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Dendroecological studies of tree growth, climate and spruce beetle outbreaks in Central British Columbia, Canada

Qibin Zhang[a,*], René I. Alfaro[b], Richard J. Hebda[c]

[a]School of Earth and Ocean Sciences, University of Victoria, Victoria B.C., V8W 3P6, Canada and Royal British Columbia Museum, Victoria, B.C., V8W 9W2, Canada

[b]Canadian Forest Service, Pacific Forestry Center, Victoria B.C., V8Z 1M5, Canada

[c]Royal British Columbia Museum, Victoria, B.C., Canada V8W 9W2, and Biology and School of Earth and Ocean Sciences, University of Victoria, Victoria B.C., V8W 3P6, Canada

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Abstract

Dendroecological techniques were used in this study to compare the radial growth patterns of different conifer species and to identify regional climatic anomalies and spruce beetle (*Dendroctonus rufipennis* Kirby) outbreaks for the past four centuries in the McGregor Model Forest, central British Columbia, Canada. Tree-ring chronologies of Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco), subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), and interior spruce (*Picea engelmannii* Parry × *P. glauca* (Moench) Voss) were developed for the Model Forest. Response function analysis showed that (1) Douglas-fir is the most climate sensitive species, and its radial growth is mainly controlled by spring precipitation and early summer temperature, and (2) the ring growth of subalpine fir and spruce is negatively affected by high summer temperature. Comparisons of the tree-ring chronologies among the three species revealed dynamics of growth releases and suppressions which reflected climate variations and forest disturbance patterns in the past several centuries. The climate during the late 1750s–1800s was characterized by slightly moist springs and probably moderate summers. During the late 1860s and early 1870s, the region experienced dry springs, hot summers, and probably cold late falls. This study identified three intervals of major disturbances attributable to severe spruce beetle outbreaks: the late 1720s, 1810s–1820s, and 1960s-early 1980s. These coincided with periods of above average growth in Douglas-fir. The association suggested a possible moist spring-outbreak pattern. The multicentury tree-ring records of climate anomalies and spruce beetle outbreaks could provide insight into the dynamics of forest growth and its response to environmental changes.

Keywords: Dendroecology; Forest disturbance; Spruce beetle outbreak; Climate change

1. Introduction

The growth dynamics of forest ecosystems is affected by a complex of environmental factors which include climate, insect infestations, fire, competition among trees, soil characteristics, and others. Trees respond to these influences with corresponding changes in their annual growth rings. Therefore, a record of past influences on growth is retained in tree-rings and can be unraveled through dendroecological techniques (Fritts and Swetnam, 1989).

*Corresponding author. Tel.: +1-250-360-1874; fax: +1-250-721-6200; e-mail: qzhang1@uvic.ca

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The radial growth responses of trees to climate have been extensively studied for climate sensitive species in North America. The ring growth of coastal Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco) on southern Vancouver Island of British Columbia is sensitive to spring and early summer precipitation (Zhang, 1996). Dendrochronological studies of white spruce (*Picea glauca* (Moench) Voss), Engelmann spruce (*P. engelmannii* Parry), and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) in boreal forests of northwestern Canada and in Canadian Rockies show that the growth rings of these species are affected by summer temperature (D'Arrigo et al., 1992; Szeicz and MacDonald, 1995; Luckman et al., 1997). Insect infestations play a key role in modifying forest structure, and severe outbreaks can cause tree mortality, reduction of growth rates, reduced lumber quality, and proliferation of the understory (Veblen et al., 1991b; Alfaro and Maclauchlan, 1992). Major infestations and their effects on tree growth can be inferred by comparing tree-ring chronologies from host and non-host species (Swetnam et al., 1985; Heath and Alfaro, 1990; Alfaro and Shepherd, 1991; Veblen et al., 1991b; Weber and Schweingruber, 1995). A relationship between insect infestation and increased spring precipitation has been reported from long-term reconstruction of outbreaks and climate in northern New Mexico (Swetnam and Lynch, 1993).

Forest ecosystems of central British Columbia are sensitive to climate variations, yet there is insufficient historical and modern climate and species response data to assess the nature of forest adjustments to climatic changes (Hebda, 1997). The spruce beetle (*Dendroctonus rufipennis* Kirby) is a severe disturbance factor in these forest ecosystems, causing widespread mortality in mature spruce stands. Three outbreaks occurred in the Prince George Forest Region between 1962 and 1982 during which spruce beetles killed an estimated 18×10^6 m^3 of spruce in the region (Humphreys and Safranyik, 1993). Understanding long-term pattern of outbreaks is important for resource management. However, historical records of spruce beetle outbreaks in the region are scarce.

In this study we developed ring-width chronologies of interior spruce (*Picea engelmannii* Parry × *P. glauca* (Moench) Voss), interior Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco), and subalpine fir for the McGregor Model Forest, located in central British Columbia. Instrumental climate data were used to identify climate–growth relationships. Tree growth dynamics for the past several centuries were examined, and major climate anomalies and spruce beetle outbreaks were reconstructed and discussed.

2. Area description

This study was conducted within the McGregor Model Forest, a component of Canada's Model Forest Network, encompassing Northwood Pulp and Timber's Tree Farm License 30, northeast of the city of Prince George, in the central interior of British Columbia (Fig. 1). It occupies ≈165 000 ha of forests mostly within the Sub-Boreal Spruce (SBS) biogeoclimatic zone (Meidinger and Pojar, 1991).

The climate of the SBS zone is continental, characterized by long, cold winters and relatively short, warm and moist summers (Fig. 2). According to long-term climatic data (A.D. 1895–1992) from Fort St. James, ca. 100 km northwest of Prince George, mean annual temperature ranges from 0.4° to 4.9°C, with mean January temperature of −12.5°C and mean July temperature of 14.3°C. Mean annual precipitation ranges from 336.7 to 739.2 mm, with April receiving the lowest amount of precipitation.

The forest is dominated by interior spruce and subalpine fir, which are climate-perpetuated climax tree species for the SBS zone. Subalpine fir regenerates more readily than spruce under the canopy; however, it has shorter longevity due to its susceptibility to pathogenic fungi (Lindgren and Lewis, 1997). Douglas-fir is a shade intolerant and long-lived seral species in the SBS zone, occurring mainly on relatively dry and warm sites. Lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.), also a seral species in the SBS, pioneers extensive seral stands and is common in mature forests in the drier parts of the zone (Meidinger and Pojar, 1991).

Fire, insect attack, windthrow, and harvesting practices are the general disturbance regimes that affect forest renewal, structure, and composition. Wildfire is the dominant stand-replacing process in the SBS zone, creating a complex landscape spatial pattern with a

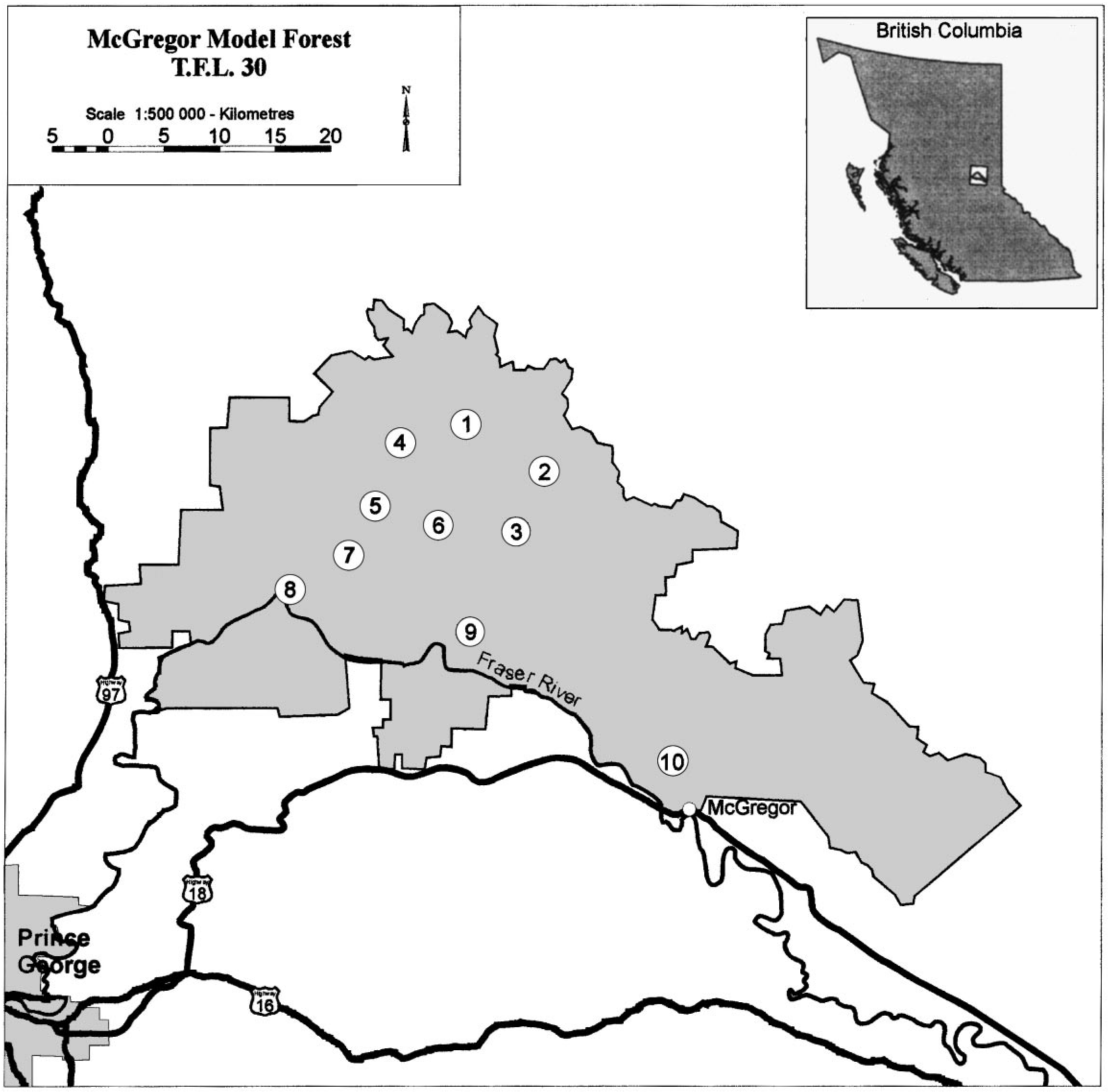

Fig. 1. Tree-ring sampling sites at the McGregor Model Forest, British Columbia.

large range in patch size and irregular disturbance boundaries (DeLong and Tanner, 1996). The average fire size for the zone ranges from 50 to 500 ha (Parminter, 1992), and the time required for fire to cycle through the zone is estimated to range from 200 to 700 years (B. Hawks, personal communication, Pacific Forestry Centre, Victoria, BC, Canada). Widespread disturbance by forest insect outbreaks is frequent and severe. The spruce beetle is the most damaging insect in the area, and can kill many mature spruce during outbreaks (Erickson and Loranger, 1983). Other insects developing outbreaks in this region include tree defoliators, e.g. eastern spruce budworm (*Choristoneura fumiferana* Clements), and the white pine weevil (*Pissodes strobi* Peck) which destroys the apical shoots of young spruce. Spruce trees have shallow root systems, and are susceptible to windthrow (Coates et al., 1994). The area has sustained selective harvesting and clearcutting since the early 1900s (Erickson and Loranger, 1983).

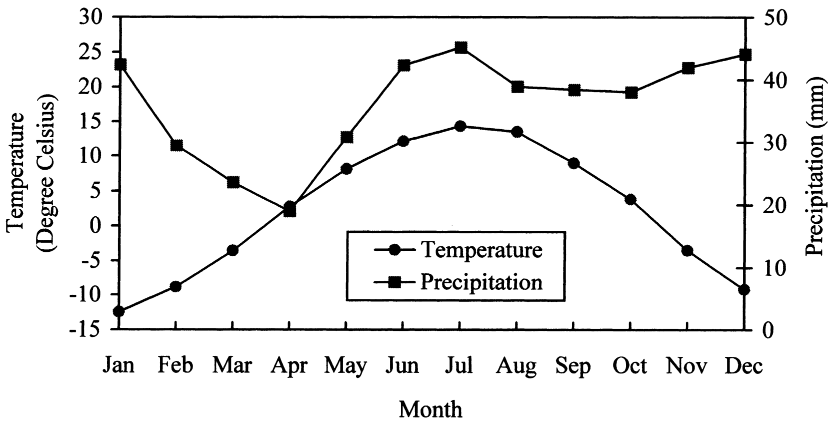

Fig. 2. Representative diagram of the climate for the SBS zone of the McGregor Model Forest (averaged for A.D. 1895–1992 using records from the weather station at Fort St. James, BC).

3. Methods

3.1. Field sampling

Increment cores and disks were collected from spruce, subalpine fir, and Douglas-fir trees in the Model Forest by Pacific Forestry Centre, Canadian Forest Service personnel, in the late summer of 1995. The cores (one core per tree) were extracted at breast height with an increment borer. The disks, 20 of spruce and two of Douglas-fir, were cut in 5 cm thickness from felled trees (at breast height) or stumps (at 50 cm above ground surface) in sites 4 to 8 and 10 (Fig. 1; Table 1). The two Douglas-fir disks, made available to us from a separate study at site 10, contained the oldest rings and were used in this study to maximize the length of tree-ring chronology. The sample stands were selected in areas that had not sustained logging, and were chosen to provide a reasonable representation of the Model Forest. The selected stands were dominated by spruce and contained a mixture of the three species. Spruce was most extensively sampled for the original purpose of examining the impacts of weevils on tree growth (Kimoto, 1996). Subalpine fir and Douglas-fir, which are non-host species for spruce beetle, were sampled for comparison of the growth patterns among species. A total of 240 spruce trees, 26 subalpine fir, and 16 Douglas-fir trees from 10 sites were sampled and these were used in the tree-ring analysis (Fig. 1; Table 1).

3.2. Tree-ring chronology development

The core and disk samples were prepared and surfaced to enhance ring boundaries before measurement. Cores were mounted on grooved wooden boards and sanded by hand with a series of sandpaper grits up to 600. Disks were prepared using a sharp 17-mm wide carving gouge. Ring-width measurement was carried out using a Measu-Chron incremental measuring system (Micro-Measurement Technology, Bangor, Maine, USA) in the Tree-Ring Laboratory of the

Table 1
Number of increment core samples and disk samples (in brackets) collected at each site in the McGregor Model Forest, British Columbia during the late summer of 1995

Species	Site number										Total
	1	2	3	4	5	6	7	8	9	10	
Douglas-fir			2	1		7	2	1	1	(2)	16
Subalpine fir	5	4	2	7	1	1	1	5			26
Interior spruce	42	39	19	34	19(7)	17(7)	17(3)	13(3)	20		240

Pacific Forestry Centre. The precision of measurement was 0.01 mm.

The measured ring-sequences were plotted and the patterns of wide and narrow rings were cross-dated among trees. The cross-dating was aided by the presence of distinctive narrow rings and the quality of cross-dating was examined by the program COFECHA (Holmes, 1983). The age-related growth trend within each ring-sequence was removed using the program ARSTAN (Grissino-Mayer et al., 1993) in which the detrending curve selected was a negative exponential curve, horizontal line, or a straight line with negative slope. Deviations from this curve were standardized to produce a set of annual growth indices for each sample. Ring-width chronology for each species was derived by averaging the growth indices for each year among different trees (Fritts, 1976). The chronology of spruce for the Model Forest was obtained by averaging nine site (sites 1 to 9) chronologies of spruce to emphasize the common features of the chronologies.

3.3. Dendroecological analysis

Relationships between climate and tree growth were detected using a computer program PRECON (Fritts, 1994) which calculates the principal components of climate data to identify the factors influencing tree growth and represents these as response functions. The climate data consisted of 98 years (A.D. 1895–1992) of monthly mean temperature and monthly total precipitation from Fort St. James, which is located within the Sub-Boreal Spruce (SBS) biogeoclimatic zone. The correlation coefficient of these climate variables between Fort St. James and Prince George, over the common period A.D. 1943–1992, averaged 0.60 for monthly total precipitation and 0.92 for monthly mean temperature (both significant at the $p \leq 0.001$ level). In addition, the climate record from Fort St. James provided the longest series in the region; therefore, it was considered as the best representation of the regional climate for this study. The tree-ring data of Douglas-fir, subalpine fir, and spruce used in the response function analysis were residual chronologies in which the autocorrelation of ring-widths had been removed by fitting a first-order autoregressive model to each ring-series so as to emphasize the effects of climate on tree growth (Grissino-Mayer et al., 1993).

The history of forest disturbances was reconstructed by examining and comparing the differences in ring-width indices of different species. The analysis of climate–growth relationships in this study provided information on the effects of climate on tree growth. Short-term (<5 years) growth increases were attributed to transient, above normal, positive environmental effects on growth. Veblen et al. (1991b) indicated that growth rates of released spruce and subalpine fir trees after beetle attack remained high for >40 years. Therefore, sustained (>5 years) growth increases in surviving spruce and subalpine fir were attributed to spruce beetle removal of competing spruce. Growth suppressions in these species might be caused by climate factors or might be the consequence of insect defoliators. However, except for the western hemlock looper, *Lambdina fiscelloria lugubrosa* (Hulst), little defoliator activity has been documented in the area in the last 50 years.

4. Results

4.1. Ring-width chronologies

The ring-width chronologies of Douglas-fir, spruce, and subalpine fir for the McGregor Model Forest and the statistics describing the three chronologies were presented in Fig. 3 and Table 2. Douglas-fir had the longest chronology due to its longevity and its resistance to moderate surface fires as a result of its thick bark. Spruce, which became established primarily after stand-replacing fires, had an age ca. 200 years younger than the oldest Douglas-fir. Subalpine fir is susceptible to pathogenic and decay fungi infection (Lindgren and Lewis, 1997); therefore, it had the shortest chronology length. Spruce exhibited the highest mean ring width and standard deviation, reflecting its fast growth relative to the other species and the variable influences of environmental factors. Subalpine fir had the highest mean sensitivity, indicating that it had high interannual variability in ring-widths and was sensitive to yearly environmental changes (Fritts, 1976). All the three species exhibited high first-order autocorrelation, suggesting the existence of low frequency variation in the chronologies caused by

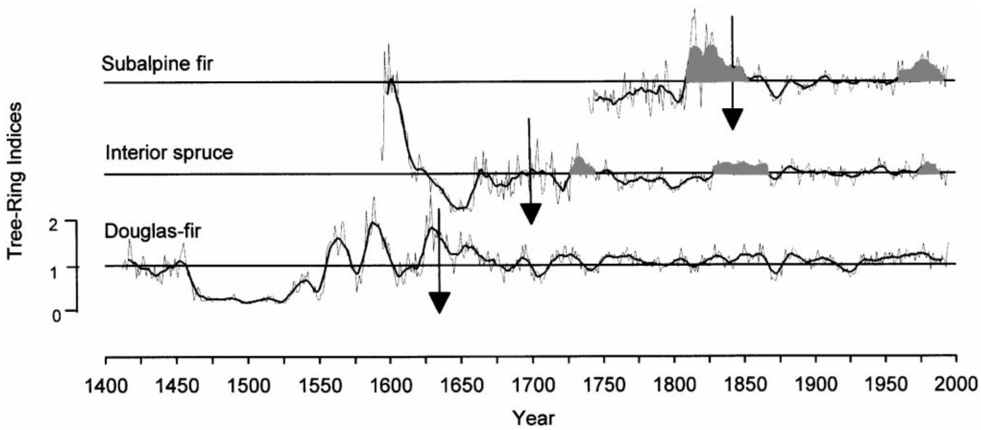

Fig. 3. Ring-width indices of subalpine fir, interior spruce, and Douglas-fir at the McGregor Model Forest, British Columbia. Superimposed on the ring indices are smoothing lines derived from a centered 10-year moving average. The vertical arrows indicate the earliest year with five sample replications. The shaded intervals in subalpine fir and spruce represent growth release attributable to major disturbances, e.g., spruce beetle outbreaks. The Douglas-fir chronology is indicative of climate variations (see text).

propagation of climatic effects from one year into following years or by long-term effects of insect infestations (Swetnam and Lynch, 1993).

4.2. Climate–tree growth relations

The response functions of Douglas-fir, subalpine fir, and spruce ring-width chronologies with monthly mean temperature and monthly total precipitation, for interval A.D. 1895–1992, were presented in Fig. 4. Radial growth of Douglas-fir was positively correlated with precipitation in May of the growth year, with precipitation and temperature in the previous November, and was negatively correlated with temperature in June, July, and the previous July. Ring growth of subalpine fir was negatively correlated with temperature in June and precipitation in July. Ring growth of spruce was negatively correlated with temperature in July and the previous August.

All three species showed negative correlations between growth and high summer temperatures. This suggested that increased evapotranspiration and water loss induced by high temperatures reduced the radial growth of these species. The positive effect of spring precipitation on ring-width growth of Douglas-fir suggested that water availability during the growing season is one limiting factor for radial growth of Douglas-fir, an observation consistent with information from other regions (Zhang, 1996). The positive effect of high late fall temperature and precipitation on ring-width growth of Douglas-fir suggested that warm and moist days in late fall favour active photosynthesis and continuous food storage, leading to large ring-width in the following year (Fritts, 1976; Waring and

Table 2
Statistics for tree-ring chronologies of Douglas-fir, subalpine fir, and interior spruce in the McGregor Model Forest, British Columbia

Species	Douglas-fir	Subalpine fir	Interior spruce
Entire chronology length	A.D. 1414–1995	A.D. 1740–1995	A.D. 1594–1995
Length with minimum 10 trees	A.D. 1767–1995	A.D. 1878–1995	A.D. 1742–1995
Length with minimum five trees	A.D. 1634–1995	A.D. 1838–1995	A.D. 1698–1995
Mean ring width (mm)	1.31	1.46	1.66
Standard deviation	0.657	0.737	0.805
Mean sensitivity	0.185	0.245	0.206
First-order autocorrelation	0.858	0.799	0.832

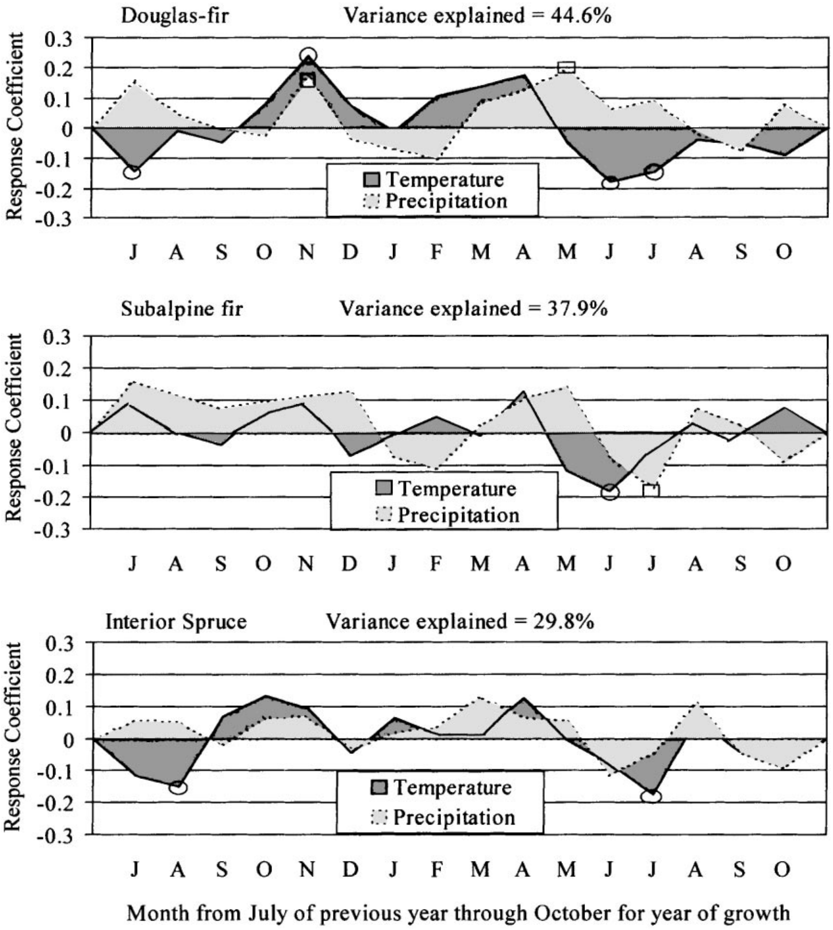

Fig. 4. Response functions of the McGregor Model Forest tree-ring chronologies. Monthly climate variables for the interval A.D. 1895–1992 are used to explain the variance in tree-rings. The labeled points represent a significant (95% level) effect of either temperature or precipitation on growth.

Franklin, 1979). The inverse association of ring-width growth of subalpine fir with July precipitation was contrary to expectation, and might be related to collinearity among predictor variables of growth or to the limitation of the autoregressive models used (Fritts and Dean, 1992). No significant coefficients were found between the growth of spruce and precipitation, which suggested that the radial growth of this species might not be sensitive to the range of variation in precipitation in the study area. It should be noted that non-climatic factors, e.g. insect infestation and competition among trees, may degrade the climate–growth relationships. Therefore, the response functions presented here gave a conservative estimate of the climate–growth relations. The proportion of variance in tree-rings explained by climate was 44.6% for Douglas-fir, 37.9% for subalpine fir, and 29.8% for spruce, i.e., tree-rings of Douglas-fir contained the highest amount of climate information, followed by subalpine-fir, whereas spruce provided the least climate information.

4.3. History of forest growth anomalies

Comparisons of the tree-ring chronologies of Douglas-fir, subalpine fir, and spruce and their relationships with the environmental factors provided useful clues for the history of forest disturbances in the

McGregor Model Forest. All chronologies had smaller sample sizes in the early years. Therefore, less confidence should be placed on inferences based on chronology intervals with less than five sample replications.

The chronology of Douglas-fir was the oldest, dating back to A.D. 1414 (Fig. 3). It showed that there was a century-long period of low radial growth during the late 1450s to the late 1550s. Although there was only one sample for this interval, it was interesting to note that this century-long suppressed growth also occurred in the ring-width chronology of Douglas-fir on southern Vancouver Island ($\approx$630 km southwest from the McGregor Model Forest) in the same interval, where it was interpreted as a result of a long period of dry springs (Zhang, 1996). The agreement between these distant chronologies suggested that the growth of Douglas-fir during the late 1450s to the late 1550s was influenced by a large-scale climatic phenomenon of dry springs and probably cold late falls which might have affected much of British Columbia.

Extremely high values of growth indices of spruce occurred in the early 1600s, indicating that the sampled trees were growing under open conditions probably created by stand-replacing fires or some other disturbances such as severe spruce beetle outbreaks (Heath and Alfaro, 1990; Veblen et al., 1991a). The following extreme low growth during the 1630s to 1650s indicated that the sampled trees might have been suppressed by increased competition among trees or by disturbances such as defoliation by insects, possibly eastern spruce budworm which presently defoliates spruce in the northern forest of B.C. (Erickson and Loranger, 1983). The growth indices of non-host Douglas-fir during this period were above average, suggesting moist springs and warm late falls.

A rapid decrease and sustained low radial growth of spruce occurred in the late 1710s to late 1720s which was followed by a period of above-average growth lasting until the mid-1740s. The climate during the late 1710s to late 1720s was characterized by moist springs, warm late falls and probably cool summers as suggested by the above average growth of Douglas-fir. Therefore, this decade of severe growth suppression of spruce was not caused by climate factors, but by either insect outbreaks such as spruce defoliator infestations or by other factors such as windstorms which could cause damage to trees' root systems. Coates et al. (1994) indicated that strong windstorms promote the build-up of spruce beetle populations and create stressed trees that may be more susceptible to beetle attack. Thus, the radial growth pattern of spruce in the 1710s to 1740s suggested a possible spruce beetle outbreak in the late 1720s, after which the growth release for the surviving trees was a result of reduced competition among trees.

The long period of growth reduction in spruce during the late 1750s to late 1820s suggested a state of increased tree to tree competition as recruitment increased overall tree density in the area sampled. This interval of growth reduction was followed by four decades of growth release which might have been caused, again, by spruce beetle infestations which thinned this overstocked forest. Lindgren and Lewis (1997) presented a chronology for this area based on samples collected from site 3. They reported a description of dying forests and desolate landscapes found in a fur trader's diary in 1836, and also hypothesized a major spruce beetle outbreak in the 1820s. By comparison of the ring growths in spruce, subalpine fir, and Douglas-fir, we provided additional evidence supporting the hypothesis of spruce beetle outbreak in the 1820s. The subalpine fir, which is sensitive to canopy disturbance (Veblen et al., 1991b), showed prolonged slow growth in the 1740s to 1800s, but then exhibited an abrupt and significant release in the 1810s–1820s. The former suggested closed canopy structure and intense competition among trees, and the latter suggested large removal of overstory spruce, possibly by spruce beetle infestation (Veblen et al., 1991a). The growth of Douglas-fir, a climate sensitive species, during the late 1750s to 1820s was slightly above average, suggesting that no severe climate anomalies occurred in the period to either suppress or release tree growth in the area. The delayed growth release in spruce compared to the release in subalpine fir might be caused by the lag in response of spruce to beetle disturbance, or it might simply be an anomaly caused by the small number of samples ($n = 2$) in subalpine fir for this period. In summary, the tree-ring growth features of these three species suggested a dense canopy structure and moderate climate during the late 1750s–1800s, and a large scale spruce beetle outbreak in the 1810s–1820s.

The chronologies of Douglas-fir, spruce, and subalpine fir (non-host for spruce beetles) showed synchronous growth reductions during the late 1860s and early 1870s. This suggested that the reduced growth might have been caused by large-scale climate anomalies. Based on the response functions of the three species to climate factors (Fig. 4), the climate in the late 1860s to early 1870s might have been characterized by severe dry springs, hot summers, and probably cold late falls. Such dry springs and hot summers in the years around 1870 were also reported from several tree-ring studies of climate in the Pacific Northwest region (Graumlich, 1987; Wiles et al., 1996; Zhang, 1996).

The growth release of subalpine fir since the 1960s indicated reduced competition from overstory spruce. The canopy disturbance agent during this period was three confirmed spruce beetle outbreaks as recorded in 1963–1965, 1969–1970, and 1979–1983 (Erickson and Loranger, 1983). The effect of these outbreaks was also reflected in the ring-width indices of surviving spruce which showed increased radial growth in the 1970s. The chronology of Douglas-fir showed above average growth since the 1930s, suggesting a favorable climate for growth through the period.

5. Discussion

The radial growth rates of Douglas-fir, subalpine fir, and spruce exhibited different response characteristics to environmental factors; therefore, comparisons of growth anomalies among these three species could provide useful information on past major climate events and forest disturbances such as insect outbreaks. The reliability of the inferences was mainly dependent on the sensitivity of tree-rings to these different factors and on the degree to which the sampled tree-rings represent the regional forest. Of the three species studied in this project, Douglas-fir was the most climate sensitive species. Nearly half of the ring-width variation in Douglas-fir could be explained by climate variables, whereas the remainder was attributed to local factors such as microclimate, local soil conditions, and competition among trees. Subalpine fir and spruce were sensitive to forest disturbances such as severe insect outbreaks. In this study, only major climate events and moderate to severe insect infestations were reconstructed from tree-ring chronologies of the three species. The confidence of these reconstructions was limited in the earlier periods when the sample sizes declined below five trees.

Tree-ring data in non-host and climate sensitive species and in host species are especially useful in studying long-term climate-insect infestation patterns because they provide replicated observations of past outbreaks and climatic fluctuations (Swetnam and Lynch, 1993). Our study showed that the occurrence of spruce beetle outbreaks in the 1960s to early 1980s and the suspected occurrences in the 1810s–1820s and the late 1720s happened in periods of moist springs as deduced from the Douglas-fir chronology. The same positive relationship between spring precipitation and outbreak was also found in a study of western spruce budworm (*Choristoneura occidentalis* Freeman) outbreaks in northern New Mexico, USA (Swetnam and Lynch, 1993). However, a negative relationship between precipitation and western spruce budworm outbreaks was reported in British Columbia (Thomson et al., 1984). Thus, the exact mechanisms of weather-outbreak association are not clearly understood.

This study also supported the finding of Kimoto (1996) that the severe insect infestations in this study area during the late 20th century are not primarily a consequence of present day forest management practices. Such severe spruce beetle outbreaks occurred several times during the 17th–19th centuries. Severe disturbance by spruce beetle played a role in shaping the forest structure, composition, and renewal by causing mortality of infested spruce, reducing competition among trees, and accelerating the growth rates of survivors and understory tree species. Mature spruce forest with dense canopies and moist weather were favorable to spruce beetle activity and dispersal, thus were more suitable to the development of outbreaks. More extensive sampling of old growth host and non-host species is required to provide long-term and reliable records of outbreaks and climate variations. These records can improve our understanding of the patterns of outbreaks as well as their relationships with climate.

6. Conclusions

Our study demonstrated that tree-ring chronologies of Douglas-fir, subalpine fir, and spruce can provide useful information on past forest growth dynamics, climate variations, and spruce beetle outbreaks. Douglas-fir was the most climate sensitive species, followed by subalpine fir. The climate during the late 1750s–1800s was characterized by slightly moist springs and probably moderate summers. The synchrony of suppressed growths of all three species during the late 1860s and early 1870s suggested dry springs, hot summers, and probably cold late falls. The spruce forest was probably infested by spruce defoliators during the 1630s–1650s, and was infested by spruce beetle in the late 1720s, 1810s–1820s, and 1960s-early 1980s as inferred by comparisons of the growth anomalies among the three species. The spruce beetle outbreaks occurred during period of above average spring precipitation, suggesting a possible weather–outbreak relationship. Further investigation of long tree-ring records will improve our knowledge of forest growth dynamics and their relationships with the environmental factors.

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