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Original article

Tree-ring characteristics of subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) in relation to elevation and climatic fluctuations

Bernhard Erich Splechtna[a,*], Jaroslav Dobrý[a,b] and Karel Klinka[a]

[a] Forest Sciences Department, University of British Columbia, Vancouver, B.C. V6T 1Z4, Canada
[b] Institute of Botany, Czech Academy of Sciences, 252 43 Pruhonice, Czech Republic

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Abstract – To determine the influence of elevation and year-to-year climatic fluctuations on radial growth and tree-ring properties of *Abies lasiocarpa*, we sampled dominant trees in 49 second-growth stands on mesic sites in British Columbia. The earlywood, latewood, and total ring width, and latewood and maximum density decreased significantly with increasing elevation. Since no significant trend was observed for latewood percentage and ring density, decline in maximum density will have minor impacts on wood quality of high and low-elevation *Abies lasiocarpa*. The correlation and response functions indicated that response to climatic factors changed with elevation. Although mesic sites within the study area were not expected to be water deficient, ring width decreased with the occurrence of warm and dry spring weather in low-elevation. Low summer temperature limited ring width in high-elevation and maximum latewood density and latewood width in low- and high-elevation, albeit the relationship was much stronger in high-elevation.

Abies lasiocarpa **/ dendrochronology / radial growth / response function / wood density**

Résumé – Caractéristiques des cernes annuels chez *Abies lasiocarpa* ((Hook.) Nutt.) en fonction de l'altitude et des variations climatiques. On a échantillonné les arbres dominants au sein de 49 peuplements de seconde venue sur des stations moyennes de la Colombie-Britannique, afin de déterminer l'influence de l'altitude et des variations climatiques sur la croissance radiale et les propriétés des cernes annuels chez *Abies lasiocarpa.* La largeur de la zone de bois initial, de la zone de bois final ainsi que la largeur totale du cerne, de même que la densité du bois final et la densité maximale diminuent de façon significative lorsque l'altitude augmente. Puisqu'on n'observe aucune tendance significative pour le pourcentage de bois final ou la densité des cernes, une baisse de la densité maximale n'aura qu'un impact mineur sur la qualité du bois chez *Abies lasiocarpa*, en haute comme en basse altitude. Les études de corrélation et de fonction reactionnaires indiquent que la réponse aux facteurs climatiques varie selon l'altitude. La largeur des cernes diminue en l'occurrence d'un printemps chaud et sec en basse altitude, bien qu'on se n'ait pas attendu une pénurie d'eau sur des stations moyennes de la région d'études. Des températures estivales basses limitent la largeur des cernes à haute altitude ainsi que la densité maximale du bois final et la largeur du cerne du bois final chez les arbres à faible et à haute altitude, bien que la relation soit plus forte à haute altitude.

Abies lasiocarpa **/ dendrochronologie / croissance radiale / fonction de réponse / densité du bois**

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* Correspondence and reprints: B.E. Splechtna, Trewaldstr. 1, A-3370 Ybbs/Donau, Austria. +43 7412 53565, fax: +43 7412 53565, e-mail: bsplechtna@aon.ac.at

1. INTRODUCTION

Subalpine fir [*Abies lasiocarpa* (Hook.) Nutt.] is one of the major timber crop species in the boreal climate of the montane forests and the central and southern, subalpine forests of British Columbia; thus silviculturists need information about its growth and the factors affecting it. Only very recently, the first height growth and site index functions for high-elevation subalpine fir were developed [9], relationships between subalpine fir site index and primary site factors were examined [4], and the decline in subalpine fir site index with increased elevation and latitude was quantified [35]. However, little is known about the variation in radial growth and tree-ring properties of subalpine fir in relation to site factors.

In the central region of interior British Columbia, subalpine fir grows from the lowest elevation (approximately 600 m) to tree line (over 1900 m). Considering this elevation range and the decline in subalpine fir site index (tree height (m) @ 50 years (breast height age)) in the Engelmann spruce – subalpine fir zone with increasing elevation – about 1 m in height with every 100 m increase in elevation and 1.4 m in height with every 1° in latitude [35] – it is logical to expect a decline in radial growth and changes in tree-ring properties from the montane to subalpine forest. However, it is not clear what will be the change in tree-ring properties of subalpine fir with increasing elevation, and whether the same climatic factors will affect low- and high-elevation trees in the same way.

Although the processes of wood formation remain unclear [43, 53], radial growth appears to be directly influenced by terminal growth and the subsequent production of growth hormones (e.g. auxins) and photosynthates, with environmental factors exerting an indirect influence on tree-ring formation. Secondary wall thickening of latewood cells is widely independent of cell expansion and appears to be regulated mainly by the amount of available photosynthates [1, 2, 40]. In humid climates, the decrease in maximum latewood density with decreasing temperature was explained by a combination of cool temperature and short growing season, the former adversely affecting photosynthesis, the latter resulting in a short time-period available for latewood formation [13, 61]. If cool temperature and short growing season adversely affect latewood formation, then the latewood width and the mean maximum density of the trees growing in high elevations or at high latitudes can be expected to be lower than in low elevations or at low latitudes [41]. As a corollary, we may expect a decline in the percentage of latewood and the mean ring density with increasing elevation [61].

In contrast, there are reports of a negative relationship between ring width and ring density in conifers [20, 42, 47, 63]. This relationship suggests slower-grown high-elevation conifers may have denser wood than low-elevation conifers. However, the literature concerning this issue is inconclusive, probably because of differences between species, the complexity of factors regulating the processes of wood formation, and differences in the approaches used to investigate these relationships [20, 33, 63]. Since wood density provides an excellent means of predicting end-use characteristics of wood [33], silviculturists need to know if and how wood density of timber crop species varies with environmental factors.

Dendrochronological studies conducted in forests close to the upper or northern tree-line suggested summer temperature is the principal tree growth-limiting factor, where growth is measured as ring width or maximum density [6, 13, 17, 21, 32, 55, 56, 59, 62]. However, recent studies conducted in boreal forests distant from the northern tree-line found that ring width of white spruce (*Picea glauca* (Moench) Voss) and jack pine (*Pinus banksiana* Lamb.) was negatively correlated with summer temperature and fire weather conditions [39]. Brooks et al. (1998) [7] used tree-ring widths to compare growth – climate relationships of two tree species growing at the northern and southern boundaries of the central Canadian boreal forests. For black spruce (*Picea mariana* (Mill.)) cool and wet conditions were favorable on both sites, whereas ring width of jack pine was positively related to high summer temperatures and increased spring precipitation regardless of latitude. This suggests that the response to climate change may be species-specific in the boreal forest [7] and emphasizes the need for investigating climate – growth relationships of different species in the same area.

Considering the importance of density as an index of wood quality, the role of climate as the major determinant of tree growth, and the concerns about the impact of climatic change on forest growth, the aim of the present study was to quantify the influence of local and regional climate on growth and wood quality of subalpine fir. The specific objectives were to determine (1) how tree-ring properties vary along an elevation gradient, using elevation as surrogate for local climate, and (2) which climatic variables affect the variation in tree-ring properties in low- and high-elevation subalpine fir. The first objective was achieved by relating tree-ring properties averaged over a 30-year period to elevation and the second objective by using dendrochronological methods.

2. MATERIALS AND METHODS

The study area encompassed central and southern British Columbia, specifically the montane Subboreal Spruce (SBS) zone (53° 50' to 54° 35' N; 121° 40' to 124° 10' W) and subalpine Engelmann spruce – subalpine fir (ESSF) zone (49° 30' to 55° 50' N; 115° 10' to 127° 40' W) [45] (*figure 1*). The climate of both zones is continental boreal; with short, wet summers and long, cold winters in the SBS zone, and with very short summers and very long, cold, snowy winters in the ESSF zone [37]. In the central region, the climatic zonation follows a gradient of increasing elevation from the SBS to ESSF to AT (Alpine Tundra) zone, with subalpine fir being present in both SBS and ESSF zones (ranging from about 600 m to sometimes over 1900 m asl.); however, in the southern region, fir is mainly present in the ESSF zone which extends from about 1 450 to nearly 2 300 m asl.

All 55 study stands were located in naturally established, unmanaged, single-storied, even-aged, subalpine fir-dominated stands which were without evidence of a history of observable damage. The stands ranged from 49 to 110 years at breast height and represented the mid-seral stage in secondary succession following wildfire or the intermediate stages in stand development, i.e., stem exclusion or understory reinitiation stages [48]. The stands were located throughout the study area to cover the widest range in climate conditions in the SBS and ESSF zones, i.e., extending from drier to wetter and warmer to colder variations of boreal climate in British Columbia.

Along the elevation gradient we constructed a climosequence (i.e. a series of ecosystems with similar environmental and biotic factors, differing only in climate) [44] by selecting study stands on sites that were typical of the vegetation zone [18, 37, 58]. Thus, study sites were located on flat areas, gentle slopes, or mid-slopes (to minimize the influence of aspect) and had mesic edaphic conditions, i.e., soils were freely drained and had a moderately deep to deep rooting zone (50 – 100 cm) and a loamy texture with coarse fragment content less than 50% by volume [52].

In each stand, a 20 × 20 m (0.04 ha) plot was established to represent an individual ecosystem relatively uniform in soil, vegetation and stand characteristics. The soil moisture and nutrient conditions were evaluated using the methods described by Green and Klinka (1994) [26]. The elevation of each plot was measured using a Thommen altimeter; latitude, longitude, and zone for each plot were identified according to its location on topographic and biogeoclimatic zone maps. To account for the temperature change with latitude, elevation was adjusted by adding a 100 m to the measured elevation for every degree of latitude north of the reference latitude of 49° N. This adjustment was based on a latitude-elevation relationship found for the spruce-fir forest along the Appalachian mountains [11].

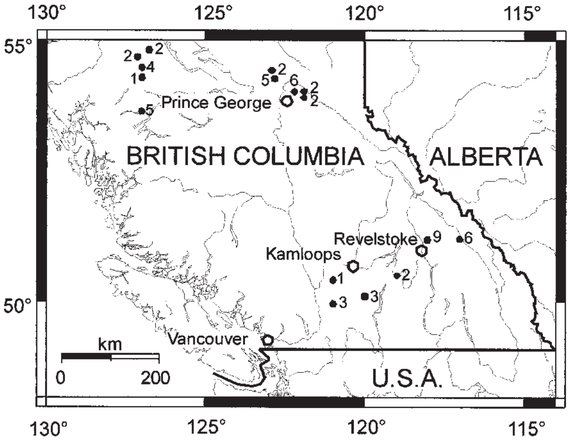

Figure 1. Sampling locations within British Columbia. The number of study stands in each location is indicated.

In each sample plot, three dominant, large diameter subalpine fir trees were felled and a breast-height (130 cm) disc taken for analysis. Sampling only dominant trees reduced potential variation in tree-ring characteristics caused by competition [51]. Since tree-ring characteristics vary also along the stem [41], breast height was used as a convenient reference height to control for this within-tree variation. Discs were transported to the laboratory, sanded, and inspected for reaction wood and other aberrant properties. Discs that showed reaction wood within the last 30 years of growth were eliminated. Consequently, 81 discs from 49 plots were selected for analysis. From each disc two radial samples (c.a. 5 mm wide) were cut from opposite directions making a set of 162 samples (data set 1). Further sample preparation followed standard dendrochronological procedures [54].

All 162 samples were submitted to Forintek Canada Corp. for X-ray densitometry, which was done according to the methodology described in Parker et al. (1980) [49]. The following measurements were taken for each tree-ring: distance from pith, earlywood width (EW), latewood width (LW), ring width (RW), earlywood density (ED), latewood density (LD), ring density (RD), minimum density (MND), and maximum density (MXD). The boundary between earlywood and latewood was defined as a fixed density value set to 0.44 g/cm^3. This value is regularly used for subalpine fir by Forintek Canada Corp. (pers. comm.) and corresponded well with the point of maximum density increase in the intra-ring density profiles of our samples. We calculated latewood percentage (LW%) from latewood width and ring width.

For the analysis of tree-ring – elevation relationships, we calculated the arithmetic mean of EW, LW, RW, ED, LD, RD, MND, and MXD for each ring from the two radii of each sample tree. Next, we calculated the arithmetic mean for each tree-ring variable for a 30-year period (1964 to 1993) and used these means in correlation and regression analyses [57]. In correlation analysis a significance level of $p \leq 0.05$ was chosen. Prior to the analysis, tree-ring variables were examined for normal distribution using probability plots and checked for linearity of relationships using scattergrams [8]. In sequential regression analysis, we used age and RW as covariates [60]. Because data set 1 included samples with a relatively wide range in age (49 to 110 years), and high-elevation trees tended to be older than low-elevation trees of the same height, we prepared another set (data set 2) that included samples with a narrower age range (61 to 89 years) to minimize the confounding effect associated with age. Data set 2 included 72 samples collected from 36 trees in 22 sample plots.

The dendrochronological analysis was based on a 47-year period time-series (1946 to 1992) for populations of both low- and high-elevation trees. Because we utilized discs that were originally sampled for height growth analysis, we could not follow standard dendrochronological procedures [23, 54]. Relating the year-to-year variation in climate to tree-ring series assumes knowledge of the exact year at which a given ring was formed. Even though the year of the last complete ring was known for the samples and the series were short, we had to crossdate the series to detect potential errors due to missing or false rings, sample preparation or measuring [23]. However, three discs sampled at each study site were not sufficient for reliable crossdating. Therefore, we merged data from adjacent plots within a 100 m of elevation (24 samples from 17 low-elevation trees (c.a. 700 m asl.) and 28 samples from 18 high-elevation trees (c.a. 1950 m asl.)). This was justified because we had sampled only on sites featuring similar topographic and edaphic conditions. The low-elevation (montane) set included samples from the SBS zone (near Prince George, 53° 53' N, 122° 40' W) and the high-elevation (subalpine) set included samples from the ESSF zone (near Revelstoke, 50° 58' N, 118° 11' W).

The dating of ring-width series and other ring characteristics based on density profiles was checked by marker rings (conspicuously narrow or wide rings, that occurred in the same year in many tree-ring series) and the COFECHA program [27, 30]. Additional validation of the crossdating was provided by a high correlation ($r = 0.85$) of our high-elevation chronology with that for Engelmann spruce (*Picea engelmannii* Parry *ex* Engelm.) at Bell Mountain (53° 20' N, 120° 40' W) [56].

Although we did not expect a suppression and release growth pattern in the samples from dominant trees, plots of ring-measurement series showed low-frequency variation, which varied between series. This indicated non-climatic signals in addition to the change of tree-ring properties with age. Therefore, we detrended the series using a 20-year cubic smoothing spline [5, 15] as provided by the ARSTAN program [14, 27]. The series that were well correlated were standardized and combined to 8 residual chronologies [14, 46] using the ARSTAN program – for two data sets (low- and high-elevation trees) and four tree-ring variables (RW, LW, LW%, and MXD) for the 47-year (1946 – 1992) period. While the autoregressive models used to build the residual chronologies probably removed all low-frequency climate variation, the common high-frequency variation in the chronologies was emphasized [46].

To examine relationships between tree-ring properties, we calculated cross-correlations between the developed chronologies. We compiled monthly mean, maximum, and minimum temperature and monthly total precipitation data for the same period from climate stations in Prince George and Revelstoke, respectively. (Environment Canada, Historical and Statistical Climate Information, Vancouver, BC). The data were examined for homogeneity by the DPL-HOM program [31]. We used residual chronologies of four tree-ring variables (RW, LW, LW%, and MXD) from two locations (low- and high-elevations) in simple correlation analysis and bootstrapped response function analysis [24, 25, 28] to examine relations of year-to-year variations of climatic variables to selected tree-ring variables. After examining response functions and correlation coefficients, we used mean maximum daily temperatures and total precipitation for selected time periods in regressions on selected tree-ring chronologies.

3. RESULTS

3.1. Variation in the mean tree-ring properties along an elevation gradient

Correlations between adjusted elevation and (i) RW, EW, LW, LD, and MXD were significantly negative, (ii) LW% were significantly positive, and (iii) RD, ED, and MND were non-significant (*table I*). However, there was a significant positive correlation between adjusted elevation and breast-height age ($r = 0.45$); and correlation coefficients of the tree-ring variables with age were similar to those with adjusted elevation. The strong age – elevation relationships suggested a confounding effect associated with age on the variation in the 30-year mean tree-ring properties. Therefore, we repeated the analysis using data set 2 that had a narrower range in age than data set 1 (61 to 89 *versus* 49 to 119 years) while keeping a more or less even sample distribution along an elevation gradient.

The correlation coefficients for age and LW% with adjusted elevation were not significant when using data set 2, while the correlation coefficients for other tree-ring properties changed relatively little (*table I*). The RW, EW, and LW decreased with increasing adjusted elevation and among density properties, LD and MXD were significantly negatively correlated with adjusted elevation (r = –0.66 and –0.72, respectively). Adjusted elevation explained also a considerable amount of variation in RW, LW, and MXD in sequential regression in addition to the age, and RW effect, respectively (*table II*).

Latewood width and LW% were not significantly correlated but LW was significantly correlated with RD (r = 0.64), LD (r = 0.74), and MXD (r = 0.70). High LW% was significantly associated with high RD (r = 0.77) but not with MXD. Correlation between RD and RW was also not significant. LW% was the single best predictor of ring density ($R^2 = 0.58$, $p < 0.001$) and LW% and LW together accounted for 77% ($p < 0.001$) of the variation in ring density, indicating a potential for predicting mean ring density from easily obtainable ring properties (*table II*).

3.2. Relationship between Year-to-Year Variations in Tree-Ring Properties and Climate

There was a very weak common signal between low- and high-elevation trees in the RW, LW and LW% chronologies but a stronger common signal in the MXD chronologies, which had the cross-correlation coefficient of 0.45. When chronologies from different tree-ring characteristics were compared, there was only a partial agreement between chronologies from low- and high-elevation trees (*table III*). The negative correlation between RW and LW% chronologies for low- and high-elevation trees indicated a negative association of RW and ring density regardless of elevation. However, the correlations between chronologies of latewood characteristics (LW, LW%, and MXD) were stronger in high-elevation than in low elevation subalpine fir. On the other hand, the low-elevation RW and MXD chronologies were significantly correlated but the high-elevation chronologies were not (*table III*). These differences in

Table I. Simple correlation coefficients between adjusted elevation and tree-ring properties of subalpine fir for data sets 1 and 2. Asterisk (*) denotes significant relationships at $P < 0.05$.

Property	Data set 1 Age range 49–119 yrs. $n = 48$	Data set 2 Age range 61–89 yrs. $n = 22$
Age (at breast height)	0.45*	0.24
Ring width (RW)	–0.62*	–0.57*
Earlywood width (EW)	–0.61*	–0.55*
Latewood width (LW)	–0.47*	–0.51*
Latewood percent (LW%)	0.46*	0.08
Ring density (RD)	0.12	–0.27
Earlywood density (ED)	0.26	0.12
Latewood density (LD)	–0.52*	–0.66*
Minimum density (MND)	0.44*	0.34
Maximum density (MXD)	–0.57*	–0.72*

Table ll. Selected models for the regression of 1a) ring width (RW) and 1b) latewood width (LW) on age (AGE); 2a) ring width and 2b) latewood width on age and adjusted elevation (ELE); 3a) maximum density on ring width, and 3b) maximum density on ring width and adjusted elevation; and 4a) ring density (RD) on percent latewood (LW%), and 4b) ring density on percent latewood and latewood width. SEE is the standard error of the estimate; $N = 22$.

[1a]	RW (mm) = 2.214 – 0.0138(AGE)		
	$R^2 = 0.17$	SEE = 0.238 mm	$P = 0.031$
[1b]	LW (mm) = 0.853 – 0.0063(AGE)		
	$R^2 = 0.39$	SEE = 0.067 mm	$P = 0.001$
[2a]	RW (mm) = 2.457 – 0.0104(AGE) – 0.0003(ELE)		
	$R^2 = 0.38$	SEE = 0.206 mm	$P = 0.004$
[2b]	LW (mm) = 0.915 – 0.0054(AGE) – 0.00008(ELE)		
	$R^2 = 0.51$	SEE = 0.060 mm	$P < 0.001$
[3a]	MXD (g/cm^3) = 0.436 + 0.183(RW)		
	$R^2 = 0.52$	SEE = 0.046 g/cm^3	$P < 0.001$
[3b]	MXD (g/cm^3) = 0.624 + 0.120(RW) – 0.00007(ELE)		
	$R^2 = 0.64$	SEE = 0.039 g/cm^3	$P < 0.001$
[4a]	RD (g/cm^3) = 0.264 + 0.0036(LW%)		
	$R^2 = 0.58$	SEE = 0.015 g/cm^3	$P < 0.001$
[4b]	RD (g/cm^3) = 0.247 + 0.003 (LW%) + 0.0946 (LW)		
	$R^2 = 0.77$	SEE = 0.009 g/cm^3	$P < 0.001$

Table III. Correlations between chronologies of ring width (RW), latewood width (LW), latewood percentage (LW%), and maximum density (MXD), separately for low- (L) and high- (H) elevation subalpine fir.

	LW		LW%		MXD	
	L	H	L	H	L	H
RW	0.47	0.29	–0.47	–0.48	0.46	0.12
LW	1	1	0.48	0.61	0.69	0.80
LW%			1	1	0.22	0.57

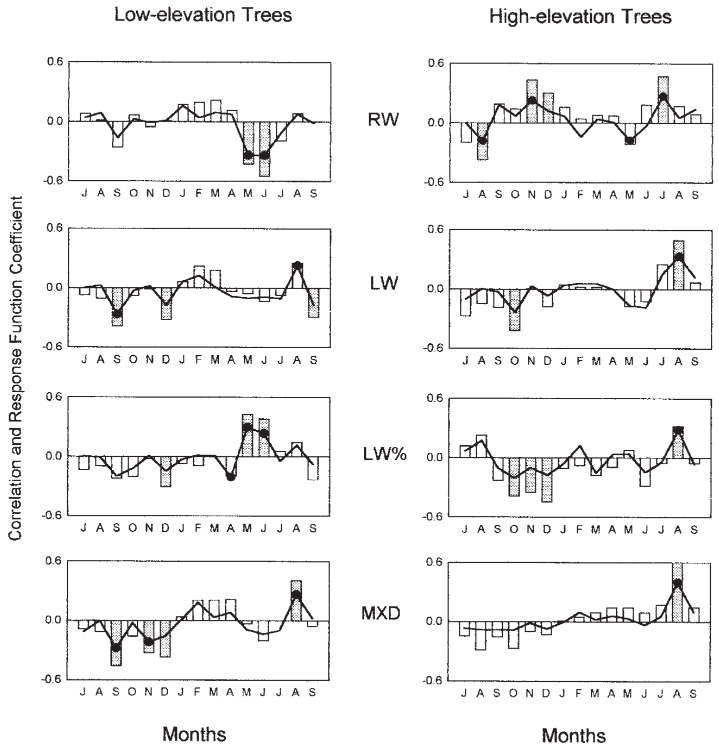

Figure 2. Mean monthly temperature – correlations (columns) and response functions (lines) of the indices of the ring width (RW), latewood width (LW), percent latewood (LW%), and maximum density (MXD) chronologies for low- and high-elevation subalpine fir on the mean monthly temperature for 15 months (July of the previous year to September of the current year) in the 1946 – 1992 period. Shaded columns indicate months of significant correlations, months of significant response are indicated by bullets.

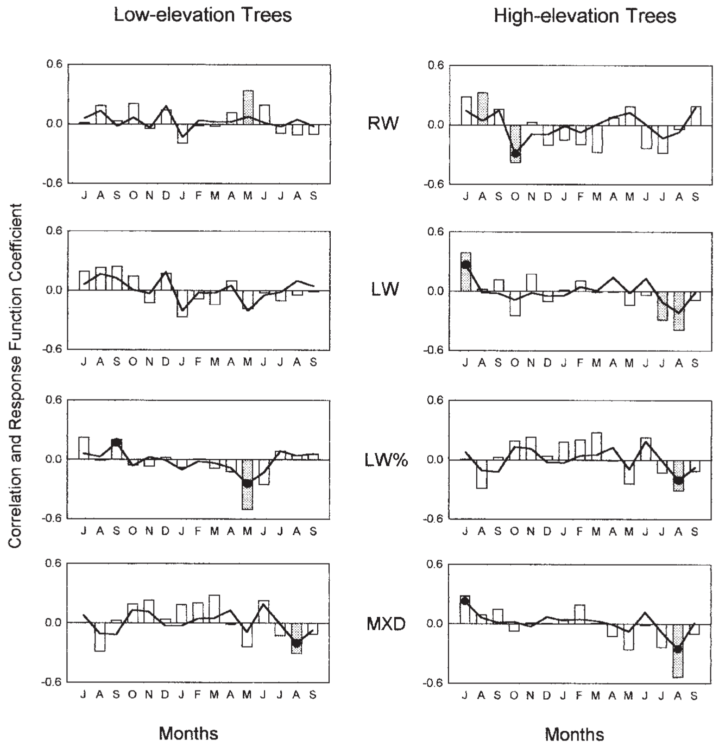

Figure 3. Mean monthly total precipitation – correlations and response functions of the indices of the ring width (RW), latewood width (LW), percent latewood (LW%), and maximum density (MXD) chronologies for low- and high-elevation subalpine fir on the monthly total precipitation for 15 months (July of the previous year to September of the current year) in the 1946 – 1992 period. Shaded columns indicate months of significant correlations, months of significant response are indicated by bullets.

correlation between chronologies indicated differences in the factors influencing wood formation in low and high elevation.

Correlation coefficients and response functions showed similar patterns and indicated how climatic factors influence the selected tree-ring properties (RW, LW, LW%, and MXD) (*figures 2 and 3*). In general, correlations and responses were stronger (i) to temperature than precipitation and (ii) in high-elevation trees than low-elevation trees. A negative response to precipitation in the current growing season was always associated with a positive response to growing season temperature, illustrating the negative association of mean monthly temperatures with monthly precipitation sums. Response functions of RW and LW% differed substantially between low- and high-elevation trees, whereas similar patterns of response were found for LW and MXD (*figures 2 and 3*).

Tree ring characteristics of low-elevation trees were mainly related to spring and summer temperatures of the current season (*figure 2*). Variations in RW were negatively related to May and June temperatures, whereas LW% showed a positive relationship with spring temperatures (accompanied by a negative relationship with May precipitation). Variations in LW and MXD were positively related to August temperatures and negatively related to fall temperatures of the previous season. In addition, MXD was negatively related to August precipitation (*figures 2 and 3*).

Tree ring characteristics of high-elevation trees were mainly related to summer temperatures of the current season (*figure 2*). Variations in RW were positively related to July temperatures of the current year and fall temperatures of the previous year, but negatively related to May temperatures of the current year and the previous year's August. There was also a negative association of RW with precipitation of the previous fall and winter. Variations in LW, LW%, and MXD were all significantly positively related to August temperature but negatively to August precipitation, indicating that latewood formation was favored by warm, sunny, and – therefore – relatively dry weather in August. In addition, LW and LW% showed a negative association with fall temperatures of the previous season (*figures 2 and 3*).

Two results from response function analysis called for a further analysis. Firstly, the negative response of RW to late spring temperature, and secondly, the large amount of variation in MXD solely explained by August temperature.

Regression analysis showed that the mean daily maximum temperature for the two month period (May and June) explained 45 % ($P < 0.001$) of the variation in RW, whereas the total sum of precipitation for May and June explained only 17% ($P = 0.004$). When both variables were used, the partial F-test for precipitation was not significant ($P = 0.59$).

To further elucidate the negative response of radial growth to high spring temperatures in low-elevation trees, we examined pointer years (years with distinctively narrow rings) in the RW chronology in relation to climatic chronologies (*figure 4*). A visual comparison of the RW chronology with the chronologies of mean daily maximum temperature for May to June and total precipitation for the same months showed that both above-average temperatures and below-average precipitation were associated with narrow rings. The use of the LW% chronology for the same comparison showed the opposite trend (*figure 4*). Clearly, precipitation and temperature were negatively correlated ($r = –0.69$) and high temperatures were always accompanied by low precipitation. However, when precipitation was low but temperatures were moderate as in the years 1965, 1978 and 1985, RW was about average.

The relationship between latewood properties, particularly MXD, and the mean August temperature of the current year in both low- and high-elevation trees was also stronger when using maximum temperature. As indicated by response functions, the strength of relationships was higher for high-elevation than low-elevation trees. A simple linear regression of MXD on the maximum August temperature for high-elevation trees yielded the adjusted R^2 value of 0.52 compared to 0.20 for low-elevation trees. *Figure 5* illustrates how closely the MXD-index followed the maximum temperature curve in high-elevation in most of the study years.

4. DISCUSSION

4.1. Variation in tree-ring properties along an elevation gradient

Radial growth (RW, EW, and LW) and latewood density (LD and MXD) of subalpine fir declined with increased elevation. The elevation gradient from montane to subalpine boreal climates in this study coincided in general with a temperature gradient [35]. The stronger correlations and responses of RW, LW, LW%, and MXD to temperature than to precipitation support the assertion that temperature (summer temperature, in particular) is the principal climatic growth factor. Decline of these properties with decreasing temperature agrees with previous findings [13, 55, 56] and may be explained by delayed growth, lower auxin levels, and reduced availability of photosynthates for cell-wall thickening [13, 41].

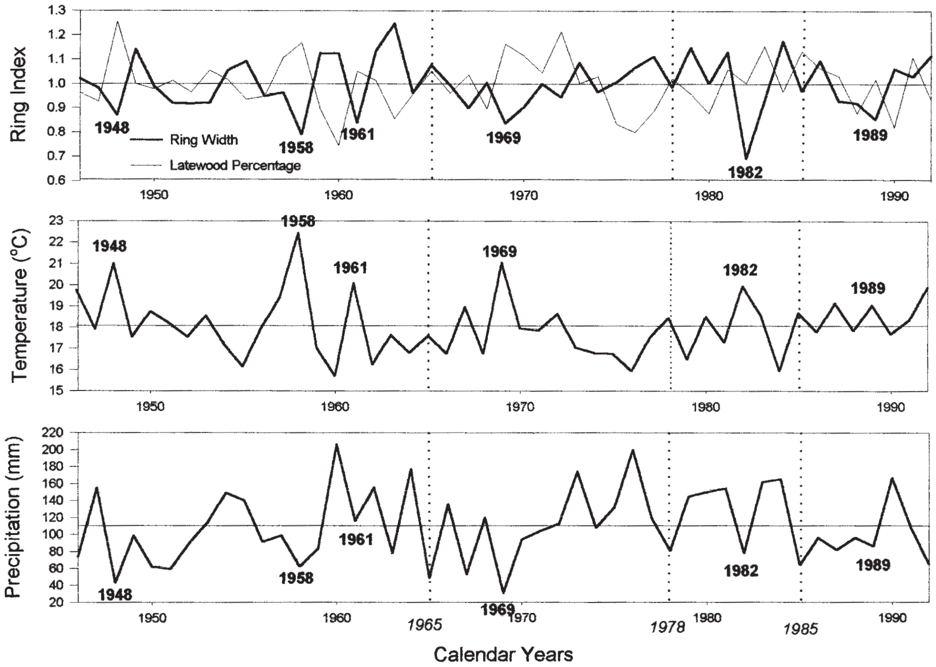

Figure 4. Comparison of the low-elevation ring width and latewood percentage chronologies (top figure) with the average daily maximum temperature for May and June (central figure) and the total precipitation for May and June (bottom figure). Pointer years for ring width are indicated by calendar years in bold print. The years of low precipitation and moderate temperature (1965, 1978, and 1985) are indicated by vertically oriented, dotted lines.

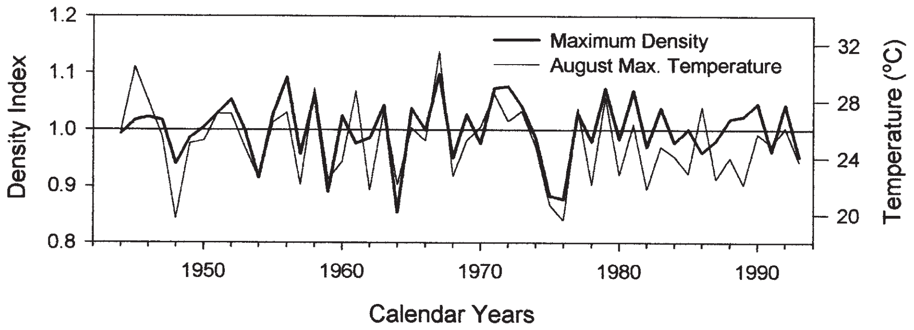

Figure 5. Comparison between the indices of the maximum density chronology and maximum August temperature of the current year for the high-elevation subalpine fir trees (Revelstoke) in the 1946 – 1992 period.

Our study, however, did not provide evidence for the presence of the negative relationship between LW% and elevation that was reported elsewhere [41, 55, 61], nor showed a significant relationship between elevation and RD. These results suggest that there is little change in density of subalpine fir wood with elevation in natural boreal forests of interior British Columbia.

However, the relationships between elevation and LW% and RD deserve a further explanation. Firstly, there is a strong association between LW% and RD. The mean RD depends more on LW% than on ED and LD because variation in ED and LD is not as large as in LW%. This assertion is based on Barbour et al. (1994) [3] and this study, which both show a strong relationship between LW% and RD (*table II*). Secondly, the relationship between LW% – and thus RD – and environment is complex because LW% is influenced by changes in both EW and LW [3, 63]. Decline in LW% with increasing elevation was explained by a shorter period of latewood-formation [61]. Schweingruber et al. (1979) [55] found a good agreement between LW and LW% chronologies of various tree species over a large area in the European Alps. We found only moderately high correlation between LW and LW% chronologies for low- and high-elevation trees (r = 0.48 and 0.61, respectively). However, simple correlation between the mean LW% and LW for the 30-year period showed only a weak positive relationship (r = 0.31) and a stronger negative relationship between LW% and EW (r = –0.53). This indicates that LW% is somewhat independent of LW, apparently more so in low- than in high-elevation trees. Which portion of the tree-ring – earlywood or latewood – determines the change in LW%, may vary from low- to high-elevation, from site to site, or from year to year. The varying relationships between LW%, LW, and RW, may explain the lack of relationship between RD and RW in our data and the inconsistent reports concerning this issue [16, 20, 33, 47, 50, 63].

4.2. Relationships between year-to year variations in tree-ring properties and climate

The dendrochronological analysis of this study differed significantly from the approach that selects study trees from environmentally extreme sites to maximize the climate signal in the tree ring series [23]. We used sites that were typical of the vegetation zone at different elevations because our focus was rather on the change of tree growth – climate relationships with elevation than on extraction of maximum climate information. The biogeoclimatic classification system of British Columbia provided a useful framework to construct a climosequence and minimize non-climatic site effects [36, 52].

After learning the change in mean ring-characteristics of subalpine fir along the temperature (elevation) gradient, we wanted to know, if tree-ring properties on low- and high-elevation zonal sites were influenced by the same climatic factors. We hypothesized that low temperature would limit radial growth in both low- and high-elevation trees, but the impact would be less pronounced in the former than the latter. However, our results indicate that, in general, low summer temperature limits wood formation processes in high-elevation trees, whereas in low-elevation trees, high spring temperatures and low August temperatures are limiting.

Many dendroclimatic studies have found RW and MXD chronologies in humid climates to be positively related with growing-season temperature [12, 23, 54, 56]. Some studies report a strong positive influence of August temperature (the time of latewood formation) on MXD [55, 59, 62], while other studies report a high spring temperature to favor the formation of dense latewood [13, 17, 19, 34, 56]. The explanation given was that favorable conditions for photosynthesis early in the growing season would result in early initiation of cambial activity and increased supply of photosynthates that, in turn, would benefit cell-wall thickening later in the season [13]. We found only August temperature to be positively related to MXD in both low- and high-elevation trees, and this relationship was stronger for high-elevation than low-elevation trees (*figures 2 and 5*). This is in agreement with our finding that MXD decreased significantly along the temperature gradient with increasing elevation.

Our data indicate that a below-normal spring temperature favors RW in low elevation-trees and an above-normal summer temperature favors RW in high-elevation trees. A favorable influence of cool growing season temperature on RW is known to occur in conifers growing in semiarid environments [10, 22, 23, 34] and the Canadian boreal forest [7, 39]. The southern limit of the western Canadian boreal forest was found to coincide with isolines of climatic moisture indices [29]. However, our study stands in the SBS zone are not moisture-limited because (i) compared to the boreal forest east of the Rocky Mountains, the SBS zone is influenced by a continental humid climate, and (ii) we sampled on mesic sites. However, springs in the SBS zone are usually dry [37] and can be warm (maximum temperature in May and June can be as high as in July or August; Environment Canada, Historical and Statistical Climate Information, Vancouver, BC). The fact that the relationship is stronger with temperature than with precipitation probably indicates an association with snowmelt. Cool spring temperatures prevent soils from drying out too quickly after snowmelt. On the other hand, dry spring spells (in our data indicated by high average daily maximum temperatures and low total monthly precipitation) occur regularly in this area (*figure 4*). The upper horizons of the soil may dry out quickly creating water stress for the trees. The water in deeper horizons of the soil may not be readily available because these horizons may be still frozen or cool soil temperatures may impede water uptake [38]. This situation seems to have a direct influence on earlywood formation, causing a higher latewood proportion in the tree-ring as indicated by the negative correlation between RW and LW% chronologies (*figure 4*).

Ring width in high-elevation trees also showed a significant negative response to May temperature but a significant positive response to June temperatures of the current year. On subalpine sites over most of the ESSF zone there is usually a high snowpack in May and soils are usually frozen (they often freeze even before the first snowfall [37]. In this situation, above-normal temperature will induce water stress and possibly desiccation [17, 32]. The presence of a strong positive response of RW to July temperature of the current year (corresponding to the spring season) and of LW, LW%, and MXD to August temperature of the current year (corresponding to the summer season) signifies that not soil moisture but temperature limits tree growth in subalpine boreal climates.

This study complements the studies describing growth responses of tree species to climatic fluctuations on different sites in temperate and boreal forests [7, 34, 56]. Our results exemplify the similarities and differences in the general growth response of subalpine fir to temperature and precipitation fluctuations at different elevations in interior British Columbia. However, response functions and correlations do not necessarily contain much information about relationships between climate and tree growth in years when other factors than climate may control wood formation. For example, in low-elevation trees, this situation becomes apparent when the spring temperature is about normal. Thus, to gain further insight into changes in wood properties with elevation, yearly variations of the relationships between tree-ring and climatic variables should be studied along an elevation gradient [34].

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