Cold Hardiness of Woody Plants

Cold hardiness, or the capability to survive exposure to winter weather, is a major consideration in the introduction of woody plants by arboreta and botanical gardens. Hardiness is usually described in relative terms in reference to a location or a temperature. A plant is said to be hardy north to southern New Jersey, or hardy north to Boston; or hardy to 0°F or to -40°F.

How Plants Are Killed

Ice forms in almost all parts of a woody plant at temperatures more than a few degrees below the freezing point of pure water. Therefore, if a plant is to be hardy to temperatures such as -20°F, the tissues of the plant must be able to withstand the stresses caused by their freezing and thawing. A key difference between a hardy plant and a non-hardy plant is believed to be where the ice forms in freezing: inside the living cells or outside of them. If ice forms inside of cells, it is almost always fatal to them, and this is probably the principal cause of frost kill in non-hardy plants.

Normally hardy tissue may be killed by moderate temperatures that are reached by a rapid rate of freezing, e.g. 10°F per minute. These tissues would tolerate much lower temperatures under slower freezing. Here again, it is believed that ice formation inside of cells, triggered by the unusually rapid drop in temperature, is the cause of tissue death. Do such rapid temperature drops occur in nature? Under normal conditions, air temperatures usually do not drop faster than 5 to 10°F per hour. However, the rapid rate of freezing mentioned above has been measured in evergreen leaves during a sunny but very cold midwinter day when shade from a structure passes over the foliage. We believe, therefore, that damage from rapid freezing does occur in nature.

In cold hardy stems and leaves, the initial freezing of water in the tissues occurs outside rather than inside the cells, and thus the freezing is not fatal. We are not certain how cells of hardy tissue avoid internal freezing. Several factors probably are involved. Cells of hardy tissue usually have a high con-
centration of sugars and salts which lower the freezing point, and thus the relatively pure water outside of the cells is encouraged to freeze first. Once the outside freezing starts, water is withdrawn from the cells to feed the outside ice, and this withdrawal effectively concentrates the cell solution and lowers its freezing temperature even more.

Another protective characteristic of hardy cells is highly permeable cell membranes. Once the outside water freezes, the cell needs to lose water freely, and often rapidly, to the outside ice in order to maintain the cell’s freezing temperature below the temperature to which it is exposed. The highly permeable membranes allow this to happen.

As water moves out of the cell, the protoplasm collapses as it does during wilting, and as this collapse progresses with lower and lower temperature, great tensions are placed on membranes and protoplasmic proteins. Since we assume that protein structures vary in different plant genotypes, species variations in resistance to these stresses might be expected, and could explain differences in degrees of hardiness.

Dr. Weiser’s group at the University of Minnesota have observed an exotherm (release of heat) at the killing point of stems of fully hardened woody plants. They interpret this as being caused by the release of water which is intimately associated with protoplasmic constituents and necessary for life. The degree of hardiness of such a stem would therefore depend on the temperature at which this “vital water” is finally released.

We have indicated that stems and leaves of hardy plants can withstand freezing of water in their tissues, provided that the ice forms outside of the cells. On the other hand, hardy flower buds apparently escape injury by avoidance of freezing; once they freeze, they are killed. Apparently, buds of certain plants are able to avoid freezing down to temperatures of −30 to −40°F. How they do this remains unknown.

**How Plants Develop Hardiness**

Many attempts have been made to explain the development of hardiness (or acclimation) by analysis of cell constituents before, during and after acclimation. It is well known that during acclimation cells commonly lose starch and accumulate simple sugars. This was originally interpreted as a major protection mechanism. It is possible that sugars in the cell protoplasm act to reduce freezing damage to vital constituents. Sugars in the cell vacuole, where most sugars accumulate, effectively lower the freezing point of cells, but only to a limited
degree — not nearly enough to account fully for the hardiness changes that occur. Other chemical changes are known to occur in the cells associated with cold acclimation, such as changes in quantity and kinds of proteins, but these changes are difficult to translate into specific benefits to the tissues.

Cell membranes are known to become increasingly permeable to water during acclimation, thus allowing water to leave the cells more readily to feed ice crystals outside of the cells. Furthermore, reduced viscosity of cell protoplasm also occurs, probably having value in providing flexibility for surviving the stresses produced by freezing. Unfortunately, we do not know the mechanisms of these changes or how to induce them.

Investigations in recent years have revealed that plant hardiness progresses in distinct stages in response to environmental changes in the fall of the year. Hardiness does not develop until growth ceases.

The first stage of cold acclimation results from short days — a photoperiod effect. The amount or degree of hardening from short days without frost is not great compared to the ultimate hardening of stems of plants such as apple, dogwood and maple. For example, stems with an ultimate hardiness of $-50^\circ F$ acclimate to about $0^\circ F$ from exposure to short days. It has also been shown that this first stage takes place most efficiently when days are relatively warm, at least at the beginning, and when leaves are present. An especially interesting finding is that the short day effect is translocated within the plant, as if it were a naturally produced hormone.

The second stage of cold acclimation, which induces further hardiness, is caused by below-freezing temperatures. Leaves play no part in this induction, and the stimulus is not translocated in the plant.

Judging from the outward appearance of the plant, we might assume that the plant's preparation for winter is a change from an active to an inactive state. There is ample evidence, however, that many chemical and physical changes take place as dormancy and cold acclimation develop. These changes result from active metabolic adjustments, rather than the mere cessation of activity.

*Root Hardiness*

Two recent trends, nursery production in containers and the use of above-ground planters in landscaping, have added a new dimension to hardiness problems of woody ornamentals. Investigations into the causes of frequent winter kill of plants
in above-ground containers revealed that roots do not develop the same degree of cold hardiness as tops. Furthermore, root hardiness does not develop at the same time as top hardiness, and apparently the degree of hardiness or lack thereof can not be predicted from the characteristics of the tops.

One of the complications is that roots of woody plants do not seem to have the same type of winter dormancy as their tops. Roots continue to grow in the fall as long as the soil is above about 40°F, and apparently they will grow throughout the winter if the soil is kept warm. Since the short-day induced first stage of acclimation is translocated in the plant, one might expect that the roots would receive and respond to this hardiness induction. We do not know if this occurs, but if it does the roots must, of course, first stop growing. Exposure to freezing induces hardiness in tops (second stage of acclimation), and a similar response might be expected in roots. Our studies suggest that this does in fact occur in roots of some plants, but unfortunately not in all species. A practical method of inducing significant hardiness in roots would be a great boon to nurseries and landscaping in northern climates.

**Hardiness to Winter Desiccation**

For purposes of plant adaptation, we may speak of cold hardiness, when we really mean winter hardiness. An evergreen that is truly winter hardy must be both cold hardy and desiccation hardy. Winter desiccation is a major cause of leaf browning, sometimes called winter "burn", of cold hardy evergreens, especially *Ilex*, *Leucothoe* and *Rhododendron* in the climatic zones represented in Massachusetts. No matter how much water is in the soil, when the water freezes it cannot be taken up by the plant. In addition, even when water is available to the roots, if the water in the stem is frozen, no water can move through the stem to supply the leaves. At the same time, leaves exposed to winter sun and wind lose water. The combination of water loss and interruption in supply results in dehydration. Differences in the amount of injury from year to year and in different locations are due to variations in time or degree of exposure to conditions of dehydration.

*Rhododendron carolinianum* 'P.J.M.' is a truly winter hardy evergreen, combining remarkable desiccation hardiness with cold hardiness. We found that 'P.J.M.' could lose up to 70% of its leaf moisture and recover without injury. In comparison, *R. 'Boule de Niege' was injured by losing about 60% , and *R. catawbiense 'Grandiflorum' was injured by losing 50% of leaf water.
Summary

The development of cold hardiness in stems and leaves of woody plants is initiated after the cessation of growth, first by a translocatable stimulus from short days. Further cold hardiness is induced by freezing. Many of the changes that take place are probably active metabolic processes, and the changes are numerous, no one of which can adequately account for freeze-tolerance. Cold acclimation does not occur equally throughout the plant, the roots being remarkably independent from the tops in this respect. Winter hardiness, especially in evergreens, involves desiccation hardiness as well as cold hardiness.

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Selected References


