8.5 to +5.5°C for 16 weeks in midwinter (Ögren 1997). Copyright Heron Publishing.

Cold stress leads to differential **gene expression,** and a wide range of cold-inducible genes have been isolated. Several of these genes occur in a wide range of plant species and contain conserved structural elements, which are probably vital for functional reasons. Their role in low-temperature acclimation, however, is not yet clear. A group of low-temperature-induced genes are homologous to the genes preferentially expressed during embryo maturation and encode mainly **hydrophilic proteins**. These genes may be involved in the osmotic stress response that is common to cold, water, and salt stress (Bartels & Nelson 1994).

Many plants that naturally occur in temperate climates go though an annual cycle of frost **hardening** and **dehardening**, with maximum freezing tolerance occurring during winter. In many woody plants, short days signal the initiation of cold acclimation, which is mediated by ABA. Freezing tolerance is accompanied by bud dormancy, which is also induced by short days, but the role of ABA in this induction is less direct (Welling et al. 1997). In herbaceous plants, frost hardening occurs by exposure to low, nonfreezing temperatures. Upon exposure to 5/2 (day/night) °C, specific mRNAs increase in abundance. It has yet to be established, however, which of the changes in gene expression are acclimations to growth at low temperature and which have a role in subsequent resistance to freeze–thaw damage. Specific **anti-freeze proteins** accumulate in the apoplast of *Secale cereale* (winter rye) and other frost-

resistant species (Hincha et al. 1997, Moffatt et al. 2006). These proteins are similar to the pathogenesis-related proteins that are induced by microbial pathogens (Sect. 3 of Chapter 9C on effects of microbial pathogens) (Griffith & Yaish 2004). They confer greater frost tolerance, as evidenced by less ion leakage from the leaves when exposed to subzero temperatures. Anti-freeze proteins that accumulate in several places in the apoplast of rye form oligomeric complexes and have the unique ability to absorb onto the surface of ice and inhibit its growth (Griffith et al. 1997, Yu & Griffith 1999). When the anti-freeze proteins are experimentally removed from the apoplast, the plant's cold tolerance is lost (Marentes et al. 1993). Hence, the accumulation of these proteins is causally linked to the increased frost tolerance; they may have an effect on the growth of ice in the cell walls (Hon et al. 1994). Exposure of *Triticum aestivum* (wheat) to low temperature induces a **dehydrin**; dehydrins are a class of proteins that are related to the products of late embryogenesis abundant genes, which we discussed in Sect. 8.3 of Chapter 3 on plant water relations. The dehydrins are found near the plasma membrane, where they may function in cryoprotection (Danyluk et al. 1998). Upon cold acclimation, a specific glycoprotein (**cryoprotectin**) accumulates in leaves of *Brassica oleracea* (cabbage) which protects thylakoids from non-acclimated leaves, both of cabbage and of other species such as *Spinacia oleracea* (spinach) (Sieg et al. 1996). Exposure to low temperature induces a specific class of proteins: lipid-transfer proteins. Although the name of these proteins suggests otherwise, they are unlikely to be involved in lipid transfer in vivo. The relationship between the putative protective role of lipid-transfer proteins and cold tolerance still needs to be determined (Doxey et al. 2006, Moffatt et al. 2006).

4. Global Change and Future Crops

Plants are frequently exposed to potential harmful radiation and adverse temperatures. Some of the protective mechanisms in plants are universal (e.g., the carotenoids of the xanthophyll cycle that protect against excess radiation). All plants also have mechanisms to avoid effects of UV radiation and repair UV damage. There is a wide variation among species, however, in the extent of the avoidance and probably also in the capacity to repair the damage. The rapid depletion of the stratospheric UV-screening ozone layer, due to human activities, imposes a selective force on plants to cope with UV.

Toxic ROS are produced when the dark reactions of photosynthesis cannot cope with the high activity of the light reactions. This may occur under high-light conditions, in combination with extreme temperatures. The xanthophyll cycle can prevent some of the potential damage by funneling off excess energy, acting as a lightning rod, at both high and low temperatures. Isoprene production possibly provides additional protection of leaves at high temperatures. Specific proteins and carbohydrates offer protection against temperature extremes. Further ecophysiological research on these compounds and on the regulation of genes that code for their production may help us to develop crop varieties that have a greater capacity to cope with extreme temperatures. Such plants will be highly desirable for agriculture in those parts of the world where extreme temperatures are a major factor limiting crop productivity.

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