

Budbreak and Winter Injury in Exotic Firs

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Abstract. Seventeen *Abies* species were evaluated for budbreak and frost injury at four locations in Michigan. Freeze tests were conducted on four species growing at the Horticulture Teaching and Research Center to determine cold hardiness levels during winter. Species differed ($P \leq 0.0001$) in their days to budbreak at all locations. Trees that had broken bud were more prone to late spring frost damage than trees yet to break bud. Species differed in chlorophyll fluorescence, bud damage, and needle damage after exposure to -44°C . Bud, foliar, and cambium damage were correlated with chlorophyll fluorescence following freeze tests. Budbreak and midwinter cold hardiness were correlated. Species breaking bud earlier displayed greater midwinter cold hardiness than species breaking bud later. Selection criteria for future *Abies* introductions to the upper midwestern U.S. should include identifying species with late budbreak to reduce risk of late frost injury.

Throughout the midwestern U.S., planting of conifers has been typically limited to a few species of trees. Trees such as douglas fir [*Pseudotsugamenziesii* (Mirbel.) Franco], norway spruce [*Picea abies* (L.) Karst.], colorado blue spruce [*Picea pungens* Englem.], scotch pine (*Pinus sylvestris* L.), austrian pine (*Pinus nigra* Arnold), and eastern white pine (*Pinus strobus* L.) are frequently used to the point of overplanting. The resulting lack of diversity has led to increased disease problems and insect pressures (McCullough et al., 1998). Recent efforts to increase conifer diversity have sparked increased interest in planting exotic conifers. Much of this interest has centered on exotic firs and their hybrids.

The use of *Abies* in the landscape and Christmas tree industries has been limited to a few species. Expanded use of *Abies* in landscapes has been limited by their perceived intolerance of many site conditions. However, *Abies* may be more tolerant of environmental conditions than originally thought as species differ in their response to soil pH (Cregg et al., 2004), drought (Guehl et al., 1991), and freezing temperatures (Sakai, 1982). Collectively, *Abies* cover large elevational and latitudinal ranges (Liu, 1971). Langlet (1963) suggests large species distribution ranges increase the likelihood of genetic adaptation to diverse environmental factors.

For future evergreen conifer introductions in the upper midwestern U.S., tolerance of freezing temperatures is a necessary charac-

teristic. Trees with adequate cold hardiness are required as average winter low temperatures range from -20 to -42°C in the upper midwestern U.S. (USDA Plant Hardiness Zone Map, 1990). Also, species with late budbreak will have reduced damage from late spring frosts.

In conifers, cold hardiness levels increase in the late fall, reach a maximum in midwinter, and decrease as temperatures rise in late winter (Ritchie, 2003). In *A. lasiocarpa* (Gordon-Kamm, 1980; van der Kamp and Worrall, 1990), *A. procera* (Owston and Kozłowski, 1981), and *A. amabilis* (Dougl.) Forbes (van der Kamp and Worrall, 1990) cold hardiness was reduced following periods of warm temperatures. Maximum cold hardiness also varies among species. For example, *A. spectabilis* (D. Don) Spach is coldhardy to -25°C while *A. balsamea* and *A. sibirica* Ledeb. are cold hardy to -70°C (Sakai, 1982). Considerable intraspecific variation has also been documented for provenances of *A. grandis* (Dougl.) Forbes (Xie and Ying, 1993) and *A. sachalinensis* (Fr. Schm.) Mast. (Eiga and Sakai, 1984). Provenance variation in cold hardiness may be related to latitude, elevation, and winter snowfall.

The direct effect of freezing temperatures is the failure of cell biological functions (Binder and Fielder, 1996; Yordanov, 1992) causing secondary limitation to the photoharvesting system (Adams and Perkins, 1993). Chlorophyll fluorescence is used to measure the efficiency by which photosystem II captures light and is often expressed as the ratio of variable fluorescence to maximum fluorescence (F_v/F_m) (Bjorkman and Demming, 1987). Chlorophyll fluorescence is useful in quantifying cold hardiness (Adams and Perkins, 1993; Binder and Fielder, 1996).

Budbreak is under strong genetic control in *A. amabilis* and *A. lasiocarpa* (Worrall, 1983) and is an adaptive response to climate conditions at the population's origin in *P. menziesii*

var. *menziesii* (Mirb.) Franc (Campbell and Sugano, 1979). First a chilling requirement and then a growing degree day (GDD) requirement must be satisfied for budbreak to occur (Campbell and Sugano, 1979; Howe et al., 2003). Northern provenances of *Acer rubrum* L. have a longer chilling requirement than southern provenances (Perry and Wu, 1960). Provenances from colder regions have a reduced GDD requirement for budbreak than provenances from warmer regions (Campbell and Sugano, 1979). For example, *Picea mariana* (Mill.) B.S.P. provenances from northern Canada broke bud 7 d earlier than provenances from the northern U.S. when grown in southern Ontario, Canada (Morgenstern, 1978).

Species that break bud earlier in the spring are more susceptible to late spring frosts than those breaking bud later in the spring (Hansen and Larsen, 2004; Leege, 2002). Timing of budbreak differs among provenances for *A. alba* Mill. (Hansen and Larsen, 2004), *A. amabilis* (Worrall, 1983), *A. grandis* (Scholz and Stephan, 1982), and *A. lasiocarpa* (Hansen et al., 2004; Worrall, 1983). High elevation provenances have reduced threshold temperatures and thus break bud earlier than lower elevation provenances when grown at lower elevations, suggesting adaptation to a shorter growing season (Worrall, 1983).

The goal of this project is to identify *Abies* species tolerant of the upper midwestern U.S. climate, and promote increased plant diversity. Objectives in this study are to 1) compare the date of budbreak between species, 2) identify differences in the degree of winter injury, and 3) test the hypothesis that midwinter cold hardiness is inversely related to budbreak.

Materials and Methods

Site locations. More than 1100 trees representing 38 species and hybrids of *Abies* were part of a true fir species trial initiated at the Kellogg Research Forest (KRF), Augusta, Mich., in early 1991. In 2002 and 2003, about 300 trees representing 17 species and hybrids (Table 1) were transplanted to three locations in Michigan: Clarksville Horticulture Experiment Station, Clarksville (CHES); Horticulture Teaching and Research Center, East Lansing, (HTRC); and Northwest Michigan Horticulture Research Station, Traverse City (NWHR) (Fig. 1). These three locations along with the KRF represent different climate regions (Table 2) in Michigan. Soils at HTRC and NWHR were loamy sand while soils at CHES and KRF were sandy loam. Trees were dug and ball and burlapped as 60 to 76 cm root balls in accordance with nursery standards. At least four trees of each species or hybrid were planted at each location with the exception of the HTRC where one to four additional trees of each species were planted when available. Trees were planted at about 4.5 m intervals in a complete randomized design at each location. In addition, at KRF four trees of each species were selected for further study.

Fertilization. In Spring 2004, sites were fertilized with granular 21–0–0 ammonium sulfate at a rate of about 133 g per tree, to lower soil

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Table 1. List of *Abies* species planted at four locations in Michigan.

Common name	Scientific name	Geographic origin	Elevation (m) ^z	Latitude (°N) ^z
Ernst fir	<i>A. chensiensis</i> Van Tiegh.	Asia	2500–3800	25–33
Korean fir	<i>A. koreana</i> Wils.	Asia	1000–2000	33–36
Needle fir	<i>A. holophylla</i> Maxim.	Asia	0–1400	33–49
Nikko fir	<i>A. homolepis</i> Sieb. et Zucc.	Asia	600–2200	33–38
Siberian White fir	<i>A. nephrolepis</i> (Trautv.) Maxim.	Asia	500–2000	35–55
Veitch fir	<i>A. veitchii</i> Lindl.	Asia	1200–3000	33–38
Balsam fir	<i>A. balsamea</i> (Linn.) Mill.	N. America	0–1500	38–59
Cannan fir	<i>A. balsamea</i> var. <i>phanerolepis</i> (Fern.) Liu	N. America	0–1500	38–59
Corkbark fir	<i>A. lasiocarpa</i> var. <i>arizonica</i> (Merr.) Lemm.	N. America	0–1700	37–39
Fraser fir	<i>A. fraseri</i> (Pursh.) Poir.	N. America	1100–2100	35–37
Noble fir	<i>A. procera</i> Rehd.	N. America	100–2700	41–48
Subalpine fir	<i>A. lasiocarpa</i> (Hook.) Nutt.	N. America	0–3500	32–64
Nordman fir	<i>A. nordmanniana</i> (Steven) Spach.	Mediterranean	1000–2200	40–44
Turkish fir	<i>A. nordmanniana</i> ssp. <i>equi-trojani</i> (Aschers. et Sint. Ex Boiss.) Coode et Cullen	Mediterranean	1000–2200	40–44
Fraser × Nikko hybrid	<i>A. fraseri</i> × <i>homolepis</i>	N. America/Asia	---	---
Korean × Balsam hybrid	<i>A. koreana</i> × <i>balsamea</i>	N. America/Asia	---	---
Korean × Veitch hybrid	<i>A. koreana</i> × <i>veitchii</i>	Asia/Asia	---	---

^zReferenced in Liu, 1971.



Fig. 1. Location of four *Abies* trials in Michigan: 1) Kellogg Research Forest (KRF), 2) Clarksville Horticultural Experiment Station (CHES), 3) Horticulture Teaching and Research Center (HTRC), and 4) Northwest Michigan Horticultural Research Station (NWHR).

pH, and insure that nitrogen was not limiting. Fertilizer was applied at CHES on 29 Apr., at HTRC on 22 Apr., and at NWHR on 11 May. On 7 July 2004, 46–0–0 urea was applied at CHES at a rate of 91 g per tree. Trees at KRF were fertilized every fall with 21–0–0 at 85 g per tree. Trees exceeding 0.9 m received 28 g of fertilizer for each additional 0.3 m in height.

Budbreak. Beginning 16 Mar. 2004 and 24 Mar. 2005, trees at each of the three outlying sites and the KRF were surveyed for budbreak, considered to have occurred once one shoot broke its bud scale. Trees were inspected weekly until all trees at each location had

broken bud. Air temperature was recorded using weather stations located at each site and available for download on the Michigan Automated Weather Network (MAWN) (<http://www.agweather.geo.msu.edu/mawn/>) website. For each inspection date, growing degree days (GDD) were calculated using a base temperature of 10 °C (Dickson et al., 2000) and the numerical integration method using the MAWN website.

Frost damage. Temperatures reached –2.2 and –2.4 °C on 3 and 4 May 2004 at the KRF after some trees had begun to break bud. Trees were visually rated on 5 May 2004 using the

following 0 to 4 scale: 0 = no shoots damaged, 1 = 1% to 25%, 2 = 26% to 50%, 3 = 51% to 75%, and 4 = 76% to 100% of shoots damaged. Shoots were considered damaged if they were brown in color or had lost rigidity. All trees in each species block (n = 7 to 42) were inspected for frost damage, in addition to the four individuals previously selected at random for the budbreak study.

Cold hardiness. Four species were chosen to measure cold hardiness and represent species with early, early-mid, mid-late, and late budbreak groups respectively: *A. nephrolepis*; *A. balsamea* var. *phanerolepis*; *A. chensiensis*; and *A. veitchii*. Shoots from the current year's growth were collected from three trees of each species at the HTRC. Samples were collected on 13 Dec. 2004, 24 Jan. 2005, and 7 Mar. 2005 with freeze tests beginning 1 to 3 d later. Twelve samples for each temperature (4 species × 3 replications) treatment were laid on moist cheese cloth, covered with aluminum foil, and rolled into bundles. A thermocouple was inserted into the stem of one sample in each bundle to measure stem temperature. Bundles were then placed into a freezer (ScienTemp, Adrian, Mich.) and stored at 2 °C until the test began. Temperatures were lowered at 3 °C·h⁻¹ and a bundle was removed at each targeted temperature until completion of the run. A control bundle was kept in a walk-in cooler at 2 °C where bundles were allowed to thaw following removal from the freezer.

In the 13 Dec. 2004 and 24 Jan. 2005 tests, a bundle was removed at each of the following temperatures: 2, –18, –21, –24, –27, –30, –33, –36, –39, –42, and –44 °C. In the 7 Mar. 2005 test, a bundle was removed at the following temperatures: 2, –6, –9, –12, –15, –18, –21, –24, –27, –30, –33, –36, –39, –42, and –44 °C. Bundles were placed in a walk-in cooler and allowed to thaw at 2 °C for 2 to 3 d and then placed in a high humidity chamber at room temperature (25 °C) for 4 to 5 d. Then samples were visually rated for needle damage, bud damage, and cambium damage using the following 0 to 2 scale: 0 = no damage; 1 = partial browning of the tissue, 2 = dead tissue.

Chlorophyll fluorescence (F_v/F_m) was measured using two needles from every sample in each temperature treatment using a portable

chlorophyll fluorescence system (plant efficiency analyzer, Hansatech Instruments Ltd., Norfolk, U.K.). Samples were clipped and dark-acclimated for 15 min before readings were taken.

Statistical analysis. Species effects on budbreak and cold hardiness damage were determined using PROC MIXED (SAS Inc., Cary, N.C.). When significant differences were indicated, means were separated using Tukey's Studentized range test (Sexton, 1998). Species and year effects on the GDD required to budbreak were determined using PROC GLM (SAS Inc.) and means were separated using the Tukey's Studentized range test. Species and location effects on the date of budbreak and GDD required for budbreak were determined by analysis of variance using a fixed effects model:

$$y_{ijk} = \mu + \alpha_i + \gamma_j + \alpha\gamma_{ij} + \epsilon_{ijk}$$

where y_{ijk} = response of the tree, α_i is the effect of species i , γ_j is the effect of the location j , and ϵ_{ijk} is the error term. Damage ratings were analyzed using non-parametric measures and with a pairwise comparison of means using the Kruskal-Wallis test (Ott, 1988). Correlation between tissue damage, F_v/F_m , and the mean date of budbreak were identified using PROC CORR (SAS Inc.).

Results

Budbreak. The date of budbreak varied with planting location ($P \leq 0.0001$), species ($P \leq 0.0001$), and year ($P \leq 0.03$) (Table 3). We observed variation in budbreak within individual trees as not all buds broke at the same time on a given tree. Budbreak began in mid to late April in both years, lasting between 29 to 49 d in 2004 and 36 to 49 d in 2005 depending upon location. Trees at southern sites began and finished breaking bud earlier than northern sites. All trees had broken bud by 17 June 2004 and 9 June 2005. In both years, *A. holophylla*, *A. lasiocarpa*, *A. lasiocarpa* var. *arizonica*, and *A. nephrolepis* were among the first to break bud at all four locations, while *A. veitchii* and *A. homolepis* were among the last species to break bud at all four locations.

Growing degree days (GDD) required for budbreak differed among species ($P \leq 0.0001$), locations ($P \leq 0.0001$), and years ($P \leq 0.04$). Trees at the southern locations accumulated GDD faster and required more GDD for budbreak than at northern locations (Table 4). Growing degree day (GDD) accumulation was initially slower in 2005 but by early June GDD accumulation was nearly equal to 2004. Fewer GDD were required at NWHRs for budbreak than at the other locations.

Species were ranked for budbreak at each location and a strong location: location correlation existed (Table 5) signifying budbreak among species was generally related at each location. Location \times species interaction for both days to budbreak and GDD was significant ($P \leq 0.0001$), indicating the rank order of some species changed among locations. For example, *A. koreana* was in the last group to break bud at CHES, HTRC, and NWHRs while being one

of the first species to break bud at KRF. In *A. koreana* \times *veitchii* and *A. fraseri* \times *homolepis*, budbreak was not closely related to the parent species, while budbreak for *A. koreana* \times *balsamea* was similar to its parents'.

Mean days to budbreak at the HTRC was correlated ($R^2 = 0.38$, $P = 0.033$) with average F_v/F_m at -44°C (Fig. 2). Trees breaking bud earlier had higher F_v/F_m values than trees breaking bud later. *Abies chensiensis* had the lowest F_v/F_m of the species included in the cold hardiness study.

Late frost damage. Late frost damage following the May 2004 freeze was related to the date of budbreak. Trees breaking bud early displayed more damage from the late spring frost than those breaking bud later ($R = 0.798$, $P < 0.01$). At KRF *A. holophylla*, *A. lasiocarpa*, *A. lasiocarpa* var. *arizonica*, and *A. nephrolepis* displayed a high percent of frost damage in a large number of trees (Fig. 3). In contrast, *A. chensiensis*, *A. fraseri* \times *homolepis*, *A. koreana*, *A. nordmanniana* ssp. *equi-trojani*, and *A. procera* displayed no frost damage. At the time of frost, the following species had not completed budbreak: *A. fraseri* \times *homolepis*, *A. homolepis*, *A. koreana*, *A. koreana* \times *balsamea*, *A. procera*, and *A. veitchii*. In both *A. homolepis* and *A. veitchii* late frost damage occurred in some trees not included in the budbreak survey but inspected for late frost damage.

Cold hardiness. Cold hardiness varied among species and by test date. Chlorophyll fluorescence values declined with decreasing temperatures ($P \leq 0.001$). Chlorophyll fluorescence (F_v/F_m) values decreased as temperatures were lowered during controlled freeze tests in *A. chensiensis* and *A. veitchii* but remained constant in *A. balsamea* var. *phanerolepis* and *A. nephrolepis* as temperatures reached -44°C . At -44°C , F_v/F_m differed among species for tests during December 2004 ($P \leq 0.002$) and January 2005 ($P \leq 0.001$), but not March 2005 ($P = 0.10$) (Table 6). Needle damage differed among species at -44°C in all tests ($P \leq 0.05$). Needle damage was greatest in *A. chensiensis* in all tests. Visible damage to needles, stem tissue, and buds was highly correlated ($P < 0.001$) with a decline in F_v/F_m values (Table 7). Damage to stem tissue and buds did not differ ($P > 0.05$) among species on any test date. Damage to needles, stem tissue, and buds were highly correlated ($P < 0.001$) with a decline in F_v/F_m values (Table 7).

Table 2. Thirty-year climate summary and USDA plant hardiness zones for four *Abies* planting sites in Michigan.

Location	Avg January low ($^\circ\text{C}$) ^z	Avg July high ($^\circ\text{C}$) ^z	Avg annual precipitation (cm) ^z	Avg annual snowfall (cm) ^z	Growing season (days) ^y	USDA hardiness zone ^y
CHES ^x	-10	28	90.7	145	147	5B
HTRC ^w	-11	28	78.5	99	150	5A
KRF ^v	-9	28	89.4	135	149	5B
NWHRs ^u	-10	27	85.1	244	135	5B

^zIllinois Dept. of Nat. Res., 2005.

^yUSDA Plant Hardiness Map, 1990.

^xClarksville Horticulture Experiment Station (CHES), Clarksville, Mich.

^wHorticulture Teaching and Research Center (HTRC), East Lansing, Mich.

^vKellogg Research Forest (KRF), Augusta, Mich.

^uNorthwest Michigan Horticulture Research Station (NWHRs), Traverse City, Mich.

Discussion

In each species, the date of budbreak was similar in both years (Table 3). However, GDD at the time of budbreak differed in both years for each species due to differences in weather conditions. Also, rank correlations between locations suggest budbreak is under strong genetic control (Table 5), which is supported by previous studies (Worral, 1983). Meeting a chilling requirement and accumulating a set number of GDD are necessary for trees to break bud (Howe et al., 2003). In both years, budbreak first occurred at southern locations in mid April and began at NWHRs in late April. The difference between the first and last species to break bud ranged between 29 and 49 d depending on location suggesting late bud breaking species such as *A. koreana* and *A. veitchii* require more GDD to break bud than species with earlier budbreak. Within species, some variation in budbreak occurred at different locations and was most prevalent in hybrids; although several species were influenced by unknown location factors.

Abies balsamea is native to the upper midwestern U.S., is prone to late spring frost damage (Lantagne and Koelling, 2004), and thus can serve as a point of reference for the species included in this study. In 2005, the following species broke bud earlier than *A. balsamea* at at least three locations: *A. holophylla*, *A. lasiocarpa*, *A. lasiocarpa* var. *arizonica*, and *A. nephrolepis*. At KRF in 2004, trees breaking bud after *A. balsamea* showed no evidence of late frost damage with the exception of *A. homolepis* and *A. veitchii*. Damage in these two species was limited to trees located on top of a hill which received more thermal time and had already broken bud. As a result, they were damaged by late spring frost while trees growing at the base of the hill had not yet broke bud and thus showed no signs of damage.

The mean number of GDD required to break bud was different ($P \leq 0.0001$) at each location (Table 4). At the NWHRs, trees required fewer GDD to break bud than more southern locations, implying that another factor in addition to thermal time may be influencing budbreak. There is some evidence that photoperiod has some influence on budbreak (Partanen et al., 1998); although its effect is debated (Worral, 1983). In 2004, daylength for trees at the NWHRs were nearly 1 h longer

when the last tree broke bud than at KRF, which perhaps can explain the difference in the GDD required for budbreak. In *P. menziesii* var. *menziesii* (Mirb.) Franc. populations from regions with similar winter temperatures, trees from regions with the largest moisture deficit broke bud earlier than the average (Campbell and Sugano, 1979). This suggests that trees from regions frequented by summer drought break bud early in the spring to complete stem elongation and set bud before summer drought conditions begin (Kaya et al., 1994). Both *A. koreana* and *A. veitchii*, two of the last species to break bud in this study, are native to regions with ample summer precipitation (Farjon, 1990) so perhaps their late budbreak is an adaptive response to a mild climate and adequate summer precipitation.

Within species, provenances can vary greatly in time of budbreak (Hansen and Larsen,

2004; Scholz and Stephen, 1982; Worrall, 1983) and cold hardiness levels (Dolnicki and Kraj, 1998; Eiga and Sakai, 1984, 1987, Xie and Ying, 1993). One of the limitations of the current study is that provenance information for each species is unknown. Moreover, it is unknown if the parent trees of the hybrids were from the same provenance as the pure species included in this study. For example, the *A. veitchii* parent of the *A. koreana* × *veitchii* hybrid is not necessarily from the same seed source as the pure *A. veitchii* included in this study, which could explain some of the inconsistencies in the budbreak between the parents and their hybrids. Also, variation within a species is not accurately represented because each species is represented by a single provenance.

Chlorophyll fluorescence (F_v/F_m) was a good indicator of cold injury during controlled

freeze tests as F_v/F_m values declined with decreasing temperatures. These results paralleled increasing needle, stem, and bud damage, which is consistent with previous studies (Adams and Perkins, 1993; Binder and Fielder, 1996). Cold hardiness between different plant organs differs in the temperature at which damage occurs (Sakai, 1982). The temperature where damage occurred was different for buds, stems, and needles. However, damage variables and F_v/F_m values were strongly correlated suggesting that while the temperatures that damage different organs may vary, relative cold hardiness is related (Table 7).

Many studies show differences in cold hardiness among species and provenances (Eiga and Sakai, 1984, 1987; Sakai, 1982; Xie and Ying, 1993). As expected, trees included in the cold hardiness study also varied in the temperature at which they displayed damage

Table 3. Budbreak date of 17 *Abies* species grown at four locations in Michigan in 2004 and 2005.

Species	2004				2005			
	CHES ^x	HTRC ^w	KRF ^y	NWHRSt ^u	CHES	HTRC	KRF	NWHRSt
<i>A. nephrolepis</i>	April 20 a ^z	April 24 abc	April 22 a	May 4 a	April 20 a	April 20 a	April 20 a	April 28 a
<i>A. lasiocarpa</i> var. <i>arizonica</i>	April 22 a	April 23 ab	April 22 a	May 4 a	April 19 a	April 20 a	April 20 a	May 1 ab
<i>A. holophylla</i>	April 23 a	April 21 a	April 22 a	May 6 ab	April 20 a	April 20 a	April 20 a	May 3 ab
<i>A. lasiocarpa</i>	April 29 ab	April 22 ab	April 22 a	May 6 ab	April 30 abcd	April 26 ab	April 20 a	April 29 a
<i>A. balsamea</i>	May 2 abc	May 1 abc	NR ^y	May 10 ab	April 24 ab	May 2 abc	April 26 abc	May 10 abc
<i>A. koreana</i> × <i>veitchii</i>	May 3 abc	May 3 bcde	April 26 ab	May 17 abcde	May 2 abcd	May 5 bcd	April 22 ab	May 18 abc
<i>A. bal.</i> var. <i>phanerolepis</i>	May 5 abc	May 3 bcde	NR ^y	May 15 abcde	April 28 abcd	May 5 bcd	April 27 abc	May 15 abc
<i>A. nordmanniana</i>	May 5 abc	May 5 cdef	NR ^y	NR ^y	April 27 abc	May 9 bcde	May 4 abcd	NR ^y
<i>A. koreana</i> × <i>balsamea</i>	May 5 abc	May 26 i	May 3 abc	June 4 e	May 6 abcd	May 26 fg	May 2 abc	May 25 bc
<i>A. fraseri</i> × <i>homolepis</i>	May 12 bc	May 7 defg	May 5 abc	May 25 bcde	May 9 abcd	May 9 bcde	May 8 bcde	May 18 abc
<i>A. procera</i>	May 12 bc	May 12 defgh	May 7 bc	May 13 abcd	May 9 abcd	May 18 defg	May 10 cde	May 30 c
<i>A. nord.</i> ssp. <i>equi-trojani</i>	May 12 bc	May 14 efgh	May 5 abc	May 27 cde	May 1 abcd	May 12 cdef	May 8 bcde	May 22 abc
<i>A. chensiensis</i>	May 14 bc	May 12 defgh	May 3 abc	May 13 abcd	May 10 bcd	May 10 bcde	May 10 cde	May 17 abc
<i>A. homolepis</i>	May 16 c	May 18 ghi	May 12 c	May 20 abcde	May 18 d	May 24 efg	May 20 de	May 25 bc
<i>A. fraseri</i>	May 17 c	May 16 fghi	NR ^y	May 29 cde	May 10 abcd	May 15 cdefg	May 11 cde	May 20 abc
<i>A. koreana</i>	May 19 c	May 22 hi	May 2 abc	May 27 cde	May 17 cd	May 25 fg	May 10 cde	May 20 abc
<i>A. veitchii</i>	May 19 c	May 22 hi	May 14 c	June 3 de	May 17 cd	May 28 g	May 24 e	June 1 c

^zMeans within columns followed by the same letter were not statistically different, $\alpha = 0.05$, Tukey Studentized range test.

^yNo records were available for trees listed as NR.

^xClarksville Horticulture Experiment Station (CHES), Clarksville, Mich.

^wHorticulture Teaching and Research Center (HTRC), East Lansing, Mich.

^yKellogg Research Forest (KRF), Augusta, Mich.

^uNorthwest Michigan Horticulture Research Station (NWHRSt), Traverse City, Mich.

Table 4. Mean growing degree days required before budbreak in 17 *Abies* species grown at four locations in Michigan in 2004 and 2005.

Species	2004				2005			
	CHES ^x	HTRC ^w	KRF ^y	NWHRSt ^u	CHES	HTRC	KRF	NWHRSt
<i>A. nephrolepis</i>	114 a ^z	128 a	150 a	81 a	153 a	148 a	176 a	102 a
<i>A. lasiocarpa</i> var. <i>arizonica</i>	119 ab	124 a	150 a	95 ab	153 a	148 a	176 a	102 a
<i>A. holophylla</i>	122 ab	117 a	150 a	83 a	153 a	148 a	176 a	106 a
<i>A. lasiocarpa</i>	170 abc	123 a	150 a	110 ab	163 ab	175 ab	176 a	113 a
<i>A. nordmanniana</i>	182 abcd	209 abc	NR ^y	NR ^y	159 a	204 ab	227 ab	NR ^y
<i>A. bal.</i> var. <i>phanerolepis</i>	193 abcd	179 ab	NR ^y	157 abc	162 ab	180 ab	201 a	162 abc
<i>A. koreana</i> × <i>veitchii</i>	198 abcde	179 ab	163 a	169 abc	197 abc	180 ab	177 a	181 abc
<i>A. koreana</i> × <i>balsamea</i>	223 abcdef	447 f	220 ab	286 c	218 abc	310 de	224 a	242 abc
<i>A. balsamea</i>	226 abcdef	167 a	NR ^y	114 ab	158 a	193 ab	181 a	142 ab
<i>A. nord.</i> ssp. <i>equi-trojani</i>	269 bcdef	310 cde	221 ab	214 abc	180 abc	231 abcd	231 ab	206 abc
<i>A. fraseri</i> × <i>homolepis</i>	270 bcdef	223 abc	246 ab	201 abc	210 abc	208 abc	231 ab	198 abc
<i>A. procera</i>	272 bcdef	285 bcd	247 ab	146 abc	223 abc	252 bcd	251 abc	284 bc
<i>A. chensiensis</i>	292 cdef	285 bcd	208 ab	146 abc	237 abc	219 abcd	251 abc	168 abc
<i>A. homolepis</i>	317 cdef	355 def	325 b	184 abc	276 c	306 cde	324 bc	219 abc
<i>A. fraseri</i>	331 def	325 cde	NR ^y	220 abc	220 abc	248 bcd	270 abc	189 abc
<i>A. koreana</i>	347 ef	403 ef	233 ab	249 bc	264 bc	310 de	258 abc	194 abc
<i>A. veitchii</i>	364 f	396 def	342 b	299 c	266 c	351 e	348 c	324 c

^z Means within columns followed by the same letter were not statistically different, $\alpha = 0.05$.

^yNo records available for trees listed as NR.

^xClarksville Horticulture Experiment Station (CHES), Clarksville, Mich.

^wHorticulture Teaching and Research Station (HTRC), East Lansing, Mich.

^yKellogg Research Forest (KRF), Augusta, Mich.

^uNorthwest Michigan Horticulture Research Station (NWHRSt), Traverse City, Mich.

^vBase temperature 10 °C.

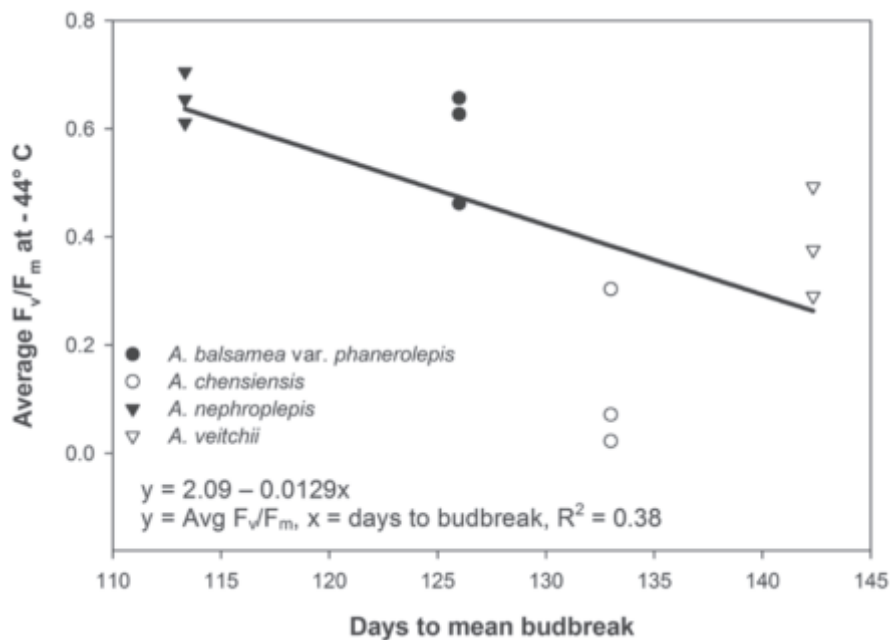


Fig. 2. Comparison of average chlorophyll fluorescence (F_v/F_m) at -44°C and days to mean budbreak in four *Abies* species growing at the Horticulture Teaching and Research Center in December 2004, January 2005, and March 2005.

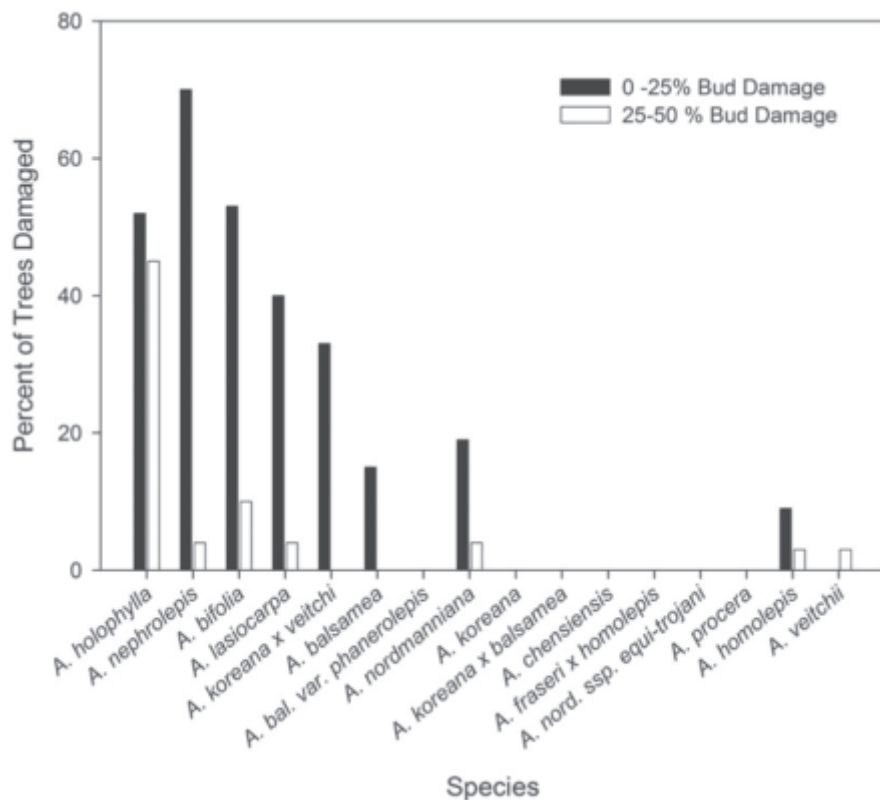


Fig. 3. Frost damage to recently emerged shoots at the Kellogg Research Forest, 5 May 2004.

to freezing temperatures. One limitation of the current study was the inability of the programmable freezer to be lowered beyond -44°C . From a practical standpoint, this is near to the lowest annual temperatures in the coldest regions of the upper midwestern U.S. In most years, species showing no signs of damage should be able to survive most winters if given the necessary time to acclimate.

During the fall, the degree of cold hardiness in trees gradually increases, reaches a maximum during midwinter, and gradual declines (Ritchie, 2003). Bud damage in the March test indicates internal development processes related to budbreak may have begun, and warmer temperatures likely reduced cold hardiness levels leading to increased freeze damage. Needle damage ratings were

the lowest in January (Table 6). Typically January temperatures were the lowest so more conditioning lead to greater cold hardiness. Increased damage in December and March was likely due to incomplete acclimation and the start of deacclimation leading to less cold hardiness. Stem damage ratings did not differ among species suggesting cambium tissue was adequately insulated at -44°C , the lowest temperature possible in our controlled freeze test. Chlorophyll fluorescence (F_v/F_m) declined progressively between each test suggesting that repairs to cold damage did not begin until growth began again in the spring. Chlorophyll fluorescence (F_v/F_m) at -44°C differed significantly among species in December and January, but not March.

Other factors being equal, trees from colder regions are cold hardy at lower temperatures (Sakai, 1982) and break bud earlier in a common site, due to a reduced chilling and thermal time requirement, than trees from warmer regions. Worrall (1983) suggests this may be an adaptation allowing trees to complete their growth before fall frosts in cold regions with short growing seasons. In the present study, date of budbreak and F_v/F_m readings at -44°C were strongly correlated for the individual trees included in the cold hardiness experiment. Trees with maximum cold hardiness levels were among the first species to break bud in the spring while species with reduced cold hardiness were among the last (Fig. 2), suggesting trade-offs between midwinter cold hardiness and the GDD required to break bud.

In summary, species varied in their tolerance of freezing temperatures and in the date they broke bud. Strong correlations existed between the temperatures at which different plant tissues showed visual signs of damage. Species that were among the first to break bud in the spring withstood colder winter temperatures than trees breaking bud later. Species breaking bud early in the spring were more likely to be damaged by late spring frosts. Budbreak should continue as an important selection criterion for conifer species introduced to the landscape and Christmas tree industries in the upper Midwest. Species such as *A. homolepis*, *A. koreana*, and *A. veitchii* were among the last species to break bud at all locations and should be considered for future introduction. Additional studies should focus on identifying provenances with late budbreak and adequate cold hardiness for species with desirable ornamental characteristics such as *A. lasiocarpa*

Table 5. Pearson correlation coefficients for budbreak of 17 *Abies* species at four locations in Michigan.

Location	HTRC ^y	KRF ^x	NWHR ^w
CHES ^z	0.71***	0.61***	0.53***
HTRC		0.60***	0.71***
KRF			0.58***

^zClarksville Horticulture Experiment Station (CHES), Clarksville, Mich.

^yHorticulture Teaching and Research Center (HTRC), East Lansing, Mich.

^xKellogg Research Forest (KRF), Augusta, Mich.

^wNorthwest Michigan Horticulture Research Station (NWHR), Traverse City, Mich.

***Significant at $P \leq 0.0001$.

Table 6. Mean chlorophyll fluorescence (F_v/F_m) values and needle damage ratings of four *Abies* species following controlled freeze tests to $-44\text{ }^\circ\text{C}$.

Species	F_v/F_m			Needle damage		
	December*	January**	March ^v	December*	January*	March*
<i>A. bal.</i> var. <i>phanerolepis</i>	0.627 a ^z	0.657 a	0.462	1.0 a ^u	0.0 a	0.3 ab
<i>A. nephrolepis</i>	0.611 a	0.654 a	0.705	1.0 a	0.0 a	0.0 a
<i>A. veitchii</i>	0.375 a	0.492 a	0.291	1.7 a	0.7 a	1.7 bc
<i>A. chensiensis</i>	0.022 b	0.071 b	0.304	2.0 b	2.0 b	2.0 c

^zMeans within a column followed by the same letter were not significantly different, $\alpha = 0.05$, Tukey studentized range test.

^vMeans within a column followed by the same letter were not significantly different, $\alpha = 0.05$, Kruskal-Wallis.

*Shoots collected on 13 Dec. 2004.

**Shoots collected on 24 Jan. 2005.

^uShoots collected on 7 Mar. 2005.

^uRating scale 0 = no damage, 1 = partial browning of the tissue, 2 = dead tissue.

*Significant at $P \leq 0.05$ and indicates significant species effects for controlled freeze test that month.

Table 7. Pearson's correlation coefficient for needle, stem, and bud damage and chlorophyll fluorescence (F_v/F_m) in four *Abies* species growing at the Horticulture Teaching and Research Center in March 2005 following controlled freeze test.

	Needle damage	Stem damage	Bud damage
F_v/F_m	-0.60***	-0.69***	-0.46***
Needle damage		0.77***	0.65***
Stem damage			0.68***

***Significant at $P \leq 0.0001$.

and *A. lasiocarpa* var. *arizonica*.

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