Climate-induced yellow-cedar decline on the island archipelago of Haida Gwaii

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Abstract. The global rise in temperature and associated changes in climate have led to decline of forests around the globe, across multiple species and ecosystems. Yellow-cedar (Callitropsis nootkatensis) decline is one of the most severe in North America. We found abundant evidence of tree decline and mortality on Haida Gwaii across multiple watersheds and over a range of elevations. This decline on Haida Gwaii parallels the broader yellow-cedar decline in terms of spatial distribution, symptoms, magnitude, and timing. However, Haida Gwaii has a more temperate climate and ephemeral snowpack than declining yellow-cedar forests in Alaska where the link to climate was first uncovered. Given these important differences, we investigated several possible drivers both at the local and at the regional scale, using population demography, dendrochronology, and daily weather data. We explored stand dynamics as a driver and tested the known link to climate. Our results are inconsistent with stand dynamics as a driver of elevated decline and mortality. Neither increased competition nor aging of a cohort explains the decline. Alternatively, the magnitude and timing of the decline are consistent with well-documented long-term directional trends in regional climate. Onset of basal area increment decline and mortality have been accumulating over time, with increased rates since the 1980s. Our sites were located at the edge of the expected range of mortality, and we found only four thaw–freeze events over the past ~80 yrs. However, superposed epoch analysis using daily weather data revealed that mortality and onset of decline events were associated with warmer winter conditions, consistent with the drivers from Alaska. Rather than isolated extreme thaw–freeze events, warmer winter temperatures on Haida Gwaii may mean less cold hardening throughout the winter, which exposes yellow-cedar’s fine roots to varying degrees of freezing damage over multiple winter thaw–freeze cycles, causing physiological stress, tree decline, and eventual death.

Key words: Callitropsis nootkatensis; climate change; dendrochronology; forest decline; Haida Gwaii; tree mortality; yellow-cedar.

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INTRODUCTION

Changes in climate, including warming temperatures and droughts, have led to forest declines around the world (van Mantgem et al. 2009, Angers et al. 2010, 2015, Cohen et al. 2016). One of the most severe examples in North America is yellow-cedar (Callitropsis nootkatensis (D. Don) Oerst. Ex D. P. Little), which has experienced widespread tree mortality and canopy decline in the middle of its latitudinal range for over a century (Hennon et al. 2012). More than 400,000 ha of declining forests have been mapped in southeastern Alaska and the north to mid-coast of
British Columbia (BC) since the late 1980s (Buma et al. 2017), collectively referred to as yellow-cedar decline. Most mortality has occurred in open canopy forests with poorly drained soils on warm (south and southwest) aspects, at low elevations in more northerly latitudes and slightly higher elevations in more southerly latitudes (Hennon and Shaw 1997, Hennon et al. 2006).

The driver of yellow-cedar decline is regional climatic warming, rather than local biotic factors (Hennon et al. 1990a, b). At the tree level, symptoms of yellow-cedar decline appear first in the root systems, followed by crown thinning, bole lesions, and eventual death (Hennon et al. 1990b). Extensive research in Alaska has eliminated root pathogens as the primary cause (Hennon et al. 1990b, Hennon and Shaw 1994). Rather, yellow-cedar’s physiology makes it uniquely susceptible to fine root damage and tree decline, particularly with warmer winter temperatures and reduced snowpacks in recent decades (Hennon et al. 2012). Increasing late-winter temperatures are leading to earlier dehardening of yellow-cedar, which takes place earlier than co-occurring species in response to warming temperature (Schaberg et al. 2011). Snowpack acts as an insulating layer protecting yellow-cedar’s fine roots (Schaberg et al. 2008), which are abundant in the shallow horizons of wet soils (D’Amore et al. 2009, Schaberg et al. 2011). Reduced snowpacks make the shallow roots of yellow-cedar more vulnerable to periodic severe late-winter and early-spring freeze events that cause fine root injury, which subsequently results in moisture stress, crown symptoms, and eventual tree death (Hennon et al. 2006, 2010). Consistent with this mechanism, Beier et al. (2008) found that in southeastern Alaska, nine of the top ten years with most extreme thaw–freeze impact of the second half of the 20th century occurred since 1983 and that the most extreme example of a thaw–freeze event coupled with low snow cover occurred in 1987. Though Beier and colleagues did not look at dead trees, all surviving trees contained a marker year of exceptionally low growth in 1987, and chronologies from declining sites increased after this year, possibly due to competitive release of surviving trees.

Mortality in recent decades may reflect background decadal-to-multi-decadal climate variation, acting synergistically with regional warming. An important influence on the climate of coastal Alaska and BC is the Pacific Decadal Oscillation (PDO), an ocean–atmospheric climate regime that may be exacerbating yellow-cedar decline in its positive (warm) phase. Pulses of tree mortality in the 1970s and 1980s (Hennon and Shaw 1994) correspond to the 1977 shift in the PDO from negative to positive phase (Mantua and Hare 2002). Similarly, on Haida Gwaii there was a divergence in growth response to climate after the 1977 shift; where healthy yellow-cedars experienced increasing growth in response to warmer growing season temperatures, while trees experiencing decline or that had died did not (Comeau et al. 2019). In addition, all yellow-cedars became negatively associated with January temperature and positively associated with winter precipitation, consistent with the thaw–freeze hypothesis (Comeau et al. 2019). During the positive phase, regional climate is warmer, and the snow–rain threshold is elevated so that lower-elevation forests have shallower and less persistent snowpacks making yellow-cedars more vulnerable to thaw–freeze events. Mortality following this climatic shift is consistent with the hypothesis that warming climate is a primary driver of yellow-cedar decline.

The elevated levels of yellow-cedar decline and mortality observed in the last decade on the Haida Gwaii archipelago along the north coast of BC are of great concern (CHN and BC 2011). Although yellow-cedar mortality exhibits similar spatial patterns compared with the adjacent mainland of BC and Alaska, the proposed mechanisms of climate-driven decline may not adequately explain the decline on Haida Gwaii. The wet–hypermaritime climate of Haida Gwaii is heavily regulated by the Pacific Ocean, with cool moist summers and wet winters with little snowfall (Banner et al. 2014). Much of Haida Gwaii exists within the snow–rain threshold, where winter temperatures typically range between −2°C and 2°C (Buma et al. 2017), which is not cold enough to freeze yellow-cedar’s fine roots that are cold hardy to −5°C (Schaberg et al. 2008, 2011). Snowpack along the coast is usually ephemeral, with more snow falling at higher elevations (Banner et al. 2014). However, yellow-cedar decline has rapidly affected 29,688 ha of forest on Haida Gwaii (tallied from 2006 to 2017, personal communication Stefan Zeglen), from
the mountains of Graham and Moresby Islands, down to sea level in the north.

This research addresses the fundamental question: What is causing yellow-cedar decline on Haida Gwaii? Before addressing the primary hypothesis that climate is driving yellow-cedar decline, we tested the alternative that stand dynamics are responsible for the observed increase in declining and dead yellow-cedars. High rates of competition and self-thinning associated with stand development disproportionately affect young or small-statured trees. Alternatively, senescence of a cohort of trees can lead to increased mortality of old and large trees (Franklin et al. 2002). Therefore, at sites exhibiting crown symptoms and tree death, we quantified the magnitude of decline and compared the relative abundance, age, and size of healthy, declining, and dead yellow-cedars to assess the potential effects of stand dynamics.

We tested the primary hypothesis that climatic change is responsible for the yellow-cedar decline on Haida Gwaii due to low snowpack that makes yellow-cedars vulnerable to thaw–freeze weather events. To differentiate potential climatic influences at a range of temporal scales, we used dendrochronology to uncover the timing of mortality and the onset of tree decline in basal area increment of individual trees. Increased rates of mortality and onset of tree decline in recent decades would parallel the most intense climate warming (IPCC 2014), with important impacts on regional temperatures and snowpack. We used daily weather data to test for the frequency of thaw–freeze events over the 20th century, which have the potential to damage the fine roots of yellow-cedar and lead to decline and death. Finally, we analyzed the winter weather conditions in years prior to onset of decline and mortality to test for a link between winter climate and yellow-cedar decline on Haida Gwaii.

METHODS

Study area

This research was conducted on Graham Island, Haida Gwaii, which is the largest of over 150 islands that make up the archipelago off the north coast of British Columbia. The climate is wet–hypermaritime, with cool moist summers and wet winters, with little snowfall. The mean annual temperature is 8.0°C ± 1.1°C (± standard deviation) at Langara on Haida Gwaii (54°15' N 133°03' W, 42.7 m above sea level), with narrow daily, seasonal, and annual ranges (Environment Canada Weather Archives 2020). On Haida Gwaii, yellow-cedar is commonly found in wetter boggy sites, with a more open canopy, but can also be found at lower densities on more well-drained sites. Yellow-cedar regenerates and competes well in deep, slightly acidic, moist soils (Parish and Thomson 1994) and is commonly associated with western redcedar (*Thuja plicata* Donn ex D. Don.), Sitka spruce (*Picea sitchensis* (Bong.) Carr.), western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), or mountain hemlock (*Tsuga mertensiana* (Bong.) Carr.) at higher elevations.

Site selection

To address questions about the drivers of yellow-cedar decline, we used a purposive approach to select sample sites with declining and dead yellow-cedar. Potential study sites were identified using the most recent aerial overview survey and aerial photographs taken in 2015, combined with knowledge gained from local experts. From aerial observation and ground truthing, we confirmed that numerous patches of forest exhibited symptoms of yellow-cedar decline and eliminated sites dominated by dead western redcedar and western hemlock. Limited road access prevented some sites from being accessed for reasons of safety and efficiency. We identified and sampled 13 suitable sites in the southern portion of Graham Island and two additional sites near the north coast of the Graham Island (Fig. 1). These sites were distributed across multiple watersheds and over a range of elevations and aspects where decline has been documented (Table 1). Each site was located adjacent to a water feature such as a stream or wetland. The sampled forests contained declining yellow-cedar as a codominant species, mixed with Sitka spruce, western hemlock, and western redcedar. None of the sites exhibited evidence that wind, fire, insects, or pathogens were driving mortality at the stand level.

Data collection

To assess population dynamics and drivers of decline, we conducted a census of yellow-cedars in two contiguous 50 × 20 m transects per site.
oriented along contour lines to ensure the sampled areas were as homogeneous as possible with respect to the biophysical traits and evidence of yellow-cedar decline.

To represent yellow-cedar population structure, we conducted a census of trees with diameter at breast height (dbh) ≥10 cm within each transect and estimated tree density in each of three health status classes. Standing trees were classified as healthy if they had full, green crowns, declining if they had discolored foliage or were partly defoliated, or dead if they lacked
We took increment cores from 25 to 30 trees at each site to enable tree-ring analyses to detect internal evidence and to quantify the timing, duration, and severity of basal area increment decline. We cored the first 15 healthy yellow-cedars (except two sites where only 10 and 14 healthy trees were available to sample) and the first 15 declining or dead yellow-cedars along the transects at each site. One core, sampled ~115 cm above the ground, was taken from each tree, and diameter at core height was measured. We aimed to intercept the pith, and, where possible, we included the bark or outer cambium. Trees with decayed outer rings or heartwood that obscured rings were replaced with the next tree along the transect in the same health status class. For transects with fewer than 15 healthy or 15 declining and dead yellow-cedars that were suitable to core, additional trees were sampled and cored from outside of the transect. These supplemental trees were not included in density calculations or other representations of population structure.

Table 1. Physical attributes of 15 study sites located in declining yellow-cedar stands on Haida Gwaii, British Columbia, Canada.

| Site ID | Location (decimal degrees) | Elevation (masl) | Slope† | Angle (°) | Aspect |
|---------|-----------------------------|-----------------|--------|-----------|--------|
| 1       | 54.02N 131.97W              | 45              | N/A†   | N/A†      |        |
| 2       | 54.00N 132.08W              | 87              | N/A†   | N/A†      |        |
| 3       | 53.64N 132.72W              | 243             | 11     | NE        |        |
| 4       | 53.60N 132.61W              | 278             | 12     | NE        |        |
| 5       | 53.58N 132.55W              | 370             | 6      | NW        |        |
| 6       | 53.54N 132.59W              | 356             | 19     | NE        |        |
| 7       | 53.54N 132.57W              | 253             | 23     | NE        |        |
| 8       | 53.53N 132.26W              | 321             | 8      | N         |        |
| 9       | 53.40N 132.37W              | 365             | 15     | NW        |        |
| 10      | 53.37N 132.34W              | 198             | 10     | NW        |        |
| 11      | 53.37N 132.35W              | 311             | 12     | E         |        |
| 12      | 53.35N 132.34W              | 207             | 14     | N         |        |
| 13      | 53.34N 132.36W              | 310             | 11     | E         |        |
| 14      | 53.31N 132.22W              | 437             | 9      | NE        |        |
| 15      | 53.28N 132.09W              | 410             | 13     | S         |        |

Note: Study sites are numbered by location from north to south. † No slope data for two sites in the north.

Dendrochronological methods

The cores were air-dried, glued onto wooden supports, sanded with progressively finer sand paper to 600 grit, and scanned at a resolution of 2400 or 3200 dpi. Ring widths were measured (to 0.001 mm) using the program CooRecorder (version 7.8, Larsson 2014a), and narrow rings were cross-checked under a microscope. We confirmed crossdating by assembling ring-width chronologies for each site using the programs CDendro (version 7.8, Larsson 2014b) and COFECHA (Holmes 1983). Crossdating improved the quality of age estimates by accounting for missing or false rings. For cores that were close to but did not intercept the pith, the number of missed rings was estimated based on the dimensions of the rings closest to the pith (Duncan 1989). Samples were excluded from the age analyses if the number of missed rings exceeded one third of the total number of rings, if the heartwood decay was abundant, or if the radius of a tree exceeded the length of the increment borer.

Crossdating allowed us to assign a calendar year to the outermost ring, indicating the year of death of snags and cessation of radial growth of some living trees. We took a conservative approach and assessed the quality of each outer-ring date, as follows. Dates assigned to trees with clearly distinguishable outer rings that were crossdated with their site chronology were considered accurate. Dates assigned to crossdated outer rings that were extremely narrow or showed evidence of decay were considered best estimates. We eliminated trees for which the outer rings were poorly correlated with the site chronology.

For analyses of growth trends over time, we calculated basal area increments from ring widths. This approach removes the age- and size-related trends in ring widths that result from adding the same amount of wood to an increasing diameter, while maintaining year-to-year and longer-term variation. Basal area increments were calculated from the pith to the bark by subtracting the cross-sectional area in year $t$–1 from that in year $t$ (LeBlanc 1990, Phipps 2005). For cores that did not include the pith, the distance to the pith was calculated from geometric measures of arced rings (Duncan 1989) or the length of the core was subtracted from half of the diameter at coring height (minus average bark
Comparisons among healthy, declining, and dead trees

We undertook three tests to determine whether tree decline and death could be attributed to stand development. First, to test for significant differences among the healthy, declining, and dead populations of trees, we compared the frequency distributions of age, dbh, and basal area using the two-sample Kolmogorov-Smirnov tests (KS test) for all pairwise combinations (Kolmogorov 1933, Smirnov 1939). Second, we used analysis of variance (ANOVA) to determine whether the mean diameters of declining or dead trees were significantly different from healthy trees. Third, the observed number of healthy, declining, and dead trees in the overstory versus understory was compared with predicted values derived assuming equal proportions in all classes using contingency tables and the chi-squared goodness-of-fit statistic. For these three tests, evidence that tree decline and death affected small or young trees in the understory more acutely than large or old trees in the overstory would indicate competitive exclusion of small-statured trees. Alternatively, disproportionate effects on old trees would indicate senescence.

We tested for internal symptoms of yellow-cedar decline in two ways. First, by assessing the outer-ring date of each tree, we identified living trees, including trees classified in the field as healthy or declining, that were no longer forming annual rings. Second, to determine the timing of the onset of basal area increment decline in individual trees, we identified breakpoints in the basal area increment series of individual trees that differentiated periods of increasing and decreasing growth during the 20th century. Breakpoints were identified using the segmented (Muggeo 2008) package in R (R Core Team 2020), which fits a piecewise regression model to each basal area increment series using an iterative approach (Muggeo 2008, R Core Team 2020). We tested for breakpoints from 1901 to 2015; however, some trees established after 1901 or stopped ring formation before 2015. Therefore, we tested for (a) three breakpoints in samples that included ≥80 yrs between 1901 and 2015, (b) two breakpoints in samples with 40–79 yrs, and (c) one breakpoint in samples with ≤39 yrs. The pattern of growth during each segment was characterized as decreasing or increasing based on the slope of the line, and the start and end dates of each segment indicated the duration in years that the growth pattern persisted. The last pattern of growth ended when rings stopped forming or at the year of sampling.

Mortality rates can be estimated from outer rings, with the assumption that there is an equal chance of sampling a tree and accurately dating its rings, whether that tree died recently or in the distant past. In reality, mortality records are incomplete and less reliable through time due to loss of small trees and progressively older snags as outer rings decay or the snags fall (Cline et al. 1980, Angers et al. 2010), a phenomenon that is compensated for by the low decay rate and persistence of yellow-cedar snags (Stan et al. 2011). Annual mortality rates were calculated as the number of trees that died in each calendar year (based on outer-ring dates) divided by the sample depth or the number of living trees that could have died each year within the 15 transects. Decadal mortality rates were calculated by averaging the annual mortality rates in each decade.

Weather data

Weather data were acquired for the Langara station (54.255° N, 133.058° W, 43 masl; Environment Canada Weather Archives 2020), the longest, most complete daily weather record on Haida Gwaii that begins in 1936. The elevation of the Langara station is similar to our lowest elevation study sites (45 masl). To represent the full range of elevations of our study sites, we extrapolated the Langara temperature record to 437 masl using a standard environmental lapse rate of 0.65°C 100 m⁻¹. We calculated the mean temperature of the coldest month, and mean winter temperature, defined as the mean temperature of the three coldest months, December to February, at 43 and 437 masl.
Thaw and freeze variables were calculated from the two daily temperature records (43 and 437 masl) following methods developed by Beier et al. (2008). Mean daily temperature (MDT) was used to estimate the number of growing days (MDT \( \geq 5^\circ C \)) and freezing days (MDT \( \leq 0^\circ C \)) for each year (1937–2015) from 1 February to the last day of freezing. 1 February was chosen as a start date following Beier et al. (2008), as research suggests that this is the earliest that yellow-cedar begins dehardening (Schaberg et al. 2005, 2008) and severe foliar injury to yellow-cedar saplings commonly occurs from March to April. We used the minimum criteria of \( \geq 3 \) growing days followed by \( \geq 1 \) freezing day (Beier et al. 2008), allowing a gap of one day of neutral temperature (0\(^\circ\)–5\(^\circ\)C) in between the growing and freezing days (Buma 2018).

To estimate the thawing intensity each year, we calculated growing degree-days (GDD) as cumulative growing degree-days (GDD) and cumulative cooling degree-days (CDD) as cumulative cooling degree-days (CDD), respectively, and both variables were calculated for the weather data at 43 and 437 masl. Using the sea function of the dplR package (Bunn 2008, Bunn et al. 2020) in R (R Core Team 2020), we tested whether onset of decline or mortality events were associated with anomalous thawing or freezing intensities during event years or up to three years prior to events. Analyzing three years prior to events tested for potential lagged effects between weather anomalies and measurable impacts on tree growth and death.

**RESULTS**

**Death and decline across all size and age classes**

A total of 1016 yellow-cedars were sampled, 26% of which were healthy, while 27% were declining and 47% were dead. At the site level, the density of yellow-cedar ranged from 125 to 740 trees/ha and the proportion of declining and dead trees ranged from 59% to 86%, with healthy trees making up only 14% to 41% (Table 2). Death and decline affected trees of all sizes (dbh 10–140 cm, \( n = 1016 \)) and ages (29–1004 yr, \( n = 377 \)), but there were also healthy live trees across the range of sizes and ages (Fig. 2). The distributions of dbh, basal area, and age did not differ significantly among the three health status categories (Figs 2a–c, \( P > 0.05 \) for all pairwise KS tests). However, the mean dbh of declining trees (29.4 ± 8.1 cm; mean ± standard deviation) was significantly smaller than healthy (33.1 ± 10.1 cm) and dead (32.8 ± 8.7 cm) trees (ANOVA, \( F = 4.00, P = 0.020 \)), while the dbh of healthy and dead trees did not differ significantly. The height class was determined for 1011 living and dead trees (five snags were severely decayed). Density of yellow-cedar was similar in the overstory (179 ± 72 trees/ha) and understory (158 ± 134 trees/ha). However, dead trees were more abundant in the overstory, while healthy and declining trees were more abundant in the understory than expected by chance (chi-squared = 20.27, \( P < 0.001 \); Fig. 2d).

**Differences in tree-ring versus canopy evidence of decline**

We determined the outer-ring date on 306 of 325 living (healthy or declining) trees; 19 trees were excluded due to suppressed outer rings or...
poor crossdating. Many living trees had not produced a ring (at the location the core was taken) for up to 99 yrs (Fig. 3). Twenty of the 213 (9.4%) live trees with crowns that appeared healthy and 52 of the 93 (55.9%) of trees with declining crowns had not produced a ring at the year of sampling. Of the 72 living trees no longer producing rings, the last ring formed between 2000 and 2014 for 48 trees and between 1916 and 1999 for 24 trees.

Changes in growth during the latter 20th century

One to three breakpoints were detected in the growth of 403 trees that were alive during the 20th century. The majority of trees (n = 232, 57.6%) switched to a decreasing pattern of growth during the second half of the 20th century (Fig. 4). These switches were common in the 1940s, 1960s, and 1980s, then relatively continuous after the 1990s. Of all trees that switched to decreasing growth, 50% entered this pattern after 1980. Fewer trees (n = 171, 42.4%) exhibited an increasing final pattern of growth. Both the direction (chi-squared = 9.75, P = 0.008) and duration (chi-squared = 14.98, P = 0.020) of the final pattern of growth differed significantly among health status classes. More declining trees had decreasing growth, and more healthy trees had increasing growth than expected by chance. For persistent growth patterns (duration ≥ 15 yr), more healthy trees increased in growth and more declining trees decreased in growth than expected by chance. The numbers of dead trees with increasing or decreasing growth prior to death, regardless of duration, were similar to those expected by chance.

Mortality rates increased in the 1980s

We accurately determined the outer-ring date of 70 snags, and best estimates were made for another 49 snags, yielding years of death between 1724 and 2015. Calculated annual and decadal mortality rates increased starting in the mid-1900s, with an abrupt increase after 1980. The background decadal mortality rate from 1860 to 1940 based on all outer-ring dates was 0.07% (range = 0.03–0.13%), increased to 0.24% from 1950 to 1980, and to 0.60% from 1990 to 2010. Decadal mortality peaked at 0.80% in the 2000s.

Sites relative to the range of transitional mortality

The mean temperature of the coldest month was 3.2°C (range −3.3°C to 7.2°C) at 43 masl and 0.7°C (range −5.8°C to 4.7°C) at 437 masl. Thus, our study sites on Haida Gwaii are generally warmer than the range of transitional mortality for yellow-cedar, defined as locations where mean temperature of the coldest month varies from −5°C to 0°C (Buma 2018). The mean winter temperature (three coldest months) was 3.6°C (range −0.3°C to 6.4°C) at 43 masl and 1.0°C (range −2.8°C to 3.8°C) at 437 masl. The highest elevation study sites fall
within the expected range of yellow-cedar mortality, defined as mean winter temperature between −2 and 2°C (Buma et al. 2017), while the lower study sites were generally warmer. From 1937 to 2015, 57 yrs included freezing days (mean temp ≤0°C) after 1 February, while 22 yrs had no freezing days at 43 masl. Over the same period, 76 yrs had freezing days after 1 February, while 3 yrs did not, at 437 masl. As expected, mean GDD was considerably higher at 43 masl (284.4°C) than at 437 masl (9.2°C), and mean CDD was considerably lower at 437 masl (−26.6°C) than at 43 masl (−8.1°C; Table 3).

Over time, the trend toward greater cumulative CDD and therefore less freezing was more pronounced at 437 masl than at 43 masl. Cumulative GDD from 1 February until last day of freezing varied greatly from year to year across elevations, with no strong trend over time. From 1 February to 30 April, growing days became warmer and more frequent, but as the period when freezing occurred ended earlier, the overall cumulative GDD remained similar.

We detected only four thaw–freeze events at 43 masl (1937–2015) and none at 437 masl. Thaw–freeze events occurred at 43 masl in 1940 (6 growing days: 1 gap day: 6 freezing days), 1966 (14:1:1), 1991 (6:0:3), and 2014 (3:1:4). None of these event years overlapped with those identified in Alaska (Beier et al. 2008).

**Mortality and onset of decline**

There were 20 mortality events between 1937 and 2000 and 29 onset of decline events between 1937 and 1998 (Fig. 4). There were fewer mortality events in the 1940s and 1950s, and a greater
number of mortality events from the 1960s on. There was fewer onset of decline events in the 1950s and 1970s, with the greatest numbers of events in the 1940s, 1960s, and 1980s. Six of the top thaw–freeze events from Alaska (Beier et al. 2008) coincided with mortality events (1956, 1970, 1986, 1987, and 1995). Four of the top thaw–freeze events from Alaska coincided with onset of decline events (1941, 1983, 1992, and 1993).

SEA revealed that mortality and onset of decline events were associated with increased thawing. While mortality events followed years with more freezing, the onset of decline events followed years with less freezing. The 20 yrs with high mortality tended to occur one year after winters with significantly warmer-than-average GDD at 437 masl and significantly colder-than-average CDD at 43 masl (Fig. 5). Additionally, the 29 yrs with high rates of onset of decline tended to occur after three years of significantly warmer GDD and one year of significantly colder CDD at 437 masl (Fig. 6). Trends at 43 masl were similar, but not significant.

**DISCUSSION**

**Yellow-cedar decline on Haida Gwaii**

Yellow-cedars are declining in ~400,000 ha of forests along the coast of Alaska and BC (Buma et al. 2017), including the recent symptomatic forests of Haida Gwaii. Yellow-cedar decline was not expected on Haida Gwaii given its temperate climate and lack of persistent snowpack, which is inconsistent with the hypothesized winter climate drivers on the mainland coast of Alaska and BC (Hennon et al. 2005, 2012). However, the decline on Haida Gwaii near wetlands and in riparian forests parallels that seen on the mainland in terms of tree- and stand-level symptoms, magnitude, and timing. Observed symptoms of decline are similar, including discoloration of needles, crown thinning, and partial cambial mortality, followed by eventual death (Hennon et al. 1990b, Stan et al. 2011). Comparable to Alaska, declining stands contain dead, dying, and live, healthy yellow-cedars (Hennon et al. 1990a, Hennon and Shaw 1997). The severity of decline on Haida Gwaii mirrors declining forests in Alaska, which have experienced up to 70% mortality in some locations (Hennon et al. 1990a, D’Amore and Hennon 2006). Our results indicate evidence of severe decline across multiple geographically diverse watersheds, including crown symptoms or death in 74% of trees, and decreasing basal area increment in an additional 53% of trees with asymptomatic crowns.

*Stand dynamics do not explain yellow-cedar decline on Haida Gwaii*

We explored several lines of evidence to investigate the possible drivers of yellow-cedar decline on Haida Gwaii, both at the local and regional scale. Considering the effects of stand dynamics is critical to understand whether elevated levels of mortality can be attributed to stand development processes (e.g., van Mantgem et al. 2009, Amoroso et al. 2015). High levels of mortality among young and small-statured trees are often attributed to crowding at high tree densities, inter-tree competition, and self-thinning (Franklin et al. 1987, 2002). However, we found no support for greater proportions of decline and death among young, small, understory trees. The distributions of tree age and size did not differ significantly among healthy, declining, and dead trees. Though not significant, trees <200 yr old tended to be healthy, and living trees were more abundant than expected in the understory, although some had declining crowns. These patterns are opposite to the distributions expected if
competition and self-thinning were driving the decline and death of yellow-cedars.

Also associated with stand dynamics, elevated mortality rates can be attributed to the aging of a cohort of trees (Franklin et al. 1987, 2002). The relative abundance of dead trees in the overstory is consistent with senescence of large, and presumably old, trees. However, trees crossed a range of age classes at all sites and we found no evidence that the yellow-cedars formed even-aged cohorts that were senescing simultaneously. Years of death derived from tree rings indicated that recent high rates of mortality were not limited to the old or large overstory trees. Additionally, yellow-cedar is slow to decay and dead trees can remain standing for over 200 yrs (Kellner

Fig. 4. Frequency of yellow-cedar mortality from 1860 to 2015 ($n = 70$, top) and onset of decline from 1900 to 2013 ($n = 228$, bottom). Bars indicate annual values; lines connect the midpoint values of 31-yr moving averages.
et al. 2000, Stan et al. 2011); therefore, the over-
story included persistent snags that had accumu-
lated over many decades.

Overall, our population structure analyses showed decline and mortality were not signifi-
cantly greater among young or small trees than old or large trees. Combined, the evidence is inconsistent with stand dynamics as a driver of elevated decline and mortality of yellow-cedar. However, this pattern does mirror the increased tree mortality across the western USA and Canada that spanned age, size, and species and had no clear relation to stand dynamics, for which changes in climate were considered the most likely driver (van Mantgem et al. 2009).

**Tree-rings provide novel insights on yellow-cedar decline**

This research uses tree-ring analyses to com-
plement crown health to evaluate the decline of yellow-cedar. A switch toward decreasing growth rates from which a tree does not recover is a commonly used internal indicator of tree decline (Cherubini et al. 2002, Bigler et al. 2004, Amoroso et al. 2012, Rodriguez-Catón et al. 2016, Cailleret et al. 2017). We identified the year of onset of tree decline based on sustained decreases in the basal area increment and found that health status assigned in the field based on external crown symptoms contrasted with the internal radial growth symptoms for many yellow-cedars. Specifically, 111 trees with asymptomatic crowns had decreasing growth patterns, including 68 trees with decreasing growth that persisted ≥15 yrs. Another 20 trees with asymptomatic crowns had stopped pro-
ducing rings. These discrepancies represent early signs of decline in radial growth before crown symptoms develop or mortality occurs (Cailleret et al. 2017). Reduction in radial growth before mortality is nearly universal in trees and is especially common in gymnosperms (Cailleret et al. 2017). Partial cambial mortality leading to cessation of ring formation has been found in yellow-cedar as the tree dies (Hennon et al. 1990b, Stan et al. 2011) and species in the Cupressaceae family, such as *Thuja plicata* (Daniels et al. 1997) and *Austrocedrus chilensis* (Amoroso and Daniels 2010). Scaling up from individual trees to stands, the pattern of decreasing radial growth has been observed in declining *A. chilensis* forests (Amoroso et al. 2012) and in *Abies alba* and *Pinus sylves-
tris* forests in Spain (Camarero et al. 2015).

The onset of tree decline and rates of mortality have amplified in recent decades, from the 1980s on. Yellow-cedar basal area increment patterns switched throughout the 20th century; however, growth of most of our study trees began to decrease in recent decades, from the 1980s on. This timing parallels observed yellow-cedar decline in Alaska, which spanned the 20th cen-
tury with peaks in tree decline and mortality in the 1970s and 1980s (Hennon and Shaw 1994).

Table 3. Thaw and freeze variables derived from daily temperature records from 1937 to 2015.

| Temperature variables | Mean (range) at 43 masl | Mean (range) at 437 masl |
|-----------------------|------------------------|-------------------------|
| MDT Dec-Feb (°C)      | 3.6 (–0.3 to 6.4)      | 1.0 (–2.8 to 3.8)       |
| MDT Feb–April (°C)    | 4.7 (2.5 to 6.7)       | 2.1 (–0.1 to 4.1)       |
| Mean GDD (°C)         | 5.9 (5.0 to 6.9)       | 5.8 (5.0 to 6.9)        |
| Number of GDD (n)     | 5 (0 to 26)            | 1 (0 to 8)              |
| Cumulative GDD (°C)   | 29.0 (0.0 to 151.4)    | 6.2 (0.0 to 52.0)       |
| Mean CDD (°C)         | –1.9 (–6.3 to 0.0)     | –1.7 (–4.7 to –0.3)     |
| Number of CDD (n)     | 4 (0 to 15)            | 14 (0 to 45)            |
| Cumulative CDD (°C)   | –8.1 (–45.4 to 0.0)    | –26.6 (–88.4 to 0.0)    |

Notes: The Langara temperature record (43 masl) was rescaled to 437 masl, representing the lowest and highest elevation study sites on Haida Gwaii. Abbreviations represent mean daily temperature (MDT), growing degree-days ≥ 5°C (GDD), and cooling degree-days ≤ 0°C (CDD).
Fig. 5. Association of 20 yellow-cedar mortality events with thawing and freezing at 43 and 437 masl from 1937 to 2000. Occurrence of mortality events (vertical lines) relative to cumulative growing degree-days (GDD $\geq 5^\circ C$, red) and cooling degree-days (CDD $\leq 0^\circ C$, blue) from 1 February to the last day of freezing (top). Superposed epoch analyses (SEA, bottom panels) show associations with GDD (left) and CDD (right) at high (top) and low (bottom) elevations for event years (lag = 0) and up to three preceding years (lag = −1 to −3). Black bars indicate significant temperature departures during event years relative to non-event years ($\alpha = 0.5$).
Fig. 6. Association of 29 onset of yellow-cedar decline events with thawing and freezing at 43 and 437 masl from 1937 to 1998. Occurrence of onset of decline events (vertical lines) relative to cumulative growing degree-days (GDD ≥ 5°C, red) and cooling degree-days (CDD ≤ 0°C, blue) from 1 February to the last day of freezing (top). Superposed epoch analyses (SEA, bottom panels) show associations with GDD (left) and CDD (right) at high (top) and low (bottom) elevations for event years (lag = 0) and up to three preceding years (lag = −1 to −3). Black bars indicate significant temperature departures during event years relative to non-event years (α = 0.5).
Determining years of tree death and estimating absolute rates of mortality have greater degrees of uncertainty than detecting onset of decline. We have the greatest confidence in calculated mortality rates in recent decades, although the outer-ring dates obtained from decay-resistant trees with persistent snags provide long records of mortality going back through time (Hennon et al. 1990c, Daniels et al. 1997, Stan et al. 2011). On Haida Gwaii, the yellow-cedar snags that we crossdated with the greatest confidence had outer rings indicating years of death from 1860 to 2015. There is greater uncertainty in mortality rates moving back through time due to decay of outer rings and loss of small trees (Cline et al. 1980, Angers et al. 2010). This form of bias influenced our calculations of background mortality rates prior to 1950. For example, by including only trees for which an outer-ring date could accurately be determined, the average decadal mortality rate was 0.03% for 1860–1950. When we included the 27 snags for which best estimates of the outer-ring dates were determined, the average decadal mortality rate during the same period was 0.07%, which is comparable to the background rate of 0.08% estimated in healthy yellow-cedar forests in Alaska (Hennon and Shaw 1994). The discrepancy in our calculated mortality rates indicates the sample size of snags with outer-ring dates deemed accurate did not adequately represent the population background rate of mortality prior to 1950, despite the long-term persistence of yellow-cedar snags. Although the decadal rate of 0.07% was more realistic, it may still under-represent the actual background mortality rate. We recommend larger sample sizes that include downed logs, as well as snags, would improve accuracy of past mortality rates. Regardless of absolute mortality rates, the abrupt changes in relative mortality rates after 1980 are corroborated by multiple lines of evidence that provide strong evidence of amplified yellow-cedar decline.

**Climatic drivers of yellow-cedar decline**

With the similarities in the spatiotemporal patterns of yellow-cedar decline on Haida Gwaii and the broader decline on the mainland, the drivers may be the same as well. The proposed mechanism on the mainland is climate warming, resulting in late-winter or spring thaw–freeze events under low snowpack conditions, which can damage the shallow fine roots of yellow-cedar, leading to crown dieback and eventual death (Hennon et al. 2006, 2012). In the forests of Graham Island, Haida Gwaii, the range of mean winter temperatures at high elevations spans the rain to snow threshold (−2°C to +2°C), where mortality is expected (Buma et al. 2017), while the winter temperatures near sea level are warmer than expected for areas of yellow-cedar decline. Although our study sites are on the warmer end of expected yellow-cedar mortality, we found patches of yellow-cedar decline across multiple watersheds and the onset of radial growth decline reached back decades.

We hypothesized that discreet episodes of mortality and onset of decline would indicate periodic thaw–freeze events were driving decline. As an example of mortality in response to acute events, Amoroso et al. (2015) found peak years in *A. chilensis* mortality were associated with late spring and summer drought. However, both mortality and onset of decline of yellow-cedar at sites on Haida Gwaii appeared temporally dispersed, accumulated over time, and formed pulses with elevated rates. Peaks in onset of decline in the 1940s, 1960s, and 1990s coincided with increased growing degree-days prior to the last day of freezing. The pattern with mortality is less clear, as effects are potentially lagged.

In southeastern Alaska, where decline is more pronounced, the frequency and severity of thaw–freeze events have increased, explaining the high rates of decline since the 1980s (Beier et al. 2008). We detected fewer thaw–freeze events on Haida Gwaii, making our results more comparable to those obtained across the range of yellow-cedar (Buma 2018). No thaw–freeze events were identified further south in the range of yellow-cedar where there is no external evidence of decline, such as Vancouver Island, BC, and one to six thaw–freeze events were identified in areas with moderate to severe decline (e.g., Prince Rupert, BC; and Sitka, AK, respectively; Buma 2018). The results from Haida Gwaii are within this range of thaw–freeze events, with no events found at lower elevation and four events at higher elevation.

Rather than warm temperatures reducing snowpack to make trees more vulnerable to
discrete freezing events, we hypothesize that warm temperature effects are more direct on Haida Gwaii. We detected many more peaks in mortality and onset of decline than thaw-freeze events. Given the relatively warm temperatures and ephemeral snowpacks on Haida Gwaii, especially at low elevation, the roots of yellow-cedar may be perpetually exposed to freezing damage. Both onset of decline and mortality events lagged years with above-average growing degree-days, corresponding to warmer temperatures or numerous warm growing days during winter. While onset of decline corresponded to above-average cold degree-days (i.e., warmer temperatures or fewer freezing days), trees died following years with below-average cold degree-days corresponding to exceptionally low temperatures or prolonged freezing. Thus, warmer winter conditions make yellow-cedar vulnerable to decline, in addition to predisposing trees to the freezing conditions that drive mortality. In the absence of moderation by snowpack, warm temperatures may induce dehardening regularly. Alternatively, temperatures may not be low enough for cold hardening of roots and they remain active and vulnerable to freezing all winter. Under these conditions, root damage may result from below-freezing temperatures, even if cold weather is not extreme or prolonged (e.g., does not meet the criteria of a thaw-freeze event). The magnitude of cold weather effects may also vary, with rare extreme effects causing acute damage, and more frequent lower-severity impacts explaining the long-term accumulation of basal area increment decline and mortality that we observed.

Understanding the temporal patterns in decline and mortality provides constructive feedback on the metrics used to detect critical weather thresholds and events. The low number of thaw-freeze events identified in areas where long-term yellow-cedar decline is ongoing indicates that the current metric needs to be refined to identify all events. Alternately, cumulative winter weather conditions, indicated by metrics such as growing and cold degree-days, may prove more insightful than defining discrete events. Resolving these alternative mechanisms is challenging since most instrumental weather records are located in valley bottoms or near sea level, while declining yellow-cedar forests are at higher elevations in complex mountainous terrain. With instrumental records far from research sites, and without a strong weather station network or in situ measurements, we are limited in our ability to directly detect thaw-freeze events or other weather conditions that drive tree decline and death. Temperature and snowpack monitoring at sites with ongoing yellow-cedar decline, contrasted with healthy forests and sites predicted to be vulnerable to decline, would shed light on the microclimatic conditions hypothesized to drive the onset of decline and eventual mortality.

Demographic studies suggest that mainland yellow-cedar populations prone to decline established during the Little Ice Age (Hennon et al. 1990c, Beier et al. 2008), a relatively cool period from c.1400 until c.1880 (Mann et al. 1999, Mann 2002), when most glaciers in the region reached their maximum advance. The onset of yellow-cedar decline coincided with the end of the Little Ice Age (Hennon et al. 1990c), with tree mortality continuing through the 1900s, with peaks in the 1970s and 1980s (Hennon and Shaw 1994, Stan et al. 2011). On Haida Gwaii, most yellow-cedars at our sites (88%) established prior to 1880 and the oldest trees predated the Little Ice Age. Decline of trees of all ages has been accumulating throughout the 20th century, during which global temperatureswarmed by 0.85°C over the period 1880–2012 (IPCC 2014). The most dramatic increases in yellow-cedar decline and mortality between 1980 and 2015 correspond to the period of the greatest warming, with the period 1983–2012 likely being the warmest 30-yr period of the last 1400 yr in the Northern Hemisphere (IPCC 2014). This period also corresponds to a switch in the Pacific Decadal Oscillation (PDO) to warmer and wetter conditions with lower snowpacks, which occurred in 1976/1977 (Mantua and Hare 2002). There is evidence on Haida Gwaii of shifts in the climate growth response of yellow-cedar around switches in the PDO, including a negative response to warmer winter temperature and low winter precipitation during the warm period following 1977, consistent with the thaw-freeze hypothesis (Comeau et al. 2019). In addition, evidence that increased mortality and onset of decline follow years with warmer winter conditions suggests that a warming climate has driven yellow-cedar decline on Haida Gwaii.
The global rise in temperature has been hypothesized as a driver affecting forests across a wide variety of species, forest types, and moisture regimes (van Mantgem et al. 2009, Allen et al. 2010, 2015, Cohen et al. 2016), including examples from British Columbia (Daniels et al. 2011). The timing of yellow-cedar decline on Haida Gwaii, mainland BC, and Alaska parallels widespread increases in tree mortality and forest decline worldwide. Examples of recent forest declines are particularly well documented in semi-arid regions in southern Europe and western North America. In the case of yellow-cedar, climate-induced tree mortality is complex and somewhat counterintuitive. Warming winter temperatures induce dehardening and photosynthesis, increasing fine root vulnerability to freezing injuries that ultimately cause physiological drought and nutrient stress (Hennon et al. 2006, 2012). The effects are especially severe on sites with wet soils and open canopy conditions, where roots are more shallowly rooted and the soil is exposed to greater temperature extremes. As a result, freezing damage to dehardened fine roots has led to drought-induced decline and death of yellow-cedars, concentrated on wet sites in coastal temperate rainforests of the Haida Gwaii archipelago.

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LITERATURE CITED

Allen, C. D., et al. 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. Forest Ecology and Management 259:660–684.

Allen, C. D., D. D. Breshears, and N. G. McDowell. 2015. On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. Ecosphere 6:1–55.

Amoroso, M. M., and L. D. Daniels. 2010. Cambial mortality in declining Austrocedrus chilensis forests: implications for stand dynamics studies. Canadian Journal of Forest Research 40:885–893.

Amoroso, M. M., L. D. Daniels, and B. C. Larson. 2012. Temporal patterns of radial growth in declining Austrocedrus chilensis forests in Northern Patagonia: the use of tree-rings as an indicator of forest decline. Forest Ecology and Management 265:62–70.

Amoroso, M. M., L. D. Daniels, R. Villalba, and P. Cherubini. 2015. Does drought incite tree decline and death in Austrocedrus chilensis forests? Journal of Vegetation Science 26:1171–1183.

Angers, V. A., P. Drapeau, and Y. Bergeron. 2010. Snag degradation pathways of four North American boreal tree species. Forest Ecology and Management 259:246–256.

Environment Canada Weather Archives. 2020. Historical Climate Data. http://www.climate.weather.gc.ca

Banner, A., W. H. MacKenzie, J. Pojar, A. MacKinnon, S. C. Saunders, and H. Klassen. 2014. A field guide to ecosystem classification and identification for Haida Gwaii. Land Management Handbook, Victoria, British Columbia, Canada.

Beier, C. M., S. E. Sink, P. E. Hennon, D. V. D’Amore, and G. P. Juday. 2008. Twentieth-century warming and the dendroclimatology of declining yellow-cedar forests in southeastern Alaska. Canadian Journal of Forest Research 38:1319–1334.

Bigler, C., J. Gricar, H. Bugmann, and K. Cufar. 2004. Growth patterns as indicators of impending tree death in silver fir. Forest Ecology and Management 199:183–190.

Buma, B. 2018. Transitional climate mortality: Slower warming may result in increased climate-induced mortality in some ecosystems. Ecosphere 9:1–16.

Buma, B., P. E. Hennon, C. A. Harrington, J. R. Popkin, J. Krapek, M. S. Lamb, L. E. Oakes, S. Saunders, and S. Zeglen. 2017. Emerging climate-driven disturbance processes: widespread mortality associated with snow-to-rain transitions across 10° of latitude and half the range of a climate-threatened conifer. Global Change Biology 23:2903–2914.

Bunn, A. G. 2008. A dendrochronology program library in R (dplR). Dendrochronologia 26:115–124.

Bunn, A. G. 2010. Statistical and visual crossdating in R using the dplR library. Dendrochronologia 28:251–258.
Daniels, L. D., J. Dobry, K. Klinka, and M. C. Feller. 1997. Determining year of death of logs and snags of *Thuja plicata* in southwestern coastal British Columbia. Canadian Journal of Forest Research 27:1132–1141.

Daniels, L. D., T. B. Maertens, A. B. Stan, S. P. J. McCloskey, J. D. Cochrane, and R. W. Gray. 2011. Direct and indirect impacts of climate change on forests: three case studies from British Columbia. Canadian Journal of Plant Pathology 33:108–116.

Duncan, R. 1989. An evaluation of errors in tree age estimates based on increment cores in Kahikatea (*Dacrycarpus dacrydiodes*). New Zealand Natural Sciences 16:31–37.

Franklin, J. F., et al. 2002. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. Forest Ecology and Management 155:399–423.

Franklin, J. F., H. H. Shugart, and M. E. Harmon. 1987. Tree death as an ecological process. BioScience 37:550–556.

Hennon, P. E., D. V. D’Amore, P. G. Schaberg, D. T. Wittwer, and C. S. Shanley. 2012. Shifting climate, altered niche, and a dynamic conservation strategy for yellow-cedar in the north pacific coastal rainforest. BioScience 62:147–158.

Hennon, P. E., D. V. D’Amore, D. Witter, A. Johnson, P. Schaberg, G. Hawley, C. Beier, S. Sink and G. Juday. 2006. Climate warming, reduced snow, and freezing injury could explain the demise of yellow-cedar in southeast Alaska, USA. World Resource Review 18:427–450.

Hennon, P. E., D. V. D’Amore, D. T. Witter, and M. B. Lamb. 2010. Influence of forest canopy and snow on microclimate in a declining yellow-cedar forest of southeast Alaska. Northwest Science 84:73–87.

Hennon, P. E., D. V. D’Amore, S. Zeglen, and M. Graininger. 2005. Yellow-cedar Decline in the North Coast Forest District of British Columbia. Research Note PNW-RN-549. US Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, Oregon, USA.

Hennon, P. E., E. M. Hansen, and C. G. Shaw. 1990a. Dynamics of decline and mortality of *Chamaecyparis nootkatensis* in southeast Alaska. Canadian Journal of Botany 68:651–662.

Hennon, P. E., C. G. Shaw, and E. M. Hansen. 1990b. Symptoms and fungal associations of declining *Chamaecyparis nootkatensis* in southeast Alaska. Plant Disease 74:267–273.

Hennon, P. E., C. G. Shaw, and E. M. Hansen. 1990c. Dating decline and mortality of *Chamaecyparis nootkatensis* in southeast Alaska. Forest Science 36:502–515.

Hennon, P. E., and C. G. Shaw. 1994. Did climatic warming trigger the onset and development of yellow-cedar decline in southeast Alaska? Forest Pathology 24:399–418.

Hennon, P. E., and C. G. Shaw. 1997. The enigma of yellow-cedar decline: What is killing these long-lived, defensive trees? Journal of Forestry 95:4–10.
Holmes, R. L. 1983. Computer-assisted quality control in tree-ring dating and measurement. Tree-Ring Bulletin 43:69–78.

IPCC [Intergovernmental Panel on Climate Change]. 2014. Climate Change 2014: Synthesis Report. In Core Writing Team, R. K. Pachauri, and L. A. Meyer, editors. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. IPCC, Geneva, Switzerland.

Kellner, A. M., C. P. Laroque, D. J. Smith, and A. S. Harestad. 2000. Chronological dating of high-elevation dead and dying trees on Northern Vancouver Island, British Columbia. Northwest Science 74:242–247.

Kolmogorov, A. N. 1933. Sulla determinazione empirica di una legge di distribuzione. Giornale Dell’instituto Italiano Degli Attuari 4:83–91.

Kolmogorov, A. N. 1933. Sulla determinazione empirica di una legge di distribuzione. Giornale Dell’instituto Italiano Degli Attuari 4:83–91.

LeBlanc, D. C. 1990. Relationships between breast-height and whole-stem growth indices for red spruce on Whiteface Mountain, New York. Canadian Journal of Forest Research 20:1399–1407.

Lough, J. M., and H. C. Fritts. 1987. An assessment of the possible effects of volcanic eruptions on North American climate using tree-ring data, 1602 to 1900 AD. Climatic Change 10:219–239.

Mann, M. E. 2002. Little Ice Age. Encyclopedia of Global Environmental Change 1:504–509.

Mann, M. E., R. S. Bradley, and M. K. Hughes. 1999. Northern hemisphere temperatures during the past millennium: inferences, uncertainties, and limitations. Geophysical Research Letters 26:759–762.

Mantua, N. J., and S. R. Hare. 2002. The Pacific Decadal Oscillation. Journal of Oceanography 58:35–44.

Muggeo, V. M. R. 2008. segmented: an R package to fit regression models with broken-line relationships. R News 8:20–25.

Parish, R., and S. Thomson. 1994. Tree book: learning to recognize trees of British Columbia. B.C. Ministry of Forests and Canadian Forest Service, Victoria, British Columbia, Canada.

Phipps, R. L. 2005. Some geometric constraints on ring-width trend. Tree-Ring Research 61:73–76.

R Core Team. 2020. R: a language and environment for statistical computing [Computer software]. R Foundation for Statistical Computing, Vienna, Austria.

Rodríguez-Catón, M., R. Villalba, M. Morales, and A. Srur. 2016. Influence of droughts on Nothofagus pumilio forest decline across northern Patagonia, Argentina. Ecosphere 7:1–17.

Schaberg, P. G., D. V. D’Amore, P. E. Hennon, J. M. Halman, and G. J. Hawley. 2011. Do limited cold tolerance and shallow depth of roots contribute to yellow-cedar decline? Forest Ecology and Management 262:2142–2150.

Schaberg, P. G., P. E. Hennon, D. V. D’Amore, and G. J. Hawley. 2008. Influence of simulated snow cover on the cold tolerance and freezing injury of yellow-cedar seedlings. Global Change Biology 14:1–12.

Schaberg, P. G., P. E. Hennon, D. V. D’Amore, G. J. Hawley, and C. H. Borer. 2005. Seasonal differences in freezing tolerance of yellow-cedar and western hemlock trees at a site affected by yellow-cedar decline. Canadian Journal of Forest Research 35:2065–2070.

Smirnov, N. V. 1939. Estimate of deviation between empirical distribution functions in two independent samples. (Russian). Bulletin Moscow University 2:3–16.

Stan, A. B., T. B. Maertens, L. D. Daniels, and S. Zeglen. 2011. Reconstructing population dynamics of yellow-cedar in declining stands: baseline information from tree rings. Tree-Ring Research 67:13–25.

van Mantgem, P. J., et al. 2009. Widespread increase of tree mortality rates in the western United States. Science 323:521–524.