FROST HARDINESS AND DORMANCY IN CONIFERS

by 1/
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Abstract. The frost hardiness and dormancy of trees is briefly discussed, as well as their possible relationship. The importance of these two physiological processes in nursery cultural techniques is pointed out.

Introduction

The literature on the subjects of frost hardiness and dormancy is voluminous and must appear chaotic to the uninitiated. These subjects are being studied both biochemically and biophysically on just about all plant species from the annual herbaceous plants to the perennial woody plants. I will be dealing only with woody plants, especially conifers.

It will be helpful to define frost hardiness and dormancy before proceeding to discuss them. The frost hardiness of a tree can be defined in general terms as the lowest temperature below the freezing point to which a tree can be subjected without being damaged. The phenomenon, which enables a tree to increase or decrease its cold resistance, is called the frost hardiness process. In the literature this process is also referred to as cold acclimation, acclimation, winter or cold hardiness or cold resistance.

Dormancy is a condition of living tissue (e.g. bud) that is predisposed to elongate (or grow) but does not do so, because it requires a cold treatment before it will elongate. Dormancy, as discussed here, is also referred to as winter dormancy, winter rest or just rest and occurs in nature during late summer, fall and early winter. Other dormancy terms such as quiescence, imposed dormancy and correlated inhibition are generally used in relation to dormancy that occurs during the growing season due to adverse external (environmental) or internal (physiological) conditions.

These definitions are simplified, particularly that of dormancy, but they are well suited for woody plants, especially conifers.

Frost Hardiness

To survive, species native to temperate regions, must have a genetic potential for frost hardiness. It is this genetic potential that has to be triggered by certain environmental influences before it can express itself. The two most critical environmental factors that trigger the frost hardiness process are light (photoperiod) and low temperature.

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Two types of freezing are recognized to occur in plants and are characterized by the location of ice formation in the plant tissues. When water freezes inside the cell, it is called intracellular freezing, but when water freezes outside the cells, in the intercellular spaces, it is called intercellular or extracellular freezing. Intracellular ice formation is nearly always lethal regardless of the hardiness of the tissue or plant and is caused by rapid decreases in temperature, such as greater than 10 degrees Celsius per minute. These types of situations seldom occur under natural conditions and therefore rarely concern us. On the other hand, moderate decreases in temperature (i.e. 1 to 6 Celsius degrees per hour) cause intercellular ice formation, which may or may not be lethal, depending on the hardiness of the plant. Intercellular ice formation, therefore, concerns us greatly.

When temperature goes below the freezing point (0 degrees), the water between the cells will freeze first, forming ice crystals. Generally, some super cooling will occur down to as low as -4°C. Following the initial ice crystal formation, water will be drawn out of the cells to the enlarging ice crystals, causing the cells to shrink while the water inside the cell remains unfrozen. It is this removal of water from inside the cell that is responsible for the freezing injury. This is the reason why dehydration is now considered as the fundamental cause of freezing injury.

During dehydration there is a simultaneous 1/ decrease in cell volume (i.e. the cell shrinks), 2/ an increased concentration of cell solutes, and 3/ pH changes of the cellular sap. It was once thought that these side effects of dehydration were the cause of the freezing injury. However, it is now generally accepted that the primary effects of freezing are due to membrane disruption. Ice formation occurs **in** both hardy and unhardy tissues, but the hardy tissues survive while the unhardy tissues do not. The hardy plant is able to protect all the cell membranes from the effects of freezing, which is accomplished with a combination of chemical protection and membrane synthesis.

The frost hardiness process in our native coniferous species occurs in two or three stages (Figs. 1 and 2). The first stage occurs in early fall when the decreasing photoperiod becomes noticeable while the day temperatures are still relatively warm, but the nights are cool. The start of the first stage is associated with growth cessation, the initiation of terminal buds, and in the case of our deciduous hardwoods, the onset of autumn coloration. During this stage of frost hardiness, which is initiated chiefly by the decreasing photoperiod, increases in frost hardiness are moderate. However, as plants progress through this first stage they become increasingly responsive to low temperatures around or just below the freezing point, which initiate the second stage of frost hardiness. It is during this second stage that large increases in frost hardiness occur. The third stage of hardening is induced by temperatures of -30 to -50°C and only the extremely hardy species can be quickly lost. There is still some disagreement among frost hardiness researchers on this "stage" concept, because it does not seem to occur in herbaceous plants but does appear to be applicable to our native coniferous species.

Differences in frost hardiness within the same tree do occur. They occur between the various tissues, such as phloem, cambium and xylem, and between various tissue components such as needles, buds and bark. Furthermore, these differences change in relation to each other during the course of the year. This differential frost hardiness is one reason why it is difficult to assess total tree damage after freezing and why it is important to use more than one method for evaluating freezing damage.

The greatest differences in frost hardiness within a tree occur between the roots and top (i.e. the above-ground portion). The roots are significantly less hardy than the aerial parts of the tree and these hardiness differences can be as much as 20 Celsius degrees. Furthermore, the roots do not exhibit the same seasonal hardiness trend as the top.

The hardiness of the roots appears to be even more dependent on the environment it grows in (i.e. the soil) than the top, probably because the roots are buffered against drastic fluctuations in temperature. The soil has to freeze for the roots to become hardy and this hardiness is quickly lost when the soil thaws. A good example is in the spring. As soon as the frost is out of the ground, the roots are actively elongating and have lost their hardiness, while the tops are still very hardy. As a matter of fact, the tops will not be completely dehardened for as much as another 8 weeks.

Dormancy

The first visible signs that spruce trees are entering dormancy, which occurs anywhere from August to September, depending on location in Canada, is the appearance of translucent white budscales and the gradual cessation of shoot elongation (Fig. 3). In the early stages this process is still reversible and shoot elongation can be made to resume, but somewhere with time, a threshold point is reached after which the process becomes irreversible. It is at this point that the tree has entered dormancy and a chilling period is needed before normal growth will resume.

As yet is is impossible to determine the exact moment when this point of non-reversibility is reached, due to the lack of physiological understanding of dormancy and the factors that affect it. All that can be said at this time is that dormancy is associated with changes in the concentration of certain growth--regulating substances. How these changes are induced is also not well understood.

When the chilling requirements have been satisfied and growth does not resume, because external conditions are not favourable for growth, then the tree is in a state of imposed dormancy. Under natural conditions in southern Ontario this state is reached by January.

In most tree species dormancy can be induced by changes in temperature, such as low temperatures (+ 5°C) and/or changes in day length (i.e. short days, less than 15 hrs.). In the spruces, dormancy appears to be brought on primarily by decreasing photoperiod, because

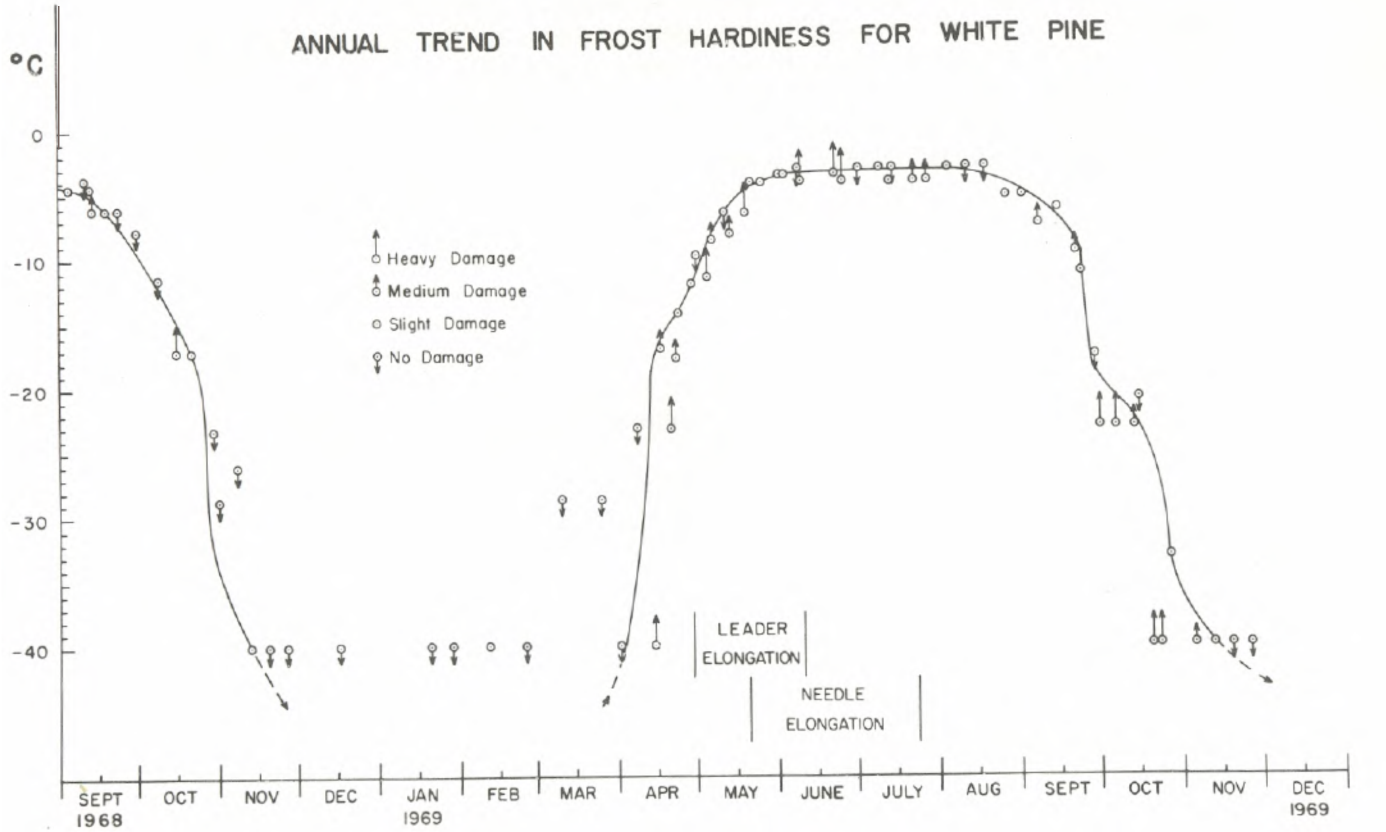


Fig. 1. Frost hardiness trend of Pinus strobus (white pine) where the frost hardiness temperature delineated is the lowest temperature to which trees can be exposed without being damaged. In general, the frost hardiness increased from late August until late November, when it had reached its maximum hardiness below -40°C. In April the dehardening rate was rapid to about -15°C after which it became more gradual to the minimum frost hardiness of about -3°C by June. The transition between the first and second stage of hardening was not detectable in October 1968 but was in October 1969. The transition is not too distinct because the time scale is calibrated in months, whereas the transition generally occurs over a period of days. The trend is truncated at -40°C (December to March) because it was not possible to conduct freezing tests below -40°C. Note that visible signs of growth occur well before the trees have totally dehardened. Trees were grown and tested near Maple, Ontario.

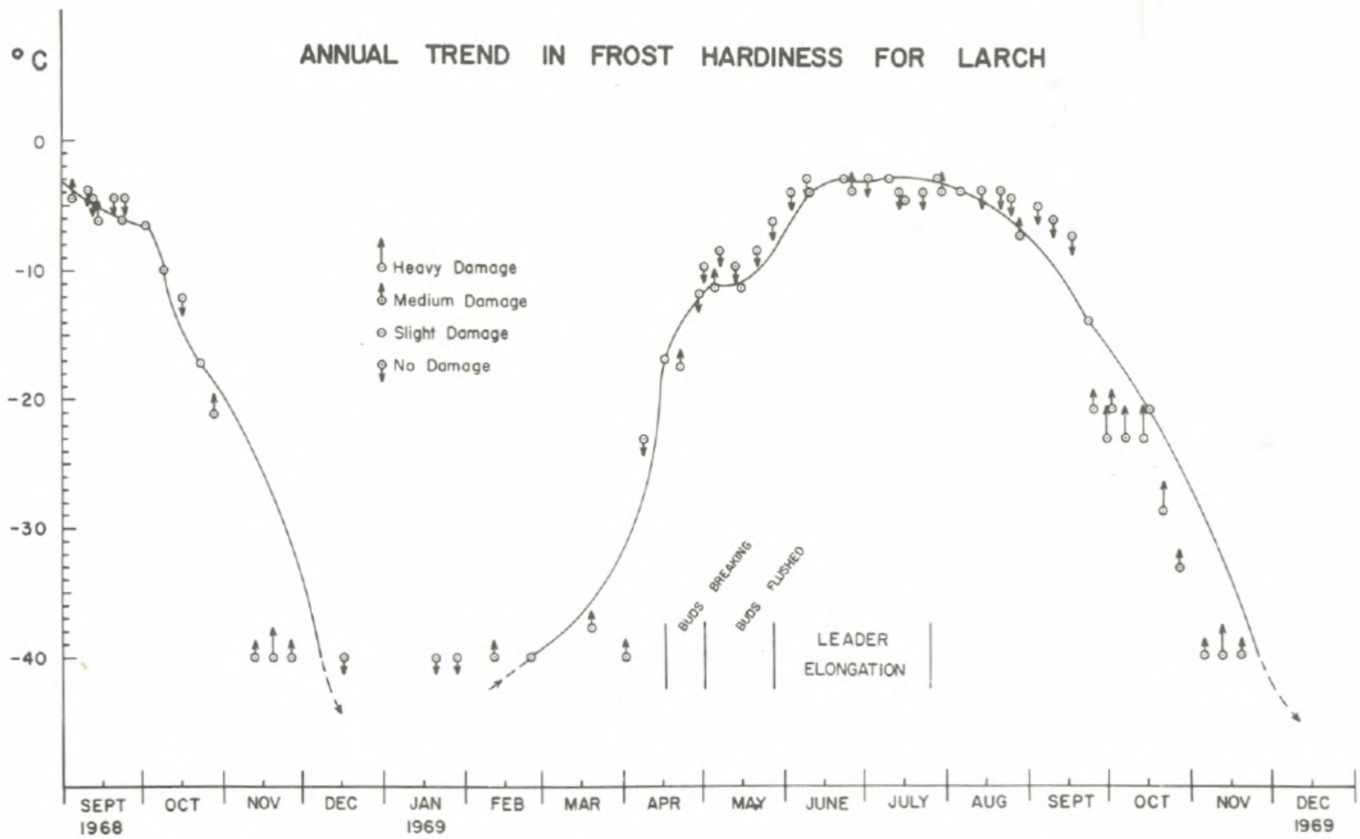
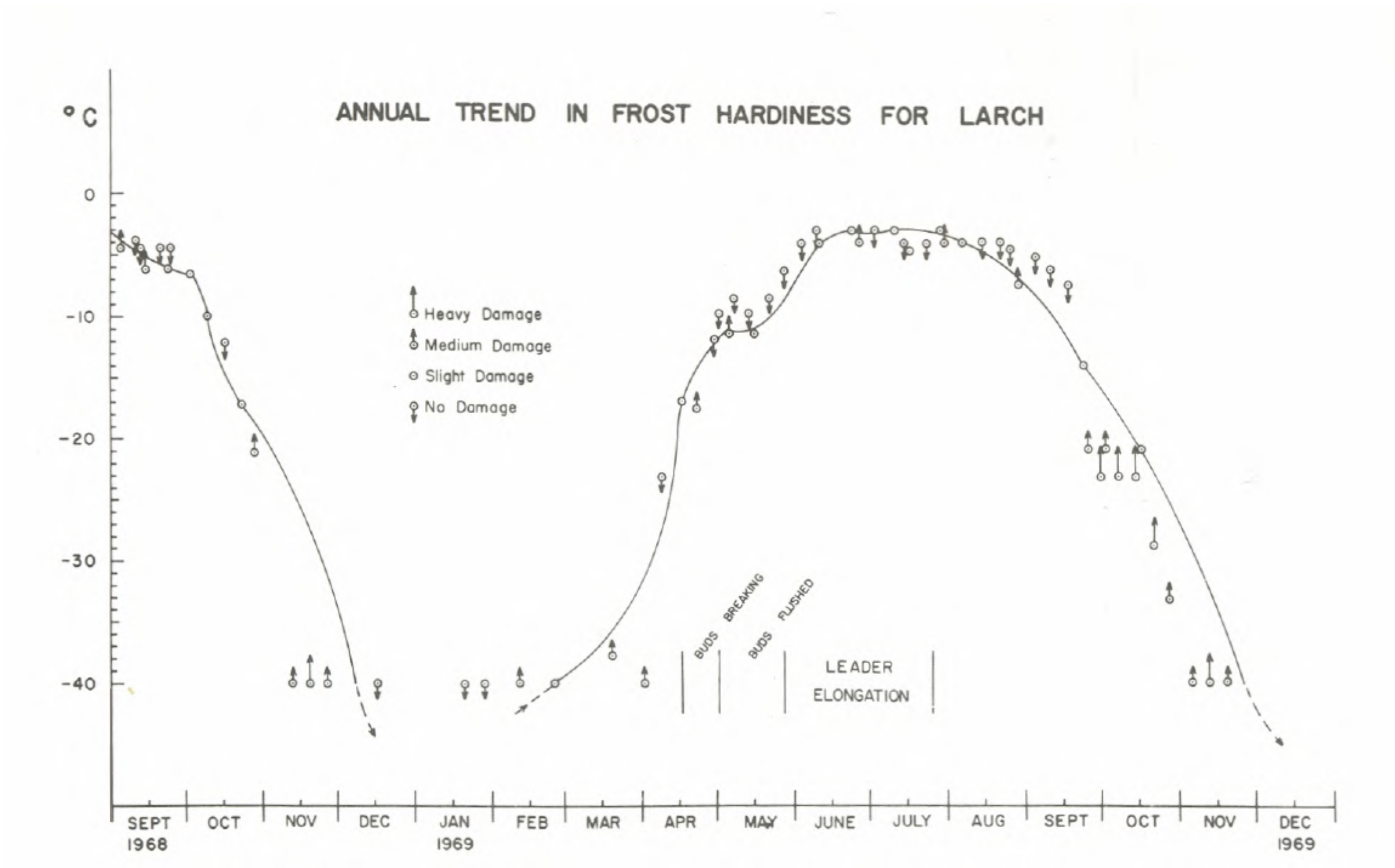


Fig. 2. Frost hardiness trend of Larix laricina (tamarack) where the frost hardiness temperature is the lowest temperature to which trees can be exposed without being damaged. In general, the frost hardiness increased from late August until December, when it had reached its maximum hardiness below -40 °C. Towards the end of February there was a gradual dehardening rate, which increased in April until May, when it levelled off at about -11 °C for several days. The minimum frost hardiness of about -3 °C was reached in June. See Fig. 1 caption for more details. The hardening and dehardening rates were more gradual in larch than in pine. Trees were grown and tested near Maple, Ontario.



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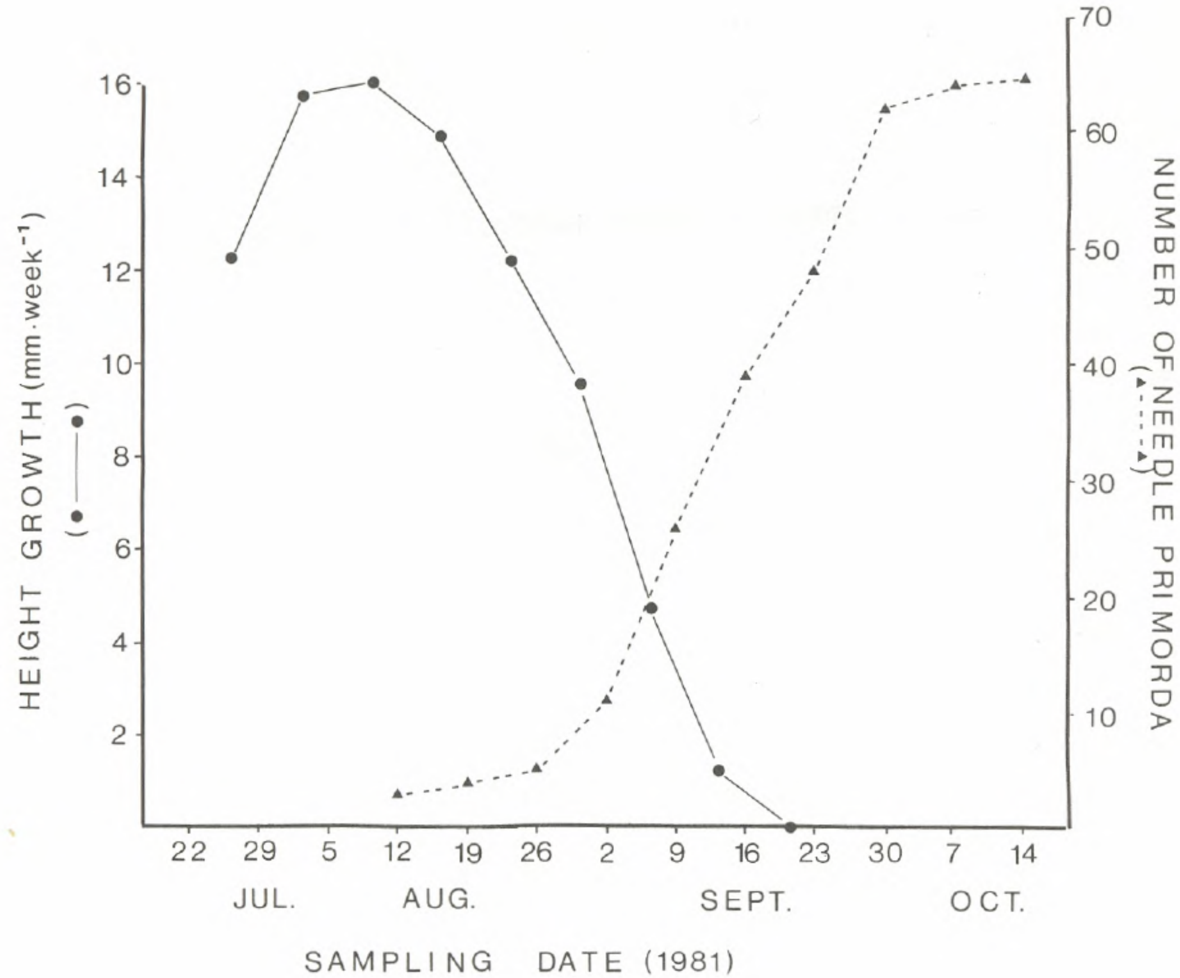

Fig. 3. Height increment of production run container-grown black spruce seedlings during July, August and September 1981, at the Swastika Tree Nursery and the subsequent needle primordia formation in bud development. Dormancy becomes irreversible somewhere between the beginning of bud development and the cessation of height growth, particularly in conifers, which are 2 years old and older (Graph is courtesy of S.J. Colombo).

spruces respond to short-day treatments quickly by means of cessation of shoot elongation and bud formation. Pines on the other hand, do not appear to respond to photoperiod as quickly, or as distinctly as the spruces, but the pines certainly become dormant. Not only are there differences in response to these environmental stimuli in dormancy induction between species but the age of the tree is also important. Mature trees respond differently to these stimuli than seedlings. This is especially noticeable in the chilling requirements before they are able to come out of dormancy.

All these differences make it impossible to make sweeping, all embracing statements on dormancy. In some instances dormancy is a photoperiodic response with some coniferous species while it is less so with others. We should remember that the effects of all environmental stimuli on dormancy are mediated through internal physiological changes. This frequently confounds the effect of an outside stimulus, because the internal conditions are often not known.

It is curious, yet interesting to note that most discussions on dormancy deal only with buds and other meristimatic tissues of the above-ground part of the tree. The roots appear to have little, if any, dormancy requirements, although they have the ability to become dormant.

The Relationship Between Frost Hardiness and Dormancy

At present the type of relationship that might exist between frost hardiness and dormancy is unknown but since both processes are complex, one can expect the relationship between them to be complex as well. These two processes have in common the same two environmental factors of light (photoperiod) and low temperature, which trigger both the frost hardiness process and dormancy induction. However, the term dormancy is restricted (or should be) to behavioural attributes of meristematic tissues only. Consequently, dormancy will be confined to the various meristematic zones, which make up a very small tissue volume of the entire tree. Frost hardiness, on the other hand, is a behavioural attribute of all living tree tissue, which has a vastly greater volume than the meristematic zones. Therefore, any relationship between dormancy and frost hardiness would depend on some sort of signal, which is transmitted either directly or indirectly from the meristematic zones to the living non-meristemati'c tissues. For instance, a decrease in secondary meristematic activity will cause an increase in reserve accumulation, which in turn, will assist the cells in their hardening process.

It has been suggested that the key factors in the induction of frost hardiness appears to be growth cessation rather than the onset of dormancy because low temperatures can stop growth and bring about some hardening without inducing dormancy. However, it appears that only dormant trees can develop a high degree of frost hardiness. Just because some trees become dormant but not frost hardy (e.g. southern pine), does not mean that there is no relationship between these two processes. The available evidence suggests that, with certain species, dormancy will be directly influenced by external factors and so influence frost hardiness indirectly, while with other species the frost hardiness will be more directly influenced by external factors. Consequently, I have suggested periodically that it might be useful for improving our understanding of the relationships between dormancy and frost hardiness to classify those species which have to go into winter dormancy in order to attain their maximum frost hardiness and those species which do not have this requirement. This is by no means an easy task since there will be considerable variation even within species, due to several factors, including geographic differences.

Most tree species in the northern temperature zone, particularly the coniferous species, go into dormancy before then attain their maximum winter hardiness. For example, in southern Ontario, under natural conditions white pine is in a state of winter dormancy by September, and the only way to break this dormancy is to satisfy the chilling requirements of the trees. In one test, I found that the chilling requirements were increasingly satisfied from September to December, so that during December the chilling requirements had been totally satisfied and the trees went from a condition of winter dormancy to one of imposed dormancy.

During this period, when the chilling requirements were being satisfied, trees increased in hardiness until they reached their maximum frost hardiness (winter hardiness) near the beginning of December (Fig. 1). This coincides approximately with the time that trees go from winter dormancy to imposed dormancy. Consequently, it is possible that when maximum frost hardiness has been attained, the chilling requirements have been satisfied. This term "imposed" could also be applied to winter hardiness, since it persists until conditions are favourable for growth.

During the dehardening period the first visible signs of growth become evident, well before the trees have fully dehardened (Figs. 1 and 2). This is particularly true for a conifer such as larch (*Larix laricina*) where the buds will flush while the young needles are still considerably frost hardy, between -11 and -17°C (Fig. 2). From these, and other observations in the literature, it is evident that the frost hardiness process lags behind the dormancy process, both in the autumn when the trees enter dormancy and increase in frost hardiness and in the spring, when the trees break dormancy and decrease in frost hardiness. This could be interpreted as suggesting that, in some tree species, dormancy is a prerequisite for frost hardiness. I suggest this to be true for most of our native coniferous species.

The relationship between frost hardiness and dormancy is not only of great physiological importance but also of immense practical importance, particularly in forest nursery practice, and merits intensive research. Even if this relationship would be weak or non-existent there would be a distinct advantage, in expressing the state of dormancy in degrees of frost hardiness, which would make the determination of dormancy more precise.

Practical Applications

How can we apply all this knowledge (or lack of it) on frost hardiness and dormancy to our forest regeneration program, and specifically to our nursery cultural practices? If we use our regular cultural practices we do not have to concern ourselves with these physiological processes. Because the trees will go into dormancy, become frost hardy and go through the winter and will come out of dormancy, deharden and resume growth as regular as clockwork. This knowledge might just enrich your total appreciation of growing trees and how trees grow.

However, our nurseries now produce a greater variety of stock types than they did a decade ago, which has resulted in increasingly diverse cultural practices. In other words, things are not as simple as they used to be and they will probably become more complex in the future. A few examples of our increased diversity are that:

1/ We are now cold-storing (approx. -3°C) bare-root stock overwinter (up to 7 months) in large quantities.

2/ We are producing a large number of containerized seedlings, which are grown (forced) on a heavily fertilized schedule in greenhouses and out-of-doors.

3/ We are introducing non-native (exotic) tree species and are hybridizing both native and non-native tree species.

With all these "new products" that are being produced in our nurseries, a knowledge of frost hardiness and dormancy has become a necessity.

Since actively growing trees are not frost hardy or dormant, it is essential that for successful overwintering, all nursery stock should be dormant and frost hardy. This is important in both the cold-storage of bare-root stock and the out-of-door overwintering of container stock. Bare-root stock should not be lifted in the fall for cold storage until the stock is fully dormant and sufficiently hardy. This applies to both the top and the root. This is just as important with the outdoor over-wintering of container stock, because their root systems are above the ground and surrounded by the cold circulating air, rather than the relatively warm insulated environment of the soil. This means that you must use the right nutrient regime (or any other cultural practice) which will ensure that all growth has stopped before inclement conditions prevail.

A good example of how changing cultural techniques will improve dormancy and frost hardiness in container stock is a project conducted by S.J. Colombo of our institute. The objective of this project was to improve bud development and reduce overwintering damage in spruce container stock. Good bud development in spruce container stock was achieved by either short-day treatment (8-hour light) or extended greenhouse culture. Good bud development reduced overwintering losses, that were as high as 40% with regular cultural practices to less than 1%. Trees with damaged tops also had reduced root growth capacity, so that by adopting proper cultural practices, the quality of the planting stock was greatly improved. Whether the reduction in root growth capacity is due to the damage to the top or due to damage to the root or a combination of both still remains to be determined.

When you are growing hybrids and exotics, dormancy and frost hardiness are important. There should be answers to some pertinent questions, such as 1/ is their maximum winter hardiness high enough for the location? 2/ do they go dormant and become frost hardy early enough in the fall so that they can keep ahead of the decreasing temperatures?, and 3/ do they retain their dormancy and frost hardiness in the spring long enough so that a prolonged mild spell in late winter or early spring does not damage or kill them?

I have not provided you with many solutions to your problems. But by providing you with a thumb-nail sketch of frost hardiness and dormancy and where these physiological processes are important, I hope that it will help you in formulating your questions. I am convinced that with cooperative efforts between the practising nurseryman and tree physiologists some of the many problems, that arise when you are growing trees, can be solved.

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