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Divergent Growth and Changing Climate Relationships of Boreal and Subalpine Spruce in Southern Yukon, Canada

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ABSTRACT. Tree-ring data for 1942–2013 were used to determine if boreal and subalpine *Picea albertiana* S. Brown emend. Strong & Hills radial growth rates changed after 1950 in southern Yukon, northwest Canada. The latter year represented the beginning of accelerated atmospheric greenhouse gas accumulation, which has subsequently caused global climate changes. Ring-width chronologies for both boreal and subalpine trees were constructed using 80 trees. Individual ring-width sequences were crossdated, age-detrended, and converted to tree ring-width indices (RWI). In 2013, boreal and subalpine RWI were 41% and 169% greater than in 1950, respectively. In contrast, elevational treeline chronologies in the region typically decreased 20%–70%. During 1942–2013, boreal and subalpine chronologies were significantly, at best modestly (r < |0.36|), and exclusively correlated with either moisture or temperature variables, respectively. Within this same time frame, RWI-climate variable correlates differed between the early and late phases of each chronology. Average pre-1969 or early-phase boreal correlations based on a 19-year moving window reached a maximum of –0.56. Late-phase chronology correlations typically shifted towards weaker associations with climate variables (typically +0.04 to +0.30). For boreal RWI, 25 of 68 tested climate variables shifted as much as 0.40–0.88 correlation coefficient units between the early and late phases of the chronologies. Subalpine RWI were correlated only with July–August precipitation during the early phase of its chronology. These changes suggest responses by spruce to climate have shifted since 1970. The modest 1942–2013 RWI-climate variable correlations likely reflect the result of these changing ecological relationships.

Key words: boreal; climate; greenhouse gas; radial growth; ring width; subalpine; white spruce; Yukon

RÉSUMÉ. Les données dendrochronologiques des années 1942 à 2013 ont été utilisées pour déterminer si les taux de croissance radiale (Strong & Hills) de l'épinette boréale et subalpine *Picea albertiana* S. Brown emendée ont changé après les années 1950 dans le sud du Yukon, situé dans le nord-ouest du Canada. La dernière année coïncidait avec le début de l'accumulation accélérée du gaz à effet de serre dans l'atmosphère, qui a fini par entraîner des changements climatiques à l'échelle mondiale. Les chronologies des largeurs de cernes des arbres boréaux et des arbres subalpins ont été élaborées à l'aide de 80 arbres. Les séquences de largeurs de cernes individuelles ont été datées par recoupement, détendancées en fonction de l'âge et converties en indices de largeurs de cernes d'arbres (RWI). En 2013, les RWI des arbres boréaux et des arbres subalpins se sont établis, respectivement, à 41 % et 169 % de plus qu'en 1950. Par contraste, les chronologies de l'élévation des limites forestières de la région ont diminué de 20 % à 70 %. De 1942 à 2013, les chronologies boréales et subalpines étaient considérablement, au mieux modestement (r < |0,36|), et exclusivement corrélées soit avec la variable de l'humidité, soit avec la variable de la température. Pendant cette même période, les corrélats de la variable RWI-climat différaient entre le début et la fin des phases de chaque chronologie. Les corrélations boréales moyennes avant 1969 ou en début de phase, basées sur une fenêtre de temps variable de 19 ans, ont atteint un maximum de –0,56. Les corrélations des chronologies de fin de phase gravitaient généralement vers des associations plus faibles avec les variables du climat (typiquement de +0,04 à +0,30). Dans le cas des RWI boréaux, 25 des 68 variables climatiques testées ont changé dans une mesure de 0,40 à 0,88 unité de coefficient de corrélation entre les phases du début et de la fin des chronologies. Les RWI subalpins ont seulement été corrélés avec les précipitations de juillet et d'août pendant le début de phase de leur chronologie. Ces changements suggèrent que les réponses des épinettes au climat ont changé depuis 1970. Les corrélations de la variable RWI-climat modestes de 1942 à 2013 reflètent vraisemblablement le résultat de ces relations écologiques changeantes.

Mots clés : boréal; climat; gaz à effet de serre; croissance radiale; largeur de cernes; subalpin; épinette blanche; Yukon

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INTRODUCTION

The consequences of global greenhouse gas-driven climate change on high-latitude North American forests were considered "highly uncertain" by the Intergovernmental Panel on Climate Change (Stocker et al., 2013:71). In northwest Canada, however, it would be expected that cold hardy trees that grow on well-drained upland sites such as *Picea albertiana* S. Brown emended Strong & Hills (2006, western white spruce) and lesser common *Picea glauca* (Moench) Voss (white spruce, both hereafter referred to as "spruce") would respond to warmer conditions by advancing beyond their current latitudinal (Esper and Schweingruber, 2004) and elevational limits (Davis et al., 2020). Other effects could include changes in stand canopy composition and structure (Roland et al., 2019) and changes in annual height (Lu et al., 2019) and radial growth rates (Barber et al., 2000). Insufficient time has passed for a major shift in the location of elevational treelines based on a less than 2 m yr^{1} average rate of upslope advance that has been reported (Danby and Hik, 2007; Davis et al., 2020). However, changes in radial growth rates as determined by tree ring-width index values (RWI) have already occurred in the most northerly of treed areas (Porter and Pisaric, 2011). Changes in radial growth rates probably began here earlier than farther south due to the greater sensitivity of high-latitude vegetation to warming climate conditions (Ito et al., 2020). In the southern Yukon region, several studies conducted at the uppermost limit of the subalpine zone or elevational treeline had radial growth rates that declined 20% – 70% after 1950, based on ring widths (Allen, 1982:129) and RWI (Lloyd and Fastie, 2002, three of four Eagle and Twelvemile chronologies; Davi et al., 2003; D'Arrigo et al., 2004; Tomkins et al., 2008; Youngblut and Luckman, 2008; Sullivan et al., 2016). Only Lloyd and Fastie (2002: one of four chronologies) and Dearborn and Danby (2018: four of 12 chronologies) reported growth increases. Increases were also reported at lower elevations in boreal areas (averages 15% – 19%) during the same time frame (Strong, 2017, 2020), with cyclic multiyear growth peaks of 25% – 45% (Strong, 2017). These different growth trends were assumed to be actual biological responses, rather than the result of different dendrochronological standardization techniques (e.g., negative exponential curves at treeline versus regional curve standardization in boreal areas) or other similar considerations.

The increase in post-1950 tree-ring growth rates at low elevations and their decline at treeline would seem ecologically inconsistent within a warming environment, which raises the question: How did spatially, elevationally, and ecologically intermediate subalpine trees respond? This perceived inconsistency in growth trends was based on higher elevations being cooler by 0.65˚C per 100 m rise in elevation (normal lapse rate), with as much or more precipitation as lower elevations (Strong, 2017:63). The most common explanation for the decline in growth near treeline has been increasing drought stress caused by globally warming atmospheric temperatures (Lloyd and Fastie, 2002; D'Arrigo et al., 2004). However, the four Dearborn and Darby (2018) treeline chronologies with increased growth were associated with southerly slopes. Such slopes are typically drier than other topographic orientations due to a greater incidence of solar radiation, which can enhance evapotranspiration demands (Strong, 2018: Figs. 2 and 4). Therefore, increased temperature-induced moisture stress would seem an unusual explanation for greater growth on southerly aspects. Regardless of the specific growth-limiting factor(s), treeline areas have harsher tree-growing conditions than lower elevations. For this reason, modeled treeline growth trends and their climate relationships are probably untrustworthy predictors of growth for less open-growing and lower elevation subalpine trees. The same would likely be true for the application of boreal growth trends and correlative relationships to subalpine trees. Recognizing and explaining temporal changes in boreal and subalpine tree growth trends are important for their management, but also because the subalpine zone could represent an area of future forest expansion in southern Yukon and northern British Columbia based on a warming climate scenario.

To determine if subalpine tree-ring growth rates of spruce have decreased or increased since 1950 and if boreal and subalpine trees have responded similarly to changing climate conditions, it would be necessary to standardize their comparison as much as possible within the context of a field study. This would include sampling boreal and subalpine trees that occur in close geographical proximity to avoid regional climate differences (e.g., timing, amount, duration, and frequency of meteorological events), which might affect tree-ring growth rates. It would also be necessary to use a common set of assumptions, age-related ring-width standardization techniques, and data analysis procedures to avoid comparison biases. Using these criteria, the objectives of this study were to (1) construct separate 1942 – 2013 ring-width (mm) and RWI chronologies for boreal and subalpine spruce in the Whitehorse area of southern Yukon (Fig. 1), (2) identify growth trend differences between the chronologies, (3) identify climate variables that are significantly ($p < 0.05$) correlated with the RWI of each chronology, and (4) determine if the relationship between RWI and individual climate variables have changed since 1950. The results from objectives 2 and 4 could identify what, if any, affect accelerated greenhouse gas accumulation (e.g., Soulé and Knapp, 2019: Fig. 3d) and resulting climate changes have had on high-latitude boreal and subalpine forests in northwest Canada.

MATERIALS AND METHODS

Study Area

The Whitehorse region has undulating to rolling topography (elevations 650 – 720 m) that occurs between

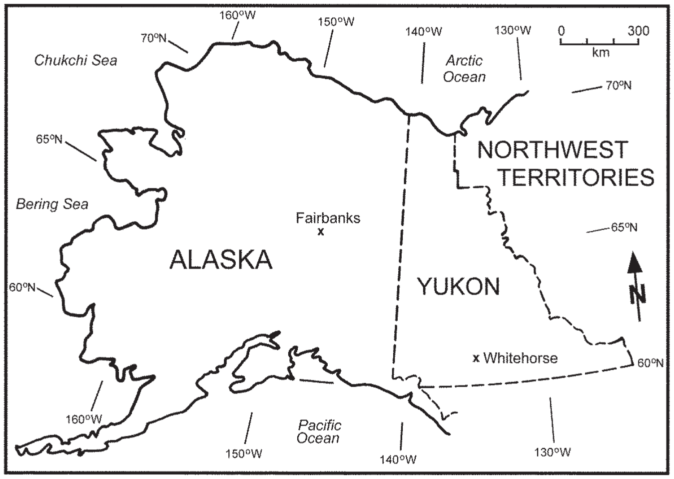

FIG. 1. Location of Whitehorse in the southern portion of Yukon, northwest Canada.

discontinuous northwest-southeast aligned mountain ridges, which reach elevations of 1500–1700 m. Well-drained upland sites at low elevations are dominated by Mid-Cordilleran Boreal forests (Strong, 2013) composed of lodgepole pine (*Pinus contorta* var. *latifolia* Engelmann ex S. Watson) and to a lesser extent spruce. Lodgepole pine stands are of postfire origin, whereas spruce can establish after disturbance or they can infiltrate established vegetation. Above 1100 m, semi-closed conifer forests become more open and transition to scattered occurrences of spruce, lodgepole pine, and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), which protrude above dense 2–3 m tall willow-birch (*Salix–Betula*) vegetation. Both trees and shrubs in this Mid-Cordilleran Subalpine zone (a.k.a. Spruce-Willow-Birch zone in northern British Columbia, Pojar and Stewart, 1991) decrease in height with increasing elevation. Mid-Cordilleran Alpine ecosystems occur above the subalpine zone, with climatic treeline at about 1450 m. Mid-Cordilleran Boreal and Subalpine ecosystems represent ~22% of Yukon (Strong, 2013).

From 1942 to 2020, the boreal forest zone within the vicinity of the Whitehorse Airport meteorological station (60˚42.567′ N, 135˚4.033′ W) had average November–October (annual) temperatures of −0.5˚C (SD 1.2), with 268 mm (SD 50) of precipitation (ECCC, 2020). May–September (summer) temperatures averaged 10.6˚C (SD 0.8). Slightly more than half of the annual precipitation fell during summer (average 153 mm, SD 43). These temperature and precipitation regimes had annual and summer heat-moisture index values of 37 (SD 9) and 101 (SD 36), respectively. Annual mean temperatures had a broad undulating temporal pattern ($R = 0.470$, $p < 0.001$), with twice as many years (68%) with above average temperatures after 1975 compared to 32% during the prior 34 years. Summer mean temperatures and annual and summer precipitation totals lacked statistically significant temporal trends ($r < 0.185$, $p > 0.05$). Yukon lacks instrumented meteorological data for subalpine areas, but it was assumed that temperatures patterns were similar though cooler, and precipitation totals were greater than boreal areas.

Tree-ring Data Collection and Processing

Twenty spruce growth-increment cores were collected from each of four boreal ($n = 80$) and four subalpine sites ($n = 80$). Except D and H, sampled sites were located within a 10 km radius of the Whitehorse meteorological station (Table 1). The exceptions were located 34 km and 37 km to the northwest, respectively. Trees were selected subjectively for coring with preference given to healthy individuals that lacked evidence of substantial past physical damage or anthropogenic disturbance and occurred on well-drained level to southerly oriented slopes. Tree locations and topographic elevations were estimated using a Garmin™ Geko 201 global positioning system. Trees were cored at heights of 60–130 cm. Use of a height other than the maximum was dictated by the position, density, and size of low-growing tree branches. Lower coring heights were also used when trees were 10 cm or less in diameter at a height of 130 cm. Collected cores were air-dried, mounted, sanded, and scanned at a density of 1000 pixels cm^{-1} prior to ring-width measurement.

Using procedures described by Strong (2017), scanned core images were imported into Adobe Photoshop® Elements 4.0 software and enlarged 83×, which was sufficient to fill the vertical view of a 30 cm tall flat-screen computer monitor with the prepared working surface of a core. The start of each growth ring was marked with a pixel, and individual rings were numbered prior to manual measurement. The precision of this measurement method has been estimated to be +0.006 mm at the 95% confidence level (Strong, 2017). Ring measurements were limited to the 1942 to 2013 period, which represented the earliest year of continuously instrumented weather monitoring at the Whitehorse Airport and the most recent ring-year that was available among all cores. Prior to analysis, ring series from each sampling site were crossdated based on a spreadsheet version of the Yamaguchi (1991) method. Crossdating was conducted using 2013 rings and three marker rings, which roughly approximated the 1st, 2nd, and 3rd quartile positions along the 1942–2013 time scale: 1958, 1979, and 1997 for boreal trees; and 1959, 1980, and 1997 for subalpine trees. Typically, all marker rings were wider than their immediately adjacent counterparts, except those of 1958. The latter has been recognized as a year of exceptionally poor ring growth in southern Yukon (Youngblut and Luckman, 2008; Strong, 2017). Other years often provided additional crossdating corroboration. The results of the crossdating procedure were reviewed using COFECHA software (March 2014 version, http://www.ldeo.columbia.edu/tree-ring-laboratory/resources/software) to identify possible errors and inconsistencies. Once crossdating was completed, the first five rings after the pith were excluded from further analysis to avoid the irregular

TABLE 1. Location and characteristics of spruce ring series collection sites in the Whitehorse region of southern Yukon.

Site	Site centre		Typical condition		
	Latitude (N)	Longitude(W)	Slope orientation	Slope gradient (%)	Elevation(m)
Boreal sites:					
A	60°44.291′	135°08.716′	Southwest	35	771
B	60°44.335′	135°03.018′	None (70%), southwest	12	666
C	60°39.862′	135°58.320′	Southwest	27	679
D	60°51.400′	135°36.283′	Southwest	14	762
Average				22	719
Subalpine sites:					
E	60°44.799′	135°13.574′	Southwest	50	1373
F	60°39.643′	135°12.893′	Southwest	31	1303
G	60°41.606′	134°55.517′	Southwest	34	1373
H	60°56.205′	135°34.407′	South-southwest	40	1395
Average				39	1361

growth that often occurs during this period. Ring series intercorrelation, average sensitivity, and autocorrelation were also calculated for each dataset using COFECHA. Determining whether the datasets were strongly influenced by autocorrelation was based on Durbin-Watson (d) tests, with d-values of 1–2 considered to indicate that little or no autocorrelation occurred.

Measured ring widths (M_t) of individual series were converted to tree ring-width index values ($RWI_t = M_t/E_t$, where t represents the sequential number of individual years within a ring series, Melvin and Briffa, 2008). Expected (E_t) values were determined based on negative exponential regression modeling of raw ring-width values by series, unless a linear regression model explained 3% or more variance. If the regression *beta*-coefficient (b) of a ring series was 0 or higher, a negative exponential curve ($E_t = E_1 \exp[bt]$) was created to represent the theoretical age-related decline in its radial growth. The value for E_1 for each ring series was based on the y-intercept of the more explanatory regression model. For boreal ring series with neutral or positive temporal growth trends, *beta*-coefficients (b) were based on the site-level average among spruce with negative growth trends (range of average site-level b-values −0.0112 to −0.0197 yr^1, $n = 4$). For subalpine spruce with neutral or positive growth trends, the regional age-related growth decline rate (Fig. 2; $b = -0.0093$) was used to calculate E_t values (i.e., a regional curve standardization approach, Helama et al., 2017). This procedural difference was necessary because too few subalpine trees had a negative age-related growth trend (i.e., average $b = -0.0105$, $n = 7$).

RWI_t values were averaged to create site-level chronologies and the site-level values were averaged to create a master chronology for the boreal and subalpine ring series.

Climate Data

Meteorological data (ECCC, 2020) from Whitehorse Airport recording stations 2101300 (1942–2012) and 2101303 (2013) were used as the basis for identifying climate variables that were correlated with interannual variation in boreal and subalpine RWI. These stations

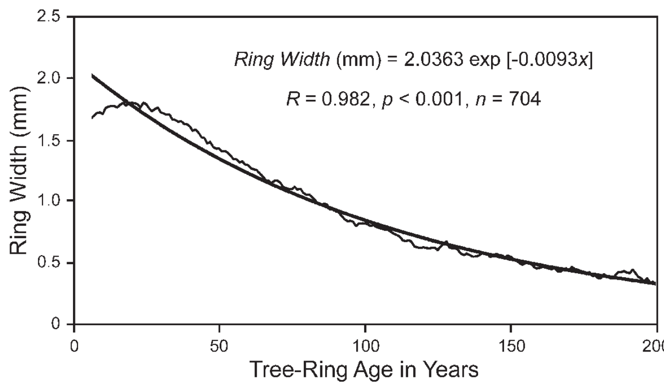

FIG. 2. Region curve standardization diagram for 5–200-year-old *Picea albertiana* ring-width sequences (narrower line) from the Tahkini Valley of southern Yukon, with a fitted negative exponential model (thicker line). Year 0 represents the core pith. The *x*-variable represents ring age relative to the pith. Regional standardization curve constructed by averaging the unpublished ring-width data associated with Fig. 4A through 4G in Strong (2017).

occurred in close proximity and at an elevation of ~706 m. Although the Whitehorse Airport has the longest and most complete meteorological record in the region, some gaps occurred within its dataset. Missing values were estimated to optimize the usefulness of the data. If four or fewer daily data values were missing for a parameter during a month and the gaps were only a day in length, the missing numbers were estimated by averaging adjacent daily values. If more daily values were missing or were longer than a single day, they were estimated from other nearby stations (2101310, 2101400, or 2101290) using regression analysis to adjust for systematic differences.

Maximum, minimum, and mean temperatures and total precipitation on an annual, summer, month, and contiguous-month (e.g., April–May, April–June, etc.) basis were compiled. Heat-moisture index (HMI) values were calculated to assess climate moisture balances, both annually (AHMI = [mean annual temperature (˚C) + 10]/[mean annual precipitation (mm)/1000]) and in summer (SHMI = mean warmest month (˚C)/[mean summer precipitation (mm)/1000]) (Wang et al., 2006). A total of 68 climate parameters were considered. Larger HMI values indicate a greater potential for climatic drought (Zhang et al., 2014:181) and the potential for more severe plant moisture deficits. November was used as the beginning of a climate year, so when calculating annual values, all winter months were chronological and represented conditions that preceded a growing season.

Statistical Procedures

The observed (*o*) frequency of increases, decreases, and no changes in temporal subalpine ring-width trends were compared based on chi-square goodness-of-fit testing ($\chi^2 = [o - \hat{e}]^2/\hat{e}$, Sokal and Rohlf, 1995), with expected ($\hat{e}$) values based on boreal frequencies. Differences in rates of temporal ring-width changes were compared using a Mann-Whitney *U*-test due to the lack of sample normality.

Pearson product-moment correlation (*r*) was used to determine the strength and directional relationship between boreal and subalpine RWI master chronologies and individual climate variables. Modeling of the temporal trend within ring-width (mm) and RWI chronologies was based on either linear or polynomial regression, depending on their complexity. These models were used to identify and illustrate trends in the data. Preference was given to polynomial models, when they explained 5% or more variance (R^2) than a corresponding linear model (r^2). Statistical testing and correlation analyses were done using STATISTICA version 5 software (StatSoft Inc., 1995). Linear and polynomial regression modeling of chronologies was based on Microsoft Excel 2003 chart and trend functions.

Product-moment correlation coefficients were also used as indices of numerical association between RWI and individual climate variables through time. These coefficients were calculated based on one-year advancing 19-year segments or moving windows of RWI (i.e., 1942–60, 1943–61 … 1995–2013). The 19-year time segment was chosen based on ad hoc testing that indicated the time frame was long enough to provide relatively stable temporal trends, but short enough to allow a large number of estimates (n = 54). The odd number of years was deliberate and allowed an equal amount of time to be represented on both sides of the median position (i.e., +9 years), which is referred to as the "reference year." Early and late phases of the chronologies were identified as a basis for estimating the amplitude of temporal change in correlation coefficients (i.e., |early phase minus late phase|). Demarcation of temporal phases was based on prolonged, quasi-stable, and covariant changes in RWI versus summer mean temperature and summer total precipitation correlations. If present, a transition period between the early and late phases of the boreal and subalpine temporal sequences was identified, based on distinct differences or abrupt changes in the degree of RWI-climate variable associations seen in discernible shifts in summer mean temperature and summer total precipitation. The resulting limits were subsequently extended to other climate variables. For purposes of summarization, correlation coefficients were classified as having no (|0–0.09|), weak (|0.10–0.29|), moderate (|0.30–0.49|), strong (|0.50–0.69|), or very strong (|0.70–1.0|) associations.

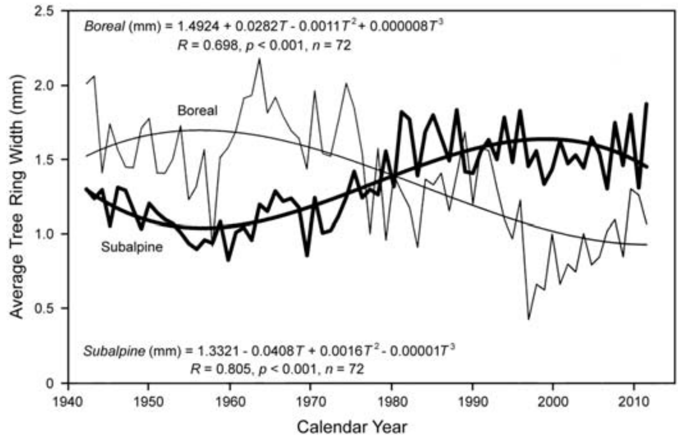

FIG. 3. Average annual tree ring widths (mm) and fitted polynomial regression models for boreal and subalpine spruce in the Whitehorse regions of southern Yukon (1942–2013).

Ordination by detrended correspondence analysis (McCune and Mefford, 1999) was used to assess relative (dis)similarity between boreal and subalpine datasets as well as among RWI site-level chronologies. The amount of variance explained by the ordination and each axis was calculated using relative Euclidean distance.

RESULTS

Ring Data Characteristics

Among 160 ring series, 95% of 624 rings used for crossdating were correctly classified based on the established criteria. Most of the inconsistencies (26 of 32) were associated with subalpine ring series. Eighty-eight of the 160 series had ring sequences that spanned the 1942–2013 time frame. The remaining ring series were of a shorter duration. Both boreal and subalpine chronologies included at least 31 series in 1942, with all 80 series represented by 1967 and 1986, respectively. Three-fourths of the boreal and one-third of the subalpine trees were older than 75 years at coring height in 2013. Most ring series were from southwest aspects, with steeper slopes occurring at higher elevations (Table 1). On average, the sampled boreal and subalpine sites were separated by an elevational distance of 642 m (Table 1).

During the 1940s to early 1970s, measured boreal spruce ring widths had an average growth rate of ~1.6 mm yr^{-1}, whereas those of the subalpine were typically ~1.1 mm yr^{-1} or 31% less (Fig. 3). The growth trends of these ecologically different groups were inversed after the late 1970s, with boreal trees gradually declining and subalpine trees reaching a growth plateau of about 1.5 mm yr^{-1} (Fig. 3). Summed 1942–2013 average yearly boreal (99.3 mm, SD 0.4) and subalpine (96.3 mm, SD 0.3) ring widths were

TABLE 2. Direction and average rate of spruce ring-width (mm) changes by ecological zone in the Whitehorse region of southern Yukon during 1942–2013.

		1942–2013 radial growth trend[1]				Average annual rate of ring-width change	
Ecological zone	Number of series	Decreasing	Neutral	Increasing	χ^2 test result	Average	SD
Boreal	80	40 [2] (50%)	38 (47%)	2 (3%)	477.5 ($p < 0.001$)	–0.009 [4]	0.011
Subalpine	80	7 (9%)	41 (51%)	32 [3] (40%)		+0.012	0.024

[1] Decreasing and increasing classes were based on statistically significant ($p < 0.05$) negative and positive *beta*-coefficients of regression equations, respectively. Members of the neutral category had insignificant equations.
[2] Boreal greater than subalpine expected frequencies based on χ^2 goodness-of-fit at 0.05 probability level.
[3] Subalpine greater than boreal expected frequencies based on χ^2 goodness-of-fit at 0.05 probability level.
[4] Rates of changed based on exponential regression *beta*-coefficients or their linear equivalents. Values differ based on Mann-Whitney *U*-test ($p = 0.001$).

not significantly different (Mann-Whitney *U*-test, $n = 72$, $p = 0.345$). These chronology totals represented average annual radial growth rates of 1.38 mm (SD 0.005) and 1.34 mm (SD 0.004), respectively.

Approximately half of the boreal and subalpine datasets lacked a statistically significant ($p < 0.05$) radial growth trend between 1942 and 2013. Among those with trends, boreal spruce mostly decreased with increasing age, whereas subalpine trees mostly increased (Table 2). A 0.021 differential in beta-coefficients occurred between boreal and subalpine trees, with the latter having a slightly faster rate of change (Table 2). Among ring series with significant temporal trends, variation in ring widths was better explained 78% of the time by curvilinear exponential rather than linear regression models, although differences in their configuration were often slight. On average, exponential and linear models explained half the variance in ring widths within regression coefficients (average R^2 or $r^2 = 0.49$). Ring series that lacked significant regression models ($p > 0.05$) often had weakly curvilinear or slightly inclined linear trends.

Boreal and Subalpine RWI Chronologies

Site-level chronologies had very similar within-group RWI profiles, especially those from the subalpine (Fig. 4). The most notable exceptions were several RWIs in the central portion of chronology D and the beginning of chronology E (i.e., result of small sample size, $n = 1$), which were 0.5 to 1.0 RWI units greater than the nearest site-level value during the same year (Fig. 4). Boreal tree rings had greater series intercorrelation (0.719 versus 0.507) and average sensitivity (0.289 versus 0.215; with range of acceptability > 0.1 to < 0.4, Speer, 2010:107) than subalpine spruce. Correlations among boreal and among subalpine site-level chronologies averaged 0.70 and 0.88, respectively (Fig. 4).

Boreal and subalpine chronologies had different site-level RWI sequences based on their separate locations within a detrended correspondence analysis ordination (Fig. 5).

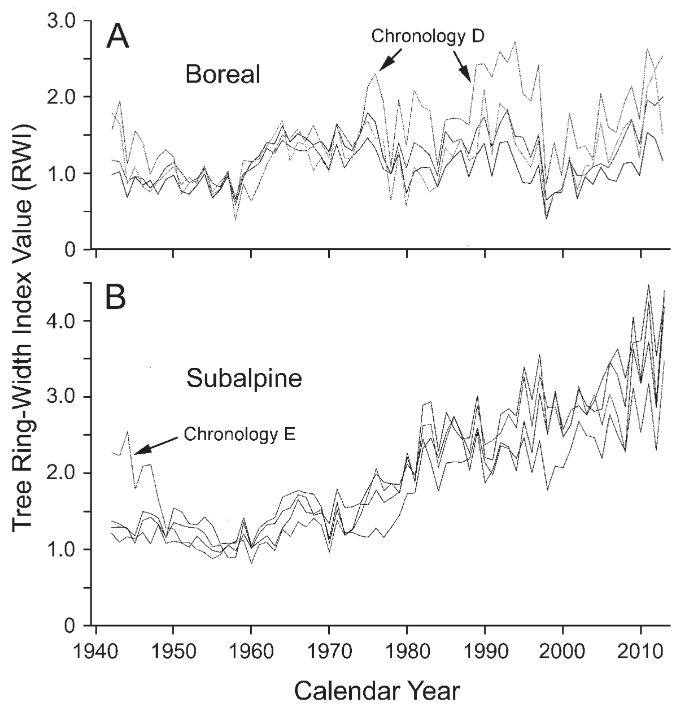

FIG. 4. Boreal and subalpine site-level tree ring-width index (RWI) chronologies from the Whitehorse region.

Overall, the ordination explained 97% of the variance in RWI among the eight site-level chronologies, with Axis 1 accounting for 96% of the total variance. Variation in site-level chronology locations along Axis 1 was very strongly correlated with differences in topographic elevation ($r = +0.976$, $p < 0.001$, $n = 8$). Elevations increased from left to right in Figure 5 (cf. Table 1).

From 1942 to 1970, age-detrended boreal and subalpine chronologies were closely aligned with respect to the direction and degree of RWI fluctuation (Fig. 6). They also had similar patterns of inter-annual fluctuation. On average, boreal spruce radial growth increased at a rate of 0.011 RWI yr^{-1} from 1951 to 2013, whereas subalpine increases

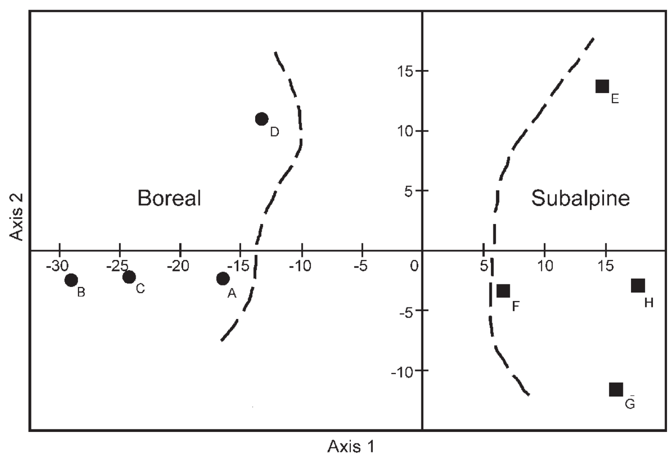

FIG. 5. Ordination of average boreal and subalpine spruce site-level tree ring-width index (RWI) chronologies from the Whitehorse region based on detrended correspondence analysis. See Table 1 for the location and site characteristics of each chronology.

averaged 0.009 RWI yr^{1} during 1951–60 and 0.054 RWI yr^{1} from 2002–13 (Fig. 6). In 2013, the regression predicted boreal RWI was on average 1.51 or 41% above the 1950 amount, whereas subalpine growth was 169% greater (Fig. 6). Despite its greater rate of growth, the standard error of estimate (SEE) for the subalpine chronology (SEE = 0.28) was similar to the boreal sequence (SEE = 0.32). Neither the boreal (autocorrelation = 0.659, d = 1.60) nor subalpine (autocorrelation = 0.615, d = 1.04) regression models were considered to suffer from notable autocorrelation.

RWI and Climate Variables

Among 68 tested climate variables, 1942–2013 boreal RWI were significantly correlated only with moisture-related variables: six precipitation and two heat-moisture indices (Table 3). Precipitation variables were positively and typically weakly correlated with RWI, whereas heat-moisture indices were moderately and inversely correlated. Month-based precipitation variables were associated with early to mid-summer, although their r-values did not differ substantially from the summer value (Table 3).

Subalpine RWI were correlated only with temperature variables (Table 3), although typically weak. These variables were either mean maximum or mean values. Maxima were correlated marginally better with subalpine RWI than mean temperatures (Table 3). Significantly correlated mean maximum and mean temperatures were associated with the April through July period (Table 3). Annual temperatures were weakly correlated with RWI.

Changing Boreal RWI-Climate Relationships

Twelve temperature variables and the summer heat-moisture index were most strongly correlated with RWI during the early phase (median reference years 1951–68) of the boreal chronology based on 19-year moving time segments (Table 4). All had inverse relationships with RWI. Among temperatures, half represented the maxima, minima, and means of the same three variables. On average, maximum, minimum, and mean variables explained similar amounts of variation in RWI (~25%). May maximum temperature was the only variable not also represented by either mean or minimum variables (Table 4). The summer heat-moisture index was as strongly correlated with RWI as the best temperature variables (Table 4). No climate variables were correlated with RWI during the late phase of the boreal chronologies at an equivalent to the $p = 0.05$ level of significance.

Summer mean temperatures ($r_{ave} = -0.32$) and total precipitation ($r_{ave} = -0.39$) had moderate opposing relationships with respect to RWI during the early phase of the boreal chronology (Fig. 7A). An 11-year transition period occurred between the early and late phases. The relative relationship between temperature and precipitation during this period became weaker and much less negative for mean summer temperature (Fig. 7A). During the late

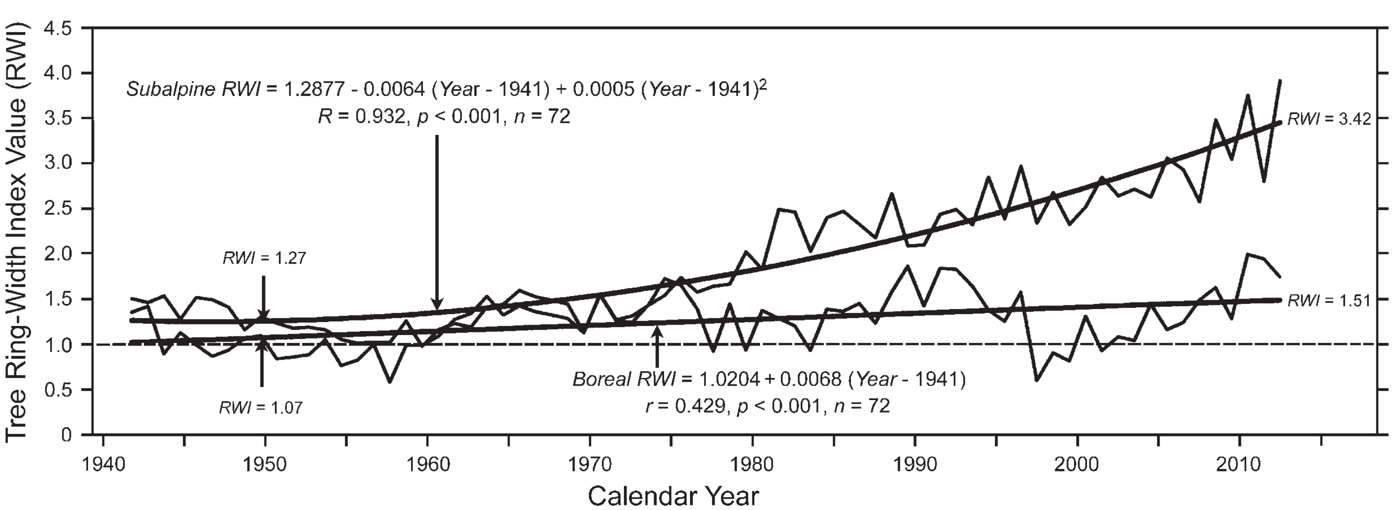

FIG. 6. Age-detrended boreal and subalpine spruce tree ring-width index (RWI) chronosequences from the Whitehorse region of Yukon, with fitted regression model. Dashed line indicates the expected RWI value after age-related detrending, when growth occurs in a stable environment.

TABLE 3. Significant Pearson product-moment correlations (r) between boreal or subalpine spruce tree ring-width index values (RWI) and climate variables measured at the Whitehorse Airport between 1942 and 2013.

Variable and time period	Boreal RWI[1] r	Boreal RWI[1] p	Variable and time period	Subalpine RWI[1] r	Subalpine RWI[1] p
Total precipitation (mm)			Mean maximum temperature (˚C)		
Annual	+0.301	0.010	Annual	+0.283	0.017
Summer	+0.256	0.030	April	+0.266	0.024
April – July	+0.260	0.028	April – May	0.292	0.013
May – July	+0.280	0.017	April – June	+0.328	0.005
July	+0.241	0.041	April – July	+0.355	0.002
June – July	+0.262	0.026	May – June	+0.267	0.023
Heat-moisture index			May – July	+0.313	0.007
Annual	–0.335	0.004	June – July	+0.262	0.027
Summer	–0.360	0.001	Mean temperature (˚C)		
			Annual	+0.256	0.028
			April – May	+0.245	0.038
			April – June	+0.282	0.016
			April – July	+0.317	0.006
			May – June	+0.243	0.039
			May – July	+0.296	0.011
			June – July	+0.277	0.021
			July	+0.236	0.046

[1] Minimum probability (p) level for inclusion < 0.05.

TABLE 4. Differences between the early and late phases of the boreal and subalpine chronologies using tree ring-width index values (RWI) and average climate variable correlations (r_{ave}) based on incrementally advancing 19-year time segments.

Variable and time period[1]	r_{ave} value: Early phase[2] (A)	r_{ave} value: Late phase (B)	Amplitude of change |A − B|	Variable and time period[1]	r_{ave} value: Early phase[3] (A)	r_{ave} value: Late phase (B)	Amplitude of change |A − B|
		Boreal RWI				Boreal RWI	
Mean maximum temperature (˚C)				Mean temperature (˚C)			
April – June	−0.457	+0.035	0.492	July	–0.471	+0.258	0.729
April – July	−0.551	+0.044	0.595	April – June	−0.464	+0.073	0.537
May – July	−0.521	+0.021	0.541	April – July	−0.553	+0.123	0.676
Mean minimum temperature (˚C)				May – July	–0.548	+0.116	0.664
April – July	−0.510	+0.179	0.689	June – July	−0.460	+0.026	0.485
May – July	−0.546	+0.215	0.761	Heat-moisture index (˚C)			
May	−0.556	+0.289	0.845	Summer	−0.564	–0.156	0.408
July	−0.540	+0.339	0.879			Subalpine RWI	
				Precipitation (mm)			
				July – August	+0.460	–0.03	0.492

[1] Included variables had either an early- or late-phase r_{ave}-value that exceeded |0.456|, which was equivalent to a probability significance level of 0.05.
[2] Boreal early chronology reference years span 1951 – 68, with the late phase from 1980 – 2004.
[3] The boundary between the early phase and the late phase is between 1969 and 1970 reference years.

phase of the chronology (reference years 1980 – 2004), both variables were weakly and positively associated with RWI (r_{ave} = +0.24 and +0.10, respectively) with an inverted relationship relative to the early phase. The amplitude of the change in the summer mean temperature relationship was almost twice that of total precipitation (Fig. 7A).

Between the early and late phases of the boreal chronology, 25 of 68 climate variables differed by 0.4 – 0.9 correlation units. The largest differentials were associated with July (0.88, Fig. 7C), May (0.84) and July – August (0.81) mean minimum temperatures. Changes in RWI-climate variable correlations between the early and late phases included shifts from negative to positive (Fig. 7C), positive to negative for May and August precipitation (Fig. 7E and 7G), and to a weaker relationship for the summer heat-moisture index (Fig. 7I).

Changing Subalpine RWI-Climate Relationships

The early phase of the subalpine RWI chronology was positively and moderately correlated only with July – August precipitation (Table 4). No variables were correlated with the late phase. The relationship between mean summer temperature and summer total precipitation was similar to their boreal counterparts, but without a prolonged transition period prior to the reversal of their positions (Fig. 7B). The pattern of change for other variables between the early and late phases of the subalpine chronology were similar to the

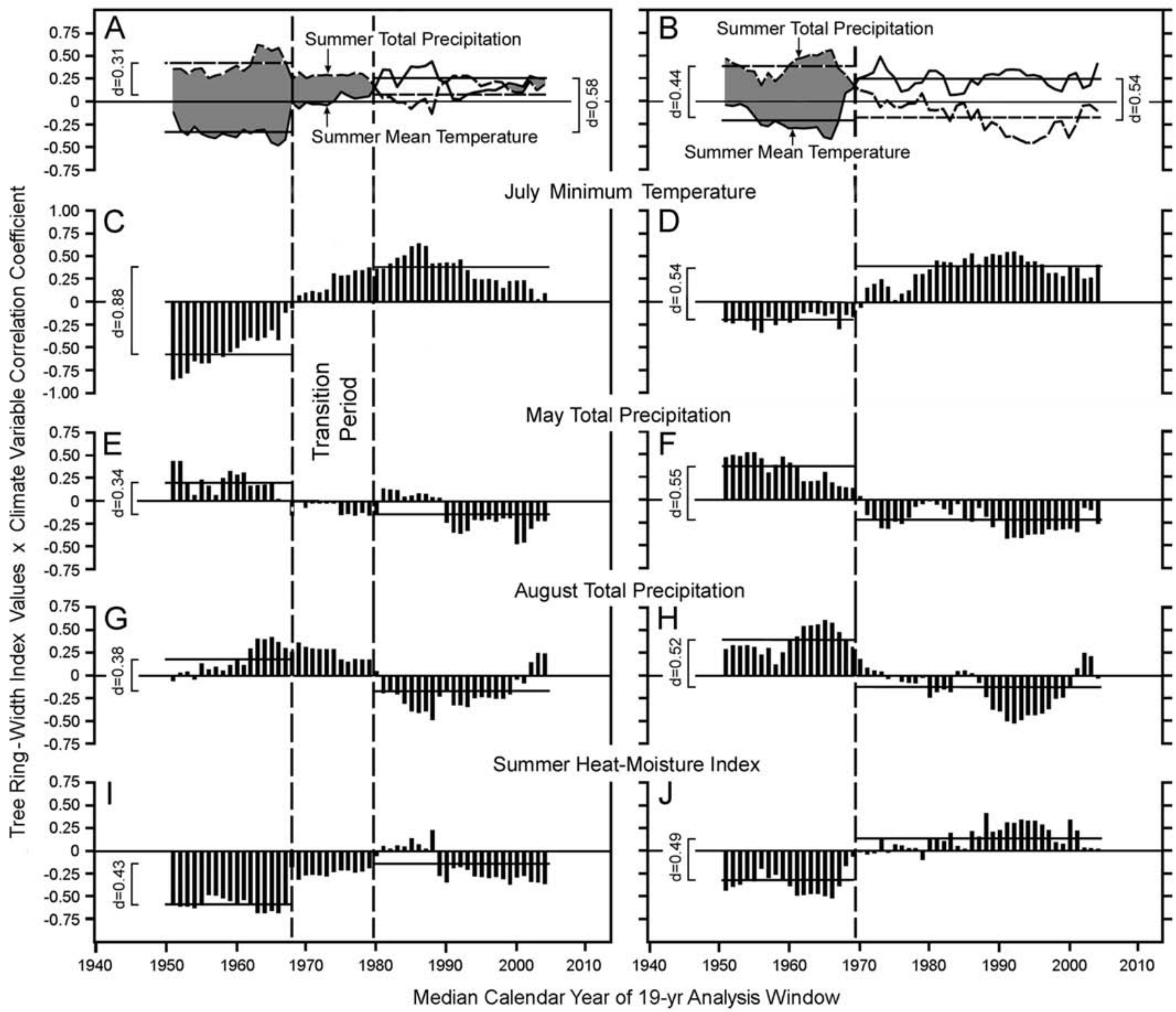

FIG. 7. Selected examples of changing spruce tree ring-width index (RWI) and climate variable relationships in the Whitehorse region based on 19-year time segments. Shaded versus unshaded areas in diagrams A and B represent inverted relationship between the presented variables. Vertical dashed lines mark the boundaries between early- and late-phases of the chronologies. Horizontal lines represent the average level of correlation for the phase (r_{ave}), with d-values indicating the amplitude of change between phases.

boreal chronology, but of a greater or somewhat greater amplitude for May precipitation, August precipitation, and summer heat-moisture index (Fig. 7F, H, and J). The exception was July minimum temperature, which had a weaker response (Fig. 7D versus 7C).

DISCUSSION

Spruce Growth in Whitehorse Region

There has been much speculation regarding the potential effect of global greenhouse gas-driven climate change on the ecology and future growth of trees in northern Canada (e.g., Price et al., 2013; D’Orangeville et al., 2018; Brecka et al., 2020). However, few studies in western Canada document the effects that have already occurred (Hogg et al., 2017), especially at high latitudes (Griesbauer and Green, 2012). Knowing what changes have already occurred could be helpful in predicting future trends. The Table 3 correlations do not point toward any particular climate variable that is consistently critical to spruce radial growth other than moisture and temperature in general and their importance during early summer. This conclusion is based on statistically significant individual climate variables explaining at most (r^2) 13% of the variance in RWI values.

Among statistically significant RWI-climate variables, those associated with early summer are likely the most important for radial growth because xylogenesis is initiated when daily minimum temperatures exceed 4°C – 5°C (Rossi et al., 2008), which usually occurs in late May to early June. Once the minimum temperature threshold is exceeded, subsequent boreal but generally not subalpine spruce radial growth is likely more sensitive to an adequate moisture supply than to heat availability. The greater importance of moisture availability for boreal spruce was represented by the more common correlation of RWI with precipitation than temperature variables (Table 3).

A small but steady temporal increase in boreal spruce radial growth rates occurred despite their presence in a semi-arid environment with very dry April – June conditions (Jätzold, 2000). This increase in growth may have occurred despite warming conditions due to a 6% Yukon-wide increase in annual precipitation between 1948 and 2012 (Streicker, 2016: Fig. 1.3), although no statistically significant trend was detected in the 1942 – 2020 Whitehorse Airport meteorological data (see *Study Area*). Values in the annual total precipitation dataset were quite varied (standard error of estimate 28%), but a visual examination did suggest the possibility of an emerging trend of increase.

The increase in boreal growth was apparent in RWI (Fig. 6), despite the decrease in measured (mm) ring widths (Fig. 3), due to the adjustment of the measured data to account for a gradual reduction in ring widths with increasing tree age (Fig. 2). In contrast, the rise in subalpine radial growth was apparent in both Fig. 3 and Fig. 6, but the magnitude of the change was more apparent when measured ring widths were adjusted for age-related decreases in growth. The 41% increase in boreal spruce RWI after 1950 was comparable to the peak growth (25% – 45%) seen in more southerly Yukon tree-ring chronologies (Strong, 2017: Fig. 5B). As well, the currently identified increases in post-1950 radial growth rates are not likely to be anomalies or errors, based on increases of up to 135% that have been reported for ponderosa pine (*Pinus ponderosa* Douglas) and western juniper (*Juniperus occidentialis* Hook.) in the northwestern United States (Soulé and Knapp, 2006, 2019).

Boreal and subalpine spruce trees were subject to the same macroclimate based on their geographical proximity. Therefore, the substantial increase in subalpine ring growth was likely due to warming temperatures in an environment with more than an adequate moisture supply. The substantial and sustained increase in RWI after the mid-1970s is an uncommon trend in far northwestern Canada (e.g., Porter and Pisaric, 2011: Fig. 3b; Dearborn and Danby, 2018:2h). Although 40% of sampled subalpine trees had increasing ring-growth trends with advancing age, the percentage with greater than expected growth would have been greater (i.e., > 40% and ≤ 91%) if trees with neutral growth trends (Table 2) had been included in the total. The rationale for their inclusion is that similar amounts of year-after-year growth (mm) represent a gain relative to the systematic decline that would be expected according to the regional pattern of negative exponential growth (Fig. 2). For subalpine trees, local environmental conditions apparently changed after 1950 based on substantially greater than expected ring growth and could become yet more favorable for spruce growth with continued climate warming. The ~18-year lag between the beginning of enhanced greenhouse gas accumulation and the shift in RWI-climate relationships (Fig. 7) probably occurred because initial climate changes were insufficient to create detectable biological responses relative to much larger interannual fluctuations in growth.

The increased boreal and substantially increased subalpine spruce RWI at least superficially conflict with the declines commonly seen in elevational treeline chronologies (see INTRODUCTION for examples). This inconsistency is not attributable to dendrochronological age-related detrending biases, because treeline and subalpine chronologies were both constructed based on the assumption of negative exponential growth. Temperature-induced drought stress is often considered the explanation for the reduction in post-1950 treeline RWI (Lloyd and Fastie, 2002; D'Arrigo et al., 2004), but there are other possibilities (Porter and Pisaric, 2011:3419). Assuming temperature-driven drought stress is a significant constraint on spruce radial growth at treeline, then lower elevation subalpine trees would be subject to proportionally greater stress because of even warmer climate conditions (i.e., less adiabatic cooling), yet growth of lower elevation ring widths increased. Concurrent subalpine RWI increases and treeline decreases might be simultaneously compatible possibilities if the evaporative effects of greater wind exposure (Müller et al., 2016) and increasing wind speeds (i.e., 15% greater since 1950; Pinard, 2007) at treeline were part of the explanation.

Changing RWI and Climate Relationships

Boreal and subalpine spruce growth rates were limited by different factors during 1942 – 2013, that is, moisture versus thermal limitations, respectively (Table 3). The greater importance of moisture for boreal spruce radial growth was previously recognized by Hogg and Wein (2005), Zalatan and Gajewski (2005), and Griesbauer and Green (2012). Despite these different limitations, RWI-climate relationships of both chronologies changed after 1968. Such changes were likely responsible for the at best weak to slightly moderate chronology correlations given in Table 3 compared to the much stronger coefficients that occurred during the early phase of each chronology (e.g., Table 4). Effectively, changing conditions disrupted the biological relationship between climate variables and RWI.

It would appear that RWI-climate variable relationship changes are not localized phenomenon. The 1969 start of the RWI-climate relationship shift approximated the 1972 date used by Griesbauer and Green (2012) to represent the same phenomenon. The slightly later date may have been the result of using a different procedure to place the limit (i.e., evolutionary response functions as opposed to the discontinuity in summer temperature and precipitation correlations, Figs. 7A and 7B), or possibly the result of the cooler and moister climate conditions that occur 3˚ latitude north of Whitehorse (Strong, 2013). Whether differences in local climate are an issue may be debatable because Yu et al. (2013) also used 1970 as the transition year for a similar analysis of Korean pine (*Pinus koraiensis* Sieb. & Zucc) in northeast China, which has a much warmer and wetter environment than Yukon. The prolonged transition period between early and late phases of the boreal as opposed to essentially none for the subalpine chronology might have occurred because of a greater supply of moisture in subalpine areas.

An unexpected feature of the early- and late-phase changes in climate relationships with RWI was the general shift towards weaker and sometimes opposing relationships relative to what previously occurred, rather than a strengthening of existing relationships. Weakened late-phase relationships signified their lesser importance in regulating tree-ring growth. Presumably, some climate variables will emerge as critical growth limiting factors (e.g., July mean minimum temperature, Figs. 7E and 7F), thus more strongly correlated with RWI, once ring widths reach an upper limit of growth relative to the availability of local resources. Many of the differences in correlation coefficients between the early and late phases of the boreal and subalpine chronologies were of larger amplitude (up to 0.88) than the less than 0.3 range in values reported by Griesbauer and Green (2012: Figs. 8 – 10). These differences could be due to the use of a longer time frame of reference (51 years versus 19 years) or regional climate differences. Distinctly different pre- and post-1950 RWI and climate variable correlations have also been reported in Alaska (Barber et al., 2004: Table V; Wilmking et al., 2004: Fig. 6) and elsewhere (Yu et al., 2013), so such changes are neither unique to southern Yukon nor associated with just high-latitude northern environments. In Yukon, RWI and climate relationships at a physiological level have probably formed and degraded numerous times since the 1890s when tree-ring growth began to stabilize after the Little Ice Age (Strong, 2017: Fig. 5B). Such changes might have occurred on an annual basis for individual variables, but not as persistently in one direction as occurred after 1967. Shifts in RWI and climate relationships may partially explain the dendrochronology phenomenon referred to as the “divergence problem” (D’Arrigo et al., 2008), which is the underestimation of reconstructed temperatures in high-latitude dendrochronological sequences after the mid-1900s.

Future Ecological Considerations

If average annual temperatures in southern Yukon warm by 2˚C or less and precipitation increases 10% – 20% during 2013 – 63 as suggested by Streicker (2016), it is possible that boreal and subalpine spruce radial growth rates could continue along their current trajectories. This possibility assumes similar rates of pre- and post-2013 temperature increase (Streicker, 2016), but more post-2013 summer precipitation to compensate for the greater evaporative potential associated with increasingly warmer ambient temperatures. If growing season precipitation increases are nearer the 10% limit or less, increased drought stress could eventually constrain subalpine and reduce boreal spruce radial growth rates.

The similarity in total tree-ring widths (Σ mm) suggests boreal and subalpine trees were equally productive during 1942 – 2013, despite different growth patterns. However, the currently greater subalpine spruce growth rate could easily outpace the future productivity of boreal spruce trees. Accompanying a greater rate of subalpine spruce growth and its more favorable growing conditions might also be an increase in tree densities as a result of infilling (Danby and Hik, 2007; Davis et al., 2020). These factors in combination could create more productive (m^{-3} ha) lower and middle elevation subalpine forest stands than their boreal counterpart (cf. Rhemtulla et al., 2002). A 2˚C increase in future temperatures could also cause a ~300 m (i.e., 2˚C/0.65˚C per 100 m) rise in treeline. However, the amount of area potentially transformable to semi-closed canopied forest due to these changes will largely depend upon the configuration of the associated topography and site conditions within the expansion zone.

CONCLUSIONS

Boreal and subalpine spruce growth rates did not decrease after 1950 as might have been predicted based on treeline chronologies compiled in the southern Yukon region. These ecosystems exist in the Whitehorse region because of local variation in landscape elevations and their corresponding ecological differences. Because of these basic ecological differences, spruce radial growth rates responded differently to recent greenhouse gas-driven climate changes. Subalpine and boreal RWI values will likely continue to diverge until moisture availability becomes limiting for subalpine spruce growth. Additional research at locations south of Yukon will be necessary to determine whether the observed substantial increase in subalpine spruce radial growth is a local or latitudinal phenomenon.

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