

## Growth characteristics of lodgepole pine associated with the start of mountain pine beetle outbreaks

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The dynamics of tree and stand growth were studied in six small but expanding mountain pine beetle outbreaks in British Columbia. Stands had exceeded a previously reported hazard threshold of age 80 years by 26 years, and a second frequently used hazard threshold of 20.5 cm mean dbh was exceeded by 37 years. However, stands had exceeded maturity, as defined by the intersection of current annual increment (CAI) and mean annual increment (MAI), by an average of only 17 years. In all cases, the beginnings of the outbreaks were coincident with a period of reduced tree growth. This reduced tree growth was difficult to detect at breast height, with a consequent failure of the periodic growth ratio to indicate susceptibility. Although the stands were past the point of maturity, the dominant and codominant trees continued to add significant wood volume, which could make surveillance for incipient outbreaks and subsequent control actions cost effective.

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On a étudié en Colombie-Britannique la dynamique de la croissance des arbres et des peuplements dans six zones, petites mais en développement, infestées par le dendroctone du pin ponderosa. Les peuplements excédaient de 26 ans un seuil de danger de 80 ans déjà signalé, et de 37 ans un autre seuil de danger fréquemment utilisé, soit un dhp moyen de 20,5 cm. Toutefois, les peuplements avaient, en moyenne, dépassé de 17 ans la maturité, comme on la définit par le recoupement de l'accroissement annuel courant et de l'accroissement annuel moyen. Dans tous les cas, le début de l'infestation a coïncidé avec une période de croissance réduite des arbres, difficile à déceler à hauteur de poitrine, ce qui a empêché le rapport périodique de croissance d'indiquer la vulnérabilité. Même si les peuplements avaient dépassé le point de maturité, les arbres dominants et codominants continuaient à produire un volume significatif de bois, ce qui pourrait rentabiliser la surveillance des infestations naissantes et leur répression subséquente.

### Introduction

The interrelationship between lodgepole pine (*Pinus contorta* Dougl. var *latifolia* Englm.) and the mountain pine beetle (MPB) (*Dendroctonus ponderosae* Hopk.) with its associated blue-stain fungi has been interpreted as a dynamic equilibrium (Safranyik *et al.* 1975). Outbreaks may, therefore, result through perturbations of the states of any of these three components. Many of the studies (see reviews of Amman 1978; Cole and Amman 1980) which have focused on the influence of the tree in this equilibrium have emphasized diameter and phloem thickness, factors which relate to survival of beetle broods and their nutrition. Other authors (Berryman 1978; Shrimpton 1978) propose that after stands exceed threshold levels for diameter and phloem thickness a frequent cause of outbreaks is a decline in tree vigor. Several hazard-rating systems have been developed to predict the time of mountain pine beetle (MPB) outbreaks. To date, these systems rely solely upon minimum thresholds and offer no information when these thresholds are exceeded. Better information

on "vigor" related tree characteristics as they apply to the onset of outbreaks is necessary.

At the individual tree level, Shrimpton (1973) indicated a relationship between tree growth dynamics, represented by the radial increment, and tree resistance. Changes in these growth rates, measured as periodic growth ratios (PGR) were studied by Mahoney (1978) in relation to beetle attack. However, because radial growth generally declines with time (Duff and Nolan 1953) problems with the PGR approach have been found (Shrimpton and Thomson 1981). At the stand level, a relationship between current annual increment (CAI) and resistance to attack by MPB has been observed (Safranyik *et al.* 1975). These authors propose that the time of intersection of current (CAI) and mean annual increment (MAI), physiological maturity, can indicate hazard from mountain pine beetle because the dynamics of tree growth are incorporated into the concept of stand maturity when defined by this time of intersection.

In the present study, we investigate the dynamics of tree and stand growth in relation to small expanding mountain pine beetle outbreaks. At an individual tree

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TABLE 1. The location, aspect, elevation, ground cover, and site classification of each study site

Plot name	Location	Aspect	Elevation (m)	Ground cover and forest type <sup>a</sup>	BCMF <sup>b</sup> site classification
Ashnola	McBride Cr.	SE	1050	Calmagrostis PLF	Good
Enderby	7 km SE of Enderby	W	450	Calmagrostis PL	Poor
Golden	Blaeberry River	S	1000	Kinikini PLF	Good
Invermere	Horsethief Creek	W	1100	Calmagrostis PLF	Medium
Kispiox	Scunsnat Creek	S	500	Kinikini PLS	Good
Riske Creek	Beecher Prairie	S	500	Calmagrostis PL	Medium

<sup>a</sup>Forest type abbreviations: PL, lodgepole pine; F, Douglas-fir; S, White spruce.<sup>b</sup>BCMF: British Columbia Ministry of Forests.

level, the detailed history of growth over the whole stem is investigated by intensive stem analysis techniques. At the stand level the dynamics are considered with reference to stand maturity. Results are discussed in relation to existing hazard-rating systems for mountain pine beetle in lodgepole pine.

### Methods

In 1979, a study site was selected in each of six areas of British Columbia which had a history of MPB activity and which were situated in zones defined as moderate or high hazard to MPB based upon climatic suitability for beetle development (Safranyik *et al.* 1975). In each area there currently existed an outbreak which had originated from a small nucleus of infested trees and had continued to spread for 2–5 years at the time of sampling.

Five of the study sites were situated in a stand at the margin of the attacked and unattacked areas, and were uniform with respect to diameter distribution, ground cover, and slope between the attacked and unattacked portions of the stand (Table 1); i.e., beetle attack was used to define the sample site. The sixth site was in the centre of a grove, having attacked trees, in a lodgepole–aspen parkland. Diameter, age, slope, and ground cover were comparable to nearby groves having attacked trees.

The dbh of each tree on a 1/5-acre (1 a = 100 m<sup>2</sup>) plot in four of the study sites was measured. The plot was situated such that it contained both attacked and unattacked trees. Twelve dominant and codominant trees, including both attacked and unattacked stems, were cut from each of the six sites. Diameter outside bark and single bark thickness were measured at 1.3 m height. Detailed procedures for discing the stems and measuring incremental growth and the programs used to compute growth are described in Thomson and Van Sickle (1980).

For the five plots with tree age greater than 100, site index was calculated by averaging their height at age 100, and for the sixth plot, near Golden, the site index was calculated by the method of Curtis *et al.* (1974). Because stocking levels

were directly comparable with growth tables for unmanaged lodgepole pine in British Columbia, the age where CAI and MAI are equal, for stems greater than 15.2 cm dbh, was determined from curves derived from the tables (Smithers 1961). The volume growth of each stem in relation to age was described by the logistic curve:

$$[1] \text{ volume} = a / (1 + e^{b+c \cdot \text{age}})$$

The relationship of CAI to individual tree age is defined by the derivative of [1]:

$$[2] \text{ CAI} = \frac{-ace^{b+c \cdot \text{age}}}{(1 + e^{b+c \cdot \text{age}})^2}$$

Curves were fitted to the CAI from age 20 by Marquardt's algorithm for nonlinear regression, and this curve projected beyond the year the trees were cut to estimate potential growth rates.

Analysis of growth patterns was carried out in relation to the radial and oblique growth sequences described by Duff and Nolan (1952). To facilitate comparisons, the radial increment on each disc in a given year was summed and averaged. The average increment for all sample trees in each plot was also obtained.

The periodic growth ratio (Mahoney 1978) was calculated for all rings on the 1.3-m disc. To evaluate the periodic growth ratio as an indicator of susceptibility, the number of ratios less than 0.9 in the 5-year period preceding the outbreak was averaged for the 12 trees on each plot. Stand hazard ratios (Schenk *et al.* 1980) were also calculated.

### Results

#### Stocking levels

Stocking data for four of the six study sites are given in Table 2 with values from Smithers (1961) yield tables for comparison. Stand ages at the years indicated for outbreak commencement are given in Table 3.

Stocking data was not obtained at Kispiox or Riske Creek. The stand at Kispiox had several small open-

TABLE 2. Comparison of observed stocking levels (stems  $\geq 15.2$  cm) compared with values from yield tables for lodgepole pine. The yield table values are enclosed in parentheses

	Stems/ha	dbh (cm)	Height (m)	Total basal area (m <sup>2</sup> /ha)	Basal area (%) other species
Ashnola	864(825)	25.2(25.9)	27.4(27.1)	43.09(43.4)	3
Enderby	975(983)	24.1(22.1)	19.7(20.7)	44.47(37.5)	1
Golden	680(755)	28.4(27.2)	26.6(28.5)	43.08(43.2)	8
Invermere	1173(944)	23.1(23.6)	25.1(23.2)	44.69(40.9)	10

TABLE 3. Site index, predicted age at intersection of CAI and MAI, age at the start of the outbreak, and number of years the trees are past the intersection of CAI and MAI. Also included is the climatic hazard zone in which the plot is located

Plot	Site index <sup>a</sup>	CAI-MAI intersection	Outbreak start	Stand age at outbreak	Climatic hazard <sup>b</sup>	Years beyond CAI-MAI intersection
Ashnola	80	82	1971	102	Extreme	20
Enderby	60	100	1974	116	High	16
Golden	90	80	1975	82	High	2
Invermere	70	88	1975	111	High	23
Kispiox	80	82	1975	119	Moderate	37
Riske Creek	60	100	1971	101	Moderate	1

<sup>a</sup>Index age, 100 years.<sup>b</sup>Safranyik *et al.* 1975.

ings. An estimate of stand density from the distribution of the 12 sampled trees and their immediate neighbours indicates approximately 750 stems/ha with an average diameter of 28.2 cm, dominant height of 26.7 m, and basal area of approximately 47 m<sup>2</sup>/ha. White spruce (*Picea glauca* (Moench) Voss) comprised approximately 10% of the basal area. Smithers' (1961) yield tables indicate 800 stems/ha with an average diameter of 26.7 cm, dominant height of 27.7 m, and basal area of 44.5 m<sup>2</sup>/ha on site 80 at 120 years of age for stems greater than 15.2 cm.

The dominant and codominant stems cut from the centre of the grove near Riske Creek had flat-topped crowns. Age and height of pine in the grove decreased from the centre, and aspen were at the margin. At an average age of 107 years, 112 trees from the centre of three groves had an average diameter of 27.6 cm and a dominant height of 19.8 m. Smithers (1961) indicates on site 60 at age 110 an average diameter of 21.8 cm and a dominant height of 20.3 m.

#### Relationship of physiological maturity to MPB attack

For each of the six plots, the calculated site index, at 100 years, predicted age where stand CAI and MAI are equal, age of trees at the start of the outbreak, and the number of years each plot has exceeded the point where CAI and MAI are equal, are given in Table 3. Site indices for the six plots varied between a low of

60 for Enderby and Riske Creek and a high value of 90 for the Golden plot. The predicted age, where CAI and MAI are equal for stands of the observed stocking and site indices, was between 80 and 100 years (Smithers 1961). All plots were at or beyond their predicted intersection point. At Golden and Riske Creek, the stands were 2 years and 1 year past physiological maturity, respectively. Three plots, Ashnola, Enderby, and Invermere, were between 21 and 26 years past physiological maturity, and the most northerly plot, Kispiox, was 37 years past physiological maturity.

#### Volume growth of individual trees

The relationship of CAI and MAI for three of the trees from Ashnola is given in Fig. 1. Curves fitted to the CAI by [2] are also shown. At the time of cutting, CAI and MAI of 36 of the 72 trees have intersected or will intersect within 20 years (e.g., Fig. 2A). Within 50 years, the number of trees where the projected CAI and MAI intersect rises to 56 (e.g., Fig. 2B). For six trees the projected CAI and MAI never intersect, and for the remaining 10 trees intersection is between 51 and 283 years (e.g., Fig. 2C).

Average growth in volume for each of the six plots during the 10 years prior to the outbreak, and projected for 10 years beyond the start of the outbreak, is in Table 4. Average volume growth on each plot, for the 10 years prior to outbreak, varied between

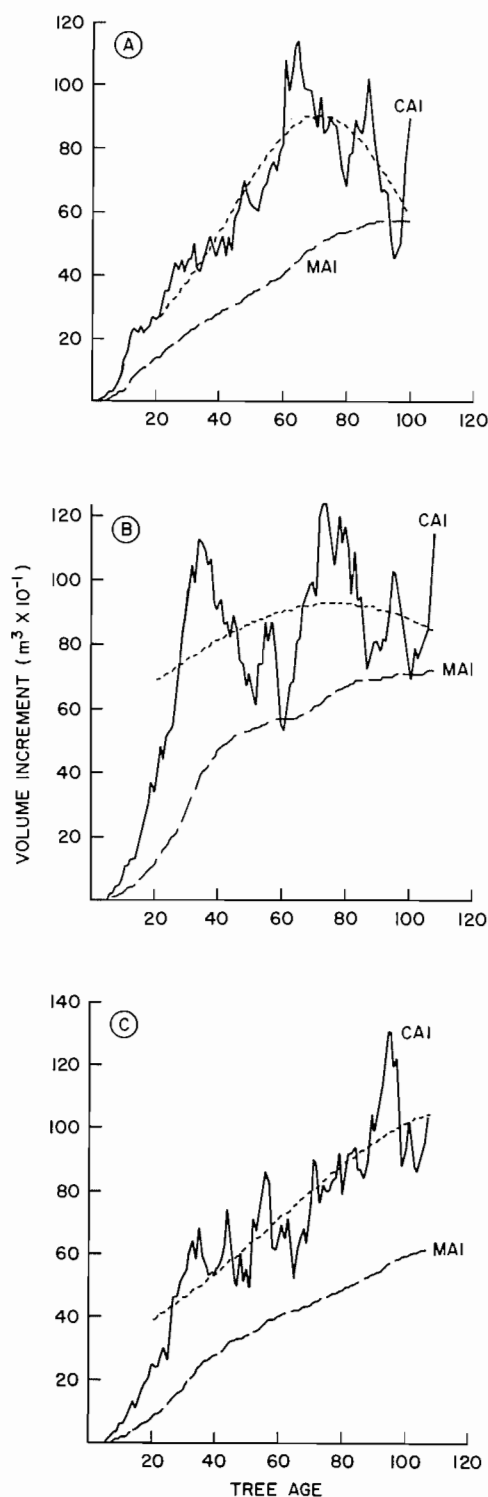


FIG. 1. The relationship between observed (solid line), calculated annual increment, mean annual increment, and age for three trees from Ashnola.

0.047  $\text{m}^3/\text{tree}$  at Enderby and 0.10  $\text{m}^3/\text{tree}$  at Golden. For 10 years beyond the start of the outbreak, projected growth in volume on each plot varied from a low of 0.037  $\text{m}^3$  at Enderby to 0.091  $\text{m}^3$  at Golden. The average increase in volume for all 72 trees in the 10 years prior to the outbreak was 0.082  $\text{m}^3$ , a 16% increase in volume. For the 10-year period after the start of the outbreak, the average projected increase in volume was 0.065  $\text{m}^3$ , an 11% increase.

Volume increase of individual trees in the 10-year period after the outbreak varied between a low of 0.02  $\text{m}^3$  at Enderby, a 10% increase, to a high value of 0.15  $\text{m}^3$  at Golden, a 13% increase. Ten of the 72 trees had volume increases greater than 15% in the 10-year period after the start of the outbreak.

#### *Relationship of radial growth rates to MPB attack*

A similar pattern of reduced growth at the time of MPB attack was found in each plot. For individual trees on each plot, the year of minimum average radial increment was the same for all trees. However, the total change in growth rate around the year of the minimum radial increment varied between trees. Some trees had as little as 12% reduction in growth rate over a 5-year period, whereas others had a 40% reduction in the same period.

For any tree, the minimal radial increment occurred in any given year between 1/10 and 6/10 of the height up the stem. The mean height (which was also the median height) of minimal increment, in the 15-year period prior to cutting the trees, was 5.6 m above ground, in relation to an average tree height of 24.1 m. The modal height for minimum radial increment was 3.4 m above ground. For some trees the 1.3-m disc did not record the year of minimum radial growth accurately even using the average of two radial traces because of growth patterns associated with the root collar or wounds.

The Riske Creek and Golden plots were experiencing a period of depressed growth when the outbreaks commenced in 1971 and 1975, respectively (Fig. 2A and 2B). Attacks were 1 and 2 years after physiological maturity, respectively. Outbreaks commenced while incremental growth on the average radial sequence was depressed, and continued to spread even though growth rates recovered.

For the Enderby plot, attainment of physiological maturity in 1958 coincided with a period when the incremental growth rate was reduced. Since that time, growth rate tended to increase until 1966 then decreased until 1975 (Fig. 2C). The outbreak began in 1974 and spread as the growth rate of trees recovered.

On the Ashnola plot, physiological maturity was attained in 1951. Since that time, growth rate decreased until 1958, recovered between 1958 and 1966, and

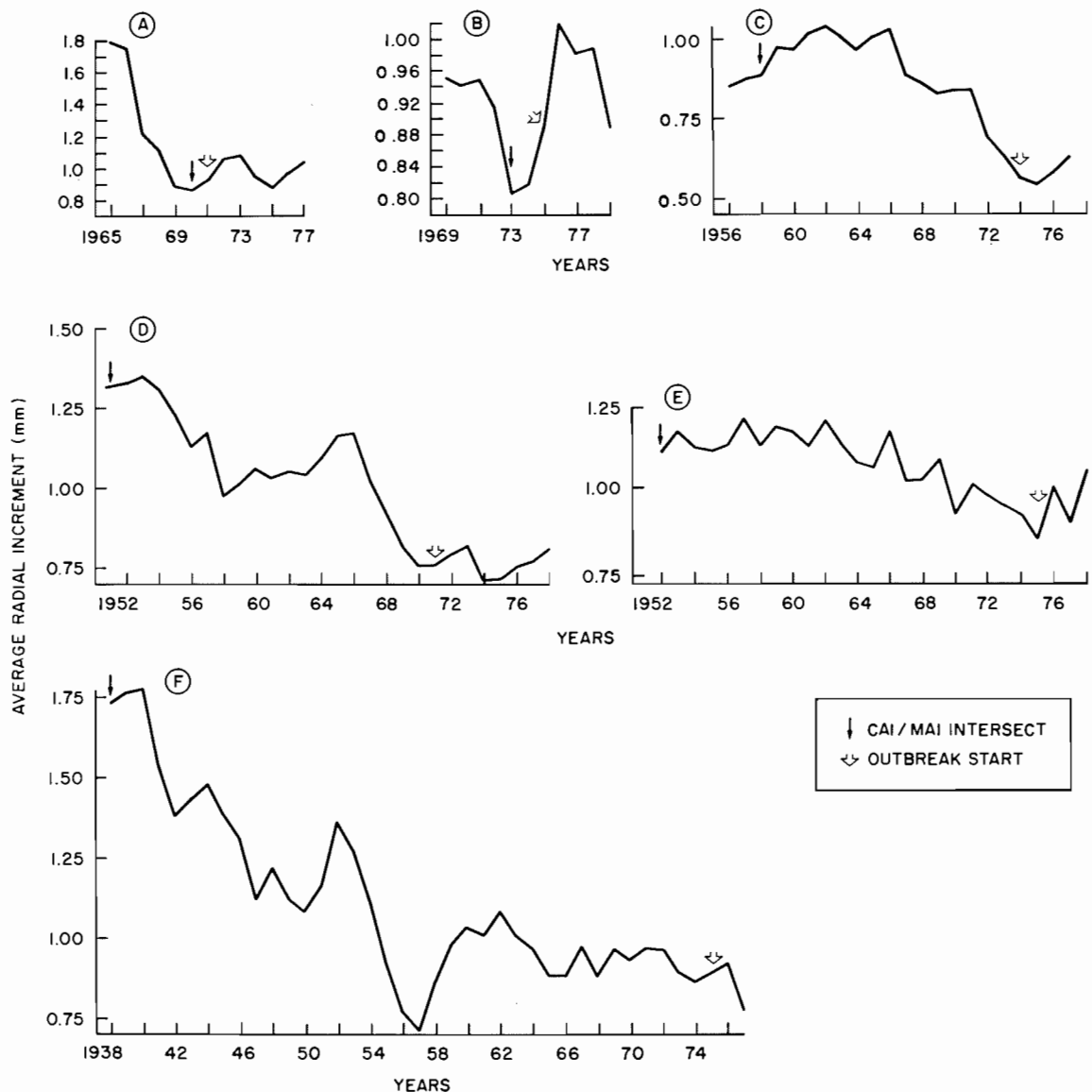


FIG. 2. Incremental growth on the average radial sequence from physiological maturity to the time of sampling for (A) Riske Creek; (B) Golden; (C) Enderby; (D) Ashnola; (E) Invermere; and (F) Kispiox.

progressively decreased until 1970 (Fig. 2D). The outbreak commenced in 1971 and has spread progressively. The growth rate since 1970 recovered partially, declined in 1974, and again partially recovered.

For the Invermere plot, growth rate since physiological maturity in 1952, has been variable. In general, growth rate remained high between 1956 and 1966 and declined between 1966 and 1975 (Fig. 2E). The outbreak commenced in 1975. Since that time growth rate recovered as the outbreak increased in size.

In the Kispiox plot, incremental growth rates have been variable since the trees were about 50 years of age

(Fig. 2F). However, the onset of the MPB outbreak in 1975 has again coincided with a period of depressed growth after the attainment of physiological maturity in 1938, and the outbreak has spread while the growth rate was recovering.

#### *Relationship of tree diameter distributions, age, periodic growth ratios, and stand hazard ratios to bark beetle attack*

The relationship of plot tree diameters to 20.5, 25.4, and 30.0 cm is given in Table 5. Diameters include single bark thickness measurements ranging from

TABLE 4. Percent volume increase in the 10-year period before outbreak and projected for 10 years after outbreak start

	Average volume (m <sup>3</sup> ) 10 years before outbreak	Average volume (m <sup>3</sup> ) in the year of outbreak start	% increase	Average volume (m <sup>3</sup> ) 10 years after outbreak start	% increase
Ashnola	0.509	0.595	16	0.666	11
Enderby	0.313	0.360	15	0.397	10
Golden	0.754	0.854	13	0.945	10
Invermere	0.433	0.511	18	0.580	13
Kispiox	0.676	0.769	13	0.836	8
Riske Creek	0.354	0.436	23	0.492	13
Average	0.506	0.588	16	0.653	11

TABLE 5. Average diameter, bark thickness, and number of stems above 25.4 and 30 cm at the start of each outbreak and the length of time the average diameter has exceeded 20.5 and 25.4 cm

	Diameter (cm)	Total bark (cm)	No. of stems at start of the outbreak <sup>a</sup>		Number of years average diameter <sup>a</sup>	
			≥25.4 cm	≥30.0 cm	>20.5 cm	>25.4 cm
Ashnola	25.6±2.2 <sup>b</sup>	1.2±0.28	8	0	34	3
Enderby	22.8±4.7	1.05±0.37	4	1	26	0
Golden	31.1±3.8	1.30±0.40	12	7	53	34
Invermere	24.3±3.6	1.15±0.19	4	1	32	0
Kispiox	29.3±3.8	1.40±0.32	10	6	51	26
Riske Creek	26.5±2.7	1.10±0.31	7	2	32	6

<sup>a</sup>Diameters were calculated from the growth profile at 1.3 m and the plot average for bark thickness added.<sup>b</sup>±SD values are given.

1.05 cm at Enderby to 1.4 cm at Kispiox (Table 5). Average age at the 0.1 m sampling height, varied from 82 at Golden to 119 at Kispiox, at the time of attack (Table 3).

On the 1.3-m disc, the majority of periodic growth ratios were less than 1.0. Of a total of 6793 ratios calculated between age 10 and the time of harvest, 4182 (62%) were less than 1.0, and 3088 (45%) were less than 0.9. For the 5-year period prior to each outbreak, ratios less than 0.9 were recorded for 1 year at Ashnola and Kispiox, 2 years at Invermere and Riske Creek, 3 years at Enderby, and 4 years at Golden. Stand hazard ratios (Schenk *et al.* 1980) were 1.58 at Invermere and Kispiox, 1.61 at Golden, 1.68 at Enderby, and 1.69 at Ashnola.

### Discussion

In this study, we allowed the MPB to pinpoint susceptible stands. We then sampled trees from the edges of small but expanding infestations. In five of the stands sampled, the outbreaks have continued to spread and salvage logging is now in progress in each area. For the sixth plot, Enderby, the stand was completely harvested in the year our samples were cut.

Stands were attacked by MPB when they exceeded

our assigned year of physiological maturity by 1–37 years. On average the attack occurred 17 years after maturity. Planned harvesting of unmanaged stands based upon recovery of the maximum volume per hectare should be possible with minimal losses to the MPB. Previously we suggested that stands should be harvested prior to the time when CAI and MAI are equal to minimize MPB losses (Safranyik *et al.* 1975). However, this point now appears the earliest at which attack might be expected. Our growth projections show that the dominants and codominants have considerable volume increase in the years immediately following the intersection of CAI and MAI. Thus, in situations where larger stems are required this volume increase may make surveillance or control actions cost effective.

The start of each outbreak has coincided with a period when the incremental growth rate had declined and the outbreaks have spread while the growth rate was recovering. The constant association with a period of reduced growth suggests a climate effect may have placed the trees under a stress, and increased their susceptibility to beetle attack and at the same time, provided improved conditions for survival and development of the insects. However, when an outbreak has been triggered, tree stress is not essential for suc-

cess of the attack. If a relationship between weather patterns and these periods of reduced growth can be shown, it may be possible to define specific time periods when a stand, which exceeds the size and age requirements of MPB is under the greatest risk of undergoing an outbreak.

The six groups of trees sampled have exceeded the 20.5-cm-diameter threshold used in hazard rating stands for MPB (Cole and Amman 1980; Cole 1978) for between 20 and 50 years. Four of the plots, Ashnola, Invermere, Riske Creek, and Vernon, have a low proportion (less than 15%) of stems greater than 30.0 cm diameter. MPB beetle outbreaks commenced on four of the plots about the time dbh reached 25.4 cm. The other two plots, Golden and Kispiox, have exceeded 25.4 cm average dbh for 26 and 34 years, respectively. MPB attacks in individual trees larger than 25.4 cm usually result in an increase in the beetle population (Safranyik *et al.* 1975). For a stand to sustain an outbreak, an estimated 22% of stems should exceed 30 cm dbh (Cole 1978). At an average stand diameter of 20.5 cm, there are usually sufficient large stems for MPB population equilibrium (Safranyik *et al.* 1975).

Age of our plots, 86–125 years, supports the 80-year-age threshold used in hazard rating for MPB in lodgepole pine stands (Safranyik *et al.* 1975; Cole and Amman 1980).

Bark thickness is a critical factor for MPB development. The bark provides shelter for adults and their developing brood and the layer of phloem, cambial, and cortical tissues (inner bark) is the source of nutrition for these insects. For all trees, the single bark thickness was well above the absolute minimum value of 1 mm necessary for beetles to attack a tree (Safranyik 1971). Amman (1969) related numbers of MPB brood produced to bark thickness of lodgepole pine. He measured bark thickness at the base of crevices. Because thin bark has minimal crevices, bark of all our trees exceeds the minimum (0.25 cm) reported value necessary to provide a nutritive layer adequate to sustain a MPB population.

Periodic growth ratios (Mahoney 1978) for the 1.3-m disc, in the 5 years prior to each outbreak were generally too high to indicate susceptibility, and ratios lower than the 0.9 threshold, at earlier times, were not associated with beetle attack. Normal tree growth results in most periodic growth ratios being less than 1.0, and the greatest growth reductions occur at an average 5.6 m up the bole, therefore, ratios measured at breast height gave very little warning of beetle attack.

The SHR proposed by Schenk *et al.* (1980) for hazard rating lodgepole pine stands is a measure of crown competition adjusted for the proportion of lodgepole pine in the stand. The stands we sampled with expanding MPB outbreaks had SHR values well in excess of

the suggested threshold value of 1.0.

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