NOTE / NOTE

Seasonal differences in freezing tolerance of yellow-cedar and western hemlock trees at a site affected by yellow-cedar decline

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Abstract: To assess whether inadequate cold hardiness could be a contributor to yellow-cedar (*Chamaecyparis nootkatensis* (D. Don) Spach) decline, we measured the freezing tolerance of foliage from yellow-cedar trees in closed-canopy (nondeclining) and open-canopy (declining at elevations below 130 m) stands at three sites along an elevational gradient in the heart of the decline in southeastern Alaska. Foliar freezing tolerance was also assessed for sympatric nondeclining western hemlock (*Tsuga heterophylla* (Raf.) Sarg.). Measurements were made in the fall, winter, and spring to evaluate if seasonal differences in cold hardiness help explain species-specific injury. Significant differences in freezing tolerance attributable to site, canopy closure, species, and the interaction of canopy closure and species were each detected for at least one sample period. However, only two results were consistent with field reports of yellow-cedar decline: (1) between winter and spring measurements, yellow-cedar trees dehardened almost 13 °C more than western hemlock trees, so that yellow-cedar trees were more vulnerable to foliar freezing injury in spring than western hemlock; and (2) stands below 130 m appeared more vulnerable to freezing injury than stands above 130 m.

Résumé : Afin d'évaluer si une résistance inadéquate au froid pouvait contribuer au dépérissement du faux-cyprès de Nootka (*Chamaecyparis nootkatensis* (D. Don) Spach), les auteurs ont mesuré la tolérance au gel du feuillage de faux-cyprès dans des peuplements fermés (non dépérissant) et ouverts (dépérissant à une altitude inférieure à 130 m), dans trois stations situées le long d'un gradient altitudinal au cœur de la zone de dépérissement dans le sud-est de l'Alaska. La tolérance au gel du feuillage a également été évaluée chez la pruche de l'Ouest (*Tsuga heterophylla* (Raf.) Sarg.), une espèce sympatrique qui ne dépérit pas. Des mesures ont été prises à l'automne, à l'hiver et au printemps pour déterminer si des différences saisonnières de résistance au froid pouvaient contribuer à expliquer pourquoi les dommages sont limités à une espèce. Des différences significatives dans la tolérance au gel attribuables au site, à la fermeture du couvert, à l'espèce et à l'interaction entre la fermeture du couvert et l'espèce ont été détectées pendant au moins une période d'échantillonnage. Cependant, seulement deux résultats sont consistants avec les rapports de terrain sur le dépérissement du faux-cyprès : (1) entre les mesures prises en hiver et au printemps, le faux-cyprès s'est désendurci de presque 13 °C de plus que la pruche de l'Ouest, de telle sorte que le faux-cyprès était plus vulnérable que la pruche de l'Ouest aux dommages causés par le gel du feuillage au printemps et (2) les peuplements situés à moins de 130 m d'altitude semblaient plus vulnérables aux dommages causés par le gel que les peuplement situés à plus de 130 m d'altitude.

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Introduction

Yellow-cedar (*Chamaecyparis nootkatensis* (D. Don) Spach) is an ecologically significant and economically valuable species that has undergone a dramatic decline in southeastern Alaska during the past 100 years (Hennon and Shaw 1997). The widespread mortality that characterizes this decline is not associated with fungi (Hennon 1990; Hennon et al. 1990), insects (Shaw et al. 1985), nematodes (Hennon et al. 1986), or viruses and phytoplasmas (Hennon and McWilliams 1999) as primary agents of tree death. However, site factors appear important to decline development, because mortality typi-

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cally occurs in and adjacent to open-canopy forests growing on wet soils at lower elevations (Hennon et al. 1990).

With no evidence of a biotic cause, current thought has focused on the possibility that one or more abiotic factors have instigated decline. In particular, freezing injury and soil toxicity (toxic substances or nutrient imbalances in the soil that kill fine roots) have been proposed as causal factors (Hennon and Shaw 1994, 1997). Because soil nutrition can influence conifer freezing tolerance (Schaberg et al. 2001, 2002), these factors may also act in concert to promote decline.

The onset of yellow-cedar decline coincided with the beginning of a period of climatic warming, and the distribution of decline parallels milder winter temperature isoclines in the region (Hennon and Shaw 1994, 1997). At least two consequences of warmer winter temperatures could predispose yellow-cedar to injury. First, warmer temperatures could induce precocious tissue dehardening and increase the risk of freezing injury when more typical low temperatures prevail. Evidence suggests that yellow-cedar is more vulnerable to direct freezing injury than some sympatric species (Silim and Lavender 1994), and may be particularly prone to temperature-dependent dehardening (Puttonen and Arnott 1994; Hawkins et al. 2001). Another consequence of milder winter temperatures would be a change in the pattern of insulative snow cover. Because ambient winter temperatures often hover around freezing, even a small alteration in temperature could cause a distinct shift in the depth and duration of snowpack. Reductions in protective snow cover would also increase possibilities for soil freezing, which would be especially damaging to roots where the depth of rooting is limited by soil water saturation (Hennon and Shaw 1994, 1997).

The sequence of symptom development for dying yellow-cedar suggests that foliar injury follows initial root injury (Hennon et al. 1990). However, for cold-hardy conifers the seasonal progression of root cold tolerance parallels that of foliar cold tolerance (Sakai and Larcher 1987), and foliar cold tolerance can be an indicator of root sensitivity to freezing damage (Coleman et al. 1992; Puttonen and Arnott 1994). Indeed, like shoots, the developmental cold tolerance of yellow-cedar roots appears to be driven largely by ambient temperature cues (Puttonen and Arnott 1994).

To evaluate the possibility that limited cold hardiness contributes to yellow-cedar decline, we measured the foliar freezing tolerance of yellow-cedar trees in closed-canopy (nondeclining) and open-canopy (declining at elevations below 130 m) stands along an elevational gradient in the center of the region affected by yellow-cedar decline in southeastern Alaska. For comparison, foliar cold tolerance was also assessed for sympatric western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), a species showing no signs of decline. Measurements were made in the fall, winter, and spring to evaluate if seasonal differences in cold hardiness help explain species-specific injury.

Materials and methods

Site description

Field sampling was conducted at Poison Cove in a roadless area on Chichagof Island, Alaska (57°31′N, 135°35′W), within the region of yellow-cedar decline. Unmanaged mixed-species forests occur from sea level to about 800 m on this south-facing slope. The study site was a mosaic of closed- and open-canopy forests. Factors contributing to open-canopy conditions were mainly poor drainage and high tree mortality at low elevations, tree death at mid-elevations, and poor drainage at high elevations. Tree mortality primarily affected one species: yellow-cedar. Concentrations of standing yellow-cedar snags predominated below 130 m in open-canopy conditions, along with surviving western hemlock, mountain hemlock (*Tsuga mertensiana* (Bong.) Carr.), Sitka spruce (*Picea sitchensis* (Bong.) Carr.), and scattered living yellow-cedar.

Temperature sensors in permanent vegetation plots of a separate study located less than 100 m from our six sampling locations were used to monitor air temperatures (Hobo recorders, Onset Computer Corp., Pocasset, Massachusetts). Air temperature was recorded hourly from fall 2002 through spring 2003.

Sample collections

We sampled trees in open- and closed-canopy conditions at three elevations: low elevation (~20 m), mid-elevation (~110 m) near the top of the concentrated mortality zone, and higher elevation (~230 m) above the mortality zone. Foliar collections were conducted during three seasons: fall (14 November 2002), winter (19 March 2003), and spring (5 May 2003). On each date we selected four living yellow-cedar and four living western hemlock trees >20 cm diameter from each elevation and canopy class per site for foliar sampling. Foliage was collected by shotgun or pole pruner from the lower crown of each tree. Foliage was sealed in plastic bags with moist paper towels and shipped in an ice-packed container to the University of Vermont in Burlington, Vermont, for cold tolerance analysis that was initiated within 48 h of collection.

Cold tolerance

Cold tolerance was assessed on the current-year foliage of western hemlock and the distal segments of primary shoots of yellow-cedar, the tissue type most commonly used for cold tolerance assessments of this species (Hawkins et al. 2001). Tissue from each tree was rinsed in iced distilled water and then chopped in 5-mm sections to produce a bulked sample. Subsamples of bulked tissue were measured volumetrically (approximately 0.3 mL or 0.1–0.2 g) into 64-cell styrene trays for freezing. Freezing stress was imposed using the methods of Strimbeck et al. (1995) and Schaberg et al. (2000). For fall and spring assessments, test temperatures ranged from 0 to –35 °C in –5 °C increments, with an additional test temperature at –60 °C to fully kill the foliage. For the winter assessment, test temperatures ranged from 0 to –48 °C in –6 °C increments, with an additional test temperature at –60 °C. The rate of freezing was –6 °C·h^{-1} for all tests. Freezer temperature was held at least 20 min at each test temperature, after which one replicate tray was removed from the freezer, placed in a precooled styrene foam container, and transferred to a separate freezer at –5 °C. After trays equilibrated to –5 °C, they were transferred in foam containers to a refrigerator at 4 °C and held until thawed. A mild detergent solution (3.5 mL of 0.1% *v/v* Triton X-100 in deionized water) at 4 °C was added to each cell, and sample

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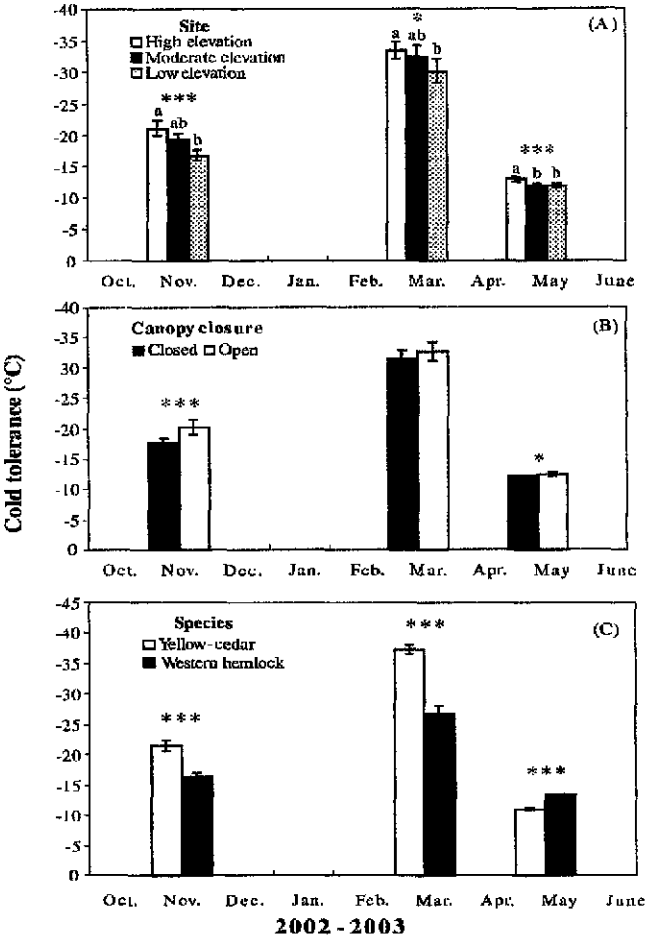
Fig. 1. The influence of (A) site, (B) canopy closure, and (C) species differences on the average cold tolerance measured as T_m (±SE) of yellow-cedar and western hemlock trees at the Poison Cove research site on three dates during the fall, winter, and spring of 2002–2003. Significance values for comparisons within sample date are as follows: *, $P \leq 0.10$; ***, $P \leq 0.01$ (ANOVA). Means with the same letter are not significantly different based on the Tukey HSD test.



trays were held in a high humidity cabinet at room temperature for 8 h. Initial conductivity of the effusate was measured using a multielectrode instrument (Wavefront Technology, Ann Arbor, Michigan), then samples were dried for at least 72 h at 50 °C to kill the tissue, soaked in fresh detergent solution for 24 h, and then the final conductivity was measured. Relative electrolyte leakage (REL), a measure of cell injury calculated as the proportion of initial to final conductivity, was used to calculate T_m, the temperature at the midpoint of a sigmoid curve fit to REL data for all test temperatures (Schaberg et al. 2000).

Statistical analyses

Because sampling occurred only at Poison Cove, any differences in cold tolerance among sites at different altitudes could have resulted from genuine elevational influences (e.g., temperature gradients) or other factors (e.g., soil or site characteristics) that covaried with elevation at this location. In recognition of this lack of specificity, "site" (not elevation) was used as a source of variation in the statistical model used to test for differences in foliar cold tolerance. Analyses of variance were used to test for differences in T_m attributable to site, canopy closure, species, and all interactions of these fixed main effects for each of the three sampling dates. Specific differences among factor means were determined using the Tukey HSD test or orthogonal contrasts. Differences were considered statistically significant if $P \leq 0.05$, unless otherwise noted.

Results and discussion

Site differences

Significant differences in cold tolerance associated with all study main effects were found for at least one of the sampling periods. Many of these findings were consistent with a priori expectations and reports in the literature. For example, despite the relatively small elevational gradient sampled (210 m), differences in cold tolerance attributable to site were detected for all sample periods (Fig. 1A). In the fall and winter, Tukey HSD results indicated that trees at the high-elevation site were more cold tolerant than trees at the low-elevation site. Although differences among site means appeared muted in the spring, within-site variance was also low. At this time, trees at the high-elevation site were significantly more cold tolerant than trees at both mid- and low-elevation sites. Although we can not specifically attribute site differences to the influence of elevation, the greater cold tolerance of trees at higher altitudes is consistent with reports for a wide range of conifers (Rehfeldt 1980; Eiga and Sakai 1984; Rehfeldt 1986; Joyce 1987), including yellow-cedar (Hawkins et al. 1994; Davradou and Hawkins 1998).

Canopy closure differences

Differences attributable to canopy closure (Fig. 1B) and the interaction of canopy closure and species (Fig. 2) were most evident in the fall and spring. In the fall, cold tolerance differences associated with both the main effect for canopy closure and the interaction of canopy closure with species were driven by the unique response of yellow-cedar relative to western hemlock. Here, although canopy closure was not associated with differential cold tolerance in western hemlock, yellow-cedar trees in open-canopy stands were more cold tolerant than trees in closed-canopy stands (Fig. 2). In the spring, there was a marginally significant main effect ($P = 0.06$) suggesting greater cold tolerance of trees in open canopies (Fig. 1B). Analysis of the canopy closure × species interaction showed a slight difference in response to crown closure between the species; however, the Tukey HSD test lacked the power to distinguish variations in response (Fig. 2). Further analysis using orthogonal contrasts revealed no difference in the cold tolerance of yellow-cedar trees in the two canopy classes ($P = 0.36$), but indicated that western hemlock in open-canopy stands were somewhat more cold tolerant than those in closed-canopy stands ($P = 0.08$).

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Fig. 2. Differences in average cold tolerance measured as T_{in} (±SE) attributable to the canopy closure × species interaction for yellow-cedar and western hemlock trees at the Poison Cove research site on three dates during the fall, winter, and spring of 2002–2003. Significance values for comparisons within sample date are as follows: *, $P \leq 0.10$; **, $P \leq 0.05$ (ANOVA). Species and canopy closure means with the same letter are not significantly different based on the Tukey HSD test.

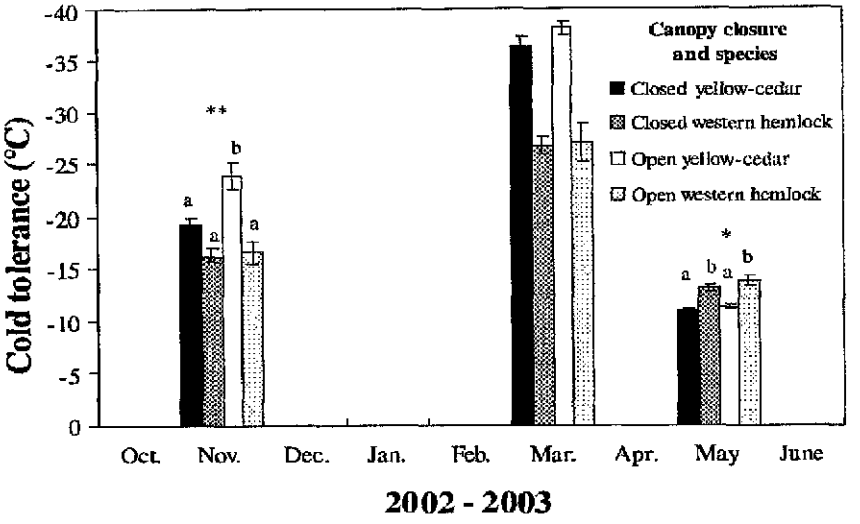
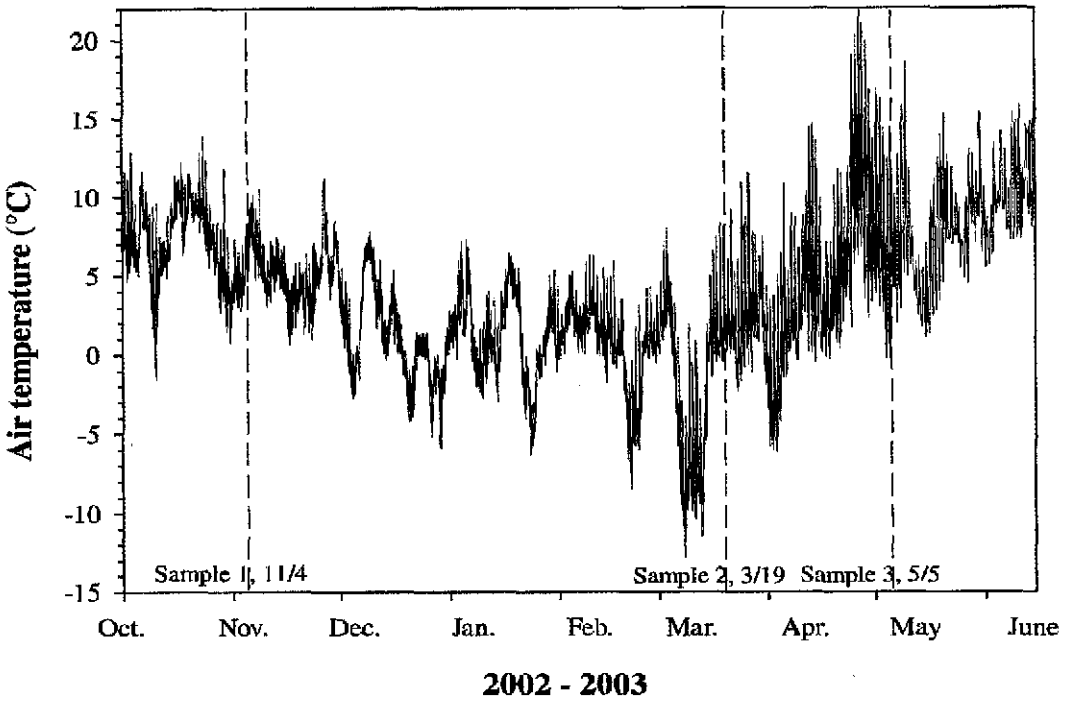


Fig. 3. Daily air temperatures recorded at the Poison Cove research site from October 2002 through May 2003. Temperatures are the means of data collected every 4 h from five thermocouple sensors.



Although the initial stages of cold hardening are influenced predominantly by decreasing day length and exposure to transient frosts, the development of additional hardiness requires a more persistent exposure to subfreezing temperatures (Levitt 1980; Silim and Lavender 1994; Havranek and Tranquillini 1995). Considering this, the lower temperatures within open-canopy stands (data not shown) could have sped the seasonal development of cold hardiness in yellow-cedar foliage. An abrupt increase in autumnal cold tolerance given appropriate temperature cues is a hallmark of species such as yellow-cedar that undergo indeterminate growth (Hawkins et al. 2001). By the spring, yellow-cedar from both canopy

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conditions had dehardened equally, whereas western hemlock in closed-canopy stands had dehardened slightly more than those in open-canopy conditions.

Species differences

Differences in cold tolerance attributable to species were highly significant on all sample dates, although the nature of these differences changed over time (Fig. 1C). In fall and winter, foliage from yellow-cedar trees was on average 5–10 °C more cold tolerant than foliage from western hemlock trees. However, in the spring this pattern was reversed, and the foliage of yellow-cedar was approximately 3 °C less cold tolerant than that of western hemlock. Indeed, in the 47 d between the winter and spring measurements, yellow-cedar dehardened an average of 26.2 °C, almost 13 °C more than sympatric western hemlock. This substantial reduction in cold hardiness followed a period of ambient warming (Fig. 3), highlighting the possibility that rapid and extreme spring dehardening could put yellow-cedar at a particular risk of freezing injury and predispose this species to damage and decline.

Species differences in cold tolerance were probably influenced by the different mixes of tissues used to assess cold tolerance. When hemlock was processed, only current-year needles were used to assess REL at the various test temperatures. However, because of its unusual growth form with overlapped scale-like leaves pressed against the stem, yellow-cedar samples included both foliar and some stem tissues. In general, conifer foliage is more susceptible to winter freezing injury than stem tissues (e.g., Rehfeldt 1978; Sakai and Malla 1981). In fact, data indicate that this tendency is specifically pertinent to the genus *Chamaecyparis*. Sakai and Okada (1971) found that twigs of *Chamaecyparis lawsoniana* (A. Murr.) Parl. were 15 °C more cold tolerant than shoot tips measured at the same time. Assuming that this pattern is also true for yellow-cedar, inclusion of stem tissue in cold tolerance tests for only this species would have disproportionately raised the apparent cold hardiness of yellow-cedar relative to western hemlock. This methodological difference could have contributed to yellow-cedar's greater estimated cold tolerance in fall and winter (Fig. 1C). Importantly, it also likely muted apparent species differences measured in spring. Furthermore, tissue-specific differences in cold tolerance likely increase in spring, because stems are slow to deharden relative to other tissues (Sakai and Larcher 1987). Especially in the spring, the inclusion of stem tissue for yellow-cedar samples probably led to an overestimation of this species' cold tolerance and an underestimation of its vulnerability to freezing injury relative to western hemlock.

In general, conifers develop adequate freezing tolerance to survive low temperature events in their native habitats. When injury does occur, it is most often associated with either delayed development of cold hardiness in the autumn or premature dehardening in the spring (Havranek and Tranquillini 1995), with spring injury often reported as the more common or more damaging (Timmis et al. 1994; Aitken and Adams 1997). Indeed, spring injury has been reported to be most common for conifer stands on warm slopes or at lower elevations (Havranek and Tranquillini 1995), areas consistent with concentrations of yellow-cedar decline (Hennon and Shaw 1997).

The particular vulnerability of yellow-cedar relative to western hemlock during spring reflects differences in the growth habit of these species. Because it exhibits indeterminate growth, yellow-cedar is vulnerable to temperature-dependent dehardening, but is also capable of enhanced shoot growth during deacclimation (Puttonen and Arnott 1994). This capacity for increased growth prior to the budbreak of sympatric species like western hemlock could provide the slow-growing yellow-cedar a needed competitive advantage. However, if, as predicted, climate change causes average spring temperatures to rise while existing low temperature extremes persist (MacCracken et al. 1991), then the ecological risks of freezing injury could outweigh any potential benefits of precocious spring growth.

Consistencies with yellow-cedar decline

Our data highlight two patterns in freezing injury susceptibility that are consistent with field reports of yellow-cedar decline: (1) that yellow-cedar trees dehardened more and sooner in the spring than co-occurring western hemlock, which made yellow-cedar more vulnerable to freezing injury at this time; and (2) that low- and mid-elevation sites were more vulnerable to freezing injury than high-elevation sites. Because of these combined influences, in the spring, yellow-cedar trees from low- and mid-elevation stands were the least cold tolerant (–10.7 ± 0.3 °C) of any classification of trees we measured. The susceptibility of yellow-cedar to spring freezing damage is also consistent with our personal observations of frost injury to potted seedlings during the spring of 2001 and 2002 grown near sea level in Juneau, Alaska. We are now assessing the vulnerability of yellow-cedar roots to spring dehardening and freezing injury.

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