PHYSIOLOGY OF PLANT TOPS DURING WINTER

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The survival of plants during the winter, or their resistance to low temperatures, is not controlled by any one environmental or physiological factor. Rather it is the combination of a number of environmental factors, both past and present, as they each, or in combination, affect the many physiological processes that interact to produce a plant response. This paper will attempt to cover some of the physiological phenomena which operate in a plant as it acclimates to freezing temperature and resists injury during winter.

Acclimation of plants. Cold acclimation of overwintering plants generally follows a two stage pattern (21). The first stage of plant acclimation to freezing temperatures appears to be induced by short days in late summer and fall (18,19). The first stage of acclimation appears to involve two distinct events; growth cessation and the initiation of the metabolic changes which facilitate the plant's response to low temperatures during the second stage of acclimation. The increase in hardiness during the first stage of acclimation is relatively small, although it may be very significant since just a few degrees of resistance in the fall may make the difference between life and death. The second stage of acclimation is apparently induced by low temperatures. Frost appears to be the triggering stimulus (19), but concurrent metabolic or physiological changes probably are more important in producing a plant which is considerably more resistant to freeze injury than during the first stage of acclimation. Metabolic changes that occur during acclimation affect the level of total protein (2,3,11); the amounts of specific enzymes (6,7,8); the degree of tissue hydration (12); the content of polysaccharides (15,16), sugars (11,13,17), and nucleic acids (2); and the nature of the membranes (15,19).

Studies of the metabolic and physiological changes accompanying hardening have led to several hypotheses on the mechanism of acclimation. Some of the mechanisms proposed are the following: inhibition of the formation of intermolecular disulfide bonds between protein sulfhydryl groups as the cells become dehydrated during freezing (10); sugars replace water in forming protective shells around sensitive proteins (6,7,17); temperature-sensitive cellular components assume more stable configuration (1); specific proteins are synthesized which interact directly with other cell components to protect them from freezing stress (7); reduced hydration of the protoplasm in the autumn increases resistance by reducing the amount of free water available for destructive ice-crystal formation (12); and increased water permeability of membranes in the autumn which permits cellular water to escape to extracellular space (9,14). There are studies of metabolic changes in plants during acclimation which can be interpreted to support most any or all hypotheses which have been proposed. Regardless of the specific mechanism, it is obvious that many physiological changes are associated with acclimation and take place in overwintering plants at a time of the year when we would expect the metabolic machinery to be operating at substantially reduced levels.

Freezing mechanisms in plant tissue. The fact that most plants freeze when their tissue temperatures drop below 0°C is important. When this occurs in tender or herbaceous plants, death usually results; however, after acclimation, hardy plants are able to tolerate extracellular ice formation in their tissues. This ice formation creates a vapor pressure deficit outside the cell and causes water to be slowly withdrawn from the cell into extracellular spaces where it freezes. The more hardy the plant is, the better it is able to tolerate the dehydration or loss of water from the cell. Plants with this type of freezing pattern, such as paper birch, red-osier dogwood, willow, and trembling aspen, can survive experimental freezing temperatures of −196°C when fully acclimated (5). In the temperate climate in which we live, we find plants which can tolerate freezing without injury from the above extreme to only a few degrees below 0°C.

Another means by which plants or plant parts survive freezing temperatures is by avoiding freezing by a process called supercooling. In general, supercooling simply refers to a liquid system which is below its normal freezing point and thus in a metastable state. For example, pure water will supercool without freezing to −38°C in the absence of a heterogeneous nucleating substance on which ice crystals can begin to form. The xylem tissue water of many fully hardy deciduous species has been shown to supercool to −40°C before freezing, even with ice in adjacent bark tissue (4). Floral primordia in *Prunus*, *Rhododendron* and *Vaccinium* flower buds also survive freezing temperatures in this manner and may not freeze when fully hardened until temperatures reach −20 to −30°C (4). In contrast to tissues which survive freezing temperatures by tolerating ice formation in their tissues, ice formation is rapid, intracellular, and causes immediate death to supercooled tissues. Supercooling probably occurs in nature because of a lack of nucleating substances necessary for ice formation within plant cells and because of ice growth barriers of some unknown form between adjacent tissues containing ice crystals and the supercooled tissues.

Mechanisms of cellular injury to plants. *Extracellular ice formation* — Hardiness of most nursery plants is related to tolerance of extracellular ice formation and to the dehydration of particular tissues during this ice formation. In hardy plants the cellular water that is removed during freezing will be absorbed during thawing without loss of metabolic activity or injury. In sensitive tissues, injury is presumed to occur when irreversible changes occur at the cellular level when excessive amounts of water have been removed during extracellular freezing. A number of hypotheses on the exact cause of injury from extracellular ice formation have been proposed but to date no single one has been fully accepted. It must also be pointed out that damage caused by freezing cannot be attributed solely to desiccation. In part, it may result from the mechanical stresses induced by the presence of ice in the tissue or by other direct effects of low temperature such as protein denaturation.

Intracellular ice formation — Injury from intracellular freezing normally occurs as a result of rapid freezing and formation of ice crystals within the cell. This occurs in non-hardy plants and in plant parts that supercool. Mechanical destruction of cell membranes and organelles is probably the most likely result of intracellular ice formation. In any case, once ice has formed within a cell, it is normally killed.

Dessication injury — Probably more nursery plants are winter-killed each year from dehydration of the tops when the root ball is frozen than from either of the mechanisms previously mentioned. This is especially true for container-grown plants whose root ball may freeze readily when subfreezing temperatures are experienced for any length of time. Following this period of freezing temperature the air and leaf temperature may rise above freezing, creating a situation in which water will move from the interior of the leaf to the surrounding air. The movement of water from the leaf to the surrounding air occurs because of a difference in the humidity in intercellular spaces of the leaf (usually 100%) and the humidity of the air. The term ascribed to this difference is vapor pressure deficit (VPD). The greater the VPD the quicker the plant will dehydrate to the point of injury. Air temperature has a marked effect on the VPD since a temperature rise will be accompanied by a decrease in the relative humidity and therefore a greater VPD. Solar radiation will also affect the loss of water from the leaf since absorbed radiation can increase the leaf temperature and thus the immediate temperature surrounding the leaf. Humidity of the air will, of course, directly affect the VPD, but the magnitude of its effect will depend on the air and leaf temperature.

Wind can have a significant effect on the loss of water from the plant since it increases the evaporation from the leaf surface. Of the environmental factors present, wind probably has the greatest effect on water loss from plants. It should be noted that injury to plants due to dessication when the root ball is frozen is similar to injury to plants when extracellular ice formation causes dehydration of plant cells.

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FACTORS AFFECTING PHYSIOLOGY OF ROOTS IN WINTER

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Roots respond to their environment. The greatest response is to temperature with rapid expansion and translocation from 25 to 35°C. As the normal temperature decreases in fall and winter, root activity slows down. Water content of root cells decreases. Sugar and mineral content increases. Roots are easily damaged by freezing, but in November normal roots become more freeze resistant due to normal hormone changes and decreased root activity.

In the container nursery, roots are not in a normal environment — they are hotter in the winter day and colder at night. Most roots are against the side of the container where the temperature changes are most severe. Without examining roots in pots by upending them, you do not realize that two plants with the same size top may be supported in one case by half a root system and in the other by a quarter root system. In the field, roots are spread over a wide shallow area with a moderated air temperature. Freezing is delayed by earth heat. A long fall season aids in the change of root function. Less water and less nitrogen also aid in making roots more freezeproof (depress injury point temperature).

In some plants cool nights and normal short days have been shown to increase hardiness of roots and stems, but each genetic strain has a different response to temperature.

Before winter, other factors affect how many roots there are and how active they are. *Drainage* of field soil or landscape site or container mix is a major factor of root vigor. Adequate soil air and water holding capacity are vital. Slope and soil amendments change drainage and thus affect root physiology. With high organic soils, wettability is a problem if they ever get dry. Capillary flow is slower than in mineral soils from wet to dry soil. This can lead to winter dessication.