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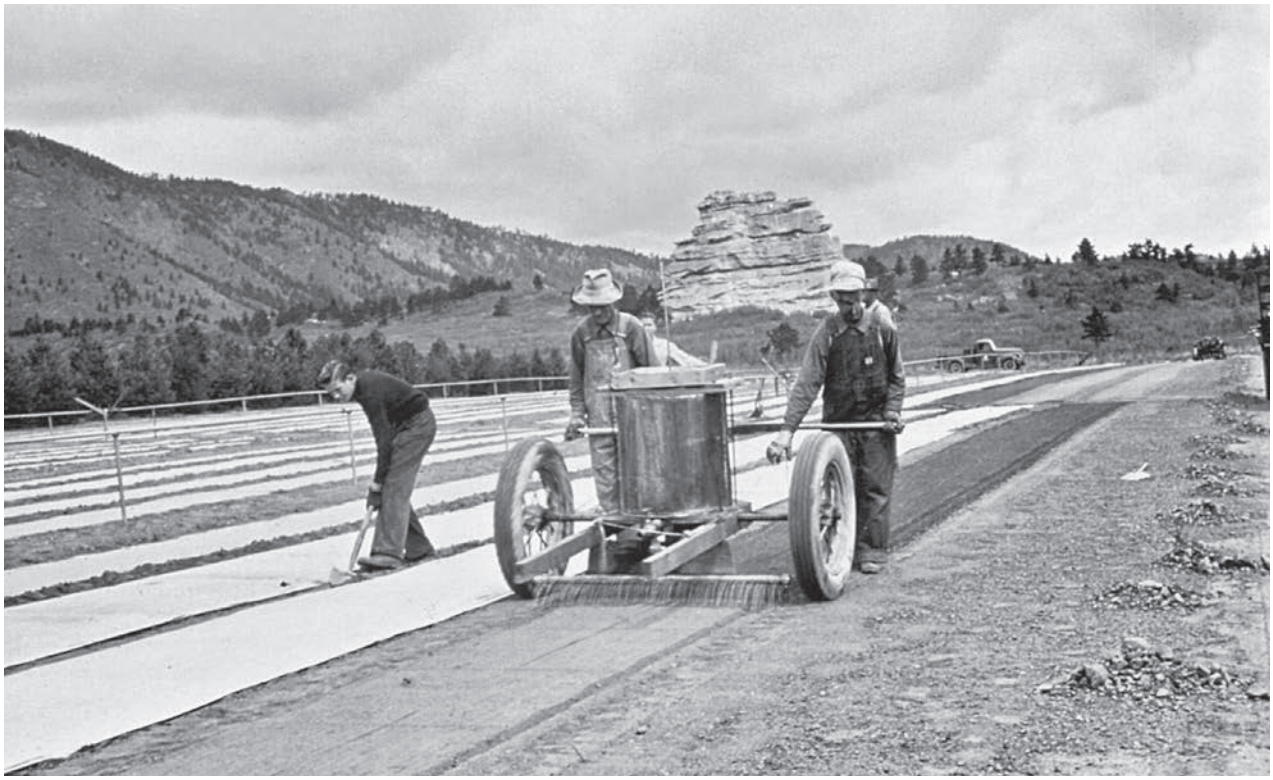

Cover Photo:
Historical photo of workers at the USDA Forest Service Monument nursery in Colorado applying acid directly to seedbeds to control damping-off.

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Forest Nursery Notes Team

R. Kasten Dumroese, Editor-In-Chief
USDA Forest Service
Rocky Mountain Research Station
1221 S. Main Street
Moscow, ID 83843-4211
TEL: 208.883.2324
FAX: 208.883.2318
E-Mail: kdumroese@fs.fed.us

Tom D. Landis, Lead Author & Editor
Forest Nursery Consultant
3248 Sycamore Way
Medford, OR 97504-9005
TEL: 541.210.8108
FAX: 541.858.61l0
E-Mail: nurseries@aol.com

Rae Watson, Requests & Mailing List
Dorena Genetic Resource Center
34963 Shoreview Drive
Cottage Grove, OR 97424
TEL: 541.767.5717
FAX: 541.858.6110
E-Mail: rewatson@fs.fed.us

Laura Hutchinson, Library Services
USDA Forest Service
North Central Research Station
1992 Folwell Avenue
St. Paul, MN 55108
TEL: 651.649.5272
E-Mail: lhutchinson@fs.fed.us

Nursery Meetings

Note: Because FNN is only printed twice a year, the following information is necessarily dated. For the most up-to-date information on meetings about nurseries, reforestation, and restoration, visit the RNGR Website: www.rngr.net

The **Second National Native Seed Conference** will be held **April 9 to 11, 2013** in Santa Fe, New Mexico. This conference will feature the latest research from around the world on a wide variety of subjects concerning plant materials used in restoration.

For more information, check out the conference website:

http://www.nativeseed.info

The **combined Northeastern and Southern Forest Nursery Association** meeting will be held **July 22 to 25, 2013** in Lafayette, Indiana. The agenda will include technical presentations and exhibits as well as tours of the Purdue University Hardwood Tree Improvement and Regeneration Center, Vallonia Nursery, and Arbor America who specialize in plantations of black walnut.

For more information, contact:

Western Forestry & Conservation Association
4033 SW Canyon Rd. • Portland, Oregon 97221
TEL: 503.226.4562
http://www.westernforestry.org/

The **Western Forest and Conservation Nursery Association** meeting will be held **August 6 to 7, 2013** in Olympia, Washington, and hosted by the Washington Department of Natural Resources. This year's theme will be "Life in the Underground: management of soils, growing media, and roots in the production of forest and conservation seedlings".

If you would like to give a presentation or just want the latest information, contact:

Diane L. Haase
Western Nursery Specialist • USDA Forest Service
333 SW First Ave • Portland, OR 97208
TEL: 503.808.2349 • FAX: 503.808.2339
E-mail: dlhaase@fs.fed.us

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).

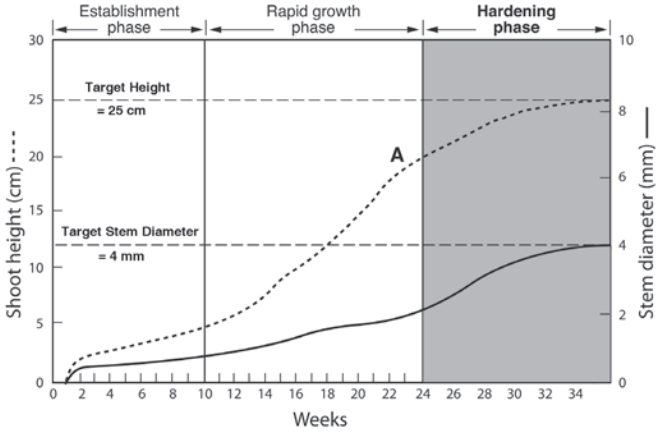

Figure 1 - The hardening phase is the last of 3 phases of nursery culture, where the objective changes from promoting fast growth to conditioning the plants to undergo the stresses of harvest, storage, and outplanting. The hardening phase usually begins when plants are 80 to 90% of their target height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

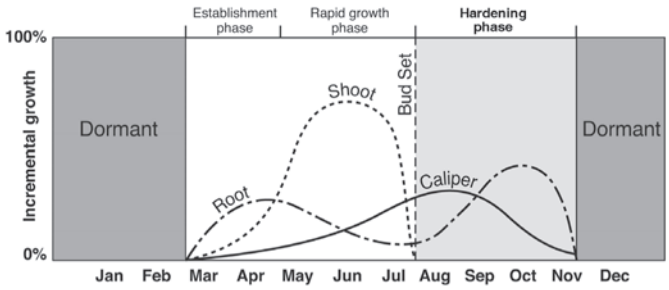

Figure 2 - Incremental growth curves are the best way to illustrate the timing of shoot, caliper, and root growth during the growing season. Target height has been reached by the Hardening Phase, when carbohydrates are shifted from the shoot meristem to the lateral meristem (caliper growth), and the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

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

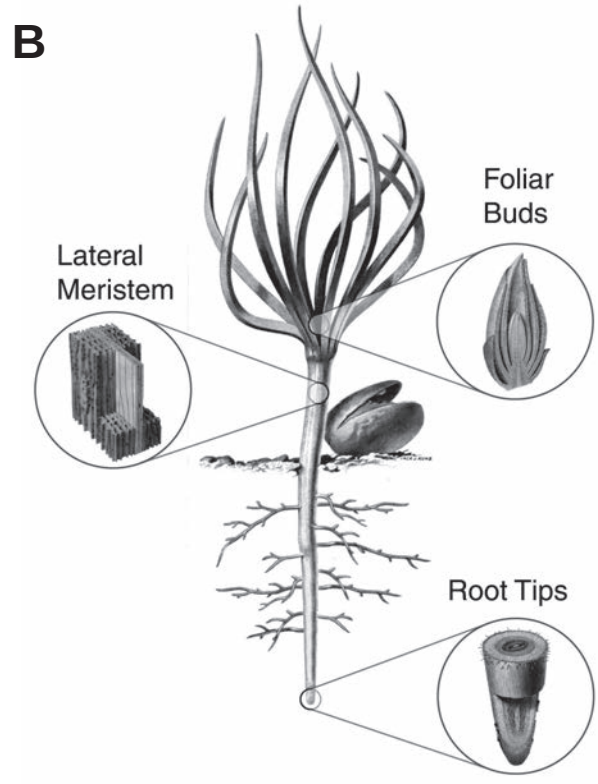

Figure 3 - Frost hardiness (A) is the most common type of hardiness, although hardy plants are resistant to all types of stresses. One of the major differences between hardiness and dormancy is that, while hardiness refers to entire plants, dormancy refers to activity of one of the three meristems: buds, 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

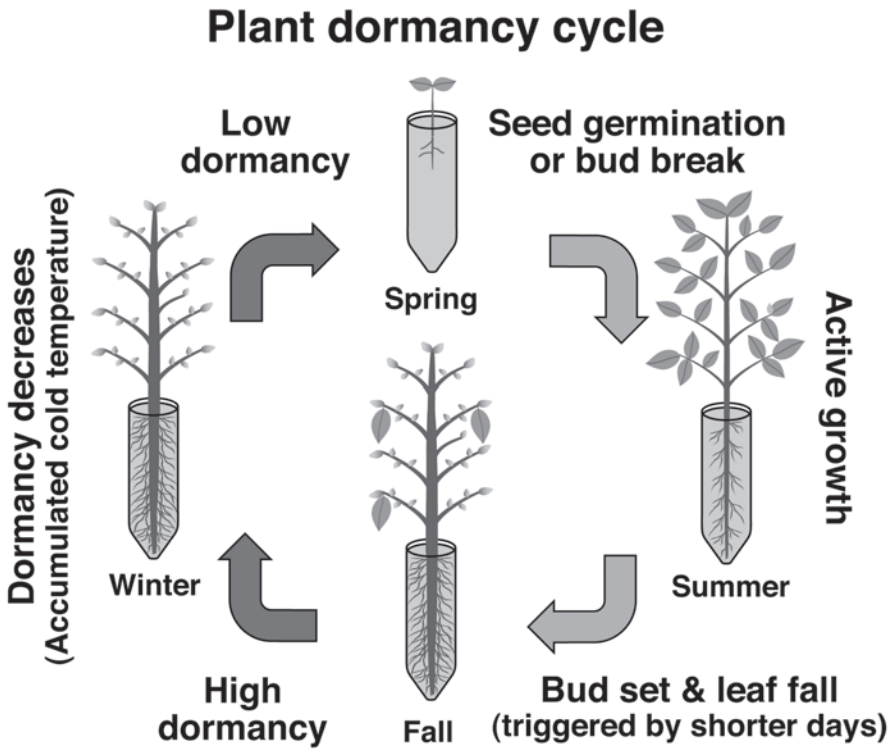

Figure 4 - The buds of perennial plants in the temperate zone go through a seasonal cycle of shoot growth and dormancy. Note that peak dormancy occurs in late fall instead of midwinter, as is often believed, and that dormancy is released by cumulative exposure to cold temperatures ("chilling requirement")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

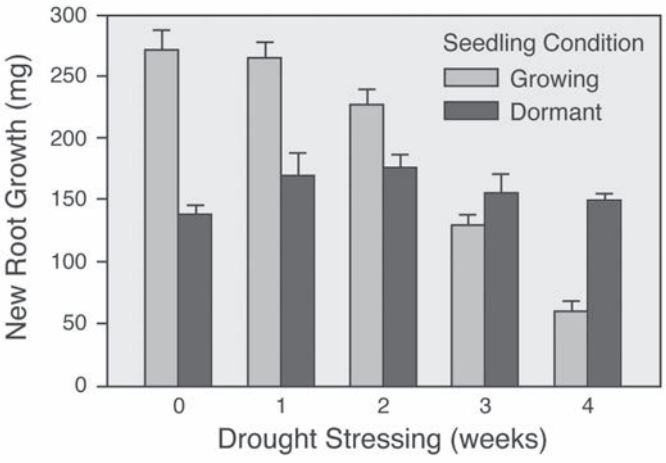

Figure 5 - When spruce seedlings were exposed to drought and then outplanted, those that were dormant had more new roots growing out from the root plug (root egress) after three weeks (modified from Helenius and others 2005).

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.

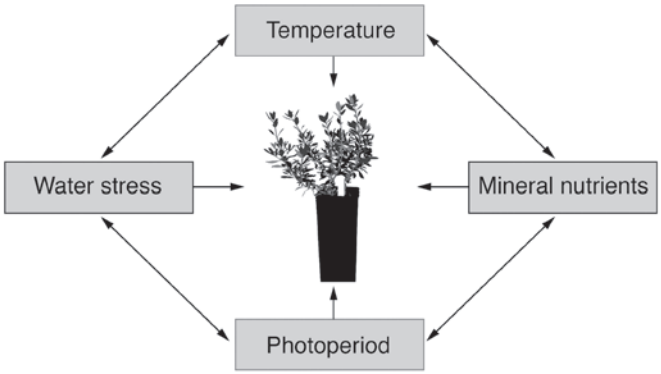

Figure 6 - Nurseries can manipulate four cultural factors to stop shoot growth and induce hardiness (Landis and others 1999).

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

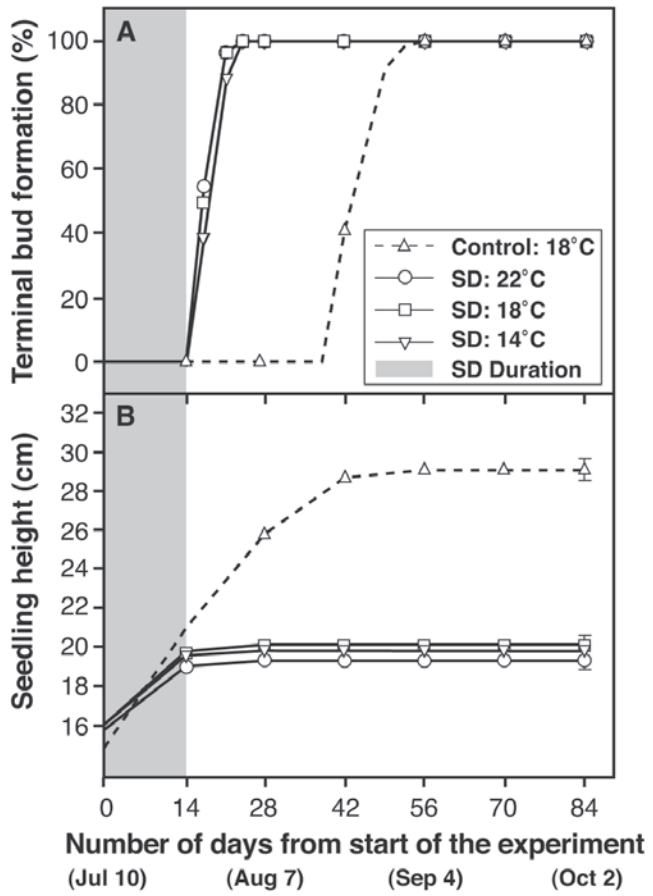

Figure 7 - Shortening photoperiod with blackout curtains, also known as short-day (SD) treatments, has proven remarkably effective in stopping height growth (A) and inducing budset (B) in conifer seedlings from high latitudes (modified from Floistad and Granhus 2010).

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 (Grossnicle 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).

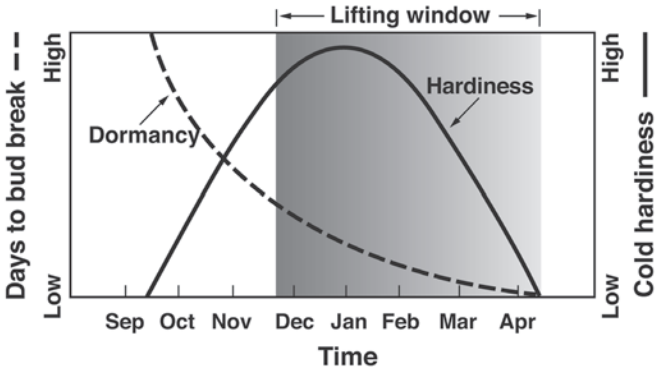

Figure 8 - Bud dormancy, as measured as days to bud break (DBB), and hardiness, as measured by cold hardiness tests, can be used to determine the best time to harvest nursery stock (the "lifting window"). However, cold hardiness tests are so much quicker and easier that they have become the standard 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.

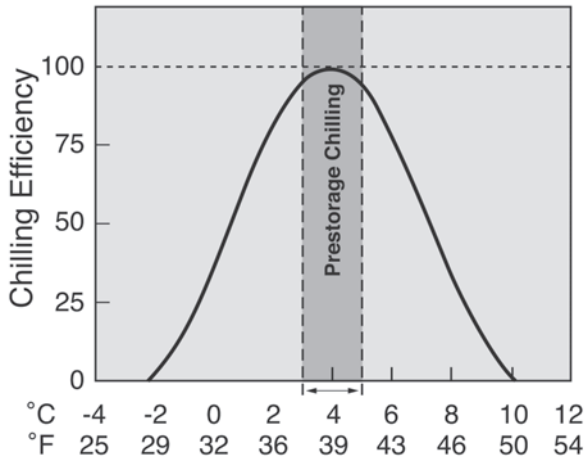

Figure 9 - Research has shown that the chilling requirement is best satisfied with temperatures above freezing, so placing container stock in refrigerated storage at 37 to 41 °F (3 to 5 °C) should augment chilling sums (modified from Landis and others 2020).

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).

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***Phytophthora ramorum*: Impacts on Forest, Conservation and Native Plant Nurseries**

by Thomas D. Landis

This article was written with the help of many experts who were gracious enough to share their knowledge and experience: Gary Chastagner and Marianne Elliott, Washington State University; Susan Frankel and Ellen Goheen, USDA Forest Service; Prakash Hebbar, USDA, APHIS; Jennifer Parke, Oregon State University; and Jane Alexander, University of California.

Phytophthora ramorum (PRAM) is a fungus-like pathogen that, although it was originally identified on ornamental plants in a German nursery (Werres and others 2001), has become a destructive forest pest in the coastal forests of California, Oregon and in other locations in Europe. Because more than 100 species of trees and shrubs from 36 different families are susceptible (Chastagner and others 2012), PRAM has the potential to become the most serious forest pest since white pine blister rust and chestnut blight. Disease symptoms on nursery stock are relatively minor and, what's most worrisome, is that many infected plants show no visible symptoms at all (Vercauteren and others 2013). Genetic testing has proven that long-range spread can be attributed to the shipping of infected nursery stock, and that PRAM can then be transmitted from nurseries to surrounding forests (Mascheretti and others 2008).

Although PRAM has not proven to be a disease with severe symptoms in nurseries, it can still have serious economic impacts due to plant quarantine regulations. At one ornamental nursery in Southern California, more than 1 million camellias worth $9 million had to be destroyed because of a PRAM infestation (Alexander 2006). PRAM has only been positively identified on ornamental nursery stock as of the current date, but it is only a matter of time until infections are discovered on forest, conservation and native plant species. Because they ship their plants directly into forests and other natural settings, forest and native plant nurseries represent a serious transmission threat. Unfortunately, this has already happened in the United Kingdom where nursery stock has been show to be the cause of a devastating forest disease outbreak in Japanese larch (*Larix kaempferi*) plantation where 3 million trees have been killed (Brasier 2012).

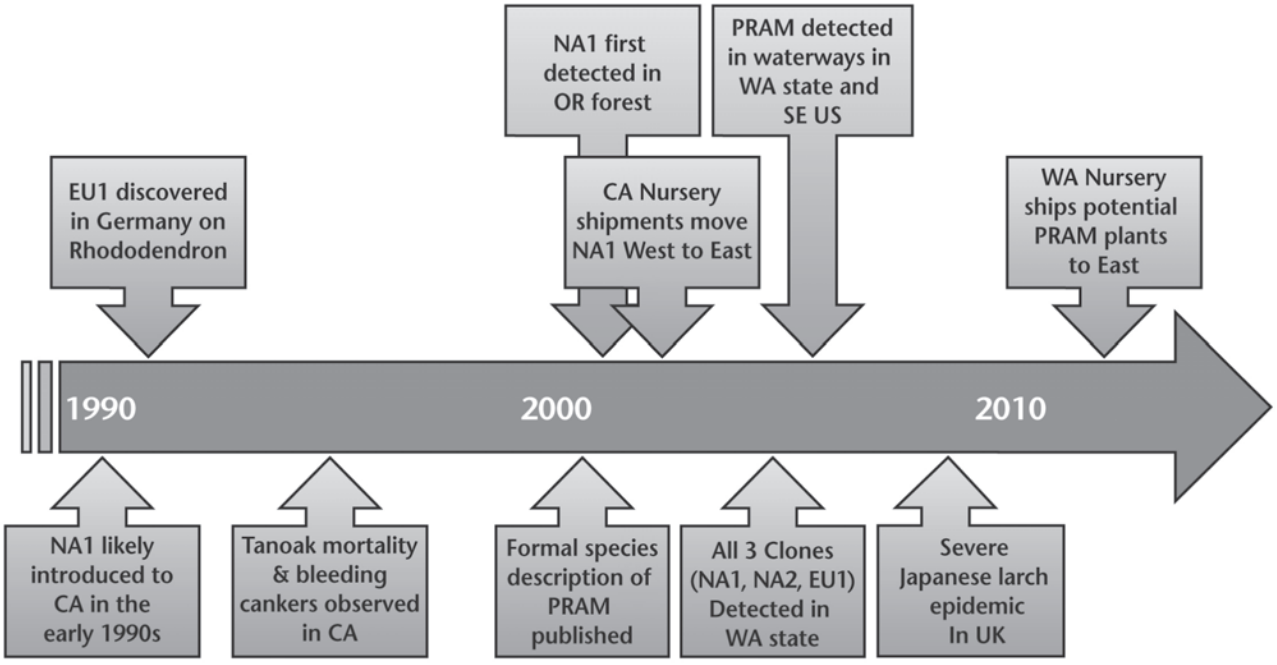

Figure 1 - Phytophthora ramorum *(PRAM) is a new and aggressive pest that affects plants in nurseries, but is much more destructive in plantations and natural forests. So far, 3 clones (EU1, NA1, NA2) have been identified (modified from Grunwald 2011).*

1. A New and Complicated Pest

Phytophthora species resemble true fungi because they grow by hyphae and produce spores, but they are actually more closely related to brown algae. Disease symptoms caused by Phytophthoras include blights, cankers, dieback, wilts, root rots, and decline. To make diagnosis even more challenging, some species cause multiple symptoms on a single host, or different symptoms on different hosts (Forest Phythophthoras of the World 2012). In nurseries, Phytophthora root rot has been a serious but well known nursery pest for decades, where the most common symptoms were root decay and lower stem canker (Cram and Hansen 2012).

What makes PRAM unusual and interesting is that nobody is exactly sure where it originally came from. Although PRAM has been identified only in North America and Europe, it is not considered to be native to either of these continents (Grunwald 2011). PRAM was first detected on ornamental nursery stock in Europe in the early 1990s (Figure 1). The first evidence that this pathogen had reached the US was the sudden oak death (SOD) epidemic in the coastal forests of northern California and southern Oregon where trees with bleeding stem cankers were dying at an alarming rate (Goheen and others 2006). The first detection of PRAM in a US nursery was on ornamental rhododendron container plants in Santa Cruz, California in December, 2000 (Alexander 2006). Based on microsatellite laboratory analysis, researchers determined that PRAM made its first appearance in California forests at 2 separate sites in northern California. Because the genetics of the forest strains were identical to those from local nurseries, this is strong evidence that PRAM entered California via the nursery trade (Mascheretti and others 2008).

Another unusual aspect of PRAM is its genetic makeup. *Phytophthora* genetics are discussed in terms of "clades", which are a group of organisms with similar features that are derived from a common ancestor. As of 2011, researchers had identified 3 clades for PRAM that were named for where they were first identified (Grunwald 2011). The European clade (EU1) was first identified on ornamental nursery plants in the early 1990s but has since been found on ornamental plantings and in the forest (Table 1). The first North American clade (NA1) was responsible for the SOD epidemic that was identified in the mid 1990s in northern California, and was subsequently confirmed in ornamental nurseries in the area. The NA2 clade was first identified on nursery stock in Washington State (Chastagner 2013) where, by 2005, the NA1 and EU1 clades were also discovered (Figure 1). Just last year, a fourth, genetically distinct clade of PRAM (EU2) was identified as the cause of an epidemic stem canker disease of Japanese larch in the United Kingdom (Brasier 2012). The European clades are of mating type A1 and the North American clades of type A2. The fact that PRAM clades of both mating types were identified in Washington State gives cause for concern but, so far, no evidence of mating has been discovered although it has been accomplished in the laboratory (Garbelotto and others 2006).

2. Symptoms

The symptoms of PRAM vary considerably in both type and intensity between different plant species and between plants in nurseries and forests; as we will discuss, this latter fact is a major concern.

2.1 Forests

Sudden oak death (SOD) is the most common disease caused by PRAM in the US, but it only affects woody plants in forests (Table 2). An unusual die-off of tanoaks (*Lithocarpus densiflorus*) in Marin County, California in early 1995 was the first evidence of SOD and the

Table 1 - Genetic clades and mating types of Phytophthora ramorum

Clade	Year Discovered	Distribution	Habitat	Mating
NA1	Early 1990s	North America	Forest, nurseries	A2
NA2	Early 2000s	Washington State, California & British Columbia	Nurseries	A2
EU1	Early 1990s	Europe & North America	Forests, nurseries, ornamental plantings	A1
EU2	2011	United Kingdown	Forests	A1
Modified from Grunwald (2011); Brasier (2012)				

Table 2 - Three diseases caused by the fungus-like pest Phytophthora ramorum *(PRAM)*

Disease	Symptoms	Host Examples	Forest Problem	Nursery Problem
Sudden oak death (SOD)	Bleeding stem cankers, tree death	Oaks, tanoak, larch	YES	NO
PRAM shoot blight	Shoot tip dieback	Redwood, Douglas-fir, white fir, red fir	YES	YES
PRAM leaf blights	Spots and necrosis on leaf edges & tips	Rhododendron, viburnum, camellia, Oregon myrtlewood	YES	YES
Modified from Goheen and others (2006); Chastagner and others (2012)				

symptoms consisted of scattered patches of dying trees with their entire crowns dead due to bleeding basal cankers. A couple of years later, other trees including coast live oaks (*Quercus agrifolia*) exhibited similar symptoms. The rapid spread of the disease in an urban-wildland interface in a highly populated area caused public concern, and all the dead trees caused a severe fire hazard. New PRAM hosts included California bay laurel (*Umbellularia californica*) and coastal redwood (*Sequoia sempervirens*) and by 2009 the host list included 109 plant species (Kliejunas 2010). Even more concerning was that PRAM was discovered in remote locations in the coastal forests of southwestern Oregon in 2001 (Goheen and others 2006).

2.2 Nurseries

Disease symptoms on nursery stock are much less severe than those of SOD, and generally consist of leaf and shoot blights (Chastagner and others 2012). In addition, host species are noticeably different in nurseries compared to forests (Table 2; Figure 2). Although ornamental cultivars of *Rhododendron, Camellia, Viburnum, Pieris,* and *Kalmia* are most commonly infected, most of these genera have native species somewhere in the US. Even more worrisome is that the "Others" category in Figure 2A contains *Aesculus*, *Pseudotsuga*, *Acer*, and *Quercus*. As far as I've been able to find out, no plants in forest, conservation, or native plant nurseries have been positively identified for PRAM as of the present date but Douglas-fir and true fir Christmas trees have been infected (Figure 2B). Considering the rapid spread of this pathogen so far and the extensive host list, all nursery workers should be vigilant and employ the latest phytosanitary procedures.

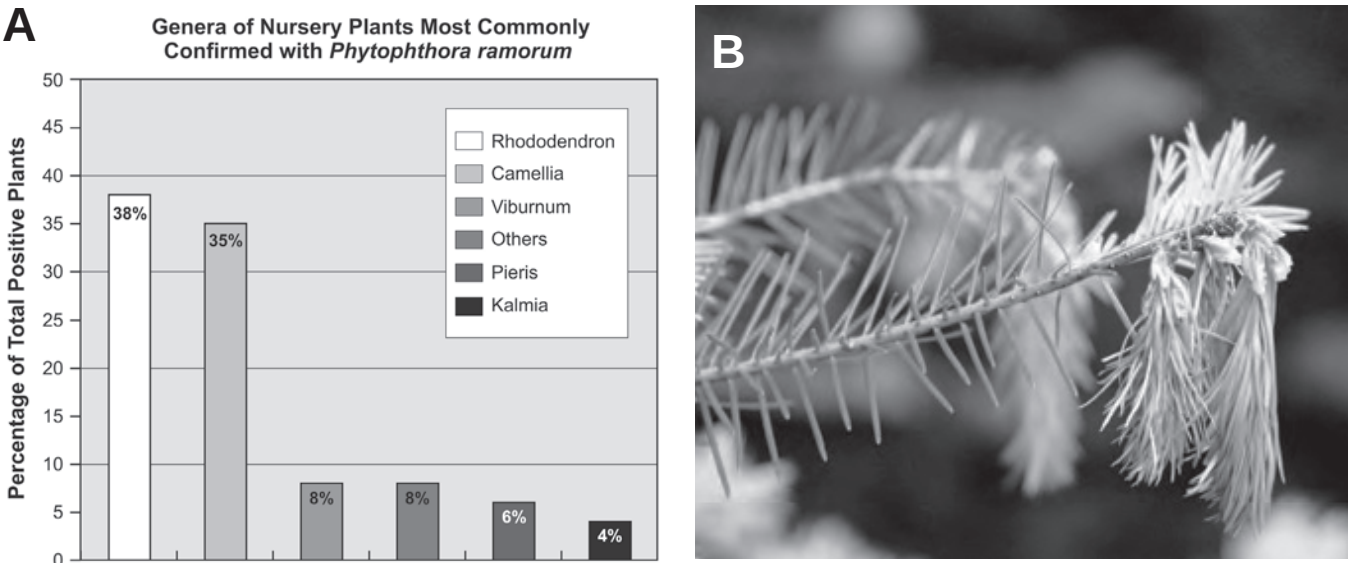

Figure 2 - Most of the nursery plants commonly infected with Phytophthora ramorum *are not produced by forest and native plant nurseries (A). However, many woody natives have been shown to be susceptible, and infections of native Christmas trees has been documented (B) (A, from USDA - APHIS 2011; B, from Chastagner 2013).*

3. Disease Spread

Phytophthora ramorum has proven to be an aggressive pathogen both in the nursery and in the natural stands. One of their unusual but operationally relevant characteristics is that all Phytophthoras produce zoospores which are able to swim in water (Figure 3A). PRAM also produces two other types of spores (Forest Phytophthoras of the World 2012). Chlamydospores are asexual structures that form in organic matter such as leaves and function as resting spores that allow the pathogen to survive periods of stress (Figure 3B). Oospores are sexual spores produced by the pairing of 2 opposite mating types (A1 & A2 in Figure 3C), but oospore formation has not been observed in nurseries where both mating types have been detected (Grunwald and others 2008). This is lucky because sexual recombination would create new challenges for controlling these pathogens.

PRAM can be spread from nursery to nursery and within nurseries in 2 different ways: on plant material or in water.

3.1 Plant material

Up until now, PRAM has spread both from nursery to nursery and from nursery to forest on infected nursery stock. This has occurred because plants infected with PRAM may or may not show visible symptoms; these latent infections have been shown to be responsible for long distance spread of this pathogen (Mascheretti and others 2008). PRAM could be transmitted between nurseries on transplants or cuttings and, because the pathogen can subsist in soil or growing media as chlamydospores (Figure 4A), could be spread on contaminated containers or even equipment. As of the present time, PRAM has not been positively identified on forest, conservation, or native plant nursery stock but, because so many plant species are susceptible, it's probably only a matter of time.

3.2 Water

Due to the ease with which the zoospores can move in water, this pathogen can easily move from plant to plant whenever free water is allowed to persist (Elliott 2012). In nurseries, this would account for most short distance spread. In research trials with container-grown *Rhododendron*, aerial dispersal of PRAM was minimal whereas spread in surface water between containers could occur over several meters (Huengens and others 2010). Another worrisome fact about PRAM is that the pathogen is able to escape nurseries in surface runoff water, presumably as

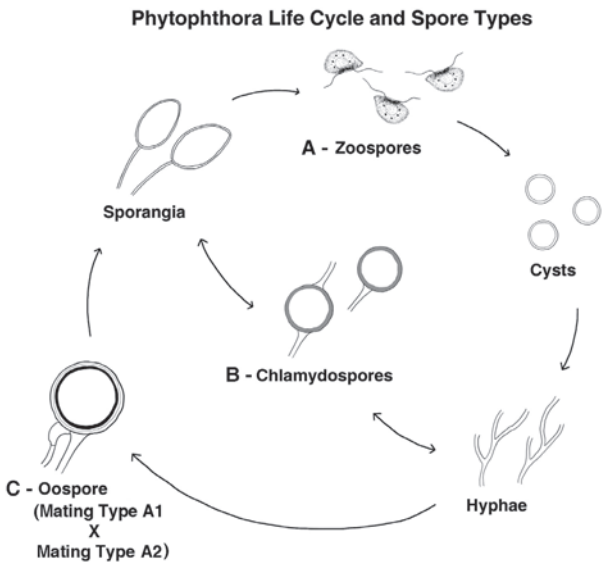

Figure 3 - Phytophthoras produce 3 types of spores: motile zoospores, which can actively disperse in water (A), chlamydospores (B), which can survive long periods in plant tissue or even organic matter, and thick walled oospores (C) that are sexually produced by the combination of the two mating types (modified from Phythophthoras of the World 2012).

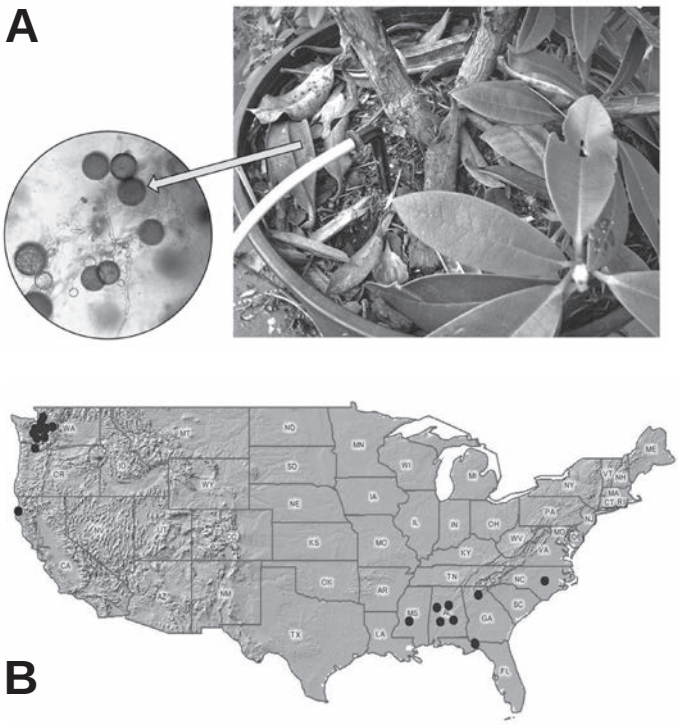

Figure 4 - Phytophthora ramorum *is spread between nurseries and from nurseries to forests in two ways: 1) On nursery stock as latent infections or chlamydospores in organic matter (A), or 2) In nursery runoff; for example, this pathogen has been detected in waterways around nurseries in 8 states (B) (A from Elliott 2012, and B from Chastagner and others 2010).*

Table 3 - Persistence of Phytophthora ramorum *in waterways in Washington State (modified from Chastagner 2013)*

County	Waterway	Year Detected						
		2006	2007	2008	2009	2010	2011	2012
King	Sammamish River		X	X	X	X	X	
	Ditch by Nursery 34		X		X	X	X	
	Little Bear Creek					X	X	
	Woodin Creek					X	X	X
	Cottage Lake Creek							X
Pierce	Rosedale Stream	X	X	X	X	X	X	
	Ditch by Nursery 45				X	X	X	
Thurston	Ditch by Nursery 41					X	X	
Lewis	Mill Creek						X	X
Clark	Ditch by Nursery 44					X	X	

zoospores, and then persist in ditches and other waterways, presumably as chlamydospores. As part of a joint project between the USDA-Forest Service and USDA-APHIS, a stream baiting survey has been underway since 2006 and PRAM has been detected in waterways in 8 states (Figure 4B). Washington State has done an intensive monitoring survey to document where PRAM has escaped nurseries to waterways (Chastagner and others 2010), and the results are troubling. PRAM has been detected in many water courses near nurseries and has proven to be very resilient (Table 3). As part of these water surveys, PRAM was detected on salal (*Gaultheria shallon*), a native forest understory plant. This is the first documented case of this pathogen escaping from an infested nursery through runoff and being spread to the surrounding forest (COMTF 2009).

4. Diagnosing *Phytophthora ramorum* in the Nursery

Many nursery diseases can be diagnosed by their unique signs and symptoms but this is not the case with PRAM. Signs and symptoms are extremely variable between hosts and are impossible to distinguish from other plant pathogens (including other *Phytophthora* species), insect damage or abiotic injury (Kliejunas 2010). The presence of the pathogen can only be confirmed through laboratory culturing on artificial media, or by molecular tests (Figure 5).

4.1 Culturing on selective media

PRAM can be isolated on selective artificial media and its identity confirmed by its unique morphological

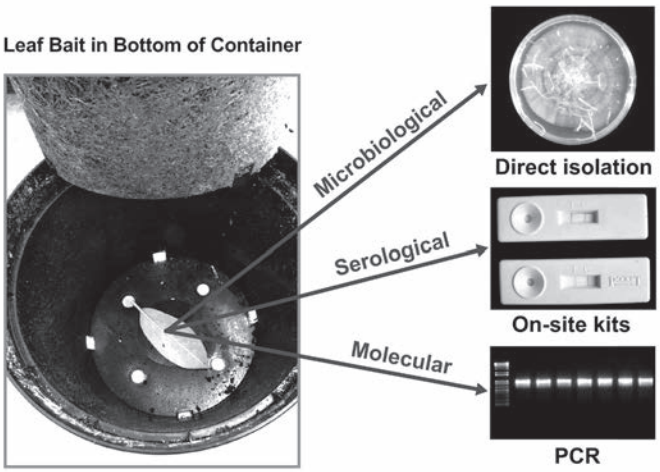

Figure 5 – Phytophthora ramorum *infections can be diagnosed by 3 different techniques (modified from Vercauteren and others 2013)*

characteristics. However, culturing from symptomatic plant material is time consuming and success may vary with the host plant. Differentiating PRAM from other *Phytophthora* species can sometimes be difficult (Kliejunas 2010).

4.2 Serological tests

The enzyme-linked immunosorbent assay (ELISA) test that uses antibodies and color change to identify a substance. An ELISA test that is specific to PRAM is not yet available, due to cross reaction with other *Phytophthora* and *Pythium* spp. (Avila and others 2010). If a large number of samples are to be processed for PRAM, ELISA can be used as a low-cost, prescreening to reduce the number of samples that will need to be processed for subsequent tests (Kliejunas 2010).

4.3 Molecular tests

Several different DNA-based molecular techniques have been used to diagnose PRAM infections, and are new variations are continually being developed (Kliejunas 2010). Both real-time and nested polymerase chain reaction (PCR) based molecular diagnostic assays have proven useful for detecting PRAM from leaf baits, and greatly reduce the turnaround time (Colburn and Jeffers 2011).

When the various diagnostic techniques were tested on camellia (*Camellia* spp.) plants at a California nursery, all the procedures were highly correlated with disease symptoms. The PCR test had the correlation, followed by ELISA, and finally culturing on selective media (Bulluck and others 2006).

The diagnostic protocols approved by the USDA APHIS-PPQ are explained in detail on their website:

http://www.aphis.usda.gov/plant_health/plant_pest_info/pram/downloads/pdf_files/DiagnosticsTable.pdf

5. Assessing the Threat

So, for us, the important question is: How big a threat is PRAM to forest and native plant nurseries? We don't have a ready answer, but looking back at past epidemics gives cause for concern (Table 4). Chestnut blight and white pine blister rust were devastating epidemics that are still affecting our forests, but these fungal diseases only affected one plant genus.

The host range for PRAM is currently at 36 plant families so the threat is potentially much greater (USDA-APHIS 2011). Pathologists consider PRAM as a generalist pathogen whose hosts include hardwood and conifer trees, shrubs, herbaceous plants, and ferns (Kliejunas 2010). Some hosts are native plants from forest environments but many of the most susceptible species as common landscape and ornamental plants. Five species of common shrubs comprise almost 95% of the confirmed PRAM infections (Figure 2), and disease

Table 4 - Comparison between previous disease epidemics and Phytophthora ramorum

Name of Pest		Date Introduced into US	Plant Hosts
Common name	**Scientific Name**		
Chestnut blight	*Cryphonectria parasitica*	Early 1900s	1 Genus: *Castanea*
White pine blister rust	*Cronartium ribicola*	Early 1900s	1 Genus: *Pinus*
Sudden oak death, Ramorum shoot or leaf blight	*Phytophthora ramorum*	Early 1990s	36 Families (and counting)

Table 5 - Annual detection of Phytophthora ramorum *in US nurseries*

Year	No. Of Positive Detections	No. Of States
2001	1	1 (CA)
2002	0	0
2003	20	3 (CA, OR, WA)
2004	176	21
2005	99	7
2006	62	11
2007	23	6
2008	28	8
2009	26	11
2010	34	13
2011 (through Sept)	25	5
Modified from Kliejunas (2010) and Alexander (2012)		

surveys showed a large variation in disease incidence among genera and specific cultivars within a genus (Tubajika and others 2006).

The explosive potential of this pest can be seen in the APHIS annual reports of the number of PRAM detections in US nurseries (Table 5). Since the initial detection in central California, the disease spread relatively slowly until 2004 when 2 large southern California ornamental nurseries shipped millions of infected container plants to other nurseries in 39 states (Frankel 2008). Inspections later that year revealed 176 nursery-related detections in 21 different states (Garbelotto and Rizzo 2005). As a result, the USDA Animal and Plant Health Inspection Service (APHIS) issued an order to inspect 1,400 nurseries that ship host plants or associated plants in California, Oregon, and Washington (Jones 2006). Even more recently, a nursery in Washington State shipped potentially infected *Gaultheria procumbens* nursery plants to customers in 30 states (Chastagner 2013).

6. Quarantine Considerations

As we discussed, the transport of nursery stock has been proven to be the primary means of long-distance spread of PRAM, and is also implicated in how the pathogen moves from the nursery to the forest. APHIS has adopted an interim federal quarantine to prevent the spread of PRAM to other parts of the U.S. Other states and countries such as Canada have also issued quarantines. APHIS maintains a website that contains the most current list of affected plant species (USDA-APHIS 2013), and has identified 3 categories of susceptibility to PRAM (Kliejunas 2010).

6.1 Regulated hosts

These are plants in which infections have been verified by Koch's postulates, which is the traditional test to confirm the a pest is the cause of the disease. Examples include: California maidenhair fern (*Adiantum aleuticum*), manzanita (*Arctostaphylos* spp.), false Solomon's seal (*Maianthemum racemosum*), Douglas-fir (*Pseudotsuga menziesii*), California black oak (*Quercus kelloggii*), and evergreen huckleberry (*Vaccinium ovatum*).

6.2 Associated plants

In this case, the plants have been naturally infected with PRAM and confirmed by culture or with PCR tests, but the infections have not been confirmed with Koch's postulates. Examples include: white fir (*Abies concolor*), vine maple (*Acer circinatum*), blueblossom (*Ceanothus thyrsiflorus*), California wood fern (*Dryopteris arguta*), Oregon grape (*Mahonia nervosa*), northern red oak (*Quercus rubra*), and Pacific yew (*Taxus brevifolia*).

6.3 Experimental hosts

These plants have been infected with PRAM in laboratory screening, but no actual infections have been documented in nature.

The issue of quarantines is complicated and frequently changing so check with your local forest pest experts or go to the following websites:

For the latest national information on PRAM: http://www.aphis.usda.gov/plant_health/plant_pest_info/pram/

For the latest PRAM information in Oregon: http://www.oregon.gov/ODA/CID/PLANT_HEALTH/Pages/sod_index.aspx

For the latest PRAM information in California: http://www.cdfa.ca.gov/plant/PE/interiorexclusion/SuddenOakDeath/

For the latest PRAM information in Washington: http://agr.wa.gov/plantsinsects/diseases/sod/

7. Implications for Forest, Conservation, and Native Plant Nurseries

Nurseries in the quarantine areas of the western states are already being impacted by PRAM, but all nurseries and nursery customers have an obligation to help stop this disease. Phytosanitation is the key to controlling the spread of any nursery pest, and can most simply be viewed as an input-output model. The basic idea is to prevent pests from entering your nursery as well as making certain that your plants are not carrying pests when they leave your nursery for sale or outplanting.

Two major approaches to phytosanitation can be employed. The systems approach is based on a Hazard Analysis of Critical Control Points and comprehensive programs that have been developed for ornamental nurseries can easily be modified for forest, conservation and native plant facilities (Parke and Grunwald 2012). A second approach based on target pests might be easier for smaller nurseries with limited funds and manpower. Here, the idea is to learn as much as possible about pests that are already found in your nursery or ones, like PRAM, that could threaten it. The following is a brief example of the target pest approach to phytosanitation.

7.1 Type of pest

PRAM a fungus-like pathogen that produces relatively minor symptoms in nursery stock, but research has shown that it can persist on plant material or even organic matter.

7.2 Method of spread

This pest produces 3 types of spores: motile zoospores, which can actively disperse in water; chlamydospores, which can survive long periods in plant tissue or even organic matter (Figure 4a); and thick walled oospores that are sexually produced by the combination of 2 mating types (Chastagner and others 2012).

7.3 Critical control points

Due to its many spore types, PRAM has multiple modes of transmission. It is most commonly spread through any type of plant material shared between nurseries including cuttings and transplants. Seed transmission has not been proven so far. Zoospores can spread through any form of water such as rain splash and surface runoff, and has been shown to persist in waterways around nurseries (Chastagner and others 2012).

By focusing on the type of pest and its methods of spread, nurseries can adapt their scouting and cultural practices to minimize adverse affects. Because their stock is outplanting directly into forests and other wild-land plant communities, nursery managers should be especially vigilant to make sure that PRAM isn't spread to or from their operation.

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Forest Nursery Pests: Damping-off

by Thomas D. Landis

Damping-off is a historical term that refers to the decay of germinating seeds and the stems of young seedlings (Figure 1A). It is also one of the oldest nursery problems—damping-off is the only disease discussed in detail in the classic nursery manual Nursery Practice on the National Forests (Tillotson 1917). Damping-off was considered "the most serious difficulty encountered in raising coniferous seedlings", and was the subject of one of the first comprehensive nursery pathology studies (Hartley and Pierce 1917).

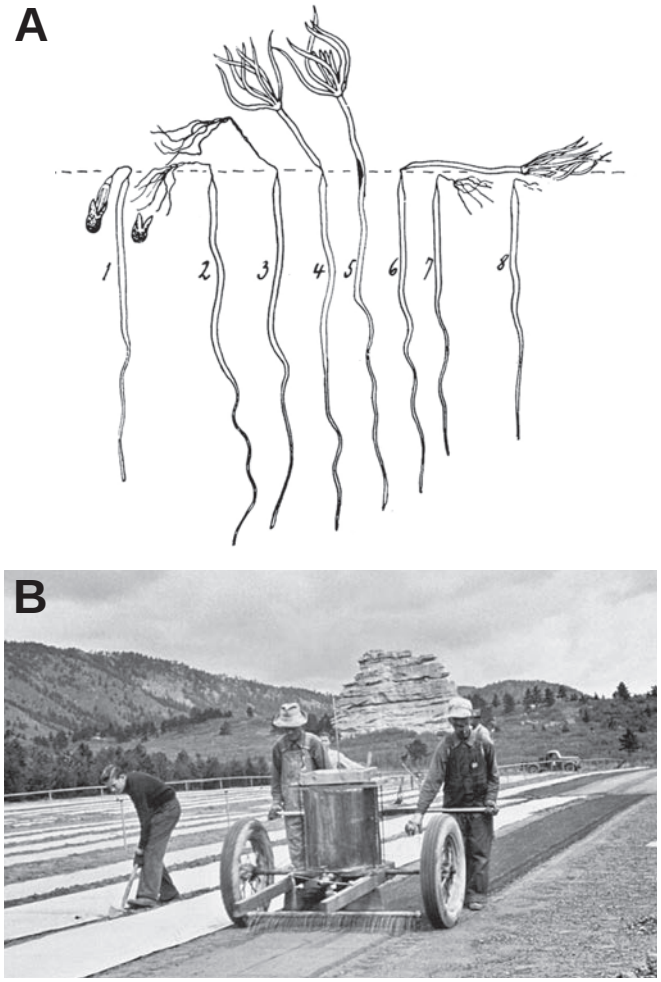


Figure 1 - The classic symptoms of damping-off include seedlings that topple over before their stems can become lignified; in this case, caused by heat injury (A). This disease was the major cause of seedling mortality in early nurseries, and research showed that lowering soil pH with direct applications of sulfuric acid was effective (B). (A - modified from Levitt 1980).

This early research revealed that lowering the pH of nursery soils helped to reduce damping-off losses, which at that time involved applying sulfuric acid directly to the seedbeds—a technique that would be frowned-upon today (Figure 1B).

1. Diagnosis and Damage

Two different types of damping-off are recognized (Figure 2), and these diseases affect plants in both bareroot and container nurseries:

1.1 Pre-emergence damping-off

This disease affects seeds and germinants before they emerge. Pre-emergence damping-off is a difficult disease to diagnose because the affected seeds are not visible; consequently, the losses are often attributed to "poor seed" (Baker 1957). If the germinants have not emerged after a reasonable period, the seed should be excavated and examined; if the seed contents are decayed, then damping-off fungi may be involved (A in Figure 2). Sometimes, germinating seeds are killed after the radicle has emerged (Figure 3A).

1.2 Post-emergence damping-off

This affects young seedlings until their stems become woody. The classic symptoms of post-emergence damping-off (B in Figure 2) include decay of the seedling hypocotyl at the ground line, causing the seedling to topple over (Figure 3B). Post-emergence damping-off symptoms can differ between different types of seedlings. With broadleaved species, the disease is expressed as necrotic areas at or below the groundline; infected seedlings wilt and die, but they often remain upright or break off just above the groundline. The symptoms of post-emergence damping-off of conifer seedlings occur at or slightly below the groundline and result in water-soaked, brownish or blackish lesions that rapidly become sunken or constricted. The specific pathogen causing damping-off cannot be determined on the basis of symptoms. Identification usually requires infected tissue culturing, which is important because knowledge of the specific pathogen may be useful in developing controls (James 2012a).

Other stresses such as heat or chemicals can produce damping-off symptoms; for instance, the surfaces of

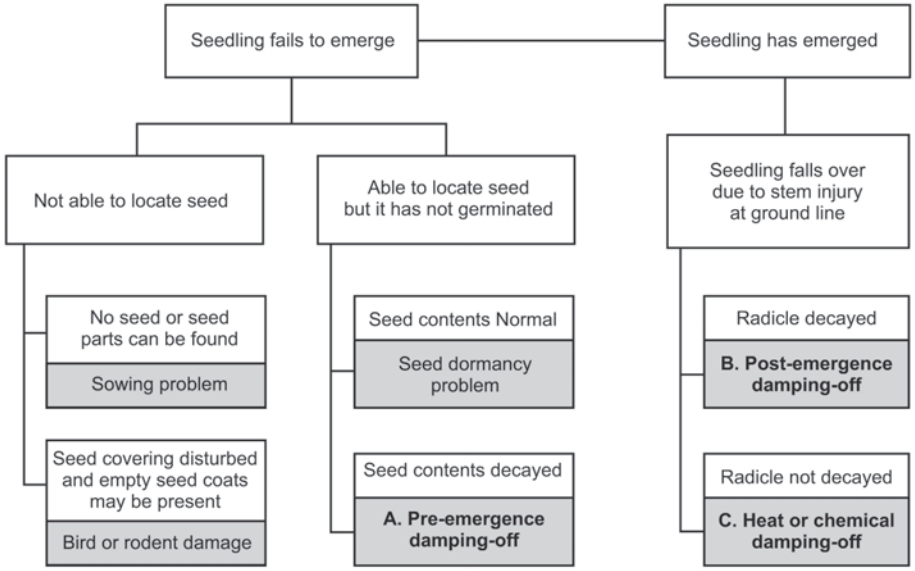


Figure 2 - Damping-off is a disease of germinating seeds (Pre-emergence - A) and young seedlings (Post-emergence - B), which also includes cotyledon blight. Although usually caused by fungi or oomycetes, stresses such as high surface soil temperatures can also cause damping-off symptoms (C) (modified from Landis and others 1990a).

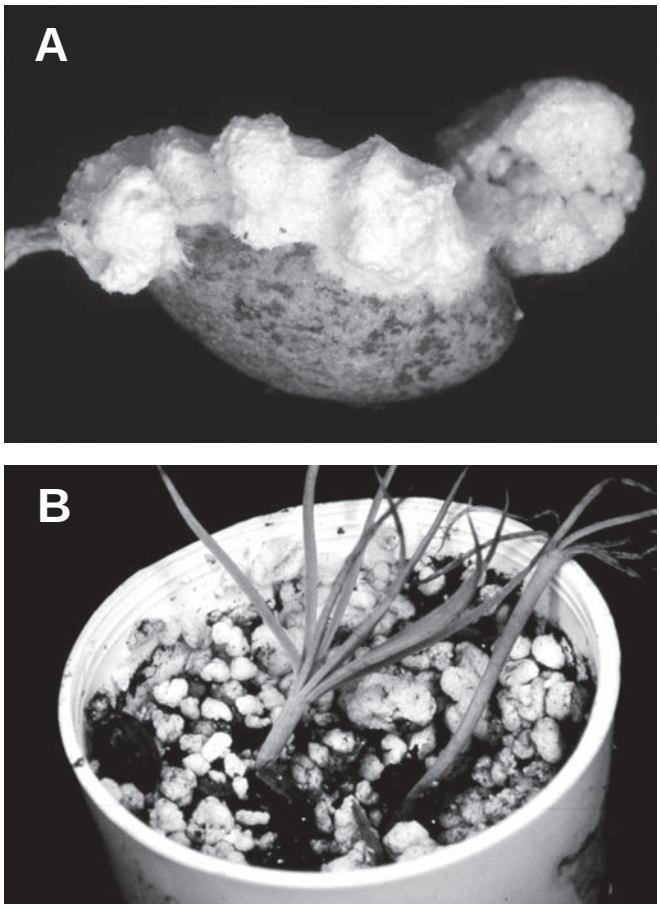


Figure 3 - In pre-emergence damping-off, germinating seeds are killed during germination—in this case by the fungus Fusarium *spp. (A). In post-emergence damping-off, decay of the stems of young seedlings causes them to topple over (B). Cotyledon blight of conifer seedlings occurs when a seedborne fungus spreads to the needle tips (C) (all photos from Landis and others 1990a).*

dark soils or mulches can become so hot that they kill seedling stem tissue (Figure 1A; C in Figure 2). The distinguishing characteristic between biotic and abiotic damping-off is the presence of decayed root tissue (Landis and others 1990a).

Another germinant disease that is usually classed with post-emergence damping-off is cotyledon blight. This decay of the tips of the cotyledons develops when seedborne fungi spread from the seedcoat during the "birdcage" stage of conifer seedling emergence (Figure 3C).

2. Hosts and Distribution

Damping-off is the most cosmopolitan nursery disease, and affects a wide variety of forest, conservation, and native plants from around the world (Table 1). Nursery stock in both tropical and temperate areas are susceptible. Most conifer and hardwood plant species are susceptible to damping-off, although some plants including junipers are not affected (James 2012a).

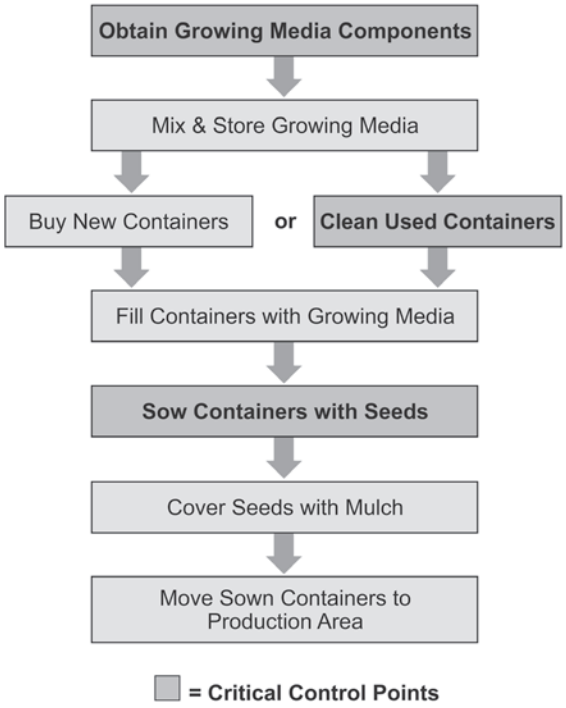
3. Causal Agents

Fungi (*Fusarium, Rhizoctonia*) and Oomycetes (*Phytophthora, Pythium*) are the most common causes of damping-off (James 2012a). However, fungi from several other genera including *Colletotrichum, Alternaria, Cylindrocladium,* and *Cylindrocarpon* have also been implicated (Table 1). Traditionally, *Rhizoctonia* spp. has been considered to be the major cause of damping-off in ornamental nurseries (Baker 1957) and is also been found causing disease of tree seedlings in foreign countries. Why it is not more commonly isolated in the US is interesting; it could be that its presence is masked by more rapidly growing fungi such as *Fusarium* spp. (Peterson 1974). The most recent literature (James 2012a) lists the most common damping-off

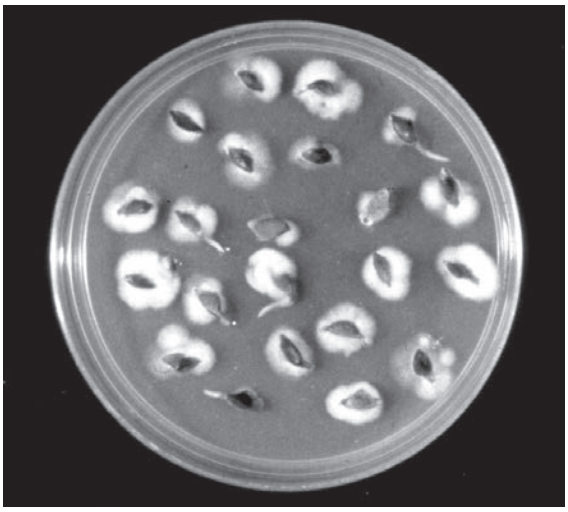
Table 1 - Damping-off is a cosmopolitan disease affecting plants from around the world

Pathogen	Host	County	Source
Fusarium spp.	*Pinus nigra*	Spain	Martin-Pinto & others (2008)
Colletotrichum acutatum, Fusarium oxysporum	*Cornus florida*	USA: Georgia	Britton (1995)
Fusarium oxysporum, Pythium spp., *Rhizoctonia solani*	*Pinus nigra*	France	Camporota & Perrin (1994)
Alternaria tenuis, Fusarium spp., *Pythium* spp., *Rhizoctonia solani*	*Eucalyptus* spp.	China	Dequn & Sutherland (1994)
Rhizoctonia solani	*Caragana arborescens*	Canada	Vaartaja & Cram (1956)
Cylindrocladium scoparium, Rhizoctonia solani	*Eucalyptus* spp.	Brazil	Ferreira & others (1997)
Rhizoctonia spp., *Pythium* spp.	*Picea smithiana*	India	Singh & others (1992)
Rhizoctonia spp.	*Pinus palustris*	USA: Florida	Starkey & Enebak (2012)
Fusarium spp.	*Pinus sylvestris*	Finland	Lilja & others (1992)
Fusarium spp., *Pythium* spp., *Thanatephorus* spp.	*Eucalyptus* spp., *Pinus caribaea, Acacia* spp.	Zimbabwe	Mazodze (1994)
Phoma herbarum, Phomopsis occulta	*Larix decidua*	France	Motta & Perrin (1994)
Fusarium spp., *Phytophthora* spp., *Rhizopus* spp.	*Santalum album*	India	Remadevi & others (2005)
Colletotrichum dematium	*Fagus crenata*	Japan	Sahashi & others (1995)
Fusarium spp.	*Pseudotsuga menziesii*	USA: Idaho	James (1987)
Phytophthora spp.	*Fagus sylvatica*	Poland	Stepniewska (2005)
Cylindrocarpon destructans	*Pinus sylvestris*	Sweden	Unestam & others (1989)
Cylindrocladium scoparium	*Pinus resinosa*	Canada	Yang & others (1995)
Fusarium spp., *Pythium* spp., *Rhizoctonia* spp.	*Acacia mangium*	Phillipines	Zethner & others (1997)
Fusarium spp., *Alternaria* spp., *Pythium* spp.	*Pinus sylvestris, Larix silbirica*	Russia	Gromovykh & others (1997)

A



B



C

Figure 4 - The Target Pest approach to phytosanitation involves analyzing each step in a nursery operation and identifying critical control points where pests can enter your nursery. This flow chart (A) shows the critical control points where damping-off pathogens can enter a container sowing operation, and where control treatments can be applied. For example, Fusarium *fungal spores can be carried on seedcoats (B), but can be eliminated by a running water rinse or quick soak in a dilute (1 bleach:10 water) bleach solution (C).*

pathogens as *Fusarium* spp., *Rhizoctonia* spp., *Phytophthora* spp., and *Pythium* spp.

Post-emergence damping-off has also been caused by abiotic stresses that damage the succulent stems of young seedlings. Heat injury was shown to cause cankers on the stems of young pine seedlings, which produced damping-off symptoms (Figure 1A).

4. Disease Management

Damping-off is a disease that can be easily contained by good phytosanitary practices because the spores of the pathogens are spread by water, soil, or growing media rather than through the air. Using the Target Pest approach to phytosanitation (Figure 4), an effective process involves confirming the pest, learning how it spreads, and then identifying critical control points.

4.1 Type of pest and method of spread

Several genera of fungi (*Fusarium, Rhizoctonia*) and Oomycetes (*Pythium, Phytophthora*) are the most common culprits, but other fungi can also be involved (Table 1). If general controls aren't effective, then confirmation of the causal agent by culturing on artificial media will be necessary (James 2012a). The mode of transmission is very different for each pest, although

spread in infected soil or growing medium is common to all species:

Fusarium spp. Spores are spread by contaminated seeds, in soil or growing media, and on used containers. The role of seed transmission can readily be seen by cotyledon blight (Figure 3C). Although airborne spores are produced, they are mainly responsible for secondary spread. Thick-walled chlamydospores help the fungus overwinter in plant debris and sclerotia are also produced (James 2012b).

Rhizoctonia spp. This fungus can be transmitted on seeds or by airborne spores, but spread by infected soil is by far the most common because the fungus overwinters in soil as sclerotia (Starkey and Eneback 2012).

***Pythium* spp.** and ***Phytophthora* spp.** These oomycetes are unique in producing zoospores which can swim in water, and both overwinter in soils or plant debris as as thick-walled oospores or chlamydospores (Weiland 2012a). Neither of these pathogens produces airborne spores, although spores can spread through water splash.

4.2 Critical control points for damping-off

Preventing the pathogens from entering your nursery is the best control but that is not always possible, especially in bareroot nurseries where all of the damping-off pathogens can persist in the soil. From a disease prevention standpoint, container nurseries are easier because containers, benches and other surfaces can be sterilized between crops (Landis and others 1990a).

Seeds. Of the primary damping-off pathogens, *Fusarium* spp. and *Rhizoctonia* spp. have proven to be carried on seeds (Figure 4B). Other less aggressive fungi, such as *Rhizopus* spp., can become problematic with some species (Table 1). Cleansing seedcoats with a running water rinse or sterilizing them with a dilute (1:10) solution of Chlorox (Figure 4C) or hydrogen peroxide prior to sowing eliminates this potential source of inoculum (Fraedrich and Cram 2012).

Soil or Growing Media. All damping-off pathogens are common soil inhabitants and so can easily holdover between crops, or they can form resting spores that can persist in plant debris for months or even years. Therefore, in bareroot nurseries, a good management strategy would be to try to sterilize soils before sowing and then use good cultural practices to keep populations low. Seedbed mulches reduce soil splash, which is one major way that *Rhizoctonia* is spread in bareroot nurseries (Starkey and Eneback 2012).

In container nurseries, most growing medium components including vermiculite and perlite are inherently sterile and the low pH of *Sphagnum* peat moss is inhibitory to damping-off pathogens (Landis and others 1990b). Bark and composts are more variable so it might be advisable to have them tested.

Irrigation or rain water. Due to their motile zoospores, *Pythium* and *Phytophthora* are most commonly spread by water. Apple or pear baits can be used to test irrigation water sources for Oomycetes and, if they are confirmed, then water treatment can be implemented. Keeping containers on raised benches prevents contact with surface water or runoff, which can be contaminated. In bareroot nurseries, selecting coarser-textured, well-drained soils for seedbeds is recommended as well as using raised beds to prevent standing water around seedlings (Weiland 2012b).

5. The Role of Environment

Most of the organisms causing damping-off are opportunistic pathogens, so disease can be lessened or even prevented by proper cultural procedures (Table 2). For example, just keeping the pH or soils or growing medium low has been an effective for preventing damping-off for more than a century (Figure 1B & 5). Likewise, keeping soils or growing media "moist, but not wet" discourages damping-off. A good discussion on which cultural practices will prevent damping-off can be found in James (2012a).

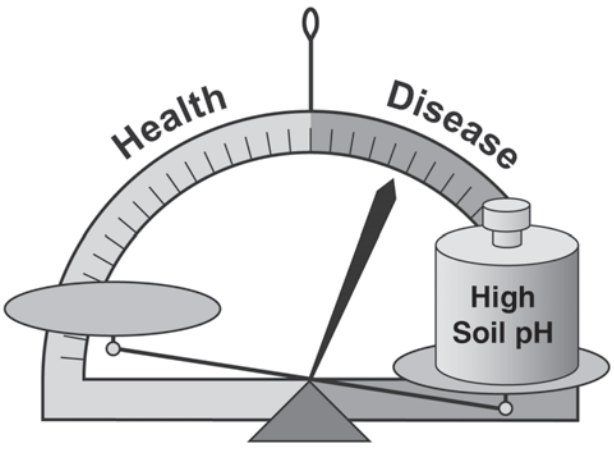


Figure 5 - Many of the pests causing damping-off are considered weak or opportunistic pathogens, which are aided by favorable environmental factors such as soils that have a high pH or don't drain well (modified from Landis 2000).

Table 2 - Environmental conditions and cultural practices affecting damping-off in forest, conservation and native plant nurseries (modified from Landis and others 1990a).

Environmental condition or cultural practice	Effect on damping-off	
	Encouraging	Discouraging
Seed quality	Dirty or contaminated; slow, weak germinants	Clean and steriIe; rapid germination and emergence
Soil or growing medium	Contaminated, fine-textured over-compacted, Alkaline: high pH (>6.5)	Pest-free, mixture of particle sizes, good porosity, Acidic: low pH (4.5-6.0)
Growing density	High (oversowing)	Low
Nutrition	Excessive fertilization, especially high nitrogen	Well-balanced fertilization especially phosphorus, potassium, and calcium
Irrigation	Frequent, heavy applications	Frequent, light applications: "Moist, but not wet"
Growing environment	High humidity, low light, extreme temperatures	Moderate humidity, adequate light, ideal temperatures

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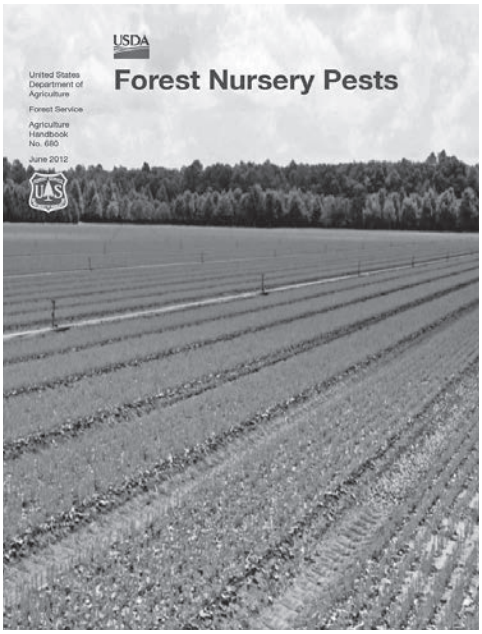

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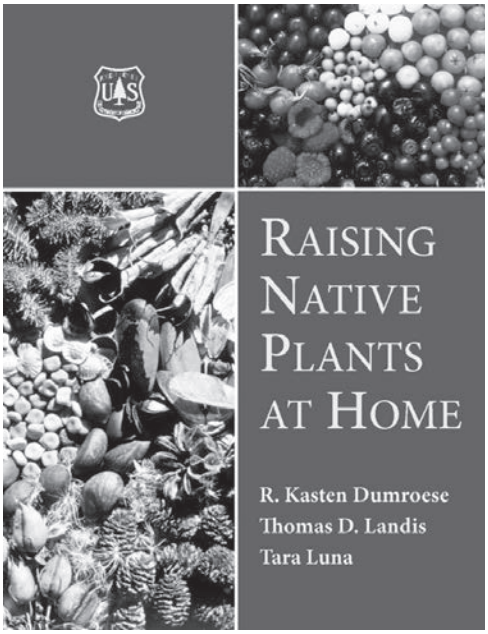

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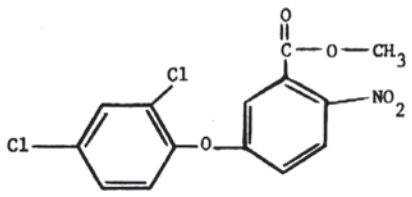

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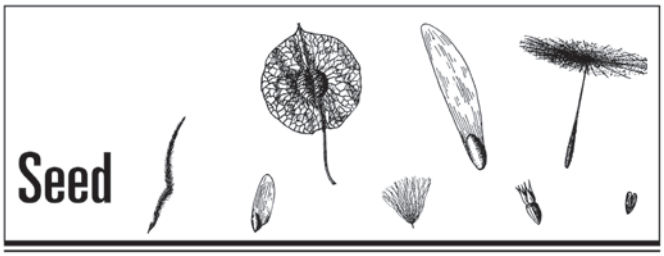

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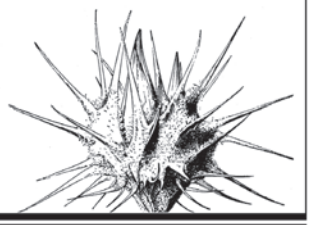

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