Exploring the Complexities of Plant Hardiness

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We often use cold-hardiness ratings as the sole indicator of plant suitability for a given region. But in actuality, a much broader range of factors determines plant performance in the landscape.

In the United States plant hardiness has usually been interpreted as cold hardiness—the ability of a given plant to survive the winter of a given region. However, even in our most northerly regions, plant survival depends on a far broader set of environmental conditions than just those found in winter. In addition to extremes of cold temperature, survival is linked to the amount and seasonal timing of precipitation, the intensity of light, the annual cycle of daylength, the texture and fertility of soil, the consistency of temperatures, and the duration and degree of high temperatures. Cold, heat, sun, clouds, drought, flood, early frosts, late ice storms, compacted soils, chainsaw-bearing contractors—all can influence a plant's hardiness.

While in any region, a plant's viability depends on its fit with this entire range of local conditions, the relative importance of each environmental factor varies geographically. In the North, tolerance to cold usually assumes the greatest importance, whereas in the South, heat hardiness is more often the limiting factor, and in most of the West, drought tolerance is the predominant influence on survival. All the same, we most often focus on cold hardiness, even in Florida and California, perhaps because at least superficially, winter damage is dramatically visible and easily understood: a cold front comes through tonight and tomorrow the plants are brown. This may explain why cold hardiness has been the focus of much horticultural research and evaluation effort, with far less attention paid to the other factors. Nonetheless, no prediction of a plant's viability can be accurate without considering the diverse combination of landscape conditions.

Dealing With Frost: Tolerance vs Avoidance

Like all forms of life, plants consist largely of water, and when temperatures drop low enough, that internal water, like all water, can freeze. Perennial plants fall into two categories based on the way they deal with frost and freezing temperatures: they can either tolerate freezing by employing a variety of physiological mechanisms; or they can avoid freezing by shedding or insulating vulnerable plant parts. Most temperate perennial plants use a combination of tolerance and avoidance to survive winter's freezing temperatures, but rely primarily on the tolerance mechanisms (which are generally more effective for surviving long periods of freezing temperatures) to protect aboveground, persistent tissues. For example, evergreen woody plants tolerate freezing in both stems and leaves while deciduous trees avoid freezing in their leaves by dropping them and tolerate freezing only in their persistent branches and trunks.

The Importance of Acclimation

A frost-hardy plant's ability to get through the winter depends on the seasonal change in its metabolism to a quiescent or dormant state

Buxus sempervirens *(boxwood) all dressed up for winter These extreme, albeit artistic, measures protect the plants against damage from snow and ice (Peter Del Tredici).*

known as *acclimation,* which is influenced by a variety of environmental factors. Acclimation is the process whereby the plant "hardens off" for winter. In order for a normally cold-hardy plant to survive the most severely cold temperatures it is genetically capable of surviving, it must complete the acclimation process before experiencing severe cold; otherwise it will be damaged. Similarly in the spring, as temperatures warm and days lengthen, plants need to deacclimate in order to resume active growth.

There are four cases in which a plant can be damaged by freezing temperatures:

1. When temperatures fall below the plant's maximum cold-hardiness limit, even after normal acclimation has occurred;
2. When premature freezing occurs before the plant has acclimated in the fall, even if the plant is potentially able to survive those temperatures in midwinter;
3. When unusually late freezes occur in the spring after the plant has deacclimated, even if it can survive those temperatures while it is hardened off in midwinter; and
4. When there are prolonged swings in temperature during the winter that cause the plant to deacclimate before the threat of severe freezing is over.

Only the first case relates to the traditional definition of cold hardiness—the definition expressed in hardiness zone maps. In the other three cases, freezing damage occurs not because the plant is located where temperatures fall below its potential maximum cold tolerance, but because its stage of acclimation is out of step with the weather. If a woody plant that is normally winter hardy to -20 degrees Fahrenheit experienced such temperatures in July, it would suffer severe damage and is likely to die. However, this same plant could experience decades with those minimum winter temperatures and thrive.

Mapping Cold Hardiness

Hardiness zone maps generally identify areas with similar average minimum temperature ranges in which, theoretically, the same groups of plants should be viable.[1] But these systems have a serious limitation. They do not take into account all of the different environmental conditions that vary from region to region, from soils to rainfall patterns, and this limitation causes problems. Consider just one example, zone 8, which encompasses Raleigh, North Carolina; Dallas, Texas; Phoenix, Arizona; and Seattle, Washington. Then compare the plants that are grown in those areas. At least twenty-five species of palm grow in Phoenix that won't grow in Raleigh. The extremes of temperature are very different even though the averages lump Raleigh and Phoenix into the same zone.

The same problem turns up in the hardiness zone maps for Europe and China that were published in Germany in the 1970s.[2] There we find Raleigh in the same zone as London. However, Raleigh has more extreme temperatures (especially during the summer), more variable precipitation, more frequent ice storms, less cloud cover and fog, and much higher light intensity year-round. These differences influence cold hardiness, and a given plant grown in England may be less cold hardy there than the same plant grown in Raleigh. Over an entire year, variables like availability of photosynthate for growth, accumulation of storage carbohydrates, timing of flowering and fruiting, and amount of root development as influenced by moisture availability, can influence a plant's ability to survive the winter. Clearly hardiness zones based on temperature alone cannot predict a plant's ability to survive.

A better system for mapping plant adaptability is the one developed by Sunset Books, called the "Sunset Zones." This system, which includes Colorado and points west, presents twenty-four zones that are defined by many variables, including high and low temperatures, dry desert winds, rainfall, and other moisture (for instance, fog cover). This system is widely used in the West and has proven very helpful there. It's especially effective at pinpointing microclimates, a critical tool on the West Coast, where great differences occur over short distances. Los Angeles alone has nine different zones.

Another excellent system is the Walter System, developed in Germany. It is based on a graphic presentation of average monthly temperatures combined with average monthly amounts and kinds of precipitation over a full year, using data collected from Walter Stations in cities all over the world. By looking, for example, at the graph for Seattle we can see not only the amount of rainfall but also the temperatures during the months of high and low rainfall. Each station graph also shows the extremes of temperature recorded for the station and altitude of the station. In just one visual image the Walter System gives a much more complete picture of what the growing conditions are for that area than the temperature-based USDA zone map can give.

[1] See Peter Del Tredici, *Arnoldia* (Fall 1990) 50 (3):16–20.

[2] Gerd Krussman, *Manual of Cultivated Broad-Leaved Trees and Shrubs*, Vol. 1. Timber Press: 1976.

Why Plants Die of Cold

To understand the importance of acclimation, we need to look at the process whereby plants die from the cold. There are several kinds of cold injury, but a primary cause of frost- or freeze-related death in woody plants is water freezing within the plant's cells. When water crystallizes and freezes within a cell, it ruptures and kills the cell. If enough cells are killed, the plant will suffer significant stress and the entire organism may die. On the other hand, if freezing is restricted to water in the intercellular spaces of the plant's tissue—that is, in the spaces between the cells, outside the boundary membranes of the cells themselves—then usually the cells are not damaged and the plant does not suffer.

The cells' contents change during acclimation such that the concentration of solutes increases. We know that adding certain solutes to water can retard its freezing, and that the higher the concentration of these solutes, the lower the temperature required to freeze the solution—this is how antifreeze works in a car radiator. In general, the intercellular solution in a woody plant—the liquid between the cells—has a lower concentration of solutes than the solution inside the cells. This difference is accentuated after acclimation, leading to more solutes in the cells. Therefore, the solution outside the cell walls freezes at a higher temperature—and earlier—than the solution inside the cell walls.

Because of this differential solute concentration, ice formation is restricted to the intercellular spaces during normal winters. If the temperature goes significantly below the plant's tolerance, however, the osmotically driven maintenance of the concentration differential between the inter- and intracellular solutions cannot be maintained; in that case, ice finally forms inside the cells, causing them to rupture and die.

The lesson here is that for plants to acclimate themselves to winter, temperatures must drop during the appropriate season and at the appropriate rate. A plant of ivy *(Hedera helix)* that has had a chance to acclimate can survive –30 degrees Fahrenheit, but it will freeze at 25 degrees Fahrenheit if that temperature occurs in the summer during active growth.

In any discussion of hardiness, it is important to remember that plants are made up of many different organs. The specific mechanisms of acclimation that result in freezing tolerance or avoidance vary among organs, and therefore hardiness does as well, which makes sense considering the different environments in which various plant organs occur. Roots, for example, are much less hardy than the shoots of woody temperate plants. Because of the insulating properties of soil, roots experience much less variation in temperature throughout the year than occurs in the air above it. This becomes an especially important consideration when dealing with container plants. The temperatures that containerized plant roots are exposed to are potentially much more extreme than those experienced by roots insulated in the soil—lower in winter and higher in summer.

There can also be significant differences in hardiness even among the aboveground parts of the plant. For example, flower buds are usually much less cold hardy than vegetative buds. Here in Massachusetts you are likely to see effects of the snowline in the spring where parts of the plant below the snowline have survived, be they floral or vegetative. But above the snowline, the flower buds may be killed while the vegetative buds will break and develop healthy foliage in the spring.

Environmental Cues for Seasonal Acclimation

The mechanisms described above—collectively referred to as *acclimation*—are triggered within the plant by environmental cues, of which the most important are seasonal changes in daylength and temperature. Differences among plant species range from the purely photoperiodic in which temperature plays almost no role to those that are purely temperature-controlled with no response to photoperiod (*i.e.*, daylength). Most plants fall somewhere between these two extremes. In

The flowering pattern of this azalea clearly demonstrates that winter's kill line coincided with its snow line (J. C. Raulston).

spring, once daylength extends beyond a certain point—known as *critical daylength*—deacclimation is initiated in photoperiodically sensitive species, active growth is triggered, and the plant will not become quiescent again until the shortened daylengths again trigger acclimation the following fall. Because the daylengths differ throughout the year at different distances from the equator, the cues that trigger spring growth (and winter acclimation as well) in a plant of Floridian provenance will be slightly different than those for a plant of Canadian provenance. In Canada, critical daylength will be much longer than in Florida. Not only is winter longer in Canada, but also the days become much longer earlier in the spring the farther north you go. So if you moved a Florida red maple north to Canada, it might begin active growth too early in the spring and thus be subject to freezing damage. On the other hand, if you moved a Canadian red maple south to Florida, the days may never get long enough to trigger active growth in the northern plant, and the plant would never break dormancy and grow.

Photoperiod responses can be influenced by artificial lights as well as by the sun. There are documented instances of delayed leaf fall in autumn on trees adjacent to streetlights, as well as premature initiation of growth on conifers decorated with large, nonflashing Christmas lights in midwinter. This is usually not a significant problem because cold temperatures generally override the influence of artificial lights.

In nonphotoperiodically triggered species, temperature is the most important cue for winter acclimation. Not only absolute tem-

Rhododendrons on Boston's Copley Plaza show dessication caused by sun and wind on parts of the plant not protected by snow (J. C. Raulston).

peratures, but also cumulative temperatures throughout the growing season play an important role, especially when we start moving plants around the globe. Many woody plants that are native to climates with long, hot summers can withstand very cold winter temperatures when grown in similar climates, yet if grown in climates with cooler summers and mild winters they are less cold hardy. In other words, the conditions for the previous season's growth can effect a plant's ability to withstand cold. This makes sense when we consider that growing conditions can affect processes like photosynthesis and carbohydrate metabolism. If a plant grows in a high light environment—for example, in the American Southwest—it may be able to store much greater quantities of carbohydrate, which may improve its ability to acclimate to severe cold. If you take the same plant, however, and grow it in a lower light climate, even one with a milder winter—Britain, for example—this same plant may not be able to survive that milder winter because the conditions of the previous growing season have prevented the plant from satisfying its physiological requirements for optimal winter acclimation.

As a specific example, crape myrtles *(Lagerstroemia indica)* are perfectly winter hardy in North Carolina where sunlight is intense, the summers are long and hot, night temperatures are high, and winter temperatures routinely drop to zero degrees Fahrenheit. But try to grow crape myrtles in England, where light is low and summers are cooler, and the plants will not survive winter, even though the temperature rarely falls below 10 degrees Fahrenheit. This is an example of the cumulative effect of annual conditions on winter hardiness.

The Significance of Provenance

We tend to characterize an entire species as being of a certain degree of hardiness. Even within a species, however, individual plants adapt to the cues that are present in their specific region at the critical transitional times of the year—for example, daylength, light intensity, cumulative temperature, or moisture conditions. When we move a plant to another region, we may interfere with those cues and prevent the plant from exhibiting its "normal" hardiness.

Reproduction from seed is a sexual process that results in genetically variable offspring. Any population of seedlings will demonstrate an amazing array of variability. For example, a row of seedling "blue" spruces will include green, blue, and gray *Picea pungens.* Part of what genetic variation is about is survival. The populations of a species now found in a given region are therefore those that adapted over many thousands of years to the specific climate of that region. If over a few hundred years the weather gets colder in part of a species' territory, seedlings that are more cold hardy will survive and those that aren't will be frozen out. The result, then, is a population that varies widely in cold hardiness from one end of its range to the other. Red maples *(Acer rubrum),* for example, occur in wild populations from Florida through Canada, but red maples of Floridian provenance are likely to be far less cold hardy than red maples of Canadian provenance. (It is important to note that the hardiness of a given seedling depends not on the location of the *nursery* where it was grown, but rather on the ancestral location of the *parent trees* from which the seed was collected.)

But the combination of evolutionary genetics and long-term climate changes can play tricks on us. For example, there are several species of plants now found growing only in Florida that are completely cold hardy at far more northerly latitudes. During the most recent glacial era, these plants germinated successfully south of the glacial front but did not survive in glaciated areas. As a result, these species retreated southward in front of the slowly advancing glaciers. This long-term process did not cause a loss of cold hardiness in the plant's genome, which had evolved preglacially in much colder environments than those in which the surviving plants were later found. As a result, one can grow *Magnolia ashei,* which is now native only to the panhandle of Florida, as far north as Chicago and Toronto. Red maples in Florida, however, are the product of continuous evolution in that region, rather than of migration from the north ahead of the glacier. Unlike *M. ashei,* therefore, a Floridian red maple seedling is not likely to perform well in Chicago or Toronto. Nonetheless, conventional thinking holds that *Acer rubrum* is significantly more cold hardy than *M. ashei.*

The Effects of Human Intervention on Cold Hardiness

Whether a plant can thrive in a specific environment depends on the interaction of the plant with its environment. In other words, we must consider not only what the environment is doing, but also what the plant is doing. Humans often influence both elements and thereby significantly affect the cold hardiness of a given plant.

It's easy to imagine how we can change the environment to influence a plant's cold hardiness—an extreme example would be to put it in a greenhouse—but it's harder to imagine how we can influence the plant itself to affect its hardiness. However, horticulturists can influence a plant's hardiness both intentionally and unintentionally. For example, watering and fertilizing late in the season, to keep plants looking attractive or to push a second flush of growth, can lead to disaster. Comparison at North Carolina State University of azaleas fertilized throughout the growing season with plants fertilized only in spring demonstrated that the heavily fertilized plants looked more attractive in the fall but suffered much greater winter damage and were less attractive the following spring. In another experiment, we promoted and distributed plants of a Japanese species of crape myrtle, *Lagerstroemia fauriei*, after finding it hardy to −10 degrees Fahrenheit. However, growers complained that their plants died after experiencing minimum winter temperatures of +10 Fahrenheit. The growers had prevented the plants from hardening off for winter by prolonging irrigation and fertilization into late fall in order to increase annual growth and, thereby, profitability. The result was that the plants went into winter with soft, nonacclimated growth that was very vulnerable to freezing damage. In effect, the plant's metabolism was affected by growing practices that created an artificial

Hardiness Evaluation for the Southeastern United States

Gardeners in the Northeast enjoy the benefits of a long tradition of plant importation and hardiness evaluation, but in the Southeast there has been very little institutional evaluation of plant adaptability and performance—until recently, that is. Just seventeen years ago, the North Carolina State University Arboretum was founded with a dual mission: determining the adaptability of new and uncommon landscape plants for use in the southeastern United States, and promoting the production and utilization of superior, adapted plants. Since 1977, the Arboretum has collected and evaluated over 9,000 plants from forty-five countries—this on only eight hard-working acres. Those eight acres currently contain over 5,000 different species and cultivars in over 450 genera.

Experience has led us to believe that the only way to test a plant's adaptability is to try growing it. This method results in large numbers of killed plants, but it has also uncovered exceptional plants that perform beautifully despite very different provenances. We've learned as much from the deaths as from the successes. It's by studying what happened that we find indications of how the plant or the environment can be modified for future success. We retain for selection and promotion those plants of significant ornamental value that have survived the various environmental stresses—and they have been many. In the years since the Arboretum was established we have experienced almost every extreme of weather including the coldest temperature ever recorded, the hottest summer, both the wettest and the driest years, and the earliest and latest frosts.

We've found wonderful surprises among both exotics and North American natives. Certainly natives have been underused and deserve greater attention and selection, but the key to the suitability of a plant lies in its adaptability, not its nativity. Many natives of the southeastern United States evolved in very specialized environments. Those from the cool, moist southern mountains often don't survive in the hot, wet summer of the Piedmont while exotics from analogous climates—for instance, humid areas of Japan and Korea—have proved very useful.

Since the Arboretum's mission is to encourage the production and use of the widest possible array of plants, our distribution and advocacy program is just as important as our evaluations. We make material available to the public, to other botanical gardens, and to the nursery trade—so far over 60,000 plants of 1,000 taxa have been distributed to nurseries and other growers around the world, and in order to move these plants to the public quickly, growers themselves have collected over 2,000,000 cuttings from the plantings.

microclimate to which the plant was not adapted.

It is especially easy to create microclimate effects in order to influence plant/environment interactions in an urban environment. The magnolias on east-west streets in Boston's Back Bay are a case in point. Magnolias on the south-facing side of the streets reach full bloom when those on the shady north-facing side are just budding up. A late freeze would kill the blooms on the south-facing side, while the blooms on the north-facing side may be only minimally damaged. By planting early blooming plants in northern exposures or under higher canopies, we can minimize this kind of damage. Likewise, since a body of water can moderate local climate considerably, planting near small water features can extend your season, just as planting near south-facing brick or stone walls can, and it shares the same potential problem—spring growth may be induced so early that the microclimate is unable to protect the new growth from severe late freezes.

The winter injury to this south-facing side of a tree trunk might have been avoided by siting it in the shade or wrapping it during the winter (J. C. Raulston)

Just as north-facing or south-facing orientation can have a major impact on plant performance, whether a plant is primarily in sun or shade can make a dramatic difference in winter survival and performance. This can be a particularly important consideration in preventing winter damage on broad-leaved evergreens, especially the damage we call winter scorch. Plants lose water through their leaves constantly in the process of transpiration. Deciduous plants drop their leaves in the winter, avoiding this problem, but evergreens must contend with it year-round. Transpiration is increased by sunlight and wind. One of the ways this happens is that sunlight on the leaf increases the difference in temperature between the leaf surface and the air, thereby increasing water loss from the leaf. In winter, when water in the soil is frozen, it is impossible for the plant replace the water that is lost from the leaves, and the leaf dessicates and may die. But if it is sited in shade the plant will be more protected from the possibility of winter scorch.

Sun scorch in winter can also occur on the south-facing side of trunks of trees. This is caused by the rapid expansion and contraction of the trunk in response to rapidly changing temperatures. Wrapping the trunk so that it is effectively shaded all winter (being sure to remove the wrap during the growing season) can help to ameliorate this problem. (Make sure to wrap from the bottom up if using a wrap of narrow width so it doesn't collect water that freezes and thaws against the trunk, damaging bark and promoting disease.)

In the final analysis, the complexities of plant hardiness lie in the maze of environmental conditions that both plant and gardener must negotiate each year. Because these conditions vary so greatly, even from one neighboring landscape to the next, and because humans can drastically alter the immediate growing environment of a plant, there is only one sure way to determine if an individual plant will thrive for you: you must try it in your own garden. To paraphrase the great English plantsman Sir Peter Smithers, I consider every plant hardy until I have killed it myself.

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