



Cold tolerance of black spruce, white spruce, jack pine, and lodgepole pine seedlings at different stages of spring dehardening

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Abstract

Understanding tree vulnerability to freezing temperatures will help resource managers to mitigate the effects of climatic variability. To test the effectiveness of tissue dehardening curves to represent whole seedling responses, we tested the cold tolerance of 4 conifer species to a range of freezing temperatures, -15 , -25 , and -35 °C in late March, and -5 , -10 , and -15 °C in early May. Results show that, after a 30-min exposure to freezing temperatures, needle mortality started at -25 °C in late March (early spring dehardening) before budbreak activation and at -10 °C in early May (late spring dehardening) when pine buds had flushed and white spruce (*Picea glauca*) buds had started swelling. Freezing temperatures delayed the timing of budbreak; increased needle, terminal bud, and seedling mortality; and reduced shoot growth and number of top laterals. White spruce and lodgepole pine (*Pinus contorta*) were more sensitive to freezing in terms of needle, terminal bud, and seedling mortality and growth reduction. The effects of March freezing were generally detected in the first year, whereas those of the May freezing were still evident in the second year on the shoot growth of black spruce (*Picea mariana*) and jack pine (*Pinus banksiana*). Although they seem relatively hardier based on first year post-freezing assessments (i.e., less immediate physical damage from freezing), black spruce and jack pine may have sustained more internal or physiological shock/damage. Our study results support the use of tissue cold hardiness–forcing temperature relationships to assess the risk of freezing damage for conifer seedlings.

Keywords Spring dehardening · Freezing temperatures · Tissue cold hardiness · Boreal conifers

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Introduction

Climate change may increase the range and variability of temperatures (Schär et al. 2004; Rigby and Porporato 2008), especially at higher latitudes and during winter months (Bonsal et al. 2001; Robeson 2004; Park et al. 2014). Periods of unseasonably high temperatures during winter can result in earlier loss of cold hardiness (dehardening) and increased risk of freezing damage, especially when followed by seasonal temperatures (Man et al. 2009, 2013a). Such winter freezing is generally extensive, affecting trees of all species and sizes across large areas (Cayford et al. 1959; Hiratsuka and Zalasky 1993; Man et al. 2009, 2013a), and can pose a significant threat to forest health (Bella and Navratil 1987; Man et al. 2013b). Because of its relatively infrequent occurrence, dormant season freezing damage has not been adequately studied (Hiratsuka and Zalasky 1993; Man et al. 2009, 2013a, 2016) and is often mistaken for winter desiccation (drying) or winter drought damage (e.g., Cayford et al. 1959; Bella and Navratil 1987; Hiratsuka and Zalasky 1993; Berg and Chapin 1994). Post-freezing needle loss and bud mortality are normally assessed in the first year (Cayford et al. 1959; Man et al. 2009, 2013a) and growth loss and tree mortality in the first few years post-freezing (Bella and Navratil 1987; Man et al. 2013b). Reported damage, however, is not linked to specific freezing temperatures and, therefore, generally not useful for assessing and predicting damage (Man et al. 2017a).

Man et al. (2017a) examined changes in cold hardiness after artificial dehardening of black spruce (*Picea mariana* (Mill.) B.S.P.), white spruce (*Picea glauca* (Moench) Voss), jack pine (*Pinus banksiana* Lamb.), and lodgepole pine (*Pinus contorta* Dougl. ex. Loud.) seedlings. Cold hardiness assessments were made on pine needles and spruce shoots (buds removed) and related to forcing temperatures (cumulative growing degree hours above 0 °C or thermal accumulation). As spring dehardening is driven primarily by forcing temperatures after the fulfilment of chilling requirements (Hänninen 1995; Man and Lu 2010; Sjøgaard et al. 2008), these cold hardiness–forcing temperature relationships can be valuable for assessing the effects of freezing temperatures and predicting the risk of freezing damage (Man et al. 2017a). Therefore, we conducted whole seedling freezing experiments on black spruce, white spruce, jack pine, and lodgepole pine at different stages of spring dehardening and compared the results against cold hardiness predicted from the previously reported tissue cold dehardening curves (Man et al. 2017a). Our objective was to determine whether tissue cold dehardening curves could be used to predict whole seedling responses to freezing temperatures, as suggested by Burr et al. (2001).

Methods

Seedling materials

Lodgepole pine seedlings were initially grown in containers in a greenhouse at Tree Time Services Inc./Coast to Coast Reforestation in Smoky Lake, Alberta, Canada (54° 07'N, 112° 28'W), using seeds of open-pollinated wild trees from southwest of Whitecourt, Alberta (54° 04'N, 115° 41'W). Black spruce, white spruce, and jack pine seedlings were initially grown in containers at the Millson Forestry Service Inc. in Timmins, Ontario (48° 28'N, 81° 24'W), using seeds from seed orchard trees established for the nearby Martel Forest area (47°50'–48°28'N, 82°15'–83°25'W). After cold storage, 1-year-old container seedlings were shipped to the Ontario Forest Research Institute in Sault Ste. Marie, Ontario

(46° 30'N, 84° 18'W) in early June 2013, where they were transplanted into 4" square (10 cm sides × 15 cm deep) pots filled with 2:1 peat moss/vermiculite (v/v) mixture and grown in the greenhouse. The seedlings received natural photoperiods with temperatures 2–5 °C above ambient and were watered as required using an automated mobile irrigation system, supplemented with hand watering, and fertilized weekly with 20-8-20 (N-P-K) (Plant Products Co Ltd, Brampton, ON) at 100 ppm N for a month before being moved outdoors in early July. They were kept outdoors for 3 summers with weekly watering and biweekly fertilization following standard nursery practices (20-8-20 at 100 ppm N before mid-August and 20-20-20 at 50 ppm N from late August to mid-October), and received winter snow cover from late December to late March and natural hardening and dehardening under ambient photoperiod and temperatures. Average height and basal diameter of the 4-year-old seedlings before whole seedling freezing tests were 76.4 cm and 9.9 mm for black spruce, 61.5 cm and 9.5 mm for white spruce, 75.3 cm and 11.5 mm for jack pine, and 66.2 cm and 11.1 mm for lodgepole pine, respectively.

Seedling freezing tests

Whole seedling freezing tests were conducted at 2 stages of natural dehardening in spring using the outdoor-grown seedlings. The first freezing test was carried out during the early stage of spring dehardening (March 19–21, 2016) when cumulative forcing temperatures (cumulative growing degree hours > 0 °C since January 1) was about 1500 and no sign of budbreak was evident in seedlings. Based on the tissue cold hardiness–forcing temperature relationships for the 4 species (Man et al. 2017a), tissue cold hardiness was –31.0 °C for black and white spruce, –28.1 °C for jack pine, and –24.8 °C for lodgepole pine. The second freezing test was conducted during late stage of spring dehardening (May 2–4, 2016) when cumulative forcing temperature was about 5800, lodgepole pine and jack pine had flushed, and white spruce buds had started swelling. Based on Man et al.'s (2017a) dehardening curves, tissue cold hardiness was –13.4 °C for black spruce, –10.7 °C for white spruce, –11.5 °C for jack pine, and –9.8 °C for lodgepole pine.

During the March freezing test, outdoor night temperatures were about –5 °C. Whole seedlings were covered with large plastic bags and conditioned at 0 °C overnight before they were exposed to testing temperatures of –15, –25, and –35 °C in a programmable freezer (Thermotron® SM-32-C, Holland, MI). During the May freezing test, outdoor night temperatures were near 0 °C and seedlings were directly exposed to testing temperatures of –5, –10, and –15 °C. These temperatures were chosen to cover the species' cold hardiness as determined from their tissue dehardening curves (Man et al. 2017a). The temperature inside the freezer was reduced at 5 °C h⁻¹ for the March freezing test and 3 °C h⁻¹ for the May freezing test; the latter allowed for better differentiation of cold hardiness changes at the late stage of spring dehardening (Man et al. 2017a). After 30 min at target temperature, seedlings were conditioned for 2 h at –10 °C for testing temperatures below –10 °C and held at 0 °C overnight before being returned outdoors. Each freezing temperature was replicated 3 times (days), with 4 seedlings from each of the 4 species per replication. For both freezing tests, unfrozen outdoor seedlings were used as controls and seedlings in freezing treatments were covered with 1.75-inch fibreglass around pots to minimize the effects of freezing temperatures on roots (Bigras and Dumais 2005).

After the freezing tests, seedlings were returned outdoors and fertilized and watered as described above. Percentage needle death was visually assessed 1 month after the March freezing and about 8 days after the May freezing, when needle browning and

mortality became clearly visible (Man et al. 2017a). The time (cumulative growing degree hours > 0 °C) to terminal bud flush, terminal bud mortality, and seedling mortality were recorded for individual seedlings after bud flush was complete. The length of the new terminal and top laterals and number of new top laterals were assessed in the fall after height growth was complete. Time to budbreak was not assessed on pine seedlings following the May freezing test as bud flush had occurred before the tests. Seedlings used in the tests were over-wintered outdoors, generally under snow from late December to late March, and were measured for shoot growth and number of top laterals at the end of the second growing season post-freezing. The post-freezing growing seasons were normal, with the summer maximum high temperature of 30.1 °C and winter minimum low temperature of -24.4 °C.

Data analysis

Time to budbreak, seedling mortality, terminal bud mortality, growth of terminal shoots and top laterals, and the number of new top laterals were compared among the 4 testing temperatures using 1-way ANOVA with Proc GLM in SAS Release 9.4 (SAS Institute Inc., Cary, NC). Individual tree observations (except for bud and seedling mortality) were averaged by testing temperatures before the analysis, which was done separately by species, testing season, and post-freezing growing season. The effects of testing temperatures were considered significant when $P < 0.05$ and pairwise comparisons of means were conducted using Tukey's method.

Results

The March freezing caused $> 20\%$ needle mortality on black spruce and white spruce at -25 and -35 °C and $> 40\%$ needle and $> 25\%$ seedling mortality on lodgepole pine at -35 °C (Figs. 1 and 2), and delayed time to budbreak for all species except jack pine at -35 °C (Fig. 3). First year shoot growth decreased as freezing temperature decreased for black spruce and white spruce for both terminals and top laterals, and for lodgepole pine for terminals (Figs. 4 and 5). The March freezing, however, did not affect second year shoot growth (Figs. 4 and 5) and reduced number of top laterals only for black spruce (Fig. 6).

The May freezing caused $> 40\%$ needle mortality on all 4 species at -10 and -15 °C and terminal bud mortality on white spruce at -15 °C (Figs. 1 and 7). First year terminal and top lateral growth decreased with decreasing freezing temperatures on all 4 species, except for jack pine, whereas second year growth was reduced only on black spruce and jack pine (Figs. 4 and 5). The May freezing did not affect time to budbreak for black spruce and white spruce (Fig. 3) or the number of top laterals in any of the 4 species (Fig. 6). After both the March and May freezing, dead pine needles remained attached longer than spruce needles and were more noticeable because of their size and colour change.

Discussion

Results of whole seedling freezing tests showed that, among the 4 boreal conifers tested in this study, jack pine was most tolerant of freezing temperatures. This difference was particularly true in March when jack pine was the only species that did not show

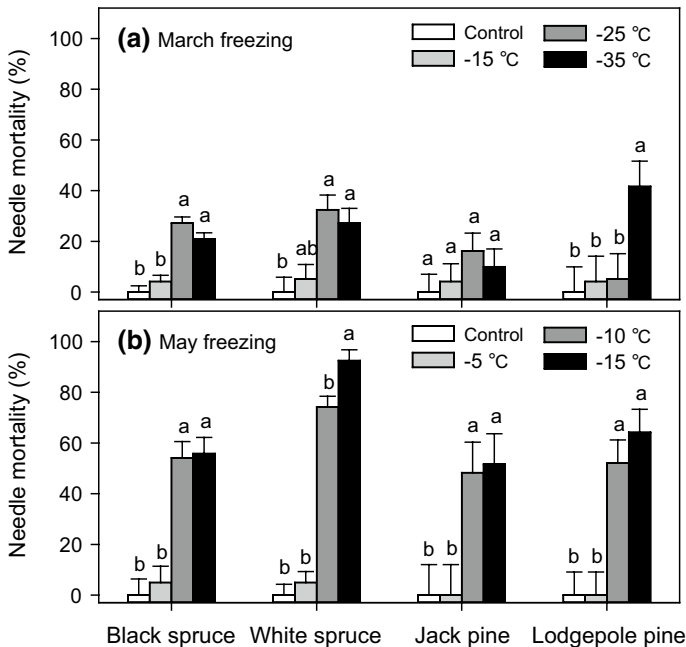


Fig. 1 Post-freezing needle mortality (least square mean \pm SE) by testing season (March vs. May), species, and testing temperature. Bars topped by different letters indicate significant differences among testing temperatures ($P < 0.05$) by testing season and species (modified from Man et al. 2017a, Fig. 6)

substantial damage from freezing temperatures as low as $-35\text{ }^{\circ}\text{C}$ for any of the all seedling attributes assessed. In contrast, white spruce was least tolerant with the greatest reduction in first year shoot growth after the March freezing at $-35\text{ }^{\circ}\text{C}$ and the largest increase in needle and bud mortality after the May freezing at $-15\text{ }^{\circ}\text{C}$. These results are consistent with findings by Bella and Navratil (1987) who reported relative growth losses in white spruce and lodgepole pine following a winter drying event in Alberta, as well as findings on the cold tolerance of white spruce, black spruce, and jack pine seedlings in late fall (Bigras and Margolis 1997), and reports from assessments of natural freezing events in late spring (Man et al. 2009, 2013a). The low tolerance of white spruce may relate to its earlier budbreak relative to black spruce (O'Reilly and Parker 1982; Man et al. 2017a, b) and, therefore, quicker loss of cold hardiness, as well as to possible differences in cold tolerance between white spruce buds and needles (Bannister and Neuner 2001), as needle and shoot cold hardiness between black and white spruce is similar during spring dehardening (Man et al. 2017a).

Based on needle and seedling mortality after being subjected to $-35\text{ }^{\circ}\text{C}$ during March freezing, the second most cold sensitive species was lodgepole pine. This result is consistent with those from tissue cold hardiness assessments (Man et al. 2017a) and field observations of cold damage in Colorado following a January freezing event (Halfpenny and Ozanne 1989). Lodgepole pine is more sensitive to winter warming and temperature fluctuations and dehardens faster than other conifers as demonstrated in controlled-environment studies (Nilsson 2001; Ögren 2001; Man et al. 2016). Lodgepole pine was not more vulnerable to freezing than the other 3 conifers in early May, perhaps

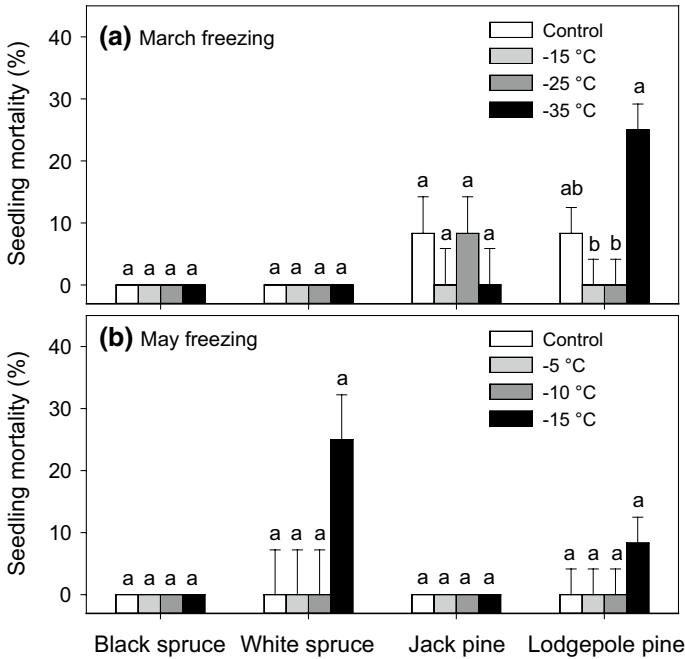


Fig. 2 First year seedling mortality (least square mean \pm SE) by testing season (March vs. May), species, and testing temperature. Bars topped by different letters indicate significant differences among testing temperatures ($P < 0.05$) by testing season and species

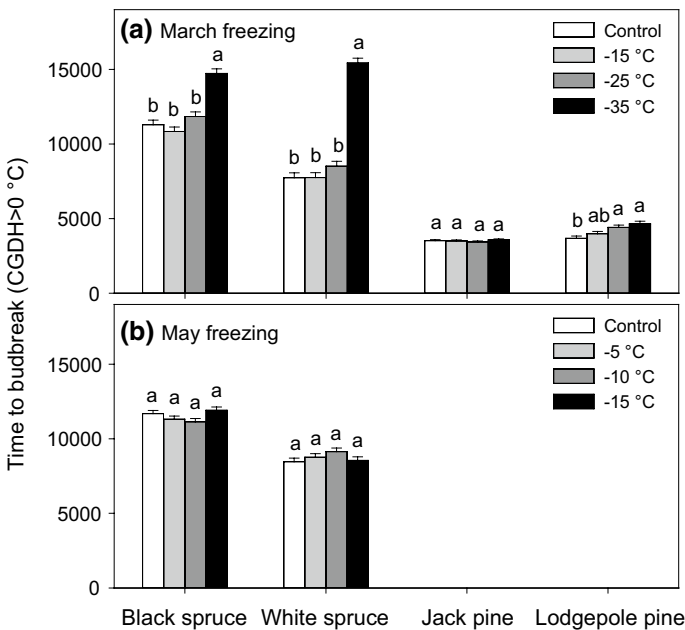


Fig. 3 First year time to budbreak (*CGDH* cumulative growing degree hours > 0 °C) (least square mean \pm SE) by testing season (March vs. May), species, and testing temperature. Bars topped by different letters indicate significant differences among testing temperatures ($P < 0.05$) by testing season and species

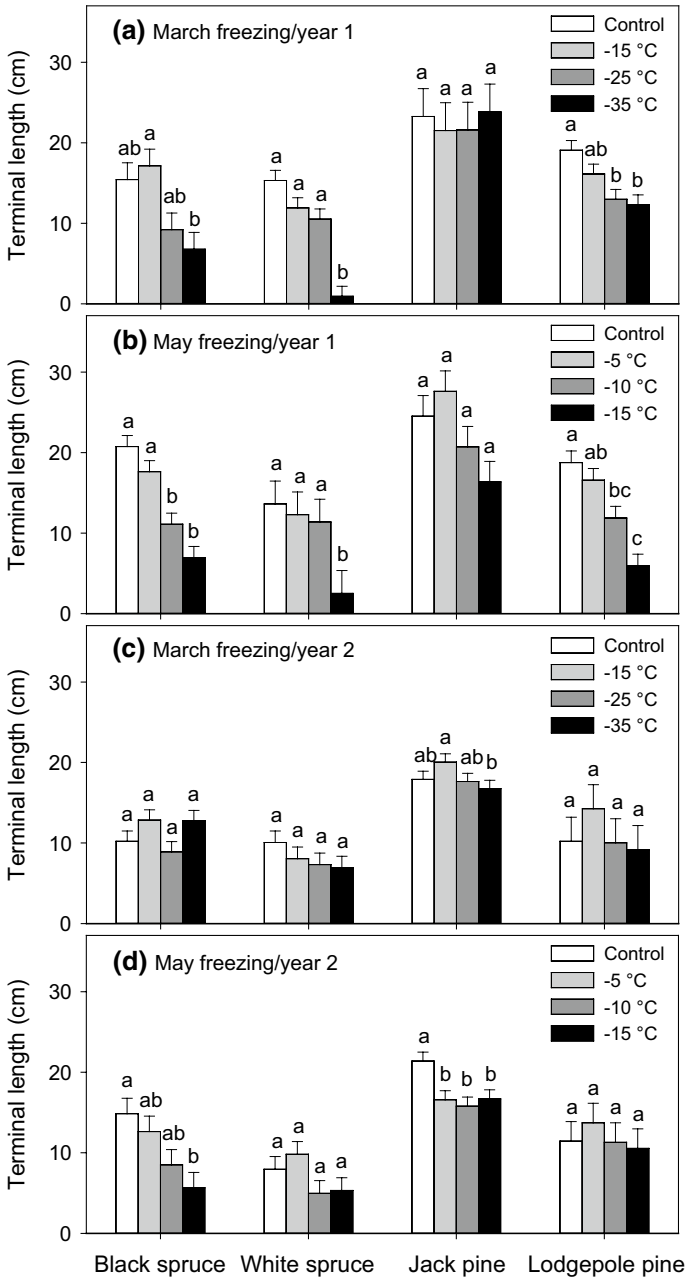


Fig. 4 Mean terminal length of survived seedlings (least square mean \pm SE) by testing season (March vs. May), species, testing temperature, and post-freezing growing season (year 1 vs. year 2). Bars topped by different letters indicate significant differences among testing temperatures ($P < 0.05$) by testing season, species, and post-freezing growing season

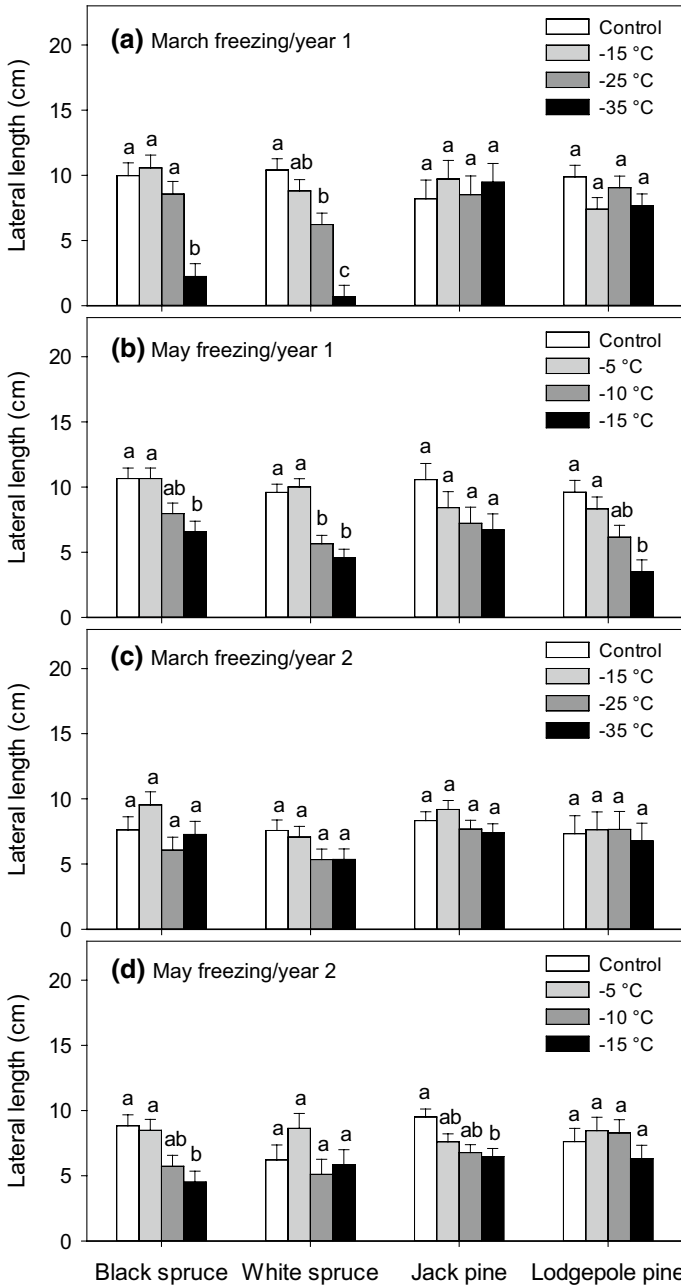


Fig. 5 Mean top lateral length of survived seedlings (least square mean \pm SE) by testing season (March vs. May), species, testing temperature, and post-freezing growing season (year 1 vs. year 2). Bars topped by different letters indicate significant differences among testing temperatures ($P < 0.05$) by testing season, species, and post-freezing growing season

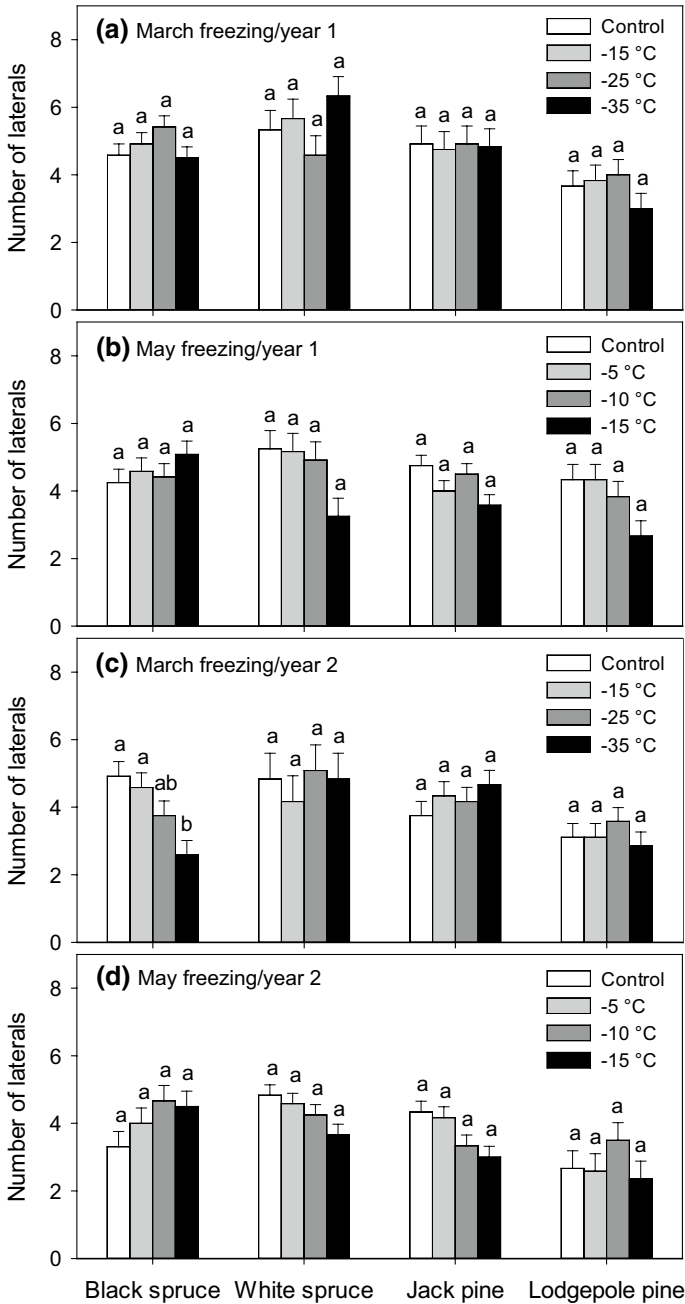


Fig. 6 Number of top laterals (least square mean \pm SE) by testing season (March vs. May), species, testing temperature, and post-freezing growing season (year 1 vs. year 2). Bars topped by different letters indicate significant differences among testing temperatures ($P < 0.05$) by testing season, species, and post-freezing growing season

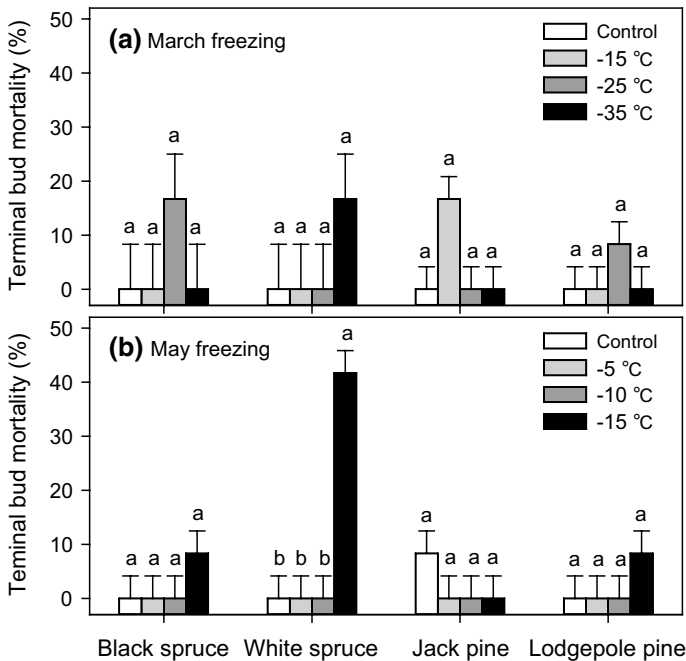


Fig. 7 First year terminal bud mortality of survived seedlings (least square mean \pm SE) by testing season (March vs. May), species, and testing temperature. Bars topped by different letters indicate significant differences among testing temperatures ($P < 0.05$) by testing season and species

because all species have lost much of their cold hardiness and become equally vulnerable at late spring dehardening. Dead needles stayed much longer and were more visible on pine trees, which may help explain why red belt damage is more often reported on lodgepole pine (Henson 1952; Robin and Susut 1974) even though other conifers are also damaged (Bella and Navratil 1987).

Although the conifers species we tested have been reported to have maximum cold hardiness well below -40 °C in mid-winter (Man et al. 2017a), they lose their hardiness rapidly with forcing temperatures in spring (Bigras et al. 2001; Man et al. 2017a). Needle mortality started to occur at -25 °C in late March and -10 °C in early May, consistent with predictions of the tissue cold dehardening curves for the 4 species (Man et al. 2017a) and observations of damage caused by natural winter freezing events (Cayford et al. 1959; Man et al. 2009, 2013a). As shown by Bigras and Hébert (1996) in black spruce, the swollen buds of white spruce continued to flush after a short exposure to -10 °C, despite substantial needle mortality. The significant increases in terminal bud mortality at -15 °C for white spruce may suggest that swollen buds of late flushing spruce trees are less hardy than flushed buds of early flushing pine trees. This difference may result from dissimilar dehardening dynamics, i.e., spruce trees reach their minimum cold hardiness at budbreak (Peace 1962; Holzer 1969; Nienstaedt and King 1969) while pine trees continue to deharden until the stage of rapid shoot elongation (Glerum 1973; Man et al. 2017a).

Our results demonstrate that conifer seedlings are more vulnerable to freezing temperatures at the later stages of cold dehardening in spring, as shown by more damage in early May than in late March. This change in the vulnerability is due to the progressive loss of

cold hardiness in spring (Man et al. 2017a) and is consistent with the timing of freezing damage observed in the field (Cayford et al. 1959; Robin and Susut 1974; Man et al. 2009, 2013a). Black spruce and jack pine, the 2 relatively hardy conifers based on the first-year freezing damage assessments continued to show negative effects on shoot growth in the second year. This finding differs from field observations that indicate height growth is not usually affected by winter freezing, despite continuous effects on diameter growth for several years (Bella and Navratil 1987; Man et al. 2013b). This finding may suggest that species do not differ substantially in cold tolerance at late spring dehardening, i.e., tree species that show less immediate visual damage may sustain more and long lasting internal physiological shock (e.g., may affect bud formation and thus following year's growth).

The results of this study are consistent with those predicted from the tissue cold dehardening curves with spring dehardening (Man et al. 2017a). The observed seedling damage at different freezing temperatures match field observations of winter freezing events in terms of needle, bud, and tree mortality, and temperature conditions (Cayford et al. 1959; Bella and Navratil 1987; Halfpenny and Ozanne 1989; Man et al. 2009, 2013a, b). The level of freezing damage varies with the stage of dehardening (as measured by cumulative forcing temperatures), freezing temperatures, tree species, and organs (i.e., needles vs. buds). All these factors should be considered when assessing and predicting freezing damage with tissue dehardening curves (Bannister and Neuner 2001; Bigras et al. 2001; Man et al. 2017a). These dehardening curves may also serve as tools for assessing species phenological match with the changes of temperature regimes when considering climate change induced natural or assisted migration.

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