

ISSN: 0976-3031

*International Journal of Recent Scientific
Research*

Impact factor: 5.114

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COLD CLIMATE REGION**



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Volume: 6

Issue: 10

**THE PUBLICATION OF
INTERNATIONAL JOURNAL OF RECENT SCIENTIFIC RESEARCH**

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ISSN: 0976-3031

Available Online at <http://www.recentscientific.com>

International Journal of Recent Scientific Research
Vol. 6, Issue, 10, pp. 7098-7102, October, 2015

**International Journal
of Recent Scientific
Research**

REVIEW ARTICLE

ICE FORMATION AND PROPAGATION IN PLANTS OF COLD CLIMATE REGION

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ARTICLE INFO

Article History:

Received 16th July, 2015
Received in revised form
24th August, 2015
Accepted 23rd September, 2015
Published online 28st
October, 2015

ABSTRACT

Freezing is a major environmental stress, inflicting economic damage on crops and limiting the distribution of both wild and crop species and risk of frost extinction. Plants in cold areas have developed several mechanisms of resistance to freezing temperatures during winter. Therefore, understanding freezing and how it is overcome by plants is of extensive practical importance.

Key words:

Nucleation, Infra-red video thermography, INA bacteria, Infrared Differential Thermal Analysis, Antifreeze proteins, Sub zero temperature.

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INTRODUCTION

Ice formation is a common stress of all high altitude plants. During the ice formation plants are damaged by cold temperatures as well as exhibit freeze damage, i.e. frost injury. In addition there is another hazard to plant i.e., snow cover, which is an important factor mitigating low air temperature extremes. Plants in cold areas have developed mechanisms of resistance to freezing temperatures during winter (Levitt, 1972). At near subzero temperatures, water in apoplastic spaces in plant freezes. However, cells have developed mechanisms to prevent intracellular water from freezing, since intracellular freezing is lethal for all living cells (Mazur, 2004).

Another important fact is that at high altitudes the probability and occurrence of low and freezing temperatures is not only restricted to the winter period but can occur throughout the whole year. Thus the control of frost injury to such plants is obligatory for their survival.

This survival ability is achieved by avoiding ice formation within plant body. One way to do this is to warm the plant to temperatures above the freezing point of the tissue. Alternatively, plants can supercool to some extent below 0°C and avoid damaging ice formation.

Mechanism of Freezing in Plant

Plants and plant parts freeze when they cannot avoid nucleation and cannot prevent the growth of ice. Before discussing the mechanism we should know about nucleation and nucleators.

Nucleation

Nucleation is defined as the phenomenon in which water molecules come together to form a stable ice nucleus, either spontaneously called homogeneous nucleation, or catalysed by another substance called heterogeneous nucleation. Homogeneous nucleation is unlikely takes place at temperatures just below 0°C but, in contrast, in a moist climate, heterogeneous nucleation is difficult to avoid. The amount of pure water needed to generate a single stable ice nucleus by homogeneous nucleation at modest sub-zero (Celsius) temperatures is extremely large. The amount falls rapidly with a drop in temperature. The amount falls further as the temperature is reduced until the homogeneous nucleation temperature of -38.5°C is reached, at which point homogeneous freezing is likely even in a very small volume of water. This sets a lower limit to freeze-avoidance for plants and their organs and tissues. Even for single cells, if they have not frozen or been freeze-dehydrated at a higher temperature, then they

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will freeze internally near -40°C (the homogeneous nucleation point being depressed by solutes).

Ice nucleation in most plant tissues begins on the surface of the cell-wall, in water transporting vessels or in the extra-cellular spaces (Guy, 1990). Ice crystals spread throughout the extra-cellular regions (Burke *et al.*, 1976) causing a rapid rise in the solute concentration of the extra-cellular solution. Thus, a water potential gradient is established, with liquid water moving out of the cell (Mazur, 1969). The cell acts as an osmotic system, with the osmotic concentration inside increasing as water diffuses out through the plasmalemma, dehydrating the cell. The protective effect of extra-cellular freezing is due to gradual dehydration which prevents intra-cellular freezing. When these ice crystals melt, most water is likely absorbed by the adjacent cells. Cell death can be caused either by a severe dehydration that produces coagulation of the protoplasm (Modlibowska, 1962a) or by disruption of cell membranes and other cellular components by ice crystals (Burke *et al.*, 1976). This disruption is usually manifested as acidity and/or discoloration of the affected tissue (Burke *et al.*, 1976). However, cells with highly viscous contents, such as any cells dehydrated by growth of extracellular ice, are likely exceptions. These may form a glass (vitrify) rather than freeze. Vitrification occurs in cells of deeply frozen plants. It is much popular, and this may explain how some tree species can survive temperatures down to liquid nitrogen and liquid helium temperatures. Substances which are heterogeneous in nature, can act as nucleators. These include:

1. Ice Nucleation-Active (INA) Bacteria;
2. Other Biological Molecules and Structures; and
3. Organic and Inorganic Debris.

Nucleators may be on the plant surface (extrinsic) or, in some cases, within the plant (intrinsic). To proper function, a potential heterogeneous nucleator must be in contact with water. Consequently, if the plant surface is dry, extrinsic nucleators will be ineffective. However, during radiation frosts in many climates, moisture will tend to condense onto plant surfaces, so giving an opportunity for any heterogeneous nucleators present on the plant surface to function. Snow and sleet can also initiate freezing in plants. (Ashworth *et al.*, 1985)

Nucleators operating in nature are partly understood. INA bacteria commonly found on plants comprise strains of several species (such as *Pseudomonas syringae* and *Erwinia herbicola*), which produce a protein able to nucleate freezing at temperatures as high as -2°C . However, the presence of INA bacteria is not a universal explanation of nucleation of ice in plants. Sizes of INA bacterial populations vary greatly between plant species, sites, climates and seasons, and only a small percentage of cells in a population are effective nucleators. Lindow, 1990 argued that a very small population of INA bacteria could nucleate freezing throughout citrus trees since once nucleated freezing would spread rapidly. However, this argument would not carry to herbaceous plants, where each leaf (in grasses) or main shoot (in a dicot) would freeze separately because of the higher temperature of the crown compared to the leaves. It is difficult to study nucleators produced by plants;

attempts to isolate the causal agent often result in a reduction or loss of activity.

However, plants themselves do contain non-bacterial nucleating agents and some of these agents function at high freezing temperatures e.g. in *Prunus* at about -2°C . Some Afro-alpine species and some *Opuntia* contain polysaccharide nucleators operating above -4°C . In laboratory tests of freezing-tolerance, the absence of surface moisture can result in artifactual super-cooling. Consequently, researchers carrying out IRVT followed by freezing tests often ensure nucleation by applying a fine spray of water to the plants. IRVT showed that even a single droplet of water on a leaf of herbaceous species, it can freeze first, before the plant. When surface water is present, surface nucleation is not inevitable; nucleation of holly leaves can occur either from frozen surface droplets or internally in the petiole or midrib, and ice then spreads from there. Laboratory tests often give lower nucleation temperatures than those reported under natural conditions and so it can be unreliable indicators of behaviour in the field. For example in high alpine plants this could occur at between 2.6°C and 3.5°C when thermally insulated thermo-couples were used and at between 5.2°C and 6.3°C in *Loiseleuria procumbens* and *Rhododendron ferrugineum*, respectively, when thermo-couples were not insulated. These observations seem to overestimate the supercooling capacity of plants, as much milder subfreezing air temperatures between 0.6°C and 2.6°C are reported to result in ice nucleation in plants in the field (Neuner and Hacker, 2012).

However, the measurement of realistic ice nucleation temperatures is somewhat tricky.

Firstly, until now it has not been possible to simulate the environmental conditions that prevail during naturally occurring radiative cooling situations in the field, where the plant is always the coldest part.

Secondly, detachment is known to provoke supercooling. Measurements on plant parts may, hence, overestimate the supercooling capability.

Thirdly, when freezing exotherms are recorded by the use of thermocouples, freezing is recorded on a single spot. Ice can nucleate anywhere in the plant, but this will usually take place in the coldest part of the plant which need not be at the measurement spot of the thermocouple. Ice spreads rapidly at rates of up to 27 cm/s and the ice wave will reach all parts that are colder than 0°C immediately. Hence, the temperature at which ice nucleation occurs in the plant is always a range of temperatures rather than one single temperature.

Fourthly, thermal insulation of the thermocouple is usually used to increase the probability that small freezing exotherms can be detected. But this thermal insulation will protect the investigated part from fast cooling and hence it will not be the coldest part during freezing. Additionally, at least for some species it cannot be excluded that ice nucleation can also occur extrinsically, i.e. surface ice may grow into the plant. If a species is nucleated extrinsically, a result deviating from the natural situation will be obtained. External ice does not

necessarily induce intrinsic freezing as the external ice has first to propagate into the plant. This can occur through stomates in some species like *Phaseolus vulgaris*, *Prunus domestica*, *Malus domestica* etc., but in other species this is only possible via a damaged cuticle or other lesions as in *Rhododendron sp.*, *Lolium perenne* and *Poa supina* P. *alpina* etc. The role of extrinsic ice nucleation is still not fully understood.

Pattern of Ice propagation and Whole plant Freezing

Many workers studied the patterns of ice propagation in whole plants by using Infrared Differential Thermal Analysis. Under the experimental conditions woody dwarf shrubs, herbs, rosette and cushion plants show a single ice nucleation anywhere in the plant, which is usually sufficient to produce freezing of the whole individual. The time necessary from initial ice formation until the whole plant was frozen is approximately 0.2–7.2 min in woody plants and herbs and could last up to about 1 h in cushions. (Neuner *et al.* 1999)

The principle pattern of ice propagation was usually found to be independent from the location of initial ice nucleation. Initially ice spreads rapidly at a rate of up to 27 cm/s throughout the vascular tissue as soon as ice has contact with the water in the xylem. Only in a second step does freezing of extracellular water in other tissues occur. This freezing pattern is exemplarily shown for a reproductive shoot of *Rhododendron ferrugineum*, where after freezing of the water in the xylem tissue, ice encroaches into the mesophyll and other adjacent tissues. In mesophyll cells this second freezing step induces functional disturbances in the thylakoids, however, in most plants they are recognizable only after a significant time lapse, i.e. 20–30 min after detection of initial ice formation in the mesophyll, and are very likely to be caused by freeze dehydration of mesophyll cells (Neuner *et al.* 1999)

In the late flower bud stage, ice propagates unhindered into the reproductive structures. In contrast to most other plant growth forms, graminoids show a distinctly different whole plant freezing pattern. In graminoids each leaf requires a separate ice nucleation event, as there is no connection of the vascular tissue between the various leaves of the tussock. This prolongs the time necessary for freezing of the whole tussock. Under the experimental setup whole tussock freezing took between 60–80 min. This slow freezing could have ecological significance for frost survival. In frost dehardened tussocks, leaf supercooling could also be important for frost survival, given that this supercooling also persists in nature when under radiation frost surface ice forms. Controlled ice seeding experiments with INA bacteria dissolved in water droplets on grass leaves showed that ice propagation into the leaf tissue from the surface was inhibited as long as leaf surfaces were undamaged. This indicates that grass leaf supercooling is possible under natural conditions where formation of surface ice due to radiative cooling conditions is likely. (Neuner *et al.* 1999; Hacker *et al.* 2011)

During a late spring frost at a low altitude site (680 m) it was observed that this holds true for natural night frost conditions, as within a tussock of *Dactylis glomerata* the older leaves were found frozen stiff in the morning, but the youngest leaves in the

centre of the same tussock must have supercooled during a night frost of -2 °C, as they did not show any intrinsic ice, this despite frozen rain droplets on the leaf surface.

Occurrence of Ice Barriers

Some plants are also adapted with the problem of freezing and they can nullify the stress by different mechanisms. Ice formation in plants can be induced by either intrinsic (Andrews *et al.*, 1986; Gross *et al.*, 1988) or extrinsic (Lindow *et al.*, 1984; Lindow *et al.*, 1996) sources. Once ice has been initiated, barriers and avenues to ice propagation, both within the plant and at the plant surfaces, determine the subsequent pattern of ice formation and are a factor in the survival mechanism (tolerance of extracellular ice or avoidance of ice by supercooling) employed by a given plant tissue or organ. Barriers to ice propagation within a plant can be permanent or temporary (i.e., propagation is impeded until growth of ice crystals can continue). Some barriers may also only be present at particular times of the year, or upon completion of particular stages of development. Supercooling of the buds of some temperate woody species appear to be, at least in part, related to cell shape and structure in the bud axis area (Ashworth, 1982; Quamme *et al.*, 1995) and a lack of vascular differentiation (Ashworth, 1982, 1984; Ashworth *et al.*, 1992) during the dormant period. In wheat (*Triticum aestivum* L.), the propagation of ice was impeded for several hours at stem and rachis nodes (Single, 1964). Avenues to ice propagation require areas (Pearce, 2001) and pores (Ashworth and Abeles, 1984) large enough for ice crystals to grow. Wounds, cracks in the cuticle and epicuticular waxes, lenticels, and open stomata have all been suggested as possible entry points for extrinsic sources of ice, while extracellular spaces and xylem vessels are thought to function as pathways of internal ice propagation. Two important mode to nullify the stress are discussed below.

Production of Antifreeze factors

Some plants are able to produce factors that can inhibit ice formation or its growth such as cereal cell wall polysaccharides and antifreeze proteins (AFPs). AFPs are defined by their ability to modify freezing *in vitro*, and the name does not necessarily indicate their function *in vivo*. AFPs produced by cereals have strong sequence similarity to the pathogenesis-related protein. Infrared video thermography of some leaves during freezing in a cooling controlled environment chamber revealed that freezing is exothermic and thus can be detected by detecting warming (Hacker *et al.* 2011). An infrared imaging camera is generally used to monitor exothermic events in the freezing leaves. The image displays temperature as false-colours (Le Grice *et al.*, 1993) running from 'cold' colours (pink and blue) to 'warm' colours (yellow and red). The full activity of AFPs probably depends on the formation of oligomers containing more than one type of AFP. The cereal leaf AFPs were found in apoplasmic extracts and the extracellular location of the glucanase-like AFP was confirmed by immuno-localization, indicating their role relates to ice outside the cell. It is unlikely that the role of AFPs is to prevent plants from freezing. Cereal leaves and leaves of many other species do not use a freeze-avoidance strategy. Plant AFPs would not effectively prevent freezing since they only lower

the temperature at which ice is stable by 0.3 °C. However application of infiltration of a fish antifreeze protein (AFP) into leaves lowered the freezing temperature by 1.8°C. On the other hand, expression of fish AFPs in transgenic plants has not resulted in improvement in survival attributable to anti-freeze effects. So the role of intrinsic plant AFPs is, probably to control rather than prevent freezing (Wisniewski *et al.*, 1997).

Structural Ice Barriers

In the vegetative tissue of plants other than graminoids, structural ice barriers are known to be present. For instance, in buds of some cold hardy conifers, the spread of ice into the meristematic tissue is efficiently prevented. These ice barriers are also present in cold hardy buds of timberline conifers such as *Pinus abies*. There spreading of ice into the bud meristem is prevented during formation of extraorgan ice masses in the cavity beneath the crown. The same frost survival mechanism was found for *L. decidua* but not for *Pinus cembra* buds whose survival mechanism, and that for other species from the genus *Pinus*, is still under discussion (Zwiazek *et al.* 2001).

In reproductive tissues of some species during certain developmental stages, ice propagation barriers appear to be present that prevent the propagation of ice from the vegetative tissue into the flower or flower primordial tissue. In the flowering stage of *Rhododendron ferrugineum*, for example, ice can propagate nearly unhindered into the florets, however, this is not the case in the flower bud during winter. Spreading of ice into the florets of the flower bud of *Rhododendron* species must somehow be prevented, probably by structural ice barriers (Ishikawa and Sakai, 1981; Price *et al.*, 1997). Similar observations were made for *Prunus* and *Forsythia* flower buds, where the supercooling ability of floral primordial depended on the existence of a functional xylem. When xylem continuity between the floral bud and the subtending stem was established, ice could propagate from the frozen stem via the vascular system and nucleate the water within the primordia.

A similar ice barrier preventing the spreading of ice into the flower bud tissue was found in some alpine woody species such as *Loiseleuria procumbens* and *Calluna vulgaris* during winter time. However, the occurrence of ice barriers between vegetative and reproductive organs may not be a distinctive feature of frost sensitive plant. Preliminary results obtained for spring-flowering lowland plants show that ice barriers between shoots and reproductive organs can also be found in lowland species such *Corylus avellana* and even in herbs such as *Anemone nemorosa*.

As these species flower during seasonal periods with a high frost probability at low altitudes, this adaptation appears to be crucial for survival of the reproductive organs. In fruits of *Silene acaulis* single ovules freeze independently from each other and at much lower temperatures than the fruit, indicating the existence of an ice barrier. The structural nature of these ice barriers is still under investigation. (Rodrigo, 2000)

Thermal Ice Barriers

For frost sensitive cushion plants a thermal ice barrier has been

detected. In cushion plants a thermal gradient builds up during freezing, where the flower heads are coldest and the vegetative parts and the shoots inside the compact cushion body remain significantly warmer. This gradient may be even more pronounced under natural radiative cooling conditions and may allow these inner shoots to maintain a non-freezing temperature. If ice nucleation occurs in a single flower, this thermal ice barrier prevents the spreading of ice from a frozen flower into the others, which means that for each single flower a separate ice nucleation event is necessary. The typical freezing pattern, as characteristically observed in cushion plants, showing these thermally functioning ice barriers is shown exemplarily for cushions of *Silene acaulis* and *Saxifraga moschata* (Neuner and Hacker, 2012). A lack of sufficient ice barriers against extrinsic ice nucleation could be involved in the particularly low frost resistance of early developmental stages of high altitude plants such as germinating seeds and seedlings. The rhizodermis (root epidermis) seems to be unable to protect the seedling from ice entrance, which is in contrast to the epidermis of shoots and cotyledons where ice cannot enter. In this way, these early stages will be ice-nucleated as soon as the rhizodermis has contact with extrinsic ice masses. During germination at the soil surface, the rhizodermis may come into contact with frozen soil water, the risk will decrease with protrusion of the root into the soil (Zwiazek *et al.* 2001).

CONCLUSIONS

In winter frost survival of plants is strictly intermeshed with snow cover and micro-site exposure. There is also a risk of frost extinction of a species. But approach to improving freezing-tolerance, these plants lead to change in life forms and developmental stages of plant organs and tissues. A small improvement in freezing-tolerance may be economically important and achievable by manipulating a single aspect of structure or physiology especially in susceptible species. An improved understanding of freezing tolerance could aid the improvement of breeding programs searching for hardier cultivars and the development of cultural conditions leading to avoidance of frost damage, as with the development of antifreeze compounds to inhibit premature ice nucleation under field conditions (Wisniewski *et al.*, 1997b). However the mechanisms involved in freezing-tolerance are not fully understood, because their supercooling capability in nature is difficult to simulate in laboratory tests. Particularly for meristematic tissues in buds and reproductive organs, which do not tolerate ice formation at all during some developmental stages, ice protection via ice barriers seems to be the only mechanism to ensure survival and the reproductive success, respectively (Hacker *et al.* 2011). Sufficient snow cover not only thermally insulates plants from low air temperature extremes but reduces the daily leaf temperature amplitudes and the number of freeze-thaw cycles they experience (Neuner *et al.* 1999).

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How to cite this article:

Anup Kumar Sarkar.2015, Ice Formation And Propagation In Plants Of Cold Climate Region. *Int J Recent Sci Res.* 6(10), pp. 7098-7102.

*International Journal of Recent Scientific
Research*

ISSN 0976-3031



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