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Evaluation of soil saturation, soil chemistry, and early spring soil and air temperatures as risk factors in yellow-cedar decline

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Abstract

Yellow-cedar (*Callitropsis nootkatensis* (D. Don) Oerst.) is a valuable tree species that is experiencing a widespread decline and mortality in southeast Alaska. This study evaluated the relative importance of several potential risk factors associated with yellow-cedar decline: soil saturation, soil aluminum (Al) toxicity or calcium (Ca) deficiency, and air and soil temperature. Data were collected from permanent vegetation plots established in two low-elevation coastal forests exhibiting broad ranges of cedar mortality. Measurements of each risk factor were contrasted among classified forest zones to indicate if there were strong links with decline. Hydrology alone is weakly associated with yellow-cedar decline, but could have a predisposing role in the decline by creating exposed conditions because of reduced forest productivity. Yellow-cedar decline is not strongly associated with soil pH and extractable Al and Ca, but there appears to be Ca enrichment of surface soils by feedback from dead yellow-cedar foliage. Air and soil temperature factors are strongly associated with decline. Based on these results, an hypothesis is presented to explain the mechanism of tree injury where exposure-driven tree mortality is initiated in gaps created by soil saturation and then expands in gaps created by the tree-mortality itself. The exposure allows soils to warm in early spring causing premature dehardening in yellow-cedar trees and subsequent freezing injury during cold events. Yellow-cedars growing in the protection of shade or snow are not preconditioned by this warming, and thus not as susceptible to cold injury. Yellow-cedar decline appears to be associated with regional climate changes, but whether the cause of these changes is related to natural or human-induced climate shifts remains uncertain. Management implications, the possible role of climate, and recommended research are discussed.

Key words: aluminum, calcium, soil temperature, yellow-cedar decline

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Introduction

Yellow-cedar (*Callitropsis nootkatensis* D. Don (Oerst.)) is a valuable ecological, social, and economic tree species in Southeast Alaska (Hennon & Harris, 1997). Recently, yellow-cedar was moved from the genus *Chamaecyapris* Spach, based on its affinity with a newly discovered tree species in northern Vietnam (Little & Schwarzbach, 2004). Wood and bark from yellow-cedar have historic and contemporary cultural value to Native people in British Columbia and Alaska (Stewart, 1984) and its wood is consistently the most commercially valuable of any tree grown in Alaska. Widespread yellow-cedar mortality (Fig. 1), commonly referred to as yellow-cedar decline, affects this tree at over 2500 mapped locations covering 200 000 hectares throughout Southeast Alaska (Fig. 2, Hennon & Shaw, 1997; Wittwer *et al.*, 2002). Yellow-cedar decline is generally absent in other portions of the yellow-cedar range to the northwest in Prince William Sound (Hennon & Trummer, 2001); to the south through most of British Columbia, Washing-

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Fig. 1 The Poison Cove study site illustrating the appearance of intensive yellow-cedar mortality.

ton, and Oregon; in the eastern and northern portions of Southeast Alaska; and at higher elevations within the distribution of yellow-cedar decline in southeast Alaska. Recently, we found concentrated patches of yellow-cedar decline south of the Canada-Alaska border, extending 150 km south into British Columbia (Hennon *et al.*, 2005). The lack of understanding on the cause of tree death has hampered efforts to predict the extent of future mortality and develop management strategies for this valuable tree species.

Reconstruction of the temporal pattern of tree death through a combination of ground surveys (Hennon *et al.*, 1990b) and time-since-death dating of snag classes (Hennon *et al.*, 1990c) showed that a high rate of tree mortality began in the late 19th century and has continued until the present. Yellow-cedar suffers a disproportionate mortality rate on these sites relative to other associated tree species (Hennon *et al.*, 1990b). Symptoms appear first in the root systems followed by crown thinning and bole lesions (Hennon *et al.*, 1990d), indicating that the primary stress factor may be in the soil environment. The crown usually dies as a unit, either slowly, thinning up to 15 years, or quickly in a few years, leaving a full crown of dead foliage. Previous research on higher fungi (Hennon, 1990; Hennon *et al.*, 1990d); Pythiaceious fungi (Hamm *et al.*, 1988; Hansen *et al.*, 1988); nematodes (Hennon *et al.*, 1985); viruses or phytoplasmas (Hennon & McWilliams, 1999); insects (Shaw *et al.*, 1985); and bear feeding injury to trees (Hennon *et al.*, 1990a) suggests that biotic agents are not the primary cause of tree death.

Generally, yellow-cedar is stress tolerant (Antos & Zobel, 1986) enduring poor-quality sites in soils that are saturated or near saturated and exhibit nutrient deficiencies. Yellow-cedar mortality indicates that one or more sources of stress have shifted beyond a critical biological tolerance threshold over a large area. Given the evidence provided by the symptoms and site features, there are indications that some type of belowground factor may be involved in yellow-cedar decline. Thus, we designed this study to evaluate the relative importance of potential soil-related risk factors associated with yellow-cedar decline: soil saturation, soil Al toxicity and/or Ca deficiency, and soil temperature. As a general introduction, below we review the rationale for studying each of the risk factors.

Soil saturation

Yellow-cedar decline appears to be associated with poorly drained soils, but this relationship is primarily based on observations of aerial photographs and using understory plants as indicators of soil drainage (Klinger, 1988; Hennon *et al.*, 1990b; Klinger, 1996). Aerial photographs taken between 1926 and 1976 at several decline sites indicate a progressive expansion of yellow-cedar decline from low gradient wetland sites to adjacent, higher gradient slopes (Hennon *et al.*, 1990b). This expansion suggests that the initial yellow-cedar decline was concentrated in areas of saturated, poorly drained soils and has expanded into the fringes of somewhat poorly drained soils. Previous studies did not establish

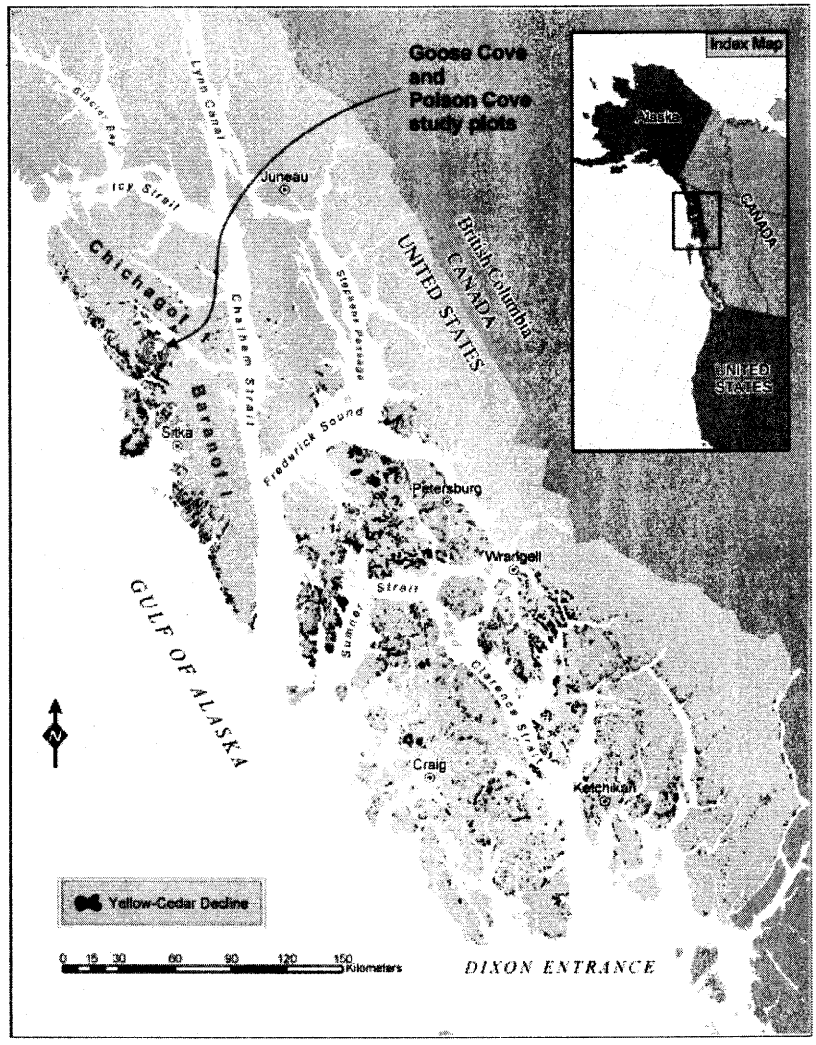

Fig. 2 Distribution of yellow-cedar decline in Southeast Alaska and location of study sites.

a tight link between yellow-cedar decline and soil saturation (Klinger, 1988; Hennon *et al.*, 1990b; Johnson & Wilcock, 2002).

Soil acidity (pH), aluminum, and calcium

Soil forming processes that result in increased soil saturation and subsequent acidification lead to extensive bog and scrub climax vegetation communities in southeast Alaska (Zach, 1950; Lawrence, 1958; Neiland, 1971). Alhough there is evidence of forest invading bogs (Dachnowski-Stokes, 1941; Heusser, 1960; Stephens *et al.*, 1970), sphagnum invasion following decreased soil drainage is believed to limit forest productivity in the region (Banner *et al.*, 1983; Klinger, 1990; Asada *et al.*, 2003) and may be a factor in yellow-cedar decline. Yellow-cedar is closely associated with saturated soils and the abundance of yellow-cedar decline appears to increase along hydrologic (Hennon *et al.*, 1990b) and pH gradients (Klinger, 1988). Increased soil acidity and subsequent Al toxicity, is compatible with the current information on tree symptoms and site characteristics of yellow-cedar decline. Aluminum toxicity has been associated with fine root death (Scott & Fisher, 1989) through direct toxicity to roots (Kochian, 1995) and may lead to inefficient cation and water uptake owing to the loss of adsorption sites on the fine roots (Foy, 1983).

Ca deficiency is one key aspect of increased Al concentrations and subsequent toxicity. Aluminum saturation in soils blocks cation exchange sites, leading to decreased Ca availability because of leaching (Lawrence *et al.*, 1995; Lawrence *et al.*, 1997). Increased soil Ca concentrations can ameliorate Al toxicity (Alva & Sumner,

1989), but Ca accumulation in plant tissue may lead to Al accumulation in the soil solution. Calcium accumulation in yellow-cedar tissue combined with leaching losses through groundwater transport may affect cedars more severely than other species. Calcium plays a role in many regulatory processes in plants, but its lack of internal mobility in plants makes adequate soil availability critical (McLaughlin & Wimmer, 1999). Western redcedar (*Thuja plicata* Donn) accumulates Ca in its foliage (Kranabetter *et al.*, 2003) and both yellow and red cedars have an affinity for Ca and Mg rich sites (Krajina, 1969). Live foliage and leaf litter from Port Orford-cedar (*Chamaecyparis lawsioniana* (A. Murr.) Parl.) tend to have higher concentrations of Ca and higher Ca : Mg ratios than foliage of trees in the Pinaceae (Ovington, 1954; Zobel *et al.*, 1985).

Freezing injury

There are indications of recent intensified warming at high latitudes (Chapman & Walsh, 1993) that is influencing tree species in the Pacific Northwest (Peterson *et al.*, 2002) and Alaska (Barber *et al.*, 2000). The onset of yellow-cedar decline during the late 19th century (Hennon *et al.*, 1990c) coincides with a period of climatic warming (Hebda, 1995). The distribution of yellow-cedar decline aligns with warm winter temperatures (Hennon & Shaw, 1994), and is limited to lower elevation in many areas (Hennon *et al.*, 1990b). Research on yellow-cedar regeneration in British Columbia reveals a susceptibility to freezing injury triggered by temperature-induced dehardening (Kamm & Kohn, 1980; Hawkins, 1993; Hawkins *et al.*, 2001). Injury can occur in foliage and/or roots (Puttonen & Arnott, 1994). Recently, our initial examination of the seasonal cold tolerance of yellow-cedar in Southeast Alaska revealed that yellow-cedar is cold hardy in fall and winter, but is more susceptible to freezing injury than sympatric western hemlock in spring (Schaberg *et al.*, 2005). Thus, yellow-cedar trees growing at low elevations in the warmer regions of Southeast Alaska during this warmer climate may be stimulated to deharden prematurely in spring and suffer freezing injury.

The timing of soil freezing and warming may be critical in the possible susceptibility of trees to freezing injury. Although native trees are generally adapted to freezing conditions and protected from significant injury, the depth and duration of soil freezing under open and closed canopy forests in southeast Alaska is unknown. Seasonal soil temperatures are influenced by soil saturation (Jury *et al.*, 1991), canopy cover (Childs *et al.*, 1985) and snowpack (Jordan, 1991). Saturated soils require more heat energy to warm and dissipate heat energy more slowly than unsaturated soils leading to more moderate daily temperature changes. Snowpack insulates the soil and prevents freezing deep in the soil profile, but many of the soils in southeast Alaska have deep, porous organic horizons that can fill with air when unsaturated. The air then cools much more rapidly than the soil matrix and may lead to the possibility of freezing if snow is not present to provide insulation (Alexander, 1991). Given that forested trees are shallow rooted, particularly on poorly drained soils, their roots may be susceptible to freezing leading to the interaction between open canopy conditions and insolation of the soil surface.

Our overall study objective was to develop a plausible hypothesis around the most promising factor in yellow-cedar decline to focus research effectively in the future. Our ability to address each potential risk factor in depth is restricted by our broad approach, difficult logistics, and limited previous knowledge of each factor. Our general approach was to test the strength of association between the risk factors and measures of tree mortality from two watersheds impacted with the decline problem over a wide range of forest conditions to provide a focus for future intensive investigations on the most promising risk factors or interactions among these factors. Also, the research approach uses stands with yellow-cedar that are already experiencing decline, which makes it difficult to discriminate between possible causes of decline and the effects of the decline on the trees. Specifically, we attempted to (1) contrast measurements of the soil risk factors among several classified zones (i.e. healthy and dead conditions along a forest productivity series) and (2) evaluate risk factors by correlating each with the proportion of the forest that was dead.

Materials and methods

Site description

Field sampling was conducted at two watersheds in southeast Alaska (Fig. 2), Goose Cove on Baranof Island (57°30′N, 135°32′W) and Poison Cove on Chichagof Island (57°31′N, 135°35′W). The Goose Cove site has a northern aspect and is limited by a ridge at 130 m elevation to the south and west and flanked on the eastern side by poorly drained soils. The Poison Cove site has a southerly aspect with a large bowl containing areas of poor drainage at low elevation and another small area of poor drainage at 250 m elevation. These watersheds have high concentrations of dead trees typical of yellow-cedar decline but also surrounding forests that appear largely healthy. Both are roadless and presumably in a pristine state with no history of timber management.

Vegetation plots and classification

A systematic grid of permanent vegetation plots was established at both study locations in 2001. The plot placement was designed to encompass a broad expanse of yellow-cedar forests throughout the watersheds. Plots were arranged along intersecting 100 m gridlines from the beach fringe forest extending to geographic barriers such as large streams and ridges. All live and dead trees ≥25 cm diameter at breast height (DBH) were measured in these 1/30 ha (10.3 m radius) plots; smaller trees (≥15 cm DBH) were measured in a central, nested plot (1/90 ha, 6 m radius). A total of 69 and 63 plots were sampled at Goose and Poison Coves, respectively. We used alternating vegetation plots (i.e. 1/2 the plots) to create a grid of plots 144 m apart for measurements of soil saturation, soil chemistry, and soil and air temperature.

Measurements of trees included DBH (to nearest mm) and height (to nearest dm) measured with a criterion impulse ranging laser. Snag class (Hennon *et al.*, 1990c) and height to break (if broken) were recorded for dead trees. Dead uprooted trees were noted as such. Species were recorded for live and dead trees; distinguishing dead trees often required observing bark or smelling wood cut with a hatchet. Data from these plots were used to calculate live and dead basal area values ($m^2 ha^{-1}$), and percent basal area dead. Downed dead trees were not included in these calculations because the decline problem results in dead standing trees that generally remain upright for 80 years or more (Hennon *et al.*, 1990c).

We classified the vegetation at both study areas using color infrared images at a 1:8000 scale. Forest zones were classified visually by degree of canopy closure and concentration of dead trees. This resulted in zones mapped as bog (nearly treeless), scrub (open canopy forest), productive dead (previously closed-canopy forest but high concentration of large dead trees), and productive live (closed-canopy forest composed primarily of live trees) (Fig. 3). We also distinguished higher (≥150 m) and lower (<150 m) elevations for these zones at Poison Cove because of our observation that cedar decline is generally limited to <150 m in the Peril Strait area. The productive dead zone was not detected above 150 m. The Goose Cove watershed was entirely low elevation and was thus mapped as four types of zones.

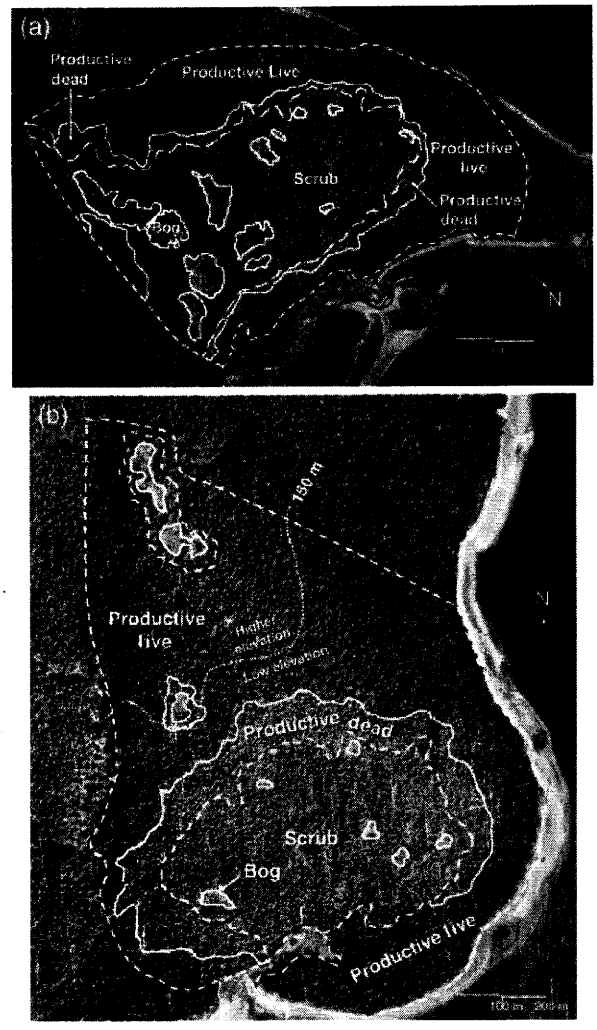

Fig. 3 Classification of the Goose Cove (a) and Poison Cove (b) study sites into zones based on canopy cover and concentration of dead trees. The distinction between higher and lower elevation areas at Poison Cove is made because of the general absence of yellow-cedar decline above 150 m in the Peril Strait area. The entire small watershed at Goose Cove is below 150 m elevation.

Soil hydrology

Water table heights within the soil profile were measured with two wells (schedule 40 PVC pipe) at 30 plots at each site placed at depths of 50 cm at azimuths of 90° and 270°, 8 m from plot center. Well measurements were taken in July, August, and September during the summer of 2002. The water table height from the two wells at each plot was averaged to determine mean plot water table depth. The average of the three measurements was used as the soil saturation depth for each plot.

Soil chemistry

Soil samples were taken from 30 vegetation plots at each study site. Three small pits were dug within each plot for soil subsampling. In order to reduce sample

variability, the subsample locations were established at half the largest plot radius (5 m) from plot center along three fixed compass directions of 0°, 120°, and 240°. Soil samples were taken within two depths corresponding to the upper (0–15 cm) and lower (15–25 cm) rooting zone. The three subsamples were then mixed to provide one composite sample at each depth for each plot.

Extractable cations were determined on all samples and analyzed by inductively coupled plasma mass spectroscopy (ICP–MS) (Robertson *et al.*, 1999). This method was modified by using 0.5 M $CuCl_2$ to extract cations from organic soil samples. $CuCl_2$ was used because of its effectiveness in displacing Al from exchange sites in organic material (Bertsch & Bloom, 1996). Mineral soil extractions were done with 1 M NH_4Cl. Extractable Al and Ca values were determined rather than solution concentrations (Cronan & Grigal, 1995) owing to the difficulty in obtaining soil solution in adequate and representative quantities at all plots. The extractable concentration of Al and Ca has been shown to be related to the dissolved concentration (David & Lawrence, 1996) and has been applied as a surrogate indicator in forest decline risk analysis (Wargo *et al.*, 2003).

Air and soil temperature

Ground surface air temperatures (10 cm above ground) and soil temperatures (15 cm deep) were recorded at 4 h intervals with automated devices (Hobo Temperature Pro, Onset Computer Corp.). These devices were deployed in fall 2001 through summer 2003 in the center of the 35 Goose Cove and 28 Poison Cove plots. Additional devices were deployed in selected plots to represent each of the classified forest zones; these devices recorded soil temperature at 7.5 and 30 cm depths at 4 h intervals and air temperature hourly at 2 m above ground. Some devices failed to produce data because of water infiltration or animal damage (i.e. rodents and bears).

Temperature data were examined to determine the number of freeze-thaw events and duration of freezing for near-surface air and soil at 15 cm depths. Air temperature data were converted to daily minimum, maximum, and range values (i.e. daily max–min) for some analyses. These values were used to calculate monthly means and displayed graphically as means for the different forest zones. Daily minimum and maximum values and soil temperature data were converted to 7-day running means to display general temperature patterns over the 2 year study. Cumulative 'degree days' were calculated from 4 h interval soil data for March through May as an indication of early spring warming using a minimum threshold of 0 °C.

Summary statistics on air and soil temperature variables for the growing and non-growing season (May–September and October–April, respectively), the four seasons (fall: September–November, winter: December–February, spring: March–May, and summer: June–August), number of freeze-thaw events, duration of freezing, and cumulative spring degree days were used in the statistical tests described below.

Statistical analysis

Analyses of variance (ANOVA) and Tukey's multiple comparison tests (GLM procedure ver. 9.1, SAS, 2003) were used to test for differences among forest zones for basal area (BA) values (total BA, percent BA dead for all tree species, percent BA dead for yellow-cedar); mean water table depth; mean soil Al and Ca concentration; mean soil Al:Ca ratio; seasonal mean air and soil temperature; average daily minimum, maximum, and range (max–min) for air temperature; and soil spring degree days.

Each of the hydrologic, soil, and temperature variables above was independently correlated (Pearson correlation) with total BA, percent BA dead, and percent yellow-cedar BA dead from plots (CORR procedure, SAS ver. 9.1, 2003) to test for correlations of these variables and forest conditions. Only plots $\geq 20\,m^2\,ha^{-1}$ total BA were included in these tests as these contained sufficient numbers of trees to calculate percent dead BA values. All tests were conducted separately for Goose Cove and Poison Cove and all results were judged to be significantly different at $P < 0.05$.

Results

Forest trees and classification

The classification of both watersheds from images, with emphasis on forest cover and tree death, was generally supported by summary statistics from plot tree data. ANOVA and Tukey's multiple comparison tests indicated significant differences (all $P < 0.001$) in live and dead BA for all trees, and for dead yellow-cedar alone at Goose Cove and Poison Cove. As expected, we found a gradient of increasing total tree BA (live + dead) from bog, scrub, productive dead, and productive live zones except the latter two zones did not differ at both sites (Fig. 4). Live tree BA also increased significantly across this gradient of zones at both Goose and Poison Coves, respectively. The death of yellow-cedar in the decline zones, where cedar had dominated, reduced cedar live basal areas to low levels, similar to that of healthy zones where cedar was not a major component.

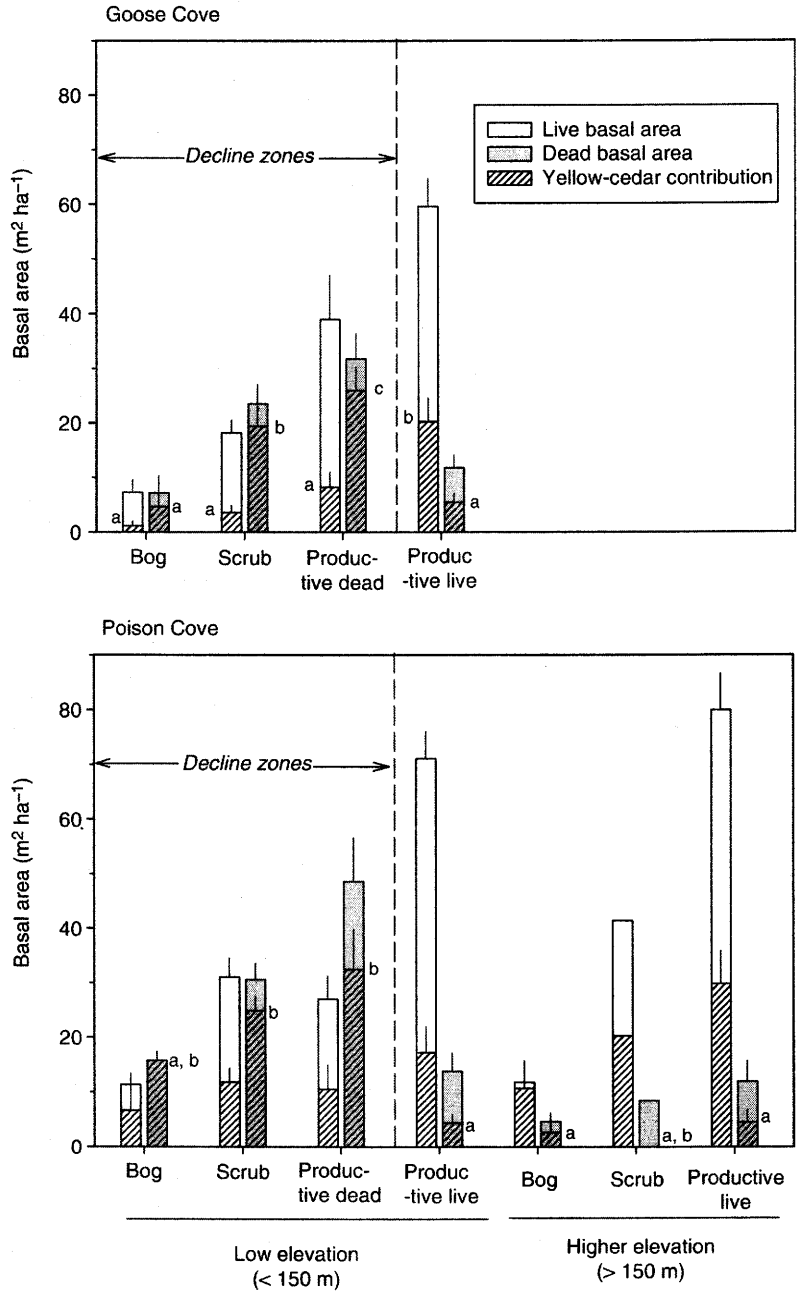

Fig. 4 Mean live and dead basal area of all species, and contribution by yellow-cedar (inset bars and error bars), by classified forest zones at Goose and Poison Cove. Error bars are one standard error. The high elevation scrub zone at Poison Cove was represented by only one plot. The basal area of live yellow-cedar was not generally significantly different in the ANOVA test by zone at Poison Cove. Forest zones with the same letter did not differ significantly by Tukey HSD test in live cedar basal area, or dead cedar basal area. Significant differences accounting for all species are not shown. Mean and error values for total basal area (live + dead) also not shown but were highly significant at both sites ($P = 0.0001$).

Dead tree BA reached a maximum value in the productive dead zone and a minimum in all apparently healthy zones and the less productive bog zones at both sites (Fig. 4). Yellow-cedar comprised most of the overall tree mortality in the dead zones, but not in the other, apparently healthy zones where dead hemlock was more abundant. The percent BA dead was remarkably consistent among dead zones, especially for

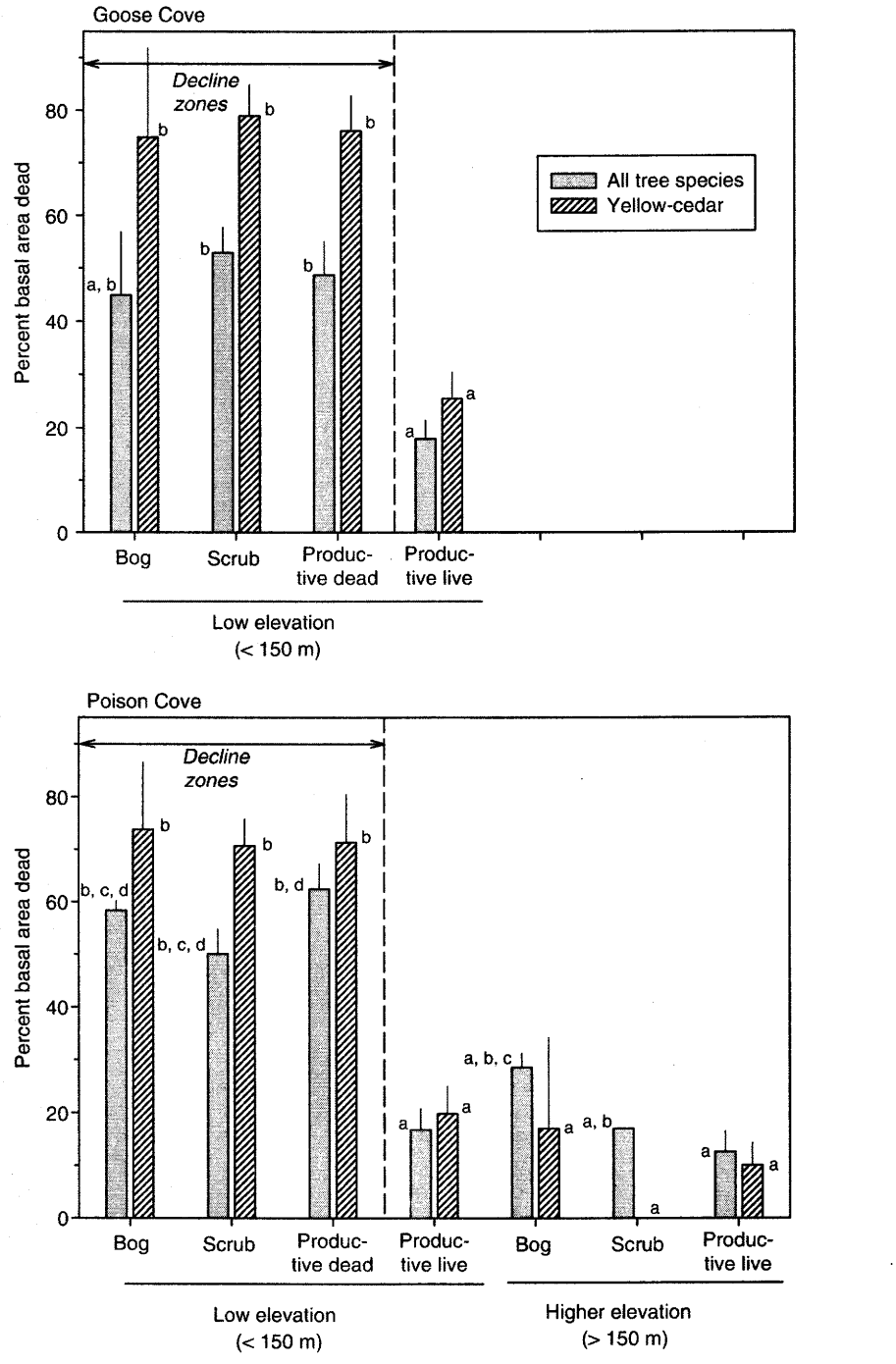

Fig. 5 Mean percent basal area dead for yellow-cedar and all species differed significantly by classified forest zones at Goose Cove and Poison Cove as indicated by ANOVA. Error bars are one standard error. The high elevation scrub zone at Poison Cove was represented by only one plot. Forest zones with the same letter did not differ significantly in dead basal area by the Tukey HSD test (i.e. comparing zones for basal area dead for all species and also for yellow-cedar alone).

yellow-cedar, which was found in a tight range of 71–79% dead at both sites (Fig. 5). In contrast, the zones judged to be healthy on the classified images (productive live at both sites, and all zones above 150 m at Poison Cove) generally had BA dead percent values from 5% to 25%.

The frequency distribution of yellow-cedar snag classes (Fig. 6) revealed a pattern skewed towards

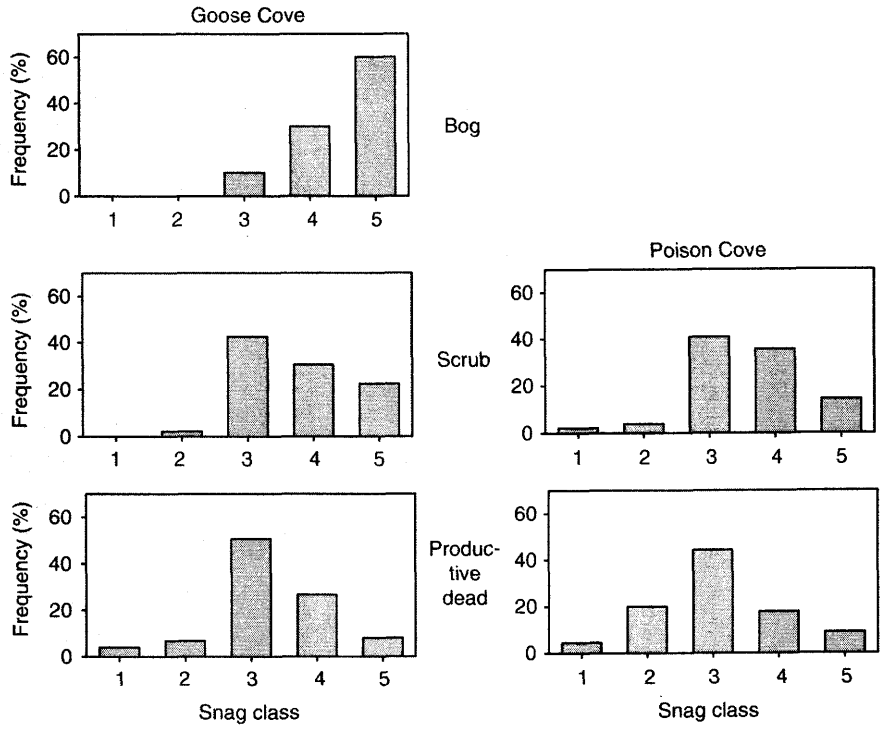

Fig. 6 Frequency distribution of percent occurrence for standing dead yellow-cedar trees (snags) in five deterioration classes (dead 4, 14, 26, 54, and 81 years for classes 1 through 5, respectively (Hennon *et al.*, 1990a)) in three dead trees zones mapped at Goose Cove and Poison Cove. Bog plots at Poison Cove were too few to generate sufficient numbers of snags for inclusion.

primarily old dead trees that died before 1950 in bogs, old and intermediate snags in scrub zones, and a more normal distribution of snag classes including recently killed trees in the productive dead zone.

Soil saturation

Depth to water table, or soil saturation, increased along the BA gradient from productive to scrub and bog zones at both Goose Cove and Poison Cove (Fig. 7). There was a significant difference in soil saturation among zones at Goose Cove ($P = 0.0003$), but not at Poison Cove ($P = 0.13$). Goose Cove had two saturation levels within the four zones, while the trend at Poison Cove was toward three saturation levels among the four forest zones (Fig. 7).

Total BA significantly decreased with increased soil saturation at Goose Cove ($P < 0.0001$) and Poison Cove ($P = 0.0005$) (Fig. 8a, b). There was also a significant decrease in percent dead BA with increasing soil saturation at Poison Cove ($P = 0.0003$), but not Goose Cove ($P = 0.08$) (Fig. 8c, d). There was no clear association between soil saturation and the proportion of yellow-cedar mortality (Fig. 8e, f). A high rate of yellow-cedar mortality was spread over a wide range of soil saturation conditions both below (>30 cm) and above

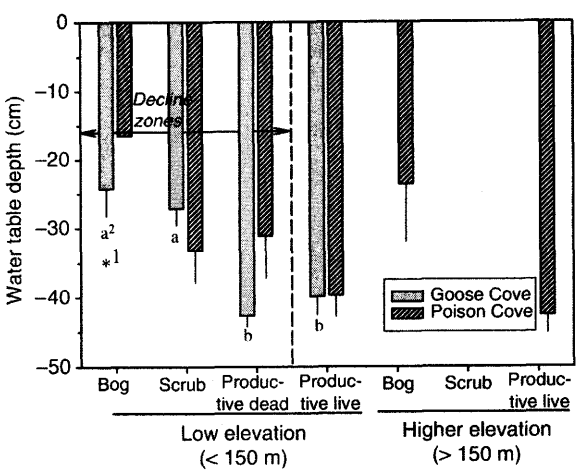

Fig. 7 Average water table depths measured in wells at Goose Cove and Poison Cove. [1]Significance for comparisons among classes: * denotes $P \leq 0.05$ at Goose Cove (ANOVA). [2]Water table depths with the same letter are not significantly different based on the Tukey HSD test.

(<30 cm) the rooting zone (Fig. 8e, f). The soils at the scrub and productive dead zones at Poison Cove were saturated at or below the effective rooting zone and the soil saturation in the productive dead forests at Goose

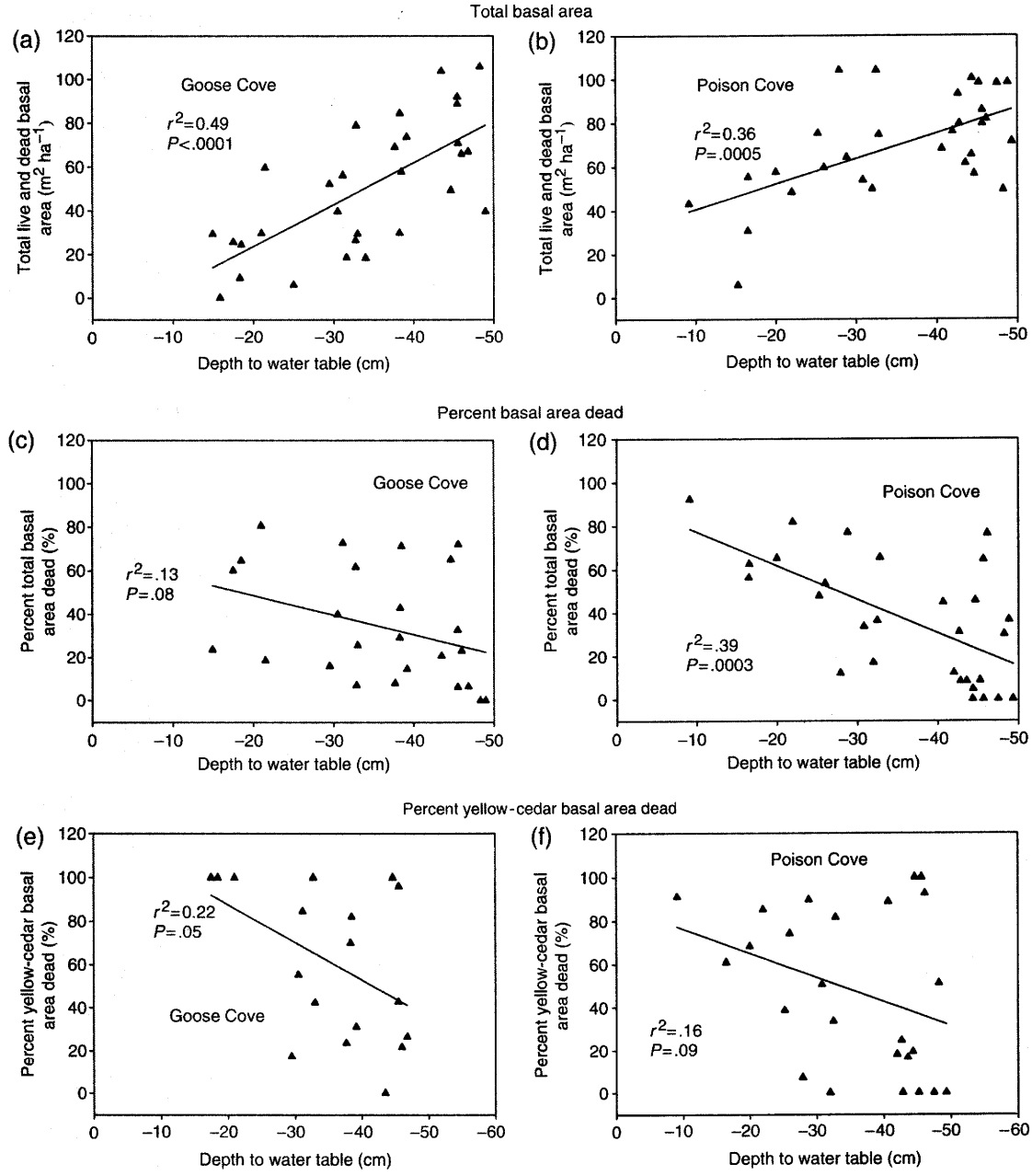

Fig. 8 Relationships of average water table depth with total basal area (a, b), percent basal area dead (c, d), and percent yellow-cedar basal area dead (e, f) at Goose Cove and Poison Cove.

Cove were similar to the productive live zone (Fig. 7). There was less mortality in well-drained soils compared to saturated soils in all trees as well as yellow-cedar trees.

Extractable Al and Ca

Extractable Al is abundant and highly variable among the classified forest zones at Goose Cove and Poison Cove (Fig. 9). There are no significant differences in extractable Al among the zones at Goose Cove (15 cm $P = 0.32$; 25 cm $P = 0.83$) or Poison Cove (15 cm $P = 0.62$; 25 cm $P = 0.75$). The aggressive $CuCl_2$ extractant magnified the possible pools of soluble Al leading to the high extractable quantities. The extractable Al in the productive dead zone at Poison cove was noticeably lower than other lower elevation classes (Fig. 9a, b). This relationship was also apparent in the Al : Ca values

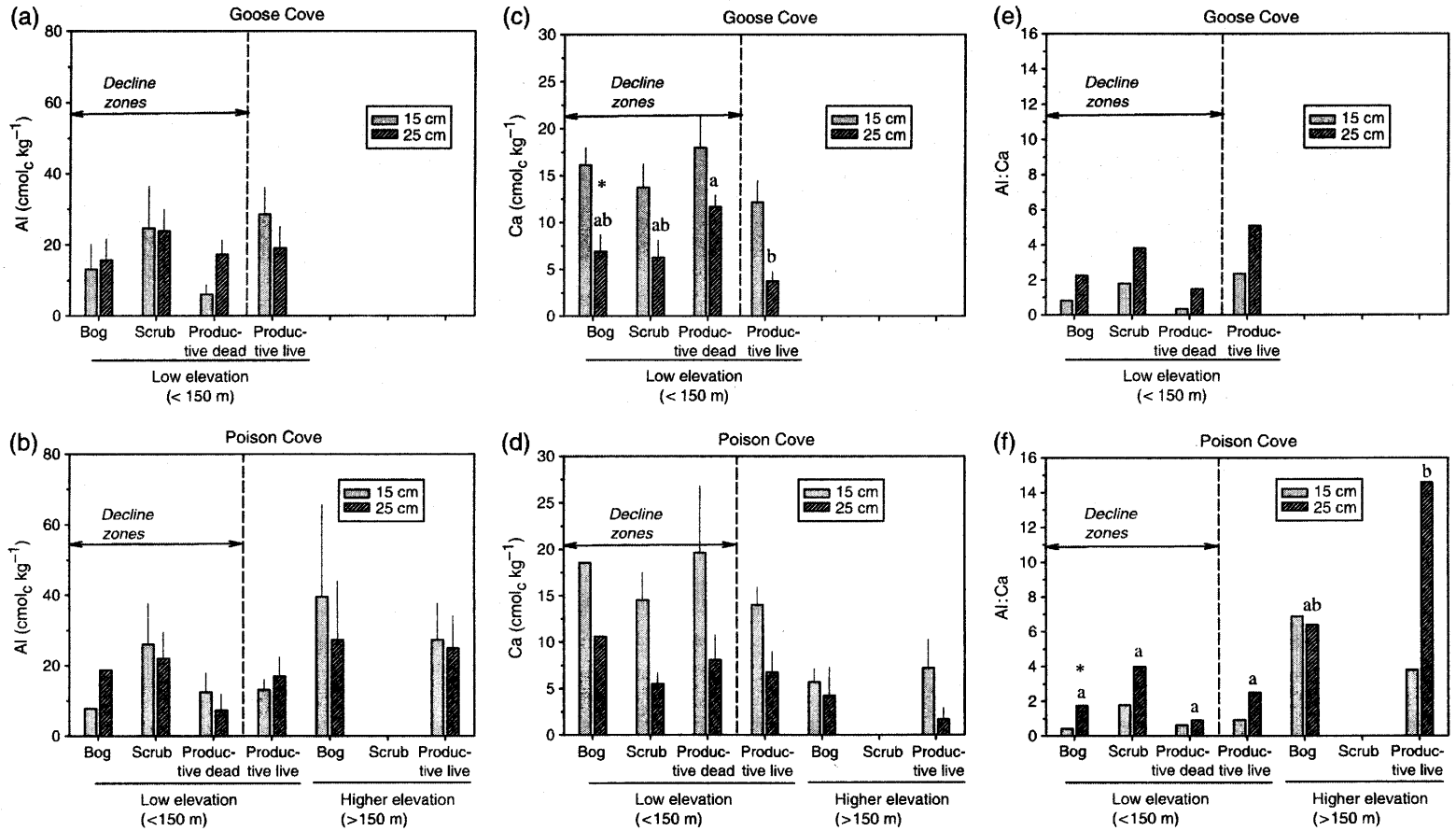

Fig. 9 Extractable Al, Ca, and the Al:Ca in classified forest zones at Goose Cove and Poison and Cove. Error bars indicate one standard error. *denotes significant ($P \leq 0.05$) effect at 25 cm depth for Ca and Al:Ca based on ANOVA. Extractable values with the same letter are not significantly different based on the Tukey HSD test.

Table 1 Pearson correlation coefficients and probability functions for relationships between extractable Al, Ca, and Al:Ca ratio with percent dead yellow-cedar basal area

	15 cm			25 cm		
Cation	*r*	*p*	*n*	*r*	*p*	*n*
Goose Cove						
Al	−0.15	0.54	18	0.09	0.71	18
Ca	0.31	0.21	18	0.35	0.15	18
Al:Ca	−0.32	0.19	18	−0.29	0.24	18
Poison Cove						
Al	−0.02	0.94	25	−0.22	0.29	25
Ca	0.40	0.05*	25	0.25	0.22	25
Al:Ca	−0.29	0.15	25	−0.44	0.03*	25

*Significance at the $P < 0.05$ level.

(Fig. 9e, f). The most extractable Al was located in the productive live zone at Goose Cove and the high elevation bog and high elevation productive live zones at Poison Cove (Fig. 9a, b).

Extractable Ca values for Goose Cove and Poison Cove were similar to reported values from the region and other similar studies (Heilman, 1968; Gonzalez, 1981; Stednick, 1984; Bormann & Sidle, 1990; Alexander *et al.*, 1994; David & Lawrence, 1996; Kranabetter & Banner, 2000). Extractable Ca has a tendency to increase with increasing decline at both sites. Calcium was positively correlated with increasing percentage of dead yellow-cedar BA at 15 cm depth at Poison Cove, but not at Goose Cove (Table 1). There was also a negative correlation of percent dead yellow-cedar BA with Al:Ca at 25 cm depth at Poison Cove that was driven by the high Ca levels at this depth (Table 1). The accumulation of Ca at 25 cm depth was significantly different among zones at Goose Cove, but not Poison Cove (Fig. 9c, d). There were no significant differences in Ca among zones at 15 cm depth, though there were greater mean Ca concentrations in the productive dead zones at both sites.

The Al:Ca ratios at both sites were above the theoretical risk threshold proposed by Cronan and Grigal (1995) in most forest zones at both depths (Fig. 9e, f). The Al:Ca ratio at 15 cm depth did not significantly differ by forest zones at Goose Cove ($P = 0.39$) or Poison Cove ($P = 0.31$) (Fig. 9e, f). One exception was the low-elevation productive dead zones at both sites. This relationship was influenced mostly by the extractable Ca in this zone compared to the other low elevation zones. By contrast, the low mortality, high elevation zones at Poison Cove had extremely high Al:Ca ratios (Fig. 9e, f) and relatively low extractable Ca values (Fig. 9c, d) compared with the low-elevation zones.

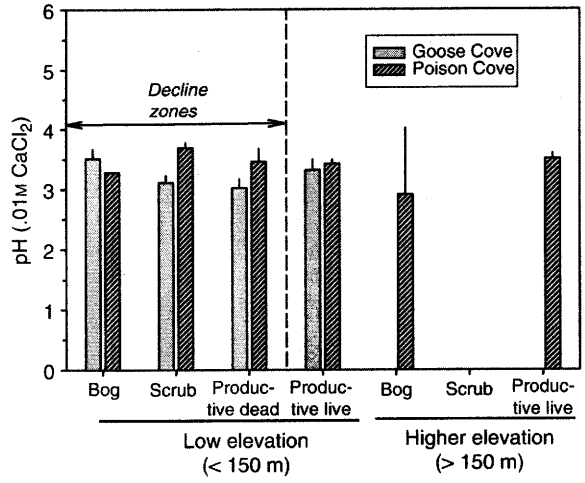

Fig. 10 pH means by classified forest zone at Goose Cove and Poison Cove. Error bars are one standard error. Means did not differ significantly at either site in the ANOVA test.

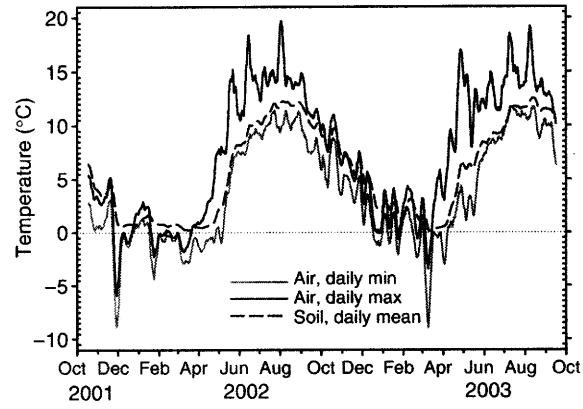

Fig. 11 Seven-day running mean air temperature 10 cm above ground for minimum and maximum values and soil temperature 15 cm below ground averaged for temperature devices at Goose Cove and Poison Cove.

Soil acidity (pH)

All of the plots revealed an extremely acidic soil environment with most mean pH values from 3.0–3.5 (Fig. 10). Goose Cove had a significantly lower pH associated with an increase in both live ($P = 0.04$) and total BA ($P = 0.01$), but not dead yellow cedar BA ($P = 0.50$). The pH at Poison Cove was not related to live ($P = 0.56$), total BA ($P = 0.94$), or percent yellow-cedar basal area dead ($P = 0.32$). Poison Cove had slightly higher pH values than Goose Cove in all zones except the bogs. Goose Cove had the lowest pH in the scrub and productive dead zones while the bog plots had the highest pH among all forest zones. The high elevation

Table 2 Mean air (a) and soil (b) temperature (15 cm depth), total duration of freezing, and number of freeze–thaw cycles for different forest zones at Goose Cove and Poison Cove during nongrowing season (October–April) and growing season (May–September).

	n	Temperature (°C)	≤0 °C* (days)	Freeze (cycles)	*n*	Temperature (°C)
(A) Ground surface air						
Goose Cove	Nongrowing 2001–2002				Growing 2002	
Bog	7	−0.1 (0.1)[a]	124	55	6	10.9 (0.4)
Scrub	11	−0.0 (0.1)[a]	130	32	7	10.8 (0.2)
Productive dead	5	0.2 (0.1)[a,b]	115	39	4	10.4 (0.2)
Productive live	9	0.3 (0.1)[b]	97	37	7	10.0 (0.1)
Goose Cove	Nongrowing 2002–2003				Growing 2003	
Bog	4	2.7 (0.2)	65	83	2	7.8 (0.6)
Scrub	5	2.9 (0.1)	51	51	5	8.0 (0.2)
Productive dead	3	3.0 (0.1)	47	34	5	7.6 (0.0)
Productive live	8	3.1 (0.1)	47	28	6	7.2 (0.2)
Poison Cove	Nongrowing 2001–2002				Growing 2002	
Low elevation (<150 m)						
Bog	1	0.4	143	38	0	
Scrub	8	0.2 (0.1)	127	30	7	10.4 (0.1)[c]
Productive dead	4	0.0 (0.2)	130	29	3	10.1 (0.1)[b,c]
Productive live	8	0.3 (0.1)	95	23	6	9.9 (0.1)[b,c]
Higher elevation (>150 m)						
Bog	1	−0.3	174	26	1	8.4[a]
Scrub	1	−0.5	154	16	1	9.0[a,b]
Productive live	4	0.1 (0.1)	107	17	4	9.5 (0.1)[b]
(B) Soil (15 cm depth)						
Goose Cove	Nongrowing 2001–2002				Growing 2002	
Bog	7	1.7 (0.1)	1	<1	5	10.4 (0.2)[b]
Scrub	11	1.3 (0.2)	23	1	6	10.1 (0.4)[b]
Productive dead	5	1.5 (0.2)	13	1	4	9.6 (0.4)[a,b]
Productive live	10	1.4 (0.2)	28	7	8	9.0 (0.2)[a]
Goose Cove	Nongrowing 2002–2003				Growing 2003†	
Bog	4	4.0 (0.1)	2	<1	2	7.8 (0.6)[b]
Scrub	5	3.9 (0.2)	1	<1	5	7.5 (0.4)[b]
Productive dead	3	4.3 (0.1)	1	<1	2	6.9 (0.2)[a,b]
Productive live	8	3.9 (0.1)	10	2	6	6.2 (0.1)[a]
Poison Cove	Non-growing 2001–2002				Growing 2002	
Low elevation (<150 m)						
Bog	1	2.0	0	0	0	
Scrub	8	1.5 (0.2)	2	<1	7	9.9 (0.2)[b]
Productive dead	4	2.1 (0.1)	0	0	3	8.6 (0.0)[a]
Productive live	7	1.7 (0.2)	4	2	4	9.6 (0.1) [a,b]
Higher elevation (>150 m)						
Bog	1	0.7	0	0	1	8.7 [a,b]
Scrub	1	1.1	0	0	1	8.3[a,b]
Productive live	5	0.9 (0.3)	37	4	2	8.2 (0.2)[a]

*Cumulative duration, expressed in days, of temperatures at or below 0 °C.

†Sampling during the 2003 growing season at Goose Cove occurred only through June.

Equipment failure produced insufficient sampling at the Poison Cove site in the second year of sampling and values are not shown. Values in parentheses are one standard error. Values with the same letter did not differ significantly by the Tukey HSD test where ANOVA indicated a general forest zone effect

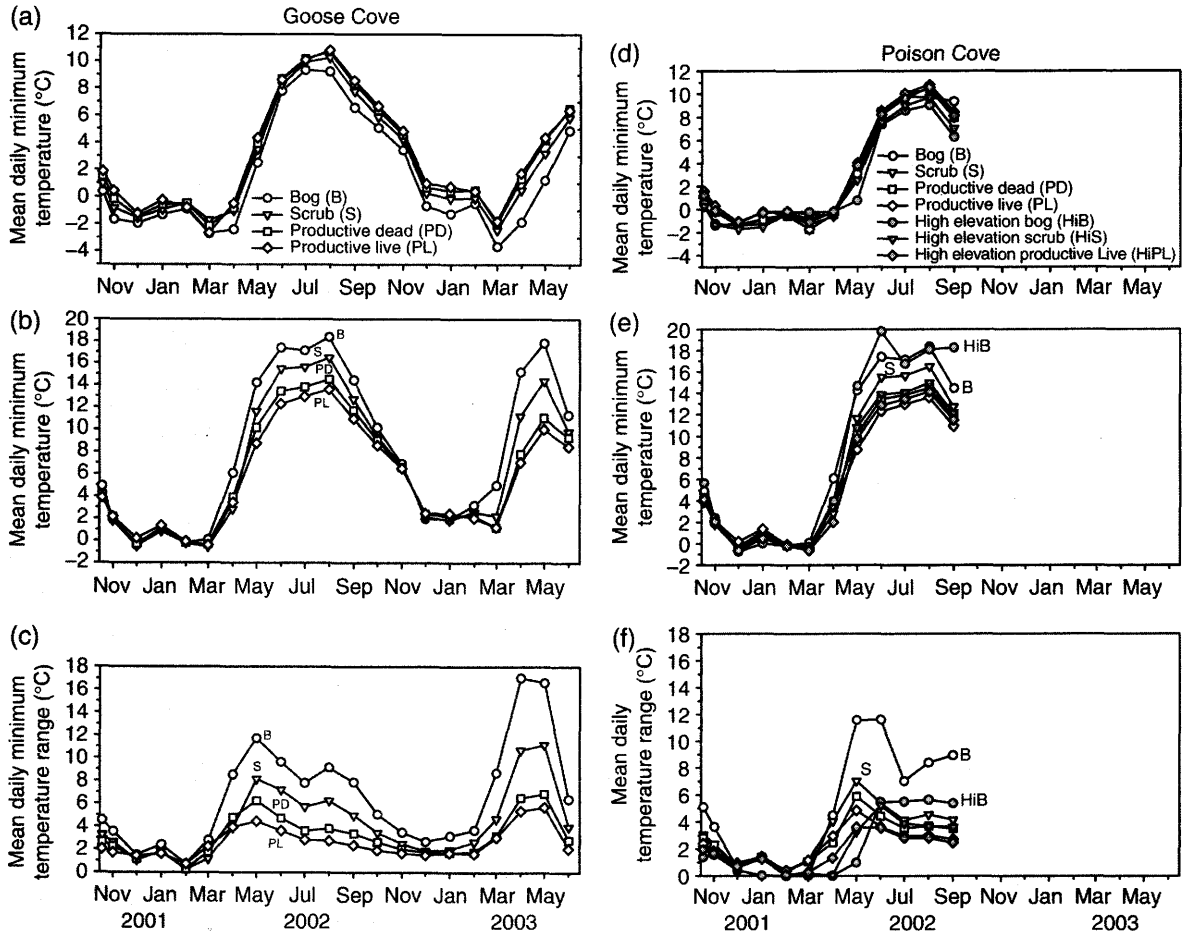

Fig. 12 Monthly mean air temperatures: (a, d) daily minimum, (b, e) daily maximum, and (c, f) daily range recorded near the ground surface on plots in classified forest zones at Goose Cove, Baranof Island, and Poison Cove, Chichagof Island, respectively. Labels for months are shown at the beginning of each month.

bogs at Poison Cove had the most variability, but the lowest overall mean pH.

Air and soil temperature

Ground surface air and soil temperatures indicated a gradual period of cooling from September to December (Fig. 11). Winter temperatures for both air and soils were generally low from December through about March with alternating cycles of warm, low-pressure weather followed by cold, high pressure. Freeze–thaw cycles were evident for air temperatures, but overall mean temperature for soils at 15 cm depth was never below 0 °C. The 2002–2003 winter was notable in that the coldest air and soil temperatures recorded were in March. Late March or early April marked a departure to higher maximum air temperatures, greater ranges between min and max air temperatures, and the most rapid prolonged change (i.e. increased warming) in soil temperature for the year.

Mean ground air temperature for growing and non-growing seasons had small tendencies consistent with exposure in the forest zones (i.e. colder during non-growing season and warmer in the growing season in zones with less cover), but significant differences were only found for the 2001–2002 non-growing season at Goose Cove and the 2002 growing season at Poison Cove (Table 2).

Seasonal mean values of daily minimum, maximum, and range differed significantly by forest zone (most P values <0.007) for fall, spring and summer of the first sampling year at both Goose and Poison Cove (Fig. 12, expressed as monthly values). These values were all consistent with the expected exposure in different zones; for example, bogs had lower minimum values, greater maximum values, and exaggerated range values. April and May revealed the greatest separation of

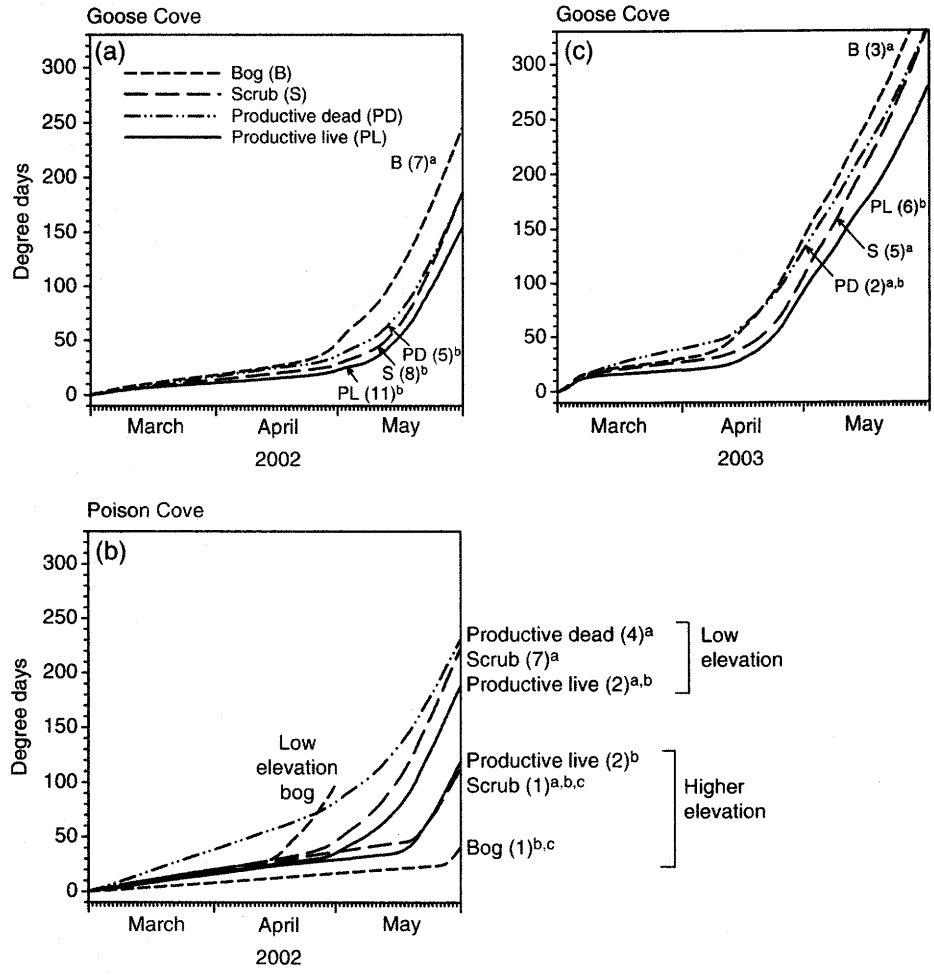

Fig. 13 Cumulative degree days (>0°) of soil temperature at 15 cm depth for forest zones from March 1 through the end of May for two spring intervals at Goose Cove (a, c) and one spring interval at Poison Cove (b). Lines are composed of daily values which represent sum of means from the plots in each forest zone. The single device in the low elevation bog did not record data past April in 2002 at Poison Cove. The number of plots sampled are given in parentheses. Each ANOVA indicated a significant zone effect; zones with the same letter did not differ significantly by the Tukey HSD test in cumulative degree days at the end of May.

these values by forest zone (Fig. 12), with mean daily range values being the most divergent.

Mean soil temperatures in the rooting zone (15 cm deep) were significantly different by forest zone during the 2002 ($P = 0.0008$) and 2003 ($P = 0.003$) growing seasons sampled at Goose Cove and the single growing season 2002 ($P = 0.015$) sampled at Poison Cove (Table 2). At Goose Cove during both years, the bog and scrub zones were slightly, but significantly warmer than the more protected productive live zone, with the productive dead zone between and not different. A significant relationship among zones was also found at Poison Cove with the dead low elevation scrub soils the warmest, but sampling was not sufficient to clearly differentiate the greater number of zones. Mean soil temperatures during non-growing seasons did not differ significantly by forest zone at either site ($P = 0.08$–0.42), but mean values were >2.3 °C warmer during the 2003–2003 season than the previous season in all zones. Duration of freezing (<0 °C) and number of freeze-thaw cycles did not differ significantly by forest zone for either air or soil at either site, although there was a tendency for a greater number of air freeze-thaw events in the bog zones (Table 2). Freezing at the soil depth of 15 cm did not occur on most plots with the exception of the productive live zone where it was common in the more aerated soils.

The smaller number of devices deployed (e.g. one device per forest zone) to measure soil temperature at 7.5 cm depths revealed the common occurrence of freezing at this shallow rooting zone. Soil temperatures dropped to about −2 °C at 7.5 cm depth at all zones

Table 3 Pearson correlation coefficients and probability functions for significant relationships between ground air or soil temperature variables and live basal area, percent dead basal area (for all tree species) and percent dead basal area for yellow-cedar at Goose and Poison Cove sites

		Live basal area ($m^2 ha^{-1}$)						All species basal area (BA) dead (% of total BA)						Cedar basal area dead (% of total cedar BA)					
		Goose			Poison			Goose			Poison			Goose			Poison		
Temperature variable	Value	*n*	*r*	*p*	*n*	*r*	*p*	*n*	*r*	*p*	*n*	*r*	*p*	*n*	*r*	*p*	*n*	*r*	*p*
Ground Air Temp																			
*Means of daily min, max**																			
Fall 2001	Min	32	0.77	0.0001	28	0.48	0.01	26	−0.73	0.0001				18	−0.85	0.0001			
	Max							26	−0.39	0.05							24	0.51	0.01
	Range	32	−0.70	0.0001	28	−0.63	0.0003	26	0.59	0.002	28	0.63	0.0003	18	0.76	0.0002	24	0.60	0.002
Winter	Min	32	0.42	0.02	27	0.54	0.003				27	−0.51	0.007	18	−0.46	0.05	23	−0.57	0.004
2001–2002	Max	32	0.60	0.0003	27	0.66	0.0002	26	−0.62	0.0008	27	−0.54	0.004	18	−0.68	0.002			
	Range							26	−0.39	0.05									
Spring 2002	Min																		
	Max	32	−0.38	0.03													23	0.49	0.02
	Range																23	0.48	0.02
Summer 2002	Min	24	0.55	0.005	27	0.38	0.04												
	Max	24	−0.70	0.0002	27	−0.71	0.0001	21	0.71	0.0003	26	0.61	0.001	13	0.74	0.004	23	0.55	0.007
	Range	24	−0.69	0.0002	27	−0.74	0.0001	21	0.67	0.001	26	0.59	0.001	13	0.71	0.006	23	0.47	0.03
Fall 2002	Min	25	0.69	0.0001	23	0.43	0.04	22	−0.52	0.01				14	−0.71	0.005			
	Max	25	−0.66	0.0004	23	−0.60	0.002	22	0.64	0.001	22	0.68	0.0005	14	0.77	0.001	20	0.74	0.0002
	Range	25	−0.69	0.0001	23	−0.78	0.0001	22	0.62	0.002	22	0.70	0.0003	14	0.77	0.001	20	0.61	0.004
Winter	Min	20	0.72	0.0003	20	0.61	0.005	17	−0.57	0.02	19	−0.48	0.04	10	−0.79	0.006			
2002–2003	Max							17	−0.58	0.02									
	Range	20	−0.63	0.003	20	−0.59	0.007				19	0.51	0.03	10	0.70	0.03	17	0.55	0.02
Spring 2003	Min	16	0.69	0.003	11	0.80	0.003				10	−0.68	0.03	9	−0.83	0.006	10	−0.76	0.01
	Max	16	−0.56	0.02	11	−0.76	0.007				10	0.65	0.04				10	0.63	0.05
	Range	16	−0.61	0.01	11	−0.88	0.0003				10	0.69	0.03	9	0.68	0.04	10	0.70	0.03
Soil temperature (15 cm depth)																			
Cumulative degree days†																			
March 2002	DD	32	−0.43	0.01	25	−0.44	0.03				25	0.53	0.006				25	0.41	0.05
April 2002	DD	32	−0.47	0.007	24	−0.44	0.03				24	0.52	0.01						
May 2002	DD	29	−0.64	0.0002				23	0.60	0.003	19	0.58	0.009				18	0.57	0.01
March 2003	DD																		
April 2003	DD																		
May 2003	DD	16	−0.60	0.01				14	0.60	0.02				10	0.76	0.011			

*Values are means derived from daily minimum (min), maximum (max), and range = max−min.

†Cumulative degree days (DD) >0 °C from March 1 to the end of the month listed.

Not shown are significant correlations between air and soil temperature variables and forest basal area variables during growing and non-growing seasons.

during the March 2002 cold weather, except for the drier soils in the productive live zone, which reached −8 °C. This period was preceded by warmer soils during February and early March, 2003, with the dead forest zones (i.e. bog, scrub, productive dead) reaching + 4 °C while the productive live zones were + 2 °C and the high elevation bog and scrub zones were close to zero and presumably covered by snow. Thawing at this depth after the cold period in mid-March occurred first in the dead forest zones (low elevation bog in late March; then productive dead, scrub in early April), followed closely by productive live in early April. Thawing at this shallow depth was delayed until the end of April at the high elevation zones.

Forest zones had significantly different cumulative spring soil degree days at 15 cm depths by the end of April 2003 at Goose Cove ($P = 0.05$), the end of May 2002 for Goose and Poison Cove ($P = 0.003$ and $P = 0.002$), and the end of May 2003 at Goose Cove ($P = 0.0009$). At Goose Cove, soils in the productive live zone lagged behind the other zones in spring warming (Fig. 13). The bog soils warmed at a faster rate than the other zones in spring 2002, but the productive dead zone had the most rapid soil warming in March and early April in 2003. Soils in the productive dead zone showed faster warming in March through most of April at Poison Cove in 2002. We suspected that the pronounced difference between this and other zones might be an error in one of the devices, but these warm values were driven by three devices of the four plots in this zone. Soil warming in the three higher elevation zones lagged far behind that of the other zones at Poison Cove in 2002, indicating that the scrub and productive live zones in these areas did not emerge from snow until past mid May and the bog zone not until the end of May.

Significant models were developed regressing percent dead basal area (for all trees and for yellow-cedar alone) with the temperature variables for Goose and Poison Coves listed in Table 2. In some cases, important variables could not be included in models because n values were too low. Also, many of the temperature variables were interchangeable in the models and including or removing them seemed arbitrary. Thus, we place more emphasis on the individual correlations presented below of temperature variables with percent basal area dead for interpretation of temperature as a risk factor.

Many air and soil temperature variables were correlated with live basal area and percent basal area dead (Table 3). In the interest of space, Table 3 does not show correlations involving mean, minimum, and maximum values for growing and nongrowing seasons for both air and soil temperature. Of the 157 significant correlations ($P < 0.05$), the sign of the Pearson R-value in all cases but two was consistent with the moderating influence of live basal area and more exposure in plots with a greater percentage of dead trees. The relationship of these two measures of forest condition, live basal area and percent basal area dead (the latter as expressed by all tree species or yellow-cedar alone), with the various temperature variables was nearly always opposite (Table 3). For example, greater basal live area was correlated with cooler summer temperatures, warmer winter temperatures, smaller daily ranges, and slower accumulation of soil degree days. Conversely, percentage basal area dead was correlated with cooler winter temperatures, warmer spring and summer temperatures, more extreme daily ranges, and greater accumulation of soil degree days. The two exceptions to this pattern were air temperature values in the transitional fall season when the relationship between temperature and site factors is more difficult to predict.

Discussion

Soil saturation

Yellow-cedar decline was previously associated with soil saturation (Hennon *et al.*, 1990b). This observation was based on the association of cedar stands with marginal, often saturated sites where cedars are more competitive than hemlock or spruce (Neiland, 1971). Soil saturation influences the occurrence and productivity of vegetation communities from open peatlands to upland forests in the region (Asada *et al.*, 2003). Successionally, yellow-cedar appears late in the colonization of soils and is linked to increased soil saturation (Ugolini & Mann, 1979). Soil saturation influenced the total live and dead tree basal area at Goose Cove and Poison Cove, but was weakly associated with the percentage of dead yellow-cedar basal area. Hydrology, acting alone, was not a strong risk factor. The extensive soil water table measurements over a wide range of cedar decline in this study showed that yellow-cedar mortality was present in both saturated and unsaturated soils.

Soil saturation may play an indirect role in decline by providing open canopy structure due to reduced tree productivity. Overall tree basal area, and the corresponding canopy cover, increased from very poorly drained peatland soils in treeless bogs to unsaturated soils in productive forests. The spatial and temporal distribution of dead yellow-cedar trees forms a radiating pattern of tree mortality from a core of trees killed decades ago in poorly and moderately drained soils in the bog and scrub zones to a higher concentration of more recently killed trees in the adjacent productive dead zone. Any possible predisposing influence of an open canopy condition would have been present well before the initiation

of decline and is reflected in the bog-scrub-productive tree gradient in our classified forest zones.

Extractable Al, soil acidity and Ca

The symptoms of dying yellow-cedar trees are consistent with toxic reactions of plants to Al, but we found no clear link between yellow-cedar decline and extractable Al, Ca, or Al:Ca. The bog and scrub sites are generally poor sites for tree growth, yet yellow-cedar has competed well with other tree species in these acidic, wet soil environments (Krajina, 1969). The high extractable Al concentrations may lead to decreased uptake efficiency in the rooting zone, but do not appear to be completely deleterious to cedar alone. These high extractable Al values may lead to more soluble Al and an increased activity of Al in solution, but the abundance of organic matter and high concentrations of Ca in the soils may be acting to offset any increased Al activity in the surface soils. Also, soil acidity did not appear to follow a trend with extractable Al indicating that there was not an interaction in these variables. The paludification gradient did not lead to excessively low pH, nor did cedar decline intensify with lower pH. These results do not support the hypothesis that soil acidity is a significant factor in decline as proposed by Klinger (1988, 1990).

There is little evidence from this study that extractable Ca in the soil directly influences yellow-cedar mortality. However, Ca seems to be important to yellow-cedar and the death of yellow-cedar trees influences the Ca cycle. Both western redcedar and yellow-cedar show a great affinity for Ca (Krajina, 1969), but their ability to exploit soil Ca pools and translocated Ca in tissues is unknown. The critical biological threshold for Ca deficiency in yellow-cedar is not well known, and more information on the chemistry of Ca bioavailability and associated tree physiological processes would be useful in future evaluations of the ecology of yellow-cedar–soil interactions. This is especially important as it appears that much of the available soil Ca cycling in yellow-cedar forests may be controlled by feedback from cedar death. The productive dead zones at both Goose Cove and Poison Cove had high levels of Ca at 15 cm depth, probably because of the concentration of numerous recently killed yellow-cedars in these areas. These dead and dying trees have large amounts of dead foliage that can release Ca. The feedback mechanism of senescing cedar foliage may have confounded any trend of decline related to extractable Ca (David & Lawrence, 1996).

Temperature and implication of exposure

Air and soil temperatures emerged as the leading possible risk factors with yellow-cedar decline. The forest zones with abundant dead yellow-cedar had temperatures that were higher in the spring and summer, lower in winter, and had greater daily ranges. Temperature values correlated with the proportion of dead yellow-cedar basal area in the same fashion. Air and soil temperatures respond primarily to exposure. Open canopies provide inlets for solar radiation that warm vegetation and the soil surface and also allow more rapid loss of energy at night. Dense forest canopies intercept solar radiation by shading during warm periods and insulate the loss of energy during cold periods, thus creating buffered, less extreme temperature conditions. Soils located under open canopies warm more quickly in spring than the soils under dense canopies, as expressed by the rapid accumulation of soil degree days in the open canopy forest zones. The surface of these soils is also exposed to slightly colder night temperatures due to less insulation from the canopy.

Snow may also play a role in protecting against exposure, at least to the lower bole and roots of trees, and the soil environment. The higher elevation bog complex at the Poison Cove site is of interest because it is an open-canopy bog-scrub community dominated by live yellow-cedar. Snowpack persisted through April and May for the 2 yr sampled, respectively, which greatly delayed the onset of soil warming in spring. The presence of late winter or early spring snow may explain the elevation limits of yellow-cedar decline (Hennon *et al.*, 1990b, Hennon & Shaw, 1994).

As described above, open canopy conditions were produced primarily by hydrologic forces in bog and scrub communities before yellow-cedar decline initiated. The hydrologic driven exposure may have facilitated the early stages of decline, but then gave way to tree mortality-driven exposure in the surrounding forest zones. Once trees are killed, the loss of crown cover leads to a more open canopy condition and adjacent trees, even those in a closed-canopy forest, are then in an exposed position. This phenomenon could explain the perimeters of yellow-cedar decline expanding from bog and scrub communities to the edges of the productive dead zone (Hennon *et al.*, 1990b) in a manner similar to the wave mortality of *Abies* species in the eastern United States (Sprugel, 1976) and Japan (Kohyama, 1984). Thus, exposure was originally driven by soil saturation, but subsequently was, and still is, driven by a feedback mechanism of tree death. Interestingly, the drier soils at the perimeters of decline patches, where tree death is recent and severe, appear to experience especially rapid spring warming.

Freezing

Exposure-induced warming could have several possible consequences for the physiology of the yellow-cedar trees. Freezing injury to trees is often caused by delayed

cold hardiness in fall or premature dehardening in spring (Havranek & Tranquillini, 1995), with the latter more common or damaging (Timmis *et al.*, 1994, Aitken & Adams, 1997). Thus, yellow-cedar trees subjected to warmer air or soil temperatures in the forest zones with decline may deharden earlier in spring than trees that have cooler soils protected by shade or snow. The influence of late winter and early spring warming that could trigger loss of cold tolerance corresponds to evidence that the most dramatic climatic changes may involve winter and spring warming (Chapman & Walsh, 1993). Also, the loss of fine roots to freezing injury may disrupt the coupled cycle of nutrient mineralization and uptake by fine roots (Tierney *et al.*, 2001).

Any freezing injury could be to shallow roots of yellow-cedar trees. We found freezing conditions at 7.5 cm deep in soils where decline occurs, but not at the 15 cm depth. Along with creating open canopy conditions that affects temperature, soil saturation may also play a role in the susceptibility of tree roots to freezing injury. Elevated water tables impede deep root penetration and concentrate roots near the soil surface in poorly drained soils. The death of near-surface roots to freezing, especially if repeated frequently, would challenge the tree's resources to replace roots and could explain the slow tree death that is often exhibited.

Yellow-cedar displays plasticity as a response to temperature in a number of traits, including seed and cone development (Cherry & El-Kassaby, 2002). The indeterminate growth of yellow-cedar foliage and shoots (i.e. no buds or bud scales) allows for rapid responses to environmental clues. This responsiveness to temperature could be due to the species' adaptation to shorter growing seasons at higher elevation (Owens & Blake, 1985).

Role of climatic warming

Yellow-cedar has been shown to be particularly prone to temperature-dependent dehardening (Kamm & Kohn, 1980; Hawkins *et al.*, 2001), including the loss of cold tolerance in roots (Puttonen & Arnott, 1994). In a recent study of cold tolerance at our Poison Cove study site, the foliage of yellow-cedar was found to be 5 °C–10 °C more cold hardy than western hemlock in fall and winter, but dehardened rapidly (i.e. 26 °C in 47 days) in spring, 13 °C more than western hemlock, to become more susceptible to freezing injury (Schaberg *et al.*, 2005). We are expanding this initial study to evaluate the influence of soil temperature on dehardening of both foliage and root tissues and explore the link between adequate Ca supply and decreased cold tolerance similar to recent research on red spruce (*Picea rubens* Sarg.) (Schaberg *et al.*, 2000).

The initiation of yellow-cedar decline in about 1900 (Hennon *et al.*, 1990c) approximately coincides with warming in the late 1800s (Heusser, 1952) that marked the end of the Little Ice Age (1400s–1800s, Hebda, 1995). The yellow-cedar trees that have died in declining forests are nearly all older than 100 years, and their ages (Hennon & Shaw, 1994) indicate that they regenerated during the Little Ice Age. Perhaps seasonal snow conditions now present above 150 m, where cedars appear healthy, are similar to those that occurred down to sea level when today's yellow-cedar trees regenerated, but those trees at lower elevations are now vulnerable without snowpack persisting into spring. In British Columbia, where yellow-cedar is known as a higher elevation species, the species periodically colonizes areas that form cold air drainages and maintain late spring snowpack (Lertzman, 1992).

Conclusions and yellow-cedar management

The most promising risk factor related to yellow-cedar mortality is exposure-driven air and soil temperature. This study has allowed us to generate an hypothesis to explain yellow-cedar decline. Soil warming in late winter or early spring is facilitated by canopy openings that allow soils to warm, which could trigger dehardening of yellow-cedar trees and lead to freezing injury. Injury could be to foliage, or to shallow roots concentrated near the soil surface. Mortality occurred initially in exposed trees in open-canopy forests influenced by soil saturation, but subsequently spread as a form of tree mortality-driven exposure into adjacent trees growing on moderately well drained soils. Yellow-cedar decline may have developed because of regional climate warming and decreased winter snowpack at low elevations, along with frequent late winter/early spring temperature fluctuations.

Our working hypothesis is based on associations of temperature variables with tree mortality in two watersheds. Future research needs to expand this work geographically to determine whether these relationships can be confirmed throughout the range of yellow-cedar decline. We recommend studying the interactions among exposure, snowpack, and yellow-cedar phenology in a range of bioclimatic zones and elevations in Southeast Alaska. We have satisfied the present objective of narrowing the areas of future investigations and have elevated a leading hypothesis, but the specific mechanisms of tree injury of yellow-cedar decline have not been determined. We must stress that our hypothesis is based primarily on associations. It is conceivable that temperature is *responding* to the death of overstory yellow-cedar trees, not causing it. Also, warmer temperatures could influence some aspect of the soil environment, besides dehardening and freezing, such as microbial activity, that could damage

yellow-cedar roots. This highlights the need to continue direct study of yellow-cedar phenology and freezing mechanisms. Cold tolerance assessments need to provide better resolution of the timing of freezing susceptibility for different tissues (i.e. roots, stems, foliage) of yellow-cedar. Also, we need to evaluate if ambient weather conditions are sufficient to both precondition trees to predispose them to injury (i.e. initiate dehardening) and to actually cause the damage.

Future management of yellow-cedar forests will rely on information on the cause of yellow-cedar decline and the contributing role of climate, predictions of where decline will and will not occur, and successional trajectories of decline-impacted forests. Also, if this is a climate-controlled phenomenon, then yellow-cedar decline provides a good example of how minor shifts in climatic conditions have drastic implications for a species and its forest community.

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