Integrated Control

of

Scolytid Bark Beetles

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Proceedings of the IUFRO Working Party
and XVII International Congress of Entomology Symposium,
"Integrated Control of Scolytid Bark Beetles"
Vancouver, B.C., Canada, July 4, 1988.

Technical Editor: Mary C. Holliman
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UNDERSTANDING SCOLYTID PROBLEMS IN LODGEPOLE PINE FORESTS: THE NEED FOR AN INTEGRATED APPROACH

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Abstract

Bark beetles (Coleoptera: Scolytidae) are the most serious insect threat to maintaining optimum productivity of lodgepole pine stands (Pinus contorta Dougl. var. latifolia Engelm.) because of their capacity to infest and kill trees within a single growing season. The most common species involved in the management of lodgepole pine forests throughout the Western United States and Canada are the mountain pine beetle (MPB) (Dendroctonus ponderosae Hopkins), the pine engraver beetle (Ips pini Say, Pityophthorus confertus Swaine, Pityogenes knechteli Swaine, Ips latidens LeConte), the lodgepole pine beetle (Dendroctonus murrayanae Hopkins), and the red turpentine beetle (D. valens LeConte).

At low population levels, MPB are difficult to locate. In unmanaged stands, these associated bark beetles infest small-diameter, suppressed and diseased trees or trees girdled by porcupines. The MPB infests only the basal 1 or 2 m of bole avoided by the associated species, but with phloem thick enough to support suboptimal MPB brood development. Measures of single-tree endemic MPB infestations to characterize lodgepole pine infested by these populations indicated many infested trees had roots infected by Armillaria mellea (Vahl. ex. Fr.), sensu lato. Additionally, fire-scarred lodgepole pine with advanced infections of Poria asiatica (Pilat) Overholts are also susceptible to attack by the MPB.

In single-tree MPB infestations, the upper bole is often infested first in May by one or more of the associated bark beetles, usually Ips pini, Pityophthorus confertus, or Pityogenes knechteli. The MPB follows this initial infestation in July, infesting the portion of the bole uninfested by these associates, usually the basal 1 to 2 m. The role of olfactory stimuli is unclear. These findings suggest that at this point in their population dynamics, endemic MPB populations benefit from concentrating in the basal portions of these trees. Infestation of host trees that are weakened by root and stem infection minimizes the likelihood of infesting trees with a higher degree of resistance in the form of resin exudation.

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If these factors governing the dynamics of endemic MPB populations prove to be the key elements involved in triggering MPB outbreaks, development of preventive strategies should be directed at scolytid populations within root and stem disease centers. Regardless of the strategies employed, to be successful it will be necessary to integrate knowledge of the dynamics of stand development from sapling through the pole stage with that of the associated scolytid complex.

Introduction

Bark beetles (Coleoptera: Scolytidae) are considered the most serious insect threat to maintaining optimum productivity of lodgepole pine stands (Pinus contorta Dougl. var. latifolia Engelm.) because of their capacity to infest and kill trees within a single growing season (Amman and Safranyik 1985). The seven most common species involved in the management of lodgepole pine forests throughout the Western United States and Canada are the mountain pine beetle (MPB) (Dendroctonus ponderosae Hopkins), the pine engraver beetle (Ips pini Say, Pityophthorus confertus Swaine, Pityogenes knechteli Swaine, Ips latidens LeConte), the lodgepole pine beetle (Dendroctonus murrayanae Hopkins), and the red turpentine beetle (D. valens LeConte).

Of these seven species, the mountain pine beetle causes the greatest threat to the productivity of lodgepole pine stands because it commonly kills most lodgepole pines 15.2 cm and larger diameter at breast height (d.b.h.) within a stand (McGregor et al. 1987; Amman and Cole 1983). The duration and severity of MPB outbreaks are influenced by weather, site, and stand and tree conditions (Amman and McGregor 1985). At the outbreak level, trees 15.2 cm or greater continue to be killed until stand or tree conditions are altered sufficiently to deprive the beetle of susceptible host trees (McGregor et al. 1987; Amman and Baker 1972).

Although methods exist for suppressing MPB infestations, including logging and application of insecticides, none are entirely suitable for suppressing outbreaks over the extensive areas currently infested in Western United States and Canada. Prevention of outbreaks is a more sensible approach to limit tree killing by bark beetles (Lorio 1984). Development of such strategies is dependent upon the identification and understanding of the interaction of factors that govern the dynamics of low or "endemic" level populations. Such populations are considered here as that level of abundance at which tree killing is well below a threshold considered "tolerable" to the land manager--usually single, widely scattered trees. Outbreak levels are those at which tree killing greatly exceeds tolerable levels and is characterized by groups of infested trees commonly totaling 150/ha.

A portion of the research devoted to the mountain pine beetle has been focused on the dynamics of low level MPB populations. Once factors responsible for allowing populations to reach outbreak levels have been identified, guidelines can be developed that provide land managers with alternatives for keeping tree killing at tolerable levels. Findings to date indicate that survival of low level MPB populations is affected by the population dynamics of several other species of bark beetles that commonly infest lodgepole pine. However, these species are often of lesser or secondary importance because they commonly infest diseased or injured trees or logging debris that have little merchantable value. Further, the influence of these other species on endemic MPB populations suggests that development of effective preventive strategies for the MPB will require the integration of knowledge of the interaction of factors affecting stand development from sapling through the pole stage. This paper reviews the knowledge of interactions between low level MPB populations, the associated scolytid complex, and stem diseases and root rots, with particular reference to factors that may contribute to the development of MPB outbreaks.

Researchers are locating infestations consisting of single lodgepole pines infested by the MPB, measuring site and tree conditions, and removing bark samples to assess factors affecting MPB survival. Although the documentation of factors affecting this population is slowed by the difficulty of locating single-tree infestations, several interactions and associations are evident.

Lodgepole Pine Bark Beetle Complex

Pityogenes knechteli Swaine, *Pityophthorus confertus* Swaine, and *Ips pini* Say are the most common associates of the MPB. They are frequently referred to as secondary bark beetles because they usually infest shaded limbs and saplings and small poles that are stagnated, have been injured by wind, snow, or lightning, or are dying from the effect of tree competition or root or stem diseases (Amman and Safranyik 1985; Furniss and Carolin 1977; Amman, Amman, and Amman 1974; Sartwell, Schmitz, and Buckhorn 1971; Reid 1957).

All three species have one to two generations per year in lodgepole pine, and parents may establish a second brood. Brood that reaches the adult stage before the onset of winter overwinters in the litter and stumps near the host tree. As a result, the emergence and initial flight of all three species take place prior to that of the mountain pine beetle (Amman and Safranyik 1985; Amman 1978; Reid 1957).

Another species in the complex infesting lodgepole pine, *Ips latidens* LeConte, is generally less abundant and infests trees weakened by other agents, including stem diseases and mechanical injury (Furniss and Carolin 1977). The remaining species in the complex, the lodgepole pine beetle (*D. murrayanae* Hopkins) and the red turpentine beetle (*D. valens* LeConte), are not considered aggressive and seldom kill standing green trees. They infest the base of the tree bole or freshly cut stumps, as evidenced by the large pitch tubes. At high attack densities, these beetles can weaken trees enough that the trees can be killed by other agents, including bark beetles (Amman and Safranyik 1985; Hall 1983).

The MPB is the most aggressive bark beetle infesting lodgepole pine. During the course of an outbreak, it may kill 90% of the large-diameter trees in a stand (McGregor et al. 1987). It usually has one generation per year, although 2 years may be required to complete its life cycle at higher elevations where temperatures are cooler. Emergence and flight generally take place in July and August, after peak emergence and flight of the associated species. When MPB are not sufficiently abundant to overcome the resistance healthy trees exhibit in the form of resin exudation, the attacking adults may be "pitched out" as they bore into the inner bark, or the resin may flood egg galleries and kill the eggs.

During the outbreak levels when the MPB is infesting large-diameter trees (>15.2 cm), P. knechteli, P. confertus, and I. Pini infest the tops and limbs of trees infested by the MPB. When the outbreak subsides and this material is no longer available, these species may kill some of the apparently healthy trees remaining (Evenden and Gibson 1940). Their observations also suggest that the first generation of P. knechteli infests the tops of trees killed by the MPB the previous year. The second generation infests the tops of trees newly attacked by the MPB. When newly attacked trees are scarce, as is the case during the endemic phase, they often infest green trees.

At very low population levels, MPB are difficult to locate. In unmanaged stands, these associated bark beetles infest small-diameter, suppressed and diseased trees or trees girdled by porcupines (Amman and Schmitz 1988). The MPB infests only the basal 1 or 2 m of bole avoided by the associated species, but with phloem thick enough to support suboptimal MPB brood development (Amman and Cole 1983). As these small-diameter trees die and comprise a progressively smaller component of a stand, the MPB frequently attacks the lower bole of larger diameter trees infected with advanced stem or root disease.

The principal factor controlling MPB brood survival and production in lodgepole pine is the quantity or thickness of the phloem tissue because it is the food of the developing larvae (Amman 1972, 1969). Phloem thickness is positively correlated with tree diameter (Amman 1969). In the laboratory, brood production ranged from an average of 23 MPB/930 cm^2 for phloem 1.27 mm thick to an average of 138 MPB/930 cm^2 for phloem 4.32 mm thick.

Interactions Among Bark Beetles and Tree Disease

Initial surveys in the Wasatch National Forest, Utah, to locate single-tree endemic infestations of MPB revealed more than half of such trees were infected with stem disease or at least one species of the associated bark beetles (table 1). Recently an effort was made to compare the degree of dwarf mistletoe (Arceuthobium americanun Nutl. ex. Engelm.) and comandra blister rust (Cronartium comandrae) PK infection among pairs of similar size lodgepole pine--one attacked by MPB and the other not--within the Shoshone and Sawtooth National Forests. Infestations at the time of these measurements consisted of scattered groups of three to four trees in the Shoshone Forest, whereas those on the Sawtooth consisted of a single group of 18 trees. Trees attacked by the MPB had, on the average, higher comandra blister rust ratings and were growing a little faster than the uninfested check tree ($P < 0.05$)

Table 1. Characteristics of single lodgepole pine infested by the MPB at four locations within the Wasatch National Forest, Utah

Study site	n	Comandra rust		Dwarf mistletoe		Associated bark beetles	
		No.	%	No.	%	No.	%
Lost Creek	14	8	57	13	92	10	71
Burnt Fork	15	8	53	6	40	9	60
Hoop Lake	5	5	100	--	--	4	80
Alturus Lake	14	9	64	14	100	8	57
Total	48	30	62	33	77	31	65

(Rasmussen 1987). Six of 18 MPB-attacked trees had comandra blister rust infection, while only one of the 18 unattacked trees was infested. Although the MPB showed no preference for trees infected with dwarf mistletoe, the infection does stimulate tree growth in the area of the infection that results in thicker phloem within the swollen area (Amman 1978). When MPB infests trees with dwarf mistletoe infection sites on the bole, these swellings with thicker phloem produce significantly more beetles per unit area than in the remainder of the tree. However, in trees with medium to heavy mistletoe infections in the crown, phloem is significantly thinner than in uninfected trees (Roe and Amman 1970). Analysis of the effect of dwarf mistletoe infection on outbreak level MPB populations revealed lodgepole pine stands with the least infection suffered the greatest tree killing because, on the average, trees in those stands had thicker phloem (McGregor 1978). The type of tree commonly infested by endemic MPB populations is shown in figure 1.

Although root pathogens have been implicated repeatedly as important biotic agents responsible for predisposing conifers to bark beetle attack, definitive evidence documenting the extent of their involvement has been difficult to obtain (Cobb et al. 1974). Understandably, the time and effort required to excavate root systems to document the incidence and severity of these rots have slowed efforts to gain a meaningful understanding of their role in the dynamics of bark beetle populations.

Armillaria mellea (Vahl. ex. Fr.) Kummer, sensu lato,[2/] infection causes butt rot, growth reduction, and perhaps eventual death of the infected tree (Morrison 1981). Some suspect that A. mellea is the most common root pathogen infecting lodgepole pine (Krebill 1975). In northern Idaho, this pathogen caused a high percentage of the rot in

[2/]Recent taxonomic and genetic studies have segregated several biological species in the Armillaria mellea complex (Wargo and Shaw 1985). Techniques for determining the biological species of diploid field isolates were not available when this study was completed.

FIG. 1. Lodgepole pine commonly infested by endemic MPB populations. Note dead top resulting from comandra blister rust canker and broomed branches indicating presence of dwarf mistletoe.

roots of western white pine (*Pinus monticola* Dougl.) but was not thought to increase the probability of attack by the mountain pine beetle (Ehrlich 1939). However, Kulhavy, Partridge, and Stark (1984) excavated entire root systems of white pine (*Pinus monticola* Dougl.) with explosives and found a strong association between the presence of *A. mellea* and MPB. They postulated that establishment of *A. mellea* is aided by infection from another pathogen, blister rust (*Cronartium ribicola* Fisch.), that girdles the bole, causing a decline in host condition.

Examination of 16 lodgepole pine stands in central Idaho revealed that, although *A. mellea* was occasionally present in root systems within the study area, none of the trees were infested with bark beetles, including the mountain pine beetle (Kulhavy, Partridge, and Stark 1978). These results were in keeping with an earlier study that found the incidence of root diseases and infestation by MPB did not show a strong correlation in mature stands of lodgepole pine (Partridge and Miller 1972). In contrast, investigation of an apparent association between fire-scarred lodgepole pine and the fungus *Poria asiatica* (Pilat) Overholts in Oregon revealed that trees with advanced stages of this disease were susceptible to attack by MPB (Gara et al. 1985; Geiszler et al. 1980).

Preliminary measures of single-tree endemic MPB infestations to characterize lodgepole pine infested by these populations indicated many infested trees had roots infected by *Armillaria mellea* (Vahl. ex. Fr.) Kummer, sensu lato, prompting a more systematic sample. A total of 42 trees were examined on 20 plots. Of 21 trees with visual indicators of parasitic *A. mellea* infection, 19 were infested by MPB, while only three of 21 trees with no visible *A. mellea* indicators were infested (table 2) (Tkacz and Schmitz 1986). The associations were significant at the $P < 0.05$ level. Statistical analysis of the association of comandra rust and dwarf mistletoe with *A. mellea* and MPB showed this association was not statistically significant.

In this preliminary survey, mature lodgepole pine infected with *A. mellea* were infested by endemic population levels of the mountain pine beetle with greater frequency than uninfected lodgepole pine. The results emphasize the need to determine the mechanism by which those host trees are located. Geiszler et al. (1980) found that during the first few years of an outbreak, more fire-scarred lodgepole pines than unscarred were killed by MPB. More recently, measures of MPB host-selection behavior showed that dispersing beetles preferentially select fire-scarred trees, primarily those infected by *P. asiatica* (Gara, Geiszler, and Littke 1984). In contrast, field experiments by Moeck, Wood, and Lindohl (1981) that were designed to determine whether pioneer beetles detect diseased hosts by olfaction, resulted in no significant difference in landing rates of the mountain pine beetle on ponderosa

Table 2. Contingency table comparing the number of trees infested by MPB with the presence of parasitic *Armillaria mellea* (AM) infection in a selected lodgepole pine stand, Wasatch National Forest, Utah, 1983 to 1984

	MPB infestation category			
A. mellea Incidence	Live (not infested)	Currently infested	Dead	Subtotal
AM present[1]	2	11	7	21
AM absent	18	1	2	21
Subtotal	20	12	10	42

Chi-square value = 24.73

[1]Presence determined by existence of external indicators of *A. mellea* mycelial fans on roots of host tree or by laboratory culture yielding *A. mellea* isolates.

pine infected with the root pathogen *Verticicladiella wageneri* Kendrick. In one instance on the Wasatch Forest in Utah, endemic MPB populations were attracted to a severely *A. mellea* (sensu lato)-infected lodgepole in such numbers that 26 lodgepole pines surrounding this tree were ultimately infested, although attack densities were below normal and some of these surrounding trees were unsuccessfully attacked (figure 2).

More recently, stand surveys have detected this association of *A. mellea* with endemic MPB populations in other lodgepole pine forests in Montana and Wyoming. Stand surveys conducted in the Wasatch Forest in Utah suggest a similar association exists between the associated bark beetles and *A. mellea*.[3]

FIG. 2. Lodgepole pine infested by endemic MPB populations. Note presence of mycelial mat (A) with adjacent MPB egg galleries (B).

[3] Nash, B. L., Schmitz, R. F., and Tkacz, B. M. 1987. Association of *Pityophthorus* spp; *Pityogenes* spp., and *Ips* spp. with lodgepole pine infected with *Armillaria* root rot in the Uinta Mountains, Utah. Unpublished Report, Intermountain Research Station, U.S. Department of Agriculture, Forest Service, Ogden, Utah. 3 pp.

Infested Tree Characteristics Common to Endemics

Blackman (1931) suggested when MPB populations infesting ponderosa pine (Pinus ponderosae Lawson) in the Black Hills killed three or fewer trees in a group, the population could be considered endemic or low level. In an attempt to determine whether the number of trees killed in a group was a measure of the aggressiveness of the population involved, he compared the growth rates of infested trees in group-kills composed of different numbers of trees with nearby uninfested trees. He found when group-kills had fewer than seven trees, their rates of growth were less than adjoining noninfested trees. In contrast, when groups contained more than seven trees, the growth rates of the infested trees were greater than nearby uninfested trees. An exploratory analysis of single, widely scattered lodgepole pines infested by the MPB suggested mean annual growth for the last 10 years and phloem thickness of infested trees were less than uninfested trees.[4/]

Initial evaluation of single-tree endemic MPB infestations within the Wasatch National Forest, Utah, confirmed that phloem thickness in these trees is generally too thin to support optimum beetle survival (table 3). In general, phloem thickness must be $\leq$2.5 mm before the number of progeny produced per unit area exceeds the number of attacking beetles (Amman and Cole 1983; Amman 1972). Attack densities in these endemic infestations are approximately a third of the density at which optimum survival is recorded. The number of emergence holes recorded per 930 m² is a fifth that expected at optimum survival rates (Amman and Cole 1983).

Table 3. Mean phloem thickness in single tree endemic MPB infestations in relation to attack and emergence densities for three sites, Wasatch National Forest, Utah.

Study site	n	Phloem thickness	Attacks	Emergence holes
		mm	Per 930 cm²	
Lost Creek	14	1.8	8.0	2.5
Burnt Fork	15	1.8	7.9	3.8
Poison Mountain	8	1.8	8.4	3.2

[4/] Lenhard, Gerald. 1980. Identification of selected characteristics of lodgepole pine trees useful in predicting the probability of attack by the mountain pine beetle. Unpublished Report. Intermountain Forest and Range Experiment Station, U.S. Department of Agriculture, Forest Service, Ogden, Utah. 10 p.

Role of Olfactory Stimuli in Endemics

During periods of low population levels of the MPB, scattered single trees are infested. If these populations are to survive and reproduce sufficiently to increase in number, it is essential they concentrate on suitable host trees. Observations of infestation patterns in single-tree MPB infestations reveal the upper bole is often infested first in May by one or more of the associated bark beetles, usually Ips pini, Pityophthorus confertus, or Pityogenes knechteli. The MPB follows this initial infestation in July and, at very low population densities, infests only the basal 1 to 2 m of the bole.

The fact these beetles coinhabit the same trees, although separated by different flight periods and portions in the tree bole, suggests they may share a common component in their pheromone bouquets or may respond to kairomones produced by the tree under attack in the form of monoterpenes in exuded resin. An alternative explanation is that pheromonal specificity is not the principal isolating mechanism among these sympatric species. Isolation of pheromone components of the mountain pine beetle has received greater attention than that for the associated bark beetles; nine volatiles released by female MPB feeding in lodgepole pine phloem have been isolated (Libbey, Ryker, and Yandell 1985).

More recent experimentation revealed that male D. ponderosae exposed to myrcene vapors produce large quantities of ipsdienol (Hunt et al. 1986). Ipsdienol is also the aggregation pheromone of the pine engraver, Ips pini (Birch et al. 1980; Lanier et al. 1980). Additionally, linalool, an isomer of ipsenol, is produced by male Ips pini. Production of ipsdienol by both D. ponderosae and I. pini suggests this component of the two pheromone bouquets may be used in interspecific communication.

Field tests in southwestern British Columbia revealed that attraction of D. ponderosae to an attractive lure composed of myrcene, trans-verbenol, and exo-brevicomin was significantly reduced with the addition of (±)- and sometimes (s)-(+)-ipsdienol (Hunt and Borden 1988). The authors suggest that a 97% (s)-(+)-ipsdienol produced in large quantities by male MPB may function as an antiaggregation pheromone, allowing males to contribute to the regulation of attack density, spacing, and termination of the attack on host trees. These tests also indicated that trans-verbenol or exo-brevicomin, both produced by MPB, may inhibit response of I. pini to (±)-ipsdienol, suggesting these pheromones may be functioning as repellent allomones to reduce interspecific competition (Hunt and Borden 1988). Myrcene may have a similar function in this geographic area.

Recent field tests in Utah of the same MPB lure composed of myrcene, trans-verbenol, and exo-brevicomin resulted in the response of I. pini tabulated below:

	MPB lure	MPB lure with verbenone	Verbenone alone	Unbaited trap
Ips pini	83	11	17	20

The response recorded in Utah would seem to suggest that at least a portion of the *I. pini* population in this area is not affected by the presence of *trans*-verbenol, *exo*-brevicomin, or myrcene.

The pheromone system of *I. latidens* has not been subject to isolation. However, field tests of synthetic pheromones for other bark beetles provide some idea of pheromones that have elicited response. The beetle has responded to isolated ipsenol and isolated ipsenol with synthetic *cis*-verbenol, but response was interrupted when isolated ipsdienol was added (Wood et al. 1967). In another test, it responded to (+)-ipsdienol, never to racemic or (-)-ipsdienol or to bolts containing male *I. pini* (Birch et al. 1980).

Discussion

Knowledge accumulated to date regarding the relationship of endemic MPB populations to associated scolytids suggests these associates play an important role in maintaining low level MPB populations and perhaps triggering outbreaks. During periods of low population levels of MPB, single scattered trees are infested. It is essential during these periods that enough MPB find a suitable host if the population is to survive. Infestation patterns in single trees reveal the upper bole is often infested first by one or more associated bark beetles, usually *Ips pini*, *Pityophthorus confertus*, or *Pityogenes knechteli*. The MPB frequently follows this initial attack and, at very low population densities, infests only the lower 1 to 2 m of the bole. These findings suggest that at this point in their population dynamics, endemic MPB populations benefit from concentrating in the basal portions of these trees. Infestation of host trees that are weakened by root and stem infection minimizes the likelihood of infesting trees with a higher degree of resistance in the form of resin exudation. Trees with high resistance might pitch out the few attacks per unit area that are typical of this population level, or flood the egg galleries, thereby killing the eggs and larvae.

At the same time, selection of these host trees limits brood productivity because of the thin phloem present in the basal 1 to 2 m of these trees. However, as these stands mature, fewer of these small-diameter diseased and suppressed trees with thin phloem remain in the understory. As a result, the probability increases that the surviving MPB populations will be attracted to larger diameter trees with phloem tissue that will support increased brood productivity.

If the factors governing the dynamics of endemic MPB populations discussed herein prove to be the key elements involved in triggering MPB outbreaks, development of preventive strategies should be directed at scolytid populations within root and stem disease centers. Regardless of the strategies employed, to be successful it will be necessary to integrate knowledge of the dynamics of stand development from sapling through the pole stage, with particular emphasis on the interaction of disease.

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Acknowledgments

Thanks are due John Schmid, Rocky Mountain Forest and Range Experiment Station, U.S. Department of Agriculture, Forest Service, Fort Collins, Colorado; Ken Gibson, Northern Region, Forest Service, Missoula, Montana; and Borys Tkacz, Intermountain Region, Forest Service, Ogden, Utah, for critical review of an earlier manuscript.