

An interpretation of the interaction between lodgepole pine, the mountain pine beetle and its associated blue stain fungi in western Canada

L. Safranyik, D.M. Shrimpton, and H.S. Whitney

Excerpt from: Management of Lodgepole Pine Ecosystems Symposium Proceedings, 1975, pgs 406-428
Conference Date: October 9-11, 1973, Pullman WA USA.

Transcribed from original printed text by Jordan Burke, Faculty of Forestry, UBC, 2016.

Full Citation:

Safranyik, L.; Shrimpton, D.M.; Whitney, H.S. 1975. An interpretation of the interaction between lodgepole pine, the mountain pine beetle, and its associated blue stain fungi in western Canada. in D.M. Baumgartner, editor. Management of Lodgepole Pine Ecosystems Symposium Proceedings, October 9-11, 1973, Pullman, Washington, USA. Washington State University Coop. Extension Service, Pullman, WA. Pages 406-428

ABSTRACT

The interaction between lodgepole pine (*Pinus contorta* Dougl.) and the mountain pine beetle (*Dendroctonus ponderosae* Hopk.), with its associated blue stain fungi (*Ceratocystis montia* Rumb. and *Euophium clavigerum* Robinson and Davidson), is described, as are consequences of this interaction for lodgepole pine trees and stands. A map of hazard ratings for western Canada based upon climatic variables affecting this interaction is proposed. Finally, guidelines for management of lodgepole pine to minimize losses from the mountain pine beetle are included.

1 Introduction

In western Canada, between 1950 and 1970, the mountain pine beetle (*Dendroctonus ponderosae* Hopk.) destroyed an estimated 1.3 million cu. ft. of timber a year, or about 3 percent of the average annual cut of lodgepole pine (*Pinus contorta* Dougl.). The monetary loss is, however, far greater than the volume loss indicates because high-value trees are usually killed by the beetles. The mountain pine beetle, recorded only from southern parts of the range of lodgepole pine, probably occurs over more of the range of lodgepole pine in British Columbia than indicated in Fig. 1. The most frequent and extensive outbreaks occurred in south central and southeastern British Columbia (Powell 1966). At present, there are no satisfactory methods to reduce losses.

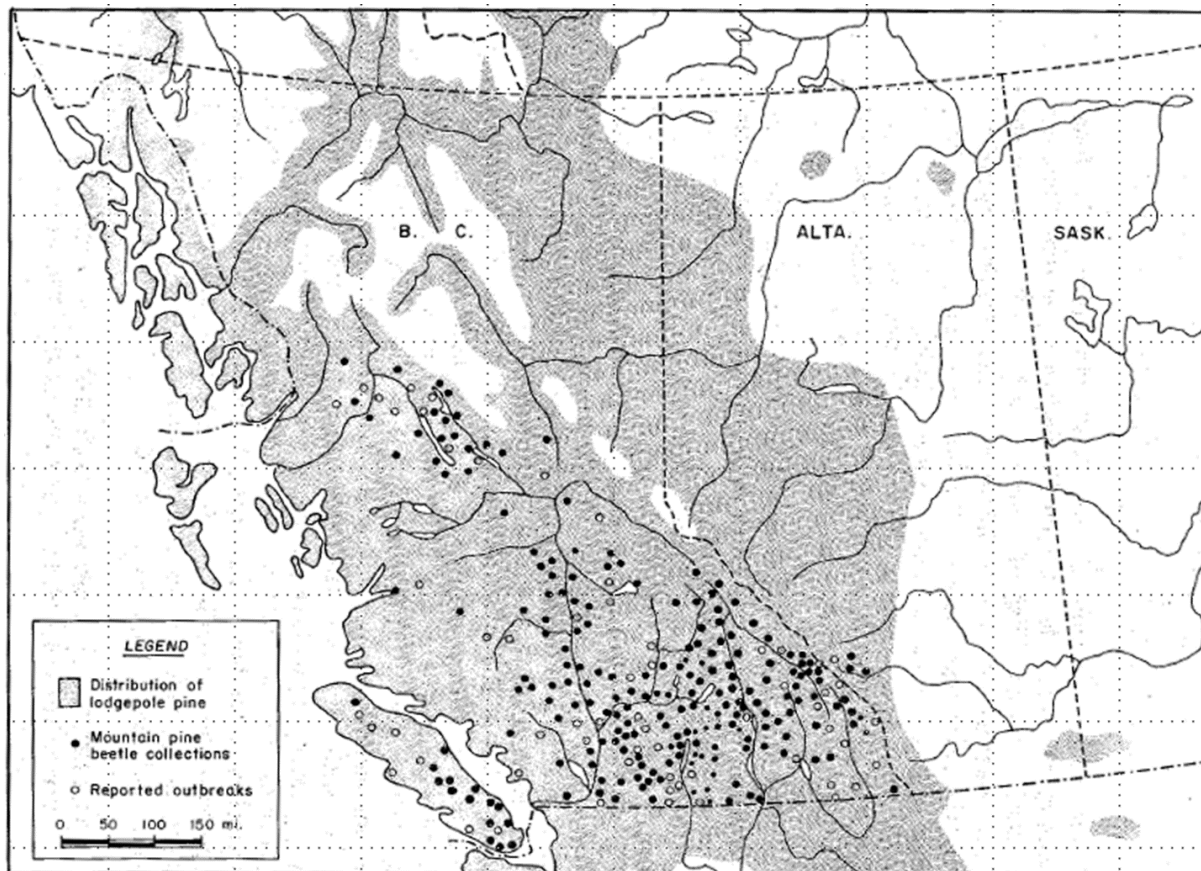


Fig. 1. The distribution of lodgepole pine and the known distribution of mountain pine beetle in western Canada.

The process of tree killing involves (a) inoculation by the beetle of the phloem region of the host with blue stain fungi (*Ceratocystis montia* Rumb. and *Europhium clavigerum* Robinson and Davidson) and killing of living tissues by these fungi, and (b) active resistance of trees to injury from the invading organisms. Thus the interaction between the host and the beetle-blue stain fungi complex is a dynamic process during the colonization phase. Once the tree is killed and beetles and fungi are established, the tree serves a passive role in providing food and shelter for the established organisms.

Numerous aspects of the biology of the mountain pine beetle, its association with certain fungi, and the specific effects these organisms have on lodgepole pine trees and stands have been described (Amman and Baker 1972; Brown 1956; Cole and Amman 1969; Reid 1963; Reid et al. 1967; Roe and Amman 1970;

Rumbold 1941; Shrimpton 1973; Whitney 1971). Also, specific effects of several climatic factors in the lives of beetles, fungi, and trees have been recorded (McCambridge 1971; Powell 1969; Reid and Gates 1970; Rumbold 1941; Somme 1964; Wygant 1940). The need for synthesis of an overall concept of bark beetles killing coniferous trees has been pointed out by several workers (Berryman 1972; Northeastern Forest Experiment Sta. 1970; Shea 1971; Wygant 1959). In this paper, we describe the interaction between lodgepole pine and the mountain pine beetle with its associated blue stain fungi, and develop 3 comprehensive hypothesis regarding consequences for the beetle population of this interaction in relation to tree and stand parameters, weather, and natural enemies. We used this hypothesis to develop an index of outbreak chance and management guidelines to reduce potential losses of lodgepole stands that have a high beetle hazard.

2 The interaction between lodgepole pine and the mountain pine beetle with its associated fungi

The disease process is characterized by a mutual dependence between the bark beetle and the blue stain fungi and by a synchrony of their development in the attacked tree.

The mountain pine beetle normally attacks lodgepole pines in midsummer and chews into the phloem region of the tree. The tree responds with a flow of resin from severed resin ducts. Beetles usually carry several different microorganisms into the tree, but two blue stain fungi, *C. montia* and *E. clavigerum*, are consistently present. The beetles have a special repository, which empties through their mouths, to carry spores of these fungi. The blue stain fungi are specialized in that they produce sticky spores that adhere here and there on the surface of beetles. Thus, spores of the blue stain fungi are inoculated into trees by the activity of beetles beneath the bark. These spores germinate quickly and penetrate living cells in both phloem and xylem. Trees continue to respond to this with a flow of liquid resin from resin ducts damaged by the attacking organisms. Living cells next to the wound may produce additional liquid resin and other substances, normally present only in the heartwood, more in response to the onset of fungal growth than to injury from the beetles. Primary resin seeping from damaged resin ducts slows the attacking organisms, but the production of secondary resins by ray cells is a continuing process that can prevent establishment. When this tree response is rapid and massive and the phloem and sapwood next to the wound become impregnated with resinous substances, beetles are killed or repelled and inoculated fungi are confined and die. When trees show little or no resinous response to attack, the fungi quickly kill living host cells and no further - response is possible. The fungi penetrate the ray cells and spread radially and vertically in the bole much faster than circumferentially; circumferential spread is enhanced by mining of beetle larvae. In a few weeks, large sectors of sapwood become colonized; the tree goes into a rapid decline and dies as a girdle of nonfunctional sapwood is affected. The crowns of such trees may stay green for up to 12 months.

A few hours after female beetles begin boring into a tree, they release an aggregating pheromone that triggers a mass attack of the tree. A male joins a female soon after the egg gallery is successfully started. After mating, borings are packed into the base of the gallery and the female burrows vertically, up the stem. Eggs are laid singly in niches along the sides of the gallery and hatch about two weeks later. Larvae mine feeding galleries circumferentially, about 90 degrees to the egg gallery, in the inner bark that is being colonized by blue stain fungi. Larvae develop through four instars and broods normally overwinter in the larval stages. The following spring, larvae resume feeding. When mature, they construct, and pupate in, an oval-shaped chamber. During pupation, fruiting bodies of the blue stain fungi line the walls of the pupal chamber. The young beetles need to feed on this fungal growth to complete their maturation. Transfer of blue stain fungi to green trees is ensured when the oral mycangium is charged

during feeding of the new adults and by contact with sticky spores that adhere to various parts of the new beetle's body. Mature beetles bore through the bark to the outside and fly to attack living trees. There is normally one generation per year.

3 Our understanding of the dynamics of the host tree. Beetle-blue stain fungi interaction in lodgepole pine

Mountain pine beetle populations and lodgepole pine stands have apparently coexisted for a long time. The similarity of distribution of lodgepole type by age classes (Continuous Forest Inventory of B.C. 1957) between areas with low and high beetle hazard suggests that beetle activity has had no major effect on the regeneration or survival of lodgepole pine. Therefore, the primary ecological function of the interaction between lodgepole pine and the mountain pine beetle with its associated blue stain fungi seems to be preparation for the successional forest types through cropping the stands. This interaction is a dynamic process which, we postulate, has a primary effect on variations in beetle population size and quality in space and time. In the beetle-blue stain fungi association, the beetle benefits by obtaining a means to diagnose and overcome the resistance of the host, by obtaining nutritional and physical conditioning of the phloem for successful establishment, and by obtaining a component of its diet essential for maturation. The fungi benefit by obtaining dispersal and inoculation into their host trees. When lodgepole pine stems were inoculated in the field with several phytophagous fungi, the blue stain fungi associated with the mountain pine beetle elicited the fastest and greatest response from the tree. Thus, after initiation of the gallery, the blue stain fungi quickly diagnose the availability of the tree for the beetle. After establishment, the tree provides food and shelter for beetles and fungi. There is no further threat to the beetle from resinosis because of the tree-killing action of the fungi. Diameter-related physical properties of the stem, such as the thickness and nutritional capacity of the phloem; total bark thickness, roughness, and area; and the rate of drying of the outer sapwood, govern the beetle-producing potential of a given tree. Natural enemies, competition for food and space among broods and with other phloem feeding insects, and climatic factors further affect the full expression of this potential. However, the effects of these nonhost factors on brood production are also modified by physical properties of the tree. We believe that climatic factors have major effects on the establishment and survival of the beetles because brood development and survival are temperature limited, and certain climatic events also have direct influences on the fungi and the tree response.

On the average, lodgepole pine stands with most stems greater than 10 inches dbh have a brood-producing potential greater than their capacity to absorb beetles. In such stands, buildup of mountain pine beetle populations is largely dependent on the availability of such trees for colonization. We believe this availability is initially controlled by the level of stand resistance. When stand resistance declines either through advanced age or stress, and many large dbh trees become available for colonization, a situation conducive to outbreaks is created, especially if climate favorable for brood survival prevails. Once beetle population density has reached a certain level in the stand, tree resistance is no longer a major controlling factor, because beetles and fungi will colonize most trees through the phenomenon of mass attack. These high populations usually maintain their momentum until most of the large diameter trees are killed, because high populations can rebound from occasional, large proportionate reductions, i.e., from extreme winter temperatures or from direct suppression operations.

How does stand dynamics affect the level of stand resistance and beetle activity? Individual tree response, as manifested by the production of resinous substances following injury to the living cells by beetles and blue stain fungi, and the level of stand resistance are related to stand age. The level of stand

resistance increases up to 40-60 years and then declines (Fig. 2). Maximum level of stand resistance corresponds approximately to maximum current annual increment (Smithers 1962) and the culmination of basal area growth of fully stocked stands on any physiographic site (Horton 1956). There is considerable seasonal variation in the level of stand resistance; this is highest in early July, and declines throughout the period of beetle flight in southeastern British Columbia (Fig. 3). The synchrony of beetle flight with the period of declining stand resistance, is important for the maintenance of endemic populations. In stands, supporting endemic populations, the resistance of individual trees is related to their diameter growth (Fig. 4). On the other hand, epidemics are possible only if the majority of attacked trees are greater than 12-13 inches dbh (Cole and Amman 1969). Therefore, one of the necessary conditions for an outbreak in a stand is a decline in the level of resistance of large dbh trees.

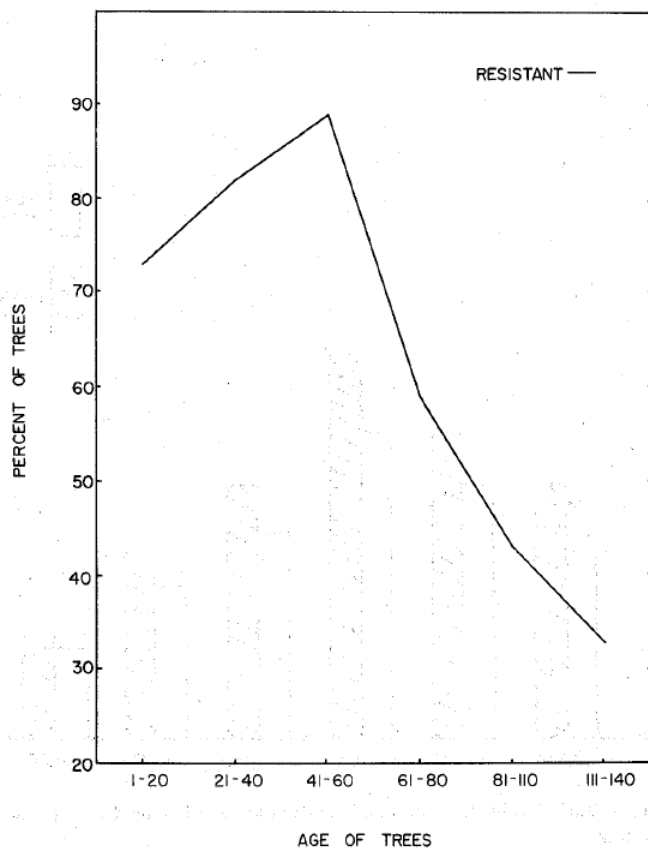


Fig. 2. Change in frequency of resistant lodgepole pine for different aged trees.

Diameter is expected to be a reliable index of the capacity of trees to produce beetles because the potential of individual trees to absorb beetles is related to dbh. Furthermore, diameter-related physical characteristics of the host have a major effect on development and survival of both beetles and fungi. Cole and Amman (1969) found a relationship between dbh and numbers of beetles produced by individual trees in western Wyoming and eastern Idaho. In southeastern British Columbia, we also found that the ratio of attacking to emerging beetles is related to tree dbh (Fig. 5). This relationship was determined by sampling trees for attack and emergence density at intervals along the infested part of boles. The density of emerging beetles was either measured directly by catching beetles in emergence traps, or on old infested trees by calculating the emergence density from the density of emergence

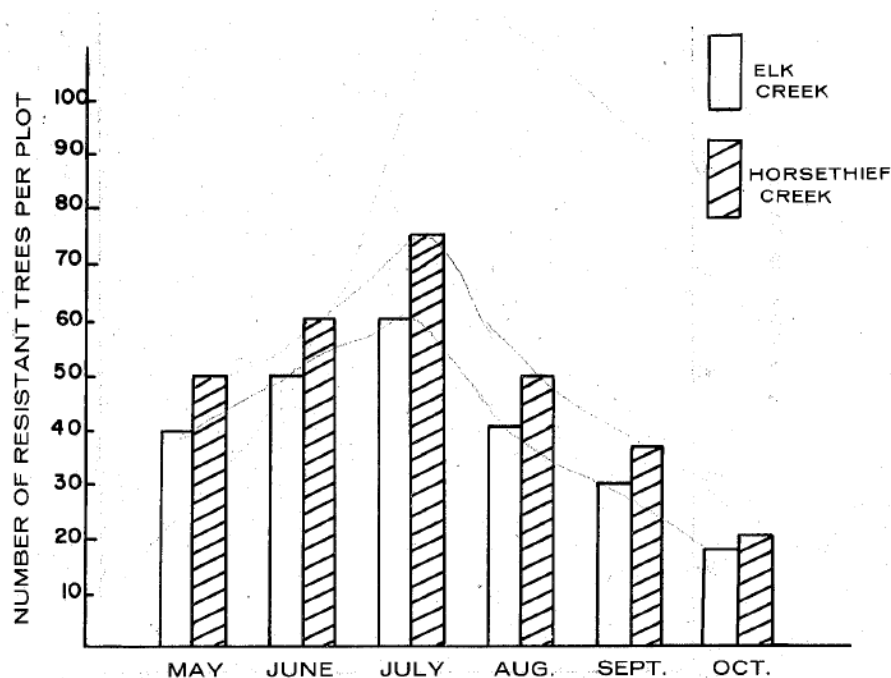


Fig. 3. Variation in the number of resistant lodgepole pine during the summer months.

holes (Reid 1963). The density figures were weighted by the infested surface areas from midpoint to midpoint between sample locations. Totals for the trees were computed by summing over the infested bole area. The equations for total attacks (YA) and emergence (YE) are as follows:

$$YA = 0.85 \text{ DBH}^{2.51}$$

$$YE = 0.003 \text{ DBH}^{5.20}$$

In deriving the equation for YE, we assumed that there will be zero emergence from infested trees less than 3 inches dbh. YA was multiplied by 1.6 to compensate for the sex ratio (the average sex ratio is about 1 male to 1.7 females $(1.7+1)/1.7 \cdot 1.6$) and the ratio $YE/(1.6)YA$ was computed for various values of dbh. The resulting curve is an expression of the emergence/attack versus dbh relationship for individual trees (Fig 5). On the average, trees less than about 10 inches dbh will not produce even replacement numbers of beetles. Brown (1956), assuming a 1:1 male to female ratio, calculated that only trees greater than 10.5 inches dbh produced more beetles than the numbers attacking these trees during an epidemic in southeastern British Columbia. Cole and Amman (1969), after making some assumptions about the relationship between tree dbh and the minimum number of beetles required to kill a tree, calculated that trees greater than about 11 inches dbh will produce more beetles than required to kill a tree. The agreement between our results and those of Brown, and Cole and Amman is satisfactory considering the differences in approach.

In deriving the relationship between mean stand dbh and brood productivity, we made the following assumptions: Tree dbh is normally distributed with a coefficient of variation = 30 percent; the probability of a tree in a dbh class being infested is the same every year and conforms to the curve given in Cole and Amman (1969); the relationship between the emergence/attack ratios of individual trees and dbh is the same as in Fig. 5. The relation between beetle productivity of stands and average stand dbh is such that production decreases with a decrease in coefficient of variation. The 30 percent

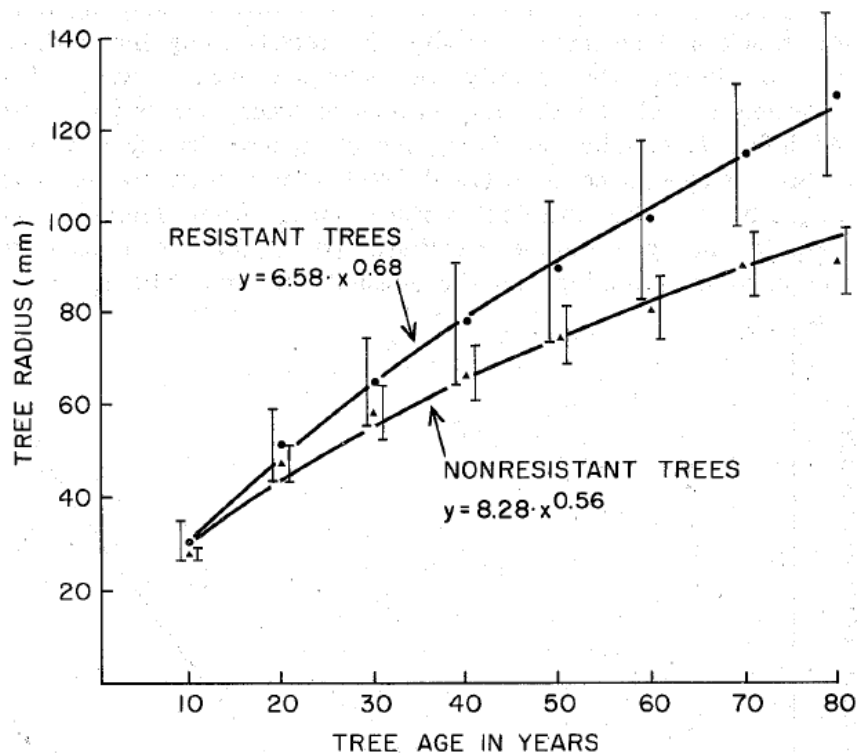


Fig. 4. Cumulative radial growth for resistant and nonresistant lodgepole pine trees from 51 to 90 years old.

coefficient of variation of dbh is higher than the highest variability observed by us in infested stands (26 percent). However, a 30 percent coefficient of variation was selected to try to simulate the lower limit of average stand dbh in which we might expect population buildup. The relationship between beetle productivity and average stand dbh is given in Fig. 5. This relationship indicates that stands greater than about 8 inches dbh are potentially capable of supporting outbreak levels of populations. This does not mean that there will be no beetle activity in stands less than 8 inches dbh. In such stands, outbreak chance is generally low. However, in areas climatically favorable for development and survival of beetles and associated blue stain fungi, persistent low level beetle activity may eventually deplete the large diameter component of these stands.

It is well documented that, following an outbreak, the percentage of trees killed is related to dbh (Cole and Amman 1969; Hopping and Beall 1948). Such a relationship from infested stands of the Banff National Park is shown in Fig. 6. The slopes of such lines indicate about 4.0 to 9 percent increase in the percentage of infested trees with each inch increase in dbh above 5-6 inches. These relationships are useful for assessing potential threat to the stand from the mountain pine beetle and for predicting stand depletion. It may be misleading to interpret the consistency of these relationships to mean that the beetle purposefully selects the largest dbh trees, because the relationship between the number of killed trees in a dbh class and their basal area is approximately linear (Fig. 7). This means that the largest number of trees will be killed in the diameter class representing the greatest basal area. This diameter class will usually be lower than the diameter of the largest trees in the stand. This finding strongly suggests that attacks occur approximately in proportion to the "barrier" presented to the flying beetles, i.e., the total cross-sectional areas in a dbh class.

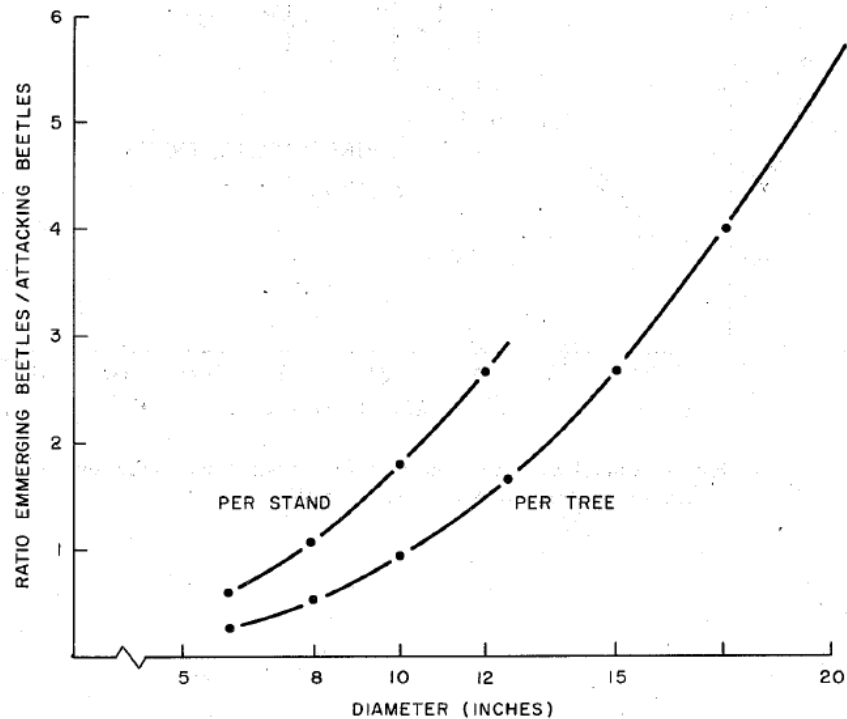


Fig. 5. Ratio of emerging to attacking beetles as related to tree and stand diameter.

4 Opportunity for outbreak as governed by climate

Because of the many and varied effects of climate on lodgepole pine and the mountain pine beetle-blue stain fungi complex, a suitable climate must, prevail before there is a continuous threat to lodgepole pine from the mountain pine beetle. Consequently, we have attempted to define areas in western Canada according to climatic suitability for the mountain pine beetle. This approach to rating areas for outbreak chance was supported by the observation that during "outbreak years" high level beetle activity often prevails over extensive areas that presumably contain a variety of stand conditions.

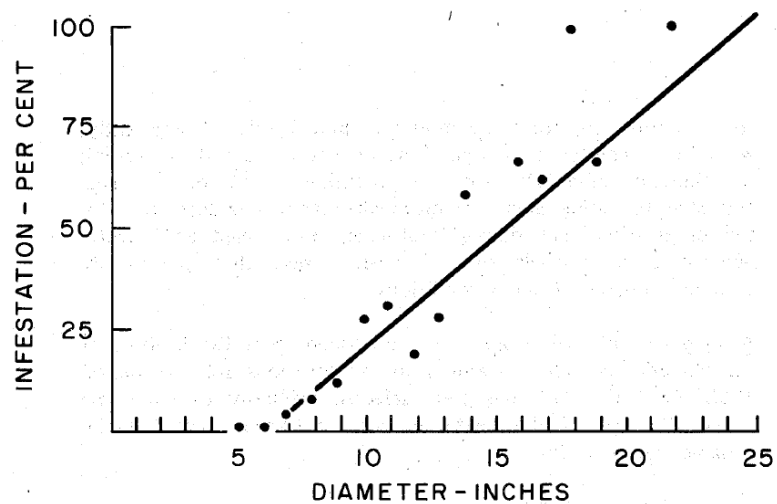


Fig. 6. Relation between trees killed and the diameter at 4.5 feet.

A map of outbreak chance was developed from the analysis of six climatic variables measured at 42 locations for the period 1950-1971. The locations were selected primarily to cover the expected range of the beetle in western Canada. The climatic variables are as follows:

A. Principal variables

P₁: More than 550 degree-days heat accumulation above 42 degrees F. from August 1 to the end of the effective growing season (Boughner 1964) and more than 1,500 degree-days heat accumulation within the effective growing season from August 1 to July 31 the following year.

P₂: Minimum winter temperatures higher than -40 degrees F.

P₃: Average maximum August temperatures greater than or equal to 65 degrees F.

P₄: Total precipitation during April, May, and June less than the long-term average for these months.

B. Modifying variables

X₁ = Variability of growing season precipitation (coefficient of variation).

X₂ = Average annual water deficit (National Atlas of Canada, 1970).

The numerical values of X₁ and X₂ were arbitrarily converted to relative scales Y₁ and Y₂, respectively, as shown in the following table:

| Precipitation variability (CV = %) = X₁ | Index = Y₁ | Water deficit (in.) = X₂ | Index = Y₂ |
|---|------------------------------|--|------------------------------|
| >45 | 1 | <0 | .2 |
| 40-45 | .9 | 0-4 | .4 |
| 35-40 | .7 | 4-8 | .7 |
| 30-35 | .4 | 8-12 | .9 |
| <30 | .2 | >12 | 1 |

P₁ was defined on the basis of the following assumptions: 1,500 degree-days is an index of minimum heat accumulation required by beetles between successive peak flights, and 550 degree-days was taken as the minimum heat requirement from peak flight to 50 percent hatching of eggs. If neither of these heat requirements are met, population buildup cannot occur because broods will either be forced into a two-year cycle and overwinter in the pupal and/or adult stages or the majority of broods will have to overwinter as eggs. Eggs, pupae, and adults are more susceptible to freezing than larvae which are the normal overwintering stage. In defining P₂, -40 degrees F. was taken as the minimum air temperature threshold for population increase because complete mortality results when larvae are exposed to temperatures from -30 to -36 degrees F. for short periods (Somme 1964; Wygant 1940). In defining

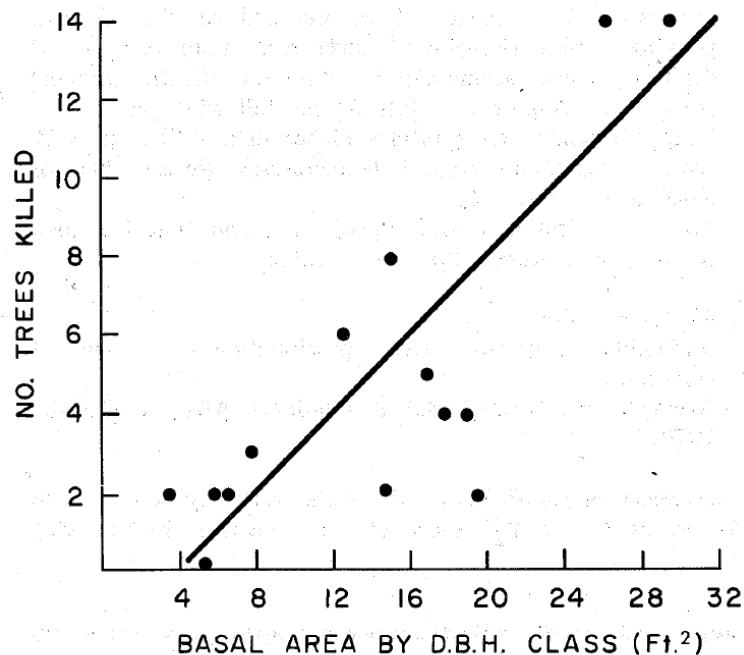


Fig. 7. Relation between number of trees killed and total basal area by diameter classes.

P_3 , it was assumed that when the frequency of hourly maximum temperatures above 70 degrees F. during August is 5 percent or less, a protracted flight period will result and attack success will decline. The lower threshold for flight by the mountain pine beetle is about 67 degrees F. (McCambridge 1971) and flight commonly occurs at temperatures above 70 degrees F. For convenience, an average maximum temperature for August of 65 degrees F. was taken as an index of the threshold frequency of maximum hourly temperatures. We interpret variable P_4 as a measure of tree response and of favorable conditions for beetle development and survival during spring. This variable was established on the basis of correlative evidence; high beetle activity followed periods with two or more consecutive years of below average precipitation from April to May over large areas in western Canada. The variability of growing season precipitation (X_1) was included because P_4 is defined in terms of deviation from the average. Variability about the average as well as the magnitude of mean precipitation has important effects on the host tree and the beetle-fungi complex. The average annual water deficit (X_2) effects the growing conditions for lodgepole pine as well as the development and survival of beetles and fungi. P was defined as the number of years with the joint occurrence of P_1 — P_4 in runs of two or more consecutive years divided by the total number of years. The index of outbreak chance (F) was then derived as follows:

$$F = P \times \sqrt{(Y_1 \times Y_2)}$$

The values of F range from 0 to 1. This scale was calibrated to correspond with relative levels of outbreak chance by comparing the index values with outbreak frequency (Powell 1966). We noted that outbreaks have not been recorded from areas with an F value of zero. On the other hand, areas in south central British Columbia, where the most frequent and destructive outbreaks occurred, had F values greater than 0.35. Therefore, F values of 0 and 0.36+, respectively, were assigned to "very low" and "extreme" outbreak chance classes. The ranges of F corresponding to the "low," "moderate," and "high"

outbreak chance classes were increased geometrically from 0 to 0.35. The following are the relative levels of outbreak chance and the corresponding index values:

| Outbreak chance | Range of index (F) |
|-----------------|--------------------|
| Very low | 0 |
| Low | 0.01-0.05 |
| Medium | 0.06-0.15 |
| High | 0.16-0.35 |
| Extreme | 0.36+ |

In mapping the distribution of outbreak chance classes, the final positioning of boundaries was influenced by topographic features and the distribution of mean values of the climatic variables that were used for the development of the index. The map of outbreak chance is shown in Fig. 8. It is stressed that in each hazard class there is a mosaic of other classes due to local effects of climate, host, and site. Thus it is the average outbreak chance over each area that is portrayed by the hazard map. Because of the location of the weather stations used, the hazard map is valid to about 2,500 ft. in the northern limits of the beetle's distribution and about 4,000 ft. in southern British Columbia. Above these elevations, outbreak chance is less than indicated. When compared to the distribution and frequency of past outbreaks, the hazard map is a reasonable representation of outbreak potential for western Canada. With better understanding of the effects of the host-beetle-blue stain fungi interaction and how it is influenced by weather, it may be possible to devise a more precise index of outbreak chance. However, a shortcoming of this approach is that it cannot be used for yearly evaluation of "population buildup." Buildup is, of course, also strongly related to tree and stand parameters.

5 Preventive management

Experience with the direct control of mountain pine beetle epidemics by chemical sprays, salvage logging or other techniques aimed at reducing beetle numbers, indicates that the effects of suppression work are temporary. Thus, these control techniques are primarily useful for holding stands until all the potentially susceptible trees can be removed (Roe and Amman 1970). Used in this way, direct control techniques will complement management practices aimed at preventing population buildup through prevention of stand susceptibility.

Based on the foregoing discussion regarding the effects of weather and stand dynamics on the beetle-blue stain fungi complex, we derived the following guidelines for reducing potential losses from the mountain pine beetle. Within the two lowest outbreak chance classes, the threat from the beetle in ma stands is generally low and, therefore, the chance of such stand depletion need not be included in long-range management plans.

In areas with the three highest outbreak chance classes, the formulation of long-range management goals and silvicultural practices for stands should include the probability and severity of stand depletion by the mountain pine beetle. For this purpose, all stands in these three hazard classes should be treated the same way, at least until more detailed maps of outbreak chance are available and the index of outbreak chance has been field tested. In view of the relatively high probability of recurring infestations

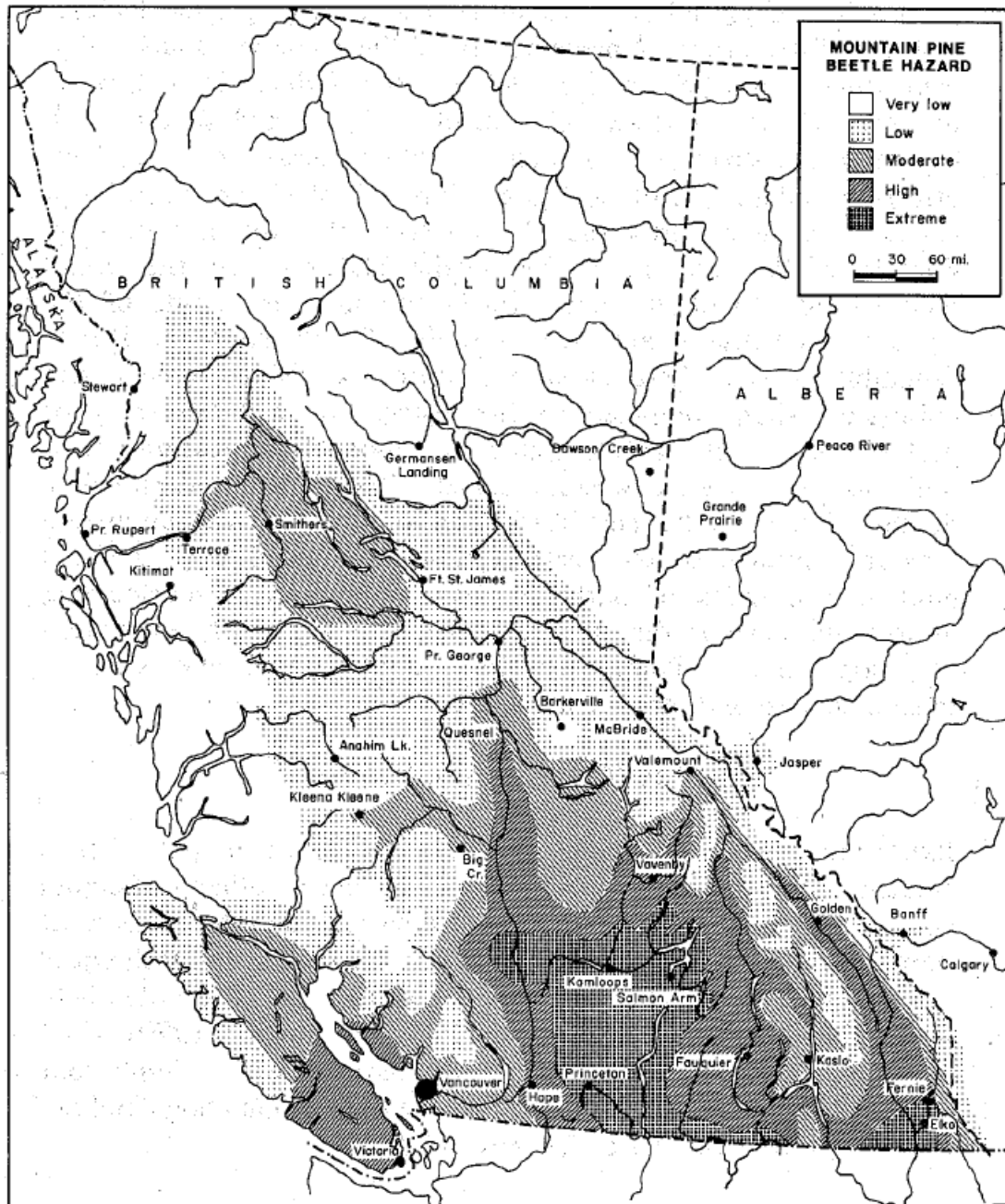


Fig. 8. Beetle outbreak hazard of western Canada.

in mature lodgepole stands in these areas, rotation age based upon maximum cubic foot wood production per acre is the best guideline to follow to minimize losses. This rotation age is conveniently defined by the intersection of current and mean annual increments, and it occurs at about 80 years on good to medium sites (Smithers 1962), and corresponds with stand diameters between 6.0 and 10.0 inches. Eight inches is our predicted minimum stand diameter that will support an outbreak. This approach to setting the rotation age is supported by survey evidence. In western Canada, outbreaks have not been reported from stands younger than 60 years; they rarely occurred between 60 and 80 years, but frequently occurred in stands older than 90 years. On the poorest lodgepole sites, outbreaks

will rarely develop in stands of any age, mainly because of the lack of large diameter trees to support an increasing population. However, persistent low level beetle activity may eventually deplete much of the large dbh component of these stands. Implementation of this proposed guideline requires planned harvesting and regeneration. Priority of cutting should be given to stands with the largest average dbh growing at the lowest elevations.

To grow stands above eight inches dbh, the relation between trees killed and diameter (Fig. 6) and the chance of occurrence of outbreaks need to be assessed locally from survey records as outlined by Roe and Amman (1970). When survey data are lacking, the index of climatic outbreak chance (F) could be calculated and taken as outbreak probability. Outbreak probability multiplied by the proportion of trees killed in a dbh class during outbreaks (Fig. 6) is an estimate of the chance for a tree being killed. When this probability is unacceptably high, the alternatives are conversion to successional types or clearcutting and regeneration, preferably to mixed lodgepole pine. This cutting should be in small blocks, so that similar age classes should not be adjacent to each other.

6 Epilogue

The phenomenon of bark beetles-killing forest trees is a complex interaction of organisms responding to changes in their environment. Successful management of this pest problem requires input from a range of disciplines and a systems analysis approach is indicated. Our strategy, in this paper, was to assemble existing knowledge from past and current research to produce a conceptual statement of the total system, cohabitation of lodgepole pines and mountain pine beetles, and forest management implications thereof. We believe this is a prerequisite to the generation of a realistic predictive model that will aid in management decisions relevant to bark beetle depredation of our forests.

Amman, Gene D. and Bruce H. Baker.
1972. MOUNTAIN PINE BEETLE
INFLUENCE ON LODGEPOLE
PINE STAND STRUCTURE. J.
For. 70:204-209.

Berryman, A. A.
1971. RESISTANCE OF
CONIFERS TO INVASION BY
BARK BEETLE-FUNGUS
ASSOCIATIONS. Bioscience
22:598-602.

Boughner, C. C.
1964. DISTRIBUTION OF
GROWING DEGREE-DAYS IN
CANADA. Can. Met. Memoirs. 17.
Met. Br., Dept. of Transport. 40 p.

Brown, G. S.
1956. POPULATION TRENDS IN
THE MOUNTAIN PINE BEETLE
AT WINDERMERE CREEK,
BRITISH COLUMBIA. Interim
Report 1954-6. For. Biol. Lab.,
Victoria, B.C. 20 pp.

Cole, W. E. and Gene D. Amman.
1969. MOUNTAIN PINE BEETLE
INFESTATIONS IN RELATION
TO LODGEPOLE PINE
DIAMETERS. USDA Forest
Service Research Note INT-95. 7
pp.

CONTINUOUS FOREST INVENTORY OF BRITISH COLUMBIA.

1957. Department of Lands and
Forests. British Columbia, Canada.

Hopping, G. R. and G. Beall.
1948. THE RELATION OF
DIAMETER OF LODGEPOLE
PINE TO INCIDENCE OF
ATTACK BY THE BARK
BEETLE, *DENDROCTONUS*
MONTICOLAE HOPKINS. For.
Chron. 24:141-145.

Horton, K. W.
1956. THE ECOLOGY OF
LODGEPOLE PINE IN ALBERTA
AND ITS ROLE IN FOREST
SUCCESSION. Can. Dept.
Northern Affairs and National
Resources, Forestry Branch, For.
Res. Div. Tech. Note No. 45.

McCambridge, F. W.
1971. TEMPERATURE LIMITS
OF FLIGHT OF THE MOUNTAIN
PINE BEETLE, *DENDROCTONUS*
PONDEROSAE. An. Ent. Soc.
America 64:534-535.

NATIONAL ATLAS OF CANADA.
1970. Department of Energy,
Mines, and Natural Resources.
Ottawa, Canada.

Northeastern Forest Experiment
Station.

1970. TOWARD INTEGRATED
CONTROL. Proceedings of the
Third Annual Northeastern Forest
Insect Work Conference, Upper
Darby, Pa. 129 pp.

Powell, J. M.

1966. DISTRIBUTION AND OUTBREAKS OF *DENDROCTONUS PONDEROSAE* HOPKINS IN FORESTS OF WESTERN CANADA. Canadian Forestry Service, Information Report A-X-2. Calgary. 19 pp.

1969. HISTORICAL STUDY OF THE RELATION OF MAJOR MOUNTAIN PINE BEETLE OUTBREAKS IN WESTERN CANADA TO SEASONAL WEATHER. Canadian Forestry Service, Information Report A-X-23. Calgary, Canada. 11 pp.

Reid, R. W.

1963. BIOLOGY OF THE MOUNTAIN PINE BEETLE, *DENDROCTONUS MONTICOLAE* HOPKINS, IN THE EAST KOOTENAY REGION OF BRITISH COLUMBIA III. INTERACTION BETWEEN THE BEETLE AND ITS HOST, WITH EMPHASIS ON BROOD MORTALITY AND SURVIVAL. Can. Entomol. 95:225-238.

_____, and H. Gates.

1970. THE EFFECT OF TEMPERATURE AND RESIN ON HATCH OF EGGS OF THE MOUNTAIN PINE BEETLE (*DENDROCTONUS PONDEROSAE*). Can. Entomol. 102:617-622.

Reid, R. W., H. S. Whitney, and J. A. Watson.

1967. REACTIONS OF LODGEPOLE PINE TO ATTACK BY *DENDROCTONUS PONDEROSAE* HOPKINS AND BLUE STAIN FUNGI. Can. Jour. Bot. 45:1115-1126.

Roe, Arthur L. and Gene D. Amman.

1970. THE MOUNTAIN PINE BEETLE IN LODGEPOLE PINE FORESTS. USDA Forest Service Research Paper INT-71, 23 pp.

Rumbold, C. T.

1941. A BLUE STAIN FUNGUS, *CERATOSTOMELLA MONTIUM* N. SP., AND SOME YEASTS ASSOCIATED WITH TWO SPECIES OF *DENDROCTONUS*. J. Agric. Research 62:589-601.

Shrimpton, D. M.

1973. EXTRACTIVE CHANGES ASSOCIATED WITH THE WOUND RESPONSE OF LODGEPOLE PINE TO ATTACK BY THE MOUNTAIN PINE BEETLE AND ITS ASSOCIATED MICROORGANISMS. Can. J. Bot. 51:527-534.

Smithers, L. A.

1962. LODGEPOLE PINE IN ALBERTA. Can. Dept. For. Bull. No. 127. 153 pp.

Shea, K. R.

1971. DISEASE AND INSECT ACTIVITY IN RELATION TO INTENSIVE CULTURE OF FORESTS. Proceedings, XV International Union of Forestry Research Organizations, p. 109-118.

Somme, L.

1964. EFFECT OF GLYCEROL ON COLD HARDINESS IN INSECTS. Can. J. Zool. 42:87-101.

Whitney, H. S.

1971. ASSOCIATION OF
DENDROCTONUS PONDEROSAE
(COLEOPTERA: SCOLYTIDAE)
WITH BLUE STAIN FUNGI AND
YEASTS DURING BROOD
DEVELOPMENT IN LODGEPOLE
PINE. Can. Ent. 103:1495-1503.

Wygant, N. D.

1940. EFFECTS OF LOW
TEMPERATURE ON THE BLACK
HILLS BEETLE (*DENDRO-*
CTONUS PONDEROSAE HOPK.).

Summary of a Ph.D. Thesis
submitted to the New York School
of Forestry. On file at the USDA
Rocky Mountain Forest and Range
Experiment Stn., Fort Collins,
Colorado. 57 pp., 16 figs.

1959. BARK BEETLE CONTROL.
J. For. 57:274-277.

An Interpretation of the Interaction Between Lodgepole Pine, the Mountain Pine Beetle and Its Associated Blue Stain Fungi in Western Canada

L. Safranyik, D.M. Shrimpton, and H.S. Whitney, Research Scientists
Pacific Forest Research Centre
Department of the Environment, Canadian Forestry Service
Victoria, British Columbia, Canada V8Z 1M5

ABSTRACT

The interaction between lodgepole pine (*Pinus contorta* Dougl.) and the mountain pine beetle (*Dendroctonus ponderosae* Hopk.), with its associated blue stain fungi (*Ceratocystis montia* Rumb. and *Euophium clavigerum* Robinson and Davidson), is described, as are consequences of this interaction for lodgepole pine trees and stands. A map of hazard ratings for western Canada based upon climatic variables affecting this interaction is proposed. Finally, guidelines for management of lodgepole pine to minimize losses from the mountain pine beetle are included.

INTRODUCTION

In western Canada, between 1950 and 1970, the mountain pine beetle (*Dendroctonus ponderosae* Hopk.) destroyed an estimated 1.3 million cu. ft. of timber a year, or about 3 percent of the average annual cut of lodgepole pine (*Pinus contorta* Dougl.). The monetary loss is, however, far greater than the volume loss indicates because high-value trees are usually killed by the beetles. The mountain pine beetle, recorded only from southern parts of the range of lodgepole pine, probably occurs over more of the range of lodgepole pine in British Columbia than indicated in Fig. 1. The most frequent and extensive outbreaks occurred in south central and southeastern British Columbia (Powell 1966). At present, there are no satisfactory methods to reduce losses.

The process of tree killing involves (a) inoculation by the beetle

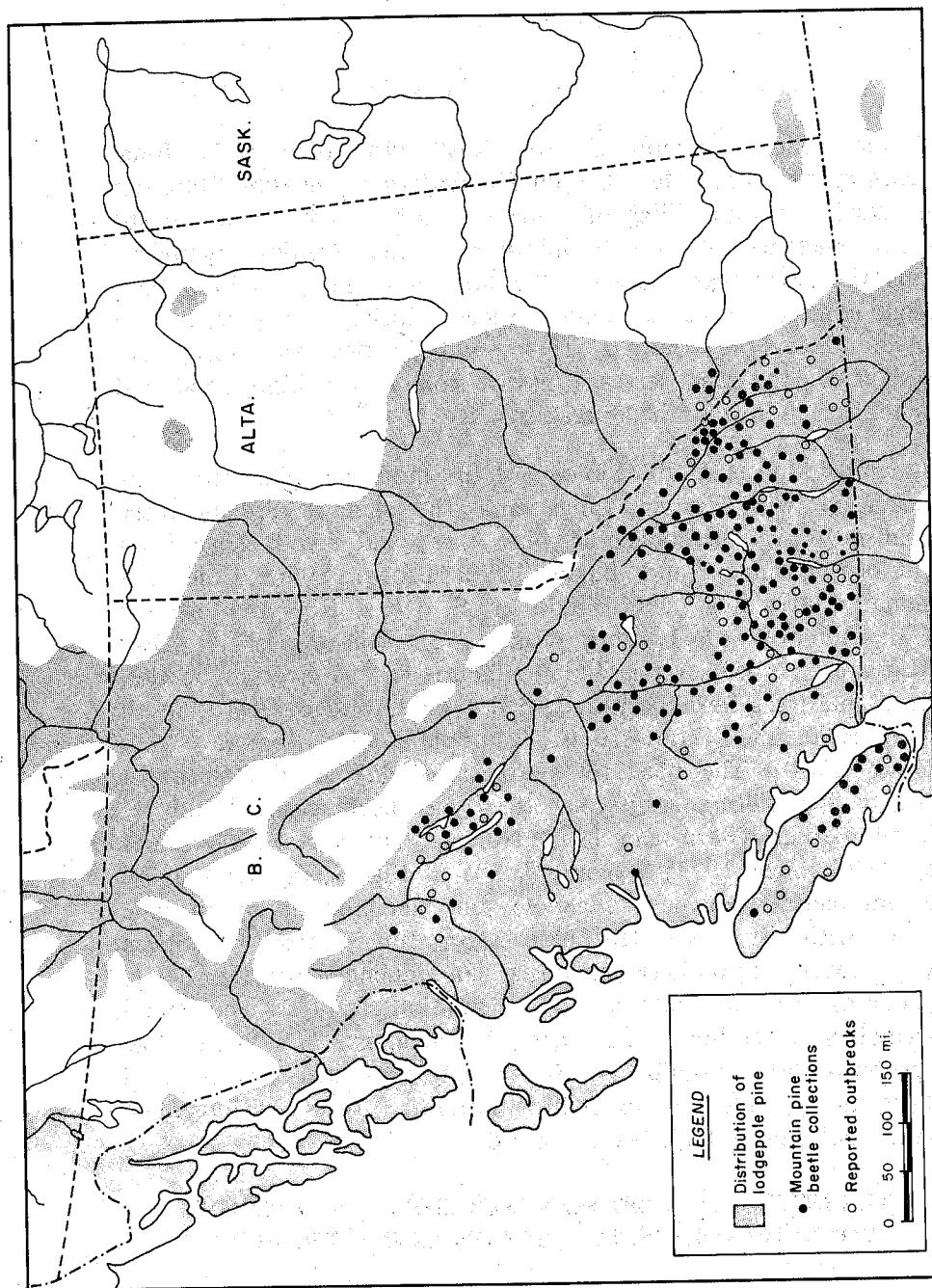


Fig. 1. The distribution of lodgepole pine and the known distribution of mountain pine beetle in western Canada.

of the phloem region of the host with blue stain fungi (*Ceratocystis montia* Rumb. and *Europhium clavigerum* Robinson and Davidson) and killing of living tissues by these fungi, and (b) active resistance of trees to injury from the invading organisms. Thus the interaction between the host and the beetle-blue stain fungi complex is a dynamic process during the colonization phase. Once the tree is killed and beetles and fungi are established, the tree serves a passive role in providing food and shelter for the established organisms.

Numerous aspects of the biology of the mountain pine beetle, its association with certain fungi, and the specific effects these organisms have on lodgepole pine trees and stands have been described (Amman and Baker 1972; Brown 1956; Cole and Amman 1969; Reid 1963; Reid et al. 1967; Roe and Amman 1970; Rumbold 1941; Shrimpton 1973; Whitney 1971). Also, specific effects of several climatic factors in the lives of beetles, fungi, and trees have been recorded (McCambridge 1971; Powell 1969; Reid and Gates 1970; Rumbold 1941; Somme 1964; Wygant 1940). The need for synthesis of an overall concept of bark beetles killing coniferous trees has been pointed out by several workers (Berryman 1972; Northeastern Forest Experiment Sta. 1970; Shea 1971; Wygant 1959). In this paper, we describe the interaction between lodgepole pine and the mountain pine beetle with its associated blue stain fungi, and develop a comprehensive hypothesis regarding consequences for the beetle population of this interaction in relation to tree and stand parameters, weather, and natural enemies. We used this hypothesis to develop an index of outbreak chance and management guidelines to reduce potential losses of lodgepole stands that have a high beetle hazard.

THE INTERACTION BETWEEN LODGEPOLE PINE AND THE MOUNTAIN PINE BEETLE WITH ITS ASSOCIATED FUNGI

The disease process is characterized by a mutual dependence between the bark beetle and the blue stain fungi and by a

synchrony of their development in the attacked tree.

The mountain pine beetle normally attacks lodgepole pines in midsummer and chews into the phloem region of the tree. The tree responds with a flow of resin from severed resin ducts. Beetles usually carry several different microorganisms into the tree, but two blue stain fungi, *C. montia* and *E. clavigerum*, are consistently present. The beetles have a special repository, which empties through their mouths, to carry spores of these fungi. The blue stain fungi are specialized in that they produce sticky spores that adhere here and there on the surface of beetles. Thus, spores of the blue stain fungi are inoculated into trees by the activity of beetles beneath the bark. These spores germinate quickly and penetrate living cells in both phloem and xylem. Trees continue to respond to this with a flow of liquid resin from resin ducts damaged by the attacking organisms. Living cells next to the wound may produce additional liquid resin and other substances, normally present only in the heartwood, more in response to the onset of fungal growth than to injury from the beetles. Primary resin seeping from damaged resin ducts slows the attacking organisms, but the production of secondary resins by ray cells is a continuing process that can prevent establishment. When this tree response is rapid and massive and the phloem and sapwood next to the wound become impregnated with resinous substances, beetles are killed or repelled and inoculated fungi are confined and die. When trees show little or no resinous response to attack, the fungi quickly kill living host cells and no further response is possible. The fungi penetrate the ray cells and spread radially and vertically in the bole much faster than circumferentially; circumferential spread is enhanced by mining of beetle larvae. In a few weeks, large sectors of sapwood become colonized; the tree goes into a rapid decline and dies as a girdle of nonfunctional sapwood is effected. The crowns of such trees may stay green for up to 12 months.

A few hours after female beetles begin boring into a tree, they release an aggregating pheromone that triggers a mass attack of

the tree. A male joins a female soon after the egg gallery is successfully started. After mating, borings are packed into the base of the gallery and the female burrows vertically up the stem. Eggs are laid singly in niches along the sides of the gallery and hatch about two weeks later. Larvae mine feeding galleries circumferentially, about 90 degrees to the egg gallery, in the inner bark that is being colonized by blue stain fungi. Larvae develop through four instars and broods normally overwinter in the larval stages. The following spring, larvae resume feeding. When mature, they construct, and pupate in, an oval-shaped chamber. During pupation, fruiting bodies of the blue stain fungi line the walls of the pupal chamber. The young beetles need to feed on this fungal growth to complete their maturation. Transfer of blue stain fungi to green trees is ensured when the oral mycangium is charged during feeding of the new adults and by contact with sticky spores that adhere to various parts of the new beetle's body. Mature beetles bore through the bark to the outside and fly to attack living trees. There is normally one generation per year.

OUR UNDERSTANDING OF THE DYNAMICS OF THE HOST TREE-BEETLE-BLUE STAIN FUNGI INTERACTION IN LODGEPOLE PINE

Mountain pine beetle populations and lodgepole pine stands have apparently coexisted for a long time. The similarity of distribution of lodgepole type by age classes (Continuous Forest Inventory of B.C. 1957) between areas with low and high beetle hazard suggests that beetle activity has had no major effect on the regeneration or survival of lodgepole pine. Therefore, the primary ecological function of the interaction between lodgepole pine and the mountain pine beetle with its associated blue stain fungi seems to be preparation for the successional forest types through cropping the stands. This interaction is a dynamic process which, we postulate, has a primary effect on variations in beetle population size and quality in space and time. In the beetle-blue stain fungi association, the beetle benefits by obtaining a means to diagnose and overcome the resistance of

the host, by obtaining nutritional and physical conditioning of the phloem for successful establishment, and by obtaining a component of its diet essential for maturation. The fungi benefit by obtaining dispersal and inoculation into their host trees. When lodgepole pine stems were inoculated in the field with several phytophagous fungi, the blue stain fungi associated with the mountain pine beetle elicited the fastest and greatest response from the tree. Thus, after initiation of the gallery, the blue stain fungi quickly diagnose the availability of the tree for the beetle. After establishment, the tree provides food and shelter for beetles and fungi. There is no further threat to the beetle from resinosis because of the tree-killing action of the fungi. Diameter-related physical properties of the stem, such as the thickness and nutritional capacity of the phloem; total bark thickness, roughness, and area; and the rate of drying of the outer sapwood, govern the beetle-producing potential of a given tree. Natural enemies, competition for food and space among broods and with other phloem feeding insects, and climatic factors further affect the full expression of this potential. However, the effects of these nonhost factors on brood production are also modified by physical properties of the tree. We believe that climatic factors have major effects on the establishment and survival of the beetles because brood development and survival are temperature limited, and certain climatic events also have direct influences on the fungi and the tree response.

On the average, lodgepole pine stands with most stems greater than 10 inches dbh have a brood-producing potential greater than their capacity to absorb beetles. In such stands, buildup of mountain pine beetle populations is largely dependent on the availability of such trees for colonization. We believe this availability is initially controlled by the level of stand resistance. When stand resistance declines either through advanced age or stress, and many large dbh trees become available for colonization, a situation conducive to outbreaks is created, especially if climate favorable for brood survival prevails. Once

beetle population density has reached a certain level in the stand, tree resistance is no longer a major controlling factor, because beetles and fungi will colonize most trees through the phenomenon of mass attack. These high populations usually maintain their momentum until most of the large diameter trees are killed, because high populations can rebound from occasional, large proportionate reductions, i.e., from extreme winter temperatures or from direct suppression operations.

How does stand dynamics affect the level of stand resistance and beetle activity? Individual tree response, as manifested by the production of resinous substances following injury to the living cells by beetles and blue stain fungi, and the level of stand resistance are related to stand age. The level of stand resistance increases up to 40-60 years and then declines (Fig. 2). Maximum level of stand resistance corresponds approximately to maximum current annual increment (Smithers 1962) and the culmination of basal area growth of fully stocked stands on any physiographic site (Horton 1956). There is considerable seasonal variation in the level of stand resistance; this is highest in early July, and declines throughout the period of beetle flight in southeastern British Columbia (Fig. 3). The synchrony of beetle flight with the period of declining stand resistance is important for the maintenance of endemic populations. In stands supporting endemic populations, the resistance of individual trees is related to their diameter growth (Fig. 4). On the other hand, epidemics are possible only if the majority of attacked trees are greater than 12-13 inches dbh (Cole and Amman 1969). Therefore, one of the necessary conditions for an outbreak in a stand is a decline in the level of resistance of large dbh trees.

Diameter is expected to be a reliable index of the capacity of trees to produce beetles because the potential of individual trees to absorb beetles is related to dbh. Furthermore, diameter-related physical characteristics of the host have a major effect on development and survival of both beetles and fungi. Cole and Amman (1969) found a relationship between dbh and numbers

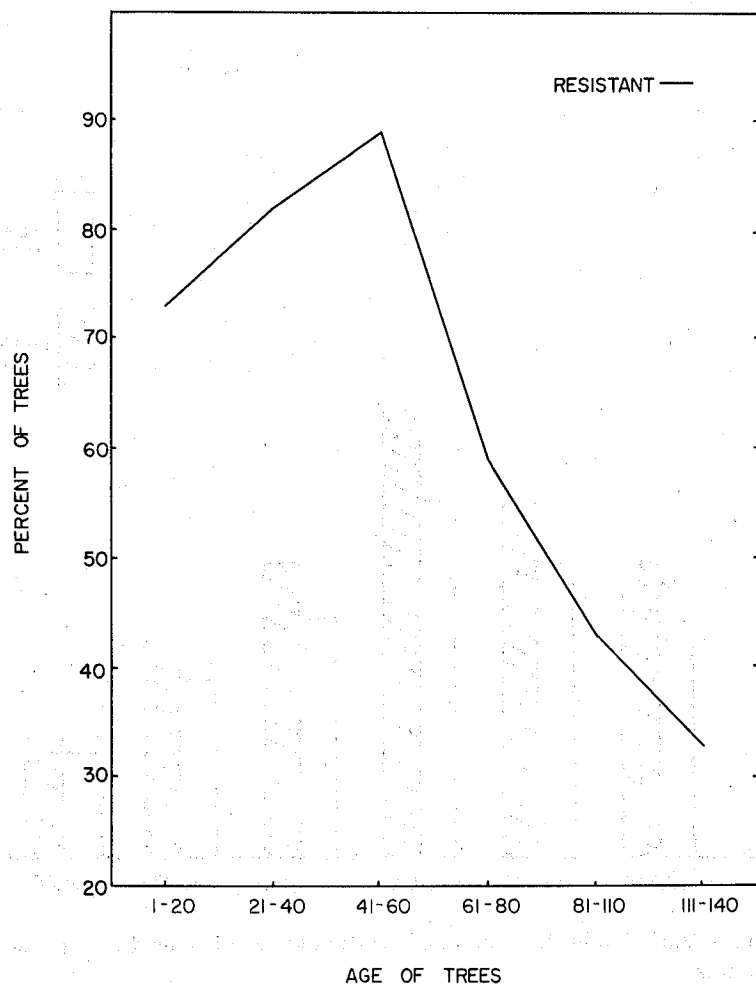


Fig. 2. Change in frequency of resistant lodgepole pine for different aged trees.

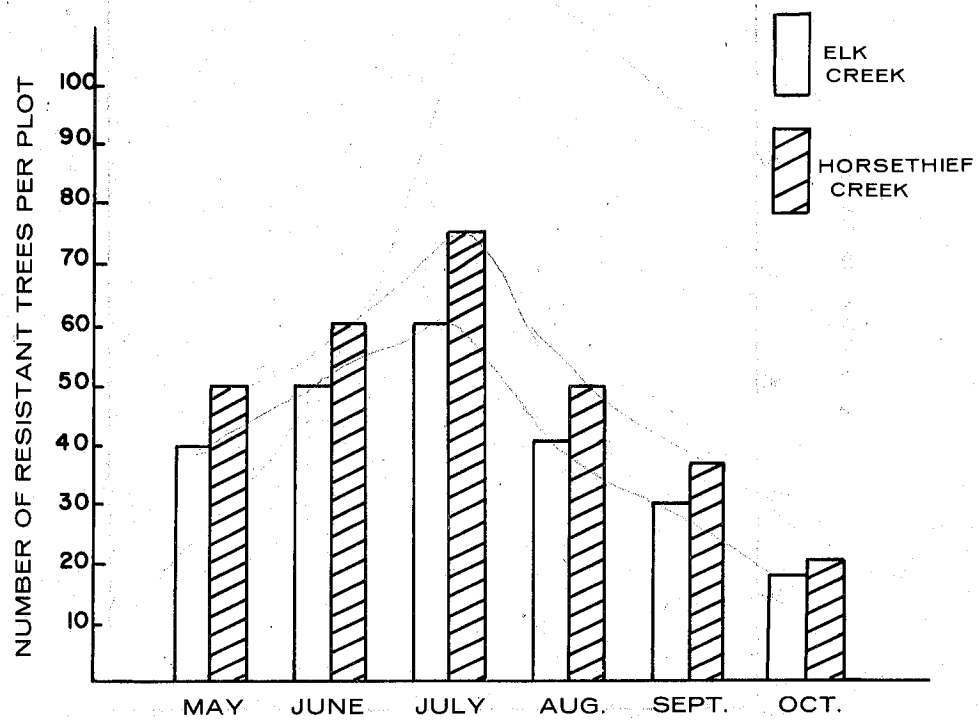


Fig. 3. Variation in the number of resistant lodgepole pine during the summer months.

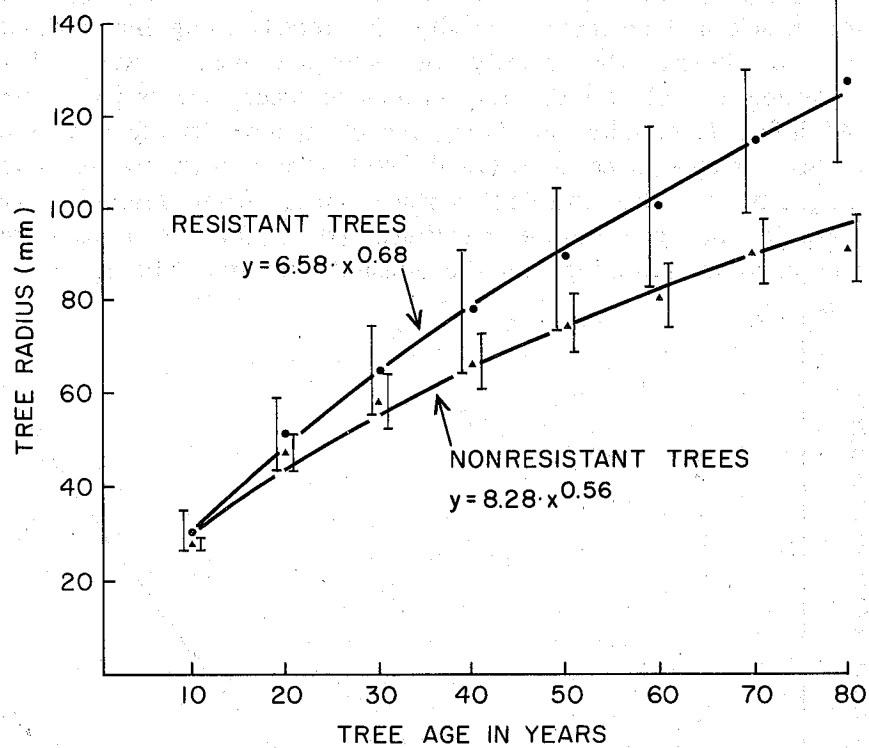


Fig. 4. Cumulative radial growth for resistant and nonresistant lodgepole pine trees from 51 to 90 years old.

of beetles produced by individual trees in western Wyoming and eastern Idaho. In southeastern British Columbia, we also found that the ratio of attacking to emerging beetles is related to tree dbh (Fig. 5). This relationship was determined by sampling trees for attack and emergence density at intervals along the infested part of boles. The density of emerging beetles was either measured directly by catching beetles in emergence traps, or on old infested trees by calculating the emergence density from the density of emergence holes (Reid 1963). The density figures were weighted by the infested surface areas from midpoint to midpoint between sample locations. Totals for the trees were computed by summing over the infested bole area. The equations

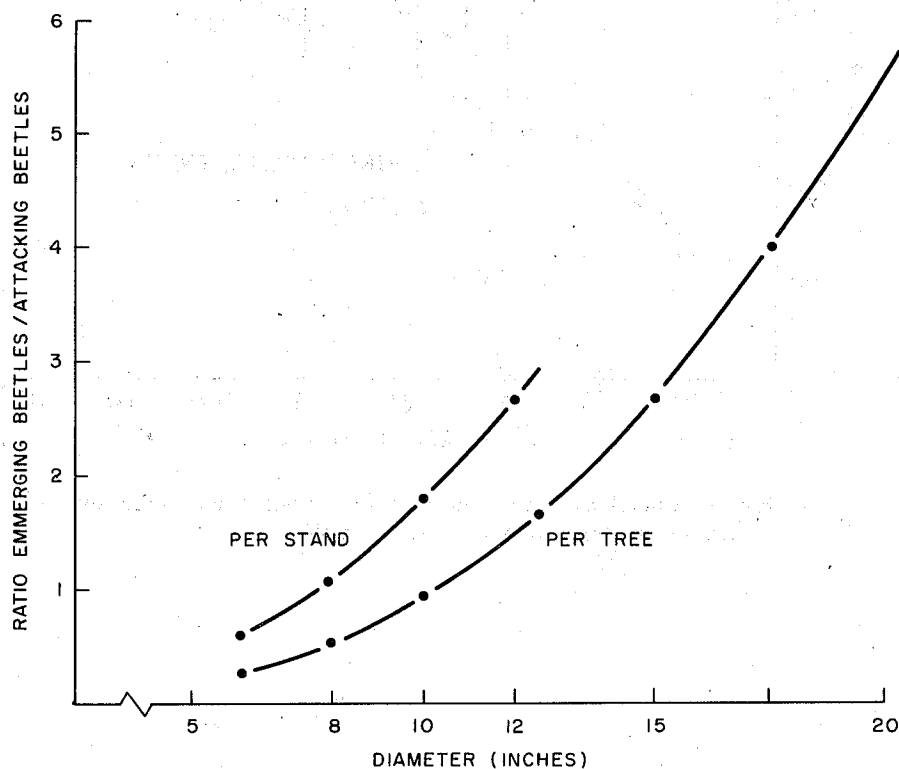


Fig. 5. Ratio of emerging to attacking beetles as related to tree and stand diameter.

for total attacks (YA) and emergence (YE) are as follows:

$$\begin{aligned} \rightarrow YA &= .85 \text{ DBH}^{2.51} \\ YE &= .003 \text{ DBH}^{5.20} \end{aligned}$$

In deriving the equation for YE, we assumed that there will be zero emergence from infested trees less than 3 inches dbh. YA was multiplied by 1.6 to compensate for the sex ratio (the average sex ratio is about 1 male to 1.7 females $(1.7+1)/1.7 \approx 1.6$) and the ratio $YE/(1.6)YA$ was computed for various values of dbh. The resulting curve is an expression of the emergence/attack versus dbh relationship for individual trees (Fig 5). On the average, trees less than about 10 inches dbh will not produce even replacement numbers of beetles. Brown (1956), assuming a 1:1 male to female ratio, calculated that only trees greater than 10.5 inches dbh produced more beetles than the numbers attacking these trees during an epidemic in southeastern British Columbia. Cole and Amman (1969), after making some assumptions about the relationship between tree dbh and the minimum number of beetles required to kill a tree, calculated that trees greater than about 11 inches dbh will produce more beetles than required to kill a tree. The agreement between our results and those of Brown, and Cole and Amman is satisfactory considering the differences in approach.

In deriving the relationship between mean stand dbh and brood productivity, we made the following assumptions: Tree dbh is normally distributed with a coefficient of variation = 30 percent; the probability of a tree in a dbh class being infested is the same every year and conforms to the curve given in Cole and Amman (1969); the relationship between the emergence/attack ratios of individual trees and dbh is the same as in Fig. 5. The relation between beetle productivity of stands and average stand dbh is such that production decreases with a decrease in coefficient of variation. The 30 percent coefficient of variation of dbh is higher than the highest variability observed by us in infested stands (26 percent). However, a 30 percent coefficient of variation was selected to try to simulate the lower limit of

average stand dbh in which we might expect population buildup. The relationship between beetle productivity and average stand dbh is given in Fig. 5. This relationship indicates that stands greater than about 8 inches dbh are potentially capable of supporting outbreak levels of populations. This does not mean that there will be no beetle activity in stands less than 8 inches dbh. In such stands, outbreak chance is generally low. However, in areas climatically favorable for development and survival of beetles and associated blue stain fungi, persistent low level beetle activity may eventually deplete the large diameter component of these stands.

It is well documented that, following an outbreak, the percentage of trees killed is related to dbh (Cole and Amman 1969; Hopping and Beall 1948). Such a relationship from infested stands of the Banff National Park is shown in Fig. 6. The slopes of such lines indicate about 4.0 to 9 percent increase in the percentage of infested trees with each inch increase in dbh above 5-6 inches. These relationships are useful for assessing potential threat to the stand from the mountain pine beetle and for predicting stand depletion. It may be misleading to interpret the consistency of these relationships to mean that the beetle purposefully selects the largest dbh trees, because the relationship between the number of killed trees in a dbh class and their basal area is approximately linear (Fig. 7). This means that the largest number of trees will be killed in the diameter class representing the greatest basal area. This diameter class will usually be lower than the diameter of the largest trees in the stand. This finding strongly suggests that attacks occur approximately in proportion to the "barrier" presented to the flying beetles, i.e., the total cross-sectional areas in a dbh class.

OPPORTUNITY FOR OUTBREAK AS GOVERNED BY CLIMATE

Because of the many and varied effects of climate on lodgepole pine and the mountain pine beetle-blue stain fungi complex, a suitable climate must prevail before there is a continuous threat

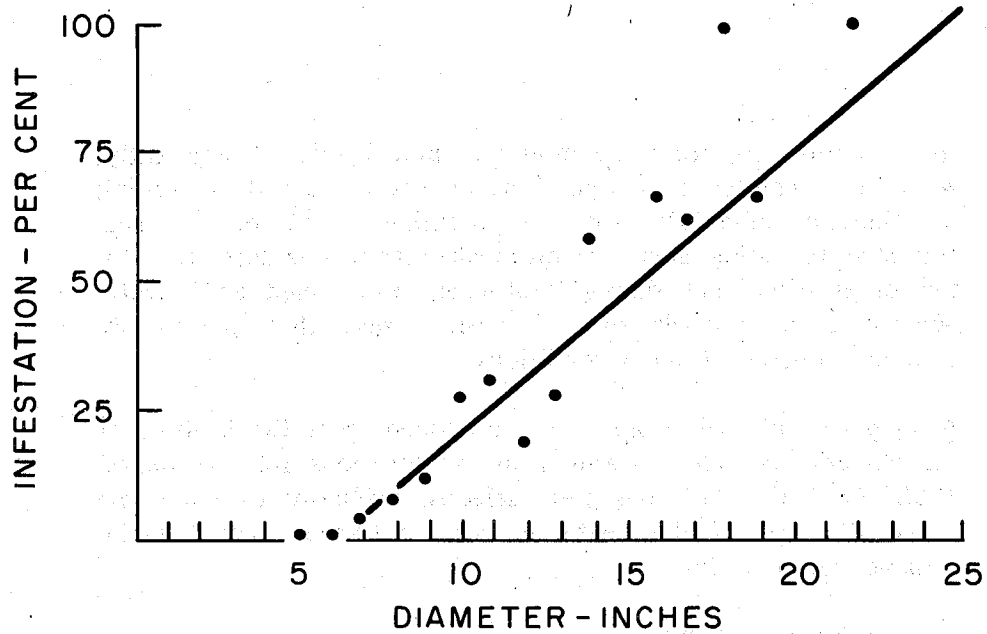


Fig. 6. Relation between trees killed and the diameter at 4.5 feet.

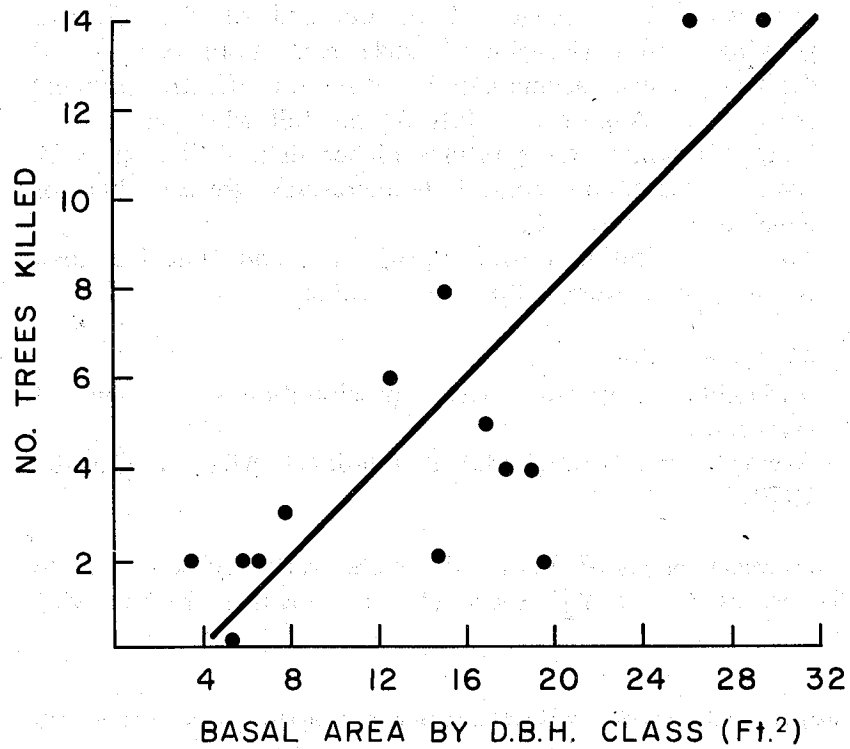


Fig. 7. Relation between number of trees killed and total basal area by diameter classes.

to lodgepole pine from the mountain pine beetle. Consequently, we have attempted to define areas in western Canada according to climatic suitability for the mountain pine beetle. This approach to rating areas for outbreak chance was supported by the observation that during "outbreak years" high level beetle activity often prevails over extensive areas that presumably contain a variety of stand conditions.

A map of outbreak chance was developed from the analysis of six climatic variables measured at 42 locations for the period 1950-1971. The locations were selected primarily to cover the expected range of the beetle in western Canada. The climatic variables are as follows:

A. *Principal variables*

- P₁: More than 550 degree-days heat accumulation above 42 degrees F. from August 1 to the end of the effective growing season (Boughner 1964) and more than 1,500 degree-days heat accumulation within the effective growing season from August 1 to July 31 the following year.¹
- P₂: Minimum winter temperatures higher than -40 degrees F.
- P₃: Average maximum August temperatures greater than or equal to 65 degrees F.
- P₄: Total precipitation during April, May, and June less than the long-term average for these months.

B. *Modifying variables*

- X₁ = Variability of growing season precipitation (coefficient of variation).
- X₂ = Average annual water deficit (National Atlas of Canada, 1970).

The numerical values of X₁ and X₂ were arbitrarily converted to relative scales Y₁ and Y₂, respectively, as shown in the following table:

¹For purposes of the climatic hazard index, a year is the period between August 1 and July 31.

| Precipitation variability (CV = %) = X_1 | Index = Y_1 | Water deficit (in.) = X_2 | Index = Y_2 |
|--|---------------|--------------------------------|---------------|
| >45 | 1 | <0 | .2 |
| 40-45 | .9 | 0-4 | .4 |
| 35-40 | .7 | 4-8 | .7 |
| 30-35 | .4 | 8-12 | .9 |
| <30 | .2 | >12 | 1 |

P_1 was defined on the basis of the following assumptions: 1,500 degree-days is an index of minimum heat accumulation required by beetles between successive peak flights, and 550 degree-days was taken as the minimum heat requirement from peak flight to 50 percent hatching of eggs. If neither of these heat requirements are met, population buildup cannot occur because broods will either be forced into a two-year cycle and overwinter in the pupal and/or adult stages or the majority of broods will have to overwinter as eggs. Eggs, pupae, and adults are more susceptible to freezing than larvae which are the normal overwintering stage. In defining P_2 , -40 degrees F. was taken as the minimum air temperature threshold for population increase because complete mortality results when larvae are exposed to temperatures from -30 to -36 degrees F. for short periods (Somme 1964; Wygant 1940). In defining P_3 , it was assumed that when the frequency of hourly maximum temperatures above 70 degrees F. during August is 5 percent or less, a protracted flight period will result and attack success will decline. The lower threshold for flight by the mountain pine beetle is about 67 degrees F. (McCambridge 1971) and flight commonly occurs at temperatures above 70 degrees F. For convenience, an average maximum temperature for August of 65 degrees F. was taken as an index of the threshold frequency of maximum hourly temperatures. We interpret variable P_4 as a measure of tree response and of favorable conditions for beetle development and survival during spring. This variable was established on the basis of correlative evidence; high beetle activity followed periods with two or more consecutive years of below average precipitation

from April to May over large areas in western Canada. The variability of growing season precipitation (X_1) was included because P_4 is defined in terms of deviation from the average. Variability about the average as well as the magnitude of mean precipitation has important effects on the host tree and the beetle-fungi complex. The average annual water deficit (X_2) effects the growing conditions for lodgepole pine as well as the development and survival of beetles and fungi.

P was defined as the number of years with the joint occurrence of P_1 – P_4 in runs of two or more consecutive years divided by the total number of years. The index of outbreak chance (F) was then derived as follows:

$$F = P \times \sqrt{Y_1 \times Y_2}$$

The values of F range from 0 to 1. This scale was calibrated to correspond with relative levels of outbreak chance by comparing the index values with outbreak frequency (Powell 1966). We noted that outbreaks have not been recorded from areas with an F value of zero. On the other hand, areas in south central British Columbia, where the most frequent and destructive outbreaks occurred, had F values greater than 0.35. Therefore, F values of 0 and 0.36+, respectively, were assigned to "very low" and "extreme" outbreak chance classes. The ranges of F corresponding to the "low," "moderate," and "high" outbreak chance classes were increased geometrically from 0 to 0.35. The following are the relative levels of outbreak chance and the corresponding index values:

| Outbreak chance | Range of index (F) |
|-----------------|------------------------|
| Very low | 0 |
| Low | 0.01-0.05 |
| Medium | 0.06-0.15 |
| High | 0.16-0.35 |
| Extreme | 0.36+ |

In mapping the distribution of outbreak chance classes, the final positioning of boundaries was influenced by topographic features and the distribution of mean values of the climatic variables that were used for the development of the index. The map of outbreak chance is shown in Fig. 8. It is stressed that in each hazard class there is a mosaic of other classes due to local effects of climate, host, and site. Thus it is the average outbreak chance over each area that is portrayed by the hazard map. Because of the location of the weather stations used, the hazard map is valid to about 2,500 ft. in the northern limits of the beetle's distribution and about 4,000 ft. in southern British Columbia. Above these elevations, outbreak chance is less than indicated. When compared to the distribution and frequency of past outbreaks, the hazard map is a reasonable representation of outbreak potential for western Canada. With better understanding of the effects of the host-beetle-blue stain fungi interaction and how it is influenced by weather, it may be possible to devise a more precise index of outbreak chance. However, a shortcoming of this approach is that it cannot be used for yearly evaluation of "population buildup." Buildup is, of course, also strongly related to tree and stand parameters.

PREVENTIVE MANAGEMENT

Experience with the direct control of mountain pine beetle epidemics by chemical sprays, salvage logging or other techniques aimed at reducing beetle numbers, indicates that the effects of suppression work are temporary. Thus, these control techniques are primarily useful for holding stands until all the potentially susceptible trees can be removed (Roe and Amman 1970). Used in this way, direct control techniques will complement management practices aimed at preventing population buildup through prevention of stand susceptibility.

Based on the foregoing discussion regarding the effects of weather and stand dynamics on the beetle-blue stain fungi complex, we derived the following guidelines for reducing potential losses from the mountain pine beetle.

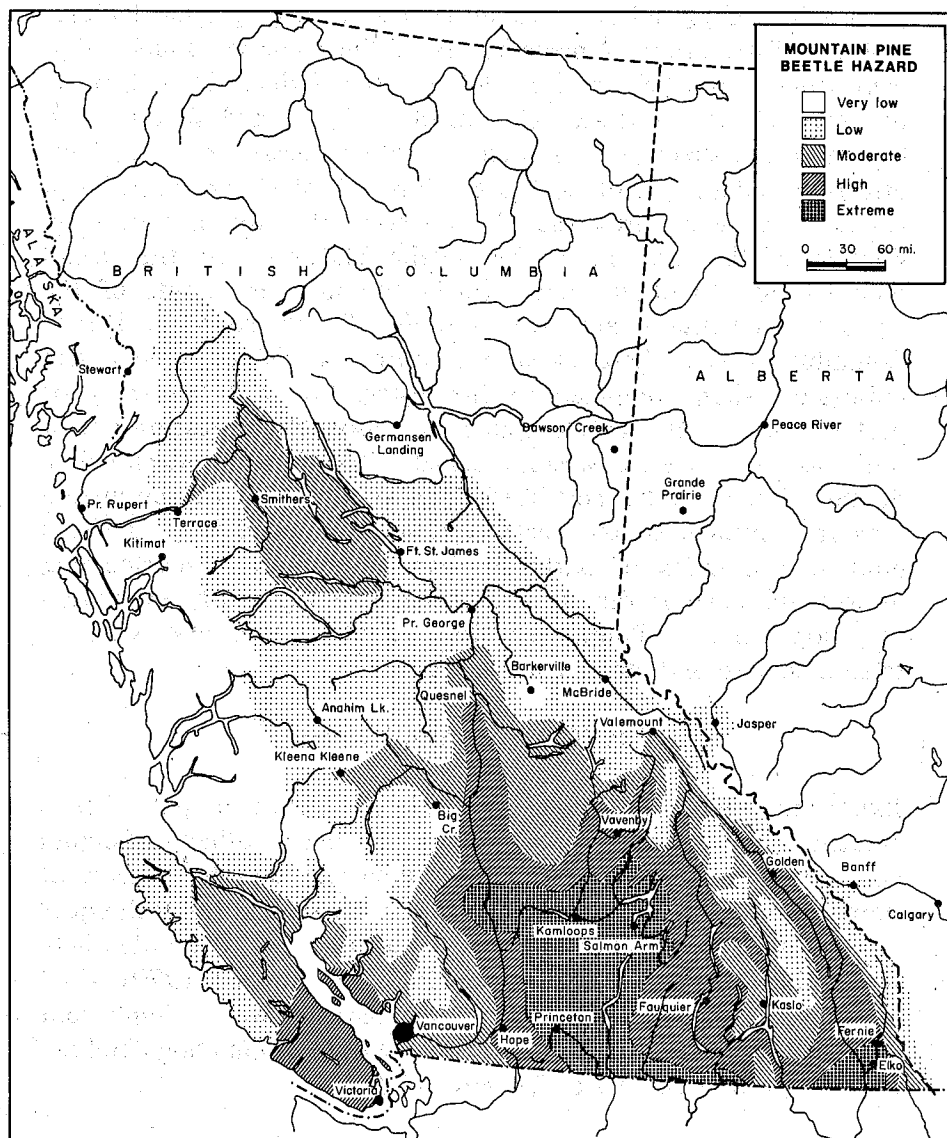


Fig. 8. Beetle outbreak hazard of western Canada.

Within the two lowest outbreak chance classes, the threat from the beetle in mature stands is generally low and, therefore, the chance of such stand depletion need not be included in long-range management plans.

In areas with the three highest outbreak chance classes, the formulation of long-range management goals and silvicultural practices for stands should include the probability and severity of stand depletion by the mountain pine beetle. For this purpose, all stands in these three hazard classes should be treated the same way, at least until more detailed maps of outbreak chance are available and the index of outbreak chance has been field tested. In view of the relatively high probability of recurring infestations in mature lodgepole stands in these areas, rotation age based upon maximum cubic foot wood production per acre is the best guideline to follow to minimize losses. This rotation age is conveniently defined by the intersection of current and mean annual increments, and it occurs at about 80 years on good to medium sites (Smithers 1962) and corresponds with stand diameters between 6.0 and 10.0 inches. Eight inches is our predicted minimum stand diameter that will support an outbreak. This approach to setting the rotation age is supported by survey evidence. In western Canada, outbreaks have not been reported from stands younger than 60 years; they rarely occurred between 60 and 80 years, but frequently occurred in stands older than 90 years. On the poorest lodgepole sites, outbreaks will rarely develop in stands of any age, mainly because of the lack of large diameter trees to support an increasing population. However, persistent low level beetle activity may eventually deplete much of the large dbh component of these stands. Implementation of this proposed guideline requires planned harvesting and regeneration. Priority of cutting should be given to stands with the largest average dbh growing at the lowest elevations.

To grow stands above eight inches dbh, the relation between trees killed and diameter (Fig. 6) and the chance of occurrence of outbreaks need to be assessed locally from survey records as

outlined by Roe and Amman (1970). When survey data are lacking, the index of climatic outbreak chance (F) could be calculated and taken as outbreak probability. Outbreak probability multiplied by the proportion of trees killed in a dbh class during outbreaks (Fig. 6) is an estimate of the chance for a tree being killed. When this probability is unacceptably high, the alternatives are conversion to successional types or clearcutting and regeneration, preferably to mixed lodgepole pine. This cutting should be in small blocks, so that similar age classes should not be adjacent to each other.

EPILOGUE

The phenomenon of bark beetles killing forest trees is a complex interaction of organisms responding to changes in their environment. Successful management of this pest problem requires input from a range of disciplines and a systems analysis approach is indicated. Our strategy, in this paper, was to assemble existing knowledge from past and current research to produce a conceptual statement of the total system, cohabitation of lodgepole pines and mountain pine beetles, and forest management implications thereof. We believe this is a prerequisite to the generation of a realistic predictive model that will aid in management decisions relevant to bark beetle depredation of our forests.

REFERENCES

- | | |
|--|---|
| Amman, Gene D. and Bruce H. Baker. 1972. MOUNTAIN PINE BEETLE INFLUENCE ON LODGEPOLE PINE STAND STRUCTURE. J. For. 70:204-209. | Boughner, C. C. 1964. DISTRIBUTION OF GROWING DEGREE-DAYS IN CANADA. Can. Met. Memoirs. 17. Met. Br., Dept. of Transport. 40 p. |
| Berryman, A. A. 1971. RESISTANCE OF CONIFERS TO INVASION BY BARK BEETLE-FUNGUS ASSOCIATIONS. Bioscience 22:598-602. | Brown, G. S. 1956. POPULATION TRENDS IN THE MOUNTAIN PINE BEETLE AT WINDERMERE CREEK, BRITISH COLUMBIA. Interim Report 1954-6. For. Biol. Lab., Victoria, B.C. 20 pp. |

Cole, W. E. and Gene D. Amman.

1969. MOUNTAIN PINE BEETLE INFESTATIONS IN RELATION TO LODGEPOLE PINE DIAMETERS. USDA Forest Service Research Note INT-95. 7 pp.

CONTINUOUS FOREST INVENTORY OF BRITISH COLUMBIA.

1957. Department of Lands and Forests. British Columbia, Canada.

Hopping, G. R. and G. Beall.

1948. THE RELATION OF DIAMETER OF LODGEPOLE PINE TO INCIDENCE OF ATTACK BY THE BARK BEETLE, *DENDROCTONUS MONTICOLAE* HOPKINS. For. Chron. 24:141-145.

Horton, K. W.

1956. THE ECOLOGY OF LODGEPOLE PINE IN ALBERTA AND ITS ROLE IN FOREST SUCCESSION. Can. Dept. Northern Affairs and National Resources, Forestry Branch, For. Res. Div. Tech. Note No. 45.

McCambridge, F. W.

1971. TEMPERATURE LIMITS OF FLIGHT OF THE MOUNTAIN PINE BEETLE, *DENDROCTONUS PONDEROSAE*. An. Ent. Soc. America 64:534-535.

NATIONAL ATLAS OF CANADA.

1970. Department of Energy, Mines, and Natural Resources. Ottawa, Canada.

Northeastern Forest Experiment Station.

1970. TOWARD INTEGRATED

CONTROL. Proceedings of the Third Annual Northeastern Forest Insect Work Conference, Upper Darby, Pa. 129 pp.

Powell, J. M.

1966. DISTRIBUTION AND OUTBREAKS OF *DENDROCTONUS PONDEROSAE* HOPKINS IN FORESTS OF WESTERN CANADA. Canadian Forestry Service, Information Report A-X-2. Calgary. 19 pp.

1969. HISTORICAL STUDY OF THE RELATION OF MAJOR MOUNTAIN PINE BEETLE OUTBREAKS IN WESTERN CANADA TO SEASONAL WEATHER. Canadian Forestry Service, Information Report A-X-23. Calgary, Canada. 11 pp.

Reid, R. W.

1963. BIOLOGY OF THE MOUNTAIN PINE BEETLE, *DENDROCTONUS MONTICOLAE* HOPKINS, IN THE EAST KOOTENAY REGION OF BRITISH COLUMBIA III. INTERACTION BETWEEN THE BEETLE AND ITS HOST, WITH EMPHASIS ON BROOD MORTALITY AND SURVIVAL. Can. Entomol. 95:225-238.

_____, and H. Gates.

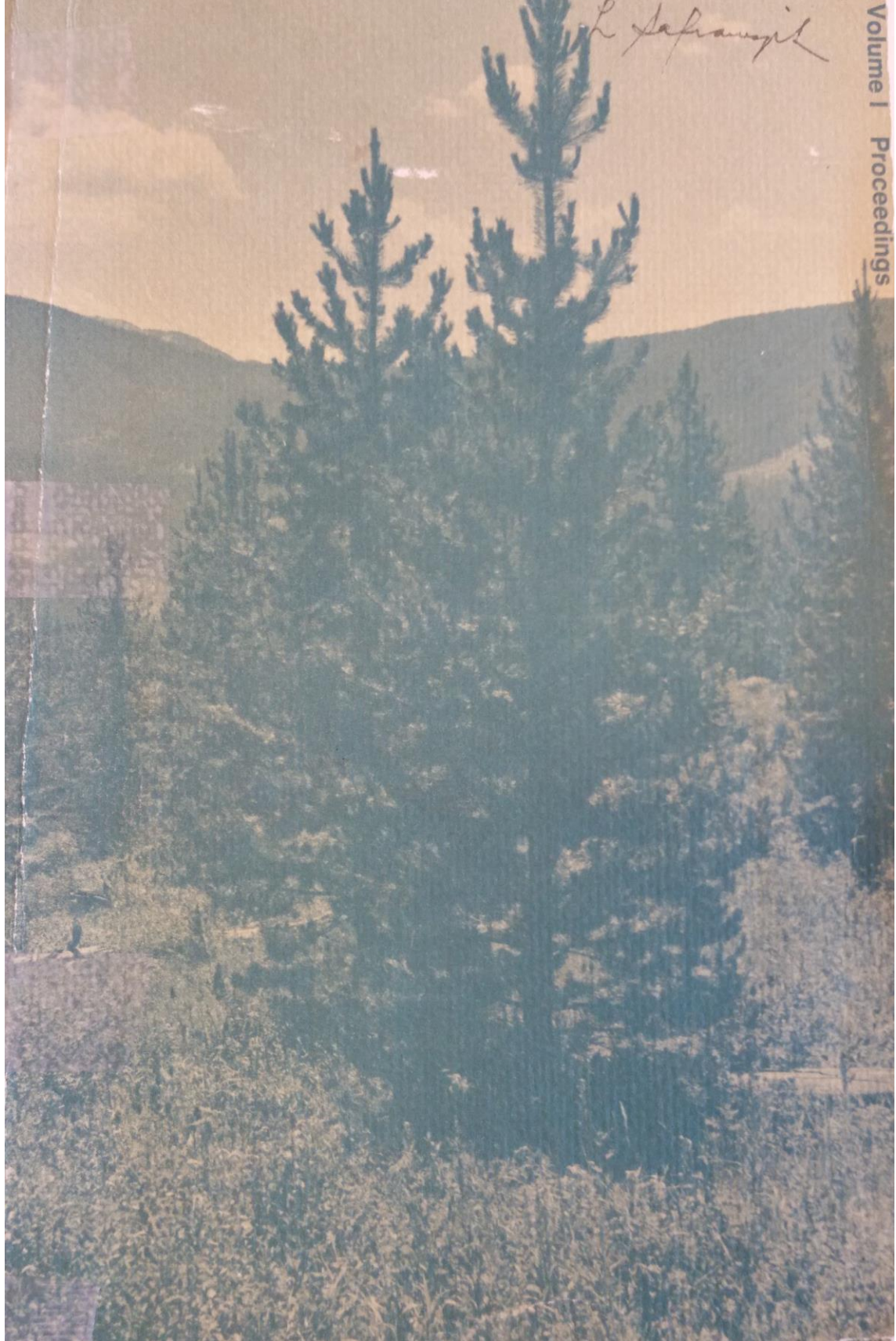
1970. THE EFFECT OF TEMPERATURE AND RESIN ON HATCH OF EGGS OF THE MOUNTAIN PINE BEETLE (*DENDROCTONUS PONDEROSAE*). Can. Entomol. 102:617-622.

- Reid, R. W., H. S. Whitney, and J. A. Watson.
1967. REACTIONS OF LODGEPOLE PINE TO ATTACK BY *DENDROCTONUS PONDEROSAE* HOPKINS AND BLUE STAIN FUNGI. Can. Jour. Bot. 45:1115-1126.
- Roe, Arthur L. and Gene D. Arman.
1970. THE MOUNTAIN PINE BEETLE IN LODGEPOLE PINE FORESTS. USDA Forest Service Research Paper INT-71, 23 pp.
- Rumbold, C. T.
1941. A BLUE STAIN FUNGUS, *CERATOSTOMELLA MONTIUM* N. SP., AND SOME YEASTS ASSOCIATED WITH TWO SPECIES OF *DENDROCTONUS*. J. Agric. Research 62:589-601.
- Shrimpton, D. M.
1973. EXTRACTIVE CHANGES ASSOCIATED WITH THE WOUND RESPONSE OF LODGEPOLE PINE TO ATTACK BY THE MOUNTAIN PINE BEETLE AND ITS ASSOCIATED MICROORGANISMS. Can. J. Bot. 51:527-534.
- Smithers, L. A.
1962. LODGEPOLE PINE IN ALBERTA. Can. Dept. For. Bull. No. 127. 153 pp.
- Shea, K. R.
1971. DISEASE AND INSECT ACTIVITY IN RELATION TO INTENSIVE CULTURE OF FORESTS. Proceedings, XV International Union of Forestry Research Organizations, p. 109-118.
- Somme, L.
1964. EFFECT OF GLYCEROL ON COLD HARDINESS IN INSECTS. Can J. Zool. 42:87-101.
- Whitney, H. S.
1971. ASSOCIATION OF *DENDROCTONUS PONDEROSAE* (COLEOPTERA: SCOLYTIDAE) WITH BLUE STAIN FUNGI AND YEASTS DURING BROOD DEVELOPMENT IN LODGEPOLE PINE. Can. Ent. 103:1495-1503.
- Wygant, N. D.
1940. EFFECTS OF LOW TEMPERATURE ON THE BLACK HILLS BEETLE (*DENDROCTONUS PONDEROSAE* HOPK.). Summary of a Ph.D. Thesis submitted to the New York School of Forestry. On file at the USDA Rocky Mountain Forest and Range Experiment Stn., Fort Collins, Colorado. 57 pp., 16 figs.
1959. BARK BEETLE CONTROL. J. For. 57:274-277.

Management of Lodgepole Pine Ecosystems

L. Safford

Volume I Proceedings



Management of Lodgepole Pine Ecosystems

SYMPOSIUM PROCEEDINGS

**Held at Washington State University
Pullman**

9-11 October 1973

**Edited by David M. Baumgartner,
Extension Forest Resources Specialist**

Washington State University Cooperative Extension Service