

# Conditioning Nursery Plants to Promote Hardiness and Dormancy

by Thomas D. Landis

Most novice growers don't give much thought to hardening or dormancy because they are much more concerned with getting seeds to germinate or cuttings to root, and then putting on enough height and stem diameter growth to meet specifications. From my point of view, however, hardening is the most important phase of nursery culture because plants that don't receive proper hardening do not store well over winter and are less likely to survive and grow after outplanting. This is even more important for forest, conservation, and native plants that will be outplanted on relatively harsh sites without subsequent watering or other supplemental treatments. This special conditioning is so important that we dedicated the last of three growth phases to hardening and dormancy induction (Figure 1).

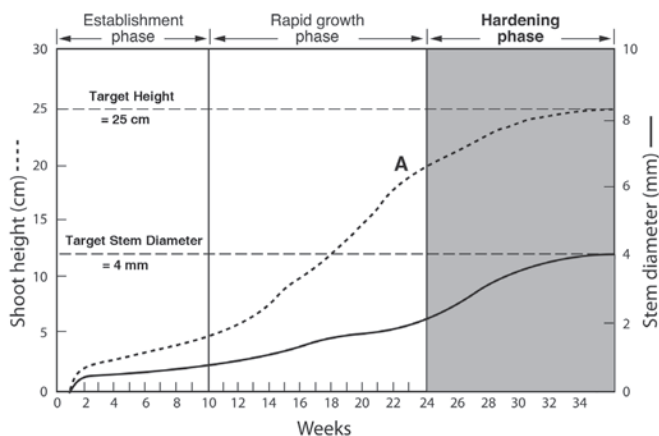


Figure 1 - The hardening phase is the last of 3 phases of nursery culture, where the objective changes from promoting fast growth to conditioning the plants to undergo the stresses of harvest, storage, and outplanting. The hardening phase usually begins when plants are 80 to 90% of their target height (A) (modified from Landis and others 1999).

## 1. The Hardening Phase

The hardening phase is the third of 3 nursery production phases and is the period of time in which the seedling shifts from shoot growth (height) to stem diameter (caliper) and root growth (Landis and others 1999). During this phase, the plants also become gradually conditioned to withstand the rigors of harvesting, shipping, and outplanting. Seedlings reach their target stem diameter during the hardening phase (Figure 1), lateral buds are set, and root growth continues until soil temperatures become

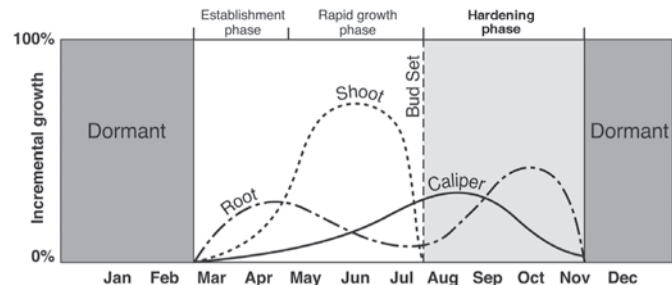


Figure 2 - Incremental growth curves are the best way to illustrate the timing of shoot, caliper, and root growth during the growing season. Target height has been reached by the Hardening Phase, when carbohydrates are shifted from the shoot meristem to the lateral meristem (caliper growth), and the roots (modified from Landis and others 1999).

too cold (Figure 2). With container stock, roots must grow enough to bind the growing medium into a firm plug that will hold up during harvesting, storage, and outplanting. The hardening phase has two different, but physiologically related, objectives that must be achieved sequentially: dormancy induction and stress conditioning.

### 1.1 Dormancy induction

Because seedling growth cannot be stopped abruptly, the hardening phase must be initiated when seedlings are approximately 80 to 90% of the actual target height to allow for this subsequent growth (A in Figure 1). While shoot growth begins to slow down, stem diameter continues to increase toward its target (Figure 2). In most species that exhibit determinate growth, bud development starts during this stage. With indeterminate species such as southern pines and junipers, a true bud does not form and the shoot simply stops growing.

### 1.2 Stress conditioning

Seedling shoots are extremely succulent after the rapid growth phase and have little stress tolerance. Therefore, they must be gradually hardened to tolerate the many stresses of harvesting, handling, storage, and outplanting. Timing and duration of the hardening phase will depend on when seedlings will be outplanted, and the types of stresses that will be encountered on the outplanting site.

## 2. Hardiness and Dormancy: Definitions and Monitoring

These two terms are commonly used in nursery work and often interchangeably. However, while both occur during the hardening phase, there are subtle, yet significant, differences between them. In addition, hardiness and dormancy are measured and monitored differently.

### 2.1 Hardiness

My favorite definition of hardiness is “a condition of durability or resistance to stress”, and the term can refer to a specific stress (for example, cold stress) or to an overall condition of stress resistance. The most common type of hardiness is to frost (Figure 3A), although a hardy plant is resistant to all types of stresses: cold, heat, moisture, salt, and mechanical. One important attribute of hardiness is that it can refer to all the various tissues of a plant (buds, foliage, stem, and roots), although the shoots become much more hardy than the roots, which are protected by the soil or growing medium (Figure 3B).

The main way that hardiness is measured is by resistance

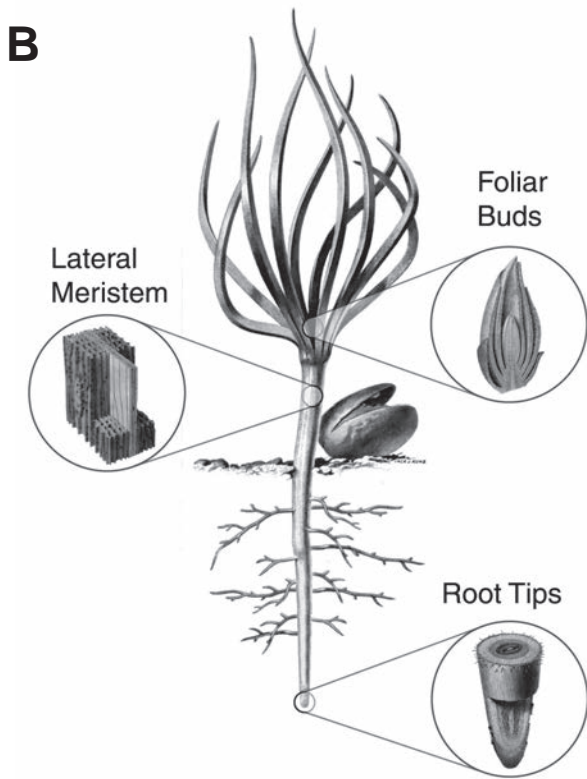


Figure 3 - Frost hardiness (A) is the most common type of hardiness, although hardy plants are resistant to all types of stresses. One of the major differences between hardiness and dormancy is that, while hardiness refers to entire plants, dormancy refers to activity of one of the three meristems: buds, lateral meristems in the stem, and root tips (B). Bud dormancy is often thought of in terms of a firm resting bud (C), but species with indeterminate growth never form buds.

to cold injury, and two cold hardiness tests are commonly used: the whole plant freezing test and the freeze-induced electrolyte leakage test (Landis and others 2010). Both tests have two steps: first, plants or plant parts are exposed to a freezing stress and, second, the amount of cold injury is rated. Cold hardiness testing is currently the second most common seedling quality test ordered by nurseries and reforestation specialists. Experience has shown that, when plants are at their maximum state of cold hardiness, they are also the most resistant to the many stresses of harvesting, handling, storage, shipping, and outplanting. In fact, recent genetic research has revealed that some of the same (dehydrin) gene complexes that are involved in cold acclimation also play a key role in resistance to water stress (Wheeler and others 2005).

## 2.2 Dormancy

Dormancy can be defined as “a state of minimal metabolic activity”, or “any time that a plant tissue is predisposed to grow, but does not” (Lavender 1984). So, when plants are dormant, they are not growing — cells are not dividing or enlarging. Dormancy is one of the oldest concepts in plant science. Nursery workers learned by trial and error that plants could be transplanted and outplanted most successfully when they

were not actively growing. In the temperate zone, this occurs during the winter.

One of the major differences between hardiness and dormancy is that, although we talk about dormant nursery stock, dormancy refers to a specific meristematic tissue, usually buds (Figure 3C). In the same plant, the buds may be dormant while the lateral meristem may not. Root meristems never truly go dormant and will grow anytime that environmental conditions, especially temperature, are favorable. So, the common nursery expression of dormant plants is a misnomer.

All nursery stock, except in the tropics, goes through a seasonal dormancy cycle (Figure 4). In spring, as day length and temperatures increase, plant buds swell and shoots begin to grow. Shoot growth is most rapid in the spring and early summer but slows down after the summer solstice as day length (photoperiod) becomes shorter. At the end of the growing season, determinate plants form terminal and lateral buds, whereas indeterminate plants just stop growing as the shoots become dormant. Dormancy is more visible in deciduous plants as their leaves change color and fall off as autumn progresses. During the winter, shoot dormancy is released by exposure to an extended period of low temperatures. Once this “chilling

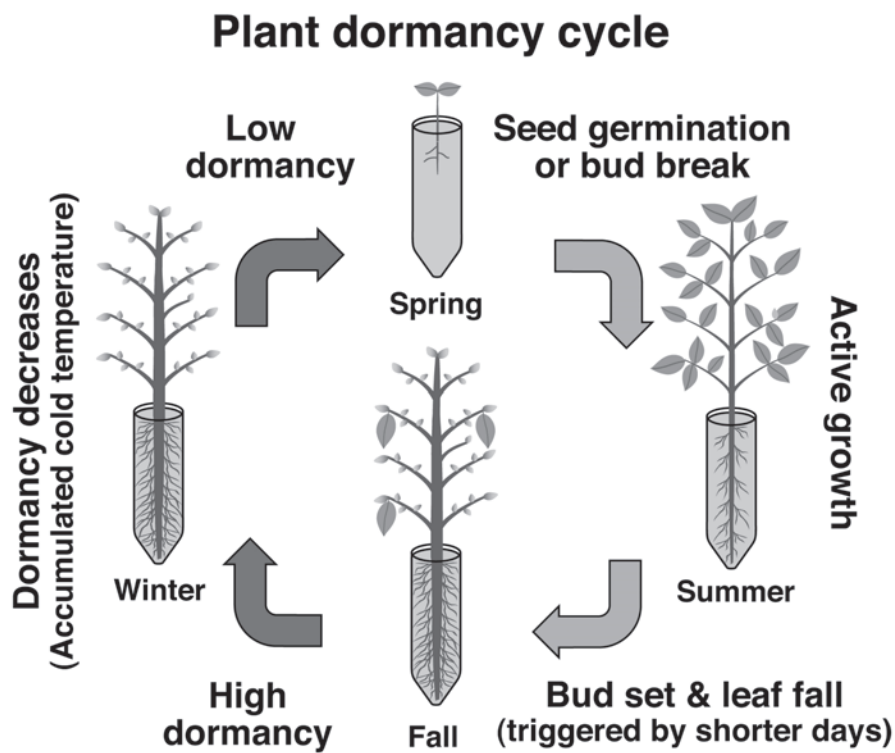


Figure 4 - The buds of perennial plants in the temperate zone go through a seasonal cycle of shoot growth and dormancy. Note that peak dormancy occurs in late fall instead of midwinter, as is often believed, and that dormancy is released by cumulative exposure to cold temperatures (“chilling requirement”) (from Jacobs and Landis 2009).



requirement” is satisfied, warm spring temperatures and will trigger bud break and shoots will begin to grow again (Jacobs and Landis 2009).

### 3. Cultural Objectives of the Hardening Phase

Nursery managers should strive for five different objectives during hardening.

#### 3.1 Manipulate seedling morphology

The first objective of hardening is to slow down and eventually stop shoot growth, while shifting carbohydrates to the lateral meristem to increase stem diameter and to the roots. This is critically important to nursery stock quality because stem diameter has consistently been shown to be the single best predictor of outplanting performance (Mexal and Landis 1990). Developing an expansive root system is also very important and root growth shows a surge during late summer and early fall (Figure 2). Shoot-to-root ratio (shoot:root) is the ratio of the dry mass or volume of the shoot to the dry mass or volume of the root system and provides an indicator of the “balance” of the plant. Shoot-to-root ratios less than 2.5:1 are usually deemed more desirable, especially on hot and dry outplanting sites where a relatively small shoot loses less water through transpiration (Landis and others 2010).

The development of large, firm buds in determinate species, such as pines, also happens during the hardening phase (Figure 3C). Although the presence and size of buds are not, by themselves, good indications of plant quality, they have traditionally been considered desirable by foresters and other customers. Perhaps the most important aspect of bud development is the number of needle primordia and this has been used as an index of plant quality (Colombo and others 2001). Some customers of conifer stock prefer their seedlings to have secondary needles, which often develop during the hardening phase; for instance, lodgepole pine (*Pinus contorta*) seedlings with secondary needles have better outplanting performance (van Steenis 1993).

#### 3.2 Minimize overwinter injuries

One of the best reasons to properly harden your nursery plants is to avoid the 3 main types of overwinter damage: cold injury, winter desiccation, and frost heaving. Early fall frosts frequently kill succulent plant tissue (Figure 3A), whereas hardy shoots are uninjured because the tissues have developed rigid cell walls and are covered with a waxing coating. Both container and bareroot stock that is

overwintered outside can be damaged by winter desiccation, which occurs during sunny, windy weather. Unfortunately, even hardy plants can be desiccated when these conditions persist for a long time. Bareroot plants can be damaged by frost heaving, especially smaller stock without a deep and extensive root system.

#### 3.3 Acclimatize stock to ambient conditions

Container nursery plants, especially those grown in greenhouses, are especially succulent and need to be gradually acclimatized to outside conditions. Moving them from the greenhouse to a shadehouse or open growing compound at the start of the hardening phase will help them develop hardy tissue that can better tolerate the stresses of lifting, packaging, and storage (Mexal and others 1979).

#### 3.4 Develop stress resistance for storage, handling, and outplanting

Hardy and dormant plants with thick walled cells and foliage covered with a protective waxy coating are much more tolerant of the many stresses they will encounter after leaving the nursery. Desiccation is the major hazard for nursery plants from the time they are harvested to when they are well established on the outplanting site. When dormant and non-dormant Norway spruce (*Picea abies*) container plants were subjected to weeks of moisture stress and then outplanted, the dormant plants produced significantly more new roots at the higher stress treatments (Figure 5).

#### 3.5 Fortify plants for outplanting

The final cultural objective for the hardening phase is to prepare plants to survive and grow after outplanting.

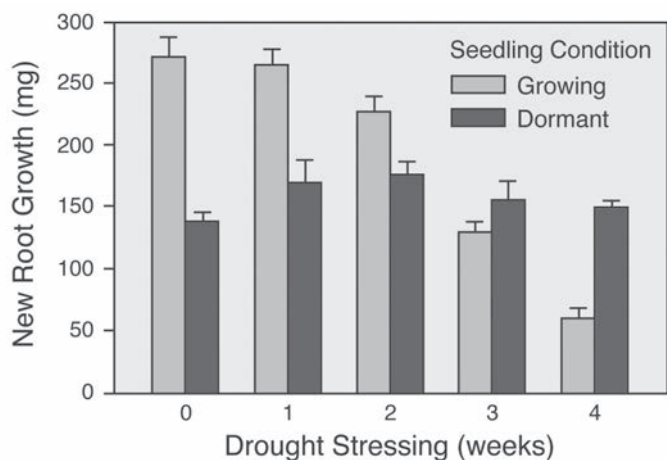


Figure 5 - When spruce seedlings were exposed to drought and then outplanted, those that were dormant had more new roots growing out from the root plug (root egress) after three weeks (modified from Helenius and others 2005).

The idea behind “nutrient loading” is that nursery plants supercharged with high levels of nitrogen will survive and grow better on outplanting sites where mineral nutrients are limiting. The process involves fertilizing seedlings during the hardening phase until their nitrogen content is in the luxury consumption area of the growth curves. Nutrient loading has been very successful with black spruce (*Picea mariana*) on sites with heavy plant competition (Timmer 1997).

## 4. Cultural Practices to Induce Hardiness and Dormancy

Nursery managers can use 4 cultural treatments to manage hardiness and dormancy (Figure 6).

### 4.1 Reduce fertilization, especially ammonium nitrogen

In general, the continued application of high nitrogen fertilizers, especially those containing ammonium, promotes succulent shoot growth and retards dormancy. For example, red maple (*Acer rubra*) seedlings grown at high (300 ppm) nitrogen levels retained their leaves about 3 weeks longer than those grown at more normal rates (Gilliam and others 1980). Just as high nitrogen is one of the primary cultural factors used to stimulate shoot growth during the rapid growth phase, lowering nitrogen levels is a logical and effective way to control height and induce hardiness (Young and Hanover 1978). Nitrate, rather than ammonium, and increased calcium levels have also proven beneficial to promote dormancy and hardiness.

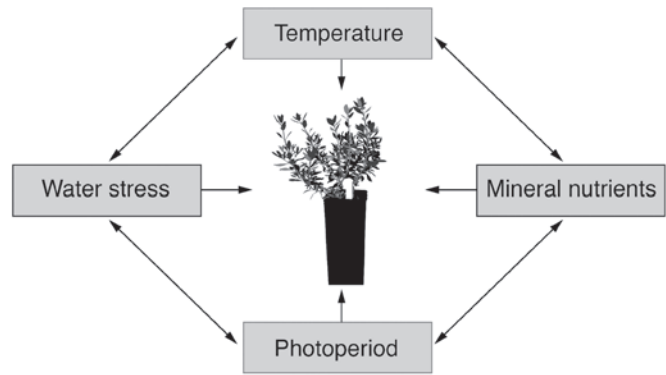


Figure 6 - Nurseries can manipulate four cultural factors to stop shoot growth and induce hardiness (Landis and others 1999).

Container growers use a “clearwater rinse” at the start of the hardening phase to flush any excess nitrogen from the growing medium, and then use a special hardening fertilization program. Calcium nitrate is a soluble fertilizer that is often used during the hardening phase (Landis and others 1999). It would be much more difficult for bareroot nurseries to quickly change fertilizers (Table 1) but avoiding high ammonium fertilizer formulations during hardening would be advisable. On the other hand, nursery stock that is nutrient deficient will not be as hardy or dormant as plants receiving proper fertilization. When exposed to freezing temperatures, Scots pine (*Pinus sylvestris*) seedlings that had received adequate fertilizer showed less cold injury than those that were nutrient deficient (Rikala and Repo 1997).

### 4.2 Induce mild water stress

Research has shown that a mild moisture stress reduces shoot growth, promotes bud dormancy, and hardens

Table 1 - Cultural treatments used to harden seedlings in bareroot and container nurseries

Growth Limiting Factors	Bareroot Nurseries	Container Nurseries
Temperature	None	1) Greenhouse - Move seedlings to shadehouse or open compound 2) Shelterhouse - Raise sides and remove roof, if possible 3) Open compounds - None
Moisture	Withhold irrigation to induce mild moisture stress as part of a comprehensive hardening program	Withhold irrigation to induce mild moisture stress as part of a comprehensive hardening program
Mineral Nutrients	Stop fertilizing with nitrogen 4 weeks before start of hardening period	Leach growing media with water; switch to low nitrogen fertilizer
Light	None, but blackout could be effective	1) Greenhouse - Turn off photoperiod lights; deploy blackout curtains 2) Shelterhouse - Turn off photoperiod lights; deploy blackout curtains 3) Open compounds - Deploy blackout curtains over hoops

the tissues of some species but this often has been difficult to achieve in nursery practice. With some species, even moderate moisture stress can be detrimental to the hardening process. For example, moisture stress had no effect on induction of shoot dormancy in western hemlock (*Tsuga heterophylla*) and actually inhibited the beneficial effects of the other dormancy treatments (O'Reilly and others 1989). One of the problems with moisture stress treatments is reaching the proper stress level uniformly for the entire crop. Because bareroot seedlings have access to a larger volume of soil, inducing a mild moisture stress is easier than with container stock that has access to a limited volume of growing media and where irrigation cannot be applied equally to every plant. Another problem is applying rather precise research results from controlled conditions to an entire crop under operational conditions. For example, a moderate plant moisture stress (PMS) treatment of -1.5 MPa induced bud set and shoot dormancy in blue spruce (*Picea pungens*) seedlings but, if the stress reached higher PMS levels of -1.8 to -2.0 MPa, foliar injury occurred (Young and Hanover 1978). Conversely, a very well designed irrigation experiment with container white spruce (*Picea glauca*) found that a mild water stress did nothing to induce frost hardiness (Carles and others 2005). So, growers should test their own species and should consider that a mild moisture stress will be most effective when applied in combination with reduced fertilization, cooler temperatures, and reduced photoperiod (Table 1).

### 4.3 Expose seedlings to cold temperatures

Most temperate zone seedlings must be able to tolerate below-freezing temperatures to avoid damage from early fall frosts and, tolerate overwinter storage. When about 80 to 90% of the crop has reached the target height and bud set is complete (Figure 1), temperatures can be lowered to begin conditioning the seedlings. Temperature modification is only possible with container plants in greenhouses (Table 1). Because the objective of this hardening phase is to slow and eventually stop shoot growth while encouraging stem diameter growth, exposing container crops to cooler temperatures is effective. This has the effect of maintaining sufficient rates of photosynthesis and respiration to promote stem diameter and root growth. The bud dormancy of most woody plants is released by long-term exposure to temperatures slightly above freezing 40 to 45 °F (-5 to 7 °C); this time/temperature treatment is known as the chilling requirement (Landis and others 2010). Some species require exposure to freezing temperatures, especially at night. Night temperatures

have been shown to be more important than day temperatures for developing cold hardiness in Douglas-fir (*Pseudotsuga menziesii*) (van den Driessche 1969).

### 4.4 Shorten the photoperiod

Both light intensity and duration are important to hardening and dormancy induction. Although sensitivity to light is most pronounced in species from higher latitudes, some response has been achieved for most temperature zone species. Shortening the daylength (photoperiod) is primarily used with container stock, especially in greenhouses (Table 1); the naturally shortening daylength is also effective with bareroot plants. Short photoperiods induce cold hardiness in many species, especially when combined with cold temperatures. A short (8-hour) photoperiod was found to induce cold hardiness levels in loblolly pine (*Pinus taeda*) comparable to seedlings that had been acclimated naturally outdoors (Mexal and others 1979).

A shortened photoperiod is one of the most effective cultural treatments triggering the termination of shoot growth and formation of buds in many conifer seedlings, especially those from high latitudes (Hawkins and others 1996). Photoperiod can be shortened in 2 ways. First, in greenhouses, just shutting-off the crop lights that were used to extend photoperiod during the rapid growth phase will induce bud set. Growers should be aware that it is the relative rather than the absolute photoperiod that is effective. For example, seedlings that were grown under a 24-hour intermittent photoperiod set buds under a 18-hour treatment even though the latter is their normal summer daylength (Landis and others 1999). Second, excluding light with blackout curtains to shorten daylength to 8 or 12 hours has proven remarkably effective in stopping shoot growth and setting buds (Figure 7). These blackout or short-day treatments have mainly been tested on conifer species from high latitudes such as Canada and Scandinavia, but they are also effective on broadleaved species such as silver birch (*Betula pendula*) (Luoranen and Rikala 1997). It would be interesting to know if species from middle latitudes would also respond to these treatments. Blackout has been successfully used to induce dormancy and hardiness in a forest nursery at approximately 40° latitude (Jopson 2007).

While blackout is very effective in terminating shoot growth and inducing budset, the timing and duration of the treatments must be coordinated with outplanting windows. Several early studies showed that blackout treatments in the fall resulted in early or irregular budbreak the following spring (van Steenis 1992). Similarly, Norway spruce seedlings outplanted in the fall showed

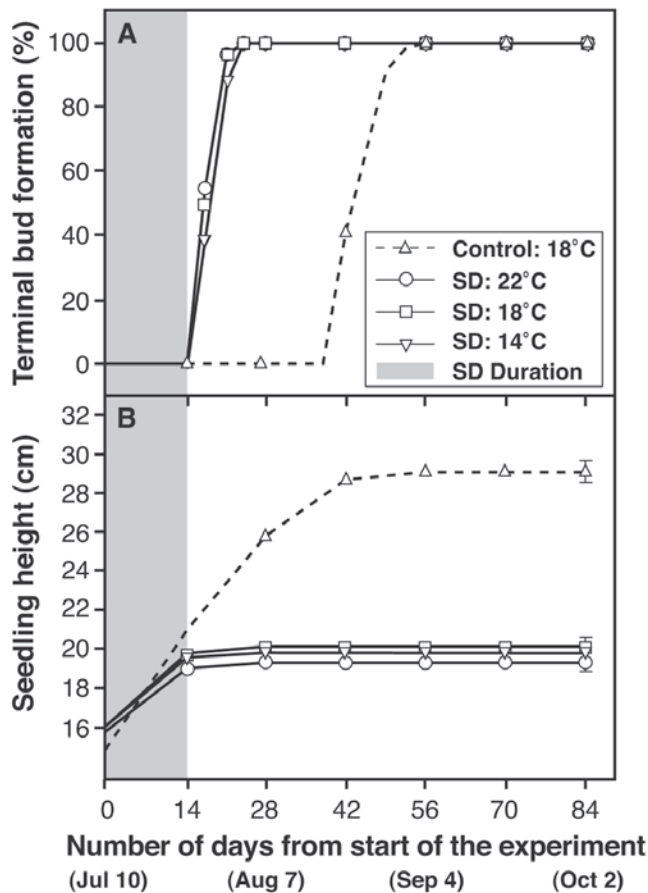


Figure 7 - Shortening photoperiod with blackout curtains, also known as short-day (SD) treatments, has proven remarkably effective in stopping height growth (A) and inducing budset (B) in conifer seedlings from high latitudes (modified from Floistad and Granhus 2010).

an increased risk of a second flush after an early-season blackout treatment (Kohmann and Johnsen 2007). In another study, seedlings that were given blackout followed by cold acclimation showed decreased frost hardiness in their lateral meristems the following spring (Floistad and Granhus 2010). Several recent research studies have examined the relationship between blackout treatments and premature budbreak after outplanting (for example, Luoranen and others 2009).

## 5. Practical Applications Regarding Hardiness and Dormancy

So, as you can see, the hardening phase is critical to producing quality nursery stock that will survive and thrive after outplanting. Here are some ways that you can apply this new information in your nursery:

### 5.1 Scheduling the hardening phase

One of the most serious mistakes that novice nursery managers make is not to allow enough time to harden stock properly. Hardening takes a minimum of 6 to 8 weeks, but the duration will depend on the timing of the outplanting window:

#### Summer outplanting (“hot planting”): 2 to 3 weeks.

These plants will be taken from the nursery before they have had the opportunity to full harden, and ambient temperatures are not low enough to be much help. Still, they should still receive several weeks of conditioning, including a mild moisture stress. Shortening of the photoperiod by blackout or short-day treatment for 2 to 3 weeks in mid to late summer is a common measure in forest nurseries to promote growth cessation and increase frost hardiness (Figure 7).

**Fall outplanting: 3 to 6 weeks.** Although they will not achieve full hardiness and dormancy, nursery stock to be outplanted in the fall must still be properly conditioned. Growers should reduce fertilization and restrict irrigation to induce periods of mild moisture stress. Again, blackout or short-day treatments for 2 to 3 weeks have shown to be effective. A new option, as discussed below, is to place the stock under refrigeration at cool, but not cold temperatures.

**Overwinter storage with winter or spring outplanting: 6 to 10 weeks.** This is the full hardening approach and adequate time should be scheduled to do the job properly. Apply all four cultural treatments: low nitrogen fertilization; periods of mild moisture stress; exposure to ambient temperatures, especially at night; and apply blackout if possible.

### 5.2 Protecting crops against fall frost injury

One of the best uses of the hardening phase is to start preparing your plants to tolerate early fall frosts. Frost damage to crops can be significant; for example, annual culling due to frost damage ranged from 5% to 30% in Quebec (Carles and others 2012). Irrigation is the most common method of protecting both bareroot and container nursery stock from frost injury. Heat is released when ice forms around shoot tissue but irrigation must continue until the risk of frost has passed (Rose and Haase 1996).

So, it would be helpful to have a reliable method to determine the cold hardiness of your plants so you could protect them if necessary. First of all, growers should check their weather records for the dates of the first frost and schedule the start of the hardening phase ac-



cordingly. Trying to force extra shoot growth into the fall to make grading specifications is a recipe for disaster. We know that plants become more cold hardy as they become more dormant and are exposed to cooler temperatures, so a measure of the amount of time that your plants are exposed to cool temperatures should be useful. Several methods of measuring accumulated exposure to cold have been used, such as chilling hours or degree hardening days. The process involves measuring the temperature each day and calculating the amount of time below a specific reference temperature. A method sometimes used in forest and conservation nurseries is to simply count the number of hours during which the air temperature is at or below a threshold value, such as 41 °F (5 °C) (Ritchie and others 1985). In Québec, bareroot white spruce seedlings are deemed ready for cold storage when the chilling sum that is based on the time below 41°F (5 °C) reaches 200 hours (Carles and other 2012). Reference temperatures will vary with nursery location and species; for example, 46 °F (8 °C) has been used for southern pines (Grossnickle 2008). The latest research combines hardening degree days below a threshold value of 58 °F (14.5 °C) measured 6.5 feet (2 m) above the crop with a measurement of the ratio of dry mass to fresh mass (DM/FM) of the upper 2 inches (4 cm) of the terminal shoot (Carles and other 2012). Considering the amount of variation in cold tolerance between species and ecotypes, each nursery should develop their own chilling sum procedure based on actual cold hardiness tests.

### 5.3 Determining lifting windows and storability

Another practical application of hardening and dormancy treatments is to establish the best time to harvest your plants, which is commonly known as the “lifting window”. This traditional concept was developed by harvesting and outplanting seedlings from late fall through early spring and measuring survival and growth (Jenkinson and others 1993). With the advent of seedling quality testing, bud dormancy and cold hardiness testing have been used to determine best time to harvest your crops and establish that they are ready for refrigerated storage. The standard test for measuring bud dormancy is a long and involved procedure compared to much easier and faster cold hardiness test (Landis and others 2010). This information shows that lifting in the late fall or early winter is preferential to waiting until late winter or early spring, especially when the plants are freezer stored (Figure 8). For example, recent research has shown that Norway spruce seedlings harvested in autumn can safely be freezer-stored for eight to nine months (Luoranen and others 2012).

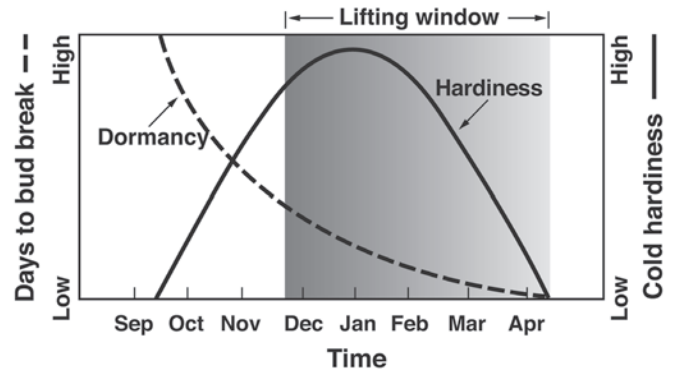


Figure 8 - Bud dormancy, as measured as days to bud break (DBB), and hardiness, as measured by cold hardiness tests, can be used to determine the best time to harvest nursery stock (the “lifting window”). However, cold hardiness tests are so much quicker and easier that they have become the standard test for determining lifting and subsequent refrigerated storage (modified from Landis and others 2010).

Container nurseries in western Canada use a “storability test” to determine if plants are physiologically ready for harvesting, packaging, and cold storage (L’Hirondelle and others 2006). Sample seedlings undergo cold hardiness tests and, if plants are cold hardy to a threshold temperature of 0 °F (-18 °C), then they are ready to withstand the stresses of storage. A similar storability test based on a freeze-induced electrolyte leakage threshold of -4 °F (-20 °C) was determined to be effective for assessing storability of pedunculate oak (*Quercus robur*) bareroot seedlings in Denmark (Bronum 2004). Of course, these temperature thresholds would have to be determined for different species in different climates.

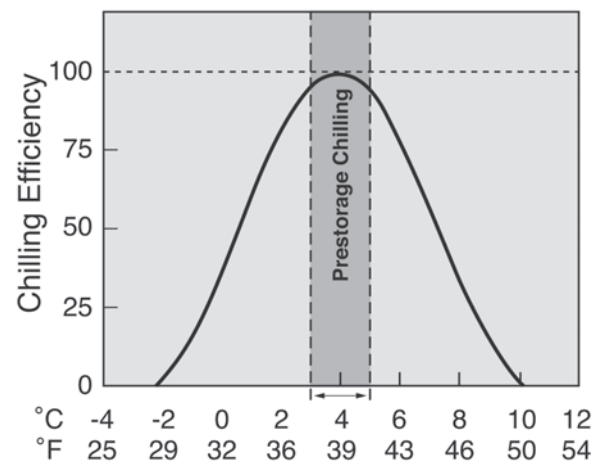


Figure 9 - Research has shown that the chilling requirement is best satisfied with temperatures above freezing, so placing container stock in refrigerated storage at 37 to 41 °F (3 to 5 °C) should augment chilling sums (modified from Landis and others 2020).



One interesting new aspect of chilling sums involves placing container stock in cooler storage to artificially augment their exposure to cold temperatures. I'm not aware of any published research or operational trials but this procedure should work. We know that the chilling requirement is best satisfied from 37 to 41 °F (3 to 5 °C) so an exposure period to these temperatures should be effective (Figure 9). The idea that refrigerated storage could substitute for exposure to cold temperatures was first proposed for Douglas-fir (Ritchie 1989) and elaborated in the Assessing Plant Quality chapter of Volume Seven of the Container Tree Nursery Manual (Landis and others 2020).

## 6. References

- Bronnum P. 2004. Does autumn climate affect the applicability of shoot frost hardiness as an operational test parameter for storability of pendunculate oak (*Quercus robur* L.) seedlings. In: Cicarese L, ed, Nursery production and stand establishment of broadleaves to promote sustainable forest management, IUFRO S3.02.00. Rome, Italy: APAT: 25-31.
- Carles SA, Lamhamedi MS, Stowe DC, Veilleux L, Margolis HA. 2012. An operational method for estimating cold tolerance thresholds of white spruce seedlings in forest nurseries. *Forestry Chronicle* 88 (4): 448-457.
- Carles SA, Stowe DC, Lamhamedi MS, Fecteau B. 2005. Turning off the tap: controlling nutrient leaching, growth and hardening of containerized white spruce seedlings through irrigation management. In: Colombo SJ, ed. The thin green line: a symposium on the state-of-the-art in reforestation, proceedings. Sault Saint Marie (ON): Ontario Ministry of Natural Resources. Forest Research Information Paper 160: 77-82.
- Colombo SJ, Sampson PH, Templeton CWG, McDonough TC, Menes PA, DeYoe D, Grossnickle SC. 2001. Assessment of nursery stock quality in Ontario. In: Wagner RG, Colombo SJ, eds. Regenerating the Canadian forest: principles and practice for Ontario. Sault Saint Marie (ON): Ontario Ministry of Natural Resources: 307-323.
- Floistad IS, Granhus A. 2010. Bud break and spring frost hardiness in *Picea abies* seedlings in response to photoperiod and temperature treatments. *Canadian Journal of Forest Research* 40:968-976.
- Gilliam CH, Stil SM, Moor S, Watson ME. 1980. Effects of three nitrogen levels on container-grown *Acer rubrum*. *HortScience* 15(5):641-642.
- Grossnickle SC. 2008. Personal communication. Brentwood Bay (BC): CellFor Inc. Research scientist.
- Hawkins CDB, Eastham AM, Story TL, Eng RYN, Draper DA. 1996. The effect of nursery blackout application on Sitka spruce seedlings. *Canadian Journal of Forest Research* 26(12):2201-2213. (6990)
- Helenius P, Luoranen J, Rikala R. 2005. Physiological and morphological responses of dormant and growing Norway spruce container seedlings to drought after outplanting. *Annals of Forest Science* 62: 201-207.
- Jacobs DF, Landis TD. 2009. Hardening. In: Dumroese RK, Luna T, Landis TD, eds. Nursery manual for native plants: a guide for tribal nurseries. Volume 1, Nursery management. Washington (DC): USDA Forest Service. Agriculture Handbook 730: 216-227.
- Jenkinson JL, Nelson JA, Huddleston ME. 1993. Improving planting stock quality—the Humboldt experience. Berkeley (CA): USDA Forest Service, Pacific Southwest Research Station. General Technical Report PSW-143. 219 p.
- Jopson T. 2007. Blackout cloth for dormancy induction. In: Riley LE, Dumroese RK, Landis TD, technical coordinators. 2007. National proceedings, forest and conservation nursery associations—2006. Fort Collins (CO): USDA Forest Service, Rocky Mountain Research Station. Proceedings RMRS-P-50: 36-37.
- Kohmann K, Johnsen O. 2007. Effects of early long-night treatment on diameter and height growth, second flush and frost tolerance in two-year-old *Picea abies* container seedlings. *Scandinavian Journal of Forest Research* 22(5): 375-383.
- L'Hirondelle SJ, Simpson DG, Binder WD. 2006. Overwinter storability of conifer planting stock: operational testing of fall frost hardiness. *New Forests* 32(3):307-321.
- Landis TD, Dumroese RK, Haase DL. 2010. The container tree nursery manual. Volume 7, Seedling processing, storage, and outplanting. Washington (DC): USDA Forest Service. Agriculture Handbook 674. 200 p.
- Landis TD, Tinus RW, Barnett JP. 1999. The container tree nursery manual. Volume 6, Seedling propagation. Washington (DC): USDA Forest Service. Agriculture Handbook 674. 167 p.
- Lavender DP. 1984. Bud dormancy. In: Duryea ML, ed. Evaluating seedling quality: principles, procedures, and predictive abilities of major tests. Corvallis (OR): Oregon State University, Forest Research Laboratory: 7-15.

- Luoranen J, Riikonen J, Rikala R, Sutinen S. 2012. Frost hardiness, carbohydrates and bud morphology of *Picea abies* seedlings after different lengths of freezer storage, Scandinavian Journal of Forest Research 27(5): 414-419.
- Luoranen J, Konttinen K, Rikala, R. 2009. Frost hardening and risk of a second flush in Norway spruce seedlings after an early-season short-day treatment. *Silva Fennica* 43(2): 235-247.
- Luoranen J, Rikala R. 1997. Growth regulation and cold hardening of silver birch seedlings with short-day treatment. *Tree Planters' Notes* 48(3/4):65-71.
- Mexal JG, Landis TD. 1990. Target seedling concepts: height and diameter. In: Rose R, Campbell SJ, Landis TD, eds. Proceedings, target seedling symposium, combined meeting of western forest nursery associations. Fort Collins (CO): USDA Forest Service, Forest and Range Experiment Station. General Technical Report RM-200: 17-35.
- Mexal JG, Timmis R, Morris WG. 1979. Cold-hardiness of containerized loblolly pine seedlings: its effect on field survival and growth. *Southern Journal of Applied Forestry* 3(1):15-19.
- O'Reilly C, Owens JN, Arnott JT. 1989. Bud development in container-grown western hemlock seedlings subjected to different dormancy induction treatments. *Forestry* 62(Suppl.):169-179.
- Rikala R, Repo T. 1997. The effect of late summer fertilization on the frost hardening of second-year Scots pine seedlings. *New Forests* 14: 33-44.
- Ritchie GA. 1989. Integrated growing schedules for achieving physiological uniformity in coniferous planting stock. *Forestry (Suppl)* 62: 213-226.
- Ritchie GA, Roden JR, Kleyn N. 1985. Physiological quality of lodgepole pine and interior spruce seedlings: effects of lift date and duration of freezer storage. *Canadian Journal of Forest Research* 15: 636-645.
- Rose R, Haase DL. 1996. Irrigation for frost protection in forest nurseries: room for improvement. *Western Journal of Applied Forestry* 11: 16-19.
- Timmer VR. 1997. Exponential nutrient loading: a new fertilization technique to improve seedling performance on competitive sites. *New Forests* 13: 279-299.
- van den Driessche R. 1969. Measurement of frost hardiness in two-year-old Douglas-fir seedlings. *Canadian Journal of Plant Science* 49:159-172.
- van Steenis E. 1993. Lodgepole pine culture: current trends in B.C. In: Proceedings, 12th annual meeting of the Forest Nursery Association of British Columbia. Vernon (BC): British Columbia Ministry of Forests: 93-96.
- van Steenis E. 1992. In: Landis TD, ed. Intermountain Forest Nursery Association, proceedings, 1991. General Technical Report RM-211. Fort Collins, CO: USDA Forest Service, Rocky Mountain Forest and Range Experiment Station: 103-105.
- Wheeler NC, Jermstad KD, Krutovsky K, Aitken SN, Howe GT, Krakowski J, Neale DB. 2005. Mapping of quantitative trait loci controlling adaptive traits in coastal Douglas-fir. IV. Cold-hardiness QTL verification and candidate gene mapping. *Molecular Breeding* 15: 145-156.
- Young E, Hanover JW. 1978. Effects of temperature, nutrient, and moisture stresses on dormancy of blue spruce seedlings under continuous light. *Forest Science* 24(4): 458-467.