The Chilling Optimum of Idaho and Arizona Ponderosa Pine Buds

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ABSTRACT: *Ponderosa pine (*Pinus ponderosa*) seedlings from Idaho (var.* ponderosa*) and Arizona (var.* scopulorum*) grown in a container nursery received optimum chilling [2,010 hr (84 days) of temperatures below 5°C]. While seedlings were in the greenhouse, days required for 50% of the population to break bud were similar for both seed sources and decreased inverse exponentially from 74 to 23 days as chilling hours accumulated to the optimum. When subsequently placed into either refrigerated or frozen storage, Idaho seedlings broke bud significantly faster than Arizona seedlings when returned to favorable environmental conditions for growth. All seedlings removed from refrigerated storage broke bud faster, were less cold tolerant, and therefore less quiescent than seedlings that had been frozen.West. J. Appl. For. 17(3):117–121.*

Key Words: Ponderosa pine, chilling requirements, container-grown seedlings.

The annual cycle of conifer growth is comprised of shoot elongation followed by dormancy. Dormancy, when "tissue predisposed to elongate does not do so" (Doorenbos 1953), has three phases that change seasonally: initial quiescence (predormancy) in late summer induced by shorter photoperiod and water stress; rest in late fall and winter; and final quiescence (postdormancy) in spring when trees will again produce shoots under favorable environmental conditions (Romberger 1963, Ritchie 1984, Lavender 1985).

During the rest phase, a seedling in favorable environmental conditions will eventually break bud. However, as seedlings accumulate time at temperatures <5°C ("chilling hours"), the number of days to break bud decreases until the chilling requirement, or chilling optimum, is reached. Once the optimum accumulation of chilling has occurred, postdormant (quiescent) seedlings will break bud rapidly when provided favorable environmental conditions. This optimum value varies between species and seed sources and is an evolutionary response to prevent stem elongation during mild winter periods that would increase the likelihood of frost damage to tender tissue (Lavender and Stafford 1985). The chilling optimum of temperate latitude forest trees varies between 0 and 2,000 hr of temperatures below 5°C (Jensen and Gatherum 1965, Steinhoff and Hoff 1972, van den Driessche 1975, Burr et al. 1989). Differences in chilling optima within species may be caused by genetic variability, perhaps related to the different elevations and geographic regions in which the seed source was found (Rehfeldt 1990). This genetic variation could in turn lead to the differences in chilling requirements between and within species.

Although Sloan (1991) examined the effect of chilling hours on ponderosa pine (*Pinus ponderosa* var. *ponderosa*) budbreak, the chilling optimum has yet to be determined. For nursery managers, target lifting (harvest) dates for their crops should occur when days to budbreak are rapidly decreasing, and cold hardiness is rapidly increasing (Burr 1990). A positive correlation exists between increased field survival and pine seedlings that have quiescent buds that elongate rapidly and uniformly after outplanting (Larsen et al. 1986). Buds are only fully quiescent if the chilling optimum has been reached. Therefore, our objective was to examine the differences in chilling optima, cold hardiness, and budbreak speed of two varieties of ponderosa pine with ambient greenhouse chilling followed by either refrigerated or frozen storage conditions.

Materials and Methods

Greenhouse Growth and Seedling Storage

Ponderosa pine seedlings from Idaho (UI Experimental Forest Flat Creek, elevation 945 m) and Arizona (Apache-Sitgreaves National Forest, Chevlon Ranger District, elevation 2,104 m) were grown from seeds in 160 cavity (90 ml) Copperblock® containers (764 cavities/m^2) (Beaver Plastics, Edmonton, Alberta) at the University of Idaho Forest Research Nursery at Moscow, ID in a 7:3 (v:v) sphagnum peat moss:Douglas-fir sawdust medium. We sowed seeds during the first week of March 1998 into 26 containers

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(13 containers of each source) resulting in about 2,000 seedlings for each source. Containers were systematically placed within a 2 × 5 m area among an operational lot of ponderosa pine. Seedlings were grown 7 months (March through September) using exponential growth fertilization (Timmer and Aidelbaum 1996) that maintained about 2.5% foliar nitrogen (N) concentration and adequate amounts of other nutrients following Wenny and Dumroese (1987). We kept greenhouse temperatures between 18 and 30°C during the seedling establishment phase in early March and then between 13 and 30°C from April through September according to our customary nursery practices for ponderosa pine (Wenny and Dumroese 1987). Photoperiod was extended (to prevent premature cessation of shoot growth) from March to June using 300 watt incandescent lights that provided intermittent all-night lighting (Landis et al. 1992) at an average irradiance of 3 μmol/(m^2/s). From October 1998 until the crop was harvested in January 1999, we set greenhouse temperature controls to mimic outdoor temperatures (generally $\leq$7°C) but kept minimum temperatures above –1°C. During January 1999, seedlings from both seed sources were extracted from the containers and randomly assigned to two storage conditions: refrigerated storage (1 to 2°C) and freezer storage (–1 to –2°C). We sealed seedlings inside 1.25 mil plastic bags that were then sealed inside a 1.5 -mil bag placed inside a plastic storage tub. The number of chilling hours, defined as the duration of time temperatures were <5°C, was determined from temperature data recorded every 15 minutes from September 1998 through May 1999.

Growth Room

Seedlings began initiating or "setting" terminal buds in June 1998 and all seedlings had buds by the end of July. A "set" bud had brown bud scales, visible with the naked eye, that covered the shoot apex. Monthly from July 1998 through May 1999 (12 sample dates), 45 seedlings >7 cm in height with terminal buds were randomly selected (either from the greenhouse or from storage containers in the refrigerator or freezer) and transplanted into 45 cavity (340 ml) Copperblock containers (215 cells/m^2) (Beaver Plastics, Edmonton, Alberta) containing the same growth medium described earlier. We avoided seedlings with lammas growth (temporary bud formation followed by stem elongation) or rosette-type needle formations at the shoot apex. Each Copperblock was divided into 3 replicates of 15 seedlings. After transplanting, we placed containers inside a growth room having 14 hr light at 20°C and 10 hr dark at 9°C. Metal halide and high-pressure sodium lights provided an irradiance of 410 μmoles/(m^2/s) at average seedling height. While in the growth room, seedlings transplanted in July, August, and September 1998 were fertilized with 1.5 mg N using Peters Conifer Grower (20N:$7P_2O_5$:$19K_2O$) during each irrigation. We irrigated when containers weighed 80% of saturated container weight (~2×/week). From October to the end of the experiment, we fertilized all previously and subsequently transplanted seedlings with 5.3 mg N. In addition, Peters Foliar Fertilizer (27N:$15P_2O_5$:$12K_2O$) was applied monthly at a rate of 2.1 mg of N/seedling (2.2 ml of foliar fertilizer per seedling) using a hand-held spray bottle. All seedlings were irrigated when container weights reached 80% of saturated weight.

Measurements

Seedlings were monitored for budbreak (bud scales separated and new needles emerged 2 mm beyond the tip of the terminal bud) every 2 days. The number of days to budbreak was recorded when 50% of the seedlings had budbreak. Each month from July 1998 through May 1999, we collected needles from three randomly selected seedlings (replicated four times; 12 seedlings total) from each seed source and storage condition (greenhouse, refrigerator, freezer) combination. Cold hardiness was determined using the freeze induced electrolyte leakage (FIEL) technique (Burr et al. 1990). For each sample date, six test temperatures were selected to bracket the expected LT_{50}.

Statistical Analysis

To determine how chilling hour accumulation affected days to budbreak, we used a two-way analysis of variance and our fixed variables were seed source (Idaho and Arizona), storage conditions [greenhouse (October 1998 to mid-January 1999); refrigerated or frozen (mid-January 1999 through May 1999)], and cumulative chilling hours (10 values from September 1998 through May 1999). Our dependent variable was days to budbreak in the growth room. Days to budbreak were transformed for both seed sources because original residuals were nonnormal. Means were transformed using $Y_t = DBB^{-0.77261}$, where DBB = mean days to budbreak and Y_t = transformed mean days to budbreak mean. When appropriate, mean days to budbreak were tested using the Ryan-Einot-Gabriel-Welsch multiple *F* test (REGWQ; SAS 1989). For cold hardiness, we used an analysis of variance, and our fixed variables were the same as described above. Our dependent variable was LT_{50}.

Results

Chilling Optimum

In the greenhouse, seedlings were first exposed to chilling temperatures in October. As cumulative chilling hours increased from October through January, the average number of days to budbreak for both populations was similar, but decreased significantly from about 74 days to about 23 days (Table 1). The number of days to 50% budbreak continued to decline, although not as rapidly, for seedlings of both seed sources after they were placed into either refrigerated or frozen storage; the number of days to budbreak decreased about another 5 days (Table 1). In general, days to budbreak for the Arizona source were unaffected by storage treatment, except that seedlings stored 3 months in refrigerated storage broke bud significantly faster than those frozen for the same duration. For the Idaho source, seedlings from frozen storage took significantly longer to break bud than those refrigerated (Table 1). For both seed sources, the significant differences in days to budbreak between storage conditions was about 2 days and may not be biologically important. On average, Idaho seedlings broke bud significantly faster (4.5 days) than Arizona seedlings, regardless of refrigerated or frozen storage conditions.

Table 1. Days to budbreak of ponderosa pine seedlings from Idaho (ID) and Arizona (AZ) for different chilling hour sums and storage location.

Sample date	Storage location	Cumulative chilling hours	Days to budbreak ID	Days to budbreak AZ	P value
Aug.–Sept. 1998	Greenhouse	0	71 a[1]	77 a[1]	0.5[2]
Oct.	Greenhouse	56	52 a	50 b	0.6
Nov.	Greenhouse	397	40 b	41 b	0.8
Dec.	Greenhouse	787	33 b	33 c	1.00
Jan. 1999	Greenhouse	1,325	27 c	28 cd	0.4
Feb.	Greenhouse	1,852	22 d	24 de	0.07
Mar. 2	Freezer	2,517	19 de	23 ef	0.0001
Mar. 2	Refrigerator	2,517	18 ef	22 ef	0.0001
Mar. 30	Freezer	3,188	18 ef	23 ef	0.0001
Mar. 30	Refrigerator	3,188	16 gh	22 ef	0.0001
Apr.	Freezer	3,859	18 efg	22 ef	0.0001
Apr.	Refrigerator	3,859	15 hi	20 f	0.0001
May	Freezer	4,502	16 fgh	20 f	0.003
May	Refrigerator	4,502	14 i	18 g	0.0001

[1] Values in the same column followed by a different letter are significantly different ($P < 0.05$) using REGWQ multiple range test.

[2] P values indicate significant differences between seed sources at each sampling date and location.

The relationship between chilling hour accumulation and days to budbreak was best described for both seed sources using the equation:

$$\text{Days to budbreak} = 90.188e^{-0.179(\text{chilling hours})^{0.265}}$$

This nonlinear transformation, using a generalized exponential fit, produced an $r^2 = 0.98$ (Figure 1). Using the chilling optimum approach of Worrall and Mergen (1967), that is, optimum is reached when an additional 10 days (240 hr) of chilling fails to reduce the days to budbreak by less than a day, the derivative of the equation indicated that days to budbreak at the chilling optimum of 2,010 hr was 23.

Cold Hardiness

Beginning in August, all seedlings became increasing tolerant to cold temperatures (Figure 2). The rate of cold hardiness development for both seed sources increased rapidly and significantly from September to December. Idaho seedlings, at most sample dates, were significantly hardier than Arizona seedlings. Both seed sources reached maximum cold hardiness at about 787 chilling hours in December: the LT_{50} was –34°C for Idaho seedlings and –26°C for Arizona seedlings (Figure 2). After this maximum cold hardiness level, and despite a continuing accumulation of chilling hours, seedlings from both seed sources became less cold hardy for the remainder of the time they spent in the greenhouse. This trend continued when seedlings were placed into either refrigerated or frozen storage. From February through April, seedlings within seed sources had similar cold hardiness values regardless of storage conditions, but by late May frozen seedlings were significantly more hardy than refrigerated stock. Frozen Idaho seedlings had a $LT_{50} = -12$°C, while

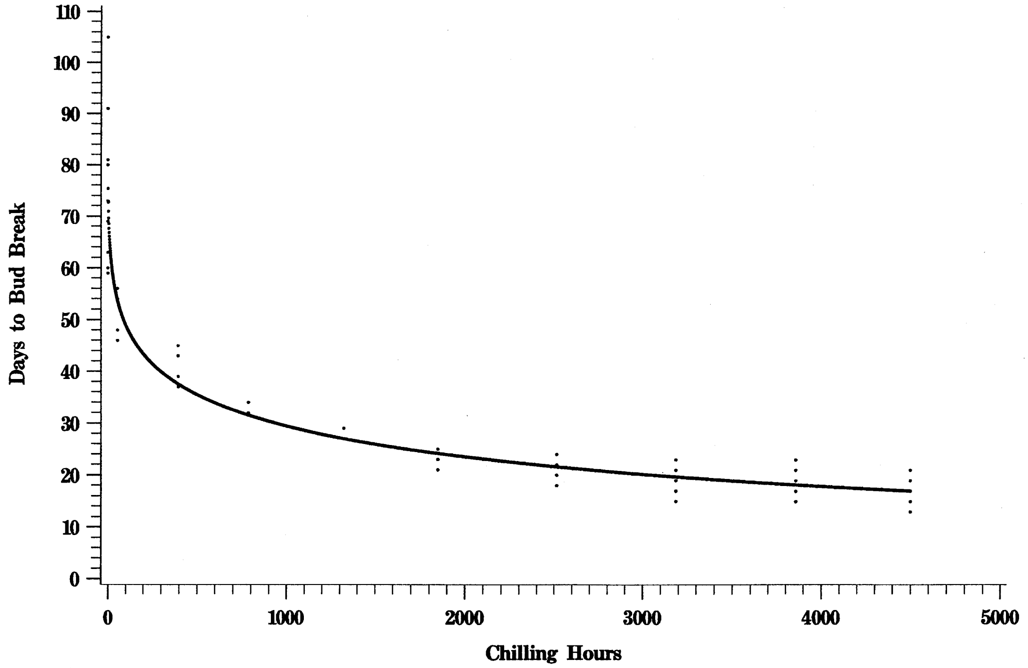

Figure 1. Days to budbreak values for ponderosa pine seedlings with accumulated hours of chilling (<5°C) during nursery production and storage. Days to budbreak (*DBB*) was best ($r = 0.98$) described by this equation: $DBB = 90.188e^{-0.179(\mathit{chilling\ hours})^{0.265}}$

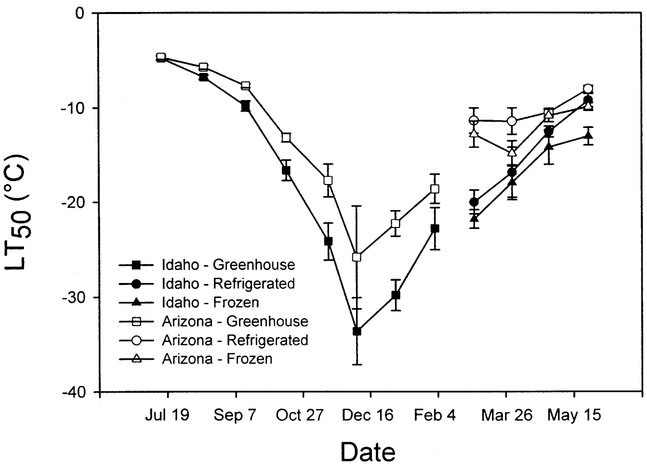

Figure 2. LT_{50} values of container-grown ponderosa pine seedlings from Idaho and Arizona during nursery production and storage. LT_{50} values were determined using the FIEL technique (Burr et al. 1990). Bars represent 95% confidence intervals.

refrigerated Idaho seedlings had a $LT_{50} = -9$ °C. The LT_{50} for the Arizona seed source was –10°C and –8°C for frozen and refrigerated seedlings, respectively.

Discussion

Our basis for determining chilling optimum was days to budbreak. Although the chilling optimum is genetically predetermined, the expression of budbreak, particularly when seedlings are stored in a greenhouse and/or grown in a growth-promoting environment, can be influenced. Greenhouses experiencing temperatures above 20°C cause a decrease in the total amount of accumulated chilling hours (van den Driessche 1975, Lavender 1981). In addition, the amount and severity of chilling interruptions (i.e., warm temperatures) in a greenhouse prior to storage will cause variations in budbreak speed of nursery-grown seedlings from year to year (van den Driessche 1975). Because greenhouse temperatures were kept below 7°C while the seedlings accumulated chilling hours, we feel little reversion occurred in our experiment. However, several factors interact to determine budbreak speed in a growth-promoting environment (Campbell and Sugano 1975, Perry 1971) including the amount of chilling hour accumulation (Ritchie 1984, Lavender 1985), temperature (Ritchie 1984, van den Driessche 1975), photoperiod (Perry 1971, Wareing 1956, Lavender 1985), and fertilizer supplementation (Perry 1971). Of these, our fertilization technique (low nitrogen rates in the earliest samples) may have increased days to budbreak in the samples that had the very lowest levels of chilling hour accumulation (<56 hr).

Our result, that Idaho and Arizona seedlings had a chilling optimum of 2,010 chilling hr (12 wk of constant chilling), is similar to other studies of coniferous species in the western United States: western hemlock (*Tsuga heterophylla*), 6 to 8 wk (Nelson and Lavender 1979); Douglas-fir (*Pseudotsuga menziesii*), 12 wk (Lavender and Hermann 1970); and western white pine (*Pinus monticola*), 14 wk (Steinhoff and Hoff 1972). Our value of 2,010 chilling hours is a sufficient benchmark for nursery managers, particularly since the stable minimum number of days to budbreak for a seed source varies among years and nurseries (Burr 1990). Further, our observation that days to budbreak decreased with accumulated chilling hours concurs with Sloan (1991) who examined days to budbreak of bareroot ponderosa pine from central Idaho that accumulated natural chilling hours. Seedlings broke bud slowly from September (157 days) to early November (111 days), but then faster from late November (55 days) to April (16 days). Although Sloan (1991) failed to monitor chilling hours and determine a chilling optimum, his data infer that chilling hour accumulation decreased days to budbreak for Idaho ponderosa pine. Interestingly, Burr et al. (1989) found that ponderosa pine from 2,300 m in Arizona could have their chilling optimum reached in 21 days without chilling hour accumulation under warm, short-day growth room conditions.

Budbreak varies within species, as evidenced by seed source and progeny tests (Worrall and Mergen 1967), even under the same chilling hour conditions (van den Driessche 1975, Sweet 1965, Worrall and Mergen 1967). Sweet (1965) found that, for 23 seed sources of coastal Douglas-fir from Washington to California, the median date of terminal budbreak could vary by 29 days.

Such variation may have developed as a survival mechanism in response to the selective action of frost relating to the elevation and geographic origin of the seed (Sweet 1965, Rehfeldt 1986, Rehfeldt 1990). With ponderosa pine found in environments that differ by up to 60 frost-free days and 60 cm in precipitation, populations become differentially adapted in numerous traits including days to budbreak, cold hardening in the fall, shoot elongation, and bud development (Rehfeldt 1986). Despite this, the greatest difference in mean budbreak between seed sources in our experiment was 6 days and occurred before any chilling hours had accumulated (August and September samples). However, Idaho seedlings broke bud significantly faster than Arizona seedlings regardless of refrigerated or frozen storage conditions, perhaps because of a higher likelihood of spring frosts occurring for the Arizona seed source than the Idaho seed source. Although the Arizona seed source is situated at a more southern latitude, the seed source is from an elevation 1,158 m higher than Idaho, allowing for greater probability of frost damage. Although optimum chilling was similar between seed sources, Idaho seedlings were more cold tolerant than Arizona seedlings, possibly due to differential genetic adaptation to their respective environments.

For both seed sources, the fewer days to budbreak for refrigerated seedlings compared to frozen seedlings were directly related to the dormancy state of the seedlings. After the rest phase, refrigerated seedlings were in a "shallower" quiescent state than frozen seedlings, evident by warmer LT_{50} values. Storage conditions affect seedling sugar concentrations that affect cryoprotection of plant tissues (Sakai and Yoshida 1968). Seedling tolerance to cold decreases as needle sugar concentration declines (Ogren 1997, Ogren et al. 1997). Cold tolerance decreases faster in higher temperature storage conditions due to greater respiratory losses of soluble sugars, demonstrated in *Pinus sylvestris* seedlings that showed a 54% decrease in needle sugar concentration at 5.5°C but only 9% at –8.5°C (Ogren 1997). Therefore, the decreased cold tolerance of refrigerated seedlings is probably due to lower soluble sugar concentrations resulting from higher respiration rates in warmer storage conditions.

The Fuchigami et al. (1982) degree growth stage model, a conceptual numerical procedure, quantifies the annual development of vegetative buds of temperate zone woody species. According to the model, cold hardiness and number of days to budbreak increase from vegetative maturity to maximum rest. At maximum rest, seedlings experience near maximum cold hardiness, no shoot growth, and the longest days to budbreak when moved to a growth-promoting environment. Our cold hardiness results concur with the model as well as the findings of Burr et al. (1989), but unlike the model, we found that days to budbreak decreased for our sources of ponderosa pine concurrently with an increase in cold hardiness development. At maximum rest, the chilling optimum had been met, similar to the results of others working with coniferous species (van den Driessche 1975, Nelson and Lavender 1979, Ritchie et al. 1985, Burr et al. 1989).

Conclusions

Growers of ponderosa pine seedlings should provide their crops with at least 2,010 hr of temperatures below 5°C to ensure maximum cold hardiness levels are reached and that seedlings are quiescent before outplanting. Seedlings stored in freezers will have "deeper" quiescence, tolerate colder temperatures, and require more days of favorable conditions before 50% budbreak is reached when compared to seedlings stored above freezing.

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