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Acclimation and Adaptive Responses of Woody Plants to Environmental Stresses

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I. Abstract

The predominant emphasis on harmful effects of environmental stresses on growth of woody plants has obscured some very beneficial effects of such stresses. Slowly increasing stresses may induce physiological adjustment that protects plants from the growth inhibition and/or injury that follow when environmental stresses are abruptly imposed. In addition, short exposures of woody plants to extreme environmental conditions at critical times in their development often improve growth. Furthermore, maintaining harvested seedlings and plant products at very low temperatures extends their longevity.

Drought tolerance: Seedlings previously exposed to water stress often undergo less inhibition of growth and other processes following transplanting than do seedlings not previously exposed to such stress. Controlled wetting and drying cycles often promote early budset, dormancy, and drought tolerance. In many species increased drought tolerance following such cycles is associated with osmotic adjustment that involves accumulation of osmotically active substances. Maintenance of leaf turgor often is linked to osmotic adjustment. A reduction in osmotic volume at full turgor also results in reduced osmotic potential, even in the absence of solute accumulation. Changes in tissue elasticity may be important for turgor maintenance and drought tolerance of plants that do not adjust osmotically.

Water deficits and nutrient deficiencies promote greater relative allocation of photosynthate to root growth, ultimately resulting in plants that have higher root:shoot ratios and greater capacity to absorb water and minerals relative to the shoots that must be supported.

At the molecular level, plants respond to water stress by synthesis of certain new proteins and increased levels of synthesis of some proteins produced under well-watered conditions. Evidence has been obtained for enhanced synthesis under water stress of water-channel proteins and other proteins that may protect membranes and other important macromolecules from damage and denaturation as cells dehydrate.

Flood tolerance: Both artificial and natural flooding sometimes benefit woody plants. Flooding of orchard soils has been an essential management practice for centuries to increase fruit yields and improve fruit quality. Also, annual advances and recessions of floods are crucial for maintaining valuable riparian forests. Intermittent flooding protects bottomland forests by increasing groundwater supplies, transporting sediments necessary for creating favorable seedbeds, and regulating decomposition of organic matter. Major adaptations for flood tolerance of some woody plants include high capacity for producing adventitious roots that compensate physiologically for decay of original roots under soil anaerobiosis, facilitation of oxygen up-

take through stomata and newly formed lenticels, and metabolic adjustments. Halophytes can adapt to saline water by salt tolerance, salt avoidance, or both.

Cold hardiness: Environmental stresses that inhibit plant growth, including low temperature, drought, short days, and combinations of these, induce cold hardening and hardiness in many species. Cold hardiness develops in two stages: at temperatures between 10° and 20°C in the autumn, when carbohydrates and lipids accumulate; and at subsequent freezing temperatures. The sum of many biochemical processes determines the degree of cold tolerance. Some of these processes are hormone dependent and induced by short days; others that are linked to activity of enzyme systems are temperature dependent. Short days are important for development of cold hardiness in species that set buds or respond strongly to photoperiod. Nursery managers often expose tree seedlings to moderate water stress at or near the end of the growing season. This accelerates budset, induces early dormancy, and increases cold hardiness.

Pollution tolerance: Absorption of gaseous air pollutants varies with resistance to flow along the pollutant's diffusion path. Hence, the amount of pollutant absorbed by leaves depends on stomatal aperture, stomatal size, and stomatal frequency. Pollution tolerance is increased when drought, dry air, or flooding of soil close stomatal pores.

Heat tolerance: Exposure to sublethal high temperature can increase the thermotolerance of plants. Potential mechanisms of response include synthesis of heat-shock proteins and isoprene and antioxidant production to protect the photosynthetic apparatus and cellular metabolism.

Breaking of dormancy: Seed dormancy can be broken by cold or heat. Embryo dormancy is broken by prolonged exposure of most seeds to temperatures of 1° to 15°C. The efficiency of treatment depends on interactions between temperature and seed moisture content. Germination can be postponed by partially dehydrating seeds or altering the temperature during seed stratification. Seed-coat dormancy can be broken by fires that rupture seed coats or melt seed-coat waxes, hence promoting water uptake. Seeds with both embryo dormancy and seed-coat dormancy may require exposure to both high and low temperatures to break dormancy. Exposure to smoke itself can also serve as a germination cue in breaking seed dormancy in some species.

Bud dormancy of temperate-zone trees is broken by winter cold. The specific chilling requirement varies widely with species and genotype, type of bud (e.g., vegetative or floral bud), depth of dormancy, temperature, duration of chilling, stage of plant development, and daylength. Interruption of a cold regime by high temperature may negate the effect of sustained chilling or breaking of bud dormancy. Near-lethal heat stress may release buds from both endodormancy and ecodormancy.

Pollen shedding: Dehiscence of anthers and release of pollen result from dehydration of walls of anther sacs. Both seasonal and diurnal pollen shedding are commonly associated with shrinkage and rupture of anther walls by low relative humidity. Pollen shedding typically is maximal near midday (low relative humidity) and low at night (high relative humidity). Pollen shedding is low or negligible during rainy periods.

Seed dispersal: Gymnosperm cones typically dehydrate before opening. The cones open and shed seeds because of differential shrinkage between the adaxial and abaxial tissues of cone scales. Once opened, cones may close and reopen with changes in relative humidity. Both dehydration and heat are necessary for seed dispersal from serotinous (late-to-open) cones. Seeds are stored in serotinous cones because resinous bonds of scales prevent cone opening. After fire melts the resinous material, the cone scales can open on drying. Fires also stimulate germination of seeds of some species. Some heath plants require fire to open their serotinous follicles and shed seeds. Fire destroys the resin at the valves of follicles, and the valves then

reflex to release the seeds. Following fire the follicles of some species require alternate wetting and drying for efficient seed dispersal.

Stimulation of reproductive growth: Vegetative and reproductive growth of woody plants are negatively correlated. A heavy crop of fruits, cones, and seeds is associated with reduced vegetative growth in the same or following year (or even years). Subjecting trees to drought during early stages of fruit development to inhibit vegetative growth, followed by normal irrigation, sometimes favors reproductive growth. Short periods of drought at critical times not only induce formation of flower buds but also break dormancy of flower buds in some species. Water deficits may induce flowering directly or by inhibiting shoot flushing, thereby limiting the capacity of young leaves to inhibit floral induction. Postharvest water stress often results in abundant return bloom over that in well-irrigated plants. Fruit yields of some species are not reduced or are increased by withholding irrigation during the period of shoot elongation. In several species, osmotic adjustment occurs during deficit irrigation. In other species, increased fruit growth by imposed drought is not associated largely with osmotic adjustment and maintenance of leaf turgor.

Seedling storage: Tree seedlings typically are stored at temperatures just above or below freezing. Growth and survival of cold-stored seedlings depend on such factors as: date of lifting from the nursery; species and genotype; storage temperature, humidity, and illumination; duration of storage; and handling of planting stock after storage. Seedlings to be stored over winter should be lifted from the nursery as late as possible. Dehydration of seedlings before, during, and after storage adversely affects growth of outplanted seedlings. Long-term storage of seedlings may result in depletion of stored carbohydrates by respiration and decrease of root growth potential. Although many seedlings are stored in darkness, a daily photoperiod during cold storage may stimulate subsequent growth and increase survival of outplanted seedlings. For some species, rapid thawing may decrease respiratory consumption of carbohydrates (over slowly thawed seedlings) and decrease development of molds.

Pollen storage: Preservation of pollen is necessary for insurance against poor flowering years, for gene conservation, and for physiological and biochemical studies. Storage temperature and pollen moisture content largely determine longevity of stored pollen. Pollen can be stored successfully for many years in deep freezers at temperatures near –15°C or in liquid nitrogen (–196°C). Cryopreservation of pollen with a high moisture content is difficult because ice crystals may destroy the cells. Pollens of many species do not survive at temperatures below –40°C if their moisture contents exceed 20–30%. Pollen generally is air dried, vacuum dried, or freeze dried before it is stored. To preserve the germination capacity of stored pollen, rehydration at high humidity often is necessary.

Seed storage: Seeds are routinely stored to provide a seed supply during years of poor seed production, to maintain genetic diversity, and to breed plants. For a long time, seeds were classified as either orthodox (relatively long-lived, with capacity for dehydration to very low moisture contents without losing viability) or recalcitrant (short-lived and requiring a high moisture content for retention of viability). More recently, some seeds have been reclassified as suborthodox or intermediate because they retain viability when carefully dried. True orthodox seeds are preserved much more easily than are nonorthodox seeds. Orthodox seeds can be stored for a long time at temperatures between 2° and –20°C, with temperatures below –5°C preferable. Some orthodox seeds have been stored at superlow temperatures, although temperatures of –40°, –70°, or –196°C have not been appreciably better than –20°C for storage of seeds of a number of species. Only relatively short-term storage protocols have been developed for nonorthodox seeds. These treatments typically extend seed viability to as much as a year. The methods often require cryopreservation of excised embryos. Responses to

cryopreservation of nonorthodox seeds or embryos vary with species and genotype, rate of drying, use of cryoprotectants, rates of freezing and thawing, and rate of rehydration.

Fruit storage: Storing fruits at low temperatures above freezing, increasing the CO_2 concentration, and lowering the O_2 concentration of fruit storage delays senescence of fruits and prolongs their life. Fruits continue to senesce and decay while in storage and become increasingly susceptible to diseases. Both temperate-zone and tropical fruits may develop chilling injury characterized by lesions, internal discoloration, greater susceptibility to decay, and shortened storage life. Chilling injury can be controlled by chemicals, temperature conditioning, and intermittent warming during storage. Stored fruits may become increasingly susceptible to disease organisms. Fruit diseases can be controlled by cold, which inhibits growth of microorganisms and maintains host resistance. Exposure of fruits to high CO_2 and low O_2 during storage directly suppresses disease-causing fungi. Pathogens also can be controlled by exposing fruits to heat before, during, and after storage. Scald that often develops during low-temperature storage can be controlled by chemicals and by heat treatments.

II. Introduction

A voluminous literature emphasizes the effects of environmental stresses on inhibiting plant growth and physiological processes, reducing yield of harvested plant products, and causing plant mortality. Plants are subjected to multiple abiotic and biotic stresses that adversely influence growing plants by inducing physiological dysfunctions (Kozlowski, 1964, 1967, 1979; Levitt, 1980; Hennessey et al., 1986; Fitter & Hay, 1987; Cherry, 1989; Jones et al., 1989; Katterman, 1990, 1992; Kozlowski et al., 1991; Mooney et al., 1991; Teller et al., 1992; Botkin, 1993; McKersie & Leshem, 1994; Schaffer & Anderson, 1994; Larcher, 1995; Smith & Hinckley, 1995; Kozlowski & Pallardy, 1997a, 1997b). Unfortunately, preoccupation with the deleterious impacts of stressful environments has tended to obscure some of their very beneficial effects on plants (Grierson et al., 1982).

Often, slowly increasing stresses induce physiological adjustments in plants that protect them from subsequent adverse responses that would occur if such stresses were abruptly imposed and continued for a long time (Kozlowski & Pallardy, 1997b). Furthermore, judicious short exposures of plants to extremes of water supply, temperature, and humidity, as well as some combinations of these, are essential for optimal plant development and/or protection of plants from subsequent environmental injury. The proper timing of such exposures is crucial.

This review will outline some examples of the benefits of extreme environmental regimes on several aspects of plant growth and protection, including alteration of the effects of subsequent stresses, breaking of dormancy, shedding of pollen and seeds, regulation of reproductive growth, and storage of pollen, seeds, seedlings, and fruits.

III. Drought Tolerance

Arid conditions, which prevail over about a third of the world's land area, exclude establishment of trees; over most of the remaining land area the growth of plants, and sometimes their survival, is reduced by periodic droughts.

Transplanted trees undergo a severe physiological shock because their capacity for water absorption is greatly decreased. This is the result of injury to roots, loss of small absorbing roots, and disruption of the previously established contact of the root system with a large volume of soil. Immediately after seedlings are outplanted their roots generally do not grow fast enough to absorb sufficient amounts of water to keep up with transpirational water losses (Kozlowski, 1967, 1982a, 1983; Kozlowski & Pallardy, 1997b).

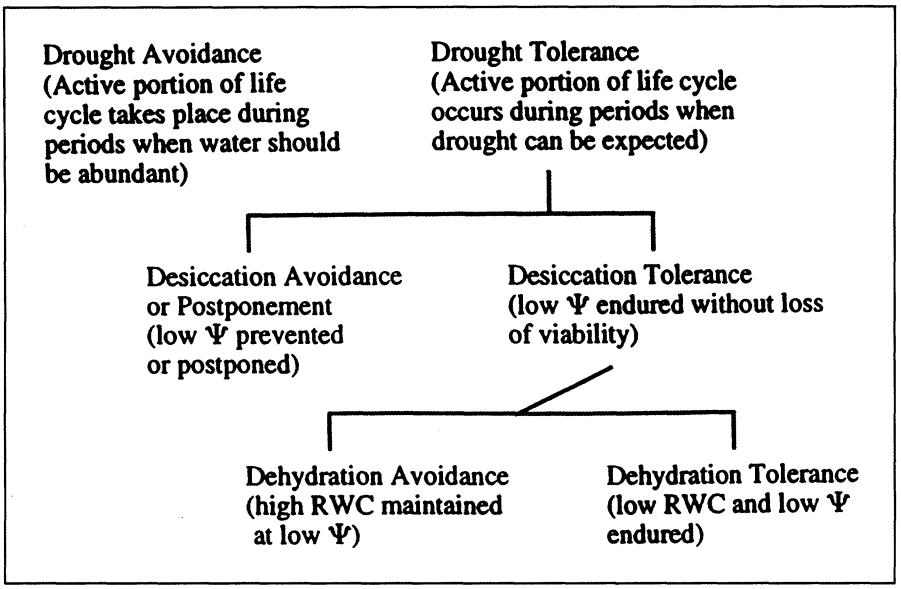

Fig. 1. General scheme of mechanisms of adaptation to drought. *Source:* Kozlowski & Pallardy, 1997a.

Plants differ widely in their capacity to cope with drought. Adaptations exist to explain these differences (Kozlowski & Pallardy, 1997a), and these can be conveniently referenced to the capacity to maintain water status (water potential, Ψ_l, and/or relative water content, RWC) (Fig. 1). Some woody plants are drought tolerant because they can either withstand extreme dehydration of protoplasm (low RWC) or avoid low Ψ_l, with the latter being more widely observed (Kozlowski, 1964, 1972b, 1976a, 1976b, 1983). Many desiccation-avoiding adaptations of woody plants have been identified in leaves (shedding; small or few leaves; small, few, and sunken stomata; rapid stomatal closure during drought; abundant leaf waxes; strong development of palisade mesophyll), in stems (twig and stem photosynthesis; low resistance to water flow in vascular tissues), and in roots (extensive root growth; high root:shoot ratios; high root-regenerating potential after transplanting) (Kozlowski, 1964, 1972b, 1976a, 1976b, 1978, 1979, 1982a; Kozlowski & Pallardy, 1997a). All these adaptations promote water homeostasis either by restricting water loss from the plant body or by increasing water absorption to replace losses by transpiration.

Levitt (1980: 2: 148) covered the early literature on drought hardening in plants (i.e., "exposure to a sublethal stress that results in resistance to an otherwise lethal stress"). Seedlings previously exposed to mild water stress undergo less injury from transplanting and drought than do seedlings not previously exposed to such stress, suggesting that the level of dehydration tolerance has been increased (Abrams, 1988c; Kozlowski et al., 1991; Kozlowski & Pallardy, 1997b). Membrane properties may respond to water-stress preconditioning. Electrolyte leakage from leaves of *Quercus* spp., *Cornus florida,* and *Acer saccharum* declined as trees were subjected to drought (Martin et al., 1987). In contrast, *Juglans nigra* did not show a reduction in electrolyte leakage when undergoing water stress. Reductions in electrolyte leakage also were demonstrated in several genotypes of *Populus* and in *Quercus macrocarpa* (Gebre &

Kuhns, 1991; Kuhns et al., 1993). *Acacia* and *Eucalyptus* seedlings that had been drought hardened by water stress had better control of water loss and were more drought tolerant than were seedlings not previously stressed (Clemens & Jones, 1978). Hence, nursery operators frequently harden seedlings to drought by decreasing the frequency of irrigation. Controlled wetting and drying cycles in the nursery in late summer and early autumn have been used to induce budset, dormancy, and drought tolerance after outplanting (Mexal & South, 1991). Potential mechanisms involved in increasing drought tolerance following development of water stress include osmotic adjustment (osmoregulation), changes in elasticity of tissues and osmotic volume, changes in root/shoot allocation of dry matter, and molecular level changes.

A. TISSUE WATER RELATIONS

The physiological and ecological significance of osmotic and elastic adjustment are best understood if placed in the context of tissue water relations. For a plant cell, total water potential, Ψ_w, has two primary components:

$$\Psi_w = \Psi_s + \Psi_p$$

where Ψ_s is the osmotic potential and Ψ_p is the turgor potential. From a simple physical perspective, a decline in Ψ_s brought about by accumulation of solutes will reduce the Ψ_w at which turgor is lost, although there are other possible effects of low Ψ_s (see below). For nongrowing cells, the role of elasticity in cell water relations can be seen by rewriting the equation above to describe the effect of a *change* in volume of cell water on total and component water potentials (Kozlowski & Pallardy, 1997a):

$$\Psi_{w_1} = \Psi_{s_\emptyset} \frac{V_\emptyset}{V_1} + \Psi_{p_\emptyset} + \epsilon \frac{V_1 - V_\emptyset}{V_\emptyset}$$

where Ψ_w, Ψ_s, and Ψ_p are as before, except that subscripts Ø and 1 refer to original and final states before and after a volume change. $V_\emptyset$ and V_1 are the volumes before and after a change in volume; and ϵ is the elastic modulus of the cell wall, which is determined by wall mechanical properties. This relationship can be scaled up to the tissue level if one remembers that the bulk elastic modulus becomes a more complex property of the tissue, depending both on cellular properties and organ geometry. The first term shows the effect of loss of volume on Ψ_s: as volume is lost, concentration of solutes will lower Ψ_s. Note that this is a passive process attributable solely to concentration of existing solutes, and it should not be considered osmotic adjustment. The last term in this equation illustrates the effect of tissue elasticity on cell water relations. Plants with high elasticity (low ϵ) can undergo a relatively large loss of water before loss of turgor; conversely, if ϵ is high, turgor may be lost with much less tissue water loss.

The ecological implications that arise from this relationship and the ways in which they are played out in nature are several (Table I). In succulents, an extreme example, selection has apparently favored adaptations for high Ψ_s and low ϵ, which traits confer the capacity to store large amounts of water internally but do not require a huge carbon investment in solutes. These traits are linked with the capacity to isolate the water in the plant body (acquired during wet weather) from an environment where Ψ_w is usually quite low. The soil water potential commonly is much lower than Ψ_s in arid- and semiarid-zone succulents; and if these plants were unable to isolate themselves from this environment, their tissues would fall far below the point of turgor loss. The adaptive fitness of other combinations of Ψ_s and ϵ also may depend on features of the habitat environment. Theoretically, in fairly xeric habitats where the light re-

Table I

Possible combinations of osmotic potential and tissue elasticity and effects on turgor maintenance and tissue dehydration.
(RWC = relative water content)

Case 1: high Ψ_s, high ϵ Turgor loss occurs at very high Ψ_w, RWC RWC declines gradually with Ψ_w	Case 2: high Ψ_s, low ϵ Turgor loss delayed somewhat to lower RWC (and slightly lower Ψ_w) than in Case 1 RWC declines steeply with Ψ_w
Case 3: low Ψ_s, high ϵ Turgor loss at intermediate Ψ_w RWC declines very little as Ψ_w drops	Case 4: low Ψ_s, low ϵ Turgor loss delayed to lowest RWC RWC declines steeply as Ψ_w drops

source is not in short supply, a combination of both low Ψ_s and high ϵ would appear most advantageous, as this set of traits best protects from tissue dehydration (low RWC) at very low Ψ_w. There is support in the literature for maintenance of high RWC at low Ψ_w as a means of protecting metabolic processes from the effects of toxic ion concentrations that may develop as tissue water is lost. For example, maintenance of volume in chloroplasts by osmotic adjustment may preserve photosynthetic capacity (Santakumari & Berkowitz, 1991) and prevent injury to chloroplasts from toxic concentrations of ions (Rao et al., 1987). If growth rate confers an advantage in a particular habitat, one might expect more elastic tissues that support the maintenance of turgor, because turgor is an important requisite for growth. Low Ψ_s will similarly support turgor maintenance, but at the metabolic cost of the solutes that must be allocated to this function. Although these patterns make sense ecologically, it must be noted that the experimental evidence for these adaptations is still relatively sketchy.

Even if kept well watered, plants will develop constitutively different levels of Ψ_s and ϵ that are apparently genetically determined. For example, Bahari et al. (1985) observed a range of Ψ_s between –1.52 and –1.95 MPa and ϵ between 3.36 and 10.37 MPa in saplings of a variety of temperate deciduous angiosperm species during a summer in which soil moisture was abundant. Osmotic adjustment occurs only if there is an active accumulation of solutes in response to drought. Evidence for this phenomenon and other tissue-level responses is discussed below.

B. OSMOTIC ADJUSTMENT

The degree of osmotic adjustment to drought varies among species and genotypes of both angiosperms and gymnosperms. While numerous species exhibit osmotic adjustment (Table II), several investigators found negligible or no osmotic adjustment in certain species. Examples of the latter condition are several Chilean evergreen shrubs, including *Cryptocarya alba, Calliguaya olorifera, Lithraea caustica,* and *Quillaja saponaria* (Poole & Miller, 1978). Hinckley et al. (1980) also concluded that osmotic adjustment in leaves of several species, including *Cornus mas, Crataegus monogyna, Olea europaea, Sorbus aria,* and *Viburnum lantana,* was of minor importance as an adaptive response to water deficits. Other species that showed little or no osmotic adjustment to drought included *Alnus sinuata* (Cline & Campbell, 1976), *Acer saccharum* (Bahari et al., 1985), *Cercis canadensis* (Buxton et al., 1985), *Juniperus virginiana* (Bahari et al., 1985), *Liriodendron tulipifera* (Roberts et al., 1980), and *Picea mariana* (Buxton et al., 1985).

As is the case with leaves, osmotic adjustment occurs in meristematic regions of roots as they are exposed to water deficits. Hence turgor may be sustained, although at a lower level

Table II

Species of woody plants showing appreciable osmotic adjustment

Species	Source
Angiosperms	
Alnus glutinosa	Seiler, 1985
Betula populifolia	Morse et al., 1993
Carya tomentosa	Parker et al., 1982
Celtis occidentalis	Abrams & Knapp, 1986
Citrus sinensis	Fereres et al., 1979
Cornus florida	Roberts et al., 1980; Bahari et al., 1985
Eucalyptus camaldulensis	Lemcoff et al., 1994
Eucalyptus behriana	Myers & Neales, 1986
Eucalytpus grandis	Lemcoff et al., 1994
Eucalyptus microcarpa	Myers & Neales, 1986
Eucalyptus nitens	White et al., 1996
Eucalyptus polyanthemos	Myers & Neales, 1986
Eucalyptus tereticornis	Lemcoff et al., 1994
Eucalyptus viminalis	Lemcoff et al., 1994
Fragaria chiloensis	Zhang & Archbold, 1991
Fragaria virginiana	Zhang & Archbold, 1991
Fraxinus excelsior	Guicherd et al., 1997
Ilex opaca	Roberts et al., 1980
Juglans nigra	Parker & Pallardy, 1985
Malus domestica	Goode & Higgs, 1973; Roberts et al., 1980; Fanjul & Rosher, 1984; Lakso et al., 1984; Wang & Stutte, 1992; Wang et al., 1995
Olea europaea	Rieger, 1995
Populus deltoides	Tschapinski et al., 1994
Populus deltoides x *P. nigra*	Tschapinski & Blake, 1989
Populus hybrids	Tschaplinski & Tuskan, 1994
Populus tremuloides	Abrams, 1988b
Populus trichocarpa	Tschaplinski & Tuskan, 1994
Quercus alba	Parker et al., 1982; Bahari et al., 1985
Quercus ellipsoidalis	Abrams, 1988b
Quercus ilex	Dreyer et al., 1990
Quercus macrocarpa	Abrams & Knapp, 1986
Quercus muehlenbergii	Abrams & Knapp, 1986
Quercus petraea	Dreyer et al., 1990
Quercus pubescens	Dreyer et al., 1990
Quercus robur	Osonubi & Davies, 1978; Dreyer et al., 1990
Quercus rubra	Parker et al., 1982
Quercus velutina	Bahari et al., 1985
Quercus stellata	Parker & Pallardy, 1988
Rosa hybrida	Augé et al., 1986
Vitis vinifera	Düring, 1985
Gymnosperms	
Picea glauca	Koppenaal et al., 1991
Picea mariana	Tunstall & Connor, 1975; Zwiazek & Blake, 1989
Pinus banksiana	Koppenaal et al., 1991
Pinus echinata	Pallardy et al., 1982; Choi, 1992
Pinus pinaster	Nguyen & Lamont, 1989
Pinus taeda	Seiler & Johnson, 1988; Meier et al., 1992
Pseudotsuga menziesii	Joly & Zaerr, 1987
Thuja occidentalis	Collier & Boyer, 1989
Tsuga canadensis	Tyree et al., 1978
Tsuga heterophylla	Kandiko et al., 1980; Buxton et al., 1985

than in unstressed roots (Pritchard & Tomos, 1993; Spollen et al., 1993). Meristematic tissues of roots are close to the water supply of the plant, and neither the hydraulic conductivity nor the gradient in water potential between the source of water and the growing tissue appears to inhibit growth under water stress (Pritchard, 1994).

The solutes involved in osmotic adjustment responses appear to vary depending on species. Sorbitol, glucose, and fructose accumulated in *Malus domestica* leaves as water stress developed (Wang & Stutte, 1992). Fructose and glucose increased in *Picea glauca* shoots and *Pinus banksiana* roots under water stress (Koppenaal et al., 1991). Osmotic adjustment in *Populus* hybrids was largely a result of increases in malic acid, potassium, sucrose, and glucose (Tschaplinski & Tuskan, 1994). Solutes contributing to osmotic adjustment in three *Populus deltoides* clones included sucrose, malic acid, glucose, fructose, myoinositol, and salicin (Gebre et al., 1994). Malate and mannitol were importantly involved in osmotic adjustment of *Fraxinus excelsior* leaves during a summer drought (Guicherd et al., 1997). If drought conditions are imposed too rapidly, the amount of osmotic adjustment often is less than if drought develops slowly (Turner & Jones, 1980; Abrams, 1988a).

C. ELASTIC ADJUSTMENT

As noted above, changes in elasticity of tissues also can regulate turgor. As water is lost from plants, inelastic tissues lose turgor faster than do elastic tissues. Hence an increase in tissue elasticity under water-stress conditions may be desirable under conditions where turgor maintenance is adaptive. On the other hand, decreased elasticity under drought tends to maintain higher levels of tissue relative water content as plant Ψ declines, protecting tissues from low RWC and possibly toxic concentrations of ions. Hence both increases and decreases in elasticity may benefit plants, depending on which response is adaptive under a given set of environmental constraints. Changes in tissue elasticity may be especially important for plants that do not adjust osmotically.

Both increases and decreases in elasticity have been reported under drought. For example, whereas elasticity increased in *Celtis occidentalis* and *Quercus muehlenbergii* leaves, in roots of *Q. macrocarpa,* and in leaves and roots of *Juglans nigra* (Parker & Pallardy, 1985, 1988; Abrams & Knapp, 1986), it decreased in shoots of *Pinus echinata* and in leaves of *Betula populifolia* (Choi, 1992; Morse et al., 1993). Sometimes changes in elasticity show opposite responses under drought in closely related plants. For example, whereas drought induced increases in ϵ of leaves of *Eucalyptus nitens,* ϵ of *E. globulus* leaves decreased (White et al., 1996). In droughted *Picea mariana* leaves, ϵ increased by 2.82 MPa (Blake & Tschaplinski, 1992). Osmotic adjustment was not important in *Pinus banksiana, Picea mariana,* or *Eucalyptus grandis,* but both high tissue elasticity and capacity to increase elasticity were important for turgor maintenance in droughted seedlings. However, initial inherent drought tolerance was more important in each species than were elastic adjustments to repeated stress (Fan et al., 1994). In contrast, Davies and Lakso (1979) noted that while seasonal osmotic potential of *Malus domestica* remained rather stable, leaf elasticity increased sufficiently to promote stomatal opening and growth. In *Quercus* there was a limit for solute accumulation (and osmotic adjustment) under chronic water stress (Kwon & Pallardy, 1989). Compensatory increases in leaf elasticity offset that influence. In *Populus deltoides* x *P. nigra,* changes in the modulus of elasticity in response to drought were numerically greater than were changes in osmotic adjustment (Tschaplinski & Blake, 1989). Elongation of *Pinus pinaster* roots was attributed to cell wall loosening at moderate water stress. Growth under severe water stress was inhibited by the inability of plants to maintain turgor (Triboulot et al., 1995). In *Malus domestica,* drought

tolerance was attributed to several adaptations, including diurnal osmotic adjustment, seasonal increases in tissue elasticity, and use of stored water (Davies & Lakso, 1979).

The mechanism by which changes in elasticity under water stress arise is not known. Wakabayashi et al. (1997) showed that osmotic stress reduced cell wall stiffening in wheat coleoptiles. This response was associated with reductions in two lignin components, ferulic and diferulic acids. In contrast, Peltier and Marigo (1999) observed a reversible increase in elastic modulus in *Fraxinus excelsior* under water stress that could be mimicked by application of 20 μmol L^{-1} abscisic acid (ABA) and counteracted by treatment with buffer solutions with acidic pH. More research is needed to explain the biochemical basis underlying documented changes in tissue elasticity under water stress.

D. CHANGES IN OSMOTIC VOLUME

Another mechanism by which Ψ_s can decline is simply through a reduction in the osmotic volume V_o (i.e., theoretically, the amount of water held in the symplast). Note that this phenomenon is not the same as the passive dehydration process that occurs during water loss from tissues, because the change in osmotic volume is obtained at full turgor, where Ψ_w is very close to zero. In this case, no import of solutes is necessary, as resident solutes are concentrated through a loss of cellular water. Conversely, increased V_o, if linked with solute accumulation, can maintain turgor across a greater range of RWC. Reductions in V_o or in the ratio of V_o to total water volume (osmotic water fraction, V_o/V_t) in droughted plants are sometimes reported (e.g., in roots of *Tsuga heterophylla,* Kandiko et al., 1980; in shoots of some families of *Pinus echinata* seedlings, Choi, 1992; in leaves of *Quercus,* Kwon & Pallardy, 1989). In contrast, increased V_o or V_o/V_t also has been reported in response to water stress (e.g., in shoots of *Betula populifolia* seedlings, Morse et al., 1993; in roots of mycorrhizal rose plants, Augé & Stodola, 1990).

E. ROOT–SHOOT ALLOCATION

Woody plants that grow on "poor" sites generally allocate a greater proportion of photosynthate to root production than do those that grow on "good" sites. The resultant changes have obvious impacts on water-absorbing capacity in comparison with transpiration by aboveground structures. For example, Keyes and Grier (1981) reported that whereas *Pseudotsuga menziesii* trees on a low-productivity site partitioned 36% of total net primary production (TNPP) to fine roots, on high-productivity sites only 8% of TNPP went to fine roots.

Both water and nutrient deficiencies often characterize such sites, and there is considerable evidence that deficiencies in both resources can lead to this shift in allocation patterns (Waring, 1991). For example, Ibrahim et al. (1997) reported greater relative allocation of dry matter to roots in young cuttings of Balsam Spire poplar (*Populus balsamifera* var. *Michauxii* (Henry) x *Populus trichocarpa* var. *Hastata* (Dode) Farwell) when plants were subjected either to low nitrogen supply or to reduced soil moisture availability. Inherent nutrient deficiencies can be exacerbated by water deficits, because soil drying restricts the cross-sectional area and increases the tortuosity of ion movement to root surfaces. The available evidence suggests that plants are often even more sensitive to nutrient deficiencies than to water stress in shifting allocation of photosynthate to root growth (Cromer & Jarvis, 1990; Waring, 1991). The metabolic aspects of photosynthate partitioning, and attendant responses to environmental stresses, are complex and likely include expression of genes related to sucrose metabolism at specific locations within the plant (Geiger et al., 1996).

F. MOLECULAR–LEVEL CHANGES

At the molecular level, study of acclimation responses of plants to water stress has usually focused on prevention of protein denaturation and preservation of membrane structure (e.g., Levitt, 1980). Many early workers focused on the possibility that SH-to-S–S transformations could promote protein aggregation. Recent research has emphasized a search for inducible "water stress proteins." Although total synthesis of proteins is usually reduced under water stress (e.g., Bewley et al., 1983; Hulbert et al., 1988), levels of some proteins increase, and certain new proteins are synthesized (Guerrero & Mullet, 1988; Bartels et al., 1990). Some researchers believe that proteins first identified with late stages of embryogenesis (during which substantial water loss occurs) may play a significant role in dehydration tolerance of the vegetative stage as well. A family of so-called dehydrin proteins (also known as the *lea* [*l*ate-*e*mbryogenesis *a*bundant] D11 family) typically accumulates under circumstances of dehydration, as occurs under conditions of drought, high salinity, or extracellular freezing (Close, 1996, 1997). There is some evidence that dehydrin protein levels under water stress (inferred from mRNA transcript abundance) are correlated with drought tolerance in higher plants (e.g., sunflower, Cellier et al., 1998). These proteins range from 100 to 600 amino acids in length and are distributed in both the nucleus and the cytoplasm. They contain one or more sequences of amino acids that form an amphipathic α-helix, resulting in hydrophobic patches on the molecule's surface. Other regions (ϕ-segments) are rich in polar amino acids and glycine. This set of properties has led to hypotheses of dehydrins as molecules that may interact with hydrophobic patches of partially denatured proteins and membrane surfaces to stabilize them and prevent protein aggregation as activity of water declines. It also is possible that dehydrins may form H-bonds in ϕ-segments with polar groups of macromolecules or participate in "exclusion reactions" with compatible solutes such as sucrose, proline, or glycine-betaine. Such reactions raise the activation energy required for protein denaturation (Campbell & Close, 1997; Close, 1997).

Another group of stress-related proteins, the ubiquitins, may also play a role in adaptive response of plants to water deficits. O'Mahony and Oliver (1999) demonstrated that mRNA transcripts of these proteins accumulate during dehydration and rehydration of a desiccation-tolerant grass (*Sporobolus stapfianus*) and moss (*Tortula ruralis*). These small proteins attach themselves to defective protein molecules, serving as a tag for selective degradation via the 26S proteasome pathway (Spremulli, 2000). In this way proteins that might otherwise cause damage during desiccation and rehydration are removed from cells. A similar role for ubiquitins in tagging proteins damaged by high temperatures has also been identified.

There is accumulating evidence that water movement across membranes in plants and animals is facilitated by specific "water channel" proteins (sometimes called "aquaporins," and "MIP-membrane intrinsic proteins") (Maurel, 1997; Schäffner, 1998). This is a large family of proteins of about 30kDa in molecular mass possessing six helical regions that cluster together and span membranes. Two vertically aligned amino acid "loops" emerge from these segments on one side. The functional channel is a tetramer of these units arranged so that the loop segments form central depressions in both sides of a membrane (Murata et al., 2000). Through this pore, water molecules appear to move easily in single file in either direction, responding to the prevailing water potential gradient. Short-term modulation of water channel activity may be effected by phosphorylation and dephosphorylation of certain serine residues of the protein (Johansson et al., 1996, 1998), and a number of investigators have reported that genes coding for water channel proteins are water-stress inducible (e.g., Yamaguchi-Shinozaki et al., 1992; Fray et al., 1994; Yamada et al., 1997). Hence it is conceivable that drought could increase

cellular permeability to water, thus increasing hydraulic conductivity of plant tissues, reducing soil-to-leaf resistances in the soil-plant-atmosphere continuum, and ultimately enhancing the desiccation-avoidance capacity in acclimated plants. Much more research remains to be done, however, before these linkages can be confirmed.

IV. Flood Tolerance

The effects of soil inundation on woody plants vary from catastrophic to beneficial, depending on the plant species and genotype, on the intensity, timing, and duration of flooding, and on a variety of site conditions (Kozlowski, 1982b, 1984; Crawford, 1989; Kozlowski & Pallardy, 1997b). The deleterious effects of flooding on seed germination (Al-Ani et al., 1985) and on vegetative and reproductive growth (Kozlowski, 1982b), often as a prelude to plant mortality (Crivelli et al., 1995; Angelov et al., 1996) are well known. The harmful effects of flooding are greatly exacerbated by the presence of salts in irrigation water, tidal waters, and salt spray along seacoasts (Shannon et al., 1994; Kozlowski, 1997). In comparison, some woody plants not only are morphologically and physiologically adapted to grow in flooded soils but also may depend on intermittent flooding for their establishment, growth, and survival.

A. IRRIGATION

Judicious, intermittent soil inundation of orchard soils by flood, furrow, sprinkler, and drip irrigation has been practiced for centuries to increase yield and improve the quality of edible fruits. Large increases in yield have been shown for apples (Goode, 1975; Landsberg & Jones, 1981), citrus fruits (Kriedemann & Barrs, 1981), grapes (Smart & Coombe, 1983), peaches (Chalmers et al., 1983), pecans (Stein et al., 1989), strawberries, and blueberries (Davies & Albrigo, 1983). Scheduling of the time and amount of water applied is crucial for fruit growth. Yields following irrigation generally reflect a greater number of fruits, but fruit size also is increased (Goode & Ingram, 1971).

Irrigation is beneficial in providing soil with water in arid regions as well as in supplementing rainfall in nonarid regions to make up small, periodic water deficits. In dry regions, irrigation increases fruit yield largely by maintaining a high soil-moisture level in the rhizosphere during fruit set. Subsequent irrigation has a lesser, though still important, benefit (Hilgeman & Reuther, 1967). In humid England, production of apples was increased by frequent, intermediate, and relatively infrequent irrigation by 40%, 46%, and 25%, respectively (Goode & Hyrycz, 1964).

B. RIPARIAN ECOSYSTEMS

Among the most valuable forest trees are the various flood-tolerant species in riverine bottomlands. They are important not only for their high productivity of biomass, hence timber, but also for their diversity, which provides a variety of ecological services, including control of floods and erosion, removal of nutrients from agricultural runoff, and alleviation of the effects of environmental pollution (Richardson, 1995).

Flood tolerance of bottomland species varies appreciably. On specific sites the predominant floodplain species of the southeastern United States vary with the degree and duration of flooding. The lowest sites that are flooded for most or all of the growing season, but have a fluctuating water table, are occupied primarily by *Taxodium distichum* and *Nyssa aquatica*. When these sites are altered by prolonged sedimentation or drainage, *Taxodium* and *Nyssa* may be succeeded by *Fraxinus pennsylvanica, Ulmus americana, Acer rubrum, Carya aquatica, Quercus lyrata,* and *Q. nuttallii*. Recent alluvial deposits often support pure stands of *Salix*

nigra (on low, wet, and fine-textured soils) and *Populus deltoides* (on higher, better-drained, and coarser sediments).

Both *Salix* and *Populus* stands in low areas often are succeeded by *Taxodium distichum, Fraxinus pennsylvanica, Ulmus americana,* and *Acer rubrum*. Subsequently these species are replaced by *Quercus lyrata, Carya aquatica,* and *Diospyros virginiana* (Putnam et al., 1960; Smith & Linnartz, 1980). At higher, only intermittently flooded sites, the major species include *Quercus michauxii, Q. falcata* var. *pagodaefolia, Q. alba,* and *Q. stellata* (Hosner, 1962; Bedinger, 1981; Office of Technology Assessment, 1984).

In the central parts of the United States the species composition of wetland forests differs with drainage and soils. Major components of bottomlands and floodplains include *Ulmus americana, Fraxinus pennsylvanica, Populus deltoides,* and *Acer saccharinum*. Associated species often are *Salix nigra, Platanus occidentalis, Celtis occidentalis,* and *Acer negundo*. In southern Illinois heavy and poorly drained soils that are flooded for up to several months annually support *Acer rubrum, Fraxinus pennsylvanica, Ulmus americana,* and *Liquidambar styraciflua*. On moderately heavy soils with lower duration of flooding *Liquidambar styraciflua, Quercus michauxii, Q. muehlenbergii, Ulmus americana, Q. falcata* var. *pagodaefolia,* and *Q. shumardii* predominate. Major species of well-drained soils and much-less-frequent flooding include *Acer saccharum, Ulmus rubra,* and *Tilia americana* (Robertson et al., 1978).

Growth and sustainability of riparian forests depend on annual advances and recessions of floods (Bayley, 1995). Periodic soil inundation and stream-channel migration protect downstream forests by transporting sediments essential for creation of favorable seedbeds and by regulating decomposition of organic matter. The essentiality of intermittent flooding and stream meandering is shown by progressive deterioration of bottomland forests following installation of dams along rivers. Dams impede meandering of streams as well as transport of water, mineral nutrients, sediments, and organic matter in ways that interfere with natural regeneration, growth, and sustainability of riverine forests (Ligon et al., 1995; Poff et al., 1997; Pollock et al., 1998; Naiman et al., 2000). Failure of regeneration of downstream forests is linked to lowered supplies of seeds, groundwater, and mineral nutrients, as well as to poor seedbeds (McBride & Strahan, 1984; Fenner et al., 1985; Duncan, 1993; Rood et al., 1994).

C. ADAPTATIONS FOR FLOOD TOLERANCE

Interactions of various morphological and physiological adaptations confer flood tolerance on certain woody plants (Hook, 1984; Kozlowski, 1984, 1997; Kozlowski & Pallardy, 1984; Crawford, 1993). Major adaptations include the following:

1. Root Regeneration

Root mortality under soil anaerobiosis is followed by initiation and growth of adventitious roots on the original root systems and/or submerged portions of stems of some flood-tolerant plants. Examples include *Betula nigra* (Kozlowski, 1984), *Fraxinus mandshurica* (Yamamoto et al., 1995), *Fraxinus pennsylvanica* (Sena Gomes & Kozlowski, 1980a), *Melaleuca quinquenervia* (Sena Gomes & Kozlowski, 1980b), *Platanus occidentalis* (Tang & Kozlowski, 1982), and *Ulmus americana* (Newsome et al., 1982; Angeles et al., 1986). Few or no adventitious roots were produced by flood-intolerant species such as *Betula papyrifera* (Tang & Kozlowski, 1982c), *Pinus halepensis* (Sena Gomes & Kozlowski, 1980d), and *Pinus banksiana* or *P. resinosa* (Tang & Kozlowski, 1983).

That flood-induced adventitious roots can compensate physiologically for decay of portions of the original root system was shown by positive correlations between flood tolerance

and capacity for production of adventitious roots (Sena Gomes & Kozlowski, 1980c), by greatly increased water uptake by plants following growth of adventitious roots (Tsukahara & Kozlowski, 1985), by oxidation of the rhizosphere and conversion of soil-borne toxins to less toxic compounds (Hook & Brown, 1973), and by increased availability to plants of root-synthesized gibberellins and cytokinins (Reid & Bradford, 1984). Although formation of adventitious roots sometimes has been attributed to increased ethylene production, formation of ethylene did not correlate well with production of adventitious roots in flooded plants in one study (Tang & Kozlowski, 1984). Furthermore, much more ethylene was produced by some flooded species than by others.

2. Facilitation of Oxygen Uptake and Transport

Some flood-tolerant species absorb oxygen through stomata or lenticels and transport it to the roots, from which it diffuses to the rhizosphere (Kozlowski & Pallardy, 1997b). When flooded, some species form hypertrophied lenticels on stems and roots. This involves accelerated phellogen activity, elongation of cork cells, dissolution of cell walls, and cell proliferation. Often all the living cells between the phellogen and the cambium are affected (Angeles et al., 1986). Lenticel formation as a flooding response has been reported for a wide variety of woody plants. Examples include *Betula nigra* (Norby & Kozlowski, 1983), *Eucalyptus camaldulensis* and *E. globulus* (Sena Gomes & Kozlowski, 1980c), *Populus deltoides* and *Salix nigra* (Pereira & Kozlowski, 1977), *Platanus occidentalis* (Tang & Kozlowski, 1982b; Tsukahara & Kozlowski, 1985), *Quercus macrocarpa* (Tang & Kozlowski, 1982a), and *Ulmus americana* (Newsome et al., 1982). Gymnosperms that produce hypertrophied lenticels in response to anaerobiosis include *Abies balsamea, Larix laricina, Picea mariana, P. pungens, P. rubens, Pinus caribaea, P. resinosa* (Hahn et al., 1920), *Pinus clausa,* and *P. taeda* (Topa & McLeod, 1986a, 1986b).

Lenticel formation appears to be fostered by ethylene that forms in response to anaerobiosis (Kozlowski, 1982b). The flood-induced lenticels promote exchange of dissolved gases in the floodwater and may also release toxic compounds (e.g., acetaldehyde, ethanol, and ethylene) from plants (Chirkova & Gutman, 1972). According to Kawase (1981), ethylene production by flooded plants is followed by increased cellulase activity, softening of cell walls, competition for water among cortical cells, and then dehydration and death of the weaker competing cells.

In response to low oxygen concentration in the root zone, many species form aerenchyma tissues in roots and stems, through which oxygen moves readily. Aerenchyma tissue, with large intercellular spaces, forms by both cell separation (schizogeny) and disintegration (lysigeny) (Angeles, 1992). Examples are *Pinus contorta* (Coutts & Philipson, 1978) and *P. serotina.* Some species also show capacity for internal stem aeration by high cambial permeability (Topa & McLeod, 1986b). Lysigenous air-space formation arises from programmed cell death of targeted cells in a process that is mediated by ethylene accumulation under low (but not zero) O_2 concentration (Jackson & Armstrong, 1999). Ethylene production is stimulated because of increases in both its immediate precursor (1-aminocyclopropane-1-carboxylic acid, ACC) and the enzymes involved in ACC synthesis and its conversion to ethylene.

Some species of mangrove produce air roots that function in oxygen uptake and transport. *Rhizophora mangle* has stilt roots with lenticels on the surface through which air is absorbed and transported to submerged roots. *Avicennia nitida* has negatively geotropic root extensions that grow upward into the air from flooded soils. These pneumatophores are covered with lenticels through which oxygen is absorbed (Scholander et al., 1955).

3. Metabolic Adjustments

Flood-tolerant plants may adapt biochemically to survive in anaerobic environments by maintaining a glucose supply and avoiding accumulation of toxic products. According to Armstrong at al. (1994) and Crawford and Braendle (1996), tolerance of anoxia may involve maintenance of substantial carbohydrate reserves and the capacity to use these substances to sustain ATP levels at low O_2, along with capacity to maintain membrane integrity during and after release from anoxia. Massive membrane lipid damage by active oxygen species and acetaldehyde derived from postanoxic metabolism of ethanol is characteristic of flood-sensitive species. In flood-tolerant species, ethanol may be eliminated by diffusion, as in *Acorus calamus*. Also, in some flood-tolerant species increased synthesis of free-radical-scavenging enzymes (e.g., superoxide dismutase) and enzymes associated with production of antioxidant compounds (e.g., ascorbic acid, α-tocopherol, and glutathione) aid in preventing lipid damage after O_2 is reintroduced into roots. Metabolic adaptations to flooding were also reviewed by Davies (1980), Jackson and Drew (1984), Marschner (1995), and Angelov et al. (1996).

Salt-tolerant plants adapt to salinity by salt tolerance, salt avoidance, and often both (Kozlowski, 1997). Very tolerant plants manage to endure high salinity through osmotic adjustment by absorbing ions from the soil and sequestering them in vacuoles or by synthesis of compatible solutes (Gucci et al., 1997).

Halophytes are strong salt excluders. They leave behind almost all the salts in the soil while absorbing large amounts of water. Because salts become concentrated in vacuoles, exposure of cytoplasm to high salinity is diminished (Shannon et al., 1994). Excess salts are excreted from leaves via salt glands or bladders. Salt glands, well known in *Tamarix* and various mangrove species, excrete mostly NaCl and small amounts of other inorganic and organic ions (Waisel, 1972, 1991). Halophytes also dilute salts by water in leaf cells (Allen et al., 1994). Some halophytes achieve salt tolerance by several mechanisms. For example, *Avicennia marina* lowers salt uptake because of low root permeability to salts, tolerates salt by maintaining normal metabolism despite a high internal salt level, and releases some of the salts it absorbs (Waisel et al., 1986).

V. Cold Hardiness

Low temperature is a dominant factor in the distribution, growth, and survival of woody plants (Grace, 1987, 1988). Sudden exposure of unhardened plants to freezing temperatures typically results in injury to their shoots, cambium, and roots and often leads to death of the plants (Kozlowski & Pallardy, 1997b). Frost hardiness of seedlings is particularly important to their development and survival when seedlings that were injured in the nursery are planted in the field, when seedlings that are not cold hardy are outplanted, or when outplanted seedlings that open buds early are exposed to freezing temperatures.

Cold hardiness varies greatly among species, genotypes, and even different parts of the same plant. Northern species (e.g., *Populus tremuloides, Betula papyrifera,* and *Larix laricina*) survived freezing to temperatures of –80° to –196°C after prefreezing to –15°C. In contrast, southern species, including *Pinus elliottii, P. palustris,* and *Quercus virginiana,* survived temperatures only down to –15°C (Sakai & Weiser, 1973).

Much variation in cold hardiness has been shown among provenances (Cannell & Sheppard, 1982; Cannell et al., 1985; Nilsson & Eriksson, 1986). Southern sources of *Pseudotsuga menziesii* set buds later and were less hardy than northern sources when both were grown in Corvallis, Oregon (Campbell & Sorenson, 1973). Skrøppa (1991) found differences in frost

hardiness between two populations of *Picea abies* that originated only 60 kilometers apart at the same altitude and longitude.

In general, reproductive structures, roots, and young leaves are particularly sensitive to cold. The shoots of *Pinus sylvestris* were hardier than roots, with the limit of tolerance at –40° and –15°C, respectively (Smit-Spinks et al., 1985). The effects of temperature on hardening of conifers to frost were determined largely by night temperatures. For example, 24°C day / 7.5°C night temperatures were as effective in inducing hardiness in *Pseudotsuga menziesii* seedlings as were continuous 7.5°C temperatures (van den Driessche, 1969).

Environmental factors that inhibit plant growth also induce cold hardiness in many species. These include low temperatures (Howell & Weiser, 1970; Gusta & Weiser, 1972; Christersson, 1978; Cannell & Shepherd, 1982; Greer & Warrington, 1982; Greer, 1983; Sakai & Larcher, 1987), short days (D'Aoust & Cameron, 1982; Greer & Warrington, 1982; Bigras & D'Aoust, 1993; Silim & Lavender, 1994), water deficits (Wildung et al., 1973; Timmis & Tanaka, 1976; Chen et al., 1977; Yelenosky, 1979), and combinations of these (Fuchigami et al., 1971).

In woody plants of the temperate zone, cold hardiness develops gradually each year, long before very low temperatures occur. Hardiness is induced in two sequential stages. In Stage I, at temperatures between 10° and 20°C in the autumn, carbohydrates and lipids accumulate. These compounds are substrates and energy sources for subsequent metabolic processes. Stage II, which is promoted by freezing temperatures, involves synthesis of proteins and membrane lipids as well as structural changes (Kozlowski & Pallardy, 1997b).

There is evidence that low but nonfreezing temperatures induce accumulation of dehydrins and other nondehydrin proteins in leaves, stems, and flowers. All three of the major chilling-responsive polypeptides of flower buds of *Vaccinium corymbosum* and *V. ashei* were identified as dehydrins or dehydrin-like proteins (Muthalif & Rowland, 1994). Seasonal patterns of accumulation of dehydrins with acclimation to cold were confirmed for bark tissues of *Prunus persica, Malus domestica, Rubus* sp. *Populus* sp., *Salix babylonica, Cornus florida, Sassafras albidum,* and *Robinia pseudoacacia* (Wisniewski et al., 1995).

The potential significance of dehydrins in acclimation to cold lies in the fact that plant cells become dehydrated during freezing because ice forms in intercellular spaces. It has been suggested that dehydrins may have a role in induction of cold hardiness in *Prunus persica* trees. More dehydrin-like proteins were found in cold-acclimated leaf tissues than in nonacclimated leaves. However, the specific role of dehydrins during development of cold hardiness itself is not known (Arora & Wisniewski, 1994). Other research has suggested that cold, but not lethal, temperature increases the capacity for cell membranes under subsequent freezing stress to undergo exocytotic extrusion rather than pinching off as endocytotic vesicles (Somerville et al., 2000). Retention of a folded but intact plasma membrane may reduce cellular damage when thawing is followed by massive osmotic water uptake by cells. Thomashow (1999) reviewed the literature on freezing tolerance genes and their regulation.

Dehardening usually occurs much faster than does cold hardening. In *Pinus sylvestris, Picea abies,* and *Pseudotsuga menziesii,* dehardening was influenced more by rising temperatures than by changes in daylength (van den Driessche, 1969; Aronsson, 1975). Greer and Stanley (1985) did not find any evidence of an interaction between daylength and temperature on dehardening of *Pinus radiata.* Once dehardening started, temperature had the major influence on loss of cold hardiness (Greer & Stanley, 1985).

The role of photoperiod in development of cold hardiness in nature varies appreciably in different species. Species that set buds usually harden extensively in response to short days. Examples include species of *Betula, Populus,* and *Cornus* (Sakai & Larcher, 1987), *Pyrus malus* (Howell & Weiser, 1970), *Pinus sylvestris* and *Picea abies* (Aronsson, 1975), *Pseudotsuga menziesii* (Timmis & Worrall, 1975), and *Pinus radiata* (Greer & Warrington, 1982).

In *Pinus sylvestris* and *Picea abies,* short days and low temperatures (2°C) were most effective for development of cold hardiness; next most effective was a combination of short days and room temperature (20°C) (Christersson, 1978). Three weeks of treatment with short days at 20°C, followed by 3 weeks under short days at 2°C, produced the same results as 6 weeks with short days at 2°C. In *Pinus sylvestris* plants at 0°C, the effects of a change in daylength and temperature were additive. It appeared that, for increased hardening, shortening of daylength was necessary before exposure to low temperature. The reverse order may result in loss of hardiness (Aronsson & Eliasson, 1970). The data emphasized the importance of exposure to short days prior to low-temperature treatment for development of cold hardiness.

In *Pinus radiata,* cold hardiness developed at a constant rate when daylength was progressively decreased below approximately 12 hours, reaching maximum hardiness at the minimum photoperiod of 9.5 hours (Greer et al., 1989). If daylength shortening ceased during this experiment, further cold hardening was arrested after a slight lag, indicating a coupling between changes in daylength and development of cold hardiness. When groups of plants were exposed to several constant daylength treatments that were sufficient to induce at least some cold hardening, the degree of cold hardiness depended directly on photoperiod length. Moreover, the rate of hardening could also be shown to depend on the rate at which daylength shortened. The data indicated that shortening of daylength controlled the first stage of the hardening process by regulating the rate of hardening.

Cold tolerance depends on many biochemical processes, and the sum of these determines the degree of tolerance. Some of these processes are hormone dependent and are induced by short days; others depend on activity of different enzyme systems and are temperature dependent (Nilsson & Eriksson, 1986).

Short days are less important for development of cold hardiness in species that do not set buds or respond only weakly to photoperiod. In *Thuja plicata* and *Chamaecyparis nootkatensis,* development of cold hardiness appeared to depend largely on temperature (Silim & Lavender, 1994). Four weeks of short days and warm temperatures had little effect on frost hardening of these species. However, low temperature increased their frost hardiness. *Thuja occidentalis,* a continental relative of *Thuja plicata,* hardened to only –10°C following 14 weeks of exposure to short days and warm temperatures (Colombo & Raitanen, 1991). Initiation and level of cold hardiness in *Pyracantha coccinea* and *Weigela florida,* which do not become very hardy in winter, were only slightly affected by short days (Williams et al., 1972).

Many forest nurseries routinely expose tree seedlings to moderate water stress at or near the end of the growth period. Such treatment accelerates budset, induces early dormancy, and increases cold hardiness (Duryea & McClain, 1984). Irrigation typically is withheld before naturally growth-inhibiting short days occur. Delay in such treatment may inhibit development of cold hardiness (Tanaka & Timmis, 1974). Cold hardiness often is induced in part because water stress prevents growth of abnormal late-season shoots such as lammas and proleptic shoots (Kozlowski & Pallardy, 1997a), which may be injured by autumn frosts. Some nursery managers monitor plant water potential to schedule irrigation; others discontinue irrigation after seedlings reach a predetermined size or on a specific date (Duryea & Landis, 1984).

Lowering the predawn xylem water potential of closely spaced *Pseudotsuga menziesii* seedlings from –0.65 to –1.2 MPa by withholding irrigation during the growth period increased the capacity for cold hardiness while decreasing shoot and root growth and accelerating budset (Timmis & Tanaka, 1976). A mild water stress of –0.5 to –1.0 MPa also increased cold hardiness of *Pseudotsuga menziesii* seedlings. The influence of this mild stress decreased as withholding irrigation was delayed from mid-July to September. For seedlings lifted in October, the mild water-stress treatment also decreased mortality of seedlings after cold storage (Blake et al., 1979). Seven days of water stress in either long or short days increased cold hardiness of

Cornus stolonifera. The increased hardiness reflected both greater tolerance of freezing and increased freezing avoidance, with the latter property associated with higher solute concentration (Chen et al., 1977). Water stress increased supercooling capacity of cold-sensitive citrus seedlings in freeze-avoidance tests and increased cold hardiness in freeze-tolerance tests. Water stress was most effective in reducing injury during freezes at temperatures higher than –6.7°C. Lower temperatures killed all plants regardless of a leaf water stress of –2.5 MPa. Combining water stress with low temperature was no more effective than either treatment alone.

In the southern United States, pine seedlings in forest nurseries may be injured by sudden autumn freezes (South et al., 1985; South, 1986). Short days can substitute for low temperatures and water stress to induce frost hardiness of *Pinus taeda*. Late-autumn planting of containerized seedlings typically resulted in vigorous growth if exposure to low temperature or short days was initiated in September or October. Approximately 42 days of hardening treatment were necessary to develop sufficient cold hardiness (Mexal et al., 1979).

VI. Pollution Tolerance

Absorption by leaves of gaseous air pollutants depends on the concentration gradient from the air to the interior of the leaf and on resistance to flow along the pollutant's diffusion path (Kozlowski, 1980). Hence, the amount of pollutant that is absorbed by leaves varies with differences in stomatal conductance, which depends on stomatal size, number of stomata per unit of leaf area, and stomatal aperture (Kozlowski & Constantinidou, 1986a, 1986b; Kozlowski & Pallardy, 1997b).

Much evidence emphasizes the importance of stomatal conductance to pollution tolerance, so only a few examples will be given. *Betula nigra* seedlings were more sensitive than *B. papyrifera* seedlings to SO_2, in part because stomatal conductance of the former species was greater (Norby & Kozlowski, 1983). *Fraxinus americana* leaves, with high stomatal conductance, absorbed more SO_2 than did *Acer saccharum* leaves, with low stomatal conductance (Jensen & Kozlowski, 1975). Susceptibility of some *Populus* clones to SO_2 was attributed to their high stomatal conductance (Kimmerer & Kozlowski, 1981). Leaf conductance in SO_2-free air of ten broadleaved trees and shrubs was used to estimate the amounts of SO_2 the plants absorbed (Winner et al., 1982).

In individual plants stomatal aperture (and hence pollutant uptake by leaves) varies diurnally and seasonally as environmental changes occur. Woody plants absorbed more air pollutants during the day, when stomata were open, than at night, when they were closed (Norby & Kozlowski, 1982). In potassium-deficient plants the stomata of *Acer saccharinum* were more closed than in plants with high potassium availability. Hence, less O_3 was absorbed by the potassium-deficient plants (Noland & Kozlowski, 1979).

Pollution tolerance can be increased when environmental stresses, particularly drought, flooding of soil, and low air humidity, close stomata and restrict pollutant uptake.

A. DROUGHT

Pollution tolerance can be increased by drought, which induces stomatal closure as a direct response to leaf dehydration (Kozlowski, 1982a) or as a response to a chemical message (most likely ABA) arising in roots subjected to drying soil (Zhang et al., 1987 ; Zhang & Davies, 1989, 1990). Suppression of gas exchange by stomatal closure in droughted plants thus impedes uptake of pollutants (Kozlowski & Constantinidou, 1986b). Unirrigated *Diplacus aurantiacus* plants had more-closed stomata than did irrigated plants. Hence, leaves of the

unwatered plants had lower capacity to absorb SO_2. The data emphasized that onset of the dry season resulted in SO_2 avoidance and higher pollution tolerance (Atkinson et al., 1988). The effects of stomatal aperture on absorption of pollutants may be inferred from an extensive literature showing regulation of CO_2 absorption of leaves by stomatal aperture (Regehr et al., 1975; Lakso, 1979; Ni & Pallardy, 1992; Kubiske & Abrams, 1993; Stewart et al., 1995; Berninger et al., 1996; Kellomaki & Wang, 1996; Epron, 1997; Fernandez et al., 1997). A decrease in photosynthesis of *Picea rubens* during drought was closely coupled with a reduction in stomatal conductance. Photosynthesis was progressively inhibited by lack of CO_2 (Seiler & Cozell, 1990).

B. FLOODING

Flooding of soil is followed by rapid stomatal closure in many woody plants (Kozlowski, 1982b; Table III), thus inhibiting absorption of air pollutants by plants and increasing their pollution tolerance. Stomatal conductance and absorption of SO_2 by *Betula nigra* and *B. papyrifera* leaves were greatly reduced by flooding, and, as a consequence, SO_2 caused less injury and less growth inhibition in flooded plants (Norby & Kozlowski, 1983).

Stomata close rather rapidly after the soil is flooded. There are many reports of stomatal closure within one to a few days after the soil is inundated. Examples include *Mangifera indica* (Larson et al., 1991), *Platanus occidentalis* (Tang & Kozlowski, 1982b), *Betula papyrifera* (Tang & Kozlowski, 1982c), *Fraxinus pennsylvanica* (Sena Gomes & Kozlowski, 1980a), and *Quercus falcata* var. *pagodaefolia* (Pezeshki & Chambers, 1985b). However, in some species stomatal closure occurs within hours after flooding. Flooding and closed stomata lowered the rate of transpiration of *Theobroma cacao* var. *catongo* seedlings within 2 hours (Sena Gomes & Kozlowski, 1986). Photosynthesis and transpiration of *Pseudotsuga menziesii* began decreasing within 4–5 hours after flooding, indicating rapid stomatal closure (Zaerr, 1983).

In amphistomatous plants the responses of adaxial and abaxial stomata to flooding may be similar or may vary appreciably, depending on species. The stomata on both leaf surfaces of *Populus deltoides* and *Melaleuca quinquenervia* closed in response to flooding (Pereira & Kozlowski, 1977; Sena Gomes & Kozlowski, 1980b). In contrast, only the stomata on the adaxial leaf surface of *Salix nigra* closed when the soil was flooded (Pereira & Kozlowski, 1977).

Pollution tolerance may be expected to vary with the duration of flooding and even with the capacity of stomata of some species to reopen during flooding. After the floodwaters drain away, pollution tolerance is reduced, because the stomata typically reopen slowly, thereby enabling uptake of more gaseous air pollutants. In *Vaccinium ashei* the closed stomata reopened when flooding was discontinued after 18 days (Davies & Flore, 1986a). When flooded for an intermediate period (10–25 days), the stomata of *Vaccinium ashei* were closed but opened when the floodwaters receded. However, after long-term flooding (30 days or more), stomatal conductance did not recover to preflooded levels after flooding was discontinued (Crane & Davies, 1988). In *Carya illinoensis* the closed stomata reopened when flooding for 8 days was discontinued but not when flooding was ended after 15 days (Smith & Ager, 1988). The resumption of normal stomatal functioning of *Fraxinus pennsylvanica* after floodwater drained away was faster after a short period of flooding than after a long one (Kozlowski & Pallardy, 1979).

In some species the stomata of flooded plants reopen during the flooding period. For example, in *Fraxinus pennsylvanica* the stomata closed rapidly but began to reopen after about 15 days of flooding. After 30 days of flooding, leaf conductance was only slightly lower than

Table III
Species of woody plants showing stomatal closure in response to flooding

Species	Source
Betula papyrifera	Tang & Kozlowski, 1982c
Betula nigra	Norby & Kozlowski, 1983
Carya illinoensis	Smith & Ager, 1988; Wazir et al., 1988
Eucalyptus camaldulensis	Sena Gomes & Kozlowski, 1980c
Eucalyptus globulus	Sena Gomes & Kozlowski, 1980c
Fraxinus pennsylvanica	Kozlowski & Pallardy, 1979; Sena Gomes & Kozlowski, 1980a
Liquidambar styraciflua	Pezeshki & Chambers, 1985a
Mangifera indica	Larson et al., 1991
Melaleuca quinquenervia	Sena Gomes & Kozlowski, 1980b
Platanus occidentalis	Tang & Kozlowski, 1982b
Populus deltoides	Pereira & Kozlowski, 1977
Prunus cerasus	Beckman et al., 1992
Quercus falcata var. *pagodaefolia*	Pezeshki & Chambers, 1985b
Quercus lyrata	Pezeshki et al., 1996
Quercus macrocarpa	Tang & Kozlowski, 1982a
Salix nigra	Pereira & Kozlowski, 1977
Theobroma cacao	Sena Gomes & Kozlowski, 1986
Ulmus americana	Newsome et al., 1982
Vaccinium ashei	Davies & Flore, 1986b
Vaccinum corymbosum	Davies & Flore, 1986b
Vaccinium spp.	Crane & Davies, 1989

it was in unflooded plants (Sena Gomes & Kozlowski, 1980a). In flooded *Taxodium distichum* plants, the stomata closed but reopened within 15 days of flooding (Pezeshki, 1993). Induction of stomatal closure by flooding, followed by stomatal opening after a period of flooding, also was reported for *Populus deltoides* (Regehr et al., 1975).

In many species the stomata of flooded plants closed without significant leaf dehydration (without a change in bulk leaf water potential), as in *Populus deltoides* (Regehr et al., 1975), *Eucalyptus globulus, Ulmus americana, Salix nigra,* and *Quercus macrocarpa* (Pereira & Kozlowski, 1977; Tang & Kozlowski, 1982a), *Melaleuca quinquenervia* (Sena Gomes & Kozlowski, 1980b), *Vaccinium corymbosum* and *V. ashei* (Crane & Davies, 1989), and *Quercus falcata* var. *pagodaefolia* (Pezeshki & Chambers, 1985b). Considerable evidence shows that stomatal closure of flooded plants results from a hormonal signal transmitted from the roots to the leaves, possibly root-synthesized ABA (Zhang et al., 1987). This view is supported by the following lines of evidence: flooding induces rapid increases in leaf ABA (Shaybany & Martin, 1977); stomatal closure and accumulation of ABA often are well correlated (Mansfield & Davies, 1981); and application of ABA to leaves is followed by rapid stomatal closure (Kriedemann et al., 1972; Davies & Kozlowski, 1975a, 1975b; Marshall et al., 1991).

C. HUMIDITY

Low humidity of the air induces stomatal closure in many species of woody plants (Table IV) and decreases diffusion of gaseous air pollutants into leaves (Mansfield & Majernik, 1970; Grace et al., 1975). The stomata of *Betula papyrifera* seedlings were more open when the relative humidity (RH) was high than when it was low. The leaves absorbed more SO_2 and were injured more when exposed to the pollutant at high RH. There was more leaf necrosis and

Table IV
Species of woody plants showing stomatal closure at low relative humidity

Species	Source
Acer saccharum	Davies & Kozlowski, 1974
Citropsis gahunensis	Khairi & Hall, 1976b
Citrus spp.	Hall et al., 1975; Khairi & Hall, 1976a, 1976b; Sheriff, 1977; Johnson & Ferrell, 1983
Eremocitrus glaucax	Khairi & Hall, 1976b
Fraxinus americana	Davies & Kozlowski, 1974
Hedera helix	Aphalo & Jarvis, 1991
Heteromeles arbutifolia	Winner & Mooney, 1980
Picea engelmannii	Johnson & Ferrell, 1983
Picea sitchensis	Grace et al., 1975
Populus spp.	Pallardy & Kozlowski, 1979, 1981
Prunus armeniaca	Schulze et al., 1972, 1974
Pseudotsuga menziesii	Meinzer, 1982; Johnson & Ferrell, 1983
Theobroma cacao	Sena Gomes et al., 1987

abscission as well as greater growth inhibition under the high-humidity regime (Norby & Kozlowski, 1982). In *Theobroma cacao* leaves, the average diffusive resistance was 26% lower at high RH (76–89%) than at low RH (39–62%). Stomatal opening and closing reflected apparent direct effects of humidity on guard cells rather than changes in bulk leaf water potential (Sena Gomes et al., 1987). In dry air the stomata of *Prunus armeniaca* closed, and they opened when transferred to moist air. Stomatal opening occurred in high RH despite a decrease in leaf water content (Schulze et al., 1972). With changes in RH from 20% to 80% and the reverse, the stomata of both *Fraxinus americana* and *Acer saccharum* opened faster than they closed. Stomatal aperture was affected more by humidity changes at low light intensity than at high light intensity (Davies & Kozlowski, 1974).

Two mechanisms have been described to explain stomatal closure in dry air. First, stomata close when guard cells lose water as leaves simply dehydrate and also because of hormonal influences. Maier-Maercker (1998) considered hydraulic signals to be more important than hormonal signals in controlling stomatal aperture. Simulations by Tardieu and Davies (1993) indicated a marginal role for hormones in control of stomatal opening and closing unless hormone levels interact with leaf water status.

ABA appears to be the major hormone involved in control of stomatal aperture. ABA is synthesized in roots and leaf mesophyll cells and transported to the epidermis, where it is associated with stomatal closure. The mechanism of the ABA effect is speculative but may involve direct effects on transport proteins in guard-cell membranes via phosphorylation reactions, changes in cytoplasmic pH, stimulation of uptake or internal release of Ca^{2+} in the cytoplasm (thereby changing the influence of a second messenger in ion transport), and interference with electrical gradients across membranes that cause ion movements (Li et al., 2000; Mori et al., 2000).

Second, stomata close without overall leaf dehydration or change in bulk leaf water potential (Sheriff, 1977; Kramer & Boyer, 1995). For example, in *Betula occidentalis,* decreases in stomatal aperture were associated with essentially constant leaf water potential (Saliendra et al., 1995). Hence stomata acted as sensors of dry air. If such a "feed-forward" mechanism operates, an almost immediate change in stomatal conductance occurs as water-vapor content of the air is altered. For example, exposure of the epidermis of turgid *Malus domestica* leaves

to dry air after a long period in moist air closed the stomata within 15 seconds (Fanjul & Jones, 1982). Such rapid stomatal responses did not appear to involve transport of K^+ from guard cells because K^+ transport lagged behind changes in stomatal aperture (Lösch & Schenk, 1978). Some researchers have suggested that the lack of a linkage between stomatal closure and ion transport as well as rapidity of the stomatal response suggest that stomatal closure occurs because of peristomatal transpiration (direct loss of water from the guard cells or from epidermal cells in the stomatal areas) (Sheriff, 1979; Saliendra et al., 1995).

The feed-forward model of stomatal control has been questioned by several investigators. Not only are stomatal responses difficult to duplicate (Meinzer, 1982), but there is no widely accepted mechanism that explains how guard cells sense "air dryness." Correlative relationships between stomatal aperture and relative humidity do not appear to reflect a cause-and-effect relationship (Aphalo & Jarvis, 1991). Mott and Parkhurst (1991), using a combination of oxygen and helium (helox) to manipulate the transpiration rates of leaves at constant values of leaf temperature and difference in the mole fraction of water vapor between leaf and air, demonstrated that guard cells responded not to water-vapor mole-fraction differences but to the transpiration rate. Monteith (1995) considered inadequate the mechanistic basis for dependence of stomatal conductance on relative humidity and also supported the concept that stomatal responses depended on transpiration rates. Meinzer et al. (1997) concluded that the simplest mechanism to account for observed responses to air dryness involves stomatal sensing of the epidermal or cuticular transpiration rate rather than the bulk leaf or stomatal rate of transpiration. Given the variability in these results, it is obvious that more research is necessary before a clear picture of the mechanism of stomatal response to dry air emerges.

VII. Heat Tolerance

It has long been known that exposure of plants to high, but sublethal, temperatures can induce acclimation or "hardening" to subsequent heat-stress events (e.g., see Levitt, 1980). For example, exposure of European beech to 55°C was accompanied by elevated resistance to later heat events (Wagenbreth, 1965). The mechanisms of injury during high-temperature episodes are several and are not completely understood. Evidence suggests that the inhibition of photosynthesis, especially the O_2-evolving, quinone-reducing complex of photosystem II (PS II), membrane injury, and protein aggregation and denaturation are primary responses to heat stress (Berry & Björkman, 1980; Havaux, 1993).

Upon exposure to high temperature, numerous organisms exhibit a shift in protein synthesis to produce a suite of specific proteins, termed heat-shock proteins (HSPs). Much of the research on HSPs has utilized bacteria, yeast, and *Drosophila* as model organisms, but plants appear to respond to heat stress in similar ways. HS proteins have been localized to cytoplasm, chloroplast, mitochondria, and endoplasmic reticulum of plant cells (Bray et al., 2000). Some HSPs (which have come to be named because of their sequence homology to original heat-induced proteins) are constitutive, being present even under moderate temperature regimes; others require a high-temperature challenge for synthesis. Although there are few studies of function of these proteins in plants, recent research with *Arabidopsis thaliana* mutants has indicated that plants lacking the capacity to accumulate HSPs are unable to acclimate (Burke et al., 2000; Queitsch et al., 2000). Some of these proteins may protect proteins from aggregation or aid in disaggregation of proteins after relief from heat stress (Bray et al., 2000). Another low-molecular-weight HSP has been linked with maintenance of electron transport through PS II during heat stress in tomato (Heckathorn et al., 1998).

Production of small-molecular-weight compounds and induction of non-HS proteins in response to high temperatures also have been reported as possible mechanisms of acclimation

to or protection from heat stress. Pools of antioxidant compounds, such as salicylic acid and glutathione, and activities of antioxidant enzymes were elevated in *Sinapis alba* seedlings exposed to 45°C for 1 hour (Dat et al., 1998). Leaves of many tree species produce isoprene, and the release of this compound increases with temperature (Rasmussen, 1970; Monson & Fall, 1989; Loreto & Sharkey, 1990; Sharkey & Singaas, 1995; Sharkey et al., 1996). Although the issue remains somewhat controversial, there is some evidence that isoprene may increase thermal tolerance of the photosynthetic apparatus to high temperature, particularly during the transient short-term episodes of high temperature that may accompany diurnal cycles (Logan & Monson, 1999; Sharkey et al., 2001). For example, it has been shown that photosynthesis of leaves of *Quercus rubra* fed an inhibitor of isoprene synthesis, fosmidomycin, were less able to recover from heat stress induced by exposure 46°C than were leaves allowed to naturally synthesize isoprene in response to this temperature (Sharkey et al., 2001). Exposure to other hydrocarbon compounds with two double bonds similar to isoprene (e.g., betadiene) was as effective or more effective in promoting recovery, while otherwise similar compounds with no double bonds (e.g., 2-methyl butane) aggravated high-temperature injury to the photosynthetic system (Sharkey et al., 2001). This result suggested that isoprene and other alkene compounds may dissolve in membranes, preventing the formation of small channels through which water may leak. Sharkey and Yeh (2001) reviewed isoprene emission from plants.

VIII. Breaking of Dormancy

Three major phases of plant dormancy have been described: ecodormancy, regulated by environmental factors; paradormancy, regulated by physiological factors outside the affected structure; and endodormancy, regulated by physiological factors inside the affected structure. These phases overlap somewhat, so the beginning and end of each cannot be precisely determined (Lang et al., 1985; Lang, 1989).

Environmental stresses play a dominant role in breaking of dormancy. In many species of woody plants, both seeds and buds require chilling for breaking dormancy. However, factors controlling seed and bud dormancy of the same species may differ appreciably (Dennis, 1996). For example, buds of most *Acer saccharinum* trees required chilling to break dormancy, but seeds did not (Ashby et al., 1991). Certain ecotypes of *Acer rubrum* did not show seed or bud dormancy (Perry & Wang, 1960; Perry, 1971), but buds of northern ecotypes became dormant and required chilling, while only some of their seeds exhibited dormancy (Farmer & Cunningham, 1981; Farmer & Goelz, 1984).

A. SEED DORMANCY

Dormancy of seeds can be broken by exposure to cold or heat, depending on the type of dormancy. Endodormancy usually is broken by chilling of moist seeds ("stratification") at temperatures of 1° to 15°C for weeks to a few months (Bewley & Black, 1982).

Acer saccharum seeds stratified at 4°C germinated after 27 days; those incubated at 15°C did not germinate at all (Hance & Bevington, 1992). Stratification increased the capacity of embryos to synthesize proteins, as also was shown for *Acer platanoides* seeds (Davies & Pinfield, 1979). At a temperature of 20°C, only 5–7% of *Pseudotsuga menziesii* seeds germinated after 42 days. In contrast, up to 73% germinated at 20°C if they were pretreated at 4°C (Taylor et al., 1993).

The efficacy of stratification depends on interactions between temperature and seed-moisture content. *Picea sitchensis* seeds incubated at 4°C and 10% moisture content did not show higher germination after transfer to 10°C than did unchilled seeds. However, after 20 weeks at

4°C and 15% moisture content, or 15 weeks at 4°C and 20% moisture content, germination was stimulated. The dormancy-breaking effect was maximal at 25% and 30% moisture content (95% germination after 15 weeks or 6 weeks, respectively, at 4°C) (Gosling & Rigg, 1990).

The degree of dormancy typically differs among seeds within a seed lot. As a practical matter, nurserymen often delay long stratification of seeds. When seeds are collected in the autumn for sowing the next spring, there may not be adequate time for seed processing, germination testing, and a long period of seed stratification. Because all seeds in a given lot do not have the same chilling requirement, dormancy of some seeds can be broken by a short period of chilling. In seeds of some species, premature germination may occur at the temperature at which the seeds are stratified (Blazich & Hinesley, 1984; Edwards, 1986).

It sometimes is desirable to arrest afterripening and postpone germination, such as when adverse weather conditions necessitate a delay in planting stratified seeds. This can be done by partial drying of seeds or by altering the temperature during seed stratification. Lowering the stratification temperature from 3° to –1° or –3°C decreased the germination capacity of *Prunus cerasifera* var. *divaricata* seeds by as much as 12%, depending on the degree to which afterripening had progressed (Tylkowski, 1985). Also by controlling seed-moisture content, premature germination could be delayed or eliminated (Edwards, 1986).

Heat-stimulated seed germination appears to be an adaptive feature in habitats with high probability of intense fires (Bell et al., 1993). Dormancy of some seeds with hard seed coats can be broken by heat. For example, in some shrubland species seed germination is induced by heat that ruptures seed coats (thereby increasing water uptake) or melts seed-coat waxes (Christensen, 1995). Hence, it is not surprising that fires stimulate regeneration of plants from soil seed banks. Fires in heathlands not only accelerated shedding of seeds but also stimulated germination of seeds stored in the soil (Specht, 1981).

Some chaparral species, including *Ceanothus cordulatus, Arctostaphylos patula, Ceanothus greggii,* and *Eriodictyon angustifolium,* germinate in response to heat from fire (Biswell, 1974, 1989; Gratkowski, 1974; Keeley & Zedler, 1978). High temperatures induced germination of *Rhus ovata* seeds by rupturing the second seed-coat layer along the edge of the seed first above the micropyle. The rupture facilitated water uptake through the underlying third seed-coat layer (Stone & Juhren, 1951). For maximum germination the seeds of the leguminous shrub *Acacia pulchella* required exposure to temperatures of 55° to 60°C (Portlock et al., 1990).

Seed dormancy of different species with hard seed coats varies appreciably in response to high temperatures. Seeds of *Macroptilium atropurpureum, Acacia farnesiana, A. macracantha,* and *Mimosa chaetocarpa* were sensitive to fluctuations in temperature. By comparison, seeds of *Crotalaria incana* and *Indigo suffruticosa* were influenced more by cumulative temperature effects on seed-coat softening (Moreno-Casasola et al., 1994). Maximum germination of *Phellodendron* seeds required alternating exposures to high temperature (35°C, 8 hours in light) and low temperature (10°C, in darkness) (Lin et al., 1994).

Convincing evidence also indicates that certain constituents of smoke can serve as a germination cue in many seeds. Exposure to cold smoke and aqueous extracts of smoke stimulate germination of seeds of numerous species, particularly those in fire-prone Mediterranean habitats in the southwestern United States and South Africa (fynbos) (Brown & Van Staden, 1997; Keeley & Bond, 1997; Keeley & Fotheringham, 1998). There is some indication that NO_2 in smoke accounts for at least part of this response (Keeley & Fotheringham, 1997); however, other gases that are known to be present in smoke and to stimulate germination, such as CO_2 and ethylene, are not involved (Bewley & Black, 1982; Jager et al., 1996; Keeley & Fotheringham, 1998). 1,8-cineole (1,3,3-Trimethyl-2-oxa-bicyclo[2.2.2] octane), an essential oil of eucalyptus leaves that is recovered from aqueous smoke extracts, also stimulates seed germination

(Adriansz et al., 2000). The mechanism by which smoke stimulates germination is unknown, although some researchers have suggested that breakdown of a subdermal cuticle-diffusion barrier by smoke may promote movement of germination promoters and/or inhibitors (Keeley & Fotheringham, 1998). Although heat-induced germination is associated with disruption of the testa allowing imbibition, exposure to smoke has no influence on this process (Keeley & Fotheringham, 1997).

Seeds of some species exhibit both endodormancy and seed-coat dormancy. Such seeds may require exposure to both low and high temperatures to break dormancy. For example, seeds of some species of *Ceanothus* required an extended period of stratification at 2°C as well as a heat shock of 100°C for 1 minute to stimulate germination (Bullock, 1982).

B. BUD DORMANCY

Like seed dormancy, bud dormancy may be broken by cold or by heat. However, dormancy of vegetative and floral buds of trees of the temperate zone is broken by winter cold. The chilling requirement is not a fixed quantity and varies with many factors, including plant species and genotype, type of bud (vegetative, flower, terminal, lateral), chilling temperature, duration of chilling, stage of plant development, daylength, and depth of dormancy (Lavender & Stafford, 1985; Cannell, 1989; Sedgley & Griffin, 1989; Kozlowski & Pallardy, 1997b).

Large differences in chilling requirements of buds of different species are shown by variations in duration of exposure to cold needed to break dormancy. Bud dormancy of *Betula pubescens, B. pendula,* and *Prunus padus* was broken in December; of *Populus tremula,* in January; and of *Alnus incana* and *A. glutinosa,* in February. Thermal time (degree days to budburst) decreased nonlinearly as the duration of chilling was increased, but this relation varied among species. The effective base temperature for accumulation of thermal time differed from 1°C in *Populus tremula* to –4°C in *Prunus padus*. Long days reduced the time to bud opening in all the above species, as well as in *Corylus avellana*. In contrast, bud dormancy of *Sorbus aucuparia* and *Rubus idaeus* did not respond to daylength (Heide, 1993a).

Breaking of dormancy of *Acer saccharinum* buds under natural conditions required exposure to temperature below 4°C for approximately 1000 hours. However, breaking of dormancy in a dark, cold room at 4°C required approximately 2000 hours of chilling. These requirements were similar to those for *Acer saccharum* and *Tilia americana* (Ashby, 1962). They differed from those for *Acer rubrum* buds, which did not have a significant chilling requirement in some parts of its range (Ashby et al., 1991).

Both chilling and long days were necessary for breaking dormancy of *Fagus sylvatica* buds. Unchilled buds sampled in October required only long days for normal budburst; buds chilled until January or March still required exposure to long days. However, buds sampled in November and December did not open under long days until after they had been exposed to a substantial period of chilling (Heide, 1993b). Although long days may compensate for lack of chilling in some species, this is not important in some countries, such as Finland, where long days do not prevail during the period of bud dormancy (Hänninen & Backman, 1994).

Chilling requirements of buds vary greatly among species and cultivars. The duration of chilling between 5° and 10°C needed to break dormancy of flower buds varies from 50 to 1700 hours for different *Prunus* species; 150 to 650 hours for *Vaccinium* species; and up to 3000 hours for some cultivars of *Pyrus* (Austin et al., 1982; Sedgley & Griffin, 1989).

Chilling requirements of vegetative and floral buds often differ appreciably. *Viburnum ashei* vegetative buds require 400 to 700 hours of chilling for budbreak. Maximum vegetative growth for Climax occurred after 450 hours of chilling below 7.2°C; of Bluebelle and Delite

after 500 hours; and of Tifblue after 650 hours. Some Climax, Bluebelle, and Delite plants flowered after 250 hours of chilling. However, these three cultivars required at least 650 hours of chilling for maximum flower development (Austin et al., 1982).

Interruption of a cold regime by high temperature can negate the effect of chilling on breaking of bud dormancy. For example, interruption of a 16-hour regime at 6°C by 8 hours at 24°C completely negated the effect of chilling on breaking dormancy of *Prunus persica* buds (Erez et al., 1979). To have a negating effect the high-temperature interruption had to be at least 4 hours long. In addition, the high-temperature interruption was effective only during the first two-thirds of the chilling period (Couvillon & Erez, 1985). In *Malus domestica,* temperatures 5° to 10°C higher than the optimal chilling temperatures for breaking bud dormancy accelerated processes leading to budbreak if they occurred after a significant portion of the chilling requirement had been received (Young, 1992).

A variety of models for predicting the effects of chilling on breaking of bud dormancy have been developed for different species. Examples include those for *Cornus sericea* (Kobayashi et al., 1982; Fuchigami & Nee, 1987), *Malus domestica* (Shaltout & Unrath, 1983; Anderson et al., 1986), and *Prunus persica* (Richardson et al., 1974). Cannell (1989) criticized some of the early models that attempted to provide quantitative relations between temperature and bud dormancy. He emphasized that optimum chilling temperatures are not constant, that both warm and subzero temperatures can have a negative effect on bud dormancy, and that chilling temperatures that alternate with warm temperatures may be less or more effective than continuous chilling temperatures in breaking bud dormancy. Erez & Couvillon (1987) proposed a two-step chilling model to accommodate the cycling of chilling temperatures with more moderate temperature when winters are not consistently cold. The first step involves conversion from the unchilled to the chilled state by chilling temperatures. This stage is reversible by high temperatures. The second stage, which is not reversible, involves conversion by moderate temperatures of the unstable intermediate formed by step 1 into a stable material. When this stable material accumulated to a certain level, rest was completed. This two-step model has been tested by computer simulation (Fishman et al., 1987a, 1987b).

Near-lethal heat stress (40° to 45°C) may release buds of woody plants from endodormancy and ecodormancy. Heat stress broke endodormancy and decreased the thermal units needed for budbreak during ecodormancy in *Populus nigra* x *P.* x *canadensis, Prunus persica* (Wisniewski et al., 1994), and *Malus domestica* (Wang & Faust, 1994). Heat stress was most effective during the early and later stages of endodormancy. Near-lethal heat stress during the late stages of ecodormancy delayed budbreak (Wisniewski et al., 1994, 1996). Temperatures that stimulated budbreak of *Populus nigra charkowiensis* x *P. nigra incrassata* in winter were lethal in early spring, indicating changes in thermotolerance of buds (Wisniewski et al., 1997). Near-lethal heat stress (47°C, 1 hour) overcame dormancy of *Cornus sericea* buds during the early and later stages of dormancy. During October and December, plants exposed to heat broke buds within 35 and 12 days, respectively (vs. 150 and 110 days, respectively, in control plants) (Shirazi & Fuchigami, 1995). The optimal high temperature for breaking endodormancy of *Prunus persica* and *Populus* sp. flower buds (37.5°C, 2 hours) was lower than that for vegetative buds (40°C, 4 hours) (Wisniewski et al., 1994).

The physiological events that occur in response to near-lethal heat stress have not been adequately characterized. The abrupt release of dormancy produces oxidizing compounds and free radicals, followed by production of antioxidants. Although several proteins are associated with changes in dormancy, the relations of these proteins to endodormancy have not been satisfactorily clarified (Wisniewski et al., 1996).

IX. Pollen Shedding

Dehiscence of anthers and release of pollen result from dehydration of the walls of anther sacs. Low relative humidity is most commonly associated with hygroscopic shrinkage and rupture of anther walls (Sarvas, 1962, 1968; Kozlowski, 1972a; Agashe & Alfadil, 1989; Hart et al., 1994). In anther sacs the endothecial layer, comprising structurally weak fibrous cells, is the most common site of dehiscence.

Pollen may be released rapidly or gradually, depending on plant species and humidity conditions (Stanley & Kirby, 1973; Stanley & Linskens, 1974). Humidity regulates both seasonal and diurnal pollen shedding, with pollen counts drastically reduced during rainy periods (Agashe & Alfadil, 1989; Hart et al., 1994). Hence pollen influx into seed orchards is greatly reduced on rainy days (Di-Giovanni & Kevan, 1991).

Diurnal variations in pollen dispersal are closely correlated with changes in humidity. In Finland, pollen shedding of *Pinus sylvestris* was maximal near noon and negligible at night. During the flowering season the relative humidity dropped at noon, usually to less than 50%, but often approached 100% during the night (Sarvas, 1962). In Australia the amount of *Pinus radiata* pollen in the air also followed a daily trend, from a maximum in the early afternoon to a minimum at night (Fielding, 1957). Diurnal release of pollen by several species of trees was similarly negatively correlated with relative humidity. In *Picea, Populus, Quercus, Salix,* and *Ulmus* there was a regular daytime maximum and nightly minimum in pollen release (Käpyla, 1984).

X. Seed Dispersal

Cones typically dehydrate and shrink before they open (Clausen & Kozlowski, 1965). *Pinus banksiana* cones dehydrated from a moisture content between 250% and 350% to only 12–15% as they matured (Beaufait, 1960). By the time *Pseudotsuga menziesii* cones were opening in early September, they had dehydrated to a moisture content of 16% (Ching & Ching, 1962).

In pines the adaxial side of the cone scale comprises largely strands of vascular tracheids extending from the cone axis; the abaxial side consists of relatively short, rectangular, thick-walled cells. The cellulose microfibrils in these short cells are oriented perpendicular to the long axis of the scale (Fahn & Werker, 1972). As cone scales dehydrate the cone opens because of differential shrinkage between the adaxial and abaxial tissues (Allen & Wardrop, 1964; Harlow et al., 1964). After cones open they may close and reopen with changes in relative humidity (Fielding, 1947).

Fire plays an important role in seed dispersal of some shrubs and trees. An estimated 1200 species in 40 woody genera retain viable seeds in their canopies for 1 to 30 years or more (LaMont et al., 1991). Cones containing viable seeds may remain on *Pinus banksiana* trees for more than 20 years (Cayford & McRae, 1983). Following fire, large numbers of seeds are released from these plants into sites rich in available resources, such as light and mineral nutrients (Gill, 1981). Hence, fires may assure regeneration of plant communities by favoring seed dispersal and seedling establishment (Bradstock, 1991).

Serotinous (late-to-open) cones have been reported in *Pinus contorta* (Lotan, 1967, 1976; Perry & Lotan, 1979; Muir & Lotan, 1985a, 1985b; Despain et al., 1996), *P. banksiana* (Teich, 1970; Gauthier et al., 1993), *P. rigida* (Givnish, 1981; Fraver, 1992; Fimbel et al., 1995), *P. clausa* (Little & Dorman, 1952), *P. pungens* (Barden, 1979), *P. torreyana, P. coulteri,* and *P. brutia* (Thanos et al., 1989), *Picea mariana* (Johnson & Johnson, 1994), and *Cupressus sempervirens* (Lev-Yadun, 1995). *Pinus sabiniana* trees were not considered to be closed-

cone pines but showed delayed seed dispersal and were functionally similar. *Sequoiadendron giganteum* also showed closed-cone tendencies (Zedler, 1986). The major species of *Cupressus* in California were characterized by a closed-cone habit or by serotinous cones. The ovulate cones remained sealed after they matured, usually accumulating on the tree until opened by fire. Species included *Cupressus abramsiana, C. bakeri, C. forbesii, C. goveniana, C. macnabiana, C. macrocarpa, C. nevadensis, C. pygmaea, C. sargentii, C. stephensonii,* and *C. bakeri* ssp. *mathewsii* (Vogl et al., 1977).

Serotiny has evolved in many species under the selective pressure of fires (Gauthier et al., 1993, 1996). *Pinus contorta* var. *latifolia* produced both serotinous and nonserotinous cones. Individual trees either were predominantly closed coned or open coned, and most stands were dominated by one of these types. Serotinous cones predominated in stands that originated after fire; nonserotinous cones, in stands that formed after disturbances that were not related to fire (Muir & Lotan, 1985a). In North Carolina the cones of *Pinus pungens* remained closed for 2 years. Then approximately 40% opened without fire, and the rest remained closed and attached to the tree for 10 years or more, with viable seeds in the oldest cones. Hence the species regenerated with or without fire (Barden, 1979). The cones of *Pinus torreyana* opened at maturity, but seeds were released from trees for up to 13 years (McMaster & Zedler, 1981).

Both desiccation and heat are necessary for seed dispersal from serotinous cones of some members of the Pinaceae and Cupressaceae (Teich, 1970; Vogl et al., 1977; Gill & Groves, 1980). Seeds are stored in serotinous cones because of the restraining resinous bonds of the scales. When the resinous material is melted by fire, the cone scales separate on drying. Hence, opening of serotinous cones is a two-part process: first the resin bonds weaken and break, and then the cone scales reflex from the cone axis (Gutsell & Johnson, 1993; Johnson & Gutsell, 1993).

Fires not only contribute to cone opening but the cones also protect seeds from high temperatures (Givnish, 1981). After exposure of closed *Pinus rigida* cones to 500°C for 3 minutes the temperature inside the cones did not exceed 100°C (Fraver, 1992). Fire also stimulates seed germination of some species (Gill, 1981). Hence, closed cones provide a means of regenerating fire-sensitive species that lack capacity for sprouting (McMaster & Zedler, 1981).

Serotiny occurs in a number of heath plants. The genus *Banksia* is characterized by woody infructescences with large follicles around the rachis (George, 1981). In Australia *Banksia ornata* depends on fire to open the follicles and release the seeds. As fire destroys the resin at the junction of the valves of the follicles, the valves reflex and seeds are released (Wardrop, 1983). At air-dry moisture contents (10–12% of dry weight) temperatures exceeding 75°C were required for opening the valves of *Banksia ornata* follicles, with the duration of exposure necessary for opening decreasing with increasing temperature (Gill, 1976). Up to 87% of the viable seeds of *Banksia burdettii* may survive and be released within 100 days of a fire, depending on fire intensity and season (Lamont & Barker, 1988).

The temperature required for follicle opening varies appreciably among *Banksia* species. When exposed for 2 minutes to temperatures in the range of 100° to 500°C, the follicles of *Banksia tricuspis* opened at a relatively low temperature (50% opened at 145°C). *Banksia hookeriana* follicles required much higher temperatures for opening (50% opened at 390°C) (Enright & Lamont, 1989).

Not all *Banksia* species depend on fire for follicle dehiscence. *Banksia ornata, B. ericifolia, B. serratifolia,* and *B. aspleniifolia* depend on fire for dehiscence of follicles and seed dispersal. By comparison, in *B. marginata* follicle dehiscence normally is seasonal and not related to fire occurrence (Gill, 1981).

After fire the follicles of some species require alternate wetting and drying for maximum seed dispersal. Wet-dry cycles were essential for seed release from 4 species of *Banksia,* whether

serotinous or not. *Banksia* seeds are held in the follicles by a two-winged plate (separator) (George, 1981). After a follicle is ruptured, the hygroscopic wings of the separator are exposed. When moistened they move together, spreading and recurving as they dehydrate. Hence, in each wet-dry cycle the separator exerts a levering action, gradually drawing the adpressed seeds out of the follicle (Cowling & LaMont, 1985).

In serotinous *Hakea* sp. plants, the high temperatures during fire did not affect survival of seeds (Bradstock, 1991). However, survival of seeds may vary appreciably with the structure of *Hakea* fruits. Seeds of large-fruited *Hakea* species (e.g., *Hakea crustablei, H. propinqua*) survived fire temperatures above 400°C (external) and 60°C (internal). In contrast, many seeds of small-fruited species (*Hakea tertifolia, H. dactyloides*) were killed. The threshold temperature for seed mortality was linearly related to thickness of the fruit wall and to dry weight of the fruit (Bradstock et al., 1994).

XI. Stimulation of Reproductive Growth

Vegetative and reproductive structures of woody plants are competing carbohydrate sinks, as shown by two major lines of evidence. First, during rapid early-season growth the shoots typically compete successfully with floral initiation for carbohydrates. However, as reproductive growth continues, both fruits and cones become the dominant carbohydrate sinks. Second, reproductive and vegetative growth are negatively, and often linearly, correlated.

Many studies show that when a heavy crop of fruits, cones, or seeds is produced, shoot growth, cambial growth, and root growth are reduced during the same year and/or the following year (Ryugo & Davis, 1959; Eis et al., 1965; Grochowska, 1973; Cripps, 1981; Dick et al., 1990; Kozlowski & Pallardy, 1997a, 1997b). In addition to preferentially mobilizing stored carbohydrates, growing reproductive structures use large amounts of currently produced photosynthate (Hale & Weaver, 1962; Mochizuki, 1962; Dickmann & Kozlowski, 1970, 1973; Davis & Sparks, 1974; Powell, 1977). Inhibition of vegetative growth by fruit growth has been dramatically illustrated in biennially bearing fruit trees (Singh, 1948; Maggs, 1963; Kozlowski & Pallardy, 1997b). Suppression of vegetative growth at a critical developmental stage results in greater partitioning of carbohydrates into reproductive structures and acceleration of their growth (Kozlowski, 1992).

Chemical growth retardants (e.g., paclobutrazol) have been useful in decreasing the sink strength of shoots, making more of the carbohydrate pool available for initiation and growth of both flowers and fruits. Many examples of increased flowering following application of triazole derivatives to fruit trees have been reported (e.g., Tukey, 1983, 1986; Webster et al., 1986; Kulkarni, 1988; Wood, 1988; Walser & Davis, 1989; McLaughlin & Greene, 1991; Griffin et al., 1993; Kurian & Iyer, 1993a, 1993b).

Correctly timed environmental stresses that impede shoot growth often stimulate growth of reproductive tissues. For example, water stress during the summer triggered flower formation, as in some *Citrus limon* cultivars (Monselise & Halevy, 1964). Root pruning, which impedes absorption of water, also induced flower initiation in citrus (Iwasaki et al., 1959). Flowers were differentiated during the stress period (Nir et al., 1972).

Leaf fall that is induced by moderate water stress prevents water deficits from developing in some tropical trees and induces anthesis during continuing drought, as in *Tabebuia neocrysantha*. Hence, anthesis is correlated with the time of leaf shedding, which typically varies with leaf age, leaf structure, and environmental conditions (Reich & Borchert, 1984). Many evergreens in tropical rain forests flower during periods of moderate drought after they have shed most of their leaves (Alvim & Alvim, 1978). In four species of wet-forest

trees of Brazil (*Erythrina glauca, Lecythis pisenis, Simaruba amora,* and *Tabebuia* sp.), flower opening occurred immediately following drought-induced leaf fall (Reich & Borchert, 1984).

Regulated deficit irrigation (RDI) involves subjecting trees to drought during very early stages of fruit development in order to reduce vegetative growth, followed by normal irrigation. Deficit irrigation can have beneficial or detrimental effects on flowering and fruiting, depending on timing and the degree of water stress imposed. Prolonged and severe water deficits generally inhibit flowering of many species. In 2 of 4 years of irrigation, the water supply (rainfall plus irrigation) accounted for 71% of the variation in flowering of *Malus* trees (Goode & Ingram, 1971). *Carya illinoensis* orchards in the southeastern United States often are amply irrigated to increase early flowering and yield of nuts (Worley, 1982; Stein et al., 1989). By comparison, short periods of drought early in the summer may favor formation of flower buds and break dormancy of flower buds in some species. *Theobroma cacao* plants developed few flowers during a dry period, but floral initiation was stimulated because flowering was exceptionally heavy during a subsequent wet or medium-wet period (Sale, 1970a). Flowering of *Theobroma cacao* also was unusually profuse when high air humidity alternated with low humidity (Sale, 1970b). Severe water stress induced flowering in *Citrus latifolia* (Southwick & Davenport, 1986). In *Pinus taeda* a period of early summer drought favored initiation of conelets (Dewers & Moehring, 1970). Abundant summer irrigation may even depress production of conelets (Bengston, 1965).

Water deficits may influence flowering of tropical trees by different mechanisms. They may directly induce flowering or inhibit shoot flushing, so that the presence of young leaves does not inhibit capacity to flower (Davenport, 1994). Whereas well-watered *Citrus latifolia* trees grew only vegetatively, those undergoing water stress flowered in amounts proportional to the degree and duration of water stress. Leafless trees also flowered in response to water stress, suggesting that the leaves were not necessary for floral induction (Southwick & Davenport, 1986).

As in *Citrus,* initiation of floral buds in *Mangifera indica* occurred after a short period of dry weather (Gongolly et al., 1957). However, water stress did not appear to be directly involved in floral induction. Rather, the water deficit inhibited shoot initiation, hence allowing existing leaves to age and decrease their inhibitory effects on flowering. Thus, the factors in young leaves that inhibit flowering were avoided (Singh, 1960; Davenport, 1990, 1994). The mechanism of floral induction in *Mangifera indica* by water stress was similar to that in *Litchi sinensis* (Menzel, 1983; Menzel & Simpson, 1990).

In some species a period of water stress appears to be necessary for breaking of bud dormancy before flowering is induced by rain or irrigation (Piringer & Borthwick, 1955). A standard management technique in Sicily, called "forzatura," involves withholding irrigation in *Citrus limon* orchards during the summer until the trees wilt. This practice accentuates summer flowering and produces a fruit crop the following summer, when prices for the fruit are high (Barbera et al., 1985). Cultivars of *Citrus limon* differ appreciably in flowering responses to forzatura treatments. The cultivars Eureka, Femminella, Villafranca, and Fino respond better than do Lisbon or Interdonata (Shalhevet & Levy, 1990).

Postharvest water stress in *Prunus persica* led to a 40% increase in return bloom over that in well-irrigated trees (Larson et al., 1988). Deficit irrigation during specific stages of fruit growth led to increased return bloom in *Pyrus communis* (Mitchell et al., 1984, 1986). In England, *Malus domestica* trees that had been subjected to severe water stress for a 2-week period beginning in late July bloomed again in mid-September, emphasizing triggering of floral initiation by drought (Jones, 1987).

Several studies showed that fruit yields were not reduced or were increased when trees were exposed to RDI during the period of rapid shoot elongation but were amply irrigated thereafter. Deficit irrigation increased fruit yield of *Prunus persica* (Chalmers et al., 1984), *Pyrus communis* (Mitchell et al., 1984, 1986), and *Malus domestica* (Durand, 1990; Ebel et al., 1993). Imposed water stress during rapid shoot growth of *Prunus persica* trees increased fruit size. However, smaller fruits were produced when water stress was imposed during the late stages of fruit growth (Li et al., 1989). Under RDI *Prunus persica* trees used approximately half as much water as did well-irrigated control trees early in the season and 30% less during the rest of the season (Boland et al., 1993). In another study, *Prunus persica* under RDI required 40% less irrigation water than did control trees (Girona et al., 1993). Caspari et al. (1994) exposed *Pyrus serotina* trees to RDI before or during rapid fruit growth. Except for the final week of RDI, fruit growth was not reduced. Fruits from trees under RDI grew faster than did those of the irrigated controls, except during the first week after RDI treatment. By comparison, fruit growth was inhibited by water stress if it developed during the period of rapid fruit growth. The decreased fruit growth rate of RDI trees during the week before full irrigation indicated that the RDI trees should have been rewatered a week earlier. Final fruit size and yield did not differ between treatments.

The effects of deficit irrigation on flowering and fruiting often vary with site conditions. RDI of *Prunus* trees on a deep soil increased both flowering and fruiting. However, although RDI increased flowering of trees on a shallow soil, it appreciably reduced fruit yield (presumably because of severe water stress and increased fruit shedding) (Lampinen et al., 1995).

Using a spatial variant of this same technique, researchers in Australia have developed a procedure, partial root zone drying (PRD), for alternating wetting and drying cycles on either side of rows of grapevines (Stoll et al., 2000). This practice stimulates synthesis of ABA in drying roots and redistributes water at night to roots in the drying zone from those in the wet zone. Subsequently, diurnal translocation of ABA from nocturnally rehydrated roots in drying soil reduces stomatal conductance and improves water-use efficiency. Shoot growth is inhibited under PRD, while fruit yields are maintained. Reduced root synthesis of cytokinins in this system may reduce shoot growth while fruit yields remain unaffected (Dry & Loveys, 1999; Stoll et al., 2000).

RDI has been used to increase the soluble solids content (SSC) of *Prunus persica* (Crisosto et al., 1994) and *Malus* fruits (Irving & Drost, 1987). A high SSC increased the retail value of *Prunus persica* fruits (Parker et al., 1991). Furthermore, the SSC of RDI *Malus* fruits remained higher than that of control tree fruits during storage. The higher levels of soluble solids and longer storage life characterized *Prunus persica* fruits from trees subjected to drought at a late stage of fruit development. However, the fruits were smaller at harvest, limiting imposition of drought during this period, except in cultivars that produced very large fruits.

In a number of species, osmotic adjustment occurs during water stress and is associated with maintenance of leaf turgor (Table II). Examples are *Malus domestica* (Fanjul & Rosher, 1984) and *Juglans nigra* (Parker & Pallardy, 1985). In *Pyrus communis,* however, osmotic adjustment did not occur during drought (Marsal & Girona, 1997). Hence, increased fruit growth in *Pyrus communis* after RDI (Mitchell et al., 1984) could not be attributed solely to maintenance of leaf turgor.

XII. Seedling Storage

Tree seedlings are routinely placed in cold storage because planting sites often are not ready when seedlings are lifted at the nursery and/or when the planting season must be ex-

tended. In the southern United States the lifting of seedlings from nurseries usually continues for about 2 months (late December to early February) whereas the planting season may last as long as 6 months (Garber & Mexal, 1980). Cold-stored seedlings often grew better and survived as long or longer than did seedlings that were not placed in storage (Hocking & Nyland, 1971).

Most seedlings are stored at temperatures 1° to 2°C above freezing or 2° to 4°C below freezing (Deffenbacher & Wright, 1954; Wakeley, 1954; Flint & McGuire, 1962; Aldhous, 1964; Mullin, 1966; Brown, 1971; Hocking, 1972; van den Driessche, 1977, 1979; Garber & Mexal, 1980; Mattson & Troeng, 1986; van Eerden & Gates; 1990; Omi et al., 1991a, 1991b). Growth and establishment of cold-stored seedlings vary with the date of lifting plants in the nursery (Stone et al., 1962, 1963; Ritchie et al., 1985; Chen et al., 1991; Drake et al., 1991), species and genotype (Cram & Lundquist, 1981; Bates et al., 1994), seedling quality (Ritchie, 1984; South et al., 1985), storage temperature, humidity, and illumination (Camm et al., 1994), seedling moisture content (Bates et al., 1994), duration of storage (Ritchie, 1982; Cannell et al., 1990), and handling of planting stock after storage (Camm et al., 1995; Kozlowski & Pallardy, 1997b)

The date on which seedlings are lifted from the nursery and placed in cold storage is critical for their survival. The root growth potential (RGP) of seedlings typically is low in the autumn, increases to a maximum in the early spring, and then decreases. The appropriate lifting date was crucial for survival after storage of seedlings of *Pinus ponderosa* (Stone et al., 1963), *Pseudotsuga menziesii* (Lavender & Wareing, 1972), and *Tsuga heterophylla* (Nelson & Lavender, 1979). *Tsuga heterophylla* seedlings lifted after mid-November were more vigorous than were those lifted in September or October (Nelson & Lavender, 1979). *Pinus ponderosa* seedlings lifted in November had higher RGP and higher survival rates after storage than did seedlings lifted in September or October (Omi et al., 1991b). Hocking and Nyland (1971) suggested that seedlings to be stored over winter should be lifted from the nursery as late as possible. The effect of date of lifting on seedling responses of cold-stored stock emphasizes that seedlings need to develop a state of physiological readiness for cold storage (Camm et al., 1994). To predict the appropriate time for lifting of seedlings for cold storage, some investigators used such components of stress resistance as cold hardiness (Colombo, 1990), chlorophyll fluorescence (Vidaver et al., 1989), level of carbohydrate reserves (Winjum, 1963; Ritchie, 1982; Cannell et al., 1990), and storage proteins (Roberts et al., 1991).

Dehydration of seedlings before, during, or after storage adversely affects their growth potential. High prestorage moisture stress delayed budbreak of *Picea glauca* seedlings (Rose et al., 1992). Storage areas often are maintained at high humidities, and/or seedlings are wrapped in plastic films (Webb & Von Althen, 1980). Root-growth potential of *Picea sitchensis* seedlings was reduced 59% by desiccation (Deans et al., 1990). Severe dehydration of seedlings reduced the moisture content of fine roots, resulting in poor rehydration of outplanted seedlings (Coutts, 1981; Insley & Buckley, 1985). Shoot- and root-water potentials of *Acer platanoides* and *Crataegus phaenopyrum* seedlings decreased during 4 weeks of cold storage. *Crataegus* was more sensitive than *Acer* to desiccation and required protection of both roots and shoots to minimize water loss (Bates et al., 1994).

Chen et al. (1991) evaluated the influence of M7, M111, MM106, and seedling rootstocks on tolerance of desiccation by *Malus* seedlings during 3 months of storage at 0°C. Only trees on MM111 rootstocks tolerated desiccation during storage followed by a 48-hour exposure to air drying. Scions on other rootstocks seldom survived.

Seedlings are typically kept in cold storage for a few days to as long as 8 months (Kozlowski & Pallardy, 1997b). Usually, long periods of storage may be inadvisable because of carbohydrate depletion by respiration (Hellmers, 1962; Ronco, 1973; McCracken, 1979a, 1979b; van

den Driessche, 1979; Ritchie, 1982, 1987; Kozlowski, 1992) and decrease in RGP (Ritchie, 1982). After 5 weeks of growth, total dry weight of *Picea sitchensis* seedlings was 416 mg in plants that had been cold-stored for 5 weeks and 244 mg after 20 weeks of cold storage (Buckley & Lovell, 1974). After 100 days of storage at 4.5°C, the dry weights of *Picea glauca* and *Pinus resinosa* seedlings decreased by 4.0% to 4.5%, respectively (van den Driessche, 1979). Reserve carbohydrates in roots and stems of *Pinus mugo* and *P. radiata* decreased steadily during 18 weeks of cool storage (McCracken, 1979a). In Scotland, carbohydrate reserves of cold-stored (0.5°C November, December, and January) *Picea sitchensis* and *Pseudotsuga menziesii* seedlings were lowered from levels of 100–150 mg g^{-1} to 40–50 mg g^{-1} (Cannell et al., 1990). Losses in dry weight of stored seedlings often are correlated with decreases in RGP and survival of outplanted seedlings. RGP of *Picea glauca* seedlings declined sharply after 22 weeks of cold storage, and of *Pseudotsuga menziesii* after cold storage for 6 months (Ritchie, 1982). Depletion of carbohydrate reserves during prolonged storage also may render plants susceptible to decay (Gutteridge & Montgomerie, 1971).

Many nursery managers routinely store seedlings in the dark. However, daily exposure of seedlings to several hours of low illumination during storage may increase cold hardiness and survival of outplanted seedlings (Lavender & Wareing, 1972). A daily photoperiod during storage improved subsequent growth and survival of *Pseudotsuga menziesii* and *Tsuga heterophylla* seedlings lifted during the autumn months. Similar treatment of seedlings lifted and stored in January did not increase survival but accelerated the onset of bud-growth initiation (Lavender, 1985). Acceleration of bud elongation also was demonstrated in winter-lifted *Pinus taeda* seedlings exposed to a daily photoperiod during storage (Johnson, 1982). The effects of photoperiod presumably are mediated by phytochrome and involve hormonal growth regulation (Camm et al., 1994).

To avoid membrane damage from rapid thawing and to allow recovery of physiological processes before planting, frozen nursery stock has been thawed at low temperature (2° to 3°C) for up to several weeks (Fraser et al., 1990). However, for some species at least, much faster thawing has been found useful. For example, for *Picea glauca* and *P. engelmannii* seedlings removed from freezer storage, recovery of water potential after thawing required only hours rather than days once ice crystals disappeared from the roots. Furthermore, rapid thawing of seedlings produced only minor effects on postplanting seedling responses. Height as well as shoot and root mass 3 months after planting did not differ between slowly thawed and rapidly thawed seedlings (Camm et al., 1995). Another reason for rapid thawing is that it decreases respiratory depletion of carbohydrates and development of molds.

XIII. Pollen Storage

Preservation of pollen is essential as insurance against poor flowering years or loss of selected plants. It also is indispensable as a gene-conservation technique and for physiological and biochemical studies (Akihama & Omura, 1986). Because the flowering period of many woody plants is short, pollen must be rapidly collected and processed for storage.

Longevity of fresh pollen of woody plants differs widely among species and genotypes (Altman & Dittmer, 1972; Bellani & Bell, 1986). For example, when pollen was stored at room temperature, its longevity varied from 16 days for *Tilia platyphyllos* to 279 days for *Pinus sylvestris* (Pfundt, 1909). Viability of *Betula* pollen decreased from 85–95% to 32–44% after storage at room temperature for 30 days and to 1.0–1.5% after 60 days (Alam & Grant, 1971). Pollens of *Citrus* and *Vitis* retained germination capacity for 4–5 years, whereas those of *Juglans* and *Corylus* were capable of germination for only a short time (Akihama & Omura, 1986).

Aside from genotypic differences, the major factors that determine longevity of pollen in storage are temperature and pollen moisture content (Stanley & Linskens, 1974). Both deep-freeze storage and storage in liquid nitrogen have been effective in preserving pollen. Storage of pollen at –15°C in commercial freezers will maintain viability of some pollens for many years. Deep-freeze storage has been used for pollens of many woody plants, including species of *Aesculus, Corylus, Diospyros, Eucalyptus, Kalmia, Malus, Populus, Prunus, Pyrus, Rhododendron, Vaccinium,* and *Vitis* (Snyder & Clausen, 1974). Pollen of *Prunus persica,* freeze dried and stored for 9 years at –20°C, showed up to 82% germination. Pollen grains of *Malus pumila* and *Pyrus serotina* kept for 9 years at room temperatures showed some but low germination capacity (Ushirozawa & Shibukawa, 1948). Germination capacity of *Picea abies* and *Pinus nigra* pollen did not decrease after 21 months in freezer storage (–18°C) or storage in liquid nitrogen (–196°C) (Lanteri et al., 1993). The viability of pollen of several *Pinus* species stored for 10 months in a deep freeze was similar to that of fresh pollen (Duffield & Callaham, 1959).

Pollen of *Pseudotsuga menziesii* was successfully stored for 2 years at –18°C if: it was air dried for 4 hours at room temperature to 8% moisture content, stored at 0°C for 30 days, sealed in a vacuum at –77°C for 1 hour, and sealed in airtight vials (Livingston & Ching, 1967). A successful and convenient method of preserving *Acacia* pollen involved vacuum drying followed by storage at –18°C (Sedgley & Harbard, 1993).

Pollen of both angiosperms and gymnosperms has been stored in a viable condition in liquid nitrogen for a very long time (Table V). In liquid nitrogen, pollen undergoes negligible metabolic changes that otherwise would lead to loss of viability. In addition, many pollen samples can be compactly preserved at modest cost. Storing pollen in liquid nitrogen is advantageous for plant breeders and gene banks for conservation of male germplasm (Barbosa et al., 1991).

Drying of pollen typically is necessary before storage. Pollen may be air dried, vacuum dried, or freeze dried (King, 1961; Akihama et al., 1979). The optimum duration of freeze drying of pollen varies appreciably among species. For example, pollen of *Juglans nigra* lost germination capacity after only 30 minutes of freeze drying (Hall & Farmer, 1971), whereas *Actinidia* pollen survived 10 hours of freeze drying (Akihama & Omura, 1986).

Cryopreservation of pollen with a high moisture content is difficult because ice crystals may form and destroy the cells. When pollen moisture content is appropriately reduced, injury generally does not occur during cooling to temperatures below –40°C and down to –196°C, followed by warming. Pollen of many species does not survive below –40°C if the moisture content exceeds 20–30% (Towill, 1985). Reduction of moisture content of angiosperm pollen below 20–30% usually is fatal, whereas pollen of most conifers is best stored in a range of 10–20% moisture content. In addition, pollen viability is retained longer when the humidity does not fluctuate much during the storage period (Harrington, 1970).

Germinability of *Pinus taeda* pollen that had been frozen for a year was 94% and 91% when the moisture contents were 9% and 7% (fresh weight basis), respectively. Germination capacity of pollen with a moisture content of 3% decreased to 71%. The reduced viability was attributed to desiccation injury to the plasmalemma and/or imbibitional chilling injury (Wang et al., 1993).

In order to preserve the germination capacity of dry-stored pollen, rehydration at high humidity is necessary after storage (Jett & Frampton, 1990; Moody & Jett, 1990). Rehydration of *Prunus* or *Pyrus* pollen at a low temperature (1°C) was more efficient than rehydration at a high temperature (Akihama & Omura, 1986). For good discussions of methods and problems of storing pollen, see Snyder and Clausen (1974), Matthews and Kraus (1981), Bramlett and Matthews (1991), and Wang et al. (1993).

Table V

Species for which pollen was successfully preserved in liquid nitrogen (–196°C)

Species	Source
Betula pendula	Jorgensen, 1990
Betula pubescens	Jorgensen, 1990
Carica papaya	Ganeshan, 1986
Cornus avellana	Connor & Towill, 1993
Juglans nigra	Farmer & Barnett, 1974
Larix decidua	Jorgensen, 1990
Larix kaempferi	Jorgensen, 1990
Larix leptolepis	Ichikawa et al., 1970
Olea europaea	Parfitt & Almehdi, 1984b
Phoenix dactylifera	Connor & Towill, 1993
Picea abies	Ahuja, 1986; Jorgensen, 1990; Lanteri et al., 1993
Picea pungens	Connor & Towill, 1993
Pinus nigra	Lanteri et al., 1993
Pinus ponderosa	Connor & Towill, 1993
Pinus strobus	Lanteri et al., 1993
Pinus sylvestris	Ahuja, 1986; Jorgensen, 1990; Lanteri et al., 1993
Pinus uncinata	Lanteri et al., 1993
Prunus sp.	Parfitt & Almehdi, 1984a
Pseudotsuga menziesii	Copes, 1985, 1987
Quercus petraea	Jorgensen, 1990
Quercus robur	Jorgensen, 1990
Simmondsia chinensis	Lee et al., 1985
Vitis sp.	Parfitt & Almehdi, 1983

XIV. Seed Storage

Seed production of many woody plants is very irregular and unpredictable (Kozlowski & Pallardy, 1997b). Seed crops vary not only among species but also among trees of the same species, as well as from year to year. Hence, plant propagators and nursery managers must store seeds in a viable condition, often for several years, in order to produce annual crops of tree seedlings. Storage of seeds also is important for preservation of species that might otherwise become extinct and for maintaining genetic diversity of species. For plant breeding, small samples of seeds must be preserved indefinitely (Pence, 1995).

Seeds generally are best collected and stored when they are physiologically mature, after they have achieved their maximum dry weight (when resources have stopped moving into seeds from the mother plant). The proteins of mature seeds can be dehydrated and rehydrated without loss of function (Harrington, 1972). As soon as seeds mature, their capacity to germinate, as well as their synthesis of proteins, lipids, and repair systems, begin to decline progressively (Osborne, 1980; Priestley, 1986). Aging seeds also show decreases in RNA, increases in chromosome aberrations (Roos, 1982), and changes in enzymatic activity, respiratory pathways, and storage compounds. The respiratory quotient (RQ) of old seeds often is high, reflecting an increase in CO_2 evolution, decrease in O_2 uptake, or both. Membranes become more permeable, as shown by greater leakage of inorganic and organic ions from seeds (Abdul-Baki & Anderson, 1972; Pukacka & Kuiper, 1988). Lowered germination capacity of stored *Pinus pinea* seeds was correlated with increased loss of reducing sugars (DeCastro & Martinez-Honduvilla, 1984) and loss of capacity for increasing levels of proteins and nucleic acids (DeCastro & Martinez-Honduvilla, 1982).

On the basis of desiccation characteristics, seeds were classified for a long time into one of two broad classes, orthodox and recalcitrant (Roberts, 1973). Orthodox seeds can retain viability for many years. They can be dried to very low moisture contents, generally to 5% and sometimes even 2% (fresh weight basis), without losing viability. Seeds of most genera of forest trees of the temperate zone were considered orthodox and included both angiosperms (e.g., *Alnus, Betula, Fraxinus, Platanus, Prunus,* and *Ulmus*) and gymnosperms (e.g., *Abies, Larix, Pinus, Pseudotsuga,* and *Tsuga*). Orthodox seeds of tropical species included those of *Acacia, Casuarina, Eucalyptus,* and members of the legume families (Bonner, 1990).

In contrast to orthodox seeds, recalcitrant seeds have a short life span. They must remain moist to retain viability, and, even when moist, they generally lose viability within a few weeks or months. Seeds originally classified as recalcitrant included those of the temperate-zone genera *Aesculus, Castanea, Corylus, Fagus, Juglans,* and *Quercus*. Seeds of recalcitrant tropical species included those of most rain-forest species and seeds of *Persea americana, Cocos nucifera, Hevea brasiliensis, Mangifera indica,* and *Theobroma cacao*.

More recent work casts doubt on the early rigid classification of seeds as either orthodox or recalcitrant. Seeds of *Carya, Corylus, Fagus,* and *Juglans* were reclassified as suborthodox because they survived when carefully dried (Ellis et al., 1985; Bonner, 1986). *Fagus* nuts showed characteristics between those of orthodox and recalcitrant seeds (Gosling, 1991). Seeds of *Neolitsia parvigemma, Lindera megaphylla,* and *Cinnamomum subavenium* showed tolerance of partial desiccation. Their sensitivity to freezing differed from that of true orthodox or recalcitrant seeds (Lin, 1996).

When dehydrated, the seeds of some tropical woody plants are sensitive to low temperatures. Examples include seeds of *Coffea arabica, Carica papaya,* and *Elaeis guineensis*. They have been classified as intermediate species (Pence, 1995). Most seeds of one cultivar of *Coffea arabica* withstood drying to a moisture content of 5–6%. Those of three other cultivars were much more sensitive to desiccation. In all cultivars, seed longevity at cool and subzero temperatures and at low moisture contents was not consistent with the storage behavior of orthodox seeds. Hence *Coffea* seeds did not conform to the storage characteristics of either orthodox or recalcitrant seeds. The mature seeds of *Elaeis guineensis* exhibited some recalcitrant characteristics. However, excised embryos could be desiccated without loss of viability and were classified as orthodox (Grant et al., 1983).

Seeds of closely related species may fall into different classes or show variable degrees of recalcitrance. For example, seeds of *Quercus acutissima* could be stored for only 2 months, whereas *Q. robur* seeds withstood storage for 42 months (Roberts & King, 1980). Seeds of *Araucaria cunninghamii* could be dried to a moisture content of 7% and were classified as orthodox. In contrast, seeds of *A. hunsteinii* showed reduced germination capacity when dried to a relatively high moisture content and hence were classified as recalcitrant (Tompsett, 1982).

Seeds of many but not all species of the genus *Dipterocarpus* are recalcitrant. Seeds of *Dipterocarpus intricatus, D. alatus,* and *D. tuberculatus* can be dried to a moisture content of 10–17%, and sometimes lower, without injury. They also have a longer storage life at these low moisture contents than at higher moisture contents. Such seeds are considered orthodox and can be safely stored at temperatures between +2°C and –20°C. By comparison, optimum temperatures for storage of recalcitrant seeds are in the range of 15° to 21°C (Tompsett, 1992).

Stored seeds lose viability because of depletion of metabolites, denaturation of macromolecules, accumulation of toxic metabolites, and attacks by microorganisms and insects (Stanwood, 1985). The lower the seed moisture content and storage temperature, the longer will seeds retain germination capacity. For storage of orthodox seeds for 5 years or less, tempera-

tures of 0° to 5°C often are adequate. For longer storage, temperatures near –15°C are preferable. The orthodox seeds of *Picea* and *Pinus* have been stored for up to 50 years at 5°C, with a loss of germination capacity of 14–34% (Wang, 1993). For details on methods of storing orthodox seeds, see Wakeley (1954), Harrington (1972), Justice and Bass (1978), King and Roberts (1979), Roberts et al. (1984), Ellis et al. (1985), Young and Young (1992), and Wang (1993).

Some orthodox seeds have been successfully stored at superlow temperatures. Storage of seeds in liquid nitrogen offers the advantage of not requiring complicated temperature and humidity controls, absence of insect and disease problems, and prolonged longevity with little or no genetic change (Styles et al., 1982). At air-dry moisture contents, the seeds of eight tree species were not damaged by exposure to liquid nitrogen. These included seeds of *Abies concolor, A. procera, Pinus lambertiana, P. ponderosa, Pseudotsuga menziesii, Thuja plicata,* and *Ulmus americana* (Stanwood, 1985). However, for seeds of many orthodox species, storage temperatures of –40°, –70°, or –196°C were not appreciably better than was –20°C (Stanwood, 1985).

Storage of nonorthodox seeds without loss of viability is much more difficult than is storage of orthodox seeds. Only relatively short-term storage protocols have been developed for truly recalcitrant seeds. These extend seed longevity from a few weeks to approximately 8–12 months. This may require cryopreservation of excised embryos (Stanwood, 1985; Gonzales-Benito & Perez-Ruiz, 1992). Freezing of immature embryos and subsequent production of somatic embryos or maturation and germination in vitro may be necessary. The use of isolated embryos renders storage of recalcitrant seeds more labor intensive than does storage of orthodox seeds (Pence, 1995).

Lack of success in cryopreservation of some recalcitrant seeds has been attributed to desiccation injury, freezing injury, or both. Removal of unfreezable water was associated with desiccation injury. However, the presence of unfreezable water was not necessarily linked to freezing injury if the moisture content of the embryo axis was less than a critical value (Berjak et al., 1992). Responses of nonorthodox seeds or embryo axes to cryopreservation may be expected to vary with species and genotype, rate of drying, use of cryoprotectants, rates of freezing and thawing, and rate of rehydration (Pence, 1995).

Bonner (1990) divided recalcitrant seeds into two categories, temperate and tropical. Temperate recalcitrant seeds cannot be dried at all but can be stored for several years at near-freezing temperatures, with only moderate loss of germination capacity. Examples are seeds of *Aesculus* and *Quercus*. Tropical recalcitrant species have moisture requirements similar to those of seeds of temperate recalcitrant species but are sensitive to low temperatures. Even short exposures to temperatures below 10° to 15°C cause loss of viability. Examples include seeds of *Hopea, Shorea,* and some tropical fruit trees.

If recalcitrant seeds are dried rapidly, the embryos can survive at much lower moisture contents than if they are dried slowly. When seeds of *Landolphia kirkii* were stored over silica gel, only 50% viability was retained after 15 days of storage (the water content of the embryo axis decreased from 220% to 120%). After 20 days only 7% were viable. However, when excised embryo axes were flash dried in 60 minutes to a moisture content of 16%, viability remained at 95%. Considerable structural damage occurred in seeds dried over silica gel, whereas structural integrity was maintained in flash-dried embryo axes (Berjak et al., 1990).

No specific method is best for storing seeds of all nonorthodox species. In some cases seeds of embryos in a desiccated or partly desiccated condition can be exposed to liquid nitrogen. This is done when the tissue can be dried enough to avoid freezing injury. When this cannot be done, tissues can be frozen while hydrated or partially hydrated, with use of cryoprotectants to

decrease freezing injury. Pence (1995) provided much useful information on storage in liquid nitrogen of seeds or embryo axes of 38 unorthodox species.

XV. Fruit Storage

Success in storage of harvested fruits depends on slowing their rates of metabolism and senescence. This typically is accomplished by storing fruits at low temperatures above freezing and by increasing the CO_2 concentration of storage chambers to 2–6% (and sometimes appreciably higher) and also lowering the O_2 concentration to 2% or 3% (Fidler & Mann, 1972; Fidler, 1973; Dewey, 1977; Smock, 1979; Weichmann, 1986; Walkins et al., 1991). The lowest possible storage temperature delays fruit ripening, maintains fruit quality, and prolongs the life of fruits (Yahia, 1994).

There are many problems in establishing the best storage environments for fruits. Different fruits continue to senesce and decay at variable rates and become increasingly susceptible to physiological diseases and to those caused by microorganisms. Because accumulation of ethylene during storage hastens senescence and deterioration of fruits, ethylene sometimes has been removed from storage chambers (Stow, 1986, 1988, 1990; Yahia et al., 1990). The response to ethylene removal often varies appreciably with cultivars. With Golden Delicious apples, the rise in ethylene during storage was delayed but not prevented by inclusion of potassium permanganate for 40 days; in Bramleys Seedling apples, potassium permanganate delayed ethylene accumulation for more than 200 days (Knee & Hatfield, 1981). Low-pressure (hypobaric) storage sometimes has been used to extend the storage life of fruits, retard production of ethylene, and inhibit some postharvest storage fungi (El Goorani & Sommer, 1981).

A. CHILLING INJURY

Fruits of many tropical plants and some temperate-zone plants may develop chilling injury before or during storage when exposed to low temperatures above freezing. Fruits especially sensitive to chilling after harvesting include apples, avocados, bananas, citrus fruits, mangos, melons, nectarines, papayas, peaches, and plums. The critical threshold temperature below which chilling injury occurs varies among fruits of different species (e.g., apples, oranges, 5°C; mangos, 10° to 13°C; limes 7° to 10°C; bananas, 12° to 13°C). Chilling sensitivity increases to a maximum at the climacteric peak and decreases thereafter (Kays, 1991). Expressions of chilling injury vary not only with species and cultivar but also with degree of fruit maturity, temperature, duration of exposure to low temperature, and environmental conditions preceding chilling (Wang, 1993). Symptoms of chilling injury may include surface lesions (pitting, sunken areas, discoloration), internal discoloration, tissue breakdown, failure of fruits to ripen, ion leakage, weight loss, increased susceptibility to decay, shortened storage life, and compositional changes that affect flavor and taste (Morris, 1982; Bramlage & Meir, 1990).

Chilling injury has been ameliorated by genetic modification, temperature conditioning, intermittent warming, use of plant-growth regulators (e.g., ABA, triazoles, ethylene, polyamines), other chemicals (e.g., fungicides, calcium, antioxidants, free-radical scavengers), and waxing of fruits (Wang, 1990, 1993).

Prestorage warming controlled chilling injury during storage of lemons (Houck et al., 1990) and limes (Spalding & Reeder, 1983). Keeping grapefruits at 17°C before placement in cold storage also reduced chilling injury (Chalutz et al., 1985). Intermittent stepwise warming of fruits during storage often has been more effective than has warming by exposure to a single warm temperature. Intermittent warming was effective on grapefruits (Hatton et al., 1981), lemons (Cohen et al., 1983), peaches, and nectarines (Anderson, 1979, 1982). Exposure to

warm temperatures must occur before chilling injury becomes irreversible. When chilling injury has progressed too long, warming often accelerates development of injury (Wang, 1993). The mechanism by which intermittent warming lessens chilling injury involves acceleration of metabolic processes that remove the toxic compounds accumulated during chilling. Exposure of chilled tissues to warm temperatures for short periods appears to repair injury to membranes, organelles, and metabolic pathways (Lyons & Breidenbach, 1987).

B. DISEASES

As fruits senesce they become increasingly susceptible to pathogens (Moline, 1984). Hence, postharvest decays are a serious problem during prolonged storage. The most common pathogens of apples were *Penicillium* spp. and *Botrytis cinerea,* isolated from 29% and 25%, respectively, of diseased apples. Two other important pathogens were *Mucor* spp. and *Cryptosporiopsis* spp., associated with 22.0% and 10.5%, respectively, of diseased apples (Sholberg & Haag, 1996). The most important pathogen of soft fruits (berries, currants, and drupes) is *Botrytis cinerea. Mucor* spp. and *Rhizopus* spp. also are of considerable importance on strawberries and raspberries (Dennis, 1983).

Cold suppresses diseases by inhibiting growth of microorganisms and maintaining host resistance by postponing fruit senescence. However, some storage diseases are not effectively controlled by cold alone. Postharvest applications of fungicides have been effective, but many have been removed from the market for possible health and environmental reasons (Sitton & Patterson, 1992).

Direct suppression of pathogens is possible using high CO_2 and low O_2 levels during cold storage (Spotts, 1984; Sommer, 1985). Controlled-atmosphere storage of apples with CO_2 concentrations greater than 2.8% reduced development of lesions associated with *Botrytis cinerea, Penicillium expansum,* and *Pezicula malaticorticis* in McIntosh, Delicious, and Golden Delicious apples kept for 61 days at 0°C. Low O_2 atmospheres were less effective for decay control. Apple firmness, soluble solids, and titratable acidity were not adversely influenced by the high CO_2 or low O_2 atmosphere treatments (Sitton & Patterson, 1992). Commercially acceptable levels of bitter pit (less than 5%) were obtained with Red Delicious apples when CO_2 concentrations in polyethylene bags exceeded 5% and O_2 levels fell to 15–10% (Hewett & Thompson, 1988).

Prolonged low-temperature storage may favor development of scald, a physiological disease of some apple and pear cultivars. Scald is characterized by browning of the skin as a result of damage to the hypodermal cells. The severity of scald is proportional to α-farnesene oxidation. Immature apples develop scald faster than do mature apples. Apples low in calcium develop more scald than do apples with higher calcium levels (Ingle & D'Souza, 1989).

Some pathogens have been effectively controlled by exposing fruits to heat before storage (Lurie et al., 1991; Mitcham & Wu, 1993; Fallik et al., 1996), during storage (Bramlage & Watkins, 1993), or after storage (Shalom et al., 1993; Conway et al., 1994). *Botrytis cinerea* was essentially eliminated in stored fruits heated to 38°C (Klein et al., 1997). Apples held for 24 hours at 42°C or 12 hours at 46°C showed reduced decay over unheated apples after 14 hours of additional incubation. The effect of heating on decay of apples caused by *Penicillium expansum* resulted not only from direct inhibition of spore germination and growth but also from formation of an inhibitory substance in the peel (Fallik et al., 1996). Heat treatment at 38°C for 4 days, pressure infiltration with 2% or 4% $CaCl_2$ solutions, and a combination of both reduced decay of Golden Delicious apples during 6 months of storage at 0°C. The heat treatment reduced decay caused by *Botrytis cinerea* by approximately 30%, while heat in combination with 2% $CaCl_2$ treatment reduced decay by near 60% (Conway et al., 1994).

XVI. Conclusions

The available evidence indicates that exposure of plants to environmental stresses frequently alters subsequent responses to the same or other stresses. Many of these responses are direct (i.e., involve heightened tolerance to subsequent episodes of the same stress, as in osmotic adjustment in water-stressed plants and induction of cold hardiness by low temperatures); others are indirect or incidental (e.g., enhanced resistance to air pollutants in water-stressed plants by stomatal closure and consequent suppression of pollutant uptake; increases in dehydration tolerance capacity in cold-hardened plants). The data also indicate that plant responses can range from the molecular (e.g., dehydrin synthesis under water stress and induction of cold hardiness) to whole-plant levels (e.g., increased root:shoot ratios in water- and nutrient-stressed plants). In many cases these responses appear adaptive and likely are products of the process of evolution under natural selection. Additionally, exposure to extreme conditions that are uncommon in nature (e.g., liquid-nitrogen temperatures) have been useful in certain situations, as in pollen and seed storage. Exploitation of these responses by humans has been a useful tool in enhancing preservation, culture, and management of plant species.

XVII. Acknowledgment

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