Variation in radial growth patterns of *Pseudotsuga menziesii* on the central coast of British Columbia, Canada

Qi-Bin Zhang and Richard J. Hebda

Abstract: Radial growth of trees in mountainous areas is subject to conditions associated with changes in elevation. We present ring-width chronologies for Douglas-fir trees (*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*) at nine sites spanning low to high elevations in the Bella Coola area of the central coast of British Columbia, near the northern limits of the species distribution, and investigate the variation in tree-ring growth patterns in relation to different elevations, using principal component (PC) analysis. We find that the first PC, which represents 55.6% of the total variance, reflects a common growth response at sites of different elevation. Response function analysis indicates that growing season precipitation is the major factor in controlling tree-ring growth. This factor explains more of the variance in low-elevation sites than it does in high-elevation ones. Temperature in August of the preceding year shows a negative relationship to ring-width growth. The second PC represents 16.7% of the total variance and reveals a distinct difference in growth response between low- and high-elevation sites. The length and temperature of the growing season seem to play an important role in tree-ring growth at sites of high elevation. Comparison of the Bella Coola records with those from southern Vancouver Island suggests that growing season precipitation influences growth of Douglas-fir on a macroregional scale, but other factors such as temperature modify the growth response at the limits of the distribution of the species.

Résumé : La croissance radiale des arbres en région montagneuse est sujette à des conditions de croissance associées aux changements d'altitude. Nous présentons des séries dendrochronologiques pour des tiges de douglas de Menzies typique (*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*) dans neufs sites dont l'altitude varie de faible à élevée. Ces sites sont situés dans la région de Bella Coola sur la côte centrale de la Colombie-Britannique, près de la limite nord de l'aire de répartition de l'espèce. Nous avons examiné la variation dans les patrons de croissance radiale en fonction de l'altitude à l'aide de l'analyse en composante principale. La première composante principale, qui représente 55,6 % de la variance totale, reflète une réaction de croissance commune dans les sites situés à différentes altitudes. L'analyse d'une fonction de réponse indique que la précipitation durant la saison de croissance est le facteur principal qui contrôle la croissance radiale. Ce facteur explique une plus forte proportion de la variance dans les sites à basse altitude que dans les sites à haute altitude. La température du mois d'août de l'année précédente montre une relation négative avec la croissance radiale. La deuxième composante principale représente 16,7 % de la variation totale et révèle une nette différence dans le comportement de la croissance entre les sites situés à basse et à haute altitude. La durée et la température de la saison de croissance semblent jouer un rôle important dans la croissance radiale dans les sites situés à haute altitude. La comparaison des données de Bella Coola avec celles du sud de l'île de Vancouver porte à croire que la croissance du douglas de Menzies est influencée à une échelle macro-régionale par les précipitations pendant la saison de croissance, mais que d'autres facteurs tels que la température modifient la réponse en croissance aux limites de l'aire de répartition de l'espèce.

[Traduit par la Rédaction]

Introduction

Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*) is a preeminent and commercially important tree species in northwestern North America, especially coastal British Columbia (Rajala 1998). It occurs over a wide latitudinal and elevation range. Tree-ring and pollen studies in coastal British Columbia show that climate change has historically affected the growth of individual Douglas-fir trees, as well as affecting forest composition and structure (Hebda 1995, 1997, 1998; Zhang 1996; Hebda and Brown 1999). Recognizing that this species has been sensitive to climatic changes and is potentially sensitive to future change, we undertook a study of climate – radial growth relationships of Douglas-fir in the Bella Coola valley, near the northern lim-

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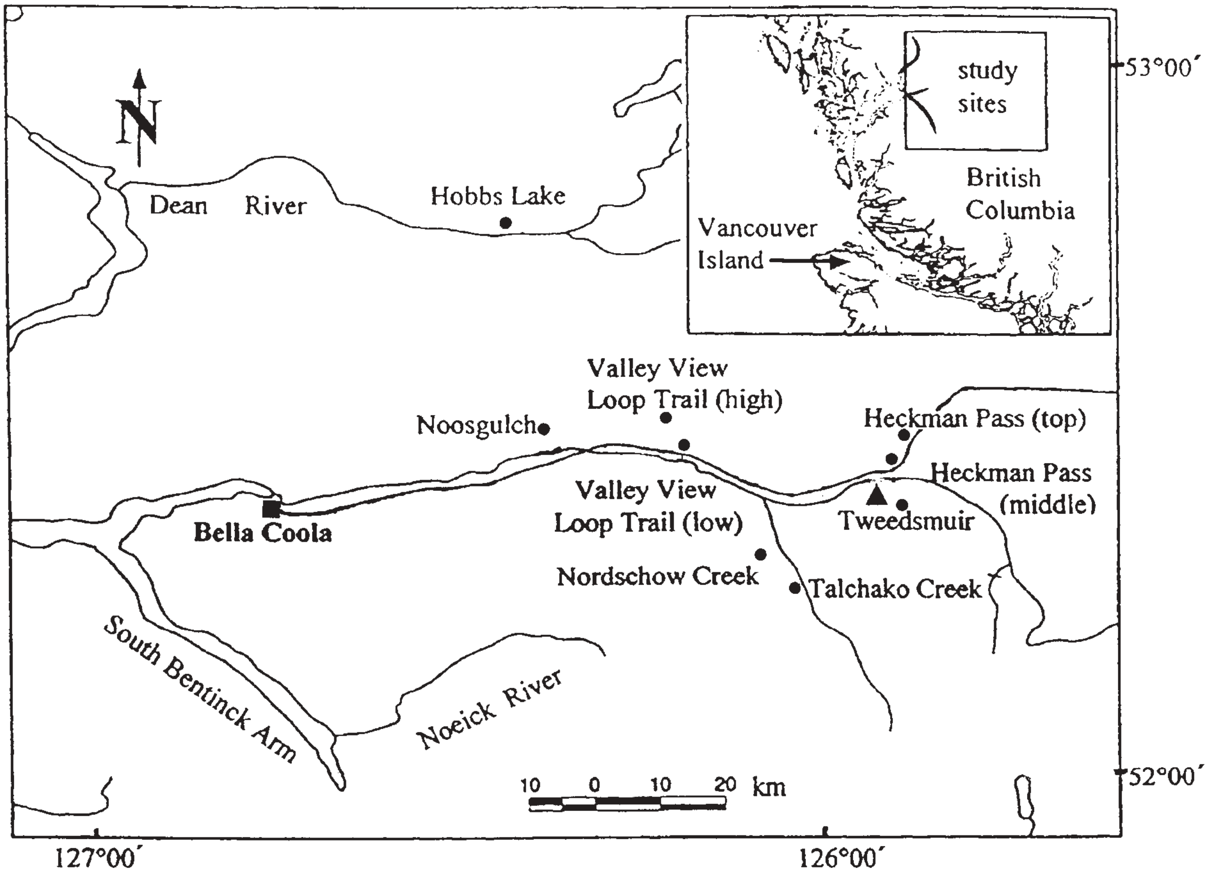
Fig. 1. Location of the nine tree-ring study sites and the weather station at Stuie–Tweedsmuir (▲) in the Bella Coola area of central coast British Columbia, Canada.



its of its range, and at sites of different elevation. Our goal was to better understand the variation in radial growth patterns of Douglas-fir in mountainous areas.

Dendroecological techniques have long been recognized as useful tools for assessing the relationships between environmental factors (including climate) and tree-ring growth and their spatial patterns (Fritts and Swetnam 1989; Zhang and Alfaro 2003). In mountainous areas, the growth conditions of trees differ with altitude; thus, the climate–growth relationships may vary with changes in altitude (Kienast et al. 1987; Yoo and Wright 2000). We note that no studies of Douglas-fir growth in relation to altitude have been carried out in the Bella Coola region. In addition, this region is located near the transition zone between two macroclimatic regimes, with summer drought figuring prominently to the south, but not so to the north (Hebda 1997, 1998). The maintenance of a sustainable forestry in the context of future climate change mandates a need to understand the response characteristics of Douglas-fir to different growth conditions.

The specific objectives of our study were (1) to provide dendrochronological data for a previously unstudied region; (2) to examine the variation in radial growth patterns of Douglas-fir among sites in the mountainous region; and (3) to identify the climatic factors most responsible for the variation in tree-ring growth. We conclude with a discussion of the climate–growth relationships of the same species under different climates in different regions to gain insights into the role of macroregional climate in tree growth.

Materials and methods

Study area

The study area is located in the inland portion of the central coast of British Columbia (Fig. 1). Deep fiords and valleys cut as much as 3 km of vertical relief into the Coast Range. Within the study area, the Coast Range abuts the high-elevation western margin of the Interior Plateau. The Bella Coola – Atnarko and Dean river systems rise in the upper reaches of the Interior Plateau, then cut through the Coast Mountain mass, reaching the sea at the head of fiords. Valley bottoms are generally flat, with terraces on the lower slopes, but the middle to upper slopes are extremely steep.

The climate changes markedly from mild rainy winters and moderate humid summers at fiord heads (such as Bella Coola) to long cold winters and short dry cool summers on the Interior Plateau. Between these two extremes, the valley bottoms and adjacent slopes experience cool to cold snowy winters and warm to hot dry summers. According to the climatic station at Stuie–Tweedsmuir, in the middle of the study area, mean annual air temperature ranges from 4.6 to 9.1 °C, with a mean January temperature of –2.1 °C and a mean July temperature of 16.3 °C. Total annual precipitation is 908–2197 mm, with 28% of the precipitation distributed in April–September. There are no long-term climatic data for mid- to high-elevation sites in the mountains of the study area, though short-term intermittent observations are available for Anahim Lake, which is located at an elevation of

Table 1. Dendrochronological characteristics of *Pseudotsuga menziesii* ring-width chronologies at nine sites in the Bella Coola area of central coast British Columbia, Canada.

Site code	Elevation (m a.s.l.)	Chronology (years)[a]	Trees (*n*)	Mean sensitivity	Serial correlation	Signal/noise ratio	First-order autocorrelation
HP1	1060	111 (1886–1996)	17	0.22	0.54	2.53	0.5
HBL	850	156 (1841–1996)	15	0.21	0.58	6.86	0.63
HP2	820	125 (1872–1996)	17	0.21	0.61	6.3	0.41
NDS	650	322 (1675–1996)	29	0.19	0.51	4.69	0.41
VV1	650	217 (1765–1996)	22	0.23	0.56	6.43	0.43
TCH	300	309 (1688–1996)	20	0.19	0.57	9.62	0.48
TWS	260	251 (1746–1996)	16	0.20	0.48	3.71	0.40
VV2	250	287 (1710–1996)	17	0.26	0.60	9.37	0.50
NSG	250	216 (1781–1996)	16	0.23	0.58	8.85	0.33

Note: a.s.l., above sea level; HBL, Hobbs Lake; HP1, Heckman Pass (upper); HP2, Heckman Pass (middle); NDS, Nordschow Creek; NSG, Noosgulch; TCH, Talchako Creek; TWS, Tweedsmuir; VV1, Valley View Loop Trail (upper); VV2, Valley View Loop Trail (lower).
[a]Ranges in parentheses.

1099 m above sea level (a.s.l.) and about 30–50 km east of the main study area (Environment Canada, unpublished station data).

Temperate coniferous rain forest of the Coastal Western Hemlock biogeoclimatic zone grows along the coast but is replaced inland under the dry valley climate by mixed conifer and deciduous forest of the Interior Douglas-fir biogeoclimatic zone. Upslope on the coast, conifer forests of the Mountain Hemlock biogeoclimatic zone occur, whereas inland there are Engelmann Spruce – Subalpine Fir (ESSF) biogeoclimatic zone conifer forests (Hebda and Allen 1993). Douglas-fir trees are rare near the ocean but predominate on valley bottoms inland near Stuie–Tweedsmuir. They grow abundantly on terraces above the valley bottom but occur mainly on well-drained, south-facing slopes with increased elevation in the ESSF zone.

Sampling strategy

We chose the sample locations to be reflective of radial growth variability between sites from low to high elevations in the Bella Coola area of central coast British Columbia. We sampled a series of nine sites from the accessible valley bottom in the Bella Coola – Atnarko drainage, up Young Creek (a tributary of the Atnarko River) to the Dean River system (accessed by helicopter), and into the middle reaches of Heckman Pass, where the upper limit of Douglas-fir distribution was reached (Fig. 1). Except for the Hobbs Lake locality, all sites are in the same valley system and subject to the same weather patterns. The sites occur mostly on moderate to steep south-facing macroslopes on bedrock or medium- to coarse-textured substrates.

At each site, 15–30 of the largest and presumably oldest trees were selected for increment core sampling. Each increment core represented a sample of the site chronology. The trees were selected subjectively, with a view to obtaining climatic signals from sensitive trees and reducing nonclimatic signals from local disturbances and competition among trees. This strategy of subjective sample selection is one of the principles in the study of dendroclimatology (Fritts 1976). The practical selection of trees was based on local conditions, such as coarse-textured soil on a slope, and minimal competition from neighbouring trees (Fritts 1976). One core per tree was extracted at breast height and in a direction parallel to the slope contour. For the few trees whose increment core contained broken pieces, an additional core from the opposing side was collected. In total, 235 increment cores were collected from 202 living Douglas-fir trees at nine sites at elevations in the range of 250–1060 m a.s.l. (Fig. 1).

Chronology development

In the laboratory, the increment cores were mounted in slotted wooden boards and polished with sandpaper of progressively finer grit. The ring widths were measured with a Windendro™ image-analysis system (Régent instruments Inc., Québec, Que.), and the measured tree-ring sequences were cross-dated and quality-checked with the software COFECHA (Holmes 1983). The cores of poor quality (e.g., fragmented, rotted, not cross-datable) were excluded from further dendrochronological analysis. For the trees with two cores, the best-quality one was selected for chronology building. The exclusion of poor-quality cores was necessary to guarantee precision of cross-dating and strengthen the useful signals in tree rings. In total, increment cores from 169 trees were selected (cores from 33 trees were excluded) for the construction of tree-ring chronologies (Table 1).

Ring-width chronology for each site was developed with the software ARSTAN (Grissino-Mayer et al. 1996), in which a double detrending method was chosen. First, a negative exponential curve was used to detrend the measured tree-ring sequences to remove the biological growth trend related to the tree's age. The subsequent tree-ring index sequences were then detrended a second time with a cubic spline of 50% frequency-response cutoff at 64 years to remove a low-frequency trend related, possibly, to stand dynamics. The ring-width indices following the double detrending were averaged together by year across different samples for each site with a robust mean calculation, to further remove the random signals related to local disturbances (Cook et al. 1990). The resulting standard tree-ring chronology for each site conserved the common signals in different samples and reflected mainly the variations in climate. The length of chronology used for analysis was chosen such that the interval had at least 10 sample replications. Chronological statistics, such as the mean sensitivity (a measure of the annual variability in tree rings), serial correlation (a measure of the amount of common signals among tree-ring sequences), signal/noise ratio (a measure of the strength of the common signals relative to the uncommon signals of noise), and autocorrelation (a measure of the association between growth in the previous year and that in the current year), were obtained to show the characteristics of the tree-ring chronologies.

Principal-component analysis of the site chronologies

The tree-ring chronologies at the nine sites at different elevations in Bella Coola area contained a variety of both local and regional environmental signals. Principal component (PC) analysis (LaMarche and Fritts 1971; Brubaker 1980) was used to summarize the regional variation in radial growth patterns carried by the nine site chronologies. This analysis was conducted by using the software PCA (Grissino-Mayer et al. 1996) and the correlation matrix of the nine site chronologies for the common interval 1886–1996. By this method, the first PC accounted for the greatest proportion of the total variance in the nine chronologies, the second PC accounted for the largest fraction of the remaining total variance, and so on. Each PC was orthogonal (unrelated) to the other and involved a linear combination of the nine site chronologies. The series of PC scores over the chronology length represented the growth variation common to the nine sites. The weight associated with each chronology conveyed information about the characteristic growth relationship between a specific site and the PC: the higher the weight, the closer the relationship (Legendre and Legendre 1998).

Climate–growth relationships

There are no sufficiently long climate records available for sites at different elevations in the region. Consequently, we chose for growth response analysis the longest regional climate record from the weather station at Stuie–Tweedsmuir (Fig. 1), at 260 m a.s.l. The climatic data used in this study consist of 89 years (1907–1995) of monthly mean temperatures and total monthly precipitation. Because the climatic conditions in the previous year usually have effects on the tree-ring growth of the current year (Fritts 1976), we examined the correlations between tree-ring growth and climatic variables from the growing season of the prior growth year to the end of the growing season in the current year. We chose the monthly climatic variables over a 13-month period — from August of the previous year to August of the current growth year (which was found to include the most important climatic factors affecting ring width) — as predictor variables, to determine their significance in affecting the concurrent ring growth. However, these variables were not used directly as regressors to calibrate with the tree-ring variable, because of the problem of intercorrelations among climatic variables (Cropper 1984). To overcome this problem, we calculated PCs on a correlation matrix of the climatic variables in the period 1907–1995 and chose the dominant PCs, determined by the PVP criterion (Guiot 1985), as predictor variables to enter into regression with the tree-ring variable (Fritts et al. 1971). The regression coefficients were converted to response coefficients by transforming the PCs back into the original monthly climatic variables. The significance of the response coefficients was tested with a bootstrap method, which assesses the variability of the coefficients based on a large number of subsamples randomly extracted, with replacement (some observations are selected several times, whereas others are absent) from the initial data set (Guiot 1991). An independent verification was done of the data from unselected observations. Such random sampling and the subsequent calibration and verification of the climate–growth model were iterated 5000 times with the program PRECON (Fritts 1994). The bootstrapped response coefficients were judged significant at $p \leq 0.05$ if their absolute values were twice their standard deviation (SD) (Guiot 1991). This method has advantages when the statistical properties of the data are not well understood or the data have autocorrelation problems.

Results

Tree-ring chronologies

Ring-width chronologies for Douglas-fir were developed for each of the nine sites in the Bella Coola area (Fig. 2). The chronological statistics are presented in Table 1. The values of mean sensitivity range from 0.19 to 0.26, indicating that the ring-width variability is relatively low at high frequency, a phenomenon typical of coastal Douglas-fir (Brubaker 1982; Zhang 2000). The values of mean serial correlation and of signal/noise ratio (for the period of 1886–1996) suggest that the individual trees at each site contained sufficient common environmental signal in their annual growth rings (Fritts and Shatz 1975). The values of the first-order autocorrelation (0.33–0.63) indicate that the chronologies contain low-frequency variance generated by climate and (or) the lag effect of tree physiology, such as needle retention and food reserves for growth in the following year (Fritts 1976).

Radial growth patterns in relation to altitudinal changes

The PC analysis of the nine site chronologies showed that the first two PCs accounted for 55.6% and 16.7% of the total variance, respectively (Table 2). Other PCs that accounted for less than 10% of the total variance described small-scale variability and were considered insignificant. The first two PCs were then used in the following analysis, to examine the spatial patterns of Douglas-fir tree-ring growth.

The weights associated with the chronologies were plotted against the site elevations to display the spatial growth patterns represented by the first two PCs (Fig. 3). For the first PC, the weights of the nine site chronologies all had positive values, which increased slightly as elevation decreased. This pattern indicates that the growth variations at all sites were positively correlated with the first PC, and the correlations were stronger at lower elevations than at higher ones. Therefore, the first PC reflected a common growth response throughout the nine sites and a larger contribution of variance from the lower elevation sites.

For the second PC, the weights of the three sites at high elevation had large and positive values, and the weights of the four sites at lower elevation had large negative values. For the two sites at middle elevation, the weight for the Nordschow Creek site was slightly above zero and the weight for the upper Valley View Loop Trail was below zero. This observation indicates that the radial growth represented by the second PC had a positive correlation with that

Fig. 2. *Pseudotsuga menziesii* ring-width chronologies at nine sites in the Bella Coola area of central coast British Columbia, Canada. See Table 1 for definitions of codes.

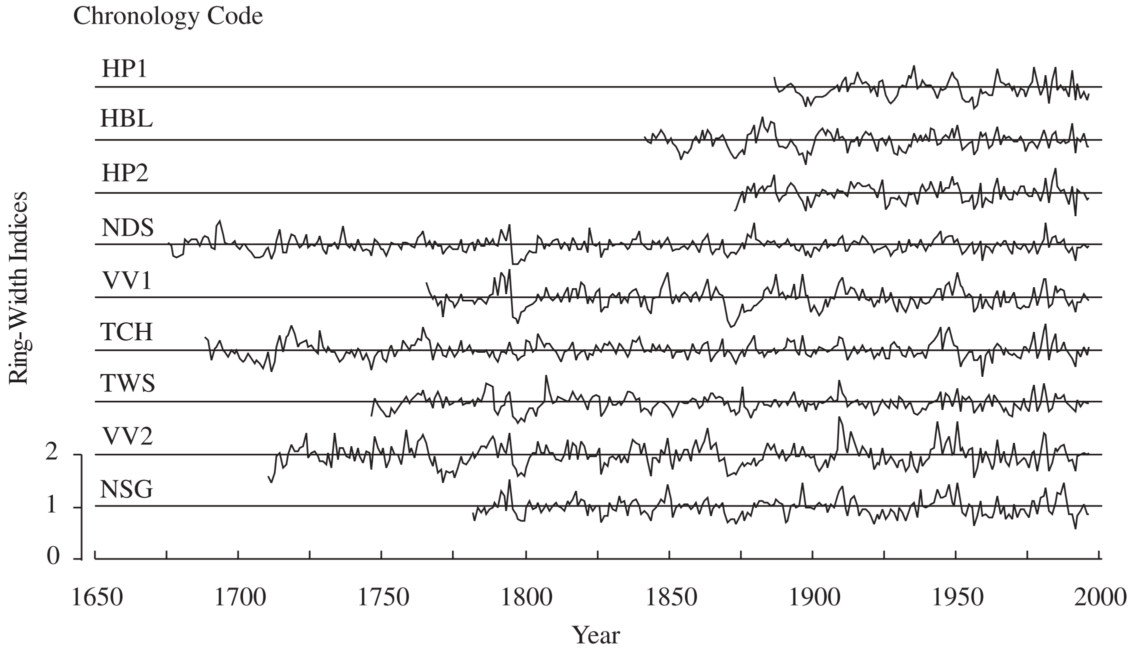


Table 2. Principal components of the *Pseudotsuga menziesii* chronologies (for the period 1886–1996) at nine sites in the Bella Coola area of central coast British Columbia, Canada.

Principle component	Eigenvalue	Variance (%)	Cumulative variance (%)
1	5.01	55.6	55.6
2	1.50	16.7	72.3
3	0.72	8.0	80.3
4	0.50	5.5	85.8
5	0.45	5.0	90.8
6	0.30	3.3	94.1
7	0.21	2.4	96.5
8	0.17	1.9	98.4
9	0.14	1.6	100.0

Note: Eigenvalue is the sum of squares of the correlations between the component and the chronologies. Variance refers to the percentage of total variance explained by the corresponding principal component.

at the three high-elevation sites, little correlation with that at the middle-elevation Nordschow Creek site, and negative correlation with that at the four low-elevation sites. The low weights for the upper Valley View Loop Trail site indicates that factors other than elevation also played a role in affecting tree-ring growth at this site. Overall, the second PC reflected a contrasting growth response pattern between sites at high and low elevation.

The growth variations represented by the first two PCs were displayed by plotting the PC scores against calendar years (Fig. 4). The most striking features of the first PC were the large positive scores (>4) in 1909–1910, 1947, 1950, 1980–1981, and 1984; and the large negative scores (< –4) in 1956, 1959, and 1991 (Fig. 4*a*). The large positive scores indicate a dominant feature of above average growth throughout the study area in those years. Likewise, the large negative scores indicate a dominant feature of below average growth throughout the study area. This spatial synchroneity of the growth pattern can also be seen by directly comparing the observed growth patterns over the nine sites. Such comparison of site chronologies showed that common intervals of enhanced growth occurred in the late 1900s, late 1940s to early 1950s, and early 1980s (apparent at low-elevation sites); and common intervals of reduced growth occurred in the 1790s, 1870s, late 1950s, and early 1990s (Fig. 2).

The scores of the second PC show variation in environmental factors not explained in the first PC (Fig. 4*b*). Positive values indicate above average growth for sites with positive masses and below average growth for sites with negative masses. Likewise, negative values mean that the sites with negative weights had above average growth and the sites with positive weights had below average growth.

Climate–growth response

Because the first PC of the tree-ring chronologies at the nine sites reflects common growth response to regional climatic variations, the scores of the first PC can be used to evaluate the regional climate–growth relationships. The growth in the previous year, called the prior growth, was used as an additional predictor variable in the response function analysis, because the tree growth showed a temporal autocorrelation in the ring-width chronologies (Table 1). The results of the response function analyses showed that the model-generated tree-ring series were highly correlated with the first PC scores for the calibration data set ($r = 0.75$) and for the verification data set ($r = 0.32$), both significant at $p \leq 0.05$. The response function explained 48% of the variance in tree-ring growth: 34% was explained by the climate variables; and 14%, by the prior growth. The radial growth of trees was positively correlated at $p \leq 0.05$ with the precipita-

Fig. 3. Weights associated with the first (*a*) and second (*b*) principal components (PCs) of site tree-ring chronologies of *Pseudotsuga menziesii* at nine sites in the Bella Coola area of central coast British Columbia, Canada.

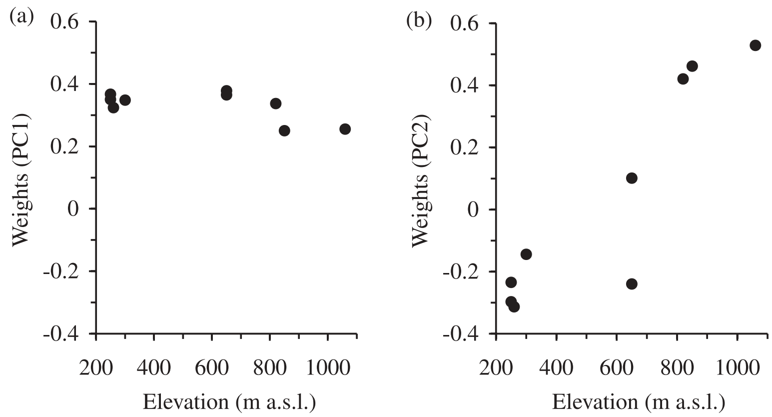
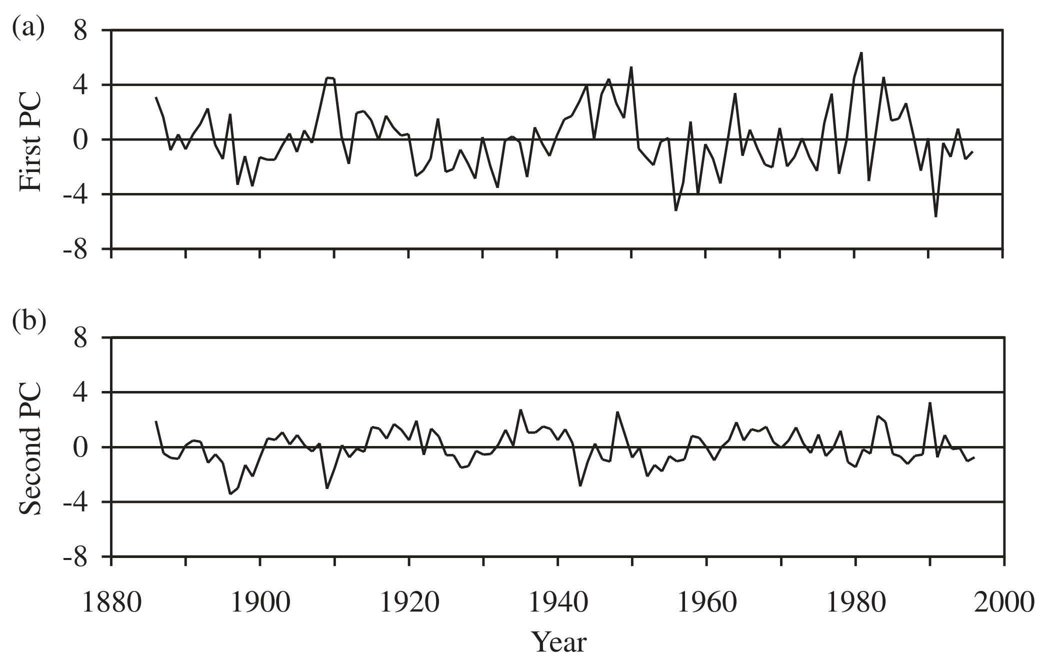


Fig. 4. The first and second principal components (PCs) of *Pseudotsuga menziesii* ring-width chronologies at nine sites in the Bella Coola area of central coast British Columbia, Canada.



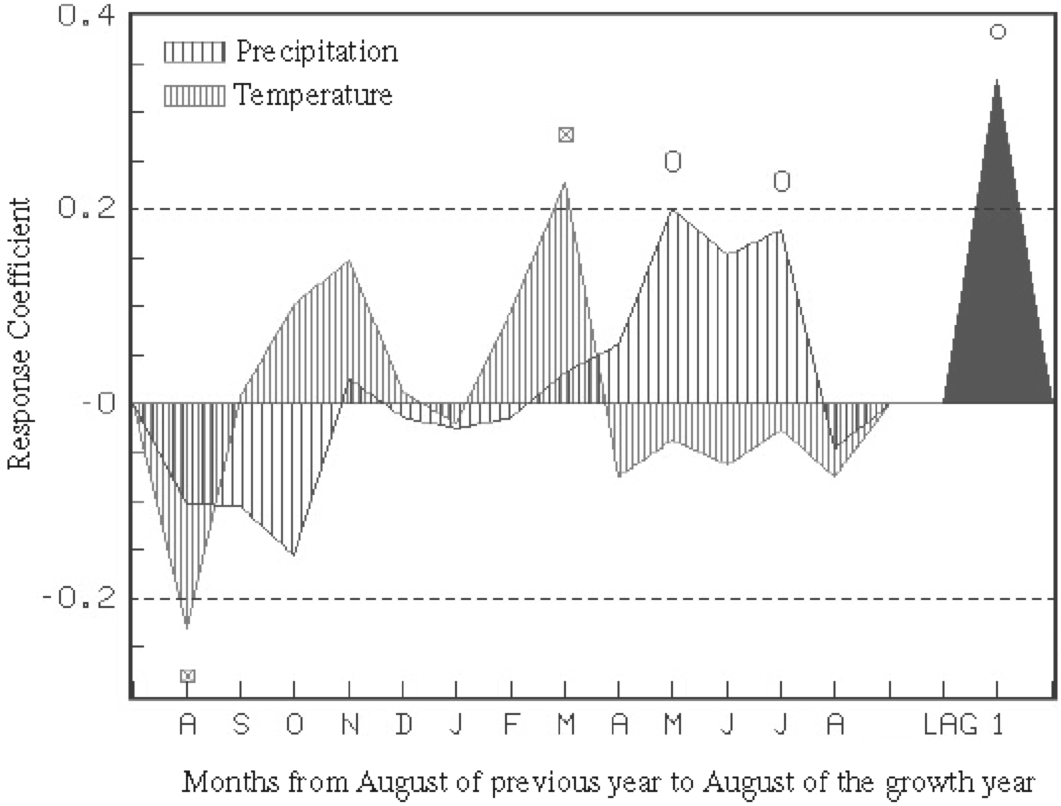
tion in May and July of the current year and with the temperature in March and negatively correlated with the temperature in August of the previous year (Fig. 5). It should be noted that the response function analysis using climate data at one low-elevation site and the first PC of nine chronologies provided only general information about the common climate–growth relationships for the region.

Discussion and conclusion

Tree-ring growth characteristics over large-scale geographical regions reveal that there were substantial differences in growth between sites (Yoo and Wright 2000). Our study shows that the radial growth of Douglas-fir at sites of different elevations within a mountainous region contains not only common signals but also differences in signals of the growth environment. This feature makes it difficult to extract large-scale climatic signals from a small number of samples at a few sites. Comparisons of growth characteristics at sites of different elevation should provide insights into the variability of growth response under a range of climatic conditions.

The first PC of the nine site chronologies in the Bella Coola area shows a common growth pattern (Fig. 3). Regional climate variation is the most likely factor for such a spatial response pattern, because all the sites in this narrow geographical area should have experienced the same relative changes as each new weather system crossed the area (Brubaker 1980; Brubaker et al. 1992; Kadonaga et al. 1999). The climate–growth relationships as reflected from the first PC showed patterns similar to those of Douglas-fir previously studied at the Heal Lake site of southern Vancouver Island, British Columbia (Zhang et al. 2000), where the elevation is about 120 m a.s.l., and where the climate is warmer and the growing season is longer than at Bella Coola. The radial growth of Douglas-fir in both regions is positively related to the growing season precipitation. Because the length of growing season in the Bella Coola area is

Fig. 5. Response function coefficients relating monthly mean temperature and total precipitation to the first principal component of chronologies for *Pseudotsuga menziesii* at nine sites in the Bella Coola area of central coast British Columbia, Canada. The coefficients that are significant at $p \leq 0.05$ (based on bootstrapping tests) are marked on the top of the monthly variables. LAG 1 refers to prior growth. The response function represents 48% of the variance in the first PC.



shorter than that on southern Vancouver Island, only May and July precipitation are significantly related to the growth of Douglas-fir in the Bella Coola area, whereas April–July precipitation affects tree growth on southern Vancouver Island. Dendroclimatic studies of Douglas-fir in the southern Canadian Cordillera (Watson and Luckman 2002) also showed that the radial growth of trees is most strongly related to water availability during the growing season months, and the precipitation signal is slightly weaker in the chronologies from more northerly sites in British Columbia and the higher elevation sites in southwestern Alberta. Studies on Douglas-fir physiology (Lassoie and Salo 1981) indicated that soil water deficits during the summer could promote persistent stomatal closure, which limits gas exchange rate and leads to reduced net photosynthesis. The results from our study suggest that the water availability in the growing season limits sustained rapid growth of Douglas-fir in the mountainous area at its northern limits of distribution and is a major radial growth-controlling factor operating on a macroregional scale.

The differences in climate–growth relationships for Douglas-fir between the Bella Coola area and southern Vancouver Island lie mainly in the nongrowing interval. High temperatures in the previous year's August had a negative influence on Douglas-fir growth in the Bella Coola area, whereas this relationship did not occur at the low-elevation site on southern Vancouver Island. This observation suggests that the influence of August temperatures of the previous year might be related to growth conditions in the mountainous area. A possible explanation is that at Bella Coola, near the northern limits of the range of Douglas-fir, high temperatures in August cause moisture stress and shorten what is already a shorter growing season than southern Vancouver Island has. Notably, Douglas-fir continues to form needle primordia within the bud in August and even into September (elongation does not take place until after winter dormancy). Reducing the number of needle primordia through moisture stress in August will directly reduce the number of needles the following year (Allen and Owens 1972). It may also be that a large amount of needle drop in the late summer and autumn as a consequence of moisture stress can proportionately reduce the photosynthetic surface at the limits of range of the species. Both of these phenomena would have a negative influence on tree-ring growth of the following year.

The positive relationship between temperature in March and radial growth in Bella Coola may be related to the length of the growing season, especially as the process of photosynthesis is active in Douglas-fir at temperatures ranging from 2 to 25 °C (Doehlert and Walker 1981). The climatic data from the Stuie–Tweedsmuir locality reveal that the mean March temperature is 3.8 °C and the SD is 1.6 °C. Thus, the area is close to the threshold for photosynthesis in March. Years with warm March temperatures and sufficient moisture will have more photosynthates produced than years with cold March temperatures, and rings will be wider. Warm March temperatures can also positively influence the rate of physiological processes preparatory to bud swelling and the timing of bud burst (Allen and Owens 1972), consequently increasing the potential for photosynthesis and the likelihood of a wide zone of earlywood and wide overall tree rings. The low values for growth indices (as represented by the first PC scores) in 1991, 1959, and 1956 correspond to low temperatures in March, dry springs, or high temperatures in August of the prior growth year. These are specific examples of limitations at the beginning and end of the growth season on radial growth at Bella Coola. In contrast, the radial growth of trees at the low-elevation site of southern Vancouver Island is positively correlated with temperature in the previous year's September and November and negatively correlated with precipitation in January, factors not significant at Bella Coola. Mild autumns and winters (mean November temperature, 6.3 °C; mean January temperature, 2.9 °C) with clear skies (less precipitation) on the Vancouver Island sites could facilitate photosynthesis (Helms 1965; Waring and Franklin 1979; Brubaker 1980; Little et al. 1995), whereas photosynthesis is unlikely to be active during the autumn or winter in the Bella Coola area, where mean monthly temperatures usually go below 2 °C in winter.

The second PC of the nine site chronologies in the Bella Coola area showed contrasting growth patterns for different sites (Fig. 3). Environmental changes associated with elevation gradient, such as a decrease in temperature and in the length of the growing season with increase in elevation, may lead to such spatial variation in radial growth (Lassoie 1982; White 1987). At tide water, Bella Coola's mean annual air temperature is 7.3 °C and mean annual precipitation is 1730 mm, whereas on the plateau at Anahim Lake, mean annual air temperature is 0.9 °C and mean annual precipitation is only 354 mm, according to observations during the 1976–1987 interval (Environment Canada, unpublished station data). In general, an increase in growing season temperature will facilitate tree growth by increasing the leaf area and the rate of photosynthesis (as a result of being closer to the optimal growing temperature) at high-elevation sites but will retard radial growth by increasing water loss (as a result of more evapotranspiration) at low-elevation sites (Brix 1967; White 1987). In our study area, the relationship of radial growth to temperature is shown clearly by year-to-year comparisons. The high temperature in March of 1984 at Anahim Lake corresponds to high tree-ring indices at high-elevation sites, and the low temperatures in March of 1976, 1982, and 1985 correspond to low tree-ring indices at high-elevation sites. Previous studies of subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) tree-ring growth in British Columbia (Splechtna et al. 2000) showed a stronger positive relationship between summer temperature and radial growth at high elevation than at low elevation. Such changing temperature response with elevation was also reported in dendroclimatic studies in western Tasmania (Buckley et al. 1997) and in the north Patagonian rain forest of Chile (Szeicz 1997). Our study suggests that the changing climate–growth response with elevation is a persistent aspect of Douglas-fir trees in the coastal mountainous areas, and it is most likely that the changes in temperature and length of growing season associated with the change in elevation are the main factors contributing to the observed growth differences. Factors other than elevation, such as slope, aspect, and local disturbance, may also interact and influence the spatial pattern of radial growth in the second PC. But within the limitations of available stands, we made every effort possible to select sites with similar site conditions. A more precise relationship of ring width to temperature for high-elevation sites would be possible if a longer high-elevation climate record and a history of stand disturbance were available, but they were not.

In conclusion, the growing season precipitation is likely a major factor limiting the growth of Douglas-fir on a macro-regional scale in coastal British Columbia. Climatic factors outside the growing season, especially temperature, may contribute to the differences between the radial growth response on southeastern Vancouver Island and that in central coast British Columbia. Tree rings of Douglas-fir at high-elevation sites, especially at the limits of species distribution, may contain information on variations in temperature and in the length of the growing season not evident from low-elevation sites. Further climatic data for high-elevation sites are needed to clarify the effects of temperature and growing season length on the radial growth of trees in this mountainous region.

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