Multiple divergent patterns in yellow-cedar growth driven by anthropogenic climate change

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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. A particularly severe example of this is yellow-cedar (*Callitropsis nootkatensis*) decline along the coast of British Columbia and Alaska, where anthropogenic climate change has led to reduced insulating snowpack, leaving yellow-cedar roots vulnerable to thaw-freeze events, resulting in freezing damage to fine roots and water stress during the subsequent growing season. This includes abundant evidence of tree decline and mortality on the islands of Haida Gwaii. Yellow-cedar decline is complex, with the potential for freezing injury over multiple years and damage that can accumulate over time. We found trees in various stages of decline, from long dead to currently declining, and multiple growth patterns at each study site. We conducted a principal component analysis and identified patterns of divergent growth and divergent response to climate among yellow-cedars within the same stands, across all sites, including three distinct periods of an onset of growth decline (1960s, 1990s, 2000s). Yellow-cedars affected by decline were decreasing in growth and negatively associated with warmer drier winter conditions, whereas yellow-cedars not affected by decline were increasing in growth and positively associated with warmer growing season temperatures. The limiting factors for declining trees, warm dry winter conditions, are consistent with the hypothesis from the mainland that climate warming has led to root freezing. Our research highlights the need to consider multiple signals within a site that would be masked by a single site-level chronology. This is especially relevant within the context of forest decline, where stressors may have differing effects on individual trees.

Keywords *Callitropsis nootkatensis* · Climate mortality · Dendroclimatology · Disturbance · Forest decline · Thaw-freeze

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1 Introduction

Forest decline is a global phenomenon that has intensified and become more widespread in the late twentieth century, largely driven by anthropogenic warming (van Mantgem et al. 2009; Allen et al. 2010; Peng et al. 2011). Forests are declining across a broad range of ecosystems and climatic conditions. Examples include coniferous *Austrocedrus chilensis* (D. Don) Pic. Serm. & Bizzarri (Amoroso et al. 2015) and broadleaved *Nothofagus pumilio* (Poepp. & Endl.) Krasser (Rodríguez-Catón et al. 2015) in northern Patagonia; *Pinus* spp. in southern Europe (Sánchez-Salguero et al. 2012) and southwestern USA (e.g., *Pinus edulis* Engelm. in Meddens et al. 2015); and a diverse range of genera in western North America undergoing increased mortality rates (Breshears et al. 2005; van Mantgem et al. 2009; Peng et al. 2011). While warming climate is a common thread among these forest declines, the exact mechanisms leading to tree dieback and death can be more complex. In addition to climate, there are often multiple interacting factors at play, including pathogens (e.g., Cherubini et al. 2002; Amoroso et al. 2015), insects (e.g., Wong & Daniels 2017), pollution (e.g., Lawrence et al. 2005), microsite conditions (e.g., Hennon et al. 2010), and genetic variation (e.g., Helama et al. 2008).

The dieback and death of yellow-cedar (*Callitropsis nootkatensis* (D. Don) Oerst. Ex D.P. Little) in the mid to northern range of its distribution is a particularly severe example of forest decline (Hennon et al. 2012). Along the coast of southern Alaska and northern British Columbia, 400,000 ha of forest have been affected by the decline (Buma et al. 2017). Evidence of yellow-cedar decline spans back to the 1880s (Hennon et al. 1990), but has intensified since the 1970s (Hennon & Shaw 1994). Research in Alaska has identified a specific sequence of weather events and climatic drivers of yellow-cedar decline. Warming temperatures over the twentieth century have reduced snowpacks, exposing shallow fine roots to freezing damage (Hennon et al. 2006, 2010). Local microsite conditions can predispose trees to freezing injury during years when a low snowpack coincides with thaw-freeze events in the late winter and early spring (Schaberg et al. 2008; Hennon et al. 2012). While large areas have experienced high levels of mortality, a subpopulation of surviving, apparently healthy trees coexist with dying and dead trees in the same stands (D'Amore & Hennon 2006; Stan et al. 2011).

On the island archipelago of Haida Gwaii, located 70 km west of the mainland, yellow-cedar decline was unexpected due to the moderating effect of the Pacific Ocean yielding an ephemeral snowpack, but mild winter temperatures and few frosts (Banner et al. 2014). However, many stands of yellow-cedar on Haida Gwaii now exhibit moderate- to high-severity decline, in which an average of 70% of trees are dying or dead (Comeau et al. 2021). Given the relatively mild climate on Haida Gwaii, we hypothesize the mechanism driving yellow-cedar decline may differ from that characterized in forests on the mainland. As with other forest declines, there are likely multiple interacting factors that have led to the decline and may influence trees in different locations in subtly different ways (Cherubini et al. 2002; Amoroso et al. 2015).

Dendrochronology can be used to pinpoint the timing of dieback and death of individual trees (Cailleret et al. 2017) and quantify rates and magnitude of decline across populations at stand and landscape scales (Amoroso et al. 2012). Tree-rings can also reveal divergent growth patterns within stands and populations, which can be an indicator of forest decline (Rodríguez-Catón et al. 2015, 2016). For example, many species in the boreal forest have exhibited divergent growth responses to warming temperatures, with a subset of trees responding weakly or negatively to increasing growing season temperatures (D'Arrigo

et al. 2008; Lloyd and Bunn 2007). Divergent growth is one explanation for differences among symptoms or health conditions of trees within the same stand.

In previous work within stands with visual evidence of yellow-cedar decline on Haida Gwaii, we have shown that yellow-cedars that have died or are visually declining grow alongside those with healthy crowns (Comeau et al. 2019, 2021). However, there are discrepancies between internal tree-ring and external crown symptoms in many trees (Comeau et al. 2021). Yellow-cedars exhibit both positive and negative responses to climatic variation and change (Comeau et al. 2019, 2021). This study tests the hypothesis that yellow-cedars within declining stands on Haida Gwaii exhibit divergent growth responses to changing climate over the period that yellow-cedar decline emerged. We used a principal component analysis (PCA), which is an effective way to identify recently divergent growth patterns and onset of decline, and can also aid in uncovering mechanisms of decline (e.g., Rodríguez-Catón et al. 2016). Given the climate-driven decline mechanism on the mainland and the fact that the timing of decline on Haida Gwaii parallels the period of greatest warming (Hennon et al. 2012; IPCC 2014), we tested whether yellow-cedars with different growth patterns responded differently to climate over the twentieth century.

2 Methods

2.1 Study area and site selection

Haida Gwaii is an archipelago along the north coast of British Columbia (Fig. 1a). The climate is wet-hypermaritime, strongly influenced by the Pacific Ocean. At sea level, the mean annual temperature is 8.0 ± 1.1 °C ($\pm$ standard deviation), with narrow daily, seasonal, and annual ranges. Mean total annual precipitation is 1967 mm, with 690 mm of snowfall, although average snow depth was 1 cm for January and February and 0 for all other months (Langara weather station, Environment Canada Weather Archives 2020). Yellow-cedar is found from low to high elevation on Haida Gwaii, and is more common on wetter sites but also grows at lower densities on drier sites.

We sampled to address the causes of yellow-cedar decline, selecting sites that exhibited crown symptoms and contained a high proportion of dead yellow-cedar. We sampled 15 sites, two on the northeastern coast and 13 in the central and southern portion of Graham Island, the largest island in Haida Gwaii (Fig. 1a). The sites associated with decline spanned multiple watersheds and a range of elevations. All sites had wet soils, often adjacent to a water feature such as a stream or wetland.

2.2 Data collection

Yellow-cedar were sampled in 100 m $\times$ 20 m transects bisecting the forest most heavily affected by decline (Comeau et al. 2019, 2021). We sampled the first 15 healthy yellow-cedars and the first 15 declining or dead yellow-cedar trees or snags encountered along each transect, with supplemental trees sampled adjacent to the transect in low-density stands. Declining trees were defined as living trees with visual crown symptoms, including needle discoloration and canopy dieback. Tree diameter at breast height (DBH, 1.3 m) and health status (healthy, declining, or dead) were recorded. One increment core, sampled at c. 115 cm above the ground, was taken from each tree. We aimed to intercept the pith and included the bark or outer cambium when possible. Sixteen of 450 trees with decayed outer

Fig. 1 **a** Location of 15 sites exhibiting yellow-cedar decline on Graham Island, Haida Gwaii. **b** Distribution of principal components (A=dark red, B=light red, C=dark blue, and D=light blue). Pie charts represent the percent of trees that make up each principal component at each site. **c** Raw basal area increment depicting mean growth patterns of four groups of yellow-cedar trees from 1674 to 2015. The inset panel depicts growth patterns from 1959 to 2015, the period used for the principal components analysis. Group A includes 119 trees positively correlated to PC1. Group B includes 107 trees negatively correlated to PC1. Group C includes 26 trees positively correlated to PC2. Group D includes 51 trees negatively correlated to PC2.

rings or abundant heartwood rot were not sampled; instead, we cored the next tree along the transect in the same health status class.

2.3 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 2014b). We crossdated each ring width series and assembled ring width chronologies for each site using the programs CDendro (version 7.8, Larsson 2014a) and COFECHA (Holmes 1983). For cores that did not intercept the pith, the number of missed rings was estimated based

on the dimensions of arced rings closest to the pith (Duncan 1989). If the estimated number of missed rings exceeded one third of the total rings, the sample was excluded from age estimations. Age was not estimated for trees with abundant heartwood rot or if the tree radius exceeded the length of the increment borer. Crossdating also allowed us to assign a calendar year to the outermost ring, indicating the year of death of snags and identifying trees with live crowns that were no longer producing rings (i.e., ring width = 0 mm). For subsequent analyses, we used basal area increments (BAI) as they provide a better estimate of forest decline than ring widths (Johnson & Abrams 2009; Rodríguez-Catón et al. 2015), and account for inherent age- and size-related growth trends, while maintaining year-to-year and long-term variation. BAI was calculated from ring widths using the inside-out method in the *dplR* package in R (Bunn et al. 2017; R Core Team 2014). For the subset of cores that did not intercept the pith, the distance to pith was estimated using the dimensions of the arced rings closest to the pith (Duncan 1989), or the cumulative ring widths were subtracted from the average radius (i.e., half of the tree diameter inside the bark at coring height). To account for asymmetrical growth, we applied a correction factor to the raw ring widths to reflect the average radius around the circumference before calculating BAI:

$$\text{Correction factor} = (\text{average radius})/(\text{cumulative ring widths} + \text{distance to pith}).$$

2.4 Dominant tree growth patterns

To identify dominant patterns in the growth of yellow-cedar, we conducted a principal component analysis (PCA) on raw BAI series using SAS® 9.4 software (SAS 2016). We used a common period of 1959–2015 (57 years) to include as many trees as possible ($n=366$). Trees that could not be crossdated ($n=21$), died or stopped forming rings before 1959 ($n=54$), or were < 50 years old ($n=3$) were excluded. For trees with live crowns but no longer producing rings, we recorded BAIs as 0 mm² from the outermost ring to 2015 (year of sampling) (Comeau et al. 2021). Following methods developed by Rodríguez-Catón et al. (2015), we retained the first two PCs that cumulatively accounted for at least 45% of the total variance in BAIs. Rather than using the original PC scores, individual BAI series (trees) were grouped according to the PC with which they had the highest absolute correlation, with a minimum r of |0.45|, and whether their correlation was positive or negative (Rodríguez-Catón et al. 2015). This yielded four groups, labelled A–D, which covered a longer period than the 57 years used to estimate the PCs. For each group, the raw BAI series from individual trees were averaged, resulting in four time-series that provided an extended perspective of long-term changes in tree growth.

2.5 Temporal variation in growth patterns

We developed standard and residual BAI chronologies for groups A–D using the R package *dplR* (Bunn 2008, 2010; Bunn et al. 2017; R Core Team 2014). Within each group, the individual BAI series were standardized using a horizontal line through the mean yielding dimensionless indices that were averaged into the four standard chronologies (A–D). Autoregressive modelling removed long-term trends, and maintained the high-frequency variation in tree growth, to enhance the common-term signal and minimize noise (Cook & Holmes 1999), yielding a residual chronology for each group. The quality of the standard chronologies from 1674 to

2015, when all included ≥ 10 samples, was assessed using three metrics commonly reported in dendrochronology (Fritts 1976): mean series intercorrelation (r), mean sensitivity, and the expressed population signal (EPS; Wigley et al. 1984).

We tested for breakpoints in the four standard BAI chronologies to identify abrupt changes and periods of increasing and decreasing growth between 1674 and 2015. We used the *segmented* package in R, which fits a piecewise regression model to each standard BAI chronology using an iterative approach (Muggeo 2008; R Core Team 2014). The number of breakpoints is specified. After testing multiple options (e.g., 2, 3, 4, or 5), we specified three breakpoints as it detected distinct, significant changes in slope magnitude or direction in each standard BAI chronology. Identifying distinct growth patterns is a meaningful way to detect onset of decline, as decreasing radial growth often precedes crown symptoms of decline and mortality (Cailleret et al. 2017) and is commonly used as an indicator of tree decline (Cherubini et al. 2002; Bigler et al. 2004; Amoroso et al. 2012; Rodríguez-Catón et al. 2016). Forest dieback processes are often complex; therefore, detecting the onset of growth decline is essential to understanding the primary causes. Identifying discrete dominant growth patterns within stands can more efficiently illuminate growth patterns related to dieback, which would not necessarily show up in the mean stand chronology.

2.6 Comparison of tree attributes among groups

We examined whether the health status, size, or age differed among the four groups exhibiting differing growth patterns. To determine whether the observed distribution of healthy, declining, and dead trees differed among groups A–D, we used a contingency table and chi-squared goodness of fit test. To test whether the frequency distributions of age (100-year classes) and DBH (10-cm classes) differed among the four groups, we conducted a two-sample Kolmogorov–Smirnov test (KS test) for all pairwise combinations (Kolmogorov 1933; Smirnov 1939). For all tests, α was 0.05.

2.7 Climate-growth relations

We compared climate-growth relations among the four PC groups for 1901–2015. We obtained monthly total precipitation and mean/minimum/maximum monthly temperature records for the 13 southern sites using the software ClimateNA (Wang et al. 2016) and averaged them to represent the dominant regional climate of the study area.

To assess relationships between the annual index values of the four residual BAI chronologies and the regional monthly precipitation and temperature records, we conducted bootstrap correlation function analysis (Blasing et al. 1984) using the R package *treeclim* (Zang & Biondi 2015; R Core Team 2014). The 12 months from the October prior to annual ring formation through September of the year of ring formation were analyzed. The period of analysis, 1901–2015, was split into four segments based on the breakpoints of each chronology; segments with < 12 years were excluded.

3 Results

3.1 Four distinct growth patterns

The PCA revealed four distinct growth patterns among sampled yellow-cedars (A–D; Table 1, Fig. 1). PCs 1 and 2 accounted for 34.65% and 14.89% of the variance in the population, respectively. The majority (62%) of trees were most strongly correlated with PC1. They formed groups A ($n=119$) and B ($n=107$) based on their positive or negative correlations with PC1 (Table 1). Another 21% of trees were most strongly correlated with PC2. Trees with positive correlations formed group C ($n=26$) and those with negative correlations formed group D ($n=51$) ($r \leq -0.45$). For the remaining 17% of trees, correlations with PCs 1 and 2 were <0.45 and they did not exhibit consistent growth patterns, so they were excluded from further analyses. Groups A, B, and D included trees from all 15 sites, whereas group C included trees from 11 sites. All four patterns were present across sites on Graham Island, with no clear relation to space (Fig. 1b). The oldest trees were 853, 908, 904, and 729 years in groups A–D, respectively (Table 1).

The standard chronologies for all four groups had a minimum of 10 samples going back to 1674 (Table 2). For the period 1674–2015, series intercorrelations ranged from 0.289 to 0.321, which are low relative to other yellow-cedars in the region (e.g., 0.46–0.51, Stan et al. 2011) as our intent was to group series by principal components, rather than choose series with the highest correlations, as is typically done in dendroclimatology. Mean sensitivity was 0.272 to 0.306 indicating modest variation in BAI from one year to the next. The EPS was above 0.85 for all chronologies starting in 1891, meaning the chronologies exhibited a coherent stand level signal throughout the period of climate-growth analysis.

Mean growth rates were similar across the four groups and relatively constant over multiple centuries, but changed during the latter twentieth century (Fig. 1c). Early in the twentieth century, all four standard chronologies exhibited an increasing growth trend, which began between 1911 and 1919 and continued for several decades (Table 1, Fig. 2). The chronologies exhibit a clear divergence starting in the 1970s (Fig. 1c), including switches in directional trends. The chronology for group A exhibited the longest term decreasing growth trend, which began decreasing rapidly in 1966, followed by a shallower decrease after 1995. The chronologies for groups B and D were most similar in pattern, although the timing of changes in their growth trends differed. Trees in chronologies B and D grew more rapidly beginning in 1985 and 1974 and then abruptly switched to decreasing growth trends in 2005 and 1996, respectively. The chronology for group C switched to a decreasing trend in 1965, similar to chronology A. Chronology C then switched from decreasing to an increasing trend in 1993, contrasting the concurrent switches to decreasing trends in chronologies A and D. After 2005, only chronology C exhibited an increasing growth pattern.

3.2 Distribution of age, size and crown health status

The distribution of healthy, declining, and dead trees differed among groups A–D, as follows (chi-squared = 107.4, $p < 0.00001$, Figure S1). Group A included fewer healthy and more declining or dead trees than expected by chance, with the lowest proportion of healthy trees and highest proportion of dead trees of the groups (24% healthy and 41% dead, $n=119$ trees). Group B included more healthy and fewer dead and declining trees,

Table 1 Yellow-cedar tree attributes and growth patterns for groups A–D. Trees were stratified according to positive or negative correlations with principal components (PC) 1 or 2. Correlation coefficients (r) are the mean correlations of individual trees in each group with the associated PC. Segmented regression was used to detect three break-points separating periods with significantly different slopes, indicating changes in growth rates, from 1674 to 2015 ($\alpha=0.05$)

Group	PC	r	n	Tree attributes (range)		Changes in growth rate 1674 – 2015							
				Age (y)	DBH (cm)	Segment 1		Segment 2		Segment 3		Segment 4	
						Slope	Break	Slope	Break	Slope	Break	Slope	Break
A	1	+0.701	119	61–853	11.9–148.0	+0.0008	1919	+0.0295	1966	–0.0475	1995	–0.0132	
B	1	–0.699	107	65–908	11.0–109.7	–0.0004	1916	+0.0090	1985	+0.1241	2005	–0.0273	
C	2	+0.653	26	67–904	10.6–76.6	–0.0012	1915	+0.0240	1965	–0.0049	1993	+0.1413	
D	2	–0.628	51	71–729	12.5–126.4	+0.0001	1911	+0.0132	1974	+0.0653	1996	–0.1156	

Table 2 Characteristics of the basal area increment chronologies for groups A–D. Mean series intercorrelation and sensitivity are for the common period 1674–2015 when all four chronologies included at least 10 trees

Group	<i>n</i>	Full length of chronology	<i>n</i> ≥ 10 (year)	Mean series intercorrelation	Mean sensitivity	EPS ≥ 0.85 (year)
A	119	1140–2015	1447	0.321	0.272	1691
B	107	1106–2015	1526	0.313	0.275	1866
C	26	1112–2015	1667	0.289	0.306	1891
D	51	1282–2015	1674	0.310	0.273	1866

with the highest proportion of healthy trees (86%, $n = 107$). Group C included more healthy trees, as many declining trees as expected by chance and no dead trees. All trees in group C produced rings through the year of sampling ($n = 26$). Finally, group D included fewer healthy and more declining trees than expected, with nearly an equal proportion of healthy (41%) and declining trees (39%, $n = 51$).

All four groups included trees of a broad range of ages and sizes (Table 1, Figure S2) and frequency distributions did not differ significantly across groups A–D ($p > 0.05$ for all pairwise tests). The declining growth patterns were not associated with tree size or age and rapidly increasing growth patterns were not associated with only the youngest and smallest trees.

3.3 Climate and yellow-cedar growth

Growth was significantly associated with temperature and precipitation although these relations varied among chronologies and through time (Figs. 3 and 4). The strongest and most consistent associations were with minimum temperature (Fig. 3); other temperature variables are presented in Figures S3–S6.

Climate-growth relations were similar for all four chronologies in the earliest two periods and diverged in the latter two periods, after 1965–1985 (Figs. 3 and 4). In the earliest time period, spanning 1901 to 1915–2019, chronologies A, B, and C responded to climate in the same way (D was excluded as the period 1901–1911 was too short). Specifically, warm March temperatures were negatively associated with growth, while wet Augusts and cool Septembers were positively associated with growth. In the second time period, spanning 1912–1920 to 1965–1985, all four chronologies exhibited increasing growth and responded to climate similarly. For all four chronologies, wet Octobers and dry Novembers were positively associated with growth, although the latter association was significant for chronologies C and D only. In three of four chronologies, warmer minimum temperatures in September were positively associated with growth, opposite to the relationship in the previous period.

There was a divergence of both growth patterns and climate-growth relations after 1965–1985. Winter temperatures became more important for chronologies A and C, and summer temperatures became more important for chronologies B and D (Fig. 3). During the 1966/1967 to 1993/1995 period, chronologies A and C exhibited decreasing growth and growth was negatively associated with warm January and April temperatures. Meanwhile, during the 1975/1986 to 1996/2005 period, chronologies B and D exhibited increasing growth trends and growth was positively associated with warm April, May, June, and July

Fig. 2 Basal area increment (BAI) standard (top) and residual (middle) chronologies for groups A–D from 1674 to 2015. The black line superimposed on each standard chronology indicates significant breakpoints identified using segmented regression analyses. The bottom panels depict sample depth or the number of trees included in each chronology over time ($n = 119$, 107, 26, and 51 for groups A–D, respectively)

minimum temperatures, with significant associations for chronology D. Average and maximum June temperatures were significant for chronology B from 1986 to 2005 (Figure S4).

Fig. 3 Correlation between monthly minimum temperature and the residual chronology for principal components A, B, C, and D over the time periods based on the identified breakpoints of each chronology. Bars are the correlation coefficients; a dot indicates significance ($\alpha = 0.05$)

Fig. 4 Correlation between monthly precipitation and the residual chronology for principal components A, B, C, and D over the time periods based on the identified breakpoints of each chronology. Bars are the correlation coefficients; a dot indicates significance ($\alpha=0.05$)

During the two decades preceding 2015, only chronology C sustained an increasing growth pattern. From 1994 to 2015, growth of chronology C was positively associated with warm spring and summer temperatures, although not significant (Fig. 3). Growth was positively associated with low winter precipitation, with February being the only significant association during this period. Conversely, low winter precipitation was negatively associated with growth for chronologies A and D, which exhibited decreasing growth starting in 1996/1997, significant in December for both chronologies, and in January for chronology D. Warm January temperatures continued to be negatively associated with the growth of chronology A and became negatively associated with growth of chronology D as well as in the most recent period, though the associations were not significant. Since growth of chronology B started to decrease in 2005, the most recent period was too short to assess climate-growth associations.

4 Discussion

4.1 Patterns of growth divergence

Yellow-cedars in declining stands on Haida Gwaii pose a particularly complex problem, as they exhibit divergent growth responses that differ among subpopulations and through

time. Over time, subsets of trees have exhibited increasing growth rates, responding positively to increasing growing season temperatures, while most trees have also exhibited periods of decreasing growth rates, associated with warm dry winter conditions.

On Haida Gwaii, we detected four distinct groups differently impacted by yellow-cedar decline. These detected patterns became established relatively recently, following more than 200 years during which the mean growth trends were similar in both magnitude and direction. This includes an increasing growth trend concurrent with warming temperatures at the beginning of the twentieth century. The divergence in growth patterns of yellow-cedars resulting in the four responses to decline at these sites is a relatively recent phenomenon becoming apparent in the 1970s. Similarly, three healthy stands of yellow-cedar exhibited a divergent response to temperature, with a marked decrease in correlation between latewood blue intensity and January to August monthly temperature after 1975 (Wiles et al. 2019). This follows similar timing to climate-growth divergence seen across multiple species and geographies in the boreal and high elevation forests of the north (Wilmking et al. 2005; Lloyd & Bunn 2007; D'Arrigo et al. 2008). Growth responses to warming temperature in trees across the circumpolar north weakened or switched direction beginning around 1940–1950 and becoming more noticeable after 1970 (D'Arrigo et al. 2004; Wilmking et al. 2005; Lloyd & Bunn 2007). By contrast, some high elevation species such as alpine larch (*Larix lyallii* Parl.) did not show divergent radial growth patterns until as late as the 1990s (Montpellier et al. 2018). However, all of these divergent growth responses appear to be unique to the twentieth century, with correlations to temperature weakening or changing direction after the mid-twentieth century (Wilmking et al. 2004, Driscoll et al. 2005, D'Arrigo et al. 2009, Wong & Daniels 2017).

4.2 Decreasing growth indicates onset of decline

Comparable to other published literature, internal symptoms of yellow-cedar decline, identified as decreasing radial growth, corresponded with the external crown symptoms observed, with decreasing growth often acting as an “early warning sign” (Amoroso et al. 2012; Cailleret et al. 2017). On Haida Gwaii, yellow-cedars affected by the earliest onset of decline were more likely to have died or to exhibit external crown symptoms, whereas yellow-cedars with more recent onset of decline were less likely to have died or exhibit crown symptoms. Trees that exhibited increasing growth at the time of sampling were all living and were the least likely to show crown symptoms. This increase in growth rate of healthy trees may be driven in part by stand dynamics, with healthy trees experiencing a growth release due to dieback and loss of neighboring trees (e.g., Stan & Daniels 2010).

Each of the four subpopulations with distinct growth patterns from 1959 to 2015 included trees which span the full range of age and size, from sites across Haida Gwaii. Three of these subpopulations exhibited decline, entering a decreasing pattern of growth in the 1960s, 1990s, or 2000s. These patterns provide evidence of three periods of onset of decline, which coincide with elevated levels of mortality reported in Comeau et al. (2021), signifying that during these three time periods, trees died and others entered decline. Mortality related to yellow-cedar decline on the mainland goes back to 1880, but has increased since 1950, with peaks in the 1970s and 1980s (Hennon & Shaw 1994). This timing corresponds to peaks in the onset of decline and mortality of yellow-cedars on Haida Gwaii in the 1980s (Comeau et al. 2021).

Group C was unique in that it was a “healthy” subpopulation made up of living trees with increasing growth and mostly asymptomatic crowns. Group C was composed of the

fewest trees ($n=26$), with a greater proportion of trees under 20 cm in DBH, but also included trees up to 904 years old. While most trees affected by a decrease in growth continued to exhibit that pattern until the end of the study period, trees in group C recovered from an early decrease in growth beginning in the 1960s, and became the only group exhibiting increasing growth in 2015. Trees in chronology C may be more resistant to decline or may be releasing due to a higher density of dead trees around them. Stem mapping at the stand level is needed to address this question.

4.3 Climatic drivers of yellow-cedar decline

Multiple lines of evidence support climate change as the most probable driver of yellow-cedar decline. Each subpopulation included trees from across sites on Haida Gwaii, where the common factor is mesoclimate. The Pacific Northwest has been warming since around the 1850s, which marked the end of a cooler period known as the Little Ice Age (Mann 2002) when glaciers in the area last reached their maxima. Correspondingly, the earliest yellow-cedar decline dates back to the 1880s (Hennon et al. 1990). Most of the yellow-cedars in this study established during this cooler time period, with 88% establishing prior to 1880 (Comeau et al. 2021). Similarly, a study of yellow-cedar at the leading edge of natural range expansion found that despite suitable habitat beyond stand edges, stand expansion is in a period of stasis with the last pulse at the end of the Little Ice Age (Krapek & Buma 2018). Warming temperatures have accelerated over time, especially during the twentieth century. The increase in growth rates of trees in all four groups beginning in the early twentieth century reflects this. The earliest onset of decline was identified as beginning in the 1960s (groups A and C). However, the most dramatic warming has occurred since the 1980s (IPCC 2014). Corroborating this, the climate data from our study sites show that the warmest winter temperatures since 1900 have occurred between 1980 and 2015, with the greatest change to January and February temperatures (Comeau et al. 2019). The greatest increases in decline and mortality of yellow-cedar beginning in the second half of the twentieth century coincide with increases in temperature. We also detected a switch in climate-growth responses around the same time. However, the strongest evidence for climate is that temporally unstable climate-growth relations corresponded to periods of increasing and decreasing growth of yellow-cedars.

High latitude and high elevation forests are typically thought to be temperature limited (e.g., Nemani et al. 2003). Many tree species have exhibited increasing growth over the twentieth century in response to warmer and longer growing seasons, with earlier snowmelt and warmer fall temperatures (Wilmking and Juday 2005; Driscoll et al. 2005; Lloyd et al. 2011), known as a “greening response” (Lloyd and Bunn 2007). This includes yellow-cedars in Alaska; a stand of healthy yellow-cedar was positively associated with growing season temperatures (Beier et al. 2008), and three stands containing healthy yellow-cedars exhibited a positive association between latewood blue intensity and growing season temperatures from 1901 to 1975 (Wiles et al. 2019). Consistent with this, yellow-cedar on Haida Gwaii exhibited increasing growth in the early twentieth century in response to a longer growing season, inferred from the positive correlation with September temperature after the mid-1910s, and in response to warmer growing season conditions in the late twentieth century, with positive associations with growing season temperature from 1975 to 2015 during periods of increasing growth. This relationship was strongest with maximum temperature for groups B and D (shown in Figures S4 and S6) and minimum temperature for group C. Moreover, Myneni et al. (1997) found that plant growth increased in the

northern high latitudes after the 1980s, concurrent with the greatest increases in growth of yellow-cedar. Conversely, during periods of decreasing growth, yellow-cedars have not been able to take advantage of warmer growing season temperatures.

Yellow-cedars on declining sites on Haida Gwaii exhibited divergent growth responses to climate after 1970. This timing mirrors that of divergence of tree growth across the circumpolar north (Wilmking et al. 2005; Lloyd and Bunn 2007; D'Arrigo et al. 2008, 2009). However, the response of tree growth and forest productivity to increasing temperatures has been highly variable both spatially and temporally. In addition to the “greening response,” some trees have shown a negative response to increasing temperatures, which has led to decreasing growth or a “browning response” (Lloyd and Bunn 2007). In most cases, growing season temperatures have had the most significant effect (D'Arrigo et al. 2004; Wilmking et al. 2004; Driscoll et al. 2005; Zhang and Wilmking 2010; Montpellier et al. 2018). Increasing growing season temperature has exceeded physiological thresholds, causing the relationship with tree growth to weaken or change direction since the mid-twentieth century (D'Arrigo et al. 2008). Negative growth responses are present across multiple species in the boreal forests, (Lloyd and Bunn 2007).

While the mechanisms for this are not fully understood, and vary by location and species (D'Arrigo et al. 2008), many negative relationships are driven by direct temperature stress or drought (Wilmking et al. 2004; Girardin et al. 2016). However, this is not the case with yellow-cedars on the wet sites that we sampled. For yellow-cedars with increasing growth rates, the positive relationship with growing season temperature is maintained through the end of the study period. Importantly, there was not a positive relationship between growing season precipitation and growth during the second half of the twentieth century (except with August precipitation for group A from 1967 to 1995). In the most recent period, when winter temperatures are at their warmest, the association with precipitation becomes most significant in the winter and spring. Unlike other circumpolar species, there is no evidence that warm growing season temperatures have become limiting to yellow-cedars in this study. Instead, warm winter temperatures and low winter precipitation were strong drivers of decreasing growth since the 1960s. This is consistent with the root-freezing hypothesis from Alaska (Hennon et al. 2012) and parallels patterns seen on the mainland, where yellow-cedars exhibited divergent climate-growth responses, with comparable limiting factors. The growth of healthy yellow-cedars on the mainland was facilitated by warmer growing season temperatures (Beier et al. 2008), while the growth of yellow-cedars at declining sites was limited by warm and dry winter conditions (Beier et al. 2008; Wiles et al. 2012).

For yellow-cedar, associations with winter are biologically relevant, although the impacts of winter conditions on tree growth and dieback are indirect. Rather than direct drought limitation due to warmer or drier growing seasons, we propose declining yellow-cedars are limited by physiological drought due to damaged roots. Growth during decreasing periods was limited by low winter precipitation and warm January temperatures. Corroborating this hypothesis, higher winter precipitation (theoretically as snow) and colder January temperatures would maintain any snowpack present insulating trees from freezing damage. In years when these conditions are particularly lacking, fine roots become damaged in the event of freezing temperatures if roots are not cold hardened (Schaberg et al. 2008, 2011). This leads to physiological drought in the summer, an indirect impact of climate that limits growth (Hennon et al. 2012).

Thaw-freeze events in conjunction with low snowpack have become more frequent in recent years in Alaska (Beier et al. 2008), though only four thaw-freeze events were identified between 1937 and 2015 on Haida Gwaii (Comeau et al. 2021). On Haida Gwaii, 1986 was a year of low growth for all four chronologies with 70–85% of trees per chronology

exhibiting negative growth; this was also ranked as the fourth highest winter for potential thaw-freeze impact from 1950 to 2004 in Alaska, based on thaw-freeze magnitude and a proxy for snow cover (Beier et al. 2008). However, we found no other correspondence among years of high thaw-freeze magnitude in Alaska (Beier et al. 2008) and thaw-freeze events on Haida Gwaii (Comeau et al. 2021) and years of low growth documented in this study. Importantly, the majority of yellow-cedar forests on Haida Gwaii exist within the snow-rain threshold, where winter temperatures range between -2 and 2 °C (Buma et al. 2017). Therefore, slight changes in temperature can have a large effect on both snowpack and the frequency of thaw-freeze events and may be difficult to identify using climate records from coastal weather stations. Corroborating this, between 1900 and 2015, winter temperatures at the study sites ranged from -10 to 7 °C, with decadal average minimum and maximum winter temperatures ranging from -4 to 2 °C. Analysis of monthly climate at these sites identified January and February as the months with the greatest warming over the twentieth century (Comeau et al. 2019). Climate change models for the region project decreased precipitation as snow, increased frequency of rain-on-snow events, elevated snowline, and reduced snowpack (Shanley et al. 2015). These small and ongoing changes in climate have had a large impact on the survival of yellow-cedar at these wet, decline-affected sites.

Given the multiple lines of evidence, we propose the driving mechanism of decline on Haida Gwaii is consistent with that on the mainland, specifically low snowpack combined with increased thaw-freeze events damaging yellow-cedar's shallow fine roots. Subsequent research should focus on snowpack accumulation and persistence, as well as fine-scale thaw-freeze cycles at sites both exhibiting and lacking evidence of yellow-cedar decline. Identifying fine-scale climatic variation, focused on the time periods when onset of decline and elevated levels of mortality occurred would also be beneficial in shedding light on the specific mechanism leading to decline on Haida Gwaii.

4.4 Fine-scale drivers of yellow-cedar decline

In addition to regional climate, there are likely also fine-scale drivers which function at the individual tree level that can act as predisposing factors to decline (Manion 1991; Manion and Lachance 1992). Both yellow-cedars which have died or have evidence of decline and those which are healthy and growing faster than at any other time in the past occur within the same stands. Limiting factors at the tree level can mediate response to a regional-scale driver, such as climate (Lloyd et al. 2017). Possible fine-scale drivers of decline include microsite conditions, pathogens, and genetics.

Wilmking et al. (2005) proposed that recent warming has led to trees becoming more sensitive to microsite differences which has caused some but not all trees at a site to become stressed by drought or other stressors. This has led to the divergence in growth among subpopulations. Additionally, microsite conditions are important in yellow-cedar decline on the mainland. Soil saturation and depth, canopy closure, aspect, snowpack, and other microenvironmental factors all influence the likelihood of yellow-cedar decline on the mainland (D'Amore and Hennon 2006; Hennon et al. 2010). It is possible that microsite conditions affect yellow-cedars on Haida Gwaii as well, especially if the root-freezing decline mechanism is the same.

Genetic variation affects how trees interact with climate, including resistance to drought and heat stress (Bansal et al. 2015; Allen et al. 2015) and tolerance of cold temperatures by way of cold hardiness (Aitken and Hannerz 2001). Pathogens have also been known to

interact with climate in forest declines (e.g., Cherubini et al. 2002; Vélez et al. 2012; Amoruso et al. 2015; Wong and Daniels 2017). Both should be studied further, to investigate their role in predisposing yellow-cedars or otherwise interacting with decline. The lack of knowledge around what predisposes or protects yellow-cedars from decline prevents accurate prediction of which trees are at risk.

5 Conclusions

Our findings highlight the importance of parsing out the multiple growth patterns that can exist within a declining stand to better understand the history and dynamics of decline over time. We uncovered four divergent growth patterns in yellow-cedars on Haida Gwaii, three of which are declining. Increasing growth over the second half of the twentieth century was driven by increasing growing season temperatures consistent with patterns from across high latitude and high elevation forests, whereas decline was driven by warmer winter temperatures and low winter precipitation, consistent with the drivers proposed on the mainland. These patterns emerged after 1965–1985, during the period of greatest climate warming. In addition to climate, there are likely multiple predisposing and contributing factors influencing decline, which are not currently understood. Subsequent research should focus on these fine-scale drivers in order to protect this important and vulnerable species.

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Author contribution Both authors contributed to conceptualization and methodology. Author 1 was responsible for the primary analysis of data and writing of the original draft. Author 2 supervised and contributed to reviewing and editing the manuscript.

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Data availability The data that support the findings of this study are available from the corresponding author upon reasonable request.

Code availability R packages used included in methods.

Declarations

Conflict of interest The authors declare no competing interests.

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