Note No. 30

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FROST, ICE-NUCLEATING AGENTS, AND FROST DAMAGE

Frost occurs in different forms whenever the temperature drops to 0 °C or lower and freezes cellular water and moisture in the air and on surfaces of vegetation. Freezing occurs during convective and radiative cooling. Convective cooling is linked with horizontal movement of northern cold air masses affecting the continental air mass. Temperatures of the horizontally moving air mass decrease with increases in altitude. Radiative cooling occurs when the temperature of the earth and calm air up to several meters above it cools to the freezing point on clear nights. Moisture in the air is then deposited on vegetation or other surfaces as crystals of ice (Court 1974). Frost occurs most often in the open countryside, especially on hilltops and valley bottoms in hilly terrain and in higher latitudes.

Ice crytals are seen as hoar frost, a deposit formed directly from water vapor during the night. Aggregates of ice crystals are known to form giant hailstones and sheets of ice during destructive ice storms (Lemon 1961). Glaze frost is the coating of ice formed when drizzle, fog, or raindrops fall on surfaces that have been cooled below the freezing point (Court 1974). Sometimes the weight of the ice breaks mature trees and brings down trees of up to pole size. All forms of frost are a hazard to crops, farmers, fruit growers, Christmas tree growers, amenity and forest nursery tree growers, and foresters. It kills buds, fruit spurs, shoots, and leaves, freezing the moisture inside them and weakening the tree growth potential.

For nearly 100 years, little progress was made in understanding frost damage in agricultural and forest crops. The unanswered question was why some plant tissues freeze at several degrees warmer while water does not freeze at -8°C. The answer to this problem would help to improve protective measures against frost. In the past 25 years some of the answers and documented contributions have come

from atmospheric, biological, laboratory, and medical centers that have developed various freezing techniques.

The susceptibility to and severity of frost damage are influenced by the water content of air and tissues and the number and properties of particles (ice-nucleating agents or INA) on plant surfaces acting as centers of condensation and freezing (Schnell 1976; Lindow et al. 1982). Biologists have discovered that certain bacteria may act as INA and mediate in frost damage at -5°C and warmer temperatures. Bacteria and yeast INA resident on plant surfaces are known to be slime formers and to live on soluble amino acids and sugars leached from healthy and damaged parts of plants as a result of nectar production and exudates from roots, pruning wounds, cankers, and dieback (Tukey and Morgan 1963; Morgan and Tukey 1964; Tukey 1970). The slime formers release their own active INA substances such as amino acids, peptides, proteins, nucleotides, and steroids, many of which have been tested in the laboratory (Power 1962). The INA organic substances protect the bacteria from temperatures colder than $-5^{\circ}C$ by freezing the externally condensed moisture and the plant tissue at a higher threshold temperature. Bacterial cells remain viable after the ice thaws.

The effectiveness of external and internal INA organic substances of plants depends on several factors: the precise number of available hydrogen bond groups, insolubility in water, and ability to break the surface tension of water. Larger molecules of organic substances are more efficient than smaller ones (Power 1962), although both appear to interplay in the physical process of ice propagation in tissues. Each organic substance has a specific threshold temperature for mediation of freezing, e.g., steroids mediate at $-1\,^{\circ}$ C and are most efficient nucleators. Some strains of bacteria and yeasts may produce and release several organic INA substances, each capable in mediating at specific threshold

temperatures. Mature plant tissues may escape frost damage by raising the proportion of non-INA organic substances in their cells to counterbalance the total external and internal INA organic substances. New growths of seedlings and shoots have little tolerance to frost, however, because their juvenile tissues produce a predominance of nonsoluble or INA organic substances that prevent loss of amino acids and sugars (Tukey 1970). Conditioning tissues toward maturity is a gradual process in frost-hardiness of seedlings.

Ice-nucleating agents within plant tissues propagate lethal ice crystals randomly and sequentially from cell to cell in rapid succession (Salt and Kaku 1967). Ice forms vertically following the distribution pattern and alignment of vital tissues. In stems 6 mm and smaller in diameter, the internal INAs propagate the ice crystals throughout the meristem and phloem system, seldom in target areas of the phleom. In stems larger than 6-mm diameter, ice nucleation usually occurs in target areas of the phloem and in axillar areas of branches where moisture condenses readily. The depth of tissues penetrated by propagating ice crystals varies with thickness of bark; in thick bark the crystals propagate to the depth of the cortex and occasionally to the cambium. Damage that results from ice propagation may reduce the growth potential of a tree and the production of fruit while the damaged areas are being repaired by new tissues.

The development of precise knowledge of INA factors may be useful in devising methods to reduce juvenility and to improve frost-hardiness of containerized conifer seedlings. Current ingredients for a frost-hardiness prescription are an 8-hour photoperiod for 10 weeks and the lowering of the temperature. Temperature requirements are best fulfilled by storing seedlings at -2° C for 10 weeks following the photoperiod treatment. The weakest link in the prescription appears to be the nutrition of containerized seedlings during the early hardening-off to satisfy the needs of cambial and

meristematic tissues. These tissues must terminate juvenility by developing buds, latewood, and periderm to protect vital cells during dormant and postdormant periods. In nature, such nutritional needs may be fulfilled by leached metabolites reabsorbed by the roots or intercepted and absorbed by stems, branches, and foliage.

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