October 1974
Reprinted 1980, 1982
PDF updated 2002

Management of Lodgepole Pine to Reduce Losses From The Mountain Pine Beetle

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

Forestry Technical Report 1

Natural Resources Canada
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Victoria, British Columbia

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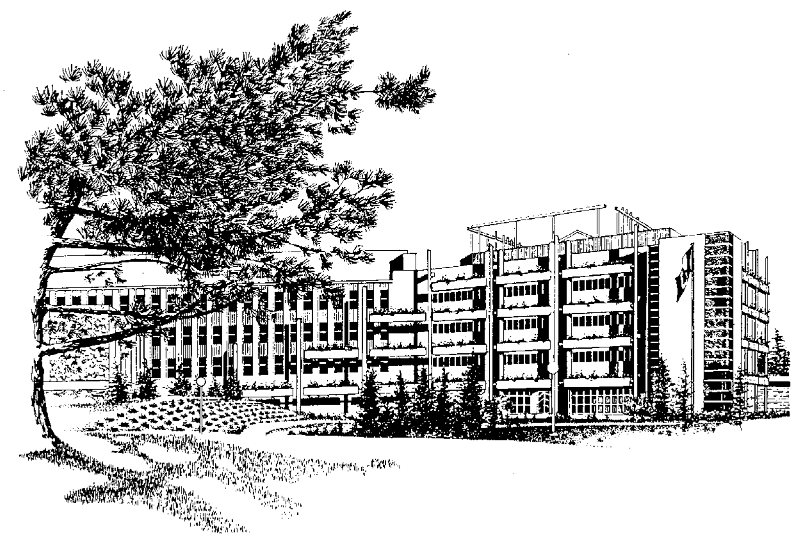

The Pacific Forestry Centre, Victoria, British Columbia

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Management of Lodgepole Pine to Reduce Losses from the Mountain Pine Beetle

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Preface

This two-part report is directed to forest managers, as well as to others concerned with the practice of forestry and the forest environment.

The first part, written in nontechnical language, covers all aspects of problems associated with the mountain pine beetle, including procedures and guidelines for coping with this insect, along with a selected reading list.

Described in the second part are the biological interactions that occur when bark beetles attack trees. This section with its bibliography forms the basis for part one and can be referred to if satisfactory decisions cannot be made with the first part alone.

If further advice is required, please contact the Pacific Forest Research Centre, 506 West Burnside Rd., Victoria, B.C. V8Z 1M5

Résumé

Ce rapport se divise en deux parties. La première partie, rédigée en termes non techniques, décrit les méthodes courantes de detecter les dommages causés par le Dendroctone du Pin ponderosa (*Dendroctonus ponderosae*); evaluer le danger, mesurer les dommages et prévoir les tendances de l'infestation. Les auteurs traitent aussi des méthodes forestières de lutte, et recommandent telles révolutions et tel reboisement afin de diminuer les pertes futures possibles.

La seconde partie décrit les informations qui existent sur les interactions biologiques qui se produisent lorsque les Dendroctones attaquent les arbres. L'influence du climat sur le Dendroctone et les effets de celui-ci sur la structure des peuplements de Pins lodgepole.

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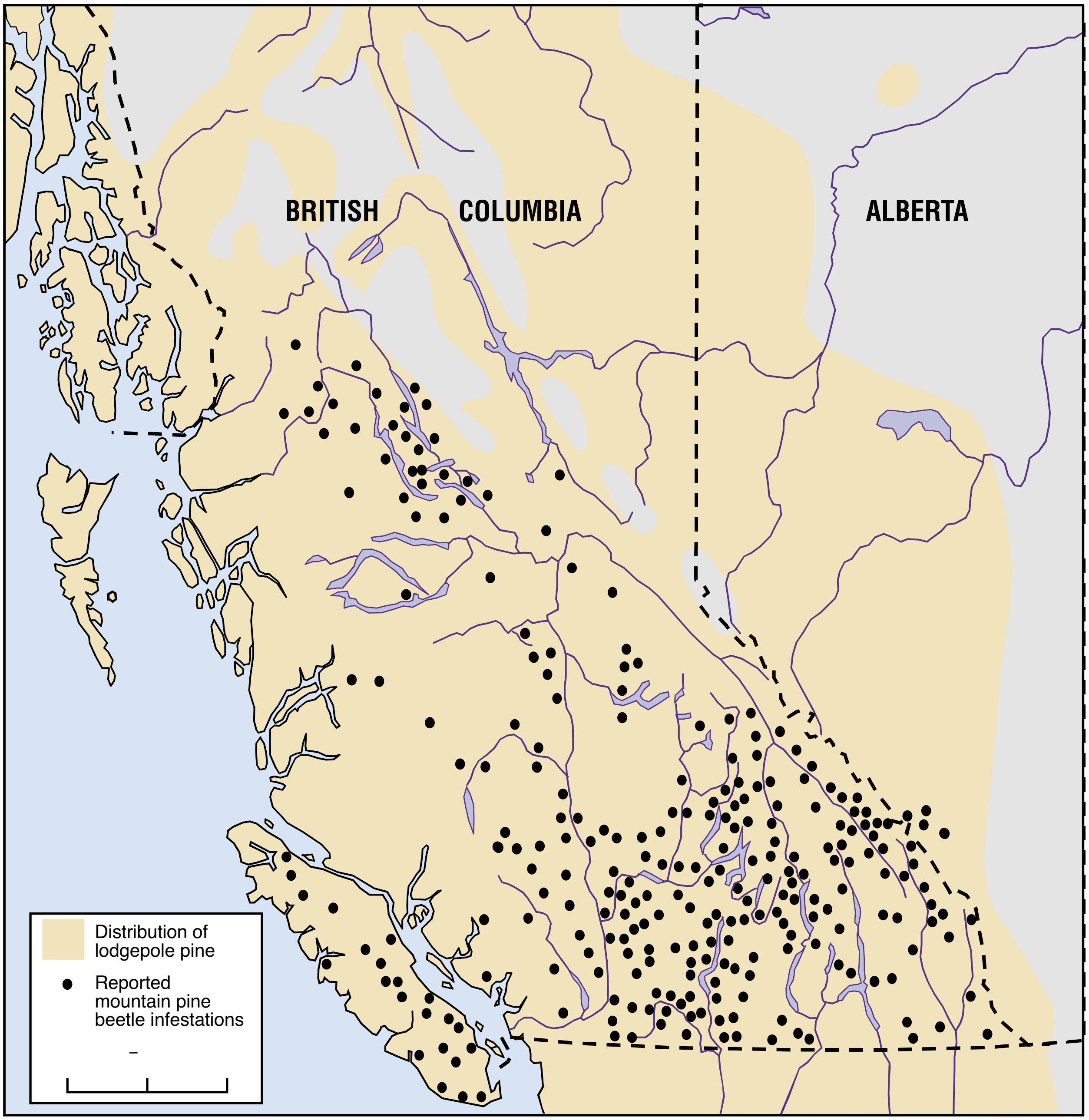


Fig. 1. The distribution of lodgepole pine and the mountain pine beetle in Western Canada.

THE PROBLEM

The mountain pine beetle (*Dendroctonus ponderosae* Hopk.) is the most serious enemy of mature pines in western Canada. Estimates of mature lodgepole pine (*Pinus contorta* Dougl.) killed by this beetle in British Columbia amounted to 1.3 million cubic feet of timber per year for the last 20 years, about 3% of the average annual cut. Moreover, the monetary loss is far greater than the volume loss would indicate because in outbreaks, the high-value trees are preferred by the beetles. If no action is taken, losses will continue because there are large areas of lodgepole pine approaching maturity in western Canada. Other effects of the mountain pine beetle are: a hastening of forest succession; a change in age and diameter distribution of lodgepole pine stands; a reduction in esthetic values, particularly in recreational areas, and an increase in fire hazard. Each can force changes in management plans. Marketing problems may result from the unplanned necessity to cut quickly large volumes of timber.

Mountain pine beetle damage has been greatest in British Columbia, in the south-central and south-eastern interior, and in southern Vancouver Island. Other areas of high beetle activity have been from Hazelton east to Stuart Lake and along the Fraser River from Quesnel to near Williams Lake. In Alberta, one outbreak has been recorded from Banff National Park. The beetle has not been recorded from the Queen Charlotte Islands or from areas north of latitude 56°N. Although unreported, it probably occurs throughout more of the range of lodgepole pine in British Columbia than is presently known (Fig. 1).

MANAGEMENT GUIDELINES TO REDUCE LOSSES

Summary

Annual aerial detection surveys of mature lodgepole pine stands and on-the-ground inspection of suspected infestations should be done in June or July. These surveys should concentrate on areas with a high beetle hazard and, if the presence of the mountain pine beetle is confirmed, damage appraisal and a forecast of infestation trend should be carried out.

The risk of monetary, social and environmental losses associated with trees being killed by beetles must be weighed against the costs of preventing or reducing these losses.

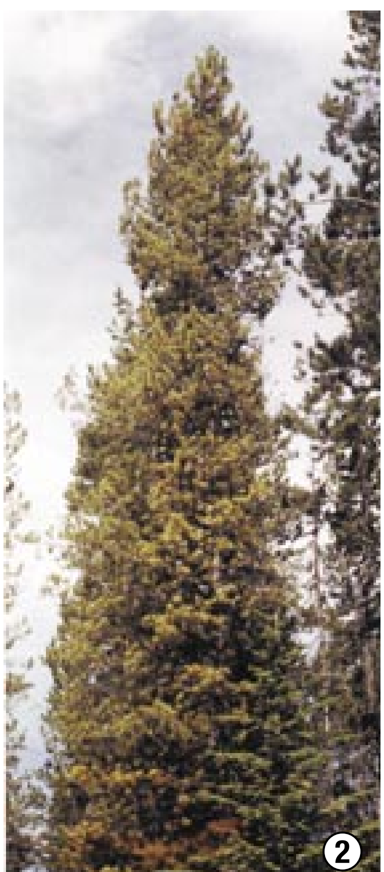
Infestations in stands with an average diameter above 8 inches (20 cm), older than 80 years, especially in areas with a high beetle hazard, are potentially epidemic. These outbreaks should be harvested immediately within boundaries containing more than one infested tree per acre. If this is not possible, because of the size of the infestation, areas with the largest diameter trees, at the periphery of the infestation, should receive cutting priority.

Long-term management plans need to consider that the larger the diameter of lodgepole pine trees, the greater is the risk that they will be killed by the mountain pine beetle.

In high beetle hazard areas, the risk will be acceptable if stands are harvested when they are between 80 and 100 years old.

Future losses can be lessened if the stand is removed by cutting a series of small blocks so that a mosaic of age classes results.

The alternative to the foregoing is to grow lodgepole pine to the desired size, accept any losses and convert to the successional type.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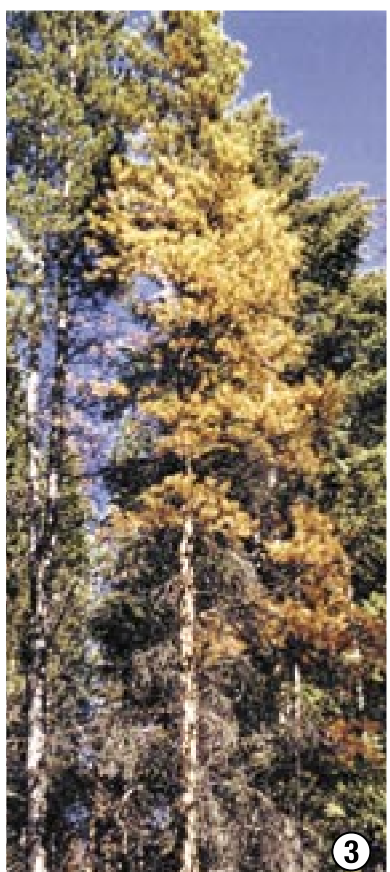
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Detection of Damage

Trees and stands infested with the mountain pine beetle are readily recognized except in the earliest stages of infestation. The symptoms are described as they develop through time, starting with the crown, then the bole and finally the inner bark and sapwood.

Symptoms of the crown

Green trees are attacked by the mountain pine beetle in mid-summer. The first noticeable foliage color change usually occurs in spring of the following year. Occasionally, following on early attack and a hot, dry summer, crowns will begin to fade in the fall. The foliage changes from green to yellow (Fig. 2) to yellow brown (Fig. 3) to red brown (Fig. 4) and then drops off the tree. In June and July of the year after attack, trees are usually yellow green or yellow brown. Some trees retain a few red brown needles for as long as 3 years following attack. This change in foliage permits detection from the air, lookout towers or other vantage points. However, trees killed by any agent, including beetles, usually show the same sequence of color changes and therefore a ground survey must be done.

Fig. 2-4. Crown symptoms of lodgepole pine attacked by the mountain pine beetle; Fig. 2. The first observable color change usually occurs in May and June the year after attack. Fig. 3. This light yellow color usually occurs in June and July the year following attack. Fig. 4. This red brown color usually occurs in July and August the year after attack.

Fig. 5-7. Bole symptoms; Fig. 5. Boring dust accumulates in bark crevices and on the ground at the base of trees. Fig. 6. Pitch tubes on the bole, each pitch tube surrounds a beetle entry hole. Fig. 7. An infested tree after woodpeckers have flaked off bark in search of beetle brood.

Symptoms of the bole

When trees with suspected beetle activity have been located, boles of these and surrounding trees should be inspected, preferably shortly after beetle attack, from late August through September. Boring dust or pitch tubes are the first signs of attack. Boring dust, extruded from beetle entrance holes, accumulates in bark crevices at the base of the tree (Fig. 5). Borings are red brown and similar in texture to sawdust from a crosscut saw, and are only extruded during the first few days of gallery construction. The borings are quickly removed by wind and rain and therefore are not always conspicuous. In some cases, pitch exudes from a beetle entry hole and forms cream colored or red brown pitch tubes, ¼ to 1 inch in diameter (0.7-2.5 cm), often mixed with bark and wood borings (Fig. 6). These pitch tubes are most apparent on the lower portion of the stem, but are often seen in the crown portion. At breast height, there are usually between 4 and 12 attacks per sq. ft. (40-130/m^2).

Trees infested by bark beetles may be readily found if woodpeckers have removed the bark in search of insects (Fig. 7). Woodpecker activity is usually highest during late fall and winter and infested trees can be easily found where bark flakes accumulate on the snow.

Symptoms of the phloem and sapwood

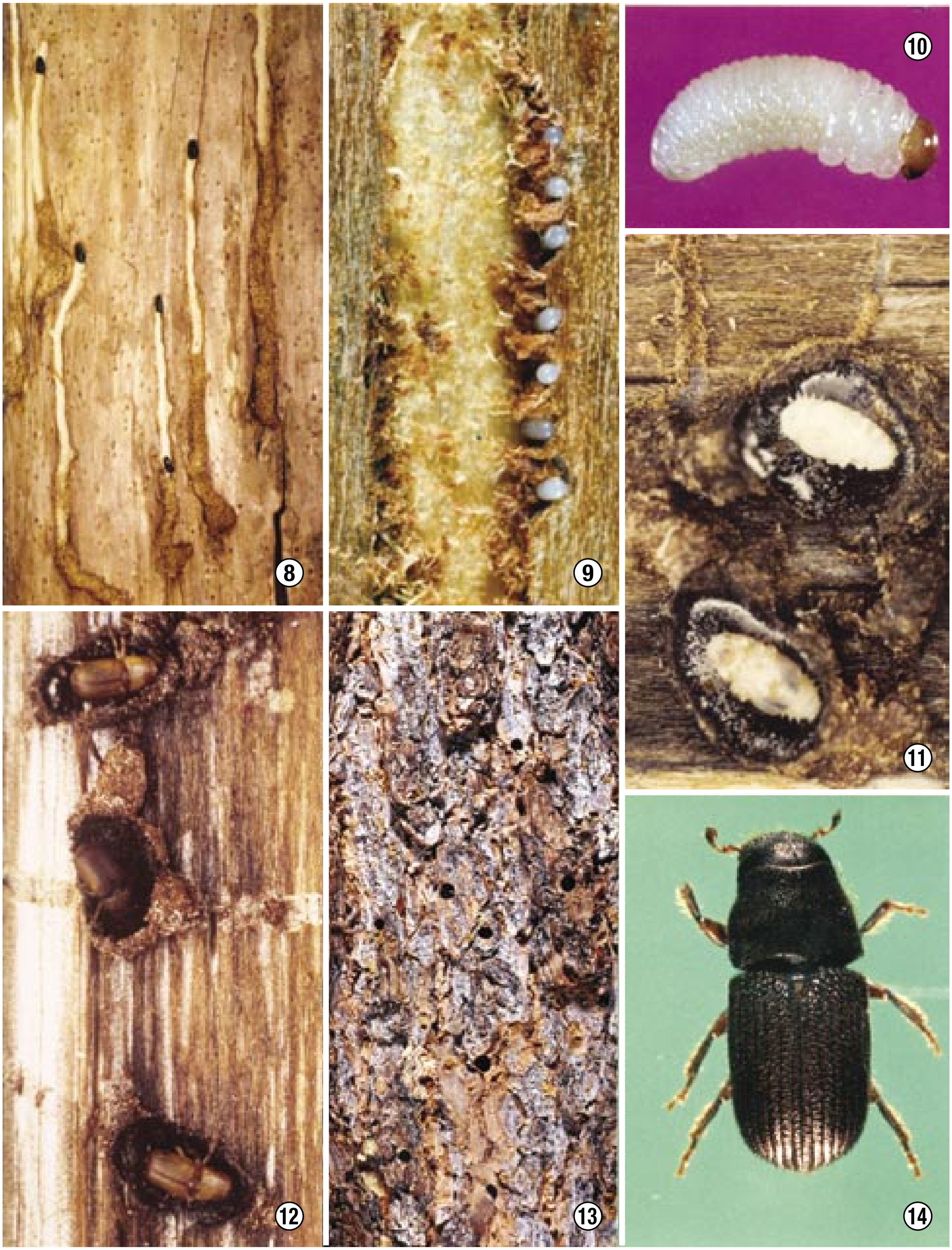
The gallery system is the most reliable indicator of mountain pine beetle activity. Its appearance will vary, depending upon the time of examination. During late summer shortly after attack, there are vertical galleries primarily in the phloem, and the sapwood may be slightly scored. The galleries have a slight hook at the bottom and are packed with borings except for the upper inch or two (Fig. 8). Completed galleries are usually about 12 inches (30.5 cm) long but occasionally reach 3 feet (91.5 cm) and contain eggs (Fig. 9) in niches along the sides. The larval mines are approximately horizontal to the parent galleries (Fig. 15). During fall, winter and early spring, parent galleries and larval mines are intermingled (Fig. 16). The latter vary from 1 to 9 inches in length (2.5-23 cm), often within the same gallery system, and increase in width further away from the parent gallery. In late spring, there is an oval pupal chamber at the end of some mines (Figs. 11 and 15). From then until emergence, larvae (Fig. 10), pupae (Fig. 11) and new adults (Fig. 12) will normally be present in each gallery system. In summer, the mature adults (Fig. 14) bore circular emergence holes (Fig. 13), about 1/10th inch in diameter (2.5 mm), through the bark and fly to a new tree. Remaining mountain pine beetles will normally be dead and the foliage of the tree will be red brown.

Within a few days of beetle attack, the sapwood behind each gallery appears dry. This is the first sign of colonization by fungi that are carried into the tree by beetles. Within 2 weeks, the fungi begin to form pigments and infected wood becomes blue stained and infected phloem turns brown. The sapwood surface is often obscured by dead phloem and boring dust. Blue stain is best observed by cutting into the sapwood (Fig. 17). However, wood is not always suitable for fungi to form pigments and although the wood may be colonized, it will not always become uniformly stained.

Detection Procedure

Detection is most successful if carried out, from the air, annually in June and July when the yellow green and yellow brown tree crowns indicate the presence of brood. Mountain pine beetle presence can be positively identified by ground surveys in late August and September when beetle attack has finished. Detection at this time involves a complete search near the old infested trees, especially when the beetle population is low. Currently infested trees are green at this time and detection can only be based on the external symptoms described for the bole. Detection for mountain pine beetle activity in B.C. is carried out annually by the Pacific Forest Research Centre. However, this is not detailed enough for forest management or control procedures, and management agencies should institute routine detection in their areas of jurisdiction.

Fig. 8-14. Symptoms under the bark; Fig. 8. Beetle galleries in phloem before eggs hatch, note the hook and borings packed at the base of each gallery. Fig. 9. Eggs in niches in the parent gallery. Fig. 10. Mature larva. Fig. 11. Pupal chamber with a pupa (p) surrounded by a mass of the associated blue stain fungus (f). Fig. 12. Newly formed adult under the bark. Fig. 13. Holes in bark (arrows) after beetles have left. Fig. 14. Mature adult.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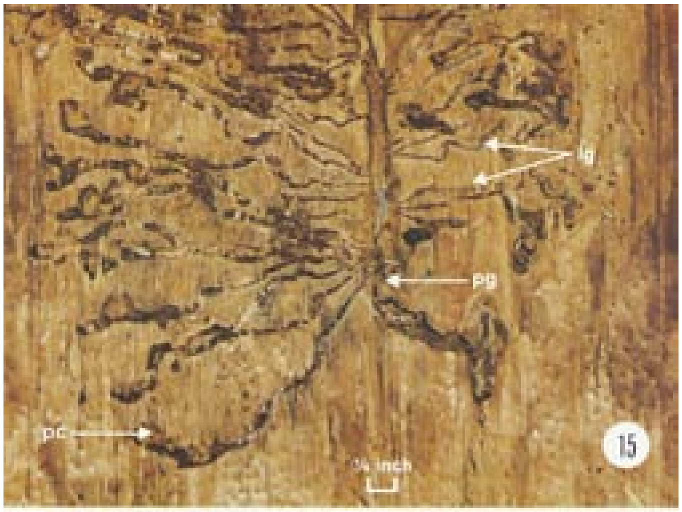

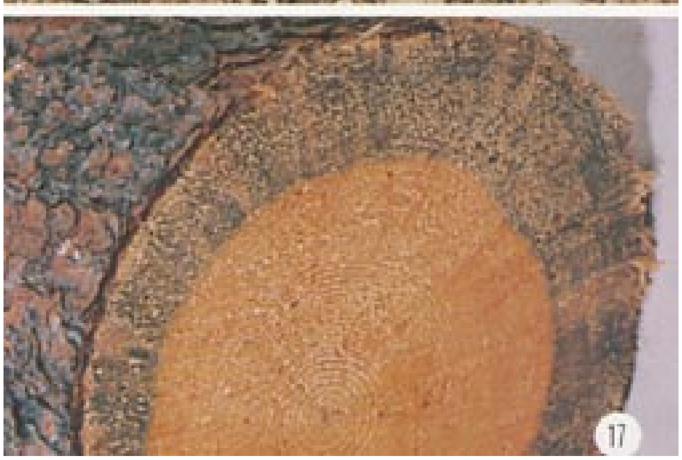

Symptoms of the stand

Low populations of the mountain pine beetle exist as discrete colonies in individual trees or small groups of trees scattered throughout the stand. These infestation loci are often found in draws or gullies, or in areas subjected to soil compaction, periodic flooding or other wide fluctuations in the water table. Exposed logging slash and stumps are generally not attacked by the mountain pine beetle. Freshly cut, decked logs in shady locations may occasionally be infested; however, beetle populations are not maintained in such.

An outbreak[1] begins from small groups of infested trees and spreads progressively from these centers (Fig. 18). Active infestations older than 2 years will have grey topped trees that have lost their foliage scattered among red and fading crowns (Fig. 19). Such increased activity by the beetle is characterized by a preference for large diameter, dominant and codominant trees and usually develops in stands older than 80 years. The majority of outbreaks develop on south- and west-facing slopes in stands where lodgepole pine is the dominant species; however, this is not a consistent relationship. Severe outbreaks can develop rapidly. Past outbreaks have lasted from 4 to 18 years, with an average of 8 to 9 years.

[1] An outbreak is defined as the time when one or more trees/acre are killed/year.

Fig. 15. An isolated gallery system in the phloem showing parent gallery (pg), larval galleries (lg) and some pupal chambers (pc).

Fig. 16. Typical intermingling of parent galleries (pg), larval galleries (lg) and brood stages in the phloem.

Fig. 17. Blue stain in the sapwood.

Fig. 18. Distribution of infestation centers (arrows) in the spring.

Fig. 19. An active infestation center in June the year after attack intermixed with trees killed in previous years.


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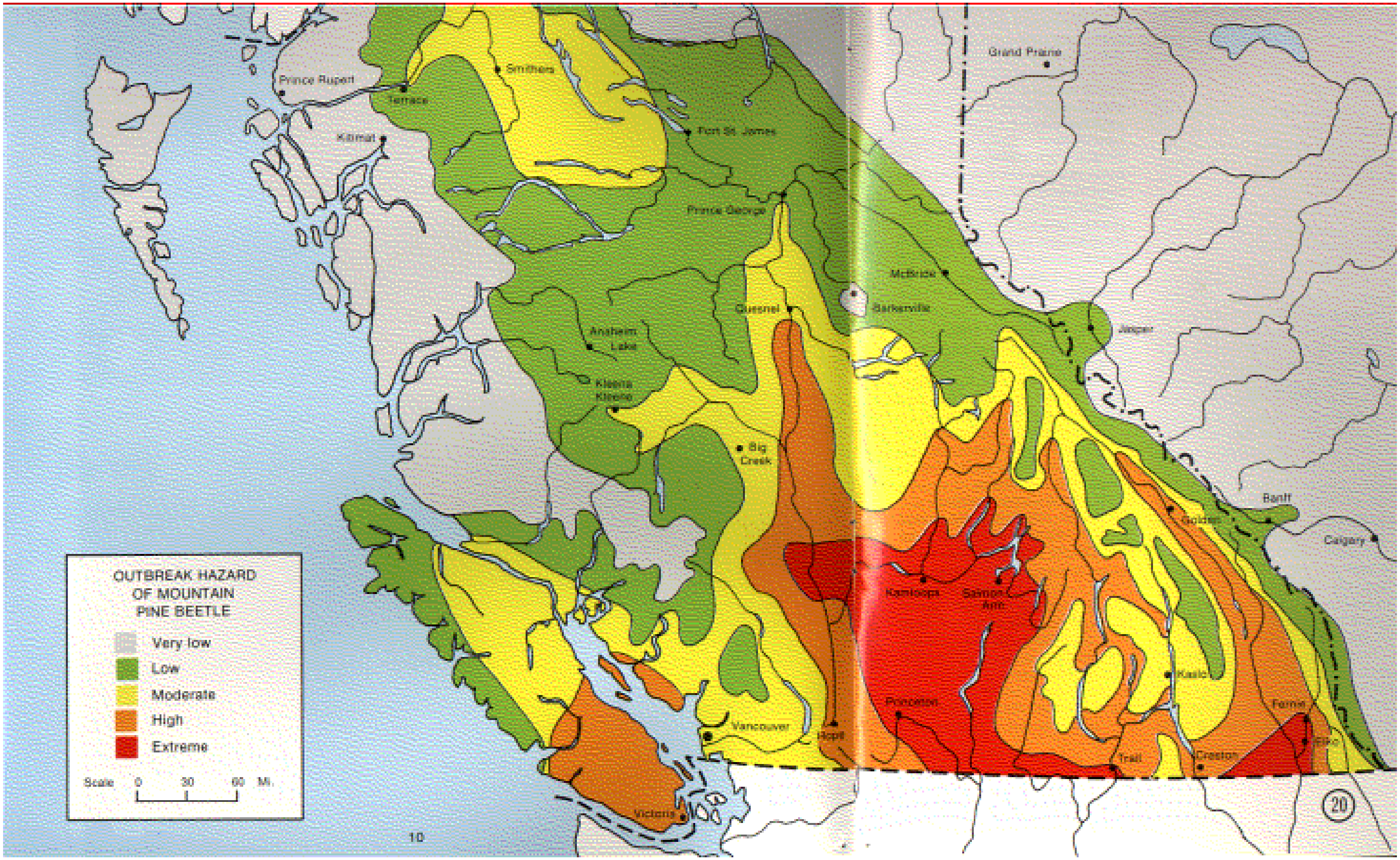

Fig. 20. Outbreak hazard map.

Hazard and Damage Assessment

To decide on what action to take when mountain pine beetle activity has been detected, three factors should be considered: the beetle hazard due to climatic effects must be assessed, the damage appraised, and a forecast of infestation trend made.

Beetle hazard due to climatic effects

A suitable climate for the beetle must prevail before it can become a continuous threat to lodgepole pine. Areas in western Canada are defined according to climatic suitability for the mountain pine beetle (Fig. 20). Areas where climate favorable for the beetle frequently occurs have a high hazard rating. Essentially these are hotter, drier areas with mild winters. Areas with a frequent occurrence of one or more climatic conditions detrimental to the beetle have a low rating. Topographic features have influenced the final positioning of boundaries on the map. It is stressed that in each area there is a mosaic of the other hazard classes due to local effects of climate. Thus, it is the expected frequency of periods favorable for an increase in the beetle population that is portrayed by the hazard map; this is independent of tree and stand conditions. As more local climatic information is obtained, a mosaic of classes in each large class should appear. The hazard map is derived for elevations up to 2500 ft (760 m) above sea level in the northern limits of beetle distribution, and roughly 4000 ft (1220 m) above sea level in southern B.C. Above these elevations, outbreak potential will be less than indicated by the map.

Damage appraisal

An estimate of loss is required for timber inventory, assessing the need for control action, and evaluating control programs. When infested trees have been detected, an aerial reconnaissance survey should be conducted in August or early September to map the limits and distribution of both damage and surrounding mature pine stands. On the ground, inspection of surrounding green trees should be done to ascertain the limits of infestation. The amount of damage can be appraised by aerial photographic techniques or by ground surveys. Aerial color photographic techniques are especially useful in remote or large areas (Fig. 18). This technique does not provide all the desired information when used by itself because green infested trees cannot be detected. However, an efficient appraisal method, based upon aerial color photography and limited ground sampling, considerably reduces the cost of the survey and increases its precision. Ground surveys can be done by conventional timber cruising techniques. Intensity of the survey depends upon the density of dead and infested trees, and size of the infestation. Volumes of uninfested trees, green infested trees and trees killed more than a year earlier are obtained for the whole area. This survey should be conducted as soon after beetle flight as possible because fresh boring dust and pitch rubes are conspicuous at this time and aid in identifying green infested trees.

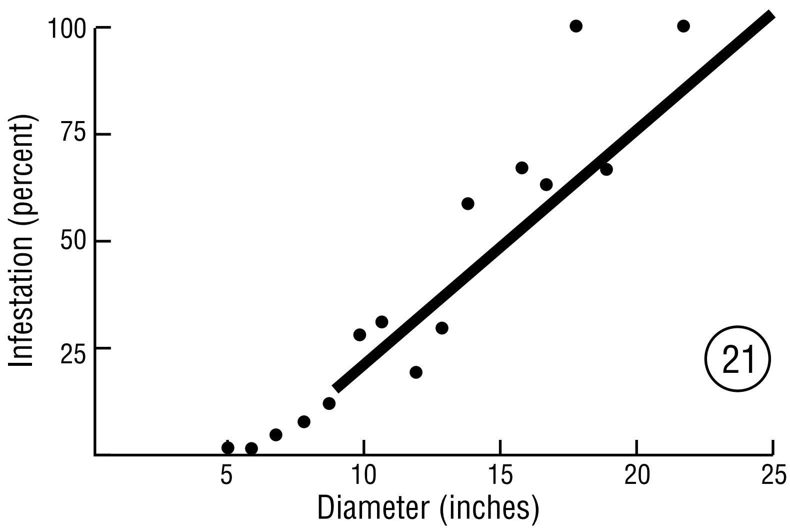

Fig. 21. Relation between percentage of trees infested and diameter at breast height (12).

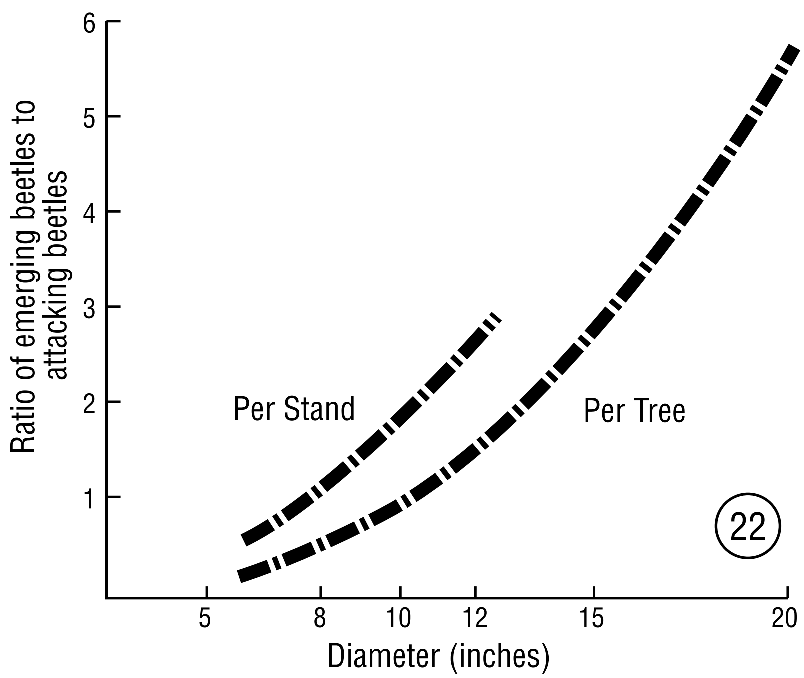

Fig. 22. Ratio of emerging to attacking beetles as related to tree and stand diameter.

Forecasting infestation trend

Infestation usually develop into outbreaks when in stands older than 80 years and with many trees over 10 inches (25.4 cm) in diameter. In such stands, final depletion increases 4-9% with each inch increase in tree diameter above 6 inches (15.2 cm) (Fig. 21). In the three highest hazard classes, the average change in beetle numbers from year to year, and hence in trees killed, will be proportional to the average stand diameter (Fig. 22). Outbreaks continue until the large diameter component of the stand is killed; the average diameter of the residual stand is usually below 8 inches (20 cm). In the two lowest hazard classes, infestations are of low intensity but persistent.

Short-range forecasts, based upon measurements of beetle density in trees in late spring, can be used to estimate more accurately the number of trees that will be infested by the emerging beetle population. This allows only 1- to 2-month lead time for planning and implementing control measures before beetles emerge to attack new trees and therefore is of limited practical use. Sometimes, a declining infestation trend can be established in the fall. Since this is almost a year before emergence, a fall survey of brood conditions carried out in conjunction with the ground detection could be of some value. Occasionally, extremely cold temperatures cause mortality of overwintering larvae above the snow line and the infestation trend may decline. Such predictions are valid only for 1 year at a time.

Reduction of Losses

The detection, identification and measurement of mountain pine beetle damage and methods for evaluating the potential threat of an infestation have been described. The question now arises: what does one do in the face of an impending outbreak? Sanitation salvage logging is recommended, especially for large outbreaks. Where a few high value trees are affected, treatment by application of insecticides, felling and burning or trapping with attractants may be useful.

Sanitation Salvage Logging

This action is favored because it utilizes timber that would be worthless in a short time and it reduces the number of beetles and their potential food source. After damage appraisal, the entire outbreak area should be clear-cut within boundaries containing more than one infested tree per acre, before flight of the new beetles. When this cannot be done, areas within the stand with the greatest density of large diameter trees at the edge of the infestation should be given cutting priority whether infested or not. Areas where the average diameter is less than 8 inches (20.3 cm) have the lowest priority. In mature stands, the best of salvage operations will not contain an extensive outbreak or prevent a recurrence in the remaining trees, especially in the three highest hazard areas. Hence, the residual stand must be re-examined on an annual basis. Salvage operations should reduce the rate of spread of an infestation. Therefore, planned clear-cutting of the entire stand or cutting the pine component to an 8 inch (20.3 cm) diameter limit are the alternatives left to management. This action can lead to unacceptably large clear-cut areas. Details of the sanitation salvage plan need to be worked out for each infestation.

Cutting of the uninfested trees in an infested area should not be done during the flight period because removal of this nearby host material will enhance the spread of the beetles. Also, to prevent dispersal of beetles, hauling and stockpiling, even in holding ponds, of infested logs should not be done during this period. Bark and edgings from infested logs contain the beetles and should be burnt or otherwise destroyed before the flight of this brood, which may or may not coincide with flight in the forest. If beetles are dispersed by hauling and stockpiling operations, any pine stands so exposed must be surveyed for beetle killed trees for a minimum of 2 years and treated if required.

Salvage operations should be done according to strict sanitation standards: Stumps cut to 1 ft (30.5 cm) or less and stems used to 4-inch (10.2 cm) top diameter. It is then not necessary to treat the infested stumps and slash. Culled, infested logs should be burned prior to flight of their brood. Likewise, when stump height is much in excess of 1 ft (30.5 cm), and most of the bark is undamaged, infested stumps should be scorched, chemically treated (see below) or debarked.

Fungal staining and checking quickly lowers the value of infested trees and therefore the salvage operation should commence as soon after beetle flight as possible. Sapwood of lodgepole pine salvaged from beetle attack is usually blue stained (Fig. 17). Young fungal growth is colorless; after about a week, pigment usually begins to develop in the fungi and this produces a blue color in the wood. Sometimes fungi never color, and the wood remains clear even though thoroughly colonized. At other times, bluing does not occur until trees are cut and logs are being processed. Blue stain fungi do not appreciably weaken the wood because they cannot utilize wood fibre for food, and the only significant detrimental effect on wood properties is a slight reduction in the modulus of elasticity. Sapwood of lodgepole pine colonized by these fungi is more rapidly and thoroughly penetrated by preservatives than non-colonized sapwood. Also, concrete poured in forms made of blue stained wood cures more rapidly. Logs from bark beetle killed trees deteriorate, similar to ordinary green logs left in the forest. Blue stain may mask the presence of rot-causing fungi in such logs. Therefore, salvage procedures should be based on rapid extraction and conversion, following by kiln drying, which will prevent further bluing.

Typically, sapwood from infested trees will begin checking by the time the foliage has turned yellow, in the spring after attack. Checking occurs earlier in trees debarked by woodpeckers and in trees on dry, exposed sites.

Other Methods

Two insecticides[2] ethylene dibromide and lindane have been used against the mountain pine beetle. However, in commercial forest applications, these insecticides are of limited value because: (1) treatment is on individual trees; thus, it is costly and difficult to treat thoroughly large areas, and a recurrence of outbreak is probable; (2) these insecticides must be handled with great care, according to strict government regulations, because of the threat to other forms of life, and (3) this method of combatting bark beetles does not yield any salvage.

Felling and burning of infested trees is an alternative to the use of insecticides. The objective is to scorch the bark deeply enough so that the broods will be killed by the heat. This method is usually limited to winter and early spring to minimize fire hazards; other disadvantages are the same as for chemical treatment. Both the above methods may, however, find useful applications in urban and suburban forestry.

Chemical attractants offer promise of control through manipulation of the beetle population. The potential of this method has been demonstrated but practical application is still experimental.

[2] Before using insecticides, consult the Provincial Entomologist, B.C. Department of Agriculture, Parliament Buildings, Victoria, B.C. for regulations concerning their use.

Preventive Management

Bark beetles will not be eliminated from lodgepole pine stands by forestry procedures. However, in commercial stands, potential losses from the mountain pine beetle can be lessened by reducing stand susceptibility. This involves the formulation of long-term management goals and silvicultural procedures. In view of the high probability of infestations in mature lodgepole stands in the three highest climatic hazard classes, it is sound policy to consider planned harvesting of the entire stand when aged between 80 and 100 years. The setting of rotation age and projected wood requirements should take into account the chance of mountain pine beetle infestation and the resulting severe depletion. In areas of severe hazard, gains made by allowing longer rotations are probably offset by losses to the beetle. Older stands with large diameter trees should be given cutting priority. In general, stands should be kept about 80 years or under, or as low as possible commensurate with the wood product requirements and economics of the operation. Rotation, based upon maximum wood production per acre, is the best guideline to follow to minimize losses from the mountain pine beetle. Harvesting should not be delayed beyond the age when current and mean annual increment are equal for a stand.

The chance for future outbreaks (Fig. 23) can be determined by considering the hazard class of the stand, the beetle history in the area, and the stand characteristics. When this chance is high, the risk of management for a certain type or size of wood may be prohibitive and an alternative sought, such as conversion to another type. This can be accomplished by selective cutting or by clear-cutting, followed by planting or seeding.

There are two other management methods that may have application in the future. Firstly, the development of mixed stands; outbreaks do occur in mixed stands, but less frequently than in pure pine stands. Furthermore, wood production in mixed stands will probably be higher, and such stands may meet recreational, wildlife and watershed requirements as well as, or better than, pure lodgepole pine stands. A mosaic of age classes in small areas is another effective silvicultural procedure. This should prevent the development of simultaneous outbreaks over large areas. In addition, with rotation based upon maximum wood production, any infestation would be confined and easily managed.

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Fig. 23. A mountain pine beetle outbreak. The pine component of the stand has been killed.

BIOLOGICAL BASIS FOR MANAGEMENT RECOMMENDATIONS

Life History and Habits of the Mountain Pine Beetle

The mountain pine beetle normally attacks living lodgepole pine trees in mid-summer. The female beetles bore through the bark and construct egg galleries in the phloem (Fig. 8). During gallery establishment, chemical attractants are released by the females, causing beetles of both sexes to aggregate at, and colonize the tree (17). A male joins the female when the gallery is successfully started. After mating, the male often leaves. The gallery entrance is plugged with boring dust, and the female beetle continues gallery construction and starts to lay eggs. Usually 60-80 eggs, about 2 eggs per cm (5/inch), are laid singly in niches along the sides of the gallery (Fig. 9) and hatch about 2 weeks later. The larvae (Fig. 10) in the inner bark mine circumferentially (Fig. 15) and develop through four stages called instars. The broods normally overwinter as larvae and complete their development the following spring. When mature, they construct an oval shaped chamber in which they pupate (Fig. 11) and change to immature beetles (Fig. 12). About mid-July, the new mature beetles (Fig. 14) bore through the bark to the outside (Fig. 13) and fly to attack living trees. There is normally one generation per year. The life cycle is illustrated in Figs. 8 - 16.

Lodgepole, western white (*Pinus monticola* Dougl.) and ponderosa (*Pinus ponderosa* Laws) pines are the major hosts. In western Canada, there are no known records of attacks on white bark (*Pinus albicaulis* Engelm.) and limber pine (*Pinus flexilis* James), but there are records from the United States. There is one record of attack on the few Scots pine (*Pinus sylvestris* L.) in B.C. At low population levels, the mountain pine beetle may show a preference for one pine species even though others are intermixed. During an outbreak, however, any acceptable host is attacked. Following an outbreak, beetle activity may or may not be confined to the pine originally preferred. A few spruce (*Picea*) and Douglas-fir (*Pseudotsuga*) may be attacked and killed, but these are not suitable hosts and broods rarely develop.

The mountain pine beetle is native to western North America. In western Canada, it occurs throughout the range of ponderosa pine, over most of the range of western white, white bark and limber pines, but only in the southern part of the range of lodgepole pine (Fig. 1).

Population Dynamics of the Mountain Pine Beetle

When mountain pine beetle populations are low, a number of factors, such as climatic effects, directly on the insect and indirectly through the tree; relations with the blue stain fungi and the tree; competition for food and space among broods; predation, parasitism and disease, interact to restrain the potential of such populations to increase. The relaxation of some of these factors may permit outbreaks to develop. The dynamics of this interaction are illustrated in Fig. 24.

Temperature effects

The rate of development of the mountain pine beetle varies with temperature. Egg hatch and growth and development of larvae mostly occur between 4.4 and 37.8°C (40-100°F) (16,22). At a constant temperature, the optimum for egg hatch (22) and brood development (H.S.W. unpublished) is 20-25.6°C (68-78°F). During cool summers, broods take more than 1 year to complete the life cycle or flight occurs late. An extended life cycle exposes the immature stages to mortality factors for longer periods. Late flight decreases the chance for eggs to hatch before winter. The likelihood of eggs surviving winter temperatures is extremely low in western Canada, except for the southern coast of B.C.

Survival of all stages of the mountain pine beetle is reduced by unseasonally cold temperatures and extremely high summer temperatures. Of all the life stages, eggs have the least tolerance to freezing temperatures, followed by pupae, adult and larvae, in that order. Eggs conditioned to low temperature are killed near -17.8°C (0°F) (22). Temperatures lower than this are common for several months in all areas except the southern coast and Vancouver Island in B.C. Mature larvae are generally more cold hardy than young larvae (L.S. unpublished). Cold hardiness changes; it is greatest in the period from December to February. Effects of cold are exerted within the first 2 to 4 hours of direct exposure. A typical seasonal mortality curve for larvae in relation to low temperatures is in Figure 25 (40). Bark and snow cover modify subcortical temperatures due to their insulating properties.

The order of susceptibility of the various stages of the brood to high temperatures is the same as that to low temperatures. Exposure to temperatures about

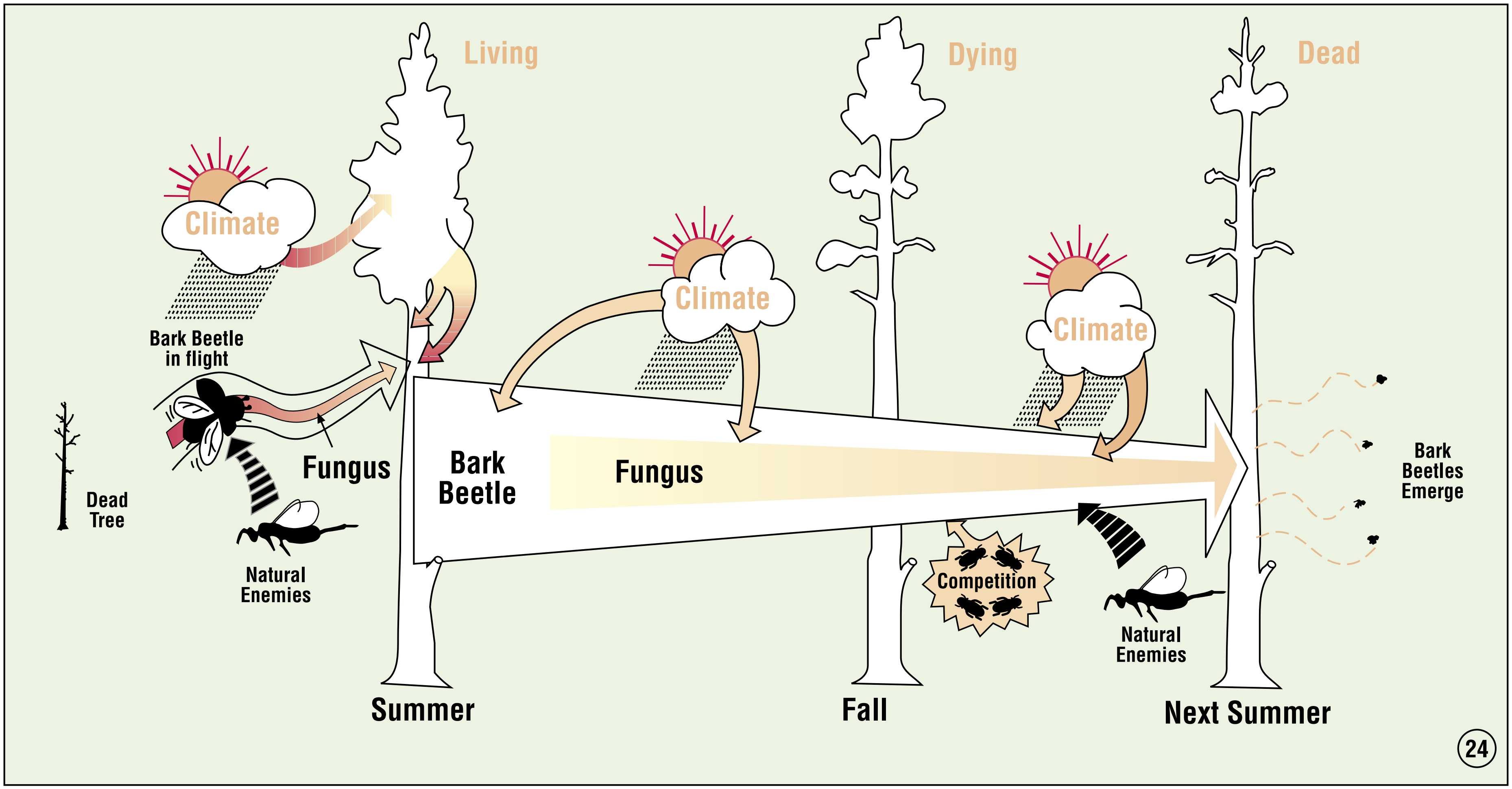


Fig. 24. Diagram of the interaction between the tree, the beetle and its associated fungi.

38°C (100°F) for prolonged periods will cause death of all stages, but the critical temperature with short exposure is above 43.3°C (110°F) (16). Such subcortical temperatures seldom occur in infested standing trees even at low elevations in the south and central interior of B.C. (18).

Beetle flight occurs when temperatures are between 19.4 and 43.3°C (67-110°F) (14). Temperatures exceeding the upper limit are rarely recorded within the range of the beetle in Canada. At high elevations and in the northern and north-western part of the beetle's distribution, maximum daily temperatures often fail to reach the lower threshold of flight during summer, thus protracting the flight period and substantially increasing adult mortality beyond the estimated 30-50% (8).

In unseasonally warm years in southern B.C., female beetles may establish two broods each in separate trees. Survival of brood from the first flight is generally low; many larvae die because trees die and dry rapidly; the remaining insects go into winter as pupae and young adults and thereby suffer heavy mortality. Survival of brood from the second flight is better because the survivors overwinter as larvae, the most cold resistant stage (20). The most favorable weather for the insect is a moderately warm fall, a mild winter, and moderate weather the ensuing spring and early summer, followed by a period of hot, dry weather in July and August (21). Therefore, an index of climatic outbreak chance and a map of outbreak hazard (Fig. 20) were constructed, based upon specific climatic factors affecting beetle survival and development (30).

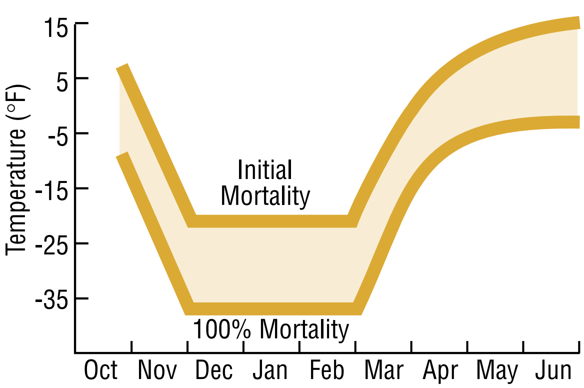


Fig. 25. Tolerance limits of larvae to 2.5 hours exposure to low temperatures (40).

Competition, predation, parasitism and disease

Spatial arrangement and density of attacks on the tree are related to thickness and roughness of bark (32), pheromone production (17), host resistance (21), host availability and size of the beetle population (29). Attack density affects gallery length, eggs per gallery and brood survival (7). Optimum brood production per unit bark area, on the average, is between 75-85 attacks per square meter (7-8 ft^2) or 2450-2880 centimeters of gallery per square meter (90-110 in/ft^2) (21) for lodgepole pine. However, the maximum brood production per female parent usually occurs at lower densities than this. Above about 96 attacks per square meter (9/ft^2) competition between larvae for food and space is sometimes great enough to prevent even replacement production of brood.

The role of predation, parasitism and disease in the population dynamics of the mountain pine beetle is not well known. In theory, each factor may regulate low populations (15), but they may also act to prolong outbreaks (27), e.g. by reducing competition. Woodpeckers and a number of predacious and parasitic insects contribute to the regulation of low populations of mountain pine beetle. Woodpecker predation is proportionately greater on low beetle populations than high populations. The effectiveness of woodpeckers is greatest when brood densities in a tree are high, regardless of the size of the beetle population. Of the insects, larvae of a fly (*Medetera aldrichii* Wheeler) and larvae and adult clerid beetles (*Enoclerus sphegeus* F.) are the most common predators; the larvae of a species of wasp (*Coeloides dendroctoni* Cushman) is the most common parasite. *M. aldrichii* larva feed on eggs, larvae and pupae of the mountain pine beetle. This predator is most numerous on the north side (21) and in the lower 50-180 cm (2-6 ft) of the bole (L.S. unpublished) in lodgepole pine. Even though they eat several immature insects (31), their effectiveness in regulating mountain pine beetle populations is not established. Adult clerid beetles (*E. sphageus*) prey on adult mountain pine beetles as they attack trees but generally consume only a small fraction of the population. Larval densities of the clerid are greatest in the north aspect (21) and in the lower 150 cm (5 ft) (L.S. unpublished) of lodgepole pine stems. Each clerid larva may consume up to 40 mountain pine beetle larvae (2). Parasitism by *C. dendroctoni* is greatest in thin barked trees on the north and east aspects of the stem. Thirty to 95% of the parasite brood overwinters and attacks the mature larvae in the spring (21). Nematodes cause adult and egg mortality and reduce the dispersive capacity and fecundity of female beetles (19). Occasionally, high beetle mortality may be caused by disease (15).

Relation between associated fungi and the mountain pine beetle

Microorganisms are intimately associated with many insects and it is known that bark beetles live beneficially with certain fungi (9). There are four fungi consistently present with the mountain pine beetle (26); two grow in phloem and the other two, the blue stain fungi, grow chiefly in the sapwood. Spores of these fungi are carried on the surface of beetles and in a specialized repository that empties through the mouth (39). The fungi are inoculated into the tree as spores slough off the beetles and by the chewing action of the beetles as they mine their gallery. In suitable trees, the spores germinate within a few hours and the mycelium starts to grow on the sides of the gallery; fungi are further dispersed by the movements of beetles in their galleries. The blue stain fungi penetrate ray and other living cells in both phloem and sapwood, thus spreading vertically and radially. The spread of fungi around the tree is due to larval mining. If fungi successfully colonize the living cells, they kill the tree and this prevents the formation of wound response substances (24). These substances, if produced, prevent beetle eggs from hatching (21) and prevent the continued growth of fungi (34). Fungal fruiting bodies line the pupal chambers (37) and the newly formed adults need to feed on this to complete their maturation (H.S.W. unpublished). The associated fungi are transmitted by these new beetles to living trees; this is ensured by the specialized mouth parts of the beetles and by surface contamination of beetles with masses of sticky fungal spores (38).

Effect of the tree on brood production

In killed lodgepole pines, the number of beetles that attacked is related to the size of the tree, as is the number of beetles emerging the following summer. Trees smaller than 12.5 cm (5 inch) in diameter are rarely attacked (Fig. 21). Trees less than 20.3 cm (8 inch) in diameter, if attacked, often survive (11). Above 12.5 cm (5 inch) in diameter, the number of beetle attacks on a tree increases as the diameter increases. Larger diameter trees are generally infested to greater heights on the stem than are smaller diameter trees (28). Regardless of diameter, the greatest density of attacks occurs in about the lower 1.83 m (6 ft) of the stem; above this zone, there is a gradual decrease in density of attacks with increasing height up the tree. This distribution of attacks occurs because beetles need a niche in the bark from which to bore an entrance hole; bark niches are more numerous near the base of the stem (32). Beetles also require total bark thickness greater than 1.5 mm (1/16 inch) before they can establish a gallery, and bark is thickest near the base of the stem. This places an upper limit on the height to which a stem can be attacked (29).

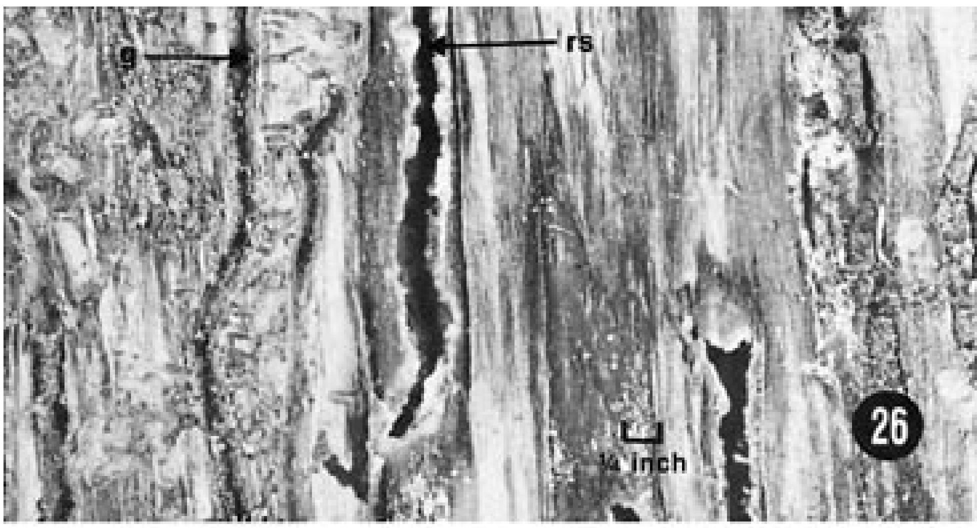
On the average, more beetles attack than emerge from any tree less than 25.4 cm (10 inch) in diameter. From trees greater than 25.4 cm (10 inch) in diameter, more beetles emerge than attack. The ratio of emerging to attacking beetles increases with increasing tree diameter (Fig. 22). There are two critical factors that determine the number of beetles produced by a successfully attacked tree. First is the nutritional capacity of the tree. Trees with thick phloem (3) and a large crown volume (28) produce the greatest number of beetles. Second, the moisture content of the stem during the entire period that insects are beneath the bark also affects brood production and emergence (21). There is an optimum rate for the infested stem to dry that ensures enough moisture for insects to complete their life cycle and emerge the summer after infestation.

Not all trees can be colonized by the beetles and their associated fungi. Trees respond to attack with an initial flow of liquid resin from severed resin ducts. Living cells next to the wound start to produce additional liquid resin and other substances normally present only in the heartwood; this is accelerated by the blue stain fungi (24). These substances are not food for beetles and fungi, and even inhibit the growth of the latter. A pliable, white "pitch tube" forms around the place where the beetle bored through the bark, and the phloem and sapwood next to the wound become impregnated with resinous substances (Fig. 26). Cells die slowly as these compounds accumulate. About 2 years after attack, this zone of dead sapwood has extended toward the centre of the tree and is continuous with, and indistinguishable from, the heartwood (Fig. 27). The pitch tube, if still present, is now yellow, hardened and shrunken. In lodgepole pine, the cambium seldom reunites over the wound and thus the trunk often assumes a fluted appearance. Sometimes a pitch pocket is formed at the original wood surface as new tissues grow over the wounded area. Trees able to prevent beetles and fungi from colonizing the stem tissues are termed "resistant". Other trees show almost no response to attack and are rapidly colonized;

such trees are termed “intermediate” (24). Trees with all grades of response have been observed, but the number in each category varies in time and space.

The tree response is a process of living cells and fluctuates with the cyclical behaviour of the tree itself. For example, there is a general rise and fall in the proportion of resistant stems throughout the growing season (23) and with advancing age of the trees (Fig. 28) (33). Competition from other species, including pine, may also affect the tree response. We have observed that outbreaks of mountain pine beetle in lodgepole pine often happen when a period of below-normal precipitation occurs in the summer preceding or in the spring before an outbreak.

Resistant trees have better diameter growth and thicker phloem than the nonresistant ones (33). Such large diameter trees (6) with thick phloem (3), when successfully attacked, give the largest increase in new beetles; therefore, when the resistance of these trees declines, a significant increase in the beetle population is possible.



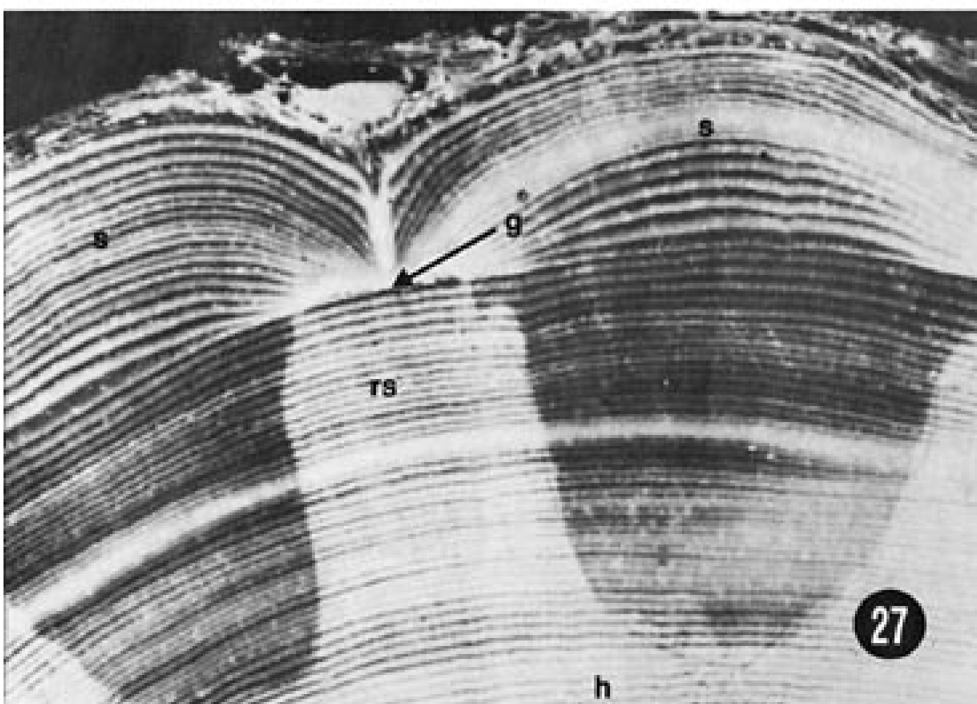


Fig. 26.Unsuccessful resin soaked mountain pine beetle galleries (rs) and successful galleries (g) in lodgepole pine.
Fig. 27. Resin impregnated sapwood (rs) behind the beetle gallery (g) becomes indistinguishable from heartwood (h) as sapwood (s) grows over the wound.

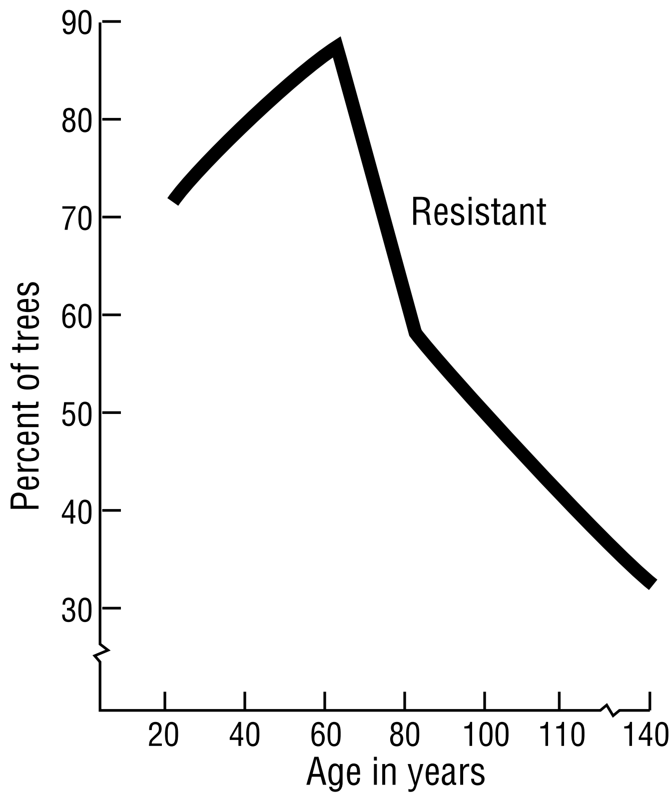


Fig. 28. Change in frequency of resistant lodgepole pines for different aged trees.

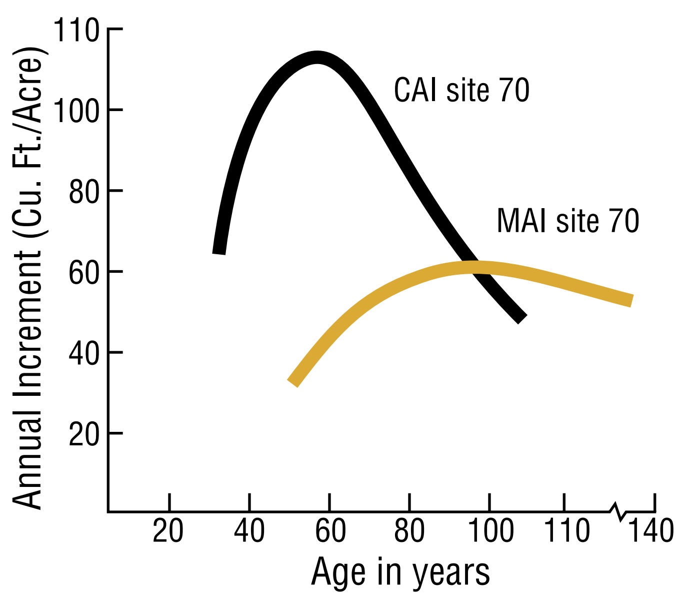


Fig. 29. Current and mean annual increment for lodgepole pine - site index 70.

When lodgepole pines received a sequence of inoculations with a blue stain fungus, some trees successfully resisted all inoculations, regardless of the inoculation density and number. Other trees resistant to the early inoculations were colonized by the fungus from later inoculations (D.M.S. and H.S.W. unpublished). Similarly, high populations of beetles can probably colonize trees that low numbers can not. Also, the seasonal synchronization of beetle flight during the period of decreasing tree response (23) will permit more trees to be colonized if an extended flight occurs. When the frequency of resistant trees in a stand is low, beetles probably have shorter distances to travel to locate a suitable tree, and losses during flight may be lessened.

Effect of the Beetle on Stand Dynamics

When trees of a given stand are grouped into diameter classes, the number killed in each class is proportional to the total pre-infestation basal area within that class (Fig. 30). As a beetle outbreak progresses through a lodgepole pine stand, the larger diameter stems are usually killed first (6). In general, the greater the number of trees above 10 inches in diameter, the greater the brood producing potential (Fig. 22), and thus the greater the likelihood of severe stand depletion. Considering the usual distribution of diameters in lodgepole pine stands, when the average stand diameter is greater than 20.3 cm (8 inches), it is estimated (30) that an increasing beetle population is possible (Fig. 22). Brood productivity tends to decline with increasing stand density (1). As a general rule, in southeastern B.C. and Banff National Park, for each inch increase in stand diameter over 6 inches, infestation intensity increased between 4 and 9% (Fig. 21). Thus, during an epidemic, the average diameter of the remaining stand will gradually decrease until the outbreak collapses (12).

Outbreaks have not been reported in stands younger than 60 years; they rarely occur between 60 and 80 years, but frequently occur in stands older than 90 (Pacific Forest Research Centre, Survey records). Resistance to attack is greatest between 40-60 years (Fig. 28) (33). This period closely corresponds to maximum current annual increment (Fig. 29) (36) and the culmination of basal area in fully stocked stands on any site (35). Resistance is low after about age 80. This coincides with the culmination of mean annual increment and an average stand diameter of 20-23 cm (8-9 inches) on most sites.

The extent, duration and intensity, and repeated occurrence of infestations are also governed by climatic factors. The most destructive outbreaks often develop during warm dry periods. Under these conditions, up to 90% of all trees may be destroyed over hundreds of square miles within 5-10 years (13). Under climatic conditions less favorable for the beetles, infestations develop less frequently and are of low intensity; however, they are persistent, as exemplified by the Babine Lake outbreak in northern B.C. that continued for some 18 years.

It has been observed that mixed stands are less prone to mountain pine beetle outbreaks than pure lodgepole pine stands (11). Once a stand has been infested, however, the presence of other species up to 36% of the stand had little effect on the depletion of lodgepole pine (4).

The mountain pine beetle is usually the first of a succession of insects to invade pines. A number of other phloem feeding insects and wood borers infest the trees after they have been killed or weakened by mountain pine beetles. For instance, high populations of *Ips* and *Pityogenes* often build up in trees killed by the mountain pine beetle. These secondary beetles rarely kill trees not previously attacked by mountain pine beetle. All of these insects perform the initial steps in decomposition of the trees (11).

After an infestation, the stand is mainly composed of trees in the intermediate and suppressed crown classes, with some slow growing dominants and codominants (25). Such trees have poor response to release (5). This selective killing of lodgepole pine

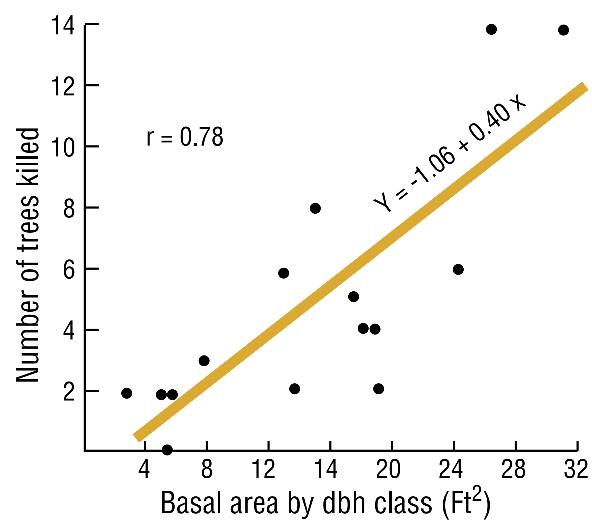


Fig. 30. Relation between number of trees killed and basal area by diameter class.

may lead to the selection of slower growing genotypes (25). Many standing and wind-thrown killed trees constitute a high fire hazard. Hopping (10) estimated from the Kootenay National Park infestation that 10% of dead trees had fallen 14 years after infestation. The rate of falling depends on a number of climatic, soil and stand factors. Beetle infestations develop repeatedly in some stands until most of the lodgepole pine is eliminated, and growth and establishment of other species may be enhanced by the openings created. At the lower elevations in the southern part of its range, lodgepole pine is succeeded by Douglas-fir and western larch, and in the north central part of British Columbia, by white spruce (Fig. 31) and alpine fir. At higher elevations, lodgepole pine is succeeded by Engelmann spruce and alpine fir. Exceptions are some rocky, dry sites where other species cannot get established (5). Such sites favor the perpetuation of lodgepole pine.

Fig. 31. Spruce regeneration following the destruction of a lodgepole pine stand by the mountain pine beetle.

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Acknowledgments

The information discussed herein results predominately from published and unpublished research in western North America during the last 70 years. Although few of the pioneers' names are mentioned in the bibliographies, the work of all contributors is gratefully acknowledged. In addition, our thanks are due to the following: British Columbia Forest Service, particularly J.R. Johnston and H.G. Bancroft, forester i/c management, forest rangers G.M. Cartwright and L.G. Taft, all of the Nelson forest district; National Parks Service of Canada, especially S. Kun, superintendent, Banff National Park; Alberta Forest Service; photographic, stenographic, editorial and biographics services, Canadian Forestry Service (NFRC, Edmonton and PFRC, Victoria), and to Forest Protection program managers R.W. Reid and D.R. Macdonald.

Special appreciation is extended to R. Jahren, PFRC, H.S. Gates and G.A. Kapaniuk, formerly PFRC, for analysis of meteorological data in developing the beetle outbreak hazard index and map.

Photo credits and illustrations; P.S. Debman, NFRC - Figs. 5, 6, 10, 14,15, 19, 26, 27 and 31; A. Craigmyle, PFRC - Figs. 7, 9, 15 and 17; R.W. Reid, NFRC - Figs. 8 and 16; R.D. Erickson, PFRC - Figs. 11 and 12; A. Dawson, PFRC - Fig. 18. Graphs, charts and general layout were done by J.C. Wiens, PFRC.

Finally, we thank E.D.A. Dyer, Drs. R.F. Shepherd and J.W.E. Harris, PFRC; Drs. G.D. Amman and W.E. Cole, U.S. Forest Service, Ogden, Utah; J.M. Finnis, B.C. Forest Service, Victoria, for their helpful criticism of the text. We, however, are solely responsible for any omissions and errors in interpretation.

Research on this subject was conducted while the authors were employed at the Northern Forest Research Centre, Edmonton, Alberta.