

Spatial Distribution of Mountain Pine Beetle Outbreaks in Relation to Climate and Stand Characteristics: A Dendroecological Analysis

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Abstract

Principal components analysis, followed by *K*-means cluster analysis, was used to detect variations in the timing and magnitude of *Pinus contorta* Dougl. ex Loud. growth releases attributed to mountain pine beetle outbreaks in 31 stands of central British Columbia. Four major growth release patterns were identified from 1970 to 2000. Variations in the timing of growth releases among clustered stands corresponded well to aerial survey data indicating the timing of beetle outbreaks in the study area. Redundancy analysis was used to determine how variations in the timing and magnitude of growth releases attributed to beetle outbreaks changed with variations in climate or stand conditions over the study area. The first RDA axis, which accounted for 39% of the variations in growth patterns among stands, was significantly ($P < 0.05$) correlated with gradients in the percentage of pine in stands killed by mountain pine beetle, summer aridity, variation in summer precipitation, distance from initial infestation site, average pine age, and maximum August temperatures. The second RDA axis explained 6% of the variations and was significantly correlated with gradients in the beetle climate suitability index, extreme cold month temperatures, and site index. Comparisons of growth release patterns with aerial survey data and redundancy analyses indicated that dendrochronological techniques are useful for identifying mountain pine beetle outbreaks in central British Columbia, particularly among stands that had a density high enough to produce a growth release signal. Provided future studies account for interannual weather fluctuations, identification of growth increases due to stand thinning caused by beetle outbreaks will be useful for reconstructing the history of beetle outbreaks over much longer time periods.

Key words: bark beetle; dendrochronology; *Dendroctonus ponderosae*; disturbance; forest health; lodgepole pine.

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The mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae), occurs in pine forests from northern British Columbia to northern Mexico. In British Columbia, lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.) is the most common host, but ponderosa pine (*P. ponderosa* Laws), whitebark pine (*P. albicaulis* Engelm.), western white pine, (*P. monticola* Dougl.) and limber pine (*P. flexilis* James) are also suitable hosts (Furniss and Carolin 1977). In mid to late summer, mountain pine beetles disperse and colonize living trees. Females carve out "J" shaped vertical galleries under the bark and, once mated, deposit eggs in niches along the main gallery. Hatched larvae feed on the phloem, mining lateral galleries as they go. Larvae usually overwinter as late-instars, and complete development to adults in the following spring (Reid 1962). Trees infested by mountain pine beetle die in one or two years

because lateral galleries mined by the larvae, and a blue stain fungus carried into the tree by the beetle, disrupt the flow of water and nutrients. Normally, beetles infest and kill the oldest and most stressed trees that are scattered throughout a forest (Safranyik and Carroll 2006). However, when climate conditions warm, populations increase and beetles mount pheromone-mediated mass-attacks that overwhelm the natural defenses of healthy trees and kill mature lodgepole pine over many thousands of hectares (Safranyik et al. 1975; Raffa and Berryman 1983).

Outbreaks of mountain pine beetle are natural disturbances that play a critical role in the development, senescence and rebirth of western North American pine forests. However, human activities have disrupted forest disturbance processes and, like many contemporary native insect outbreaks, mountain pine beetle outbreaks are having more widespread impacts than ever before. This is probably at least partly because forest management (e.g., harvest regulation, fire suppression) has increased the abundance of susceptible lodgepole pine forests, but also because warming climates seem to be expanding the geographic range within which the beetle is able to complete its life-cycle (Logan and Powell 2001; Carroll et al. 2004). In western Canada, the mountain pine beetle outbreak of the 1970s and 1980s killed approximately 2 million hectares of mature pine forests. Presently, mountain pine beetle populations are rising again. In British Columbia, they destroyed approximately 7 million hectares of pine forests from 1999 to 2004. As wood from lodgepole pine forests comprises 25% of British Columbia's timber supply, the socioeconomic impacts of beetle outbreaks are enormous. In addition to extensive timber losses, tree mortality caused by beetle outbreaks may increase the risk of wildfires, alter successional trajectories, watershed hydrology, and nutrient cycles, and have negative impacts on recreational areas (McCullough et al. 1998; US Department of Agriculture Forest Service 2000).

While mountain pine beetle outbreaks occur synchronously over large, subcontinental spatial scales (British Columbia Ministry of Forests 2005; US Department of Agriculture 2005; Campbell E and Alfaro RI, 2005, unpublished data), local variations in outbreak dynamics are likely to occur and generate varying impacts on forests. The last mountain pine beetle outbreak in western Canada occurred from approximately the mid-1970s to the mid-1980s and was fully documented through aerial surveys conducted by the Canadian Forest Service. The objective of this study was to utilize a dendroecological approach (i.e., study of tree ringwidth patterns) to describe how the occurrence and severity of beetle outbreaks vary with regional climate conditions and stand characteristics. Dendroecology has been used extensively to study the outbreak dynamics of defoliators (Bergeron et al. 2002; Zhang and Alfaro 2002) but less so for bark beetles (Veblen et al. 1991; Zhang et al. 1999), especially the mountain pine beetle (Heath and Alfaro 1990; Alfaro et al. 2004), where suspected

outbreaks are identified from increases in the radial growth of survivors that have responded to stand-wide beetle-caused host mortality. By identifying trends in occurrence and severity of past outbreaks, we hope to provide forest managers with an improved basis for predicting the occurrences and impacts of future outbreak events.

Results

Variability in *Pinus contorta* growth

Ninety-one percent of the variation in lodgepole pine growth among stands from 1970 to 1987 was captured in the first four principal components of a PCA. The Kaiser criterion indicated that higher order principal components accounted for <5% additional variance and provided the basis for selecting four groups as most appropriate for *K*-means cluster analysis. Coefficients of determination (r^2) obtained through simple linear regressions indicated that at least 70% of the variation in individual stand chronologies could be explained by a particular cluster for most stands (Table 1). Only stand 124 was not significantly ($P < 0.05$) related to any cluster and the growth ring chronology of this stand (between 1970 and 1987) was eliminated from calculations of cluster averages.

While *Pinus contorta* radial growth from 1970 to 1975 and from 1989 to 2000 varied similarly among clusters, from approximately 1975 to 1988, growth patterns were quite distinct among clusters, with substantial variation in the timing and magnitude of growth releases evident in the chronologies (Figure 1). Within cluster 1 chronologies, *P. contorta* exhibited 48% increase in radial growth from 1975 to 1977 and sustained above, or near average, growth (i.e., a tree-ring index > 1) for several years. *P. contorta* in cluster 4 stands had 60% increases in radial growth but this growth release was somewhat more gradual, occurring from 1975 to 1986. All tree-ring chronologies grew faster between 1989 and 1992, with increases in radial growth ranging from approximately 25% to 40%. This was the only period of above average growth for cluster 2 chronologies. Cluster 3 chronologies maintained below average growth from 1970 to 2000. Overall, cluster 1, 2, and 3 chronologies were significantly and positively correlated with one another indicating similar interannual fluctuations in growth from 1970 to 2000 (Table 2). An insignificant *R*-value indicated that cluster 3 and cluster 4 growth patterns were the most different (Table 2).

Comparison of growth release patterns with aerial survey data

Aerial surveys from 1970 to 2000 recorded a mountain pine beetle outbreak in every stand sampled except 104, 107, and

Table 1. Relationship between mean standardized chronologies of lodgepole pine radial growth for each stand and clustered chronologies as measured by coefficients of determination (r^2) obtained through simple linear regressions

Stand	Cluster 1	Cluster 2	Cluster 3	Cluster 4
BMC44	0.96	0.72	0.60	0.44
C101	0.66	0.44	0.43	0.16
C102	0.82	0.76	0.39	0.45
C103	0.66	0.80	0.32	0.36
C104	0.72	0.68	0.24	0.51
C105	0.59	0.76	0.18	0.50
C106	0.62	0.92	0.19	0.50
C107	0.38	0.82	0.03	0.51
C108	0.35	0.03	0.80	0.27
C109	0.51	0.11	0.84	0.06
C110	0.18	0.00	0.68	0.02
C111	0.42	0.08	0.66	0.04
C112	0.40	0.20	0.81	0.02
C113	0.33	0.27	0.26	0.26
C114	0.26	0.04	0.79	0.00
C115	0.55	0.22	0.82	0.07
C116	0.38	0.81	0.08	0.63
C117	0.43	0.81	0.11	0.65
C118	0.53	0.74	0.08	0.94
C119	0.81	0.44	0.49	0.26
C121	0.24	0.45	0.00	0.94
C122	0.16	0.56	0.01	0.30
C123	0.54	0.74	0.28	0.24
C124	0.04	0.01	0.13	0.13
C125	0.64	0.68	0.15	0.92
C126	0.64	0.86	0.26	0.55
C128	0.79	0.68	0.78	0.17
C129	0.32	0.51	0.01	0.97
C130	0.35	0.69	0.01	0.93
C163	0.71	0.47	0.33	0.26
C359	0.75	0.40	0.50	0.11

Coefficients, multiplied by 100 indicate percent variation in stand growth chronologies that is explained by each cluster chronology. Boldface values indicate the strongest relationships, which are all statistically significant ($P < 0.05$).

108 (Figure 2). These stands did, however, show periods of increased radial growth during this time. This, combined with the fact that samples were originally located in stands during an active outbreak in the late 1980s, suggests that the discrepancy may be because of observer error during aerial surveys. Alternatively, outbreaks in these stands may have been less severe and simply undetectable from the air. However, less severe outbreaks are unlikely to elicit significant growth increases and thus, warmer and moister than normal weather

Table 2. Pearson correlations (R) among clustered *Pinus contorta* radial growth chronologies obtained through K -means cluster analysis

	Cluster 1	Cluster 2	Cluster 3	Cluster 4
Cluster 1	1.000			
Cluster 2	0.845	1.000		
Cluster 3	0.786	0.469	1.000	
Cluster 4	0.644	0.795	0.176	1.000

could also explain why we observed growth increases in stands where no outbreaks were identified in aerial surveys.

The first record of a beetle outbreak in the aerial survey data occurred in 1975 among cluster 1 stands and corresponded to a major release in lodgepole pine growth at about the same time among this group of stands (Figure 1). The last aerial survey record of a beetle outbreak occurred in 1985, suggesting that populations crashed between 1985 and 1986. Outbreaks among cluster 1 stands occurred over the longest period of time, from 1975 to 1985 and corresponded to the doubling of growth among surviving trees that was sustained for several years (Figure 1). The second longest outbreak occurred among cluster 4 stands, from 1978 to 1985 and surviving lodgepole pines showed a doubling of radial growth from 1980 to 1984. Aerial survey data indicated that beetle outbreaks in cluster 2 and cluster 3 stands were shorter, restricted largely to between 1981 and 1985. Increases in growth of surviving hosts among stands in these clusters of stands began in 1989 but they were small compared to the doubling of growth found among stands in clusters 1 and 4.

Redundancy analyses

The first four RDA axes, accounted for a significant proportion of the variation (56.3%) in *P. contorta* growth among stands (Monte Carlo permutation test, $P = 0.001$). The first two RDA axes explained most of this, 38.7% and 6.3% respectively (Figure 3). The first RDA axis was significantly correlated with: distance from stand BM44 (one of the two initial sites of infestation, DISTBM), average lodgepole pine age (AVPLAGE), percentage of dead lodgepole pines in stands (%DEADPL), variability of summer precipitation (SDPPTSM), summer aridity (ARIDITY), and maximum August temperature (TMAX08) (Figure 3). The second RDA axis was significantly correlated with: site quality (SITEIND), the beetle climate suitability index (CSI), and extreme winter temperatures (EXTCO) (Figure 3).

Cluster 1 stands occurred on the upper half, and predominantly on the left portion of the ordination diagram (Figure 3). On average, these stands had greater variability in summer precipitation. Site quality (SITEIND) and climate suitability for mountain pine beetle (CSI) was also higher than average in

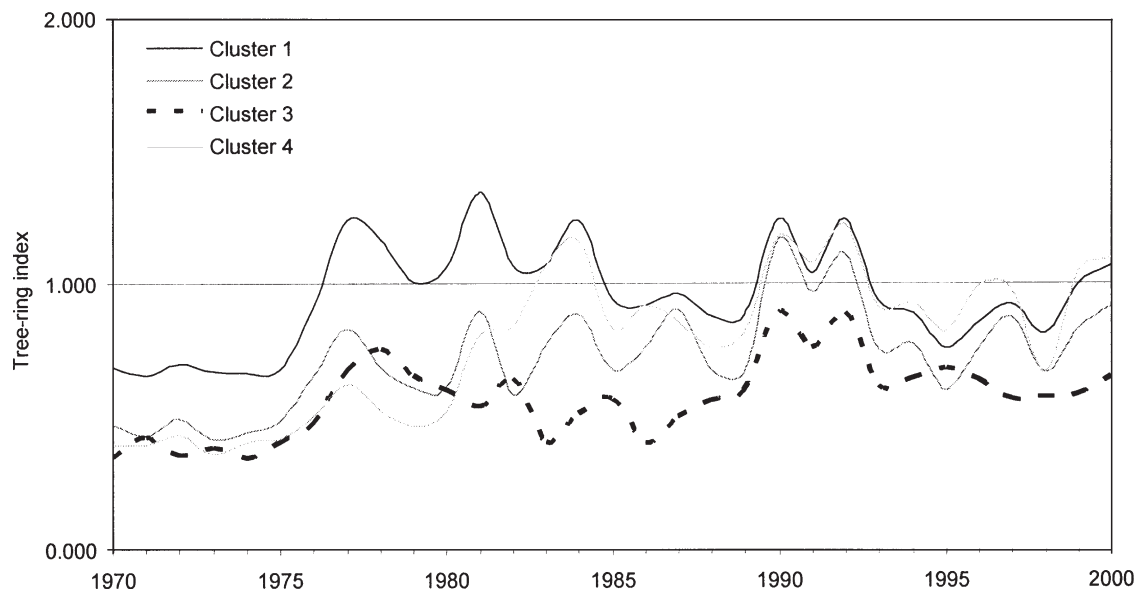


Figure 1. *K*-means cluster analysis of tree-ring growth patterns of *Pinus contorta* for stands sampled in central British Columbia.

The solid horizontal line represents average tree-ring width over the lifespan of the tree.

these stands. Cluster 2 stands occurred around the centre of the ordination graph, which represent average values for all explanatory variables. Cluster 3 stands were predominantly restricted to the lower left quadrant of the ordination diagram, where extreme winter temperatures are coldest and summer precipitations are more variable. Cluster 4 stands were predominantly restricted to the lower right quadrant of the ordination graph, where the climate was, on average more arid, with high temperatures in August.

Redundancy analysis indicated a significant relationship (Monte Carlo Permutation Test, $P=0.003$) between *P. contorta* growth release patterns and geographic location (latitude and longitude, linearized by a third order polynomial equation). Pearson correlations were used to describe the strength of linear relationships between the climate variables retained in above RDAs and latitude, longitude, and elevation (Table 3). The most suitable beetle climate (high CSI values) occurred among stands located in the eastern parts of the Chilcotin plateau. Summer precipitation was more variable in most western stands. More western stands and those at lower elevations possessed the most arid summer conditions. Extreme cold temperatures occurred among more continental, eastern stands and at higher elevations. Although variation in maximum August temperatures was not related to geographic location, it was strongly associated with elevation in this region, with the highest maximum August temperatures occurring in stands at lower elevations.

Discussion

Cluster analysis indicated four distinct tree ringwidth patterns that reflected variation in the timing and magnitude of growth releases attributed to mountain pine beetle outbreaks in the study area. The clustering techniques used are exploratory in nature and the grouping of stands into these four patterns is subject to some variations, depending on the method used. However, all the clustering methods we employed produced similar results and the selection of the number of groups for the method we finally decided to use (*K*-means partitioning) was systematic and rule-based and thus objective. Moreover, comparisons with aerial survey data indicate that these four

Table 3. Pearson correlations describing the strength of linear relationships between significant climate variables and geographic coordinates (latitude, longitude and elevation) in central British Columbia

Explanatory variable	Latitude	Longitude	Elevation
Climate variables			
CSI	-0.294	-0.640	0.004
Variability in summer precipitation	-0.171	0.352	0.208
Aridity index	0.031	0.686	-0.654
Extreme cold month temperature	-0.140	-0.522	-0.426
Maximum August temperature	-0.185	0.003	-0.816

CSI=Mountain pine beetle climate suitability index. Relationships in boldface are significant at $P < 0.05$.

	1970	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989
Cluster 1:																				
BMC44						■	■	■			■									
C109																■	■			
C113																				
C119						■		■	■			■								
C126												■	■	■	■	■				
C128								■			■	■	■	■	■					
C359																■				
Cluster 4:																				
C118										■		■	■	■						
C121											■	■	■	■	■			■		
C125												■	■	■	■					
C129									■	■			■	■	■					
C130									■				■	■	■		■			
Cluster 2:																				
C102														■		■				
C103															■	■				
C104																				
C105																				
C106													■	■	■	■				
C107														■	■	■				
C116													■	■	■					
C117													■	■	■		■			
c122																■	■			
C163										■				■	■	■				
Cluster 3:																				
C101																				■
C108																				
C110																				
C111														■	■	■				
C112															■	■				
C114																■	■			
C115																	■	■		
C123																		■	■	

Figure 2. Aerial survey data of mountain pine beetle infestations in stands sampled in British Columbia.

clusters represent tree responses that are biologically interpretable with respect to the timing and magnitude of growth releases attributed to mountain pine beetle outbreaks. We suggest that early and rapid increase of growth among cluster 1 stands represents an intense and prolonged mountain pine beetle outbreaks in those stands. Similar increases in radial growth among cluster 4 stands began 2 years later, but the release was more gradual, suggesting an outbreak of lesser

severity. Both clusters 2 and 3 did not indicate any growth increases until 1989, 4 years after the outbreak crashed because of cold winter temperatures over the province of British Columbia (Environment Canada 2002). It is possible that these growth increases represent a delayed response to canopy disturbance by beetle in these stands, as has been observed in other studies (Heath and Alfaro 1990). This delay may simply be because of the fact that the cooler winter weather

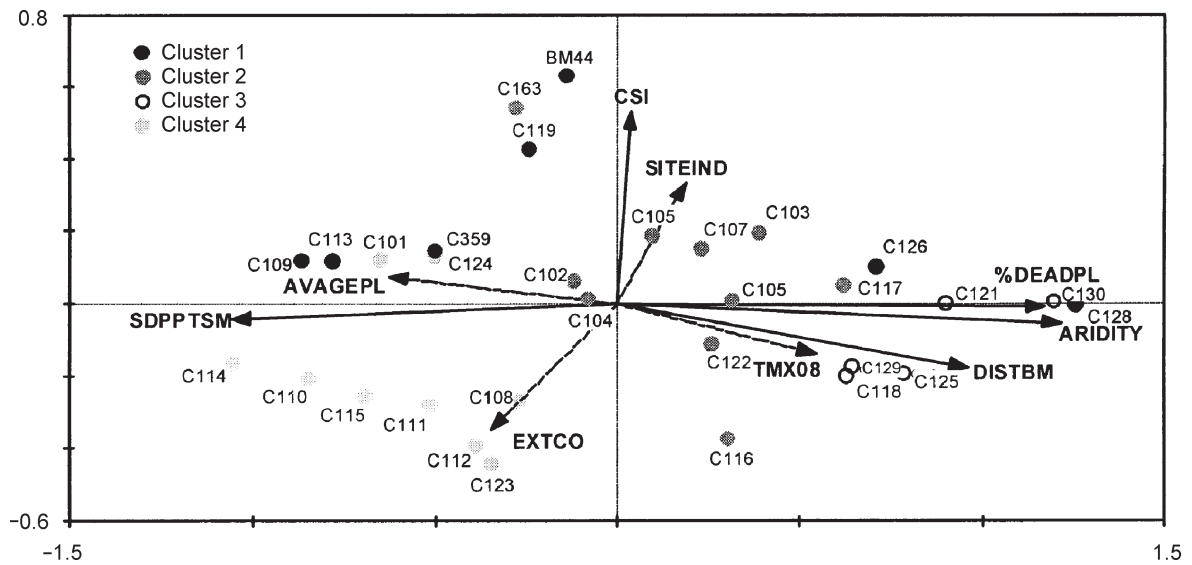


Figure 3. Redundancy analysis ordination biplot of standardized chronologies of tree ringwidths (1970–1987) for *Pinus contorta*. Dots represent the position of each stand chronology in ordination space. Results of *K*-means cluster analysis (i.e., 4 groups of chronologies) are superimposed onto the ordination and stand groups are indicated by different shading of dots. Variables significantly correlated with RDA axes are indicated by arrows (solid line = significant at $P < 0.05$ and dashed line = significant at $0.05 < p < 0.10$). The relative length of arrows corresponds to the relative influence of explanatory variables on the dispersion of stands in the ordination space.

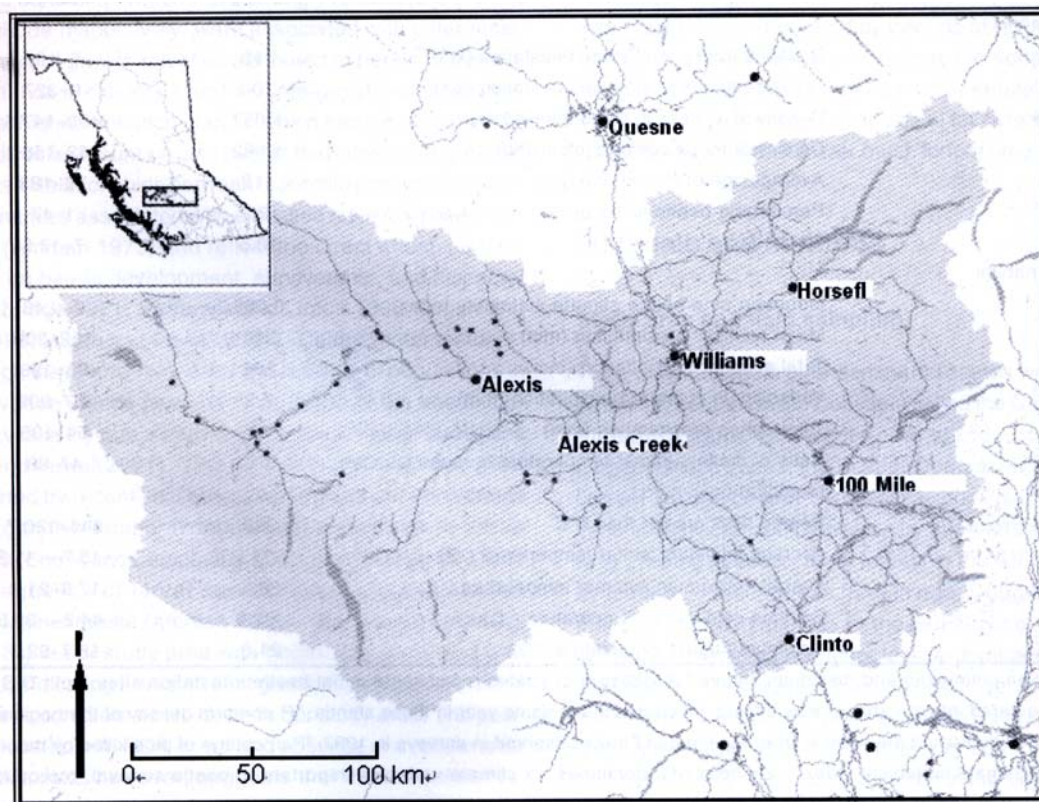


Figure 4. Geographic location of *Pinus contorta*-dominated stands sampled in the Cariboo-Chilcotin Plateau of central British Columbia.

conditions contributing to the 1985 crash of beetle outbreaks also lead to shorter growing seasons so that lodgepole pine growth was limited by temperatures between 1985 and 1987.

A few other studies have used dendroecological techniques to study the history of bark beetle outbreaks (Veblen et al. 1991; Eisenhart and Veblen 2000), including work by Alfaro et al. (2004), who reconstructed the occurrence of mountain pine beetle outbreaks in our study area. Fundamental to these historical studies is the confidence with which growth releases can be attributed to forest canopy disturbances caused by beetle outbreaks. Through comparisons with aerial survey data, this study showed that dendroecological techniques could most confidently detect beetle outbreaks in central British Columbia when they were of sufficiently long duration and/or the changes to canopy cover were severe enough to elicit an increase in radial growth (~40%). This finding lends credibility to the long-term reconstructions of beetle outbreaks described by Alfaro et al. (2004), who identified three outbreaks from 1880 onwards in our study area. Our comparisons of growth data with aerial survey data provide direct evidence that

dendroecological techniques can be an effective method for detecting important historical beetle outbreaks when no documentary archives are available.

Redundancy analysis was useful for identifying the potential sources of variation in tree-ring release patterns among stands. The type of tree-ring release pattern observed in stands was most strongly related to variations in: aridity, variability in precipitation, the percentage of pines killed by mountain pine beetle, distance to the start of the first outbreak at Bull Mountain, average pine age, and extreme winter temperatures/suitability of beetle habitat. Fundamental to detecting beetle outbreaks in tree rings is the assumption that large canopy disturbances caused by beetle outbreaks produce large growth responses. However, while cluster 3 stands exhibited the highest percentages of tree deaths attributed to mountain pine beetle, growth increases were comparatively minor. This is probably because these pine stands occur in the most arid regions of the study area where tree density is lower and stands have a more open canopy structure. Gradients in the amount and variability of precipitation, related largely to maximum August temperatures,

Table 4. Variables quantifying local stand characteristics and climatic conditions of 31 *Pinus contorta*-dominated stands sampled in central British Columbia

Explanatory variables	Description	Average	Range ^a
Stand variables			
DISTBM ^b	Distance from site of initial infestation (km)	113	0–199
DIST119	Distance from site of initial infestation (km)	104	0–327
DENALLTR	Density of all trees in stand (stems/ha)	1 057	490–147 5
DENPL ^c	Density of <i>Pinus contorta</i> (stems/ha)	1 082	462–150 1
AVAGEPL	Average age of <i>P. contorta</i> (yrs)	112	79–183
%DEADPL ^d	Percentage beetle-killed pine	20	1–47
SITEIND	Site index	10.5	7–17.5
Climate variables			
CSI ^e	Mountain pine beetle climate suitability index	0.085	0–0.48
MSP	Mean summer precipitation (mm)	200	152–309
PPTSM	Total summer precipitation (mm)	132	96–198
SDPPTSM ^f	Variability in summer precipitation (mm)	3.9	1.7–907
PPTSP	Total spring precipitation (mm)	68	54–135
Aridity index	Ratio of mean summer temperature to mean summer precipitation	68	47–88
DD>5	Degree days greater than 5°C	943	644–120 7
MINWTT	Average minimum winter temperature (°C)	–14.5	–15.7– –11.3
MAXSMT	Average maximum summer temperature (°C)	20.1	17.8–21.3
EXTCO	Extreme cold month temperature (°C)	–42.9	–44.2– –39.5
TMAX08	Maximum August temperature (°C)	21.3	18.7–22.3

^aDifference between minimum and maximum values. ^bA measure of spatial proximity to initial beetle infestation sites, both DISTBM and DIST119 were entered into the analyses as infestation started in the same year in these stands. ^c*P. contorta* density at the beginning of the outbreak calculated by adding the number of living and dead trees observed in surveys in 1987. ^dPercentage of pine killed by mountain pine beetle by 1987. ^eClimate suitability index = an index that combines six climate variables important to beetle survival, reproduction and dispersal (Carroll et al. 2004). ^fVariability measured by standard deviation.

were strongly related to the percentage of dead pines observed in stands. Drought has long been associated with the susceptibility of forests to insect outbreaks, including the mountain pine beetle, possibly because they decrease the effectiveness of natural defence mechanisms (Thompson and Shrimpton 1984; Mattson and Haack 1987).

We thought that by including variables quantifying distance to the first outbreak observed in aerial surveys, we might be able to detect a spatial effect in the timing of outbreaks that could be explained by beetle dispersal from outbreak epicentres (Aukema et al. 2006). However, distance to the first beetle outbreak was highly correlated with stronger gradients in precipitation and the percentage of trees killed by beetle, suggesting that climate and stand structure may have a more important influence on the timing of outbreaks than directional beetle movements, *per se*. Redundancy analysis on a matrix geographic coordinates also suggested a strong spatial component to the timing and magnitude outbreaks. But, statistically significant correlations between longitude and important climate gradients (e.g., extreme cold month temperatures) provide additional evidence that spatial patterns in beetle outbreaks within our study area are likely more strongly influenced by climate than beetle dispersal.

The gradients in extreme winter temperatures and an index of climate suitability, which were strongly related to elevation and longitude respectively, were associated with differences in the timing of growth releases attributed to beetle outbreaks among stands in clusters 1 and 4. Tree-growth releases indicated that higher elevation stands, which had low climate suitability indices for mountain pine beetle, had later onset of beetle outbreaks. Relationships between mountain pine beetle population dynamics associated with elevation have long been recognized (Amman 1973) and reflect the direct effects of temperature on beetle development, survivorship, and dispersal (McCambridge 1971; Safranyik and Linton 1998; Logan and Bentz 1999; Logan and Powell 2001). Colder winter temperature at high elevations may delay the build-up of populations in high-elevation stands because completion of the beetle life-cycle may take 2 years, rather than 1 year, at higher elevations (Logan and Powell 2001). This delay in beetle outbreak onset is supported by recent field surveys and computer simulations indicating both a temporal delay in the occurrence of beetle outbreaks (Eng M and Campbell E, 2005, unpublished data) and lower frequency of larval survivorship in high-elevation whitebark pine forests (Amman 1982). The climate suitability index (CSI) in our study area was negatively correlated with longitude, indicating a west to east gradient in habitats suitable for beetle to complete its life-cycle in our study area. The positive relationship with RDA axis 1 and absence of a relationship with RDA axis 2, however, suggests that the temperatures, rather than the precipitation components of this index (Carroll et al. 2004) have the greatest effect on growth release

patterns attributed to beetle outbreaks.

The relationship between tree growth release patterns and average pine age in stands is somewhat difficult to interpret but may be related to outbreak timing - cluster 1 and 4 stands had, on average, the oldest pine trees and earlier onset of outbreaks. It has long been recognized that beetle populations build faster on old pine trees because the thick bark provides abundant food as well as protection from climate extremes and natural enemies (Amman 1972; Ramussen 1976; Furniss and Carolin 1977).

In summary, dendrochronological techniques were useful for identifying growth releases caused by the 1971 to 1986 mountain pine beetle outbreak in stands of central British Columbia, particularly when stands are dense enough to produce a growth release signal. Cluster analysis identified four major growth release patterns and differences in the magnitude and duration of growth releases among each cluster were related to: the percentage of pines killed by beetle, distance from site of initial infestation, average age of pine in stands, and regional climate. Gradients in beetle climate suitability indices, extreme winter temperatures, summer aridity and variability in precipitation explained variation in growth release patterns among stands. While growth releases were strongly associated with the occurrence in beetle outbreaks, in some instances, the growth signal produced by beetle outbreaks may have been confounded by periods of favorable weather. However, using analytical techniques to separate these increases in growth from those caused by beetle-induced stand thinning, dendroecology will be useful for constructing the history of beetle outbreaks over much longer time periods.

Materials and Methods

Study area and field sampling

Thirty-one lodgepole pine-dominated stands were sampled in an area of central British Columbia called the Cariboo-Chilcotin Plateau (Figure 4). Twenty-nine stands occurred in two biogeoclimatic zones: the Interior Douglas-fir (IDF) and Sub-boreal Pine Spruce (SBPS) (Meidinger and Pojar 1991). The IDF zone is characterized by warm, dry summers and a relatively long growing season. Seral forests in the IDF are dominated by lodgepole pine, but as forests age, Douglas-fir becomes more abundant in stands. In the SBPS zone, frequent high-intensity fires maintain lodgepole pine-dominated forests over vast areas. This biogeoclimatic zone is generally located at elevations above the IDF, so the climate is harsher, characterized by cold, dry winters and cool, dry summers (Meidinger and Pojar 1991). One stand occurred in the slightly wetter ICH (Interior Cedar Hemlock) biogeoclimatic zone and another in the higher elevation Montane Spruce biogeoclimatic zone (MS).

We undertook this dendroecological research in stands where the Canadian Forest Service had previously established permanent plots to study the impact of the last (mid-1970s to mid-1980s) mountain pine beetle epidemic (Heath and Alfaro 1990; Shore and Safranyik 1996; Hawkes et al. 2005). These stands were randomly selected from a larger population of mountain pine beetle-infested stands in the study area. Stand structure and species composition data were collected from variable radius prism plots established in each stand (Stockdale et al. 2005). The basal area factor (BAF) of the prism used in establishing the plots was 2.3 or 4.6 m²/hm² to include a minimum of 8–10 trees in each plot (“in” trees). “In” trees were numbered with fluorescent paint. The diameter and height of all living and standing dead trees in each plot was tabulated. The cause of tree death was recorded when it could be discerned. Increment cores were taken from all “in” trees. Thirty of the 31 stands were initially sampled in 1987 or 1988 (Shore and Safranyik 1996) and 17 of these stands were revisited in 2001 when another 10–15 increment cores were taken and stand characteristics were re-measured. One stand located near Williams Lake was sampled in 2001 (Heath and Alfaro 1990).

Aerial survey data

Since the mid-1900s British Columbia Forest Service and Canadian Forest Service have conducted aerial surveys from fixed-wing aircraft to examine the extent of forest disturbances in the province. Damage caused by mountain pine beetle is sketch-mapped by observing foliar colour changes affecting groups of dying trees. The foliage of dying trees turns yellow to bright red in the year following attack. The following year, foliar colour fades and tree needles start to shed. Areas of dead or dying trees are marked on survey maps. These sketch-map data are digitized and summarized annually.

We used these annual aerial survey records of mountain pine beetle outbreaks to determine the occurrence and timing of outbreaks in the stands we sampled. Using ArcView GIS, we overlaid our distribution of sample stands onto annual sketch-maps of mountain pine beetle infestations, documented from 1970 to 2000. The intersection of sample points with aerial sketch-map data indicated a presence of an infestation in the stand that year.

Development of tree-ring chronologies

Increment cores collected from *P. contorta* were prepared in the laboratory following standard dendrochronology procedures (Stokes and Smiley 1968). Cores were mounted on wood planks and sanded with progressively finer sand paper (grits 220 to 600) to enhance the boundaries between annual growth rings. After mounting and sanding, tree rings were measured to the

nearest 0.001 mm and dated using Windendro or a Measu-Chron incremental measuring system. The program COFECHA (Holmes 1983) was used to detect measurement and dating errors by computing correlation coefficients between overlapping 50-year segments from individual tree-ring series. Tree-ring series that did not cross-date well with other samples within a stand (i.e., $r < 0.50$) were checked for dating or measurement errors and corrected as needed. Series that remained poorly correlated with other samples in a stand were eliminated from the dataset.

The computer program ARSTAN (Cook 1985) was used to produce a mean standardized chronology of *P. contorta* tree-ring widths for each stand sampled. Dated tree-ring series in each stand were standardized by fitting a horizontal line through the mean of each tree-ring series, that is, ringwidth was divided by the mean series ringwidth. Standardizing series by their mean preserves the long-term growth trend necessary to identify radial growth releases indicative of large canopy disturbances (Veblen et al. 1991; Eisenhart and Veblen 2000). Standardized series were averaged together to produce a mean chronology for each stand.

Statistical analyses

Cluster analysis was used to group stands where lodgepole pine had similar growth patterns from 1970 to 1987. We evaluated the results of 3 clustering techniques: i) hierarchical agglomerative (i.e., Ward's method); ii) hierarchical divisive (ordination by principal components analysis, PCA); and, iii) *K*-means partitioning. All methods produced similar results but we only present those for *K*-means partitioning (MacQueen 1967). The best number of clusters used for *K*-means partitioning was a subjective decision, but guided by results of the PCA and the Kaiser criterion (Legendre and Legendre 1998), where principal components with eigenvalues greater than one contribute the most to variation and indicate the number of groups to use. Coefficients of determination (r^2) obtained through simple linear regression were used to indicate how much variance in individual stand chronologies was explained by each cluster chronology, and Pearson correlation coefficients (R) described the strength of the relationship between each cluster chronology. To evaluate how well releases in *P. contorta* growth corresponded to mountain pine beetle outbreaks, we compared the clustered tree ringwidth chronologies with the aerial survey sketch-map data for each stand, which were grouped into the same four clusters.

Redundancy Analysis (Rao 1973), which combines multiple regression with principal components analysis, was used to detect relationships between *P. contorta* growth patterns (i.e., timing and magnitude of growth releases) in stands and regional climate conditions and stand characteristics. The program CANOCO (v.4.5, ter Braak and Šmilauer 2002) was used

to conduct RDA on a matrix of response variables, Y_{PL} , comprised of *P. contorta* tree ringwidth indices obtained from the master chronology created for each stand. Fitted values, Y_{PL} , were obtained by multiple regression of Y_{PL} on 2 sets of explanatory variables. The first set of explanatory variables, X , describe: i) stand characteristics and, ii) climate conditions important to mountain pine beetle survival, reproduction, and dispersal (Safranyik et al. 1975; Carroll et al. 2004) (Table 4). A climate model, ClimateBC (Hamman and Wang 2005), was used to generate unique climate values for each stand based on 30-year climate normals (1970–2000). The second set of explanatory variables, W , included geographic coordinates (latitude and longitude) linearized by a third-order polynomial regression equation (Legendre and Legendre 1998), and was used to test for the presence of a geographic pattern, or directionality, in the timing and magnitude of growth releases. To avoid over-fitting the final model, and yet still provide the most information possible about relationships between the response and explanatory variables, we systematically eliminated variables if they were highly correlated with others (i.e., had variance inflation factors greater than 10). Eight explanatory variables were eliminated from the final RDA: distance from stand 119 (DIST119), one of the two initial sites of infestation; density of lodgepole pine in 1987 (PLDEN87); mean summer precipitation (MSP); degree days >5 °C (DD5); minimum winter temperature (TMINWT); maximum summer temperature (TMAXSM); total summer precipitation (PPTSM); and spring precipitation (PPTSP). Relationships between variation in growth patterns among stands and explanatory variables were illustrated by superimposing the results of cluster analysis onto ordination biplot of the final RDA.

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