

Dendroecological Reconstruction of Mountain Pine Beetle Outbreaks in the Chilcotin Plateau of British Columbia

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Abstract

The mountain pine beetle (*Dendroctonus ponderosae* Hopk.) (Coleoptera: Scolytidae) is an aggressive bark beetle that periodically increases to outbreak levels killing thousands of trees. It is considered one of the major natural disturbance agents in North America. In British Columbia, the main host species is lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.), but western white pine (*Pinus monticola* Dougl.), ponderosa pine (*Pinus ponderosa* Laws.), whitebark pine (*Pinus albicaulis* Engelm.), and limber pine (*Pinus flexilis* James) are also attacked. We used dendrochronology to establish the history of canopy disturbances indicative of potential past beetle outbreaks. For this we relied on the fact that beetle outbreaks do not normally kill all the trees in a stand and that trees that survive outbreaks, experience extended periods of increased growth, visible in tree ring series as prolonged periods of release. Increased growth is thus used as a proxy for canopy disturbance. Fifteen chronologies studied in the south central area of British Columbia showed three fairly synchronous large-scale release periods which are proposed as three large outbreaks: 1890s, 1940s and the 1980s. The three releases averaged 13.8 years (Min=5, Max=23 years) in duration and recurred every 42 years (Min=28, Max=53 years), counted from the start of the release.

Introduction

The mountain pine beetle (*Dendroctonus ponderosae* Hopk.) (Coleoptera: Scolytidae) is an aggressive bark beetle whose populations periodically increase to outbreak levels in infestations that kill thousands of trees. It is considered one of the major natural disturbance agents in North America (Furniss and Carolin 1977). In British Columbia (BC), the main host species is lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.), but western white pine (*Pinus monticola* Dougl.), ponderosa pine (*Pinus ponderosa* Laws), whitebark pine (*Pinus albicaulis* Engelm.), and limber pine (*Pinus flexilis* James) are also attacked (Furniss and Carolin 1977). Occasionally, non-host trees such as Engelmann spruce (*Picea engelmannii* Parry) are attacked, but beetle populations do not persist in these occasional hosts (Unger 1993). Mountain pine beetles generally attack stands that are more than 80 years old, containing many trees of large diameter (Safranyik et al. 1974).

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Although mountain pine beetles can attack younger trees, outbreaks have not been reported in stands younger than 60 years (Safranyik et al. 1974).

The mountain pine beetle occurs from northern Mexico (latitude 30°N), north to central BC (latitude 56°N) and from the Pacific Ocean in the west, to North Dakota (Safranyik 2001). Mountain pine beetle is distributed throughout most lodgepole pine stands in BC, with infestations being the greatest in the south-central and southeastern part of the province (Safranyik et al. 1974).

The life cycle of the mountain pine beetle varies considerably (Furniss and Carolin 1977). The normal cycle takes one year to complete; however, during warmer than average summers, adult parents may re-emerge and establish a second brood in the same year. In cooler summers or at higher elevations, broods may require two years to mature. Beetle flights normally occur throughout July and into August. After locating a suitable host, females bore through the bark to the phloem and cambium region where the egg gallery is constructed. The first beetles attacking a tree use aggregating pheromones to attract additional beetles to mass attack and overcome the tree's resistance. Fungi, which are introduced by the beetle, cause blue stain in the sapwood. As the fungi become established in the phloem and xylem, they interrupt the flow of water to the tree crown and reduce the tree's ability to produce resin, which is its main defence mechanism against beetle attack. The combined action of the beetle and fungi kills the tree.

Peterman (1978) described the post-outbreak dynamics in climax lodgepole pine stands and indicated that beetle attack thins the stand and promotes increased growth among the remaining pines and other vegetation in the stand, allowing regeneration in the understory. During an outbreak, the beetles preferentially kill trees of the largest diameter (McGregor and Cole 1985). Cole and Amman (1980) investigated the characteristics of residual stands (>100 years old) in Wyoming and Idaho to determine the effect of past beetle outbreaks on stand structure. Increment cores from understory fir and spruce indicated a growth release following the death of overstorey pine trees killed by mountain pine beetle.

Roe and Amman (1970) compared the stand structure of lodgepole pine forests that had gone through beetle epidemics with those that had not. They found that by removing the largest trees in the stand, the beetle promoted succession to spruce and fir. In the absence of fire, consecutive mountain pine beetle attacks in the stand contributed to the conversion of an even-aged stand to an uneven aged stand. Similarly, Heath and Alfaro (1990) found that mountain pine beetle-attacked forests in the Cariboo Region of BC shifted in species composition from lodgepole pine-Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), to predominantly Douglas-fir.

Tree rings maintain a record of the canopy disturbance history for a locality, and are therefore useful as indicators of ecosystem function (Becker et al. 1988; Alfaro 2001), and have been used to determine past outbreaks of bark beetles (Stuart et al. 1989; Heath and Alfaro 1990; Veblen et al. 1991a, b; Zhang et al. 1999; Eisenhart and Veblen 2000) and defoliating insects (Zhang and Alfaro 2002, 2003). The identification of growth release periods in surviving host and non-host trees, synchronous with the mortality of host trees, is the most common method of historical beetle outbreak detection in tree ring series. The release is not precisely simultaneous because not all hosts are attacked nor die in the same year (Eisenhart and Veblen 2000).

In spite of its prevalence as a disturbance agent of BC forests, studies to understand the impacts of mountain pine beetle on stand dynamics are few. Heath and Alfaro (1990) measured stand structure and growth of surviving trees after an infestation, which occurred from 1971 to 1975 at Bull Mountain, near Williams Lake, BC. In addition, in 1987, the Pacific Forestry Centre established 30 research plots to measure ecological changes induced by beetle in lodgepole pine forests in south-central BC (Shore and Safranyik 1996). In 2001, a comprehensive study of beetle impacts on stand dynamics was launched in response to increased outbreaks in BC. As part of that study, in the summer of 2001, we re-measured 15 of the plots established by Shore and Safranyik (1996) (Fig. 1) in order to determine their condition in 2001, i.e., 14 years after plot establishment. The plots are located in the Chilcotin Plateau of the Cariboo Region of BC and are henceforth referred to as the Cariboo plots.

The objective of the work presented here was to determine the long-term history of mountain pine beetle outbreaks in these 15 plots. These plots cover a substantial portion of the range of mountain pine beetle in BC. For this, we used dendrochronological methods to identify release periods attributable to beetle outbreaks in increment cores collected in 2001.

Brief history of mountain pine beetle in the Chilcotin Plateau area of British Columbia

The following information on the history of mountain pine beetle outbreaks in central BC was summarized from Wood and Unger (1996) and is based on available reports, and on ground and aerial observations by the Forest Insect and Disease Survey (FIDS) of the Canadian Forest Service, conducted annually from the 1960s until 1995. Since then, with the discontinuation of FIDS, records have been less consistent.

An outbreak of mountain pine beetle was reported in the Cariboo Region of BC from 1930 to 1936 in the Tatla Lake area, when 60% to 90% of infested lodgepole pine was killed over 650,000 ha. In the 1940s beetle-killed trees were reported in the Alexis Creek area (Personal communication, Dr. Les Safranyik, Canadian Forest Service, Victoria). A series of mountain pine beetle outbreaks occurred throughout the 1970s in the Cariboo Region. In 1974, the Klinaklini River drainage had infestations, which by 1975 had spread over most of the West Chilcotin. In 1981, mountain pine beetle killed over 9 million trees on 72,800 ha of the Chilcotin Plateau.

Dendroecological Methods

In the summer of 2001, increment cores were collected and analyzed from each of 15 locations in the Cariboo Region of BC (Fig. 1).

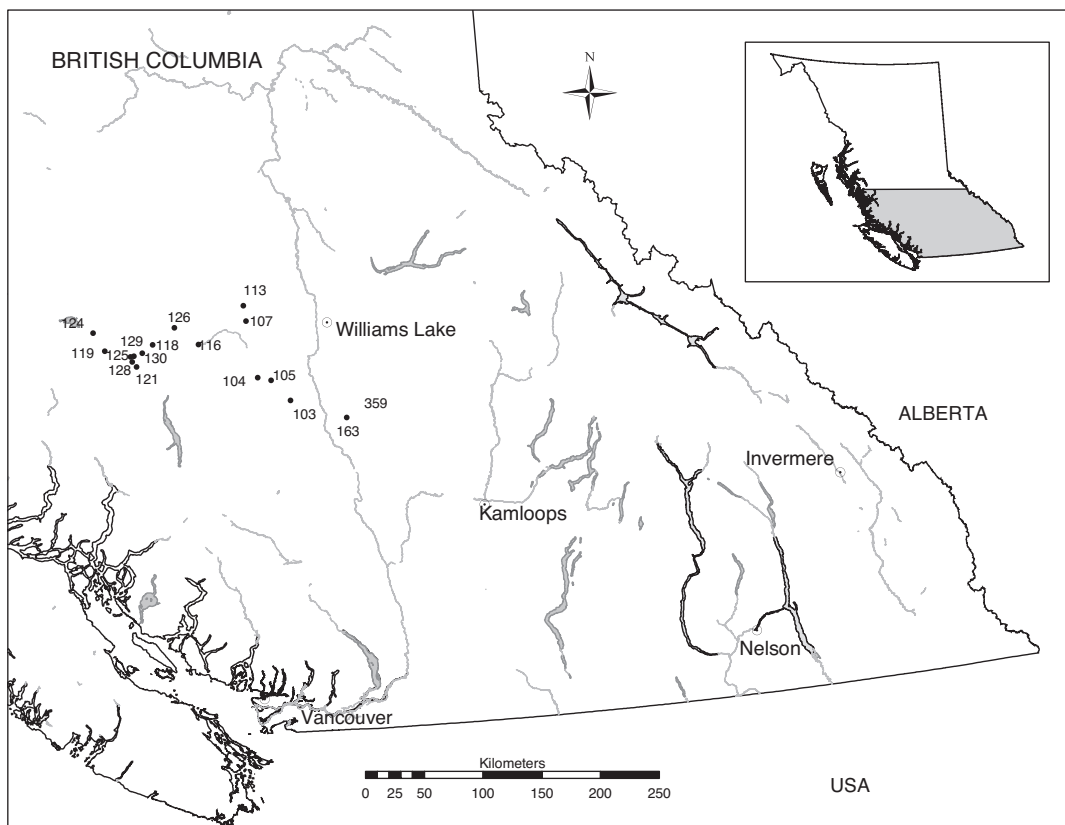


Figure 1. Map of the location of plots used to study the recurrence of mountain pine beetle infestations in lodgepole pine, in Central BC. Shaded area represents the enlarged map.

Stands were located in the Sub-boreal Pine Spruce (SBPS) and Interior Douglas-fir (IDF) biogeoclimatic zones (Meidinger and Pojar 1991) (Table 1). The SBPS zone is characterized by cold, dry winters and cool, dry summers. Mean annual precipitation ranges from 335 to 580 mm (Steen and Coupe 1997). Lodgepole pine is the climax tree species in this zone and is the most common species regenerating in the understory (Steen and Coupe 1997). The IDF zone is characterized by warm, dry summers and cool, dry winters (Meidinger and Pojar 1991). Climax vegetation on sites in the IDF zone is a Douglas-fir forest, often with intermixed lodgepole pine in the forest canopy (Steen and Coupe 1997).

Table 1. Summary data for lodgepole pine (host) stand chronologies used to study recurrence of mountain pine beetle disturbance in the Chilcotin Plateau area of BC.

Location	Stand No.	No. of cores cross-dated	BGC ¹ zone	BGC sub-zone	Chronology period	Year with >5 cores ²	Mean Serial Correlation ³
Cariboo	103	21	IDF	dk4	1890-2001	1897	0.618
Cariboo	104	21	IDF	dk4	1849-2000	1890	0.590
Cariboo	105	16	IDF	dk4	1865-2000	1869	0.569
Cariboo	107	9	SBPS	xc	1886-2000	1915	0.493
Cariboo	113	14	SBPS	xc	1758-2000	1809	0.448
Cariboo	116	19	IDF	dk4	1849-2001	1889	0.558
Cariboo	118	14	SBPS	xc	1853-2000	1867	0.456
Cariboo	119	14	SBPS	xc	1912-2000	1951	0.544
Cariboo	121	13	IDF	dk4	1901-2000	1931	0.403
Cariboo	124	16	SBPS	xc	1887-2000	1915	0.430
Cariboo	125	17	SBPS	xc	1886-2000	1905	0.454
Cariboo	126	14	IDF	dk4	1864-2000	1915	0.496
Cariboo	128	16	SBPS	xc	1865-2000	1941	0.457
Cariboo	129	18	SBPS	xc	1860-2000	1891	0.495
Cariboo	130	18	SBPS	xc	1895-2000	1906	0.493

¹Biogeoclimatic zone

²Starting year when the chronology is based on 5 or more trees

³Describes the amount of common signal within the chronology (Fritts 1976)

Increment core sample collection and preparation

Increment cores were collected from lodgepole pine as well as from non-host (these are trees not normally attacked by mountain pine beetle) Douglas-fir and interior spruce trees. In total, we collected 259 increment cores: 240 from lodgepole pine and 19 from non-host Douglas-fir and spruce. The cores (one per tree) were extracted at breast height with an increment borer parallel to the slope contour. In the field, each core was labelled with stand and plot number, tree number and species. Collected cores were transported to the Pacific Forestry Centre, Canadian Forest Service, Victoria, BC, for storage and analysis. Cores were glued and mounted in slotted mounting boards, which were labelled with tree identifiers. The surface of the cores was sanded with progressively finer sand paper (grits 220 to 600) to enhance the boundaries between annual rings.

Sample measurement and chronology development

Ring-width measurement was conducted in the Tree-Ring Laboratory of the Pacific Forestry Centre using a Windendro™ tree-ring measuring system and a Measu-Chron incremental measuring system. The precision of the measurement was 0.01 mm. The measured ring-width 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). COFECHA (Holmes 1983) detects measurement and cross-dating errors by computing correlation coefficients between overlapping 50-year segments from individual series (Eisenhart and Veblen 2000).

We standardized all cross-dated series by dividing each ring width by the mean series ring width (Eisenhart and Veblen 2000). Standardizing series by their mean preserved the long-term growth trend necessary to identify canopy disturbances (Veblen et al. 1991a). Each chronology was visually inspected for growth releases that might indicate a mountain pine beetle outbreak. After trying different methods to remove subjectivity from the process of identifying the release periods, we settled for a purely visual method, in which a release was called a mountain pine beetle release if it was abrupt and sustained over several years (Fig. 2).

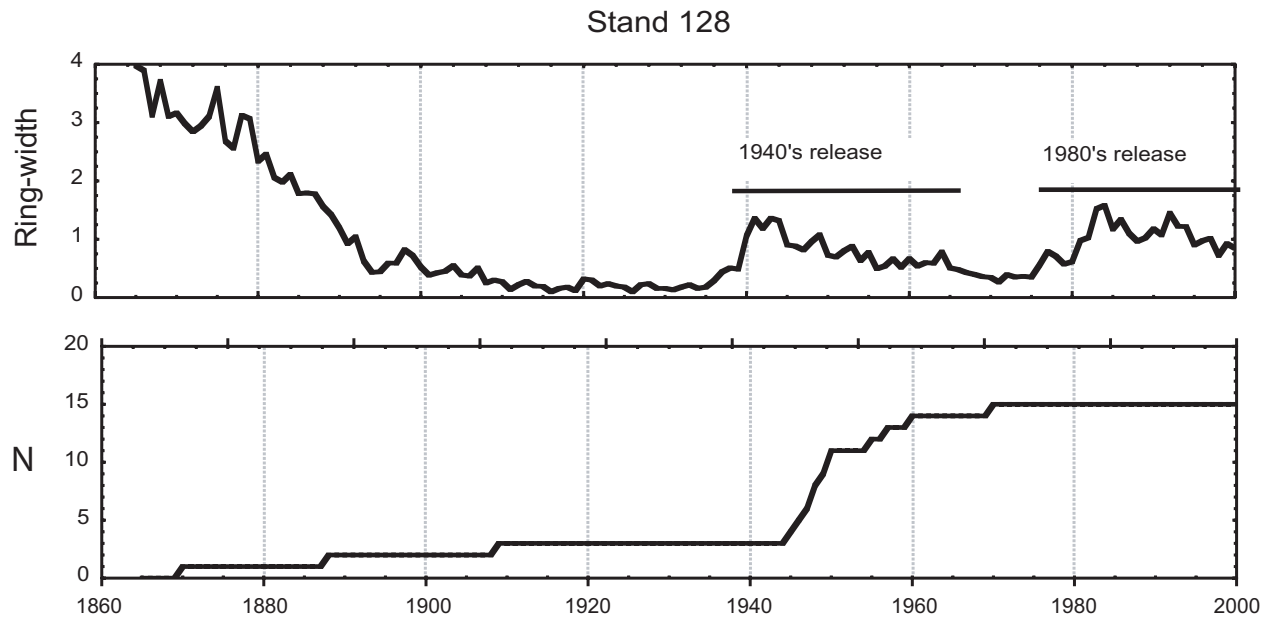


Figure 2. Example of tree ring chronology (top) and sample size for the chronology (bottom). Ring width indices for this stand (#128, Cariboo Region) clearly show two release periods attributable to canopy disturbances caused by outbreak of the mountain pine beetle (1940s and 1980s).

We defined the start of a growth release as a year that exhibited a 50% increase with respect to the mean ring width of the previous 5 years. The end of a release was defined by the year when rings returned to pre-release levels. Thus, the start and end of the release was compared only with the tree-ring indices that directly preceded the release and not to the whole chronology. Releases that lasted less than 5 years were ignored as we expected that canopy openings caused by beetle thinning would cause release periods that would last until full canopy closure was re-established. Although no data exists on the length of this process, we expected that, for severe outbreaks, it would last more than 5 years. Veblen et al. (1991a, b) used a similar method for detecting release in Engelmann spruce trees following spruce bark beetle outbreaks in Colorado.

Lodgepole pine (host) chronologies were developed for each of the 15 stands. In the initial decades of long tree-ring chronologies, when sample size is inevitably small, identification of releases is unreliable (Eisenhart and Veblen 2000). Therefore, interpretation of chronologies was limited to where the sample size was at least five trees per stand.

It was difficult to find sufficient non-host trees in the study area to build reliable chronologies for species other than pine. However, we succeeded in building two non-host chronologies: one spruce chronology for stand 113 and a Douglas-fir chronology for stand 116 in the Cariboo region. Non-host chronologies were examined for periods of release and compared to host chronologies to determine if periods of release in non-host species were synchronous with periods of release in lodgepole pine.

Searching for spatial outbreak patterns

To study the spatial synchrony of mountain pine beetle outbreaks, the entire chronologies were visually compared and the release periods attributable to beetle-induced thinning were tabulated and plotted for each sampled stand. The average start and end year of the release and the interval between initial dates of release were calculated.

Results

Outbreak history based on tree rings

Over 90% of lodgepole pine cores were successfully cross-dated and included in the tree-ring analysis. The number of cores included in the stand chronologies ranged from 9 to 21 (Table 1). Although one chronology (stand 113) contained one tree dating to 1758 (243 years old at breast height, Table 1), for most chronologies the oldest date when the sample size was at least five trees was in the 1880s. Therefore our results can be applied with confidence only to the period after this date, i.e., we provide a beetle history for the last 120 years.

On average, the 15 chronologies studied showed three fairly synchronous release periods: 1890s, 1940s and the 1980s (Tables 2 and 3, Figs. 3 and 4). The three releases averaged 13.8 years (Min=5, Max=23 years) in duration and recurred every 42 years (Min=28, Max=53 years), counted from the start of one release to the start of the next release (Table 2).

The *first release* (1890s) appears in only 5 of the 12 stands that were old enough to register this release (Figs. 3,4). The median of the initial release date for these five stands was 1893, but ranged from 1887 to 1898. The average duration of this release was 13.2 years. Examination of fire and beetle scars in discs from these areas indicates possible activity of these two disturbances simultaneously (Fig. 3). Without additional sampling and lacking written records, the causes of this release are uncertain.

The *second release* (Figs. 3, 4) appeared with relative synchrony in 13 of the 15 stands sampled and had an initial median date of 1935 (Min=1926, Max= 1959). The average duration of this release was 13.6 years (Min= 5, Max= 23 years). The start of the second release occurred, on average, 40.8 years after the start of the first release. Cross-section samples collected by Hawkes et al. (2004) showed many beetle scans in this period (Fig. 3).

The *third release* was evident in 12 of the 15 stands sampled and also appeared with relative synchrony (Figs. 3, 4). This release had a median initial date of 1982 (Min=1975, Max= 1989) and lasted, on average 14.3 years, and in some stands it still continued in 2000. This release occurred, on average, 42.9 years after the start of the second release. Cross-section samples also show many beetle scans dating in this period (Fig. 3).

Non-host. In the two stands that had both host and non-host chronologies constructed (Tables 4 and 5, Fig. 5), both species responded to canopy disturbance approximately at the same time as lodgepole pine. Similarly to lodgepole pine, release periods were evident starting in the 1890s, 1930s and 1980s. Release durations were 8, 25 and 15 years for the first, second and third releases.

Table 2. Dates of growth releases attributable to mountain pine beetle thinning of lodgepole pine stands, duration of release, and interval between releases, in the Chilcotin Plateau area of BC. Dashed line indicates that there was no interval.

Stand No.	Release Dates	Duration of release (Years)	Interval between adjacent ¹ releases (Years)
103	1939-1950	11	---
	1989-2000	11	50
104	1895-1903	8	---
	1938-1950	12	43
	1975-1985	10	37
105	1939-1950	11	---
107	1932-1944	12	---

113	1898-1904	6	---
	1926-1947	21	28
116	1887-1902	15	---
	1933-1944	11	46
	1986-1998	12	53
118	1895-1910	15	---
	1980-2000	20	---
119	1941-1946	5	---
	1975-1993	18	34

121	1932-1955	23	---
	1980-1987	7	48
124	1959-1968	9	---
	1988-1993	5	29
125	1935-1944	9	---
	1980-1997	17	45
126	1934-1951	17	---
	1975-1996	21	41

128	1939-1956	17	---
	1982-1998	16	43
129	1890-1912	22	---
	1936-1951	15	46
	1981-1998	17	45
130	1935-1953	18	---
	1982-2000	18	47

Overall			
Mean		13.8	42.3

¹Three release periods were found: 1890s, 1940s and 1980s. Intervals are between consecutive release periods.

Table 3. Characteristics of lodgepole pine growth releases attributable to stand thinning by mountain pine beetle outbreaks in the Chilcotin Plateau area of the Cariboo Region.

	First release		Second release		Third release	
	Initial year	End year	Initial year	End year	Initial year	End year
No. stands	5	5	14	14	12	12
Mean	1893	1906	1937	1951	1981	1995
Median	1895	1904	1935	1950	1982	1997
Range	1887-1898	1902-1912	1926-1959	1944-1968	1975-1989	1985-2000

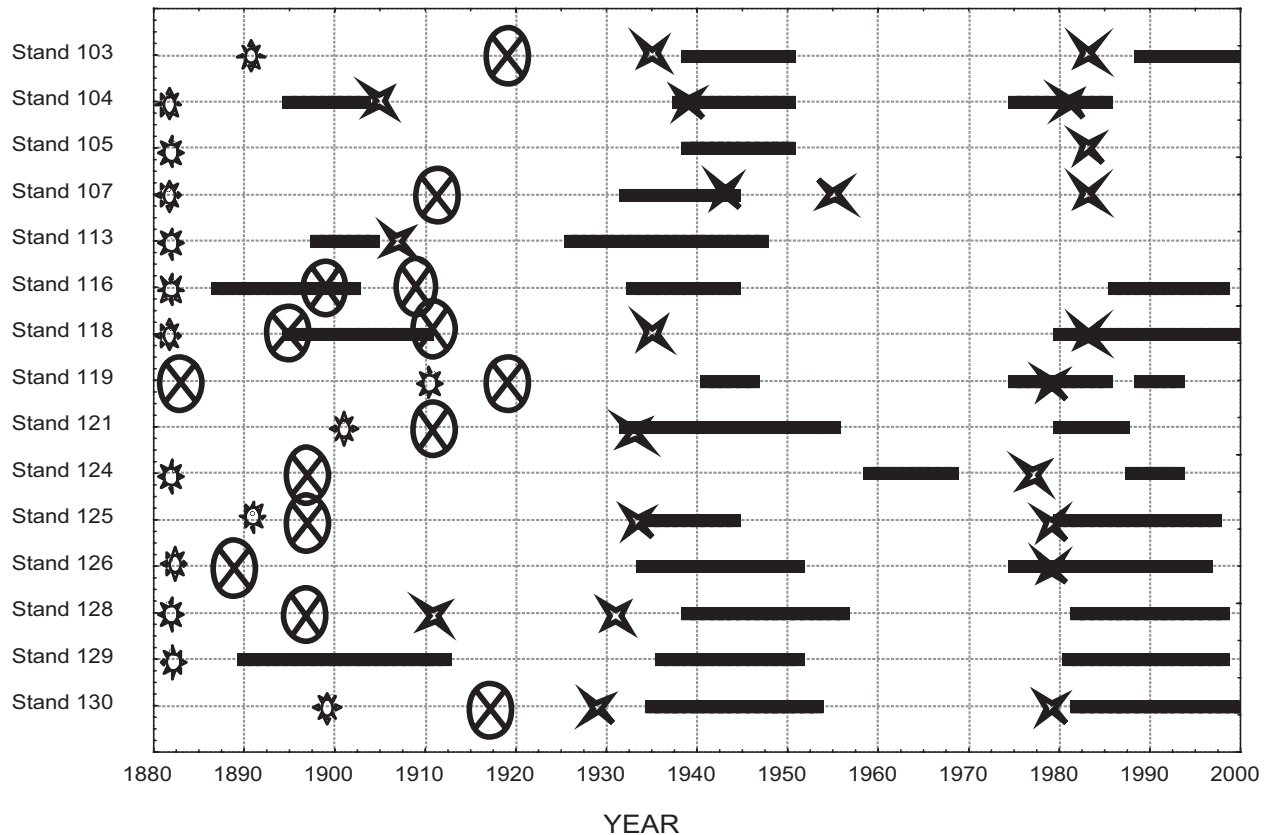


Figure 3. Release periods attributable to mountain pine beetle outbreaks in Chilcotin Plateau, BC, inferred from growth-release periods using tree-ring chronologies. Fire (circle with cross in middle) and mountain pine beetle (star shaped symbol) scar dates are given for each stand. For details of fire and beetle scars, please see Hawkes et al. (2004). Asterisk indicates start year for the tree-ring chronology.

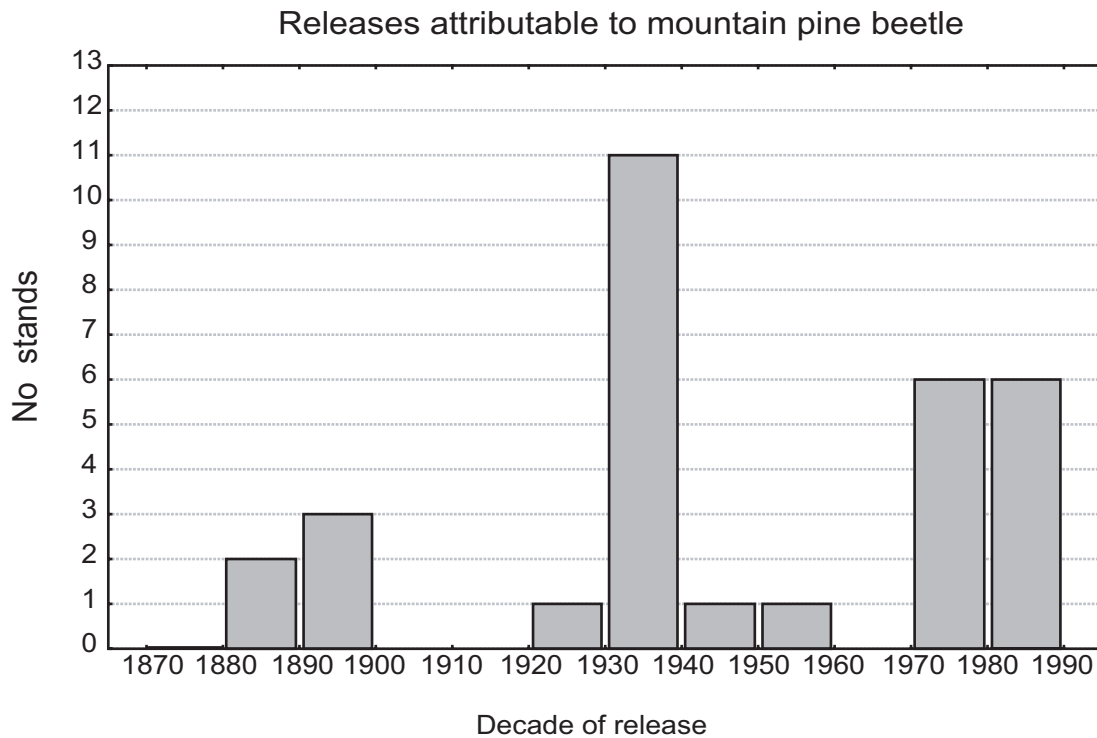


Figure 4. Histogram of the initial growth release year for 15 lodgepole pine stands in the Chilcotin Plateau area of BC. Releases are attributable to stand thinning caused by beetle outbreaks occurring in the late 1890s, 1930s and 1970s. Years indicate interval during which release occurred.

Table 4. Summary data for non-host stand chronologies used to study recurrence of mountain pine beetle disturbances in the Chilcotin Plateau area of BC.

Location	Stand No.	Species	No. of cores cross-dated	Chronology period	Mean Serial Correlation
Cariboo	113	Spruce	10	1894-2000	0.379
Cariboo	116	Douglas-fir	9	1901-2001	0.764

Table 5. Characteristics of growth releases in non-host trees attributable to mountain pine beetle thinning in the Chilcotin Plateau area of BC.

Location	Stand No.	Species	First release		Second release		Third release	
			Initial year	End year	Initial year	End year	Initial year	End year
Cariboo	113	Spruce	1896	1903	1925	1946	1975	1993
Cariboo	116	Douglas-fir	1911	1920	1932	1955	1984	1997
		Mean	1904	1912	1928	1951	1980	1995

Discussion

We identified dates of releases caused by potential mountain pine beetle outbreaks using tree ring release as a proxy for canopy disturbance (Table 2, Fig. 3). Because lodgepole stands do not grow to be very old, we were able only to examine the disturbance history from the late 19th century forward. Because of a delayed response in tree growth response to thinning, the initial date of release is not necessarily the year when mountain pine beetles began to thin the stands. Heath and Alfaro (1990) indicated that the thinning response of lodgepole pine, expressed as significant increases in ring growth, began 2 to 6 years after the start of a severe beetle outbreak and peaked 5 to 9 years after. Therefore, the potential mountain pine beetle outbreaks dates would have started 2 to 6 years prior to the initial release dates indicated in this paper.

There is some uncertainty in the dendrochronological approach when establishing mountain pine beetle disturbance history, because dendrochronology is unable to distinguish between growth releases induced by beetle thinning from above-normal periods of growth caused by better than normal climatic conditions, e.g., above-normal precipitation. In the case of dating defoliating insect outbreaks, the dendrochronology method makes it possible to separate the climatic signal from defoliator-induced growth reduction by adjusting the signal of the host tree by that of the non-host tree, as both types of trees have opposite reactions to defoliation (Swetnam and Lynch 1993; Zhang and Alfaro 2002). Separation of climatic release from beetle-induced thinning is not possible as both beetle host and non-host trees respond equally to the thinning action of the beetle (Heath and Alfaro 1990). However, we can be increasingly re-assured that the 1940s and 1980s releases are beetle-induced because the records indicate widespread infestations in the 1940s in the Chilcotin area and the 1980s plots were established in areas with ongoing beetle infestations. Also many cross-section samples from these areas contain beetle attack scars dating to the 1940's and 1980's (Hawkes et al. 2004). For complete certainty, we need samples from control areas, i.e., from areas where we know beetle outbreaks did not occur. This is impossible for the early outbreaks (1890s and 1940s), which are not well documented. In the 1980s the outbreak was very large; therefore, potential control sites occurred only in very different ecosystems, which would make comparisons inaccurate.

There is some uncertainty as to the cause of the 1890s release, as records are non-existent for this period. In addition, fire scars in four stands in the Chilcotin date to this period, suggesting that ground fires also played a role. Apart from beetle, ground fire is the only large-scale canopy disturbance capable of thinning a lodgepole pine stand. However, comparing the tree ring patterns for trees that originate from fully documented outbreaks (Heath and Alfaro 1990; Veblen et al. 1991a, b) and with the tree ring signals in this study, strongly suggests that the 1890s release also represent responses to beetle thinning.

Several of the stands did not record a release in response to the last outbreak. This could be attributed to the fact that many of the cores were sampled from trees that are old, fire scarred, infested with mistletoe, and stem and root diseases, and have been previously unsuccessfully attacked by mountain pine beetle. These trees may not have the resources (i.e., foliar biomass, live cambium, and fine root biomass) to respond to canopy disturbance in a manner that, using the criteria of this study, would be detected as a growth release.

The average interval between the first (1890s) disturbance and the second (1940s) was 41 years, and between the second and third (1980s) disturbance was 43 years. This points to a strong cyclical nature of beetle outbreaks. The cycle, recorded in the tree rings, consists of thinning of the stand by beetles which creates a strong and sustained increase in ring-width growth, followed by a gradual decline in ring width as the stand returns to full site occupancy by lodgepole pine and other species. The average length of the growth release was 13.2 (1890s), 13.6 (1940s) and 14.3 years (1980s, still ongoing in some stands).

What causes the cycle?

We hypothesize that lodgepole pine stands alternate between a susceptible state and a resistant state, on average every 42 years, with some variability between locations. Stands in the susceptible state are

overstocked, mature stands, usually older than 80 years and with many trees of large diameter. Under these conditions, trees are stressed and unable to fend off beetle attack (Safranyik et al. 1974). When conditions such as climate and proximity to active infestations (Shore and Safranyik 1992) are suitable for population increase, outbreaks develop, which gradually, over the course of an infestation, thin the stand. Surviving trees benefit from the additional space and resources made available through tree mortality, and gradually become resistant to beetle invasion. This causes the outbreak to decrease and eventually cease. Without beetle thinning, stocking increases, as trees accelerate growth and regeneration is recruited into the overstorey. Thus, gradually, over a process that may last on average 42 years, the stand again becomes susceptible to outbreaks.

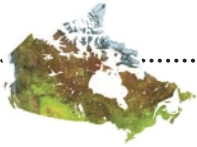
We hope that the recurrence rates established here will assist in forecasting potential outbreaks and in planning the timber supply of BC.

René I. Alfaro is a research scientist with the Canadian Forest Service, Pacific Forestry Centre.

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