

Chilling Hours: Myths and Facts

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Abstract: This paper is a critical review of over four decades of research on chilling with southern pine seedlings. For most pines, freeze tolerance, seed dormancy, and endodormancy of terminal buds are affected by natural chilling (0° to 8 °C [32 to 46 °F]). Unfortunately, in the field of reforestation, several myths have emerged regarding the importance of chilling. One myth is that chilling seedlings in a dark cooler will increase freeze tolerance of southern pine seedlings and another myth states that chilling must occur before pine seedlings can be successfully “hot-planted.” I once believed in the common myth that bud ecodormancy (a.k.a. quiescence) is directly responsible for acceptable storage potential of pines. However, a true “cause and effect” relationship does not exist. Several independent studies have shown that pine seedlings can survive four weeks of storage (2 °C [36 °F]) without a “well-formed” terminal bud and without any natural chilling. A critical analysis reveals that most chilling studies have confounded planting date, chilling, freeze tolerance, rainfall amounts, and photoperiod. Conclusions from these “confounded” studies were used to spread the ecodormancy=storage myth. To dispel this myth may prove difficult, since it requires establishment of studies that do not involve confounding factors. This paper also discusses a new theory about why root growth potential (RGP) of cooler-stored seedlings sometimes drops quickly when bareroot seedlings are lifted in the fall. The theory suggests low RGP occurs when certain fungi (e.g. *Pythium*) grow on succulent, wounded roots in a cool, dark, damp environment. Knowledge about early storage of pine seedlings would increase if research is directed at explaining why RGP can drop quickly after only 1 week of cooler storage. Data are not required to keep a myth alive; it only requires unquestioning faith in a theory.

Keywords: dormancy, freeze tolerance, seedling storage, nursery management, disease

Introduction

Pines grown in southern nurseries include sand pine (*Pinus clausa* [Chapm. Ex Engelm.] Sarg.), shortleaf pine (*P. echinata* Mill.), slash pine (*P. elliottii* Engelm.), longleaf pine (*P. palustris* Mill.), loblolly pine (*P. taeda* L.) and Virginia pine (*P. virginiana* Mill.). The range of these species is generally below 38 °N latitude (sand pine is below 31°N) and, therefore, they receive less chilling in the nursery than pines from more northern regions. A lack of chilling will delay the formation of flower buds on trees and, therefore, chilling is economically important to fruit and nut industries.

Inadequate chilling can explain slow germination of pine seed in nursery beds and it occasionally explains low outplanting survival after a hard freeze. This paper is a critical review of over four decades of research on chilling with southern pine seedlings. The discussion regarding seed stratification is brief and more detail will be placed on bud-break and freeze tolerance. A critique will be made on the often assumed relationship between bud-dormancy status and cool-storage potential of pine seedlings.

Endodormancy and Ecodormancy

Use of the word “dormancy” can be confusing since there are many definitions for this term. When asked to explain the relationship between seedling quality and “dormancy”, “few are able to articulate a clear view of what dormancy is, how it works, or how it affects quality” (Landis and others 2010). In theory, the word “dormancy” refers only to the ability of seeds to germinate or the ability of buds to elongate. However, in general practice, dormancy is used to describe a variety of conditions such as tolerance of seedlings to: desiccation, freezing temperatures, storage diseases, rough handling, high temperatures, or certain herbicides. Some believe seedlings are dormant just after shoot growth stops in the fall and they remain dormant until growth resumes in the spring. For this reason, the word dormancy will not be used in this paper (except in quotations). Instead, the words endodormancy (a.k.a. rest) and ecodormancy (a.k.a. quiescence) will be used to describe the status of terminal buds (Boyer and South 1989).

The transition date when endodormancy ends and ecodormancy begins is not easy to determine. For a species like longleaf pine, it is almost impossible to determine due to the lack of bud elongation during the first year. For the purpose of this paper, the transition date occurs when the speed of bud-break is quickest (after being placed in a warm environment with, perhaps, a 15-hr photoperiod). For example if it takes 45 days before 50% of the seedlings have signs of “broken buds” in a greenhouse, then the seedlings are still in an endodormant state. In contrast, seedlings have achieved ecodormancy if it takes ≤ 15 days to achieve 50% bud-break.

Types of Chilling

I classify above-freezing chilling into four types. Natural-light chilling occurs under a natural photoperiod. The amount of natural-light chilling obtained on a given date depends on latitude, altitude and weather. For example, seedlings grown at Delano, Tennessee would receive more natural-light chilling by 1 January than seedlings grown at Chiefland, Florida. Artificial-light chilling is used by researchers who are investigating the effect of photoperiod on seedling physiology in storage. Artificial-light chilling occurs in growth chambers, lighted greenhouses, or lighted coolers where light-bulbs are used. Typically, natural-light chilling hour studies have confounded

factors while well designed artificial-light-chilling studies are relatively free of confounding factors.

Natural-dark chilling and artificial-dark have a 24-h dark cycle (i.e. no photoperiod). Natural-dark chilling may occur when seed are heavily mulched or when seedlings are stored in an underground cellar (Dierauf and Marler 1971). Artificial-dark chilling is used by nursery managers to stratify seed and to store seedlings. Seed are chilled in a dark cooler at 2 °C (36 °F) (a.k.a. cool storage). Seedlings stored in a cooler may also be in the dark when packaged in bags or boxes. The response of seedlings to natural-light and artificial-dark chilling differs (see below).

Below-freezing temperatures can be grouped into two types. Freeze chilling occurs in the range of 0 to -2 °C (32 to 28 °F) and has a minimal effect on endodormancy status (Landis and others 2010). Hypo-chilling temperatures are below -2 °C (28°F) and most agree these temperatures do not affect the endodormancy status of seedlings.

Chilling Hours

There is no universally accepted temperature range to define a “chilling hour” and reference temperatures can vary with species and nursery (Landis 2010). Several researchers in the South count hours within a range of 0 to 8 °C (32 to 46 °F; i.e. the range used in this paper). Some managers might not record chilling if it occurs before October 15 (Lantz 1989), but in some years this could reduce the number counted by 100 hours or more (DeWald and Feret 1987). Most researchers do not count temperatures below zero since freeze-chilling affects endodormancy only to a limited extent and hypo-chilling likely has no effect. However, some researchers do include freeze-chilling and hypo-chilling when summing chilling hours (Table 1). For example, Ritchie (1989) adds time in freezer-storage to the chilling hour sum even though -2°C (28 °F) is not as effective in releasing endodormancy as 2 °C (36 °F). In contrast, a few do not even count temperatures when they are less than 1.5 °C (34.7 °F; Cesaraccio and others 2004). The temperature range selected is very important to a nursery manager since, for a given date (e.g. January 31), the number might be less than 250 hours or more than 800 hours. Using a narrow temperature range might mean that a chilling hour target (developed for a wider range) is never met at some southern nurseries (Table 1).

Table 1. Temperature ranges for 13 definitions for “chilling hours” and the respective accumulation by 31 January 2012 at Claxton, Georgia.

Maximum temperature	Minimum temperature	Hours by 31 Jan	Date for 400 chilling hr	Date for 600 chilling hr	Reference
10 °C (50 °F)	None	825	14 Dec	5 Jan	Jenkinson and others (1993)
8 °C (46 °F)	None	779	16 Dec	10 Jan	Landis and others (2010)
7.2 °C (45 °F)	None	681	30 Dec	19 Jan	Weinberger (1956)
8 °C (46 °F)	0 °C (32 °F)	657	28 Dec	10 Feb	Garber (1983)
7.2 °C (45 °F)	0 °C (32 °F)	559	5 Jan	12 Feb	Voth (1989)
7 °C (45 °F)	None	547	7 Jan	12 Feb	Olson and Nienstaedt (1957)
6.7 °C (44 °F)	None	547	7 Jan	Did not achieve	Kainer and others (1991)
6 °C (43 °F)	None	456	19 Jan	Did not achieve	Ritchie (1989)
5.6 °C (42 °F)	None	455	19 Jan	Did not achieve	Ritchie (2004)
5 °C (41 °F)	None	363	12 Feb	Did not achieve	Omni and others (1994)
4.4 °C (40 °F)	None	362	12 Feb	Did not achieve	van den Driessche (1977)
5 °C (41 °F)	0 °C (32 °F)	334	26 Feb	Did not achieve	Bailey and Harrington (2006)
4.5 °C (40 °F)	0.5 °C (33 °F)	241	Did not achieve	Did not achieve	Ezell (2011)

Fact: Natural-light and Artificial-dark Chilling Increase Seed Germination

For more than two decades, researchers at Yale University conducted germination tests with pines without stratification (Toumey and Stevens 1928). At that time, the importance of pre-treating pine seed with chilling was not well known. However, some managers realized that sowing seed in January produced more pine seedlings than waiting to sow dry seed in April (Wakeley 1935). Sowing in January allowed the seed to be chilled naturally. Other managers would soak seed in cool water for a few days prior to sowing (Schenck 1907). The importance of chilling southern pine seeds was not fully realized until Lela Barton (1928) demonstrated that artificial-dark chilling would greatly increase the speed of germination. Nursery managers now use artificial-dark chilling to increase the speed of germination of several pine species.

Fact: Natural-light and Artificial-dark Chilling Increase Bud Break

It is generally believed that natural-light chilling is primarily responsible for shifting terminal buds from a state of endodormancy to a state of ecodormancy. However, a long photoperiod can also substitute for a lack of natural-light chilling (Garber 1983).

Artificial-dark chilling can be as effective as natural-light chilling in releasing endodormancy (Carlson 1985; Ritchie 2004). Similar results were observed with hardwood seedlings (Webb 1977). However, temperatures below freezing can retard the release of endodormancy of Douglas-fir (*Pseudotsuga menziesii* [Franco]; Ritchie 1984a). Although freeze-chilling had some effects on endodormancy, these findings illustrate why some researchers do not count hours below freezing toward a chilling hour accumulation.

Some Bud-break Myths

For the southern pines, it has been said that “Most sources reach maximum dormancy after 400 chilling hours” (Lantz 1987). This myth was started by those who say all genotypes of any given pine respond to chilling in a like manner. For example, Ritchie (1984b) said the relationship between the release of endodormancy for Douglas-fir and chilling sum “does not vary appreciably among seed lots and nurseries from year to year. Therefore, once the relationship has been empirically established for a given species in a given region, dormancy status during winter can be accurately predicted from monitoring chilling sums.”

In contrast to Ritchie’s claim, the beginning of ecodormancy of loblolly pine varies by genotype (Garber 1983; Carlson 1985; Boyer and South 1989). For some genotypes, it may be less than 415 chilling hours (Garber 1983) or over 1000 chilling hours (Carlson 1985). In fact, the same seed source may enter ecodormancy at different chilling-hour times, since the number of hours apparently varies with year and likely also with nursery management (DeWald and Feret 1988). Although a lack of chilling apparently delays the onset of ecodormancy, it is wrong to assume that 400 chilling hours are sufficient to overcome endodormancy for all southern pine genotypes, in every year, and in every nursery.

Another myth is that natural-light chilling is required for pine seedlings to enter a state of endodormancy. Although natural-light chilling typically occurs while buds are entering a state of endodormancy, chilling is not required. Natural-light chilling does not cause terminal

buds of pines to become endodormant. Garber (1983) showed that endodormancy can exist in late October.

Landis and others (2010) say that “refrigerated storage has the effect of slowing the release of dormancy.” For the southern pines, this is a myth because rarely do seedlings below 36 °N latitude receive 24 natural-light chilling hours/day. In contrast, each day of cooler-storage (2 °C [36 °F]) equals 24 artificial-dark chilling hours. For example, 28 days of cooler-storage will result in 672 chilling hours while 44 days of winter at Claxton, GA (28 December to 10 February) might provide only 200 chilling hours (Table 1). Obviously, at this location the release of endodormancy of loblolly pine would be quicker for artificial-dark chilling than for natural-light chilling. Regardless, the original claim about “slowing the release of dormancy” was made in regards to freeze-chilling, not artificial-dark chilling (Ritchie 1989).

Chilling Injury Myth

Cool temperatures during the fall will affect the physiology of a number of plants. Some tropical plants may experience “chilling injury” after exposure to nonfreezing temperatures below 10 °C (50 °F; Lyons 1973). In southern pine nurseries, exposure to nonfreezing temperatures below 8 °C (46 °F) can alter needle color (Grossnickle 2012). Loblolly pine seedlings from a northern seed source may turn purple (due to an increase in the production of anthocyanin combined with a decline in production of chlorophyll) while a southern source in adjacent plots may remain green. However, it is a myth to consider the purple color to be “chilling injury.” In fact, this color change is considered to be beneficial since it indicates seedlings have acquired some freeze tolerance (Grossnickle 2012).

Fact: Natural-light Chilling Increases Freeze Tolerance

Much has been written about the development of freeze tolerance in conifers (Bigras and Colombo 2001). Most agree that chilling is required for tissues to become freeze tolerant. In general, seedlings of loblolly, slash, and shortleaf pine that are planted deep and have not received chilling may tolerate a -2 °C (28 °F) freeze. However, natural-light chilling is likely required for loblolly pine seedlings to develop a tolerance to a -6 °C (21 °F) freeze (Mexal and others 1979; South 2007). Seedlings kept in a heated greenhouse do not acclimate to that level of tolerance by December or January.

Some Freeze Tolerance Myths

The myth that placing bareroot loblolly pine seedlings in a cooler will increase freeze tolerance might be traced back to research conducted with eastern white pine (*P. strobus* L.) and red pine (*P. resinosa* Ait.) in Ontario (Racey 1988). Racey found that tolerance to long-term freezer storage (-3 °C [27 °F]) was increased when 3+0 stock was conditioned first by 4 weeks of storage in a cooler (1 °C [34 °F]), primarily for a 11 October lifting date. However, container-grown loblolly pine clones did not acquire tolerance to a -3 °C (27 °F) freeze after 5 weeks of artificial-dark chilling (Grossnickle 2012). Apparently, longleaf pine seedlings also do not acclimate with artificial-dark chilling. For example, survival of longleaf pine seedlings can be reduced when the cool-stored seedlings are outplanted just prior to a hard freeze (South and Loewenstein 1994; Pickens 2012).

Some have claimed that a well-formed terminal bud is required before a pine seedling can become tolerant to a -10 °C (14 °F) freeze. This myth can easily be proven false by observing seedlings after a hard-freeze in a nursery (South and others 1993) or

greenhouse (Duncan and others 1996). In fact, proper top-pruning of pine seedlings can increase tolerance of the stem to a freeze (South and others 1993). Apparently, the idea that setting a terminal bud was a necessary step may have come from those who claimed that endodormancy and freeze tolerance was a “cause and effect” relationship.

Lifting by Chilling Hours or by the Calendar?

Prior to 1980, nursery managers typically started lifting bareroot southern pine seedlings at about the same time each year. For example, during the late 1950s lifting at the Coosa Nursery in Alabama was near the end of November (range 17 November to 2 December). A similar period (16 November to 2 December) occurred at the Ashe Nursery in Mississippi during the late 1960s and early 1970s.

Early on, some realized that lifting stock in October or November and storing them for five months or more would kill bareroot loblolly pine seedlings (Kahler and Gilmore 1961). In contrast, seedlings lifted in late December (or early January) could be safely stored for 12 weeks in a cooler. Perhaps due to their recommendation that loblolly pine “probably should not be lifted during normal years before the middle of December for placing in cold storage,” some managers changed their target lifting date. For example, the initiation date for lifting at the Ashe Nursery during the early 1980s was mid-December. To date, researchers have not demonstrated that delaying lifting for storage till mid-January (due to a lack of chilling), is statistically better than starting to lift in late December.

It is not known why bareroot pine seedlings generally do not store well when lifted in October or early November. Several theories have emerged to explain this phenomenon. One school of thought believes that the physiological status of the terminal bud determines how long seedlings can be stored. They say terminal buds must achieve ecodormancy before they can tolerate 4 weeks or more of cooler storage. Others claim ecodormancy likely has nothing to do with the seedling storage since (1) bareroot seedlings without terminal buds can tolerate long-term storage, (2) container-grown seedlings can be stored in the fall, and (3) occasionally bareroot seedlings can be stored for 4 weeks or more when lifted in late October (Stumpff and South 1991) or early November (van den Driessche 1977). Some believe that bareroot seedlings are more vulnerable to deterioration in storage because there is greater likelihood of damage to roots during lifting in the fall (Mohammed and others 2001).

Some chilling hour myths are relatively benign (e.g. the myth that chilling is required to achieve endodormancy) since they do not impact nursery economics or regeneration success. However, when chilling hour myths delay lifting and planting windows, this can have serious economic consequences. Extending the planting season into March is not desirable for southern pines (South and Mexal 1984). An exception might occur in locations with winters that have extended periods of frozen ground. Planting in February or March would then be preferred to planting in December in the Piedmont and Mountains of Virginia (Marler 1963; Garner 1972).

Hot-Planting Myths

“Hot-planting” is a tree-planting term to describe the practice of planting seedlings within a few days of lifting (Landis and Jacobs 2008; Landis and others 2010). The term “hot” can be misleading since planting within three days of lifting can occur in any month

and these seedlings may be transported in a refrigerated van. A less ambiguous term would be “<72 hour-planting” which emphasizes the time limit between lifting and planting. The “<72 hour-planting” method can occur when temperature is below freezing (in late October), and it can occur when the air temperature is above 25 °C (77°F; in January). In a perfect world, there only would be “<72 hour-planting” of southern pine seedlings (from October to February) since cooler-storage of pine seedlings is “a necessary evil” (South and Mexal 1984).

Some believe the myth that southern pine seedlings need 200 chilling hours before they are ready for no more than 3 days of storage (Lantz 1989; Ezell 2011). However, there are numerous examples where both container-grown and bareroot seedlings have been successfully “hot-planted” without any chilling. Planting during rainy months in the summer has been successful in the USA (McGregor 1965; Jordan 1966; Goodwin 1976; Woods and others 1979; Landis and others 2010) and South Africa (Donald 1976; Rolando and Little 2005). Keys to successful “hot-planting” of loblolly pine seedlings during summer months include; machine-plant seedlings when soil moisture is adequate, plant large-diameter seedlings deep (so that the root-collar is about 15 cm below the surface and roots are closer to lower, moister soil profiles), make sure the soil is not too wet (Jordan 1966) and use lignified, container-stock when hand-planting is required. In the south, perhaps 10% of container-grown seedlings are planted prior to any chilling (Dumroese and Barnett 2004).

In some regions in North America, “hot-planting” in October or November is preferable to planting in summer. In Florida, initial survival was greater than 95% when sand pine seedlings were hot-planted in mid-November (Hebb 1982). In Oklahoma, initial survival was greater than 80% when fungicide-treated shortleaf pine seedlings were hot-planted with only 48 chilling hours (Hallgren and Ferris 1995). In one study with loblolly pine, survival was 90% when seedlings were hot-planted on October 27 (Stumpff and South 1991). Although planting failures can occur during any month for many reasons, 200 chilling hours are not required in order to achieve good survival of hot-planted seedlings, regardless of stock type.

A new myth recently emerged with the claim that shortleaf pine should be hot-planted “if they have less than 600 chilling hours.” At some nurseries, adherence to this myth would mean that nursery managers could not store shortleaf pine for most or all of the lifting season (Table 1). This myth apparently originated from assumptions based only on RGP data from one nursery and one genotype. However, conclusions regarding the need for chilling should be based on survival data obtained for “hot-planting” more than a single genotype from more than one nursery. In fact, authors of the RGP study clearly stated that “no attempt is made to define optimum lifting windows or storage length” (Brisette and others 1988). Their warning apparently had no effect, and another myth was born.

Cooler Storage Myths

Operational constraints “often necessitate prolonged storage (or holding) of seedlings” (Garber and Mexal 1980). For storage of bareroot southern pine seedlings, the “prime” lifting season is from late-December to early-February (Garber and Mexal 1980).

Kahler and Gilmore (1961) said that “loblolly pine seedlings cannot survive cold storage unless they are hardened off and dormant before being placed in cold storage.” A decade later, Lavender and Wareing (1972) said that “a period of chilling, following short-day

pretreatment, greatly increases the seedlings' resistance to the adverse effects of root damage and dark storage." Later, Weyerhaeuser researchers began to examine when loblolly pine seedlings could withstand cooler storage and they determined that one seed source could be lifted in mid-December and stored for 9 weeks (Garber and Mexal 1980). About the same time, Garber (1978) demonstrated that for another seed source, terminal buds also achieved ecodormancy by mid-December. Taken together, these independent studies were used to assume the start of ecodormancy coincided with tolerance to cooler storage. As a result, Garber and Mexal (1980) suggested that guidelines relating the stages of bud break to storage potential could be developed with a minimum amount of research. Weyerhaeuser researchers developed guidelines and nursery managers started to store seedlings based on the accumulation of chilling hours.

Instead of conducting an experiment with a testable null hypothesis, some (including me) incorrectly assumed that tolerance to storage was regulated from within the terminal bud or apical meristem. For example, Barden and Feret (1986) stated that "loblolly pine seedlings do not store well until they are fully quiescent." Instead of questioning the theory, I looked for data to support the dogma that the amount of chilling determined storage potential. Eventually, the data convinced me that the ability to survive cool storage was not related to the satisfaction of the chilling requirement for terminal buds (van den Driessche 1977; Boyer and South 1985; Stumpff and South 1991).

A common myth is that southern pine seedlings, regardless of stock type or latitude, require 400 chilling hours before they can tolerate 4 weeks of cool storage. Based on declines in RGP, DeWald and Feret (1988) said that between 400 and 500 hours of natural-light chilling are necessary for satisfactory cool storage of loblolly pine seedlings in Virginia. Based on outplanting survival for a single year, Williams and South (1995) reported that container-grown seedlings exposed to 406 chilling hours could tolerate 10 weeks of cool storage (in plastic bags) when lifted on

6 January. The magic "400" number has been mentioned in several tree planting guides (e.g. Lantz 1989), but in order to be true, the 400 number must be repeatable. However, there are no studies that show the 400 number is repeatable from different latitudes, years, or genotypes. In fact, several studies have demonstrated that container-grown seedlings have been stored for a month without any chilling (Table 2). Likewise, Boyer and South (1985) reported that bareroot seedlings could tolerate 11 weeks of cooler storage when lifted on 6 December with just 223 chilling hours. Donald and South (2002) reported good storage (4 weeks) with only 113 chilling hours and concluded that "Although chilling is beneficial to pines, since it increases the resistance to freeze injury, successful cool storage of loblolly pine seedlings may not be directly related to chilling as once believed."

Another myth says artificial-dark chilling will increase seedling tolerance to cool storage. This myth assumes that placing bareroot pine seedlings in a cooler (4 °C [39 °F]) for 17 days would harden the seedlings enough so they will then tolerate an additional 40 days of cooler-storage. This myth originates from those who claim the theory (that stress resistance increases as endodormancy weakens) applies not only to natural-light chilling, but also to freeze-chilling and artificial-dark chilling (Landis and others 2010). Some believe the theory that stress resistance of Douglas-fir seedlings (exposed to 500 natural-light chilling hours) will increase by placing the seedlings in freezer-storage for 12 weeks (Ritchie 1989). Storage data to verify this theory have not been "repeatable from year to year with different crop types (bareroot and container) and species (Douglas-fir, pines, spruces, some hardwoods) and across nurseries." In fact, when compared to seedlings left in the nursery, artificial-dark chilling can prevent an increase in seedling quality (i.e. achievement of freeze tolerance). Therefore, instead of increasing seedling quality, outplanting survival could be decreased (due to a killing hard freeze) when seedlings were lifted early and cool-stored (without receiving an adequate amount of natural-light chilling).

Table 2. Selected examples of good seedling survival of container-grown stock cooler-stored in the fall without natural chilling.

Species	Lift date	Storage length (weeks)	% survival	Reference
loblolly pine	20-Sept-2007	7	100%	South unpublished
loblolly pine	Oct-2007	4	100%	Grossnickle 2012
longleaf pine	3-Oct-2001	6	95%	Pickens 2012
longleaf pine	3-Nov-2008	4	97%	Jackson and others 2012b
shortleaf pine	3-Nov-2008	4	85%	Jackson and others 2012b
slash pine	3-Nov-2008	4	99%	Jackson and others 2012b
loblolly pine	3-Nov-2008	4	99%	Jackson and others 2012b
longleaf pine	6-Nov-2000	4 to 10	88%	South and others 2005
longleaf pine	6-Nov-2000	4 to 10	84%	South and others 2005
longleaf pine	6-Nov-2000	4 to 10	71%	South and others 2005
longleaf pine	6-Nov-2000	4 to 10	69%	South and others 2005
shortleaf pine	18-Dec-2007	4	84%	Jackson and others 2012c
slash pine	18-Dec-2007	4	83%	Jackson and others 2012c
loblolly pine	18-Dec-2007	4	88%	Jackson and others 2012c

A New Root Growth Potential- Disease Theory

A new school-of-thought regarding seedling storage has formulated a theory that may eventually replace the ecodormancy=storage theory. Researchers from this school (Jackson and others 2012a) have attempted to determine why RGP often declines rapidly when seedlings are placed in storage. Occasionally bareroot seedlings lifted in October and stored for 4 weeks can have similar RGP to non-stored seedlings. At other times, a 55% decline in RGP might occur when seedlings are stored for only one week. Understanding what factors are responsible for such diverse responses could go a long way in unraveling the reasons why results from 4 weeks of storage of October lifted bareroot seedlings have been so variable.

Some suggested that disease organisms play a major role in determining why bareroot seedlings often do not perform well after storage in the fall while container-grown seedlings can be packaged and cool-stored with acceptable survival (Table 2). Fungi (e.g. *Pythium*) might explain why the RGP can drop quickly when October lifted seedlings are placed in a cool and moist storage environment. It is known that adding too much water before storage can reduce the RGP of loblolly pine (Barden and Feret 1986). Also, when roots of Douglas-fir are kept warm (15 °C [59 °F]) in dark, cool storage (2 °C [36 °F]), seedling survival increased from 55% (cool) to 90% (warm) (Lavender and Wareing 1972). Most *Pythium* species grow well in cool, moist environments and perhaps warm roots are not conducive to their growth. Also, treating roots with certain fungicides can, under some situations, improve the storability of southern pines (Barnett and others 1988; Hallgren and Ferris 1995; Brissette and others 1996). Sometimes the correct amount of a fungicide will suppress disease and increase RGP (Hallgren and Ferris 1995). Finally, recent research indicates that RGP can be reduced in the fall when seedlings have been inoculated with certain *Pythium* species (Jackson and others 2012a). Taken together, these findings suggest the primary factor that controls storage potential of pine seedlings resides in the roots (instead of within the terminal bud).

Conclusions

Although natural-light chilling is beneficial to pines (since it increases freeze tolerance), successful cooler-storage of loblolly pine seedlings (either container or bareroot) is not directly related to the level of endodormancy. Most conclusions about natural-light chilling and cooler-storage were made from date-of-lifting studies that confounded lifting date with factors like freeze tolerance and seedling age. The conclusions were not based on studies that were designed to test a hypothesis. We need researchers who are willing to question dogmas and who are willing to expose seedling quality myths. Otherwise, we may continue to see individuals make claims about chilling that are not true.

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References

- Bailey JD, Harrington CA. 2006. Temperature regulation of bud-burst phenology within and among years in a young Douglas-fir (*Pseudotsuga menziesii*) plantation in western Washington, USA. *Tree Physiology* 26:421-430.
- Barden CE, Feret PP. 1986. Root growth potential of loblolly pine seedlings held in cold storage under differing moisture treatments. In: Schroeder RA, compiler. *Proceedings of the Southern Forest Nursery Association*. p 218-223.
- Barnett JP, Brissette JC, Kais AG, Jones JP. 1988. Improving field performance of southern pine seedlings by treating with fungicides before storage. *Southern Journal of Applied Forestry* 12:281-285.
- Barton LV. 1928. Hastening the germination of southern pine seeds. *Journal of Forestry* 26:774-785.
- Bigras FJ, Colombo SJ. 2001. *Conifer Cold Hardiness*. Dordrecht: Kluwer.
- Boyer JN, South DB. 1985. Dormancy, chilling requirements, and storability of container-grown loblolly pine seedlings. In: South DB, editor. *Proceedings of the International Symposium on Nursery Management Practices for the Southern Pines*, Auburn, (AL): Department of Research Information, Auburn University. p 372-383.
- Boyer JN, South DB. 1989. Seasonal changes in intensity of bud dormancy in loblolly pine seedlings. *Tree Physiology* 5:379-385.
- Brissette JC, Barnett JP, Gramling CL. 1988. Root growth potential of southern pine seedlings grown at the W.W. Ashe Nursery. In: *Proceedings of the Southern Forest Nursery Association*. p 173-183.
- Brissette JC, Barnett JP, Jones JP. 1996. Fungicides improve field performance of stored loblolly and longleaf pine seedlings. *Southern Journal of Applied Forestry* 20:5-9.
- Carlson WC. 1985. Effects of natural chilling and cold storage on budbreak and root growth potential of loblolly pine (*Pinus taeda* L.). *Canadian Journal of Forest Research* 15:651-656.
- Cesaraccio C, Spano D, Snyder RL, Duce P. 2004. Chilling and forcing model to predict bud-burst of crop and forest species. *Agricultural and Forest Meteorology* 126:1-13.
- DeWald LE, Feret PP. 1988. Changes in loblolly pine seedling root growth potential, dry weight, and dormancy during cold storage. *Forest Science* 34:41-54.
- Dierauf TA, Marler RL. 1971. Effectiveness of an underground storage unit for loblolly pine seedlings. *Tree Planters' Notes* 22:5-8.
- Donald DGM. 1976. The use of open-rooted pine seedlings for afforestation in South Africa. *South African Forestry Journal* 97:1-11.
- Dumroese RK, Barnett JP. 2004. Container seedling handling and storage in the southeastern states. In: Riley LE, Dumroese RK, Landis TD, technical coordinators. *National Proceedings: Forest and Conservation Nursery Associations*. Fort Collins (CO): USDA Forest Service, Rocky Mountain Forest and Range Experiment Station. *Proceedings RMRS-P-33*. p 22-25.
- Duncan PD, White TL, Hodge GR. 1996. First-year freeze hardiness of pure species and hybrid taxa of *Pinus elliotii* (Engelmann) and *Pinus caribaea* (Morelet). *New Forests* 12:223-241.
- Ezell AW. 2011. *Planting Southern Pines – a guide to species selection and planting techniques*. Mississippi State University Extension Service. Publication 1776. 16 p.
- Garber MP, Mexal JG. 1980. Lift and storage practices: their impact on successful establishment of southern pine plantations. *New Zealand Journal of Forestry Science* 10:72-82.

- Garber MP. 1983. Effects of chilling and photoperiod on dormancy release of container-grown loblolly pine seedlings. *Canadian Journal of Forest Research* 13:1265-1270.
- Garner JW. 1972. Loblolly pine seedling survival and growth study for different planting dates. Virginia Division of Forestry. Occasional Report 39. 3 p.
- Goodwin OC. 1976. Summer-planted loblolly and longleaf pine tubelings outgrow 1-0 nursery seedlings in North Carolina. *Journal of Forestry* 74:515-516.
- Grossnickle S. 2012. Personal communication. Victoria (BC). Nursery To Forest Solutions.
- Hallgren SW, DM Ferris DM. 1995. Benomyl applied to roots improves second-year survival and growth of shortleaf pine. *Southern Journal of Applied Forestry* 19:36-41.
- Hebb EA. 1982. Cold storage of Choctawhatchee sand pine seedlings: effect of lifting date and length of storage. *Southern Journal of Applied Forestry* 6:229-231.
- Jackson DP, Enebak SA, South DB. 2012a. *Pythium* species and cold storage affect the root growth potential and survival of bareroot loblolly (*Pinus taeda* L.) and slash pine (*Pinus elliottii* Engelm.) seedlings. *Journal of Horticulture and Forestry* 4:114-119.
- Jackson DP, Enebak SA, South DB. 2012b. Survival of southern pine seedlings after inoculations with *Pythium* and cold storage in the presence of peat moss. *Forest Pathology* 42:44-51.
- Jackson DP, Enebak SA, South DB. 2012c. Effects of *Pythium* species and time in cold storage on the survival of bareroot and container-grown southern pine seedlings. *ISRN Ecology* 2012:1-7 (article ID 874970).
- Jenkinson JL, Nelson JA, Huddleston ME. 1993. Improving planting stock quality – the Humboldt experience. Albany (CA): USDA Forest Service. Pacific Southwest Experiment Station. General Technical Report PSW-143. 219 p.
- Jordan RA. 1966. Off season planting. In: Jones L, technical coordinator. Proceedings of the Southeastern Area Forest Nurserymen Conferences. Atlanta (GA): USDA Forest Service, State and Private Forestry, Southeastern Area. p 74-82.
- Kahler LH, Gilmore AR. 1961. Field survival of cold stored loblolly pine seedlings. *Tree Planters' Notes* 45:15-16.
- Kainer KA, Duryea ML, White TL, Johnson JD. 1991. Slash pine bud dormancy as affected by lifting date and root wrenching in the nursery. *Tree Physiology* 9:479-489.
- Landis TD, Jacobs DF. 2008. Hot-planting opens new outplanting windows at high elevations and latitudes. *Forest Nursery Notes* 28(1):19-23.
- Landis TD, Dumroese RK, Haase DL. 2010. Seedling processing, storage and outplanting. Vol. 7, The container tree nursery manual. Washington (DC): USDA Forest Service, Agricultural Handbook 674. 200 p.
- Lantz CW, editor. 1989. Care and Planting of Southern Pine Seedlings. Atlanta (GA): USDA Forest Service. Management Bulletin R9-MB39. 44 p.
- Lavender DP, Wareing FP. 1972. Effects of daylength and chilling on the response of Douglas fir (*Pseudotsuga menziesii* (Mirb) Franco) seedlings to root damage and storage. *New Phytologist* 71:1055-1067.
- Lyons JM. 1973. Chilling injury in plants. *Annual Review of Plant Physiology*. 24(1):445-466.
- Marler RL. 1963. Tree planting survival: a 3 year study. Virginia Division of Forestry. Occasional Report 19. 8 p.
- McGregor WHD. 1965. Successful summer planting of slash pine. *Journal of Forestry* 63:208-209.
- Mexal JG, Timmis R, Morris WG. 1979. Cold-hardiness of containerized loblolly pine seedlings. *Southern Journal of Applied Forestry* 3:15-19.
- Mohammed GH, McLeod GR, Menes PA, Timmer VR. 2001. A comparison of bareroot and container stock. In: Wagner B, Colombo SJ, editors. Regenerating Ontario's Forests. Markham, Ontario, Fitzhenry & Whiteside Ltd. p 343-348.
- Olson JS, Nienstaedt H. 1957. Photoperiod and chilling control growth of hemlock. *Science* 125:492-494.
- Omni SK, Rose R, Sabin TE. 1994. Fall lifting and long-term freezer storage of ponderosa pine seedlings: effects on starch, root growth, and field performance. *Canadian Journal of Forest Research* 24:624-637.
- Pickens B. 2012. Effects of extended cold storage on the survival and performance of container grown longleaf seedlings. In: Kush JS, compiler. Proceedings of the Eighth Biennial Regional Conference. Andalusia (AL): Longleaf Alliance Report 16. p 86-91.
- Racey DG. 1988. Cold temperature conditioning of conifer seedlings prior to frozen overwinter storage. Ontario Ministry of Natural Resources. Forest Research Report 118. 12 p.
- Ritchie GA. 1984a. Effect of freezer storage on bud dormancy release in Douglas-fir seedlings. *Canadian Journal of Forest Research* 14:186-190.
- Ritchie GA. 1984b. Assessing seedling quality. In: Duryea ML, Landis TD, editors. Forest nursery manual production of bareroot seedlings. The Hague/Boston/Lancaster: Martinus Nijhoff/Dr W. Junk Publishers. p 243-259.
- Ritchie GA. 1989. Integrated growing schedules for achieving physiological uniformity in coniferous planting stock. *Forestry (Supplement)* 62:213-226.
- Richie GA. 2004. Container seedling storage and handling in the Pacific Northwest: answers to some frequently asked questions. In: Riley LE, Dumroese RK, Landis TD, technical coordinators. National proceedings: Forest and Conservation Nursery Associations. Fort Collins (CO): USDA Forest Service, Rocky Mountain Research Station. Proceedings RMRS-P-33. p 3-7.
- Rolando CA, Little KM. 2005. An assessment of factors affecting early survival and growth of *Pinus patula* and *Pinus elliottii* in the summer rainfall region of southern Africa. *Southern African Forestry Journal* 205:21-30.
- Schenck CA. 1907. Biltmore Lectures on Sylviculture. Brandow Printing Company, Albany, NY 184 p.
- South DB. 2007. Freeze injury to roots of southern pine seedlings in the USA. *Southern Hemisphere Forestry Journal* 69:151-156.
- South DB, Mexal JG. 1984. Growing the "best" seedlings for reforestation success. Alabama Agricultural Experiment Station. Forestry Department Series No. 12. 11 p.
- South DB, Donald DGM, Rakestraw JL. 1993. Effect of nursery culture and bud status on freeze injury to *Pinus taeda* and *Pinus elliottii* seedlings. *South African Forestry Journal* 166:37-45.
- South DB, Donald DGM. 2002. Effect of nursery conditioning treatments and fall fertilization on survival and early growth of *Pinus taeda* seedlings in Alabama, U.S.A. *Canadian Journal of Forestry Research* 32:1171-1179.
- South DB, Loewenstein NJ. 1994. Effects of Viterra® root dips and benomyl on root growth potential and survival of longleaf pine seedlings. *Southern Journal of Applied Forestry* 18:19-23.
- South DB, Harris SW, Barnett JP, Hains MJ, Gjerstad DH. 2005. Effect of container type and seedling size on survival and early height growth of *Pinus palustris* seedlings in Alabama, U.S.A. *Forest Ecology and Management* 204:385-398.

- Stumpff NJ, South DB. 1991. Benomyl root dips adversely affect first-year performance of stored loblolly pine seedlings. *Southern Journal of Applied Forestry* 15:133-137.
- Toumey JW, Stevens CL. 1928. The testing of coniferous tree seeds at the School of Forestry, Yale University 1906-1926. Yale University, New Haven (CT). 46 p.
- van den Driessche R. 1977. Survival of coastal and interior Douglas fir seedlings after storage at different temperatures, and effectiveness of cold storage in satisfying chilling requirements. *Canadian Journal of Forestry Research* 7:125-131.
- Voth V. 1989. The effect of nursery location latitude on California winter planted strawberries. *Acta Horticulturae* 265:283-284.
- Wakeley PC. 1935. Artificial reforestation in the southern pine region. USDA Technical Bulletin 492. 115 p.
- Webb DP. 1977. Root regeneration and bud dormancy of sugar maple, silver maple, and white ash seedlings: effects of chilling. *Forest Science* 23:474-483.
- Weinberger JH. 1956. Prolonged dormancy trouble in peaches in the southeast in relation to winter temperatures. *American Society of Horticulture Proceedings* 67:107-112.
- Williams HM, South DB. 1995. Root growth potential and field survival of container loblolly pine seedlings fall fertilized with nitrogen. In: Edwards MB, editor. *Proceedings of the Eighth Biennial Southern Silvicultural Research Conference*. Auburn (AL). USDA Forest Service, Southern Research Station. General Technical Report SRS-1. p 357-363.
- Woods FW, Hay RL, Irwin GH. 1979. Summer planting on strip mines successful. *Tree Planters' Notes* 30:22-23.