

## **What Determines a Plant's Cold Hardiness?**

*John W. Einset*

**Cold-tolerance depends upon a plant's ability to keep water from leaving its cells and freezing, which severely dehydrates the cells**

Banana plantations along Cape Cod, orange groves in the Berkshire Mountains, tropical landscaping in New England! Unlikely as these images seem, they are not entirely out of the realm of possibility, especially if more can be learned about the basic mechanisms that govern the tolerance of plants to cold. In fact, goals less spectacular than these, yet still highly significant, are achievable in the near future because both our understanding of plant physiology and our ability to manipulate plant cold hardiness have improved.

Without question, resistance to low temperatures is a major factor determining the geographic distribution of plant species. So-called *chilling-sensitive* plants, such as the tropical banana and the semitropical avocado, can be severely injured or even killed by long-term exposure to temperatures (50 degrees Fahrenheit, for example) that are well above freezing. By contrast, *chilling-resistant* plants, such as garden peas and potatoes, survive brief periods of frost but are killed when freezing conditions continue for more than about four hours. *Cold-hardy* plants, on the other hand, tolerate extended periods of freezing, and laboratory tests indicate that cold hardiness in some of these plants per-

mits them to survive at temperatures as low as minus 75 degrees Fahrenheit.

What causes such wide variations in the sensitivity of plants to cold? As a consequence of natural selection, plants native to a particular hardiness zone are adapted to the temperature extremes that occur in their environment. Remove them from that environment, and they may or may not survive. For example, banana plants kept at low, but nonfreezing, temperatures suffer an imbalance in their metabolism that kills their cells and causes brown necrotic streaks to appear on fruits. Or, hardier plants might be killed by frost that occurs during their normal period of vegetative growth. Several cultivars of rhododendrons and azaleas that are grown successfully in Georgia and the Carolinas, for instance, are killed by late frosts when they are transplanted to New England only because their tender vegetative buds initiate growth too early in spring. Other plants fail to survive because late-summer frosts kill vegetative shoots before they become acclimated to cold temperatures.

During any given year, a species of tree or shrub adapted to the north-temperate environment alternates between periods of cold

hardiness and cold sensitivity. The term *acclimation* (hardening) refers to the transition from a sensitive to a hardy condition, while *deacclimation* (dehardening) designates the hardy-to-sensitive transition. Obviously, the seasonal timing of acclimation and deacclimation is of critical importance in determining a plant's cold hardiness. The magnitude and duration of the acclimated state are also crucial. In fact, the Arnold Arboretum's hardiness zones classify woody-plant species according to the magnitude of the cold tolerance they exhibit in their acclimated states. Zone 6 plants, for instance, can withstand minimum temperatures of plus 5 degrees Fahrenheit to minus 5 degrees Fahrenheit, while plants of zones 5, 4, 3, 2, and 1 exhibit progressively greater cold hardiness. Obviously, plants in all of these categories can tolerate some below-freezing weather; it is the magnitude of their tolerance that differentiates them.

When a plant, regardless of its hardiness classification, is injured by a killing frost, several harmful processes are involved. One of the earliest and most critical processes is the formation of ice crystals in the spaces between their cells. Freezing of the water in the intercellular spaces causes water in the adjacent living cells to move out of the cells into the intercellular spaces, where it, too, freezes. The amount of ice in the intercellular spaces increases rapidly as additional water moves out of the cells. Left unchecked, the loss of water from cells causes severe dehydration. In fact, the most widely held explanation of frost damage in plants is that death is caused directly by the advanced state of cellular dehydration that results when ice forms in tissues. According to this explanation when the concentration of water in cells falls below a critical "threshold" value, protein molecules in the cells' protoplasm begin to cross-link with each other, forming a stable but nonfunctional matrix. In this permanently altered state of protoplasm, metab-

olism slows to a standstill and, since the cells die, the entire plant dies.

Apparently, species of plants that survive temperatures lethal to other species do so by preventing the dehydration caused by ice formation. One way in which they accomplish this involves "supercooling"—the absence of ice formation even during periods of freezing temperatures. Another way is for ice to form in the intercellular spaces but for the loss of water from cells to be reduced. Often, this means of frost prevention involves osmotic alterations in the protoplasm of hardy plants. Halophytes (salt-tolerant plants), for example, usually are harder than their non-salt-tolerant relatives because the higher osmotic concentration of their protoplasm effectively prevents water from leaving cells and contributing to extracellular ice crystals. Some other hardy plants generate high internal contents of organic solutes (dissolved compounds) during acclimation. Finally, certain plants are cold tolerant simply because they can recover from even the extreme dehydration that accompanies ice formation. Examples of such species are paper birch (*Betula papyrifera*), trembling aspen (*Populus tremuloides*), and several willows.

In view of all these considerations, what practically can be done to prevent freezing injury in plants? An obvious strategy is to ensure that plants are well-watered before periods of potential frost. By keeping their tissues turgid, or swollen, one might be able to prevent the extreme cellular dehydration that usually kills frosted plants. A related treatment is to spray tender plants with water whenever temperatures are below freezing. The rationale of this procedure is twofold. First, it maximizes the water content of living tissues and, second, the heat (known to physicists as the heat of fusion) given off when water on the surface of a plant freezes, counteracts the effect of freezing temperatures on water within the plant. In Massachusetts, for example, cranberry grow-

ers routinely use water sprinklers in their bogs during late-spring frosts to take advantage of the heat of fusion released when water freezes on the surface of cranberry plants. The heat released by 100 gallons of water when it freezes is approximately equivalent to the amount of heat produced by burning one gallon of fuel oil. Obviously, the sprinkler technology is an important frost-protection measure. Breeding programs to introduce hardiness genes into less hardy plants may also become extremely important in the next few years.

Other ways of preventing frost injury in plants are still in the experimental stages and therefore are not yet of practical value. Some,

in fact, are quite controversial. Researchers at the University of California, for example, are attempting to utilize genetically engineered strains of bacteria as frost-protection agents. They reason that some bacterial species called "ice-nucleating bacteria," normally associated with plants, tend to sensitize plants to freezing injury, since individual bacteria act as "nucleation centers" for the formation of ice crystals. Other bacterial species, by contrast, are nonnucleating. Displace ice-nucleating bacteria on a plant with nonnucleating ones, it is argued, and the plant should be less prone to frost injury. Unfortunately, it is still too early to judge whether theory and practice are compatible



*The paper birch (Betula papyrifera), in the Arnold Arboretum (left), and the trembling aspen (Populus tremuloides), in the San Francisco Mountains, Arizona, are cold tolerant simply because they can recover from the extreme dehydration due to the formation of ice in their intercellular spaces. Many other species are cold tolerant because they prevent dehydration of their cells in the first place. Photograph of Populus tremuloides by Susan D. McKelvey. Both photographs from the Archives of the Arnold Arboretum.*

in this case. Not only that, but several experts question the wisdom of introducing potentially harmful bacteria into the environment. They identify several important questions. Will the engineered bacteria cause undesirable plants, such as weeds, to become frost tolerant, too? Or, since the ice-nucleating bacteria normally present on plants may have beneficial but unrecognized effects on their host plants, might not their beneficial effects be abolished? Lastly, is it possible that nonnucleating bacteria could affect the weather, a prospect that could have profound consequences?

As is the case whenever basic science is used to solve practical problems, resolution

of the public's concerns about nonnucleating bacteria as frost protectants will ultimately depend on the results of controlled experiments designed to identify possible adverse environmental effects of this practice. If none are found, then significant progress will have been made on one strategy for manipulating plant cold hardiness. As usual, improved scientific understanding of a phenomenon, such as cold hardiness, if it is properly applied, has the potential of improving horticultural technology.

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John W. Einset, a staff member of the Arnold Arboretum, is associate professor of biology in Harvard University.