

THEORY AND PRACTICE OF MOUNTAIN PINE BEETLE MANAGEMENT IN LODGEPOLE PINE FORESTS

**Symposium Co-sponsored by: National Science Foundation
Washington State University
University of Idaho
USDA Forest Service**

**Held at Washington State University
Pullman, Washington
April 25-27, 1978**

**Proceedings Published by the Forest, Wildlife and Range Experiment Station,
University of Idaho, Moscow, in collaboration with:
USDA Forest Service, Forest Insect and Disease Research, Washington, D.C.,
and the Intermountain Forest and Range Experiment Station, Ogden, Utah.**

December 1978

**NOTE: BLANK PAGES HAVE BEEN REMOVED
TO CONSERVE MEMORY. I.E. 2, 6, 58, 59, 174...**

TABLE OF CONTENTS

PREFACE	xi
---------	----

ACKNOWLEDGMENTS	xii
-----------------	-----

INTRODUCTION

Ronald W. Stark	
The Mountain Pine Beetle Symposium Aspirations	3

The evolution of the symposium from a cooperative research project, an integrated pest management program involving the USDA Forest Service, the University of Idaho and Washington State University, is presented. The purpose of the symposium was to present a comprehensive state-of-the-art compendium on the current status of integrated management of the mountain pine beetle (*Dendroctonus ponderosae* Hopkins) for critical review by the users—forest managers. The aspiration of the contributors is to synthesize our current knowledge to provide a sound basis for implementation of management practices for regulation of destructive populations of the mountain pine beetle.

THE PROBLEM

Charles A. Wellner	
Management Problems Resulting from Mountain Pine Beetles in Lodgepole Pine Forests	9

Infestations of the mountain pine beetle (*Dendroctonus ponderosae* Hopkins), the most important natural factor in management of lodgepole pine (*Pinus contorta* Douglas var. *latifolia* Engelman) ecosystems, result in a number of management problems. These infestations seriously affect even flow and sustained yield and make the task of converting unmanaged to regulated forests very difficult. The result is chaos to orderly harvest. The beetles, rather than the manager, set priorities and schedule the cut. Infestations without the follow-up of fire or cutting, using an even-aged silvicultural system, hasten stands toward the climax stage in forest succession. Infestations may affect stand productivity. Too, access by big game, livestock and man may be affected. The effect on water quality and quantity is probably minimal. Infestations affect recreation and esthetics, build up high fire hazards, and may increase infections of dwarf mistletoe (*Arceuthobium americanum* Nuttall ex Engelman). Infestations create difficult utilization problems and cause special problems in areas closed to timber harvest. Because of the proclivity of the mountain pine beetle for large-diameter trees, management of lodgepole pine for timber production may face a disappointing future.

Randall M. Peterman	
The Ecological Role of the Mountain Pine Beetle in Lodgepole Pine Forests	16

Mountain pine beetle (*Dendroctonus ponderosae* Hopkins) is interpreted as a natural thinning and "harvesting" agent of lodgepole pine (*Pinus contorta* Douglas var. *latifolia* Engelman). In this capacity, the bark beetle creates fuel for the fires that are so important for the reproduction of its host tree. Furthermore, the action of the insect decreases the likelihood that dense, stagnant lodgepole pine stands will be produced in the next generation. This is because trees are "harvested" before too large a seed crop accumulates. The prevention of stagnant stands is not only of evolutionary significance to the host tree, but also of profound importance to forest managers because stagnant stands have little value for timber, wildlife or recreation. It is suggested, therefore, that in certain restricted situations we change our view of mountain pine beetle from "a pest" to "a management tool." Just as with the relatively new area of fire management, there will be some, but not all situations, in which it will be advantageous to permit *D. ponderosae* outbreaks to continue unhindered (such as in inaccessible stands or stands otherwise presently unimportant to managers). This will begin to break up the age distribution of lodgepole pine stands and at the same time help to meet management objectives by preventing stagnant offspring stands from developing. The uncertainties in this proposed use of mountain pine beetle are discussed.

The results of a project to prepare guidelines and prescribe treatment for infested lodgepole pine (*Pinus contorta* Douglas var. *latifolia* Engelmann) stands in the Umatilla and Wallowa-Whitman National Forests in northeastern Oregon are used to illustrate the potential impacts of a mountain pine beetle (*Dendroctonus ponderosae* Hopkins) outbreak on all forest resources. Resources considered are timber, fisheries and wildlife, water, soils, recreation and esthetic value. Guidelines to mitigate the effects on these were developed with respect to the treatment selected, a three-phase harvest program over a 21-year period. This management plan was selected over no action, a two-phase harvest program over a 14-year period, and a two-phase harvest program over a 22-year period as best meeting the overall management objectives.

CAUSES OF THE PROBLEM

Gene D. Amman

Biology, Ecology, and Causes of Outbreaks of the Mountain Pine Beetle in Lodgepole Pine Forests

39

The mountain pine beetle (*Dendroctonus ponderosae* Hopkins) typically produces one generation per year. The year begins with adults infesting trees and introducing blue-stain fungi into them in July and early August. Eggs are laid singly in niches on alternate sides of the vertical egg galleries. Larvae hatch and feed in the phloem, usually at right angles to the egg gallery. Larvae overwinter, then complete development in the spring. Pupation occurs in chambers made in the bark and outer sapwood. During endemic periods, beetles infest weakened and injured trees and those infested by other species of bark beetles. Epidemics appear to start when enough such trees are in proximity and emerging brood adults converge and infest a common tree or group of trees of medium to large diameter and medium to thick phloem. The beetle shows a strong preference for such trees, and its survival usually is best in them. Tree stress is not necessary for the start of epidemics. Stand characteristics associated with epidemics are 1) trees more than 80 years old, 2) average tree diameter more than 20 cm (8 inches), 3) a substantial number of trees in the stand with diameter at breast height of 30 cm (12 inches) or more and phloem 0.25 cm (0.10 inch) thick or more, and 4) stand site at an elevation where temperatures are optimum for brood development.

Homero Cabrera

Phloem Structure and Development in Lodgepole Pine

54

Thickness of phloem and presence of resin canals in lodgepole pine (*Pinus contorta* Douglas var. *latifolia* Engelmann) are important factors in the successful development of mountain pine beetle (*Dendroctonus ponderosae* Hopkins) broods. Thick phloem is closely related to tree vigor, and contains three components: phloem increment, phloem compression and phloem retention. Individual annual phloem increments make a relatively small contribution to total phloem thickness (usually less than 10%). Compression of old phloem tissue, resulting from increases in tree diameter, reduces the contribution of individual increments to phloem thickness to approximately half their original amount. Retention is the major factor affecting both the ultimate phloem thickness and the rate of change of phloem thickness. For the trees used in this study, the overall average period of phloem retention was 21.7 years, but for individual trees it may be in excess of 40 years in the lower bole. Resin canal density is a highly variable characteristic in lodgepole pine, but overall, densities are usually higher in the upper parts of the tree. Resin canal density may be a useful indicator of relative tree resistance to bark beetle attack; however, research on other pine species indicates that even short-term environmental stress may result in a substantial temporary reduction in resistance.

D. Malcolm Shrimpton

Resistance of Lodgepole Pine to Mountain Pine Beetle Infestation

64

This paper discusses the possible relationships between the mountain pine beetle (*Dendroctonus ponderosae* Hopkins) and the physiological processes of the lodgepole pine (*Pinus contorta* Douglas var. *latifolia* Engelmann) stem that act to heal wounds of the type caused by bark beetles. The resin canal system of lodgepole pine and production of secondary resins are described. The effects of moisture stress and the relationship of each resin system to maturation of the tree are also described. The interaction between tree response and the attacking beetle/blue-stain complex and the relationship between mountain pine beetle outbreak and physiological maturity of lodgepole pine are discussed.

The literature on the direct effects of climate and weather on the biology and dynamics of mountain pine beetle (*Dendroctonus ponderosae* Hopkins) populations is reviewed and discussed, with emphasis on the development of epidemics. Of the climatic effects, temperature is the most important. Typically, in the optimum range of the beetle's distribution on lodgepole pine (*Pinus contorta* Douglas var. *latifolia* Engelm.), there is enough heat accumulation each year to produce one or more generations and the frequency of adverse weather conditions is not high enough to prevent population build-up or to reduce infestations to endemic levels. In some years, however, adverse weather can cause a decline in population and damage levels, but this reversal is usually temporary and the course of outbreak is largely determined by factors other than climate. In this optimum habitat, the beetle poses a continuous threat to lodgepole pine of susceptible age and size. At high elevation and at northern latitudes, climate becomes the dominant factor controlling the distribution and abundance of mountain pine beetle populations and infestations in space and time. Beetle development is out of phase with the cold season; consequently, the least cold-hardy life stages (eggs, pupae) may enter the winter and suffer heavy mortality. Epidemics tend to be less frequent and intense, and stand depletion decreases, toward the limits of the distributional range. The northern limit of the beetle's range is bounded by the isotherm for -40°C (-40°F) mean annual minimum temperature and a zone where, on the average, heat accumulation during the growing season is less than the estimated minimum (833 degree-days C) for brood development on a 1-year cycle. The upper altitudinal limit, which ranges from about 750 m (2460 ft) near the northern limit (latitude 56°N) to about 3650 m (11,972 ft) near the southern limit (latitude 31°N), is probably delimited by similar temperature conditions.

INTEGRATION AND ANALYSIS

Walter E. Cole

Management Strategies for Preventing Mountain Pine Beetle Epidemics in Lodgepole Pine Stands: Based on Empirical Models 87

Empirical models have been prepared describing the interaction between mountain pine beetle (*Dendroctonus ponderosae* Hopkins) and lodgepole pine (*Pinus contorta* Douglas var. *latifolia* Engelm.). These models show the relationship between losses of lodgepole pine and survival of mountain pine beetle by life stages. Further, they identify stand characteristics conducive to mountain pine beetle epidemics and provide the basis for determining probabilities of infestation and resultant tree losses. This probability of infestation and tree loss can be determined for stands of varying diameter/phloem structure and can be further refined as additional information is gained. Harvesting techniques based on this probability can be applied strategically to prevent mountain pine beetle epidemics.

Alan A. Berryman

A Synoptic Model of the Lodgepole Pine/Mountain Pine Beetle Interaction and Its Potential Application in Forest Management 98

A simple graphical model is presented which displays the risk and intensity of mountain pine beetle (*Dendroctonus ponderosae* Hopkins)-caused timber mortality in terms of average stand phloem thickness, stand resistance to attack, and climate. The model provides a tool to help the forest manager understand the interaction between the beetle and the stand and, when fit to data from lodgepole pine (*Pinus contorta* Douglas var. *latifolia* Engelm.) stands, can be used to predict the likelihood of mountain pine beetle epidemics in real or simulated stands and to evaluate management alternatives.

Ronald L. Mahoney

Lodgepole Pine/Mountain Pine Beetle Risk Classification Methods and Their Application 106

Four mountain pine beetle (*Dendroctonus ponderosae* Hopkins)/lodgepole pine (*Pinus contorta* Douglas var. *latifolia* Engelm.) stand risk classification methods are tested. Their application to management is discussed. The 21 lodgepole pine test stands were located in central Idaho and western Montana. A combination of the methods tested provides improved predictions of mountain pine beetle infestations, a better understanding of host/beetle interactions, and practical alternatives for lodgepole pine/mountain pine beetle management.

Silvicultural planning requires reliable estimates of stand growth, species and tree size composition, and mortality levels. Mountain pine beetle (*Dendroctonus ponderosae* Hopkins) infestations are inherent events in the development of many lodgepole pine (*Pinus contorta* Douglas var. *latifolia* Engelman) stands. Therefore, tree mortality expected from future infestations must be considered when planning for the use of stands which may sustain appreciable beetle-caused mortality. The mountain pine beetle population dynamics simulation program (MPBMOD) has been coupled to a prognosis model for stand development (TREMOT). Together these models form a unified program (TREINS1) which can be used by forest managers and research workers to explore management alternatives designed to reduce beetle-caused losses of lodgepole pine. This paper describes how the information produced by TREINS1 can be used by timber managers. The program design, limitations, data requirements and operation are discussed.

SOLUTIONS TO THE PROBLEM

Douglas L. Parker

Detection and Evaluation Surveys for the Mountain Pine Beetle in Lodgepole Pine Forests

125

Detection and evaluation surveys are conducted by survey entomologists to gain information for advising resource managers on the need, feasibility and justification for control of damaging insect infestations. This evaluation process involves aerial and ground detection surveys and the following evaluation surveys: estimation of tree damage, determination of the relative abundance of the pest, and estimation of forest susceptibility. The survey techniques commonly used by survey entomologists to detect and evaluate mountain pine beetle (*Dendroctonus ponderosae* Hopkins) infestations are discussed.

Mark D. McGregor

Management of Mountain Pine Beetle in Lodgepole Pine Stands in the Rocky Mountain Area

129

Mountain pine beetle (*Dendroctonus ponderosae* Hopkins) is the primary bark beetle influencing management of lodgepole pine (*Pinus contorta* Douglas var. *latifolia* Engelman). Management by chemical treatment and by felling and burning of infested trees or salvage logging are rearguard techniques and do not prevent or reduce anticipated tree mortality. Methods are available for risk rating susceptible stands so management can be directed toward highest hazard stands. Characteristics such as slope, aspect, elevation, tree diameter, percent of lodgepole pine basal area with mistletoe infection, percent of lodgepole pine basal area in the stand and habitat type should be considered when risk rating stands. Suggested management strategies are discussed for areas designated for timber production, for individual trees of high value and for non-timber values.

Dennis M. Cole

Feasibility of Silvicultural Practices for Reducing Losses to the Mountain Pine Beetle in Lodgepole Pine Forests

140

A variety of standard silvicultural practices, and variations of them, have been proposed for reducing the losses caused by the mountain pine beetle (*Dendroctonus ponderosae* Hopkins) in lodgepole pine (*Pinus contorta* Douglas var. *latifolia* Engelman) forests. This paper outlines silvicultural practices deemed applicable for a variety of lodgepole pine stand descriptions and management situations; it also discusses factors that limit application and some consequences of misapplication. The necessity that silvicultural practices be compatible with the requirements of forest growth regulation and with management for other resource values is stressed, and an example is given of the role of silvicultural practices in an integrated long-range program for reducing losses.

William H. Klein

Strategies and Tactics for Reducing Losses in Lodgepole Pine to the Mountain Pine Beetle by Chemical and Mechanical Means

148

The mountain pine beetle (*Dendroctonus ponderosae* Hopkins), easily the most destructive bark beetle in the West, has ravaged the lodgepole pine (*Pinus contorta* Douglas var. *latifolia* Engelman) forests of the northern Rockies since the turn of the century. The progress of mountain pine

beetle epidemics in lodgepole pine is traced from a beginning in northern Montana in 1909 to full-scale outbreaks that progressed southward through the lodgepole pine forests of southern Idaho, western Wyoming and northern Utah. During the past two decades, the infestation pattern has reversed itself, with outbreaks recurring in parts of northern Utah, southern Idaho, western Wyoming, and back into Montana. Various control strategies employing a variety of methods, practically all of which entailed treatment of individual trees, were attempted, but at best only a few were touted as successful. The large-scale and costly control programs that were aimed at portions of large outbreaks and undertaken during the late 1950s and early 1960s in the Intermountain area failed to stop the infestations. During the 1970s, emphasis changed from individual tree control to individual tree protection. Methods are available for protecting high-value trees from beetle attacks, but they may be relatively costly and are impractical on a forest-wide basis. Individual tree treatment continues to be a management option, but a poor one. Long-lasting control can best be achieved by application of preventive techniques. In some instances, a do-nothing policy could be a viable alternative.

Harvey S. Whitney, Les Safranyik, S. John Muraro and E. David A. Dyer

In Defense of the Concept of Direct Control of Mountain Pine Beetle Populations in Lodgepole Pine: Some Modern Approaches 159

The strategy and tactics of direct control of the mountain pine beetle (*Dendroctonus ponderosae* Hopkins) are reviewed and the absolute requirement for detection of incipient infestations and diligence in treatment application is reiterated. Modern approaches to the use of explosives, the entomopathogenic fungus *Beauveria bassiana* (Balsam) Vuillemin, improvements in standing single tree burning, a mechanical debarker and microwave power are described. The current and future needs for direct control are discussed.

Gary B. Pitman, Mary W. Stock and Robert C. McKnight

Pheromone Application in Mountain Pine Beetle/Lodgepole Pine Management: Theory and Practice 165

This report reviews two uses of pheromones to effect bark beetle population changes, mass trapping and protection of susceptible host trees by disruption of host selection and colonization. A number of theoretical tactics using pheromones for suppression and protection of lodgepole pine against the mountain pine beetle (*Dendroctonus ponderosae* Hopkins) are discussed. From these tactics, application of the aggregative pheromone pondelure to high-risk trees scheduled for harvest is presently feasible. Current limitations to employing pheromones in mountain pine beetle/lodgepole pine (*Pinus contorta* Douglas var. *latifolia* Engelm.) management programs are attributed to large areas of undermanaged lodgepole pine, the high and extensive level of present mountain pine beetle epidemics, and the need for more research to identify and evaluate additional behavior regulators functioning in the pest's chemical communication system. Recent research, however, has clearly demonstrated the high potential for pheromone use in mountain pine beetle control programs.

NEW INFORMATION AND APPROACHES

David L. Kulhavy, Arthur D. Partridge and Ronald W. Stark

Mountain Pine Beetle and Disease Management in Lodgepole Pine Stands: Inseparable 177

Pest management strategies addressing only the mountain pine beetle (*Dendroctonus ponderosae* Hopkins) may lead to recurrence of mountain pine beetle, occurrence of associated insects and expansion of disease problems. The roles of diseased lodgepole pine (*Pinus contorta* Douglas var. *latifolia* Engelm.) and of lodgepole pine with flooded root zones acting as triggers of mountain pine and associated bark beetle population build-ups are presented. Silvicultural treatments for dwarf mistletoe, and to a lesser extent for the rusts and root disturbances, are presented in the context of mountain pine beetle management. We conclude that the forest manager must consider the consequences of any silvicultural prescriptions on diseases and insects.

Daniel R. Geiszler and Robert I. Gara

Mountain Pine Beetle Attack Dynamics in Lodgepole Pine 182

The "switching mechanism" by which mountain pine beetles (*Dendroctonus ponderosae* Hopkins) will kill lodgepole pine (*Pinus contorta* Douglas var. *murrayana* (Greville and Balfour) Engelm.) in groups during outbreaks was investigated. The agents causing beetles to switch from attacking a "focus" tree to attacking a "recipient" tree appear to be the sequential effects of aggregative and anti-aggregative pheromones. Analysis of the attack rates shows that recipient trees are initially attacked

more quickly than trees baited with *trans*-verbenol and α -pinene. Regression analysis shows that beetles select recipient trees on the basis of tree diameter and distance from the focus tree. Thinning prescriptions based on a tolerance interval about a regression line relating diameters of recipient trees to distance from the focus tree might be used to reduce beetle kill.

Donn B. Cahill

Cutting Strategies as Control Measures of the Mountain Pine Beetle in Lodgepole Pine in Colorado 188

Efforts to suppress mountain pine beetle (*Dendroctonus ponderosae* Hopkins) epidemics in Colorado have been carried out since the early 1900s using various methods of treating or removing beetle populations. These methods have slowed the rate of annual tree losses, but have done little to reduce total tree mortality over the course of an infestation, or to reduce the susceptibility of the stands to additional beetle attack. Based on recent research findings that demonstrated the importance of lodgepole pine (*Pinus contorta* Douglas var. *latifolia* Engelmann) phloem thickness and diameter in mountain pine beetle epidemics, stands in the Middle Park area of Colorado were cut using strategies to reduce stand susceptibility to beetle attack. Partial cutting and clearcutting, combined with the logging of infested trees, were used to reduce the inventory of larger-diameter trees. Other factors considered were dwarf mistletoe, comandra rust and visual management concerns. Losses in partial-cut areas have been reduced to 1 to 2 percent of the residual trees, whereas in unmanaged stands 39 percent of the trees have been lost.

Dennis R. Hamel

Results of Harvesting Strategies for Management of Mountain Pine Beetle Infestations in Lodgepole Pine on the Gallatin National Forest, Montana 192

Mountain pine beetle (*Dendroctonus ponderosae* Hopkins) epidemics in lodgepole pine (*Pinus contorta* Douglas var. *latifolia* Engelmann) are correlated with large-diameter, thick-phloemed trees, and decline of epidemics is associated with loss of these trees. Beetle brood production is directly correlated with phloem thickness, which is directly related to tree diameter. Probabilities of mountain pine beetle-caused losses to lodgepole pine can be developed from phloem thickness/tree diameter distribution data. Based on these probabilities, harvesting strategies were implemented in 1974 on the Gallatin National Forest to reduce average tree diameter and assess the effect on population build-up. Harvesting of four 16-ha (40-acre) blocks within heavily infested areas, based on diameter and phloem distributions, was completed in 1976. A 3-year post-harvest evaluation will determine the efficacy of this management alternative. Preliminary results indicate beetle population reductions in blocks harvested to 25- and 30-cm (10- and 12-inch) diameter limits, but population build-up in the block harvested to an 18-cm (7-inch) limit and in the block harvested on the basis of phloem thickness. Population build-ups were also noted in check blocks.

Mary W. Stock, Jerry D. Guenther and Gary B. Pitman

Implications of Genetic Differences between Mountain Pine Populations to Integrated Pest Management 197

Electrophoresis was used to evaluate genetic diversity among mountain pine beetle (*Dendroctonus ponderosae* Hopkins) populations in relation to geographic location and host trees. Populations attacking lodgepole pine (*Pinus contorta* Douglas var. *latifolia* Engelmann) in pure and mixed stands, western white pine (*P. monticola* Douglas) mixed with lodgepole *latifolia*, and lodgepole var. *murrayana* (Greville and Balfour) mixed with ponderosa pine (*P. ponderosa* Lawson) were examined. No genetic differences were detected among populations from stands of pure lodgepole var. *latifolia* or from *latifolia* mixed with ponderosa pine or white pine. In contrast, there was a larger degree of genetic difference observed between mountain pine beetles in lodgepole *murrayana* and all other populations. Further morphological, physiological and behavioral comparisons between mountain pine beetles in lodgepole *latifolia* and *murrayana* may reveal differences which contribute to variations in the insects' response to specific management practices, such as those employing pheromones.

ASSESSMENT OF RESEARCH AND APPLICATION

Maynard T. Rost

Comments on the Mountain Pine Beetle/Lodgepole Pine Symposium 205

The questions of what managers need from researchers and the extent to which this symposium met that need are discussed. The importance of preventive programs is emphasized. Ways in which managers can become more involved in solving the problem of mountain pine beetle (*Dendroctonus ponderosae* Hopkins) in lodgepole pine (*Pinus contorta* Douglas var. *latifolia* Engelmann) are suggested.

Walter R. Clark Theory and Practice of Mountain Pine Beetle Management in Lodgepole Pine Forests: A Comment	208
--	-----

William M. Ciesla The Mountain Pine Beetle/Lodgepole Pine Pest Management System: Opportunities for Putting New Knowledge into Practice	209
--	-----

Opportunities for putting new information on the management of mountain pine beetle (*Dendroctonus ponderosae* Hopkins) in lodgepole pine (*Pinus contorta* Douglas var. *latifolia* Engelmann) forests into practice are explored. These are addressed from the viewpoint of what is currently known about insect/host interrelationships, alternative pest management strategies and how they can be integrated with resource management objectives, economics and environmental constraints. In addition, an accelerated program of knowledge utilization efforts, including informal workshops, demonstrations, validation and documentation of mathematical models and greater involvement of potential users of this technology, is recommended for the final year of this research and development program.

APPENDIX I	213
-------------------	-----

APPENDIX II	217
--------------------	-----

PREFACE

The University of Idaho and Washington State University have been participants in the National Science Foundation-sponsored project, "The Principles, Strategies and Tactics of Pest Population Regulation and Control in Major Crop Ecosystems" (DEB 75-04223) since its inception. In collaboration with the Intermountain Forest and Range Experiment Station (USDA Forest Service), the objective was to develop integrated pest management strategies for the mountain pine beetle, *Dendroctonus ponderosae* Hopkins.

The final year of the NSF project seemed to be an appropriate time to determine the status of our knowledge and whether an integrated pest management system is feasible. Planning for this symposium began in 1976, and in 1978 the National Science Foundation awarded the University of Idaho a grant in support of it (DEB 77-21477). Publication of the

Proceedings was made possible by support from Forest Insect and Disease Research, Washington Office, USDA Forest Service and the Forest, Wildlife and Range Experiment Station, University of Idaho.

A somewhat unique feature of the symposium was the inclusion of an assessment of the success of the symposium (and the research efforts it represented) by individuals representing the ultimate users of integrated pest management systems. Their unedited comments are included.

While no "formula" is presented for integrated management of the mountain pine beetle, we believe that there now exists a systematic process for forest managers to incorporate into their planning and several options for operational trials to minimize the damage wrought by this forest insect.

A.A. Berryman
G.D. Amman
R. W. Stark

<i>Location of Participants</i>		<i>Affiliation</i>	
Montana	37	USDA Forest Service	65
Oregon	30	State/Prov. Forestry Agency	16
Idaho	18	Industry	15
British Columbia	14	Universities	10
Washington	13	Indian Tribal Councils	8
California	5	Bureau of Land Management	4
Utah	4	Bureau of Indian Affairs	4
Wyoming	4	USDA Combined Forest	
Louisiana	3	Pest Program	2
Colorado	2	Not Identified	9
North Carolina	1		
South Dakota	1		
Virginia	1		

ACKNOWLEDGMENTS

A symposium is only successful with the whole-hearted cooperation of the speakers and moderators, participants and support staff. We had such, in good measure, from the 39 speakers and moderators, 133 participants and the many support personnel. The former two are listed in the Appendix and to all our heartfelt thanks are due.

The arrangements and meetings were ably handled by David Baumgartner and his staff, Cooperative Extension, Washington State University.

The difficult task of assembling and editing the Symposium Proceedings was expertly done by Darline Kibbee and Susan Hieb, editors of the Forest, Wildlife and Range Experiment Station, University of Idaho.

Finally, the consistent interest and support of the National Science Foundation and the USDA Forest Service are gratefully acknowledged.

A.A. Berryman
G.D. Amman
R.W. Stark

INTRODUCTION

The Mountain Pine Beetle Symposium Aspirations

Ronald W. Stark

ABSTRACT

The evolution of the symposium from a cooperative research project, an integrated pest management program involving the USDA Forest Service, the University of Idaho and Washington State University, is presented. The purpose of the symposium was to present a comprehensive state-of-the-art compendium on the current status of integrated management of the mountain pine beetle (*Dendroctonus ponderosae* Hopkins) for critical review by the users—forest managers. The aspiration of the contributors is to synthesize our current knowledge to provide a sound basis for implementation of management practices for regulation of destructive populations of the mountain pine beetle.

INTRODUCTION

The University of Idaho and Washington State University are participants with the USDA Forest Service in a research program entitled, "The Principles, Strategies, and Tactics of Pest Population Regulation and Control in Major Crop Ecosystems," co-sponsored by the National Science Foundation (NSF) and the Environmental Protection Agency (EPA). This project began in 1972 and is administered by the University of California, Berkeley, under the leadership of Drs. C.B. Huffaker and R.F. Smith. The objectives of the project are to explore the underlying principles of pest management and to develop management systems for major crop ecosystems in the United States. The role of the mountain pine beetle group sub-project is to develop an integrated pest management (IPM) system for the mountain pine beetle (MPB - *Dendroctonus ponderosae* Hopkins) (Berryman 1975, Stark 1972). Emphasis has been placed on utilization of existing data rather than on original research. The latter has been supported only where obvious gaps existed. The IPM program terminates in March, 1979. The UI/WSU group has worked under a cooperative

agreement with the Intermountain Forest and Range Experiment Station, USDA Forest Service, whose researchers have been involved in MPB research for many years. These collaborators felt that 1978 was an appropriate year to review the accomplishments of the past 5 years, in the context of all current knowledge, from the viewpoint of the potential user—the forest manager public and private.

HISTORICAL BACKGROUND

An historical review of outbreaks since 1945 has recently been published (Crookson et al. 1977) and an excellent review of earlier outbreaks and control efforts over the past half-century is presented later in this symposium by Klein. I will confine my remarks to a brief overview of the research upon which our attempts to formulate an integrated pest management system for the mountain pine beetle are based.

Forest entomological research in the Pacific Northwest is less than 100 years old. Experiment stations at land grant universities were established by the Hatch Act in 1887 and most have developed research units in forestry. The USDA Forest Service began in 1881 as a Division of Forestry in the Department of Agriculture, and a full-fledged research branch was not established until 1911 (Daig 1976). Authorization for formal experiment stations was established by the McSweeney-McNary Act in 1928. Appropriations for the Southwestern Station were made in 1930 and for the Rocky Mountain Station in 1935. They were combined in 1953 as the Rocky Mountain Forest and Range Experiment Station at Fort Collins, Colorado (Price 1976). The Pacific Northwest Station was established (apparently prior to authorization as such) in 1925 and claims to have been the first experiment station to use computers (Daig 1976), in 1956. This demonstrates the youthfulness of the computer technology that now permits us to accomplish things our predecessors never dreamed of! The Forest Sciences Laboratory at Corvallis is only 18 years old.

During these early years, forest entomological and pathological research were in separate bureaus. It was not until 1953 that the Forest Insect Investigations Unit of the Bureau of Entomology and Plant Quarantine and the Forest Pathology Unit of the Bureau of Plant Industry, Soils and Agricultural Engineering were transferred to the Forest Service (Price 1976). Although there was considerable cooperation among the various groups concerned with forest problems, differences in approach and conflicts were inevitable. Therefore, forest protection research under one policy-making body is actually only 24 years old—a mere fledgling!

An historical account of the emerging structure of Forest Service and university research does not reflect the paucity of manpower in those formative years. The first “research” recorded on western bark beetles was by A.D. Hopkins, who at that time was the forest entomologist at the University of West Virginia. He became Chief of the Bureau of Entomology and Plant Quarantine in 1902 (Burke 1946). Until the 1920s the entire northwest forest entomological research group consisted of fewer than five people, who were responsible for all problems and all western states. Burke (1946) recounts an interesting anecdote about what may have been the first cooperative arrangement between the embryonic Forest Service and a university. About the turn of the century, the Chief of the Bureau of Forestry in the Philippines asked Gifford Pinchot, head of the Bureau of Forestry in the U.S., to get him a forest entomologist. Pinchot contacted A.D. Hopkins at the University of West Virginia, who informed him that none existed, but he would be glad to train one. He selected J.L. Webb (from Washington State University), who was at that time a field assistant in the Bureau working on the Black Hills beetle in South Dakota. Webb did not go to the Philippines, however, but stayed in the Pacific Northwest. The appointment of Webb stirred A.D. Howard, Chief of the Division of Entomology, to establish an Office of Forest Insect Research, thereby temporarily checking the development of a forest insect investigation unit in the Bureau of Forestry.

A cursory examination of the literature shows that the early years, circa 1900 to 1920, yielded primarily survey, taxonomic and general biological papers. As research facilities grew and problems persisted, detailed biological and ecological studies proliferated (1920-1950). The greatest expansion has been since World War II, with great strides made in population dynamics, biological and chemical control, quantitative techniques, forest management and computer technology.

As the resources for forestry and forest entomological research expanded, forest protection sciences emerged as specialized disciplines. As knowledge proliferated, these disciplines became more and more separated, until they became sufficient unto themselves. Broad disciplines such as entomology divided into specializations and a dichotomy appeared between “basic” and “applied” research. Emergence of these disciplines was understandable in these formative years, which persisted into the late 50s and early 60s. Paradoxically, the

original science, ecology, re-emerged about this time with a new aura of respectability and began the reunification of the forest sciences.

The products of research from slightly more than half a century have converged to provide the basis for integrated pest management (Stark 1977). One of the aspirations of this symposium is to unify and clarify our knowledge relevant to management of mountain pine beetle populations and thereby, hopefully, provide forest management with the information necessary to implement sound protection practices.

INTEGRATED PEST MANAGEMENT

Integrated pest management entails the management of populations of organisms that are capable of becoming pests; in forestry practice IPM is a part of resource or forest management (Stark 1977, 1978). It is a process in which all components and interactions of pest-host systems are studied, with a view to providing the resource manager with the information necessary for decision-making. The process includes the determination of the mechanics of the system, its societal values, its impact on all resources, and regulatory tactics and strategies that may be used and their probable effects on the pest and on related social values and ecosystems. Evaluation of the decisions implemented is the end of that process but the beginning of another—refinement of the total system model. Systems analysis is the most appropriate tool for the entire process (Stark and Gittins 1973).

The discipline of integrated pest management is still in its formative years and it is as yet unclear where the bulk of the “action” will take place. One feature of IPM is paramount: its activities are subordinate, but complementary, to resource or forest management. On the other hand, it is incumbent upon forest managers, public and private, to incorporate forest protection into their planning processes from the beginning (Brady 1978).

The total process is illustrated in Fig. 1. To the resource manager, the various components—insect population dynamics, treatment strategies, etc.—may exist only as “black boxes” providing him with various choices that he must fit into his overall policies and objectives. Hopefully, this symposium will provide the background for the resolution of procedures. The participating scientists will try, with their particular expertise, to address the problems of the manager, each contributing the latest information, which in total should provide us with information and recommendations concerning the lodgepole pine (*Pinus contorta* Douglas var. *latifolia* Engelman)/mountain pine beetle ecosystem. The management participants are expected to criticize and revise the conclusions and recommendations insofar as they relate to their particular management problems. The scientists present are not here to participate in an academic intellectual exercise, but to contribute to the development of a practical product, usable by forest managers. While the proceedings of this symposium have been reviewed by a management group, the views of those present are solicited and will be considered for inclusion as an addendum.

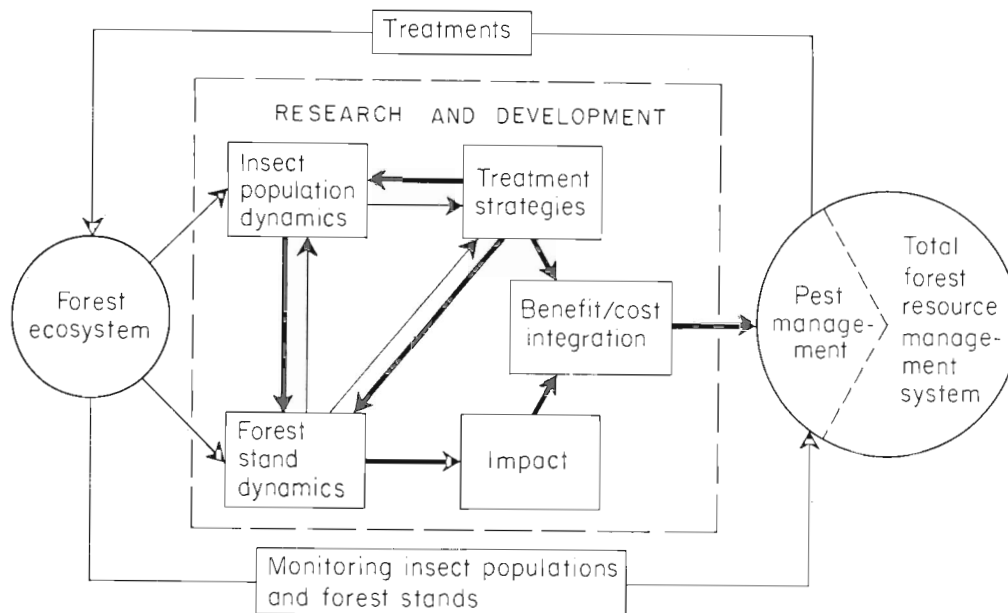


Fig. 1. Model structure of forest pest management system (Redrawn from: Integrated summary; Pine bark beetle subproject, NSF-EPA Project, Vol. 1, p. 145, U.C. Berkeley 1974).

It is inevitable that differences of opinion on the theoretical bases for control recommendations, on the control recommendations themselves and on the potential consequences of these if implemented, will occur. Our scientists, although cooperative, are not always in agreement on theory. This is to be expected and encouraged. The proof will be in the testing of **all** logical pest management systems to determine that one (or those) most suited to the particular situation.

It is obvious that the entire problem involved in the formulation of a control policy is very complicated and cannot be settled by merely laying down a few hard and fast rules as to when and where and under what conditions control work is to be recommended. Local conditions and values and quite often other considerations that are not entomological must largely determine the plans and strategies for each specific project. . . . The management of control operations must therefore vary according to local conditions within the area to be protected (Craighead et al. 1931).

With this reminder from the past that there is no single universal solution, let us begin the meat course. All contributors join me in asking your assistance in evaluation of the products of this symposium.

REFERENCES

- Berryman, A.A. 1975. Management of mountain pine beetle in lodgepole pine ecosystems: a cooperative interdisciplinary research and development project. Pages 627-650 in D. Baumgartner (ed.), *Management of lodgepole pine ecosystems*, Vol. 2. Washington State Univ. Coop. Ext. Serv., Pullman.
- Brady, J.L. 1978. Forest protection from a land manager's view. Pages 1-9 in V. Burlison (ed.) *Proc. Forest Protection Symposium*. March 15-16, 1977. Forest, Wildl. and Range Exp. Sta., Univ. of Idaho, Moscow.
- Burke, H.E. 1946. *My recollections of the first years in forest entomology*. USDA Bur. of Entomol. and Plant Quarantine, Berkeley, CA. 37 pp. (unpublished).
- Craighead, F.C., J.M. Miller, J.C. Evenden, and F.P. Keen. 1931. Control work against bark beetles in western forests and an appraisal of its results. *J. Forest.* 29:1001-1018.
- Crookston, N.L., R.W. Stark, and D.L. Adams. 1977. Outbreaks of mountain pine beetle in northwestern lodgepole pine forests—1945 to 1975. *Forest, Wildl. and Range Exp. Sta. Bull. No. 22*. Univ. of Idaho, Moscow. 7 pp + map.
- Daig, I. 1976. *Early forestry research: a history of the Pacific Northwest Forest and Range Experiment Station, 1925-1975*. USDA Forest Serv., Portland, OR. 32 pp.
- Price, R. 1976. *History of forest service research in the central and southern Rocky Mountain region, 1908-1975*. Gen. Tech. Rep. RM-27. USDA Forest Service, Ft. Collins, CO. 100 pp.
- Stark, R.W. 1972. The systems approach to insect pest management—a developing programme in the United States of America: the pine bark beetles. Pages 265-273 in P.W. Geier et al. (eds.) *Insect studies in population management*, Vol. 1. Ecol. Soc. Australia Memoirs.
- . 1977. Integrated pest management in forest practice. *J. Forest.* 75:251-254.
- . 1978. Forest protection from a scientist's viewpoint. Pages 9-14 in V. Burlison (ed.) *Forest Protection Symposium*. March 15-16, 1977. Forest, Wildl. and Range Exp. Sta., Univ. of Idaho, Moscow.
- Stark, R.W., and A.R. Gittins. 1973. *Pest management for the 21st century*. Natur. Resource Series No. 2. Idaho Research Foundation. Moscow. 102 pp.

THE PROBLEM

Management Problems Resulting from Mountain Pine Beetles in Lodgepole Pine Forests

Charles A. Wellner

ABSTRACT

Infestations of the mountain pine beetle (*Dendroctonus ponderosae* Hopkins), the most important natural factor in management of lodgepole pine (*Pinus contorta* Douglas var. *latifolia* Engelman) ecosystems, result in a number of management problems. These infestations seriously affect even flow and sustained yield and make the task of converting unmanaged to regulated forests very difficult. The result is chaos to orderly harvest. The beetles, rather than the manager, set priorities and schedule the cut. Infestations without the follow-up of fire or cutting, using an even-aged silvicultural system, hasten stands toward the climax stage in forest succession. Infestations may affect stand productivity. Too, access by big game, livestock and man may be affected. The effect on water quality and quantity is probably minimal. Infestations affect recreation and esthetics, build up high fire hazards, and may increase infections of dwarf mistletoe (*Arceuthobium americanum* Nuttall ex Engelman). Infestations create difficult utilization problems and cause special problems in areas closed to timber harvest. Because of the proclivity of the mountain pine beetle for large-diameter trees, management of lodgepole pine for timber production may face a disappointing future.

INTRODUCTION

Two hundred years ago the mountain pine beetle (*Dendroctonus ponderosae* Hopkins) carried out its natural role in the life history of lodgepole pine (*Pinus contorta* Douglas var. *latifolia* Engelman) forests without concern by anyone. It is only reasonable to believe, however, that Nez Perce, Flathead and Shoshone were frequently blocked or delayed in travels to and from buffalo country by large masses of down timber killed by the mountain pine beetle. A little more than

150 years ago, the Lewis and Clark expedition experienced severe difficulties from down timber when traveling from the Bitterroot Valley to the Clearwater country. For example, the journal (Coues 1965) for 12 September 1805, reads

The road had been very bad during the first part of the day, but the passage over the mountains, which was eight miles across, was very painful to the horses, as we were obliged to go over steep, stony ridges of hills and along hollows and ravines rendered more disagreeable by fallen timber, chiefly pine, spruce-pine, and fir.

I doubt that they recognized the possible contribution of the mountain pine beetle to the problem!

Significant difficulties of access caused by down timber were experienced by more and more white people as they penetrated the Rocky Mountains in search of furs, minerals, game and land. It is interesting that the many reports written by capable professionals at the turn of the century about the new forest reserves seldom mention forest insects as a cause of forest damage, yet these same reports show a great preoccupation—almost an obsession—with excessive damage resulting from man-caused fires.

It was not until well into the present century that the role of the mountain pine beetle in the lodgepole pine/beetle/fire cycle began to be recognized. Even Clements (1910) did not relate insects and fire, nor did Mason, in his outstanding bulletins (1915 a and b), suggest the relation of fire to heavy fuel loading caused by the mountain pine beetle. I would guess that in the northern Rocky Mountains it was the widespread and serious outbreaks of the mountain pine beetle in Montana and Idaho in the 1920s and early 1930s that really

focused attention on beetle-created fire-hazardous fuels (Flint 1924). Firefighters during these critical fire years fully realized the beetle/fire relation!

Although the possible devastating effects of the mountain pine beetle on timber supplies were recognized as early as 1912 and 1913 by those conducting control programs in the Big Hole Basin in Montana and on the Ochoco National Forest in Oregon (Mason 1915b), real concern was not expressed until lodgepole pine began to become a marketable species. This marketability has come about largely since World War II.

All of this suggests that the mountain pine beetle probably has been a normal, functioning part of lodgepole pine ecosystems almost as long as lodgepole pine has existed (Amman 1977). The mountain pine beetle has played a major role in shaping the destiny of lodgepole pine in many situations and a minor role in others. This beetle became a problem only when its activities began to conflict with land management objectives. These conflicts have increased steadily during the last 50 years until today the mountain pine beetle is a major problem in the management of lodgepole pine forests (Crookston et al. 1977).

Let us consider these management problems in greater detail.

PROBLEMS RESULTING FROM DISRUPTION OF PLANNED TIMBER MANAGEMENT PROGRAMS

Even Flow and Sustained Yield

Before discussing effects of the mountain pine beetle on even flow and sustained yield, recall that much lodgepole pine country is difficult to manage for timber products (Benson 1975, Schweitzer 1975). Lodgepole pine country usually contains many values in addition to timber, and all values must be taken into account in management. Although lodgepole pine is a high-quality timber tree, it is a small tree, often growing on rough terrain and in relatively low volumes per hectare. Consequently logging and processing costs are relatively high. Most lodgepole pine in the United States is in federal ownership. For these reasons, the timber industry and, especially, the forest products industries that can utilize small-diameter trees have been slow to show interest in much of the lodgepole pine country. At least some working circles have never reached the allowable cut of this species. Some have been able to sell their allowable cut of saw logs but few have been able to sell their allowable cut of round wood. Until round wood is merchantable in lodgepole pine country, effective timber management will be difficult.

Many of the lodgepole pine forests that suffered severe damage by the mountain pine beetle in recent years originated after extensive fires during a period of unprecedented burning in the last century. The large areas of relatively

even-aged, as well as multi-aged, mature lodgepole pine pose a severe management problem in scheduling even flow and sustained yield. Because of the uneven distribution of age classes, it is often necessary to hold large acreages of mature timber. The holding creates a requisite balance of age classes over time. In this way an even flow of timber products at a yield level indicated by volume and acreages in the working circle can be maintained. Because of repeated depredations by the mountain pine beetle, however, mature lodgepole pine forests are perishable and cannot be held for long periods. Lodgepole pine forests are neither stable nor long-lasting. Beetles disrupt even flow, and sustained yield management is difficult.

If the manager elects to harvest all of the mature lodgepole pine forests before loss to beetles, a period of cutting at a high level of output must inevitably be followed by a reduced cut over a much longer period. The result is undesirable effects on dependent timber industry and communities and perpetuation of a great imbalance in acreage of age classes. If the manager elects to hold mature stands in an attempt to develop balance of age classes for a regulated forest, large volumes of dead lodgepole pine and greatly reduced volumes per hectare may result.

Actually, in recent years, the managers of many forests have not had an alternative. The mountain pine beetle has swept through forest after forest, reducing volumes by one-third, one-half or even more. The problem is intensified by the beetle's proclivity for the largest trees in the stand. The manager has been faced with the twin problems of trying 1) to salvage dead trees while they are still merchantable and 2) to accelerate harvest of green trees before the trees are lost to the beetles. The manager is often thwarted by development costs greater than the timber can bear, environmental constraints that are hard to meet and residual volumes that are not economic to log. Recent experiences in such national forests as the Targhee (Klein 1976, Targhee N.F. 1974) and the Sawtooth (USDA Forest Service 1978, Sawtooth N.F. 1976) illustrate these problems. Without supplementary funds to build access roads, utilization of the lodgepole pine, dead or live, is often impossible. Considerations of sustained yield and even flow are obscured by the immediate problems of how to use dead timber and how to prevent additional losses.

In country economically marginal for timber production, the mountain pine beetle can so reduce volumes and growing stock that opportunities for timber production are severely affected, with consequent effects on allowable cut.

Orderly Harvest

Mountain pine beetle infestations in lodgepole pine create chaos in orderly timber management. The beetles, rather than the manager, set priorities and schedule the cut. If the working circle contains other forest types, planned harvesting in these is often reduced to shift the allowable cut for salvage of beetle-infested lodgepole pine.

Guidelines (Amman et al. 1977, Safranyik et al. 1974) of relative tree and especially stand susceptibility are proving of value (Hamel and Oakes 1977) in scheduling management actions to minimize beetle outbreaks and losses of timber and other resource values. It would appear that studies to 1) improve these guidelines, 2) develop better information on probability of attack for stands of various characteristics (Roe and Amman 1970) and 3) improve knowledge of what triggers epidemics require high priority.

Stand Productivity

Stand productivity is closely related to ecological consequences of the mountain pine beetle.

Pfister and Daubenmire (1975) recognized four successional roles for lodgepole pine:

1. **Minor seral.**—A component of young even-aged stands that will be replaced by shade-tolerant associates in 50 to 200 years.
2. **Dominant seral.**—The dominant cover type of even-aged stands having a vigorous understory of shade-tolerant species that will replace the lodgepole pine in 100 to 200 years.
3. **Persistent.**—The dominant cover type of even-aged stands that give little evidence of replacement by shade-tolerant species.
4. **Climax.**—The only tree species capable of growing on a particular environment—self-perpetuating.

The effects of the mountain pine beetle on timber productivity are somewhat different in these various situations.

The literature is replete with data showing that the mountain pine beetle infests and kills proportionately more large- than small-diameter trees (Cole and Amman 1969). The beetle attacks the trees of largest diameter each year of the infestation, until mostly small-diameter trees remain. The infestation then declines (Amman 1977). To the lodgepole pine component of the stand, this is a silvicultural catastrophe. The beetle thins from above, removes the most vigorous lodgepole pines, and leaves the poorest trees. The effect on productivity of the lodgepole pine component is poor growth of residual trees. Too, productivity is affected by additional mortality caused by sunscald, snow, windthrow or other causes. Recovery of the lodgepole pine is generally slow.

Where lodgepole pine is a minor seral component of the stand, the effect on total stand productivity may be relatively small, depending on the proportion of lodgepole pine in the stand. Other species in the stand replace lodgepole pine more rapidly than if the mountain pine beetle had not been active.

Where lodgepole pine is a dominant seral species the effect on productivity is more serious. Here the mountain pine beetle hastens the stand toward climax by releasing understory species such as Douglas-fir in some habitat types, grand fir, western hemlock or western redcedar in others, and subalpine fir or Engelmann spruce in still others. The immediate effect on productivity is the loss of lodgepole pine volume; long-range productivity may not be seriously impaired. Although other species often may not have the growth capacity of lodgepole pine over short rotations and may be more subject to heart rots, they respond much better than lodgepole pine to release. Several other species have capacity for greater size than lodgepole pine. Conversion to these species gives the advantage of developing a mosaic of stands of different species that should dampen future depredations by the mountain pine beetle.

It is in stands where lodgepole pine is persistent or climax, the latter two classes of Pfister and Daubenmire (1975), that the mountain pine beetle really plays havoc with productivity. Here other species are not present to make positive contributions to the silviculturally bleak residual stand of lodgepole pine made up of small-diameter, poor-vigor trees. Over time, some of the residual trees that survive develop a larger crown and accelerate growth; openings seed into regeneration; a multi-storied stand develops. Growth rates gradually improve. But this can only happen where dwarf mistletoe is absent. Where dwarf mistletoe is present, conditions are ideal for its development, with consequent serious effects on timber productivity.

PROBLEMS RESULTING FROM EFFECTS OF MOUNTAIN PINE BEETLE INFESTATIONS ON VALUES OTHER THAN TIMBER

Accessibility for Big Game and Livestock

Detailed studies of the effects of mountain pine beetle on all wildlife appear to be nonexistent; only knowledgeable guesses are offered (Leuschner and Newton 1974, Amman et al. 1977). The effect on wildlife in general is probably beneficial. The mountain pine beetle infestations certainly are detrimental to some species, but because infestations result in greater forest diversity, they should create a greater range of habitats favorable to more species of animal life (Berntsen 1975).

It would seem only reasonable that beetle infestations would improve forage for livestock (Basile 1975) and browse for big game to some extent. Use of range for forage and grazing depends, however, on the extent that down material from beetle infestation prevents access by livestock and big game to forage and browse.

The clearest expressions of the effects of the beetles on wildlife have to do with the problems of access and movement of big game and livestock resulting from the tangle of down, beetle-killed lodgepole pine that develops after a mountain pine beetle infestation. The seriousness of the problem depends on the quantity of trees killed per unit of land. Anyone who has had to get from here to there through a jungle of down, beetle-killed trees knows how difficult travel can be. You attempt to crawl through the down material, then give up and try moving over the top, 1.5 to 3 m above the ground, balanced from one slick tree trunk to the next. In the days of caulked boots this was almost fun. But today, after a couple of falls and skinned arms and legs, you end up cursing both the beetle and lodgepole pine.

Livestock (Basile 1975), and to a lesser extent big game, find travel difficult, too. In many stands it has been necessary to cut trails to provide livestock access to grazing lands.

From personal experience I know that moose do not like these situations. I once escaped from a big bull that was breathing down my neck by jumping into a jackstraw of beetle-killed lodgepole pines. We glared at each other through the tangle of down trees until the moose decided the quarry was not worth the effort!

Reliable information on the effect of down material on forest use by elk and deer is lacking. Lyon (1976) found that elk use in clearcuts diminished substantially when dead and down timber exceeded 0.5 m (1.7 ft) in height. It seems reasonable that deep accumulations of beetle-killed trees would impede travel of big game.

Down timber of lodgepole pine persists for long periods after trees have fallen. Case-hardened beetle-killed lodgepole pines often will last from 20 to 40 or more years (Brown 1975).

Water and Watersheds

The effect of the mountain pine beetle on water quality and quantity and the overall effect on watersheds are not known. The effects, probably, are minimal. To the extent that infestations open stands, they could increase water yields much the same as an infestation by the Engelmann spruce beetle did in the White River watershed in Colorado, where 25 years after the epidemic, annual water yields were still 10 percent greater than expected yields (Bethlahmy 1975). Locally, on sites with little ground cover, infestations may result in some erosion, but this is probably rare.

Roads to harvest beetle-killed timber are much more likely to affect water quality than the beetle infestation itself.

Esthetics

Landscape architects consider both overview appearance—that is, appearance of a forest from the outside—and close

views—appearance from inside (Litton 1975). Effects of the mountain pine beetle may be quite different from those two vantage points. The effect on overview appearance may be negligible or even beneficial. To the extent that beetle infestations introduce diversity in texture, color or form, such as by species composition changes or the color contrasts of dying and dead trees in a forest notable for its sameness, esthetic quality could be improved (Litton 1975, Murie 1966, White 1976).

At the height of the mountain pine beetle infestation in Grand Teton National Park, I stopped one day with my family at a vista point of the Teton Range. All I saw was the foreground of dead and dying lodgepole pines. My wife and children saw only the magnificent mountains and not one noticed anything amiss in the foreground.

The inside or close view effect of the beetle may be much different, depending on the extent of damage and the period of years after the killing of the lodgepole pine. Litton (1975) described interior characteristics as follows:

The visual characteristics of lodgepole pine stands at different stages of their lives are of either negative or positive value. Stand densities also influence the visual image. Pole stands, especially, if dense, are monotonous in their lack of variation. The super-densities of young or repressed lodgepole pine dog hair regeneration . . . act as repellent barriers. The old stand that breaks up with leaners and ground plane clutter of fallen trunks presents a chaotic scene. As deteriorating lodgepole pine is replaced by the regeneration of successional species, there is sign of returning visual order.

Recreation

Effects on recreation are varied and expressed mainly through effects on recreational facilities, access and scenic qualities.

Effects of the beetle on recreation probably have been most costly in damage to recreational facilities. Some campgrounds in lodgepole pine have had to be closed for campground rehabilitation.

The hazard of beetle-killed trees is of concern in all areas of intensive recreational use. The beetle infestations in national parks have created costly problems of tree removal in intensively used areas.

The beetle also has affected access to favorite recreational sites in many locations. Maintaining trails through beetle-killed stands is difficult and costly. With the great increase in numbers of backpackers, trail maintenance has become a problem of magnitude in wilderness, parks and all areas used for recreation.

Of course, scenic qualities come into direct play in recreational use.

PROBLEMS RESULTING FROM EFFECTS OF MOUNTAIN PINE BEETLE INFESTATIONS ON FIRE AND DWARF MISTLETOE

Fire

Brown (1975) published an excellent paper on fire cycles and community dynamics in lodgepole pine forests. Brown states:

One insect, the mountain pine beetle, overshadows all others as a cause of fuel build-up in lodgepole pine. Using yield table volumes and dbh-mortality relationships determined by Evenden and Gibson (1940) I calculated 60 to 90 tons per acre of beetle-killed boles on medium sites. The actual build-up on the ground of beetle-killed trees begins about 5 years after fire (Flint 1924) and proceeds for about 10 years.

The large increase in ground fuel and associated increase in the probability of large, high-intensity fires due to beetle epidemics suggests that the relationship among beetles, fire, and lodgepole pine tends to perpetuate lodgepole pine. The mountain pine beetle's strong preference for large trees gears heavy fuel build-up to a time when stands are mature or overmature. In some stands this is when climax species are developing prominence in the understory and together with the ground fuel present a high chance of crown fire. This situation operates against succession to climax stages.

The large acreages of even-aged lodgepole pine are standing evidence of the role that fire has played in the perpetuation of this species, a role that has long been recognized (Clements 1910, Mason 1915). The place of the mountain pine beetle in the lodgepole pine/beetle/fire cycle has been acknowledged often during the past 50 years (Flint 1924, Evenden and Gibson 1940, Evenden 1943, Roe and Amman 1970, Brown 1975, Amman 1977). In this period, increasingly effective fire control has largely pulled fire from the cycle.

Much has been written during the past 10 years about the effects of fire control on build-up of fuels. Some attention has been given to the effect of fire control in hastening stands of mixed species toward the climax stage in succession. This latter consequence of fire control is of equal or greater importance than fuel build-up. The condition is pervasive throughout much of the Rocky Mountain forested country. Only fire or even-aged systems of management effectively interrupt succession and favor intolerant species that usually are fast-growing and the most valuable for timber products.

In lodgepole pine forests, mountain pine beetle infestations, without the age-old follow-up of fire or cutting using even-aged silvicultural systems, speed forests on the way toward the climax stage.

Dwarf Mistletoe

Next to the mountain pine beetle, dwarf mistletoe is the most serious natural problem in the management of lodgepole pine. Although eight species of dwarf mistletoe are known to parasitize lodgepole pine, only one, *Arceuthobium americanum* Nuttall ex Engelmann, is of serious economic importance (Hawksworth 1975). Growth of *A. americanum* ranges from northern British Columbia and northern Alberta south to central Colorado and the Sierra Nevada of California. Furthermore, not only is it widely distributed; it is often abundant. This species is present in more than half the lodgepole pine in several areas (Hawksworth 1975).

According to Wicker and Leaphart (1974) and Hawksworth (1975), fire has been the primary limiting agent in spread of this disease. If fires are severe enough to kill large areas of infected trees, the parasite can be essentially eliminated from the stand except where occasional infected trees survive. Even-aged systems of silviculture, if carried out properly, can keep dwarf mistletoe in check just as effectively as severe fires.

The effect of mountain pine beetle infestations on dwarf mistletoe varies by stand condition. Where lodgepole pine is a minor seral species (Pfister and Daubenmire 1975), the effect of the beetle on dwarf mistletoe is minimal because lodgepole pine and any dwarf mistletoe it may harbor are rather rapidly eliminated from these stands in favor of more tolerant species.

Where lodgepole pine is a dominant seral species, opening of the stand by the mountain pine beetle will tend to increase and intensify dwarf mistletoe in the residual lodgepole pine stand. This can seriously retard growth of the stand and the growth of any lodgepole pine that may regenerate in openings. Ultimately the tolerant tree species replace lodgepole pine in these stands and dwarf mistletoe is eliminated as the lodgepole pine is replaced.

The most serious situations are where lodgepole pine is either persistent or climax. Here it is the only tree species and regeneration is also lodgepole pine. The effect of the mountain pine beetle in these stands is to increase dwarf mistletoe in both the residual stand and in regeneration that develops in openings. The result can be a badly diseased stand with tree growth reduced and eventual tree mortality caused by dwarf mistletoe.

OTHER PROBLEMS RESULTING FROM MOUNTAIN PINE BEETLE INFESTATION

Utilization

I have written about the problems of utilizing trees killed by the mountain pine beetle and green lodgepole pine susceptible to attack. Much lodgepole pine country is undeveloped, so access roads often are needed. Environmental constraints may be severe. Frequently, timber values, especially after a beetle infestation, are not great enough to warrant the building

of access roads. Mills to process the timber may be lacking, or if present, may not be suitable or of the right capacity to utilize the timber. Although the stud mill has been a great boon to the utilization of lodgepole pine, markets for small-diameter round wood and plants to process this material often are lacking in lodgepole pine country. Utilization of the great volumes of trees of small size, although improving, is generally a major problem.

Areas Closed to Timber Harvest

Infestations of the mountain pine beetle in lodgepole stands in areas such as parks, wilderness and other tracts where timber products are not an objective of management present a special situation. In these areas where lodgepole pine is seral, the effect of the mountain pine beetle is to speed succession to more tolerant species, gradually reducing or eliminating lodgepole pine. In forests where lodgepole pine is persistent or climax, the effect is to develop uneven-aged stands, often riddled with dwarf mistletoe. I have mentioned that fire and cutting using even-aged silvicultural systems are the only practical tools available at present to maintain lodgepole pine over large areas where it is seral, and prevent the intensification of dwarf mistletoe. In areas where cutting is not permitted, fire is the only management tool available. Even under the most ideal circumstances, fire is only a partial tool because man does not have the freedom to use it that nature had.

Saw Logs or Beetle Bait?

One of the most serious questions in the long-run management of lodgepole pine is "Will intensive management of lodgepole pine, including thinning, fertilization, genetic improvement of growth and elimination of dwarf mistletoe, to grow trees of a size that will make these management practices economically worthwhile result in simply growing beetle bait?" If management of lodgepole pine must be limited to growing trees of small size on most sites, to avoid depredations by the mountain pine beetle, then management is headed for future disappointment. Growing small-diameter trees in regions that have a surfeit of small trees does not appear to be rewarding. Markets for small-diameter round wood are improving, but growing, harvesting and processing this size wood is costly and the mountainous country where lodgepole pine is found is at a great economic disadvantage when compared with more favorable regions. Present information does not indicate a satisfactory solution to this problem. Land managers need to have the problem considered in depth and to have solutions furnished for a wide range of situations.

SUMMARY

I have reviewed a number of management problems resulting from mountain pine beetles in lodgepole pine forests. These are much the same as those problems recognized and

described by Berryman (1975) in outlining a socio-economic impact model. There are others. But these cited are sufficient to stress the point that developing integrated pest management systems (Stark 1977) for the mountain pine beetle as a part of resource management must take into account a wide array of ecological situations and management objectives. In the development of management strategies, the advice of Regional Forester Vern Hamre (1975) at the 1973 Symposium on Management of Lodgepole Pine Ecosystems applies: "Scientific and technical knowledge and application alone will not assure a sound program of management. The missing element is the public and its influence on multiple-use management programs."

QUESTIONS AND ANSWERS

- Q. Mountain pine beetle populations might spread from unmanaged susceptible stands in wilderness areas to infest adjacent managed stands which would not themselves support an epidemic. What can the forest manager do in such situations?
- A. Probably nothing at present. The Wilderness Act states, "... such measures may be taken as may be necessary in the control of fire, insects, and disease, subject to such conditions as the Secretary deems desirable." The general opposition of people to most insect control measures and the fact that there is no adequate control for the mountain pine beetle would seem to preclude control measures in wilderness at present.

REFERENCES

- Amman, G.D. 1977. The role of the mountain pine beetle in lodgepole pine ecosystems: Impact on succession. Pages 3-18 in *Proceedings in Life Sciences. The Role of Arthropods in Forest Ecosystems*. Springer-Verlag, Inc., New York.
- Amman, G.D., M.D. McGregor, D.B. Cahill, and W.H. Klein. 1977. Guidelines for reducing losses of lodgepole pine to the mountain pine beetle in unmanaged stands in the Rocky Mountains. USDA Forest Serv. Gen Tech. Rep. INT-36. Intermtn. Forest and Range Exp. Sta., Ogden, UT. 19 pp.
- Basile, J.V. 1975. Forage productivity in the lodgepole pine type. Pages 246-263 in D.M. Baumgartner (ed.). *Management of lodgepole pine ecosystems*. Washington State Univ. Coop. Ext. Serv., Pullman.
- Benson, R.E. 1975. Lodgepole pine products and utilization. Pages 602-613 in D.M. Baumgartner (ed.). *Management of lodgepole pine ecosystems*. Washington State Univ. Coop. Ext. Serv., Pullman.
- Berntsen, C.M. 1975. Management conflicts in lodgepole pine. Pages 503-515 in D.M. Baumgartner (ed.). *Management of lodgepole pine ecosystems*. Washington State Univ. Coop. Ext. Serv., Pullman.
- Berryman, A.A. 1975. Management of mountain pine beetle populations in lodgepole pine ecosystems: A cooperative, interdisciplinary research and development project. Pages 627-650 in D.M. Baumgartner (ed.). *Management of lodgepole pine ecosystems*. Washington State Univ. Coop. Ext. Serv., Pullman.

- Bethlahmy, N. 1975. A Colorado episode: Beetle epidemic, ghost forests, more streamflow. *Northwest Sci.* 49:95-105.
- Brown, J.K. 1975. Fire cycles and community dynamics in lodgepole pine forests. Pages 429-456 in D.M. Baumgartner (ed.). *Management of lodgepole pine ecosystems*. Washington State Univ. Coop. Ext. Serv., Pullman.
- Clements, F.E. 1910. The life history of lodgepole pine burn forests. *USDA Forest Serv. Bull.* No. 79. Washington, D.C. 56 pp.
- Cole, W.E., and G.D. Amman. 1969. Mountain pine beetle infestations in relation to lodgepole pine diameters. *USDA Forest Serv. Res. Note INT-95*. Intermtn. Forest and Range Exp. Sta., Ogden, UT. 7 pp.
- Coues, E. (ed.). 1965. History of the expedition under the command of Lewis and Clark, Vol. II. Dover Publications, Inc., New York. 820 pp.
- Crookston, N.L., R.W. Stark and D.L. Adams. 1977. Outbreaks of mountain pine beetle in lodgepole pine forests—1945 to 1975. *Forest, Wildl. and Range Exp. Sta. Bull.* No. 22. Univ. of Idaho, Moscow. 7 pp. + map.
- Evenden, J.C. 1943. The mountain pine beetle, an important enemy of western pines. *USDA Circ.* 664. Washington, D.C. 25 pp.
- Evenden, J.C., and A.L. Gibson. 1940. A destructive infestation in lodgepole pine stands by the mountain pine beetle. *J. Forest.* 38:271-275.
- Flint, H.R. 1924. Various aspects of the insect problem in the lodgepole pine region. *USDA Forest Serv., D-1 Appl. For. Notes* 54. Missoula, MT. 4 pp.
- Hamel, D.R., and R.D. Oakes. 1977. Evaluation of mountain pine beetle infestations, Lap, Cool, and Caribou Drainages, Yaak District, Kootenai National Forest—1976. *USDA Forest Serv., Northern Reg., State and Private Forest Rep.* 77-8. Missoula, MT. 7 pp.
- Hamre, V. 1975. Management for multiple use. Pages 651-657 in D.M. Baumgartner (ed.). *Management of lodgepole pine ecosystems*. Washington State Univ. Coop. Ext. Serv., Pullman.
- Hawksworth, F.G. 1975. Dwarf mistletoe and its role in lodgepole pine ecosystems. Pages 342-350 in D.M. Baumgartner (ed.), *Management of lodgepole pine ecosystems*. Washington State Univ. Coop. Ext. Serv., Pullman.
- Klein, W.H. 1976. Preliminary report of a survey to measure the impact of the mountain pine beetle in a lodgepole pine forest. *USDA Forest Serv., Intermtn. Reg. Rep.*, Ogden, UT. 7 pp.
- Leuschner, W.A., and C.M. Newton. 1974. Benefits of forest insect control. *Bull. Entomol. Soc. Amer.* 20:223-227.
- Litton, R.B., Jr. 1975. Aesthetic resources of the lodgepole pine forest. Pages 285-296 in D.M. Baumgartner (ed.). *Management of lodgepole pine ecosystems*. Washington State Univ. Coop. Ext. Serv., Pullman.
- Lyon, L.J. 1976. Elk use related to characteristics of clearcuts in western Montana. Pages 69-72 in J.M. Peek (chmn.). *Proc., Elk-Logging—Roads Symposium*. Forest, Wildl. and Range Exp. Sta., Univ. of Idaho, Moscow.
- Mason, D.T. 1915a. The life history of lodgepole pine in the Rocky Mountains. *USDA Forest Serv. Bull.* No. 154. Washington, D.C. 35 pp.
- . 1915b. Utilization and management of lodgepole pine in the Rocky Mountains. *USDA Forest Serv. Bull.* No. 234. Washington, D.C. 54 pp.
- Murie, A. 1966. Pesticide program in Grand Teton National Park. *National Parks Mag.* 1966 (June): 17-19.
- Pfister, R.D., and R. Daubenmire. 1975. Ecology of lodgepole pine, *Pinus contorta* Dougl. Pages 27-46 in D.M. Baumgartner (ed.). *Management of lodgepole pine ecosystems*. Washington State Univ. Coop. Ext. Serv., Pullman.
- Roe, A.L., and G.D. Amman. 1970. The mountain pine beetle in lodgepole pine forests. *USDA Forest Serv. Res. Pap.* INT-71. Intermtn. Forest and Range Exp. Sta., Ogden, UT. 23 pp.
- Safranyik, L., D.M. Shrimpton and H.S. Whitney. 1974. Management of lodgepole pine to reduce losses from the mountain pine beetle. *Can. Forest Serv. Forest. Tech. Rep.* 1. Pac. Forest Res. Centre, Victoria, B.C. 24 pp.
- Sawtooth National Forest. 1976. Cassia lodgepole: A management decision. *USDA Forest Serv., Sawtooth National Forest, Idaho.* 10 pp.
- Schweitzer, D.L. 1975. Economics of producing lodgepole pine stumpage. Pages 614-626 in D.M. Baumgartner (ed.). *Management of lodgepole pine ecosystems*. Washington State Univ. Coop. Ext. Serv., Pullman.
- Stark, R.W. 1977. Integrated pest management in forest practice. *J. Forest.* 75:251-254.
- Targhee National Forest. 1974. Targhee lodgepole: Tragedy or opportunity? *USDA Forest Serv., Targhee National Forest, Idaho.* 28 pp.
- USDA Forest Service. 1978. Biological evaluation, mountain pine beetle infestation, Cassia Division, Twin Falls Ranger District, Sawtooth National Forest, 1977. *USDA Forest Serv., Intermtn. Reg., Ogden, UT.* 4 pp.
- White, G.K. 1976. The impact of the pine beetle on recreational values. *Ph.D. diss., Washington State Univ., Pullman*, 87 pp.
- Wicker, E.F., and C.D. Leaphart. 1974. Fire and dwarf mistletoe (*Arceuthobium* sp.) relationships in the northern Rocky Mountains. Pages 279-298 in *Proc., Tall Timbers Fire Ecol. Conf.* No. 14 and Intermtn. Fire Res. Council Fire and Land Manage. Symp., Missoula, MT.

The Ecological Role of Mountain Pine Beetle in Lodgepole Pine Forests

Randall M. Peterman

ABSTRACT

Mountain pine beetle (*Dendroctonus ponderosae* Hopkins) is interpreted as a natural thinning and "harvesting" agent of lodgepole pine (*Pinus contorta* Douglas var. *latifolia* Engelm.). In this capacity, the bark beetle creates fuel for the fires that are so important for the reproduction of its host tree. Furthermore, the action of the insect decreases the likelihood that dense, stagnant lodgepole pine stands will be produced in the next generation. This is because trees are "harvested" before too large a seed crop accumulates. The prevention of stagnant stands is not only of evolutionary significance to the host tree, but also of profound importance to forest managers because stagnant stands have little value for timber, wildlife or recreation. It is suggested, therefore, that in certain restricted situations we change our view of mountain pine beetle from "a pest" to "a management tool." Just as with the relatively new area of fire management, there will be some, but **not all** situations, in which it will be advantageous to permit *D. ponderosae* outbreaks to continue unhindered (such as in inaccessible stands or stands otherwise presently unimportant to managers). This will begin to break up the age distribution of lodgepole pine stands and at the same time help to meet management objectives by preventing stagnant offspring stands from developing. The uncertainties in this proposed use of mountain pine beetle are discussed.

INTRODUCTION

This paper will discuss four topics: 1) the general behavior of mountain pine beetle (*Dendroctonus ponderosae* Hopkins) in lodgepole pine forests (*Pinus contorta* Douglas var. *latifolia* Engelm.), 2) the interpretation of this behavior in terms of the role mountain pine beetle plays in the dynamics of lodgepole forests, 3) the management implications derived from that role, and 4) recommended changes in management policy and research priorities.

MOUNTAIN PINE BEETLE BEHAVIOR

The general action of the bark beetle in lodgepole pine forests is fairly well understood. While generalizations are dangerous, especially given the variable characteristics of lodgepole pine, they are necessary in order to gain an overview. Further, generalizations are permissible as long as one determines how the conclusions drawn would differ when the exceptions to the rules are considered. The following brief review of mountain pine beetle behavior is drawn from several studies (Amman and Baker 1972; Berryman 1972, 1976; Cole and Amman 1969; Peterman 1977; Reid 1962a, b; Reid et al. 1967; Roe and Amman 1970; Safranyik et al. 1974, 1975). Adult mountain pine beetles disperse in the summer and attack mature, standing, vigorous and apparently healthy lodgepole pine trees. Insect galleries are bored through the bark and into the phloem and eggs are deposited along gallery walls. During this time, the host tree is also inoculated with blue-stain fungi, which are carried by adult beetles. These fungi, along with the mass attack behavior characteristic of *D. ponderosae*, help to decrease the effectiveness of the tree's resistance mechanism (resin production). If tree resistance is successfully overcome and if the phloem has appropriate thickness and moisture content, beetle larvae hatch and begin to dig their own galleries circumferentially through the phloem. The host tree is eventually killed by this girdling action of gallery construction and by the invasion of tree transport cells by the blue stain fungi. Tree death becomes apparent through foliage discoloration about 12 months after initial beetle attack.

The rate of build-up of mountain pine beetle populations is dependent upon attack densities, phloem thickness, tree resistance levels and climatic factors. In this sense, *D. ponderosae* populations are in part food-limited—successful brood production cannot be sustained for any length of time unless there are sufficient host trees of suitable quality. The

other source of population build-up, long-range dispersal, is relatively poorly understood.

Not all lodgepole pine trees are equally likely to be successfully attacked. Mature, large-diameter (and thick-phloem) trees receive most attacks in a given stand. Some trees within a given size and age class are able to resist beetle attacks by filling galleries with resin, thereby preventing larval and sometimes adult gallery construction. As trees become older than about 50 years, the proportion of trees in a particular stand able to resist beetles, if attacked, generally decreases with tree age. Unfortunately, we are presently unable to predict which trees in a stand will be non-resistant for a given attack density, but on a larger geographical scale, the hazard index of Safranyik et al. (1974, 1975) offers one way of assessing the chance that there will be a *D. ponderosae* outbreak.

In some areas, mountain pine beetle populations persist for many years in small pockets, doing damage to only a few trees in a stand. In other situations, *D. ponderosae* has exploded from an endemic state to outbreak conditions in about 5 years and these outbreaks have killed lodgepole pine over hundreds of thousands of acres. Outbreaks in even-aged stands of old trees of the same diameter class kill almost all trees, whereas mixed age stands lose mostly the larger trees.

Attempts to control mountain pine beetle populations through insecticides have in general not been successful in terms of saving trees (Amman and Baker 1972), but there are continuing efforts to develop other population suppression techniques, such as removing affected trees before beetles emerge, or use of pheromones.

ECOLOGICAL ROLE

Let us consider how these actions of mountain pine beetle affect the dynamics of lodgepole pine forests. Here, comments will be restricted to the most common cases, where lodgepole is in a "persistent" or "climax" role, as defined by Pfister and Daubenmire (1975). In an endemic state, the beetle serves as a natural thinning agent, killing some trees and opening up the stand (Graham 1963, Smithers 1962). This decreases the competition for light, water and nutrients among the remaining trees, which in turn results in an increase in growth. In areas where lodgepole pine releases seed annually (non-serotinous cones), the thinning action also permits establishment of lodgepole seedlings in the understory (Amman 1977). Being shade intolerant (Clements 1910, Fowells 1965), these seedlings will not grow well until the overstory is removed.

When mountain pine beetle is in an outbreak stage it acts as an efficient natural "harvesting" agent ("harvesting" in terms of killing and utilizing trees for reproduction, but leaving trees *in situ*). A large proportion of the large-diameter trees in a stand are killed within a few years, perhaps over thousands of acres if tree conditions are appropriate. The dead trees are a volatile fuel for lightning fires (Brown 1975), but from the

standpoint of lodgepole pine reproduction, such fires can be a benefit, for as is well known, lodgepole is a fire-maintained species (Armit 1966, Brown 1975, Smithers 1962). Seeds are stored in serotinous cones that open only above 45° C (113° F) (Clements 1910). However, not all lodgepole cones are serotinous; there are different proportions of these cones in different geographical locations and in trees of different ages (Lotan 1975). Just how the degree of cone serotiny affects the benefits of post-outbreak fires will be discussed later. In general, however, fires that occur in *P. contorta* stands tend to clear the soil of litter and competing species, prepare the soil for seed germination, and cause cones to release seeds (Brown 1975). Since lodgepole pine largely inhabits areas with dry summers and frequent lightning storms, naturally started fires occur with a high probability after a *D. ponderosae* outbreak (Armit 1966).

Mutch (1970) argues that many fire-adapted plant species have evolved to create highly flammable fuel sources. Perhaps mountain pine beetle is another mechanism which creates fuel (dead trees) that leads to fires, which in turn results in lodgepole pine reproduction.

When *D. ponderosae* is interpreted in this way as a natural thinning or "harvesting" agent that uses the host tree for its own reproduction while at the same time aiding the reproduction of its host, we are prompted to ask, "How much coevolution has gone on between the tree and the beetle?" Certainly mountain pine beetle is the largest source of insect-induced natural mortality on lodgepole pine (Amman 1975) and lodgepole is a major host of *D. ponderosae*, although other tree species are often attacked. It is believed by some authors that mountain pine beetle, a native to North America, has coexisted with lodgepole since the tree's earliest existence (Amman 1977, Roe and Amman 1970) and so the potential for strong coevolution has been great. There is evidence that other insect/plant relations have existed for millions of years (Opler 1973). There also are numerous examples of plant/animal interactions that have evolved to the point where plant reproduction is greatly influenced by associated specialized animals (e.g., Gilbert and Raven 1975, Smith 1970). In order to determine the ecological role of *D. ponderosae* and to examine this concept of coevolution more carefully, we need to review the characteristics of lodgepole reproduction. In doing so, we will also begin to get a glimpse of how the ecological role of mountain pine beetle affects our management outlook on that insect.

Lodgepole Reproduction

Cone production in lodgepole pine begins as early as 5 to 10 years of age (Crossley 1956, Latham 1965), and there may be anywhere from 25 to 40 seeds per cone (Armit 1966, Clements 1910, Bates 1930). Numbers of cones per tree increase with increasing crown size; therefore suppressed trees bear few cones (Baker 1950, Crossley 1956, Smithers 1962). In trees with serotinous cones, seeds are generally not released until the required high temperature is reached, and viable seeds

have been found in cones 75 years old (Mason 1915). Thus, old stands with only a relatively low percentage (say 20-40%) of serotinous cones can store a tremendous amount of seed, hundreds of thousands of seeds per acre (Lotan 1975). Fires can, of course, occur in lodgepole stands while trees are still alive, or after they have been killed by mountain pine beetles.

In this paper, we are largely concerned with the characteristics of the tree offspring generation and the effects of events in the parental generation. As illustrated in Fig. 1 for a site with average conditions, a small number of germinating seeds will produce a relatively open stand, whereas a large number of seeds will often result in an extremely dense stand, susceptible to growth stagnation (Smithers 1962). Of the North American tree species, lodgepole is the most likely to stagnate (Fowells 1965). We are all familiar with the consequences of such dense, or dog hair, lodgepole pine stands, e.g., little self-thinning as stands age, slow growth, rapid crown closure, and small tree crowns and boles—in short, trees that are not very useful to forest managers. The severity of this stagnation effect is demonstrated by examples such as that cited by Smithers (1962) where trees 90 years old were only 8.1 cm (3.2 inches) in diameter.

What processes affecting the parent stand lead to stagnation of *P. contorta* stands in the next generation? Unfortunately, we lack good field data on this question, because two pieces of information we need are missing, i.e., for a lodgepole pine stand that is presently stagnant, what was the age at which the parent stand was burned and what was its degree of

serotiny? But the lack of this kind of information need not stop us completely, for a cursory review of lodgepole reproductive characteristics points to an obvious mechanism which can lead to stagnation, i.e., the burning of a very old stand with a moderate to high proportion of cones that are serotinous. This is because cone production is closely related to crown size, which in turn increases with tree age in open stands. For example, Stand A in Fig. 2 is harvested either by man or mountain pine beetle and burned at 60 years of age, seeds are released and the next generation of trees begins to grow. When these offspring trees are, say, 70 years of age, they are relatively large and can yield considerable volume of wood. Stand B of Fig. 2 is nearby, has the same site conditions as Stand A, but is not harvested and burned until it is 100 years old. Forty more years of serotinous cone production have occurred, and when seeds are released during the fire, an extremely dense offspring generation is started which results in stagnation at an early age. At 70 years of age, these offspring trees yield far less volume of wood than the offspring of Stand A. While it is recognized that some seeds will be lost annually due to breaking off of limbs and cones, this loss will probably be a relatively small fraction of the total seed accumulation.

The validity of this hypothetical series of events depends upon the degree to which serotinous cones are produced in lodgepole pine stands. The higher the proportion of serotinous cones, the more likely it will be that stands harvested and burned at a given age will produce a stagnating stand in the next tree generation. The lower the degree of serotiny, the older the trees will have to become before they have produced enough serotinous cones to produce a stagnating off-

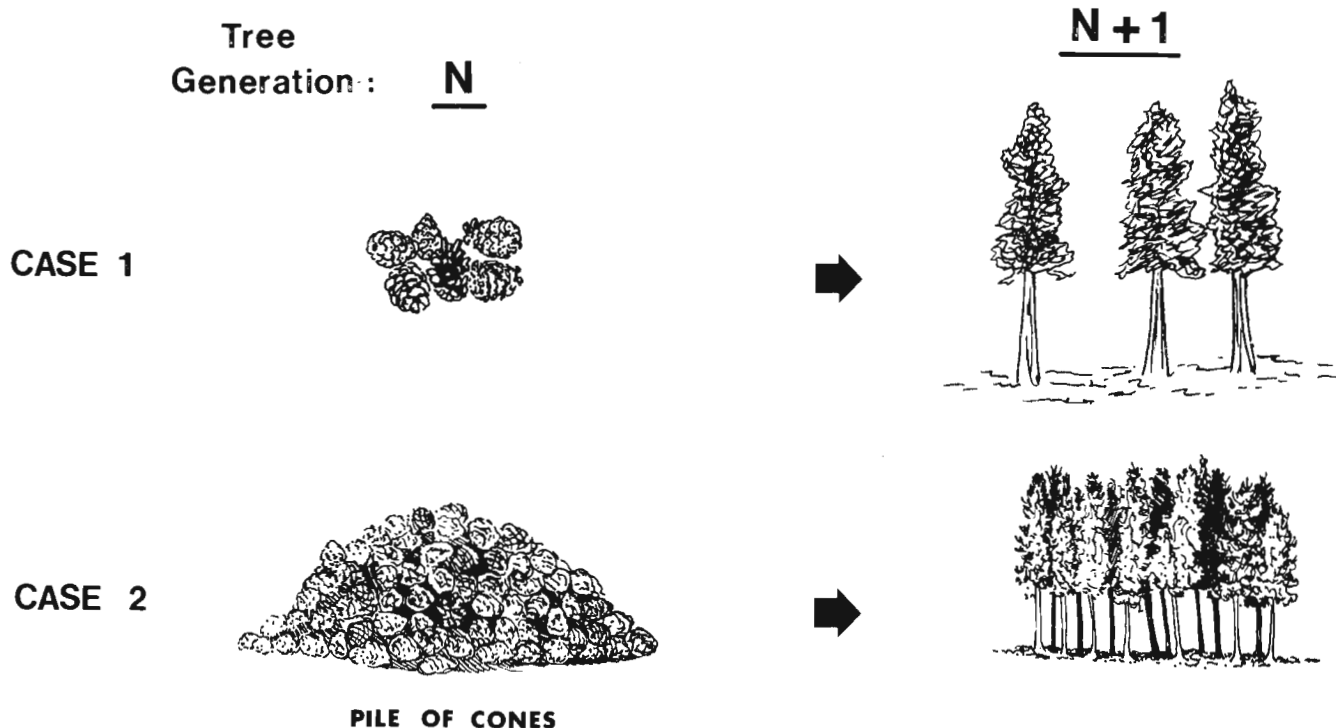


Fig. 1. A schematic illustration of how lodgepole pine seed supply affects offspring stand density.

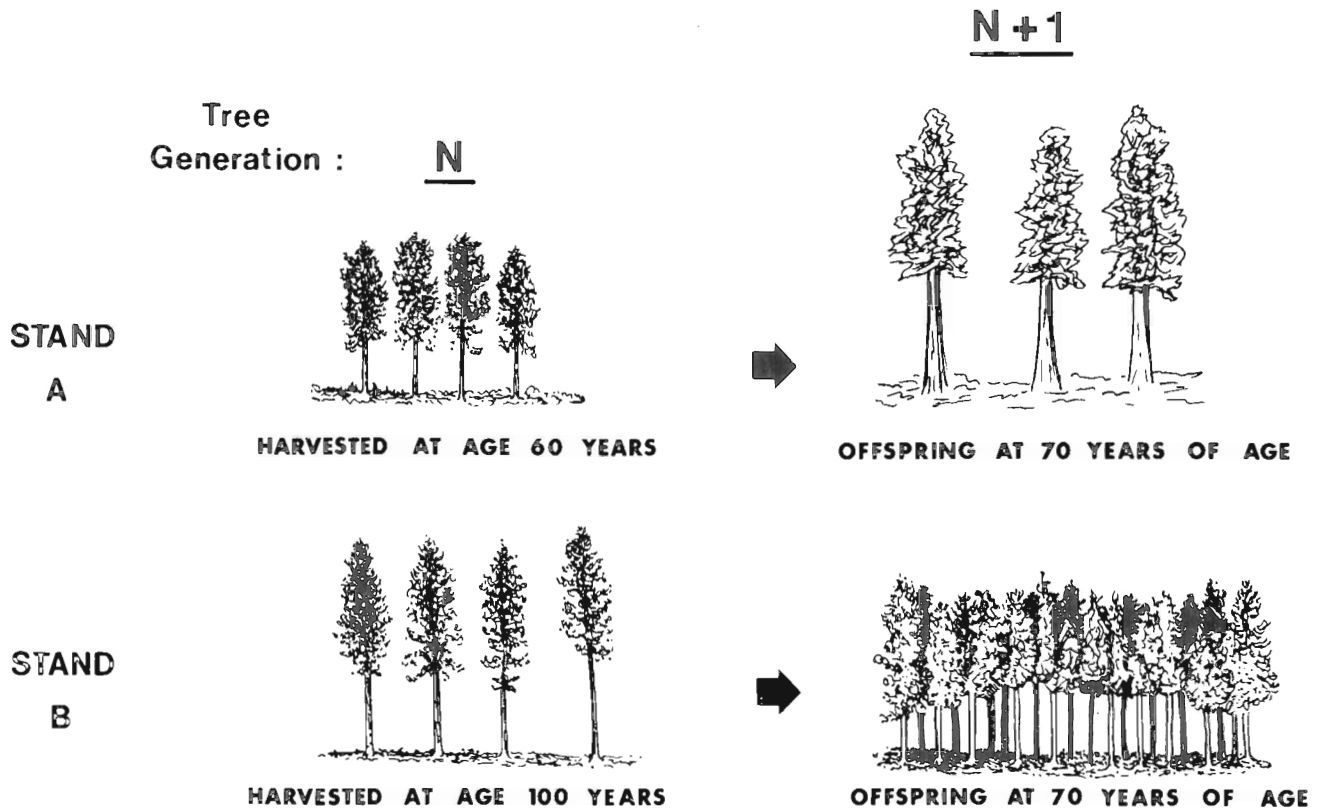


Fig. 2. Effects of age of harvest and burning of parental stands of lodgepole pine on characteristics of the offspring stands.

spring generation. Since a high degree of cone serotiny ($> 40\text{--}50\%$) is only moderately common over lodgepole pine's geographical range (Lotan 1975), the foregoing scenarios probably only apply to that subset of all possible lodgepole pine stands.

These arguments suggest that the ecological role of mountain pine beetle may be to decrease the probability that lodgepole stands with a high degree of serotiny will produce a stagnating offspring generation, by preventing the stand from getting too old. The age at which trees become less resistant to *D. ponderosae* may have evolved to create a high probability of outbreaks at a time appropriate for the trees. Such a mechanism to prevent stagnation could be of evolutionary significance to lodgepole pine for two reasons: 1) stagnant trees, like suppressed trees, have small crowns and few cones and therefore are not likely to reproduce well; 2) the trees stocked very sparsely in the generation after the stagnant stand could be outcompeted by other tree species. This interrelation between *P. contorta* and the mountain pine beetle could be advantageous to the insect because in the long run there will be fewer stagnant stands, which are unsuitable for *D. ponderosae* reproduction due to the small diameter and thin phloem of the trees (Amman 1969, Cole et al. 1976).

This interpretation of the mountain pine beetle's role has obvious significance for management, since the prevention of stagnant stands will increase the potential yield of timber when, and if, the offspring stand is harvested. By permitting

certain stands that cannot be economically harvested at present to be killed by *D. ponderosae*, there may be an increased likelihood of those stands naturally producing a harvestable offspring generation.

A Mathematical Model

A simulation model of lodgepole pine stands was constructed in order to explore some of the above speculations about generation-to-generation forest changes. In particular, the model was designed to explore the different outcomes resulting when trees become non-resistant to mountain pine beetle at various ages. The model implicitly assumes that age is a major determinant of level of resistance, and that other factors such as elevation and site quality contribute to the variance about that underlying relation. This model incorporated the effects of initial seedling density, tree competition, natural thinning mortality, growth, cone production, and age at which trees were "harvested" by bark beetles and burned. Details of the model are presented elsewhere (Peterman 1974), but in short, functional relations concerning lodgepole reproduction were derived from the existing data and literature. The model also assumed that fires occur in lodgepole stands of different ages according to the relation shown by Brown (1975: Fig. 2C)—i.e., moderate probability in young, thick stands; decreased probability as stands thin out; increased probability again as old, dead, windthrown trees accumulate.

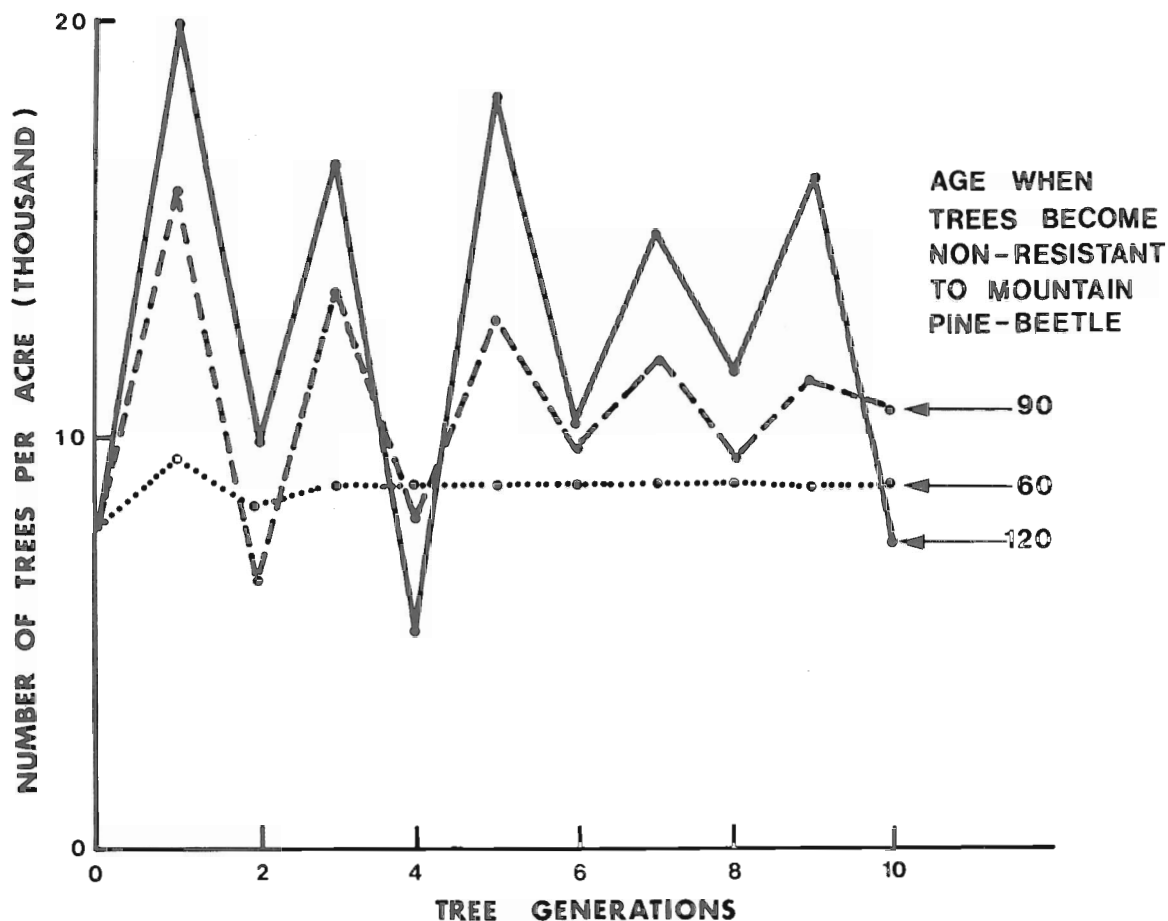


Fig. 3. Results of three different 10-generation simulations of a lodgepole pine stand, given different ages at which stands were attacked and killed by mountain pine beetle populations.

In the model, these fires were assumed to destroy the stand completely and release the tree seeds that were calculated to be held in serotinous cones at that time. Fires could occur at any randomly determined time, either before or after a *D. ponderosae* outbreak. While only a 0.4-ha (1-acre) patch of ground was considered in the model, we can easily extrapolate to larger spatial areas. All lodgepole seeds were assumed to come from the trees on that plot, since lodgepole seeds generally do not disperse more than 61 m (200 ft) from the parent tree (Dahms 1963). Competing tree species were not included in the model.

Bark beetle population dynamics were not calculated, as it was assumed that stands were killed and burned within 10 years of becoming non-resistant to the beetle. Fires were assumed to be of average intensity.

Results of the modeling exercise show that the age at which mountain pine beetle outbreaks occur greatly affects simulated lodgepole stand characteristics over several generations (Peterman, unpublished data). For example, the older trees are before they are killed by mountain pine beetle and burned, the wider the amplitude of oscillations in tree den-

sities over several generations (Fig. 3). When we look at measures of lodgepole reproductive success such as the ones shown in Figs. 4 and 5, we find that there is a very definite optimal range of ages for trees to be attacked by mountain pine beetle. Variation in site quality, which affects tree growth rates, would shift the peaks of the curves earlier or later in time. When trees are "harvested" by bark beetles before about 60 or 70 years of age, average number of trees per acre over the 10 simulated generations and minimum number of saplings per parent tree are relatively low. When beetles kill stands older than about 120 years of age, these measures of reproductive success are also relatively low because of the high degree of oscillation in stand densities from one generation to the next.

Other measures of lodgepole reproductive success have the same basic shape, with peaks in the range of 80 to 120 years. Furthermore, these results are relatively insensitive to changes of up to 60 percent in the degree of serotiny, because lodgepole is such a prolific seed producer. There is a striking agreement between these ages of peak tree reproductive success and the normal outbreak frequency of mountain pine beetle in lodgepole pine stands, which is about 80 to 100 years (Loope and Wood 1976, Safranyik et al. 1975).

Thus, on the basis of existing data on lodgepole pine reproduction, it is predicted that mountain pine beetle can prevent the production of stagnant lodgepole stands, depending on the age at which parent stands are attacked and killed. This result of mountain pine beetle attacks also contributes to the economic value of stands by keeping initial densities of trees below the level that would produce severe crowding.

Therefore, not only may mountain pine beetle outbreaks perform a vital role in the ecology of lodgepole pine forests, but that role may not be so much at odds with overall timber yield objectives as previously thought. **Under certain conditions**, and in stands not presently accessible, *D. ponderosae* may help improve forest yields in future generations.

IMPLICATIONS FOR MANAGEMENT

Based on these arguments, there may be certain situations in which it would be beneficial to shift our view of mountain pine beetle from "a pest" to "a management tool." Specifically, the bark beetle could help prevent future stagnant stands in plots that have a relatively high degree of serotiny and which are not presently important for timber

production. Such a dramatic shift in perspective certainly has precedent in forest management, as shown by two widely cited examples.

Saxony Spruce Sickness

In the late 1700s foresters in southern Germany began to change from mixed species forests to monocultures of the more economical Norway spruce. These plantations produced very well in the first rotation, but by the second generation, a decrease in production was already noticeable (Plochmann 1968, Troup 1966). This decline, caused largely by compaction and acidification of the soil, continued through two more tree generations. In the early part of this century, foresters began to change many plantations back toward a mixed forest, particularly by using species that had previously thrived in the local soil and climatic conditions (Hawley and Smith 1954). The lesson was learned the hard way that the peculiar ecological characteristics of forests derived over generations cannot be ignored.

Fire Management vs. Fire Suppression

Another well-known example more relevant to lodgepole pine deals with management attitudes toward forest fires.

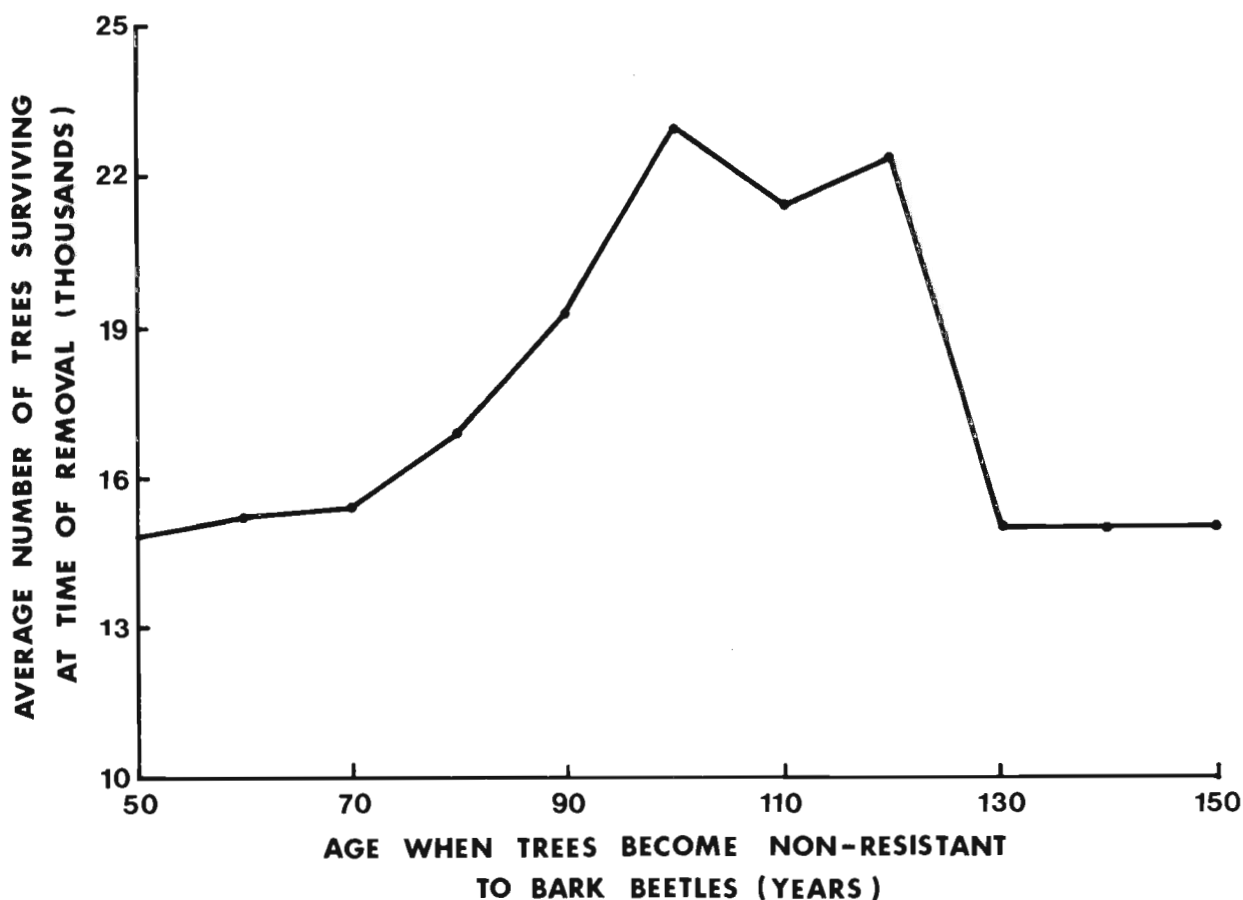


Fig. 4. Lodgepole pine reproductive success measured in relation to the age at which stands become non-resistant to *D. ponderosae* attacks. "Average number of trees at time of removal" means the number present at the time fire consumed the stand, or, if there was an outbreak, at the time the beetles attacked.

Large-scale destruction of timber by fires in the 1800s and early 1900s emphasized the "competition" between man's lumber needs and fire. Out of this evolved fire control and suppression programs that became extremely effective (Wellner 1970). It soon became apparent, however, especially in some U.S. national parks, that elimination of fires was causing a change in species composition and a dangerous build-up of fuels on the ground (Heinselman 1971; Kilgore 1976a, 1976b; Sanderson 1976). Such fuels could lead to very destructive fires if any fire ever got out of control. In the late 1960s this situation led to a widespread recognition that fire was not always at odds with management needs, e.g., under certain conditions it could be used in a positive way as a management tool both through deliberate "prescribed burns" and through the policy of letting lightning-started fires burn (USDA Forest Serv. 1972, Kilgore 1976b, Slaughter et al. 1971).

The common theme in these two examples is that our initial perceptions of the roles of the natural ecosystem components (mixed species of a certain type, and fire) were wrong. When we acted to alter the characteristics of these components to achieve our own needs more effectively, undesirable consequences followed. A shift in perspective then resulted which attempted to put those components of the system that had been altered back toward their natural configuration.

Therefore, it seems reasonable to suggest that we may have the wrong perception of forest insect pests in general, and mountain pine beetle in particular. Outbreaks may not necessarily always be bad. In fact, it may be possible to achieve

many present management objectives in certain stands by letting particular outbreaks continue unhindered by man.

In order that this view of mountain pine beetle as a management tool become acceptable, it is necessary that we use fairly long-term management objectives. We should explicitly consider how the management of a present forest will affect the characteristics of the generations of trees that will follow. To some extent this long-term view already prevails among foresters who are using fire as a management tool. Some natural fires in lodgepole pine are being left to burn out on their own in order to break up the age distribution of the forest (Loope and Gruell 1973, Loope and Wood 1976). This will create, over the next several decades, a spatial mosaic of different-aged trees that will prevent large forested areas from simultaneously becoming susceptible to mountain pine beetle outbreaks.

When *D. ponderosae* is used as a management tool, it may break up the age distribution of lodgepole forests much as fires do, and this will be particularly useful in those areas that cannot be harvested by man for some reason. The spatial mosaic of ages in the next generation will presumably decrease the probability of large-scale outbreaks of mountain pine beetle by eliminating the large contiguous regions of even-aged stands (Roe and Amman 1970, Safranyik et al. 1974). Letting some *D. ponderosae* outbreaks proceed will also reduce the chance of creating a stagnating offspring generation, thereby

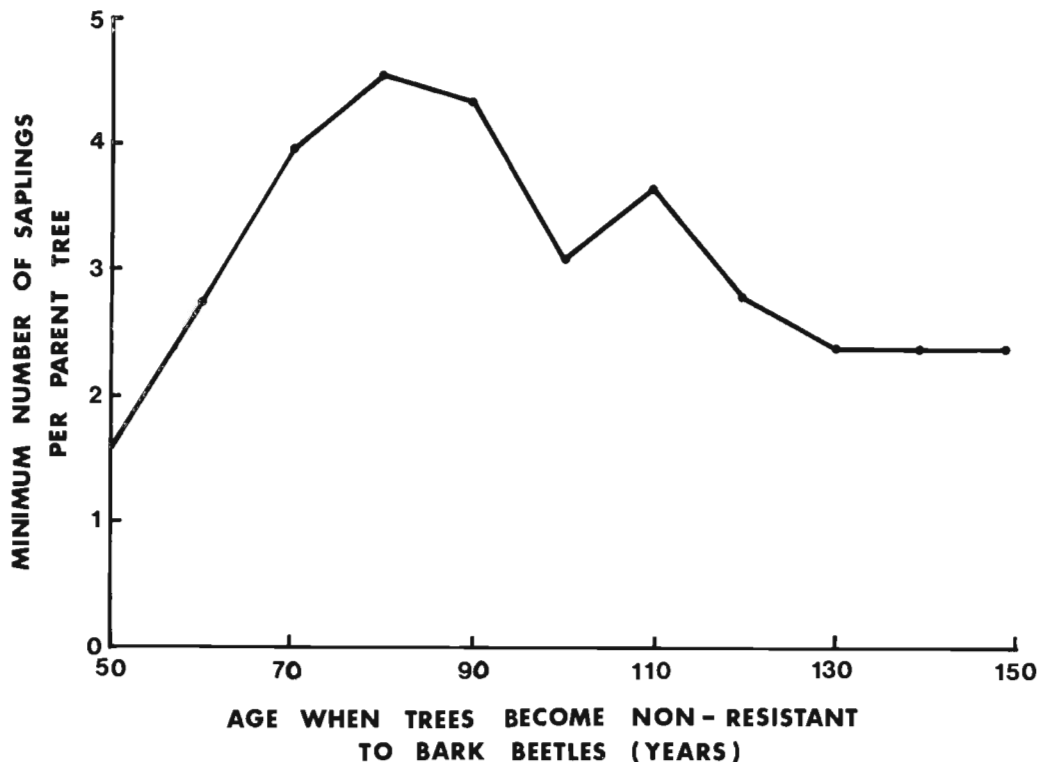


Fig. 5. Minimum number of saplings per parent tree as a measure of reproductive success for lodgepole pine.

increasing the potential volume of harvestable wood, as discussed above. Management objectives, however, are no longer simply "to maximize timber harvest"; i.e., the value of the forest for recreation and wildlife as well as for other resources is also presently considered (see papers in Baumgartner 1975, U.S. Congress 1976). But extremely dense, stagnant lodgepole stands will probably support little wildlife or recreational activity because of the lack of forage on the shaded forest floor and the impenetrable thicket of branches and tree trunks (Berntsen 1975). Thus, today's broader management objectives can also be met to some extent by the use of mountain pine beetle outbreaks, in conjunction with fire management, to prevent overcrowded stands from developing.

CAUTIONS AND RECOMMENDATIONS

The suggestion that mountain pine beetle be used in certain restricted cases as a management tool is not without its risks. Outbreaks could spread beyond the area desired and lead again to wide areas of even-aged forest in the following generation. But let us put these uncertainties into proper perspective. No management actions are taken with perfect knowledge of what will happen; this is especially true of the fire management activities being practiced today. We must not avoid taking some management action that may have great benefits in the future just because there is some risk of producing serious costs. Kilgore (1976a) points out that, as recently as 1970, this same "black-and-white" attitude was shown toward fire as a management tool, expressed in the form, "We cannot gamble with as potent a force as fire—either we must have it under full control at all times or we should not use it at all." Kilgore goes on to point out the error in this argument in a succinct statement that can equally apply to the use of mountain pine beetle as a management tool:

For however much we can learn about the role of fire in a particular forest type under a given set of fuel, weather, and topographic parameters, there will always be some risk in a decision to prescribe burn or to let a fire burn. The decision to suppress, of course, appears to have the lesser risk over the short span of time. It's the safe, traditional, status quo decision and theoretically gets no one in trouble. But in the long run, fuel accumulates and another manager at a later time faces an even tougher decision.

In our considerations of mountain pine beetle as a management tool, we can learn a great deal from fire management theory and practice. For example, it is clear that no one would recommend a blanket policy of letting all *D. ponderosae* outbreaks continue without taking action to suppress them, just as no one would suggest that all natural fires be permitted to burn (Loope and Gruell 1973). There will be certain situations that will prompt us to wait for better conditions before letting an outbreak go unchecked—region presently or in the near future important for timber production, very dry weather, old trees over large areas, etc. But with sufficient research and

compilation of existing data, such as the hazard index of Safranyik et al. in Canada (1975), it should be possible to create some decision rules for use in field situations when an outbreak begins. Such decision rules are presently used in some fire management situations (Devet 1976) to help managers decide very quickly whether to let a particular fire burn.

Again, as with fire management, the biggest problem with the application of the idea of using mountain pine beetle as a management tool is that the transition phase out of the present dangerous conditions is more difficult than the maintenance of some future forest condition. There is no simple solution to this problem. The transition phase will probably take several generations of trial "outbreaks"—some spreading too far and others being successful. The short-term costs of these failures will clearly have to be weighed against the long-term benefits. In addition, fire management will have to be used **in conjunction** with mountain pine beetle management in order to manipulate to best advantage the fuel sources arising from outbreaks.

The shortcomings of the proposed mountain pine beetle management strategy are readily apparent. But deficiencies appear in any new scheme until sufficient trials are carried out to fill in the gaps. Several areas of research are readily identified, however, as central to bridging those gaps and providing forest managers with guidelines for letting outbreaks continue. For example, how can resistance levels of trees be predicted? How large a patch of trees of given resistance is needed to create an outbreak (as opposed to an endemic population)? How large a band of resistant trees is needed around such patches to prevent the spread of the outbreak by dispersal? What are the characteristics of adult mountain pine beetle dispersal? How can the density of lodgepole pine seedlings in the next generation be more accurately predicted? How is this density affected by degree of serotiny? What offspring stand densities resulted in the past when mountain pine beetle outbreaks occurred in stands of different ages?

This type of information should be synthesized into models that can provide forest managers with predictions of the short- and long-term consequences of letting a particular infestation go unharmed, given present conditions of the forest, weather, beetle population, etc. In this way, managers can be aided in their approach to "emergency" situations.

CONCLUSIONS

The alteration of our view of mountain pine beetle as a pest to one as a management tool will not occur overnight, nor should it. There must be careful planning of experiments to provide data, careful research and a more complete synthesis of information. The proposed use of mountain pine beetle is not without its risks, but this is true of any management policy. We should welcome the chance to turn uncertainties about outbreaks into unexpected opportunities, opportunities to manipulate lodgepole pine forests to meet management objectives.

Finally, we should recall that early suggestions to use fire as part of forest management were met with derision and astonishment. It was only through the combined efforts of researchers and foresters that fire became an accepted management tool. It is hoped that the same dedication and expertise will soon be applied to the challenging new area of forestry—mountain pine beetle as a management tool.

EPILOGUE

The preceding arguments must be placed into a proper context, and that is, how significantly does the mountain pine beetle affect the dynamics of lodgepole pine, which man treats as a resource and manipulates with management policies? Just how important a competitor with man is the insect? After an examination of the literature, I have, surprisingly, found it impossible to describe that context because there is insufficient information on the following questions. What proportion of lodgepole trees are killed by mountain pine beetle every year? What fraction of those trees would have been harvestable in the future? And what proportion of lodgepole pine stands do not have climatic restrictions on the potential presence of the bark beetle? While it is clear that there can be severe devastation by the bark beetle on a small scale, the only partial answer I have found to one of these large-scale questions is that about 3 percent of the average annual cut of lodgepole pine in Canada has been killed by mountain pine beetle every year for the last 20 years (Safranyik et al. 1974).

But this one piece of information is not enough. The other questions must be answered for the whole geographical distribution of lodgepole pine to determine if mountain pine beetle greatly affects the dynamics of the potentially **harvestable** resource. Entomologists cannot properly advise forest managers until the extent of this effect is understood. Likewise, choice of management policies by foresters will be greatly influenced by this knowledge. If the insect has only marginal consequences, then perhaps the emphasis on the beetle problem should be shifted to an emphasis on forest management problems. But if the effect is significant, then perhaps some policy that uses the bark beetle as a management tool should be considered.

It is hoped that other papers in this symposium will provide this sorely needed information.

ACKNOWLEDGMENTS

I would like to thank F. Bunnell, W.C. Clark, C.S. Holling, and four reviewers, A.A. Berryman, G.D. Amman, J.E. Lotan, and R.D. Pfister, for their helpful comments on a draft manuscript.

QUESTIONS AND ANSWERS

- Q. Using mountain pine beetle as a management tool—is this not identical to thinning from above, a questionable practice in lodgepole management?
- A. I wasn't proposing to use the beetle as a thinning agent to improve the quality of non-attacked trees. Instead, I discussed the use of the beetle to kill the whole stand through fire and to thereby start a new tree generation.
- Q. Can you explain how to "turn on" a localized attack and/or control the parameters or localize the attack by using mountain pine beetle as a management tool?
- A. First, I am **not** suggesting that one should start an outbreak deliberately—only that once one begins naturally it may have some benefits. If someone did want to start an outbreak, perhaps it could be done by hauling several dozen infested boles into a "ripe," thick-phloemed stand.
- Second, I don't think we can control the amount of spread of the outbreak other than by the means outlined by other speakers in this symposium—rely on tree conditions to stop the spread, use selective cutting, etc.
- Q. Have you found that lodgepole pine reaches a greater dbh before susceptibility at higher, colder elevations where the tree should be longer lived?
- A. I have no evidence for this and (after asking) neither does anyone in the audience.

REFERENCES

- Amman, G.D. 1969. Mountain pine beetle emergence in relation to depth of lodgepole pine bark. USDA Forest Serv. Res. Note INT-96. Intermtn. Forest and Range Exp. Sta., Ogden, UT. 8 pp.
- . 1975. Insects affecting lodgepole pine productivity. Pages 310-341 in D.M. Baumgartner (ed.). Management of lodgepole pine ecosystems. Washington State Univ. Coop. Exten. Serv., Pullman.
- . 1977. Role of the mountain pine beetle in lodgepole pine ecosystems: Impact on succession. Pages 3-18 in W.J. Mattson (ed.). The role of arthropods in forest ecosystems. Springer-Verlag Proc. in Life Sciences, New York.
- Amman, G.D., and B.H. Baker. 1972. Mountain pine beetle influence on lodgepole pine stand structure. J. Forest. 70:204-209.
- Armit, D. 1966. Silvics and silviculture of lodgepole pine in the north central interior of British Columbia; a problem analysis. Brit. Columbia Forest Serv. Res. Note No. 40. Victoria. 59 pp.
- Baker, F.S. 1950. Principles of silviculture. McGraw Hill, New York. 414 pp.

- Bates, C.G. 1930. The production, extraction and germination of lodgepole pine seed. USDA Tech. Bull. No. 191. U.S. Govt. Print. Off., Washington, D.C. 92 pp.
- Baumgartner, D.M. (ed.). 1975. Management of lodgepole pine ecosystems, Vol. 1 and 2. Washington State Univ. Coop. Ext. Serv., Pullman. 825 pp.
- Berntsen, C.M. 1975. Management conflicts in lodgepole pine. Pages 503-515 in D.M. Baumgartner (ed.). Management of lodgepole pine ecosystems. Washington State Univ. Coop. Ext. Serv., Pullman.
- Berryman, A.A. 1972. Resistance of conifers to invasion by bark beetle-fungus associations. *Bioscience* 22:598-602.
- _____. 1976. Theoretical explanation of mountain pine beetle dynamics in lodgepole pine forests. *Environ. Entomol.* 5:1225-1233.
- Brown, J.K. 1975. Fire cycles and community dynamics in lodgepole pine forests. Pages 429-455 in D.M. Baumgartner (ed.). Management of lodgepole pine ecosystems. Washington State Univ. Coop. Ext. Serv., Pullman.
- Clements, F.E. 1910. The life history of lodgepole burn forests. USDA Forest Serv. Bull. No. 79. U.S. Govt. Print. Off., Washington, D.C. 56 pp.
- Cole, W.E., and G.D. Amman. 1969. Mountain pine beetle infestations in relation to lodgepole pine diameters. USDA Forest Serv. Res. Note INT-95. Intermtn. Forest and Range Exp. Sta., Ogden, UT. 7 pp.
- Cole, W.E., G.D. Amman and C.E. Jensen. 1976. Mathematical models for the mountain pine beetle-lodgepole pine interaction. *Environ. Entomol.* 5:11-19.
- Crossley, D.I. 1956. Fruiting habits of lodgepole pine. Forest Res. Div. Tech. Note No. 34. Canada Dept. Northern Affairs and Natural Resources. 29 pp.
- Dahms, W.G. 1963. Dispersal of lodgepole pine seed into clear-cut patches. USDA Forest Serv. Res. Note PNW-47. PNW Forest and Range Exp. Sta., Portland, OR. 11 pp.
- Devet, D.D. 1976. Descon-utilizing benign wildfires to achieve land management objectives. Pages 33-43 in Proc. Tall Timbers Fire Ecology Conference and Fire and Land Management Symposium, No. 14. Tall Timbers Res. Sta., Tallahassee, FL.
- Fowells, H.A. (ed.). 1965. Silvics of forest trees of the United States. USDA Forest Serv. Agri. Handbook No. 271. U.S. Govt. Print. Off., Washington, D.C. 762 pp.
- Gilbert, L.E., and P.H. Raven (eds.). 1975. Coevolution of animals and plants. Univ. of Texas Press, Austin. 246 pp.
- Graham, K. 1963. Concepts of forest entomology. Reinhold Publ. Corp., New York. 388 pp.
- Hawley, R.C., and D.M. Smith. 1954. The practice of silviculture (6th ed.). John Wiley and Sons, New York. 312 pp.
- Heinselman, M.L. 1971. The natural role of fire in northern conifer forests. Pages 61-72 in C.W. Slaughter, R.J. Barney and G.M. Hansen (eds.). Fire in the northern environment—a symposium. USDA Forest Serv., Portland, OR.
- Kilgore, B.M. 1976a. Introduction—fire management section. Pages 7-9 in Proc. Tall Timbers Fire Ecology Conference and Fire and Land Management Symposium, No. 14. Tall Timbers Res. Sta., Tallahassee, FL.
- _____. 1976b. Fire management in the National Parks: an overview. Pages 45-57 in Proc. Tall Timbers Fire Ecology Conference and Fire and Land Management Symposium, No. 14. Tall Timbers Res. Sta., Tallahassee, FL.
- Latham, J.A. 1965. The effects of spacing on development of lodgepole pine in the Manning Park area of British Columbia. B. For. thesis, Univ. of British Columbia, Vancouver. 58 pp. (unpublished).
- Loope, L.L., and G.E. Gruell. 1973. The ecological role of fire in the Jackson Hole area, northwestern Wyoming. *Quatern. Res.* 3: 425-443.
- Loope, L.L., and R.P. Wood. 1976. Fire management in Grand Teton National Park. Pages 87-98 in Proc. Tall Timbers Fire Ecology Conference and Fire and Land Management Symposium, No. 14. Tall Timbers Res. Sta., Tallahassee, FL.
- Lotan, J.E. 1975. The role of cone serotiny in lodgepole pine forests. Pages 471-495 in D.M. Baumgartner (ed.). Management of lodgepole pine ecosystems. Washington State Univ. Coop. Ext. Serv., Pullman.
- Mason, D.T. 1915. The management of lodgepole pine. *Forest. Quart.* 13:171-182.
- Mutch, R.W. 1970. Wildland fires and ecosystems—a hypothesis. *Ecology* 51:1046-1051.
- Opler, P.A. 1973. Fossil lepidopterous leaf mines demonstrate the age of some insect-plant relationships. *Science (Washington, D.C.)* 179:1321-1323.
- Peterman, R.M. 1974. Some aspects of the population dynamics of the mountain pine beetle, *Dendroctonus ponderosae*, in lodgepole pine forests of British Columbia. Ph.D. diss., Zoology Dept., Univ. of British Columbia, Vancouver. 208 pp. (unpublished).
- _____. 1977. An evaluation of the fungal inoculation method of determining the resistance of lodgepole pine to mountain pine beetle (Coleoptera: Scolytidae) attacks. *Can. Entomol.* 109: 443-448.
- Pfister, R.D., and R. Daubenmire. 1975. Ecology of lodgepole pine (*Pinus contorta* Dougl.). Pages 27-46 in D.M. Baumgartner (ed.). Management of lodgepole pine ecosystems. Washington State Univ. Coop. Ext. Serv., Pullman.
- Plochmann, R., 1968. Forestry in the Federal Republic of Germany. Hill Family Foundation Forestry Series, Dept. of Printing, Oregon State Univ., Corvallis. 52 pp.
- Reid, R.W. 1962a. Biology of the mountain pine beetle, *Dendroctonus monticolae* Hopkins, in the east Kootenay region of B.C. I. Life cycle, brood development, and flight periods. *Can. Entomol.* 94:531-538.
- _____. 1962b. Biology of the mountain pine beetle, *Dendroctonus monticolae* Hopkins, in the east Kootenay region of B.C. II. Behaviour in the host, fecundity, and internal changes in the female. *Can. Entomol.* 94:605-613.
- 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. J. Bot.* 45:1115-1126.

- Roe, A.L., and G.D. Amman. 1970. The mountain pine beetle in lodgepole pine forests. USDA Forest Serv. Res. Paper INT-71. Intermtn. Forest and Range Exp.Sta., Ogden, UT. 23 pp.
- Safranyik, L., D.M. Shrimpton and H.S. Whitney. 1974. Management of lodgepole pine to reduce losses from the mountain pine beetle. Forest. Tech. Rep. No. 1. Forestry Serv., Environment Canada. Victoria, B.C. 25 pp.
- Safranyik, L., D.M. Shrimpton and H.S. Whitney. 1975. An interpretation of the interaction between lodgepole pine, the mountain pine beetle and its associated blue stain fungi in western Canada. Pages 406-428 in D.M. Baumgartner (ed.). Management of lodgepole pine ecosystems. Washington State Univ. Coop. Exten. Serv., Pullman.
- Sanderson, J.E. 1976. The role of fire suppression in fire management. Pages 19-31 in Proc. Tall Timbers Fire Ecology Conference and Fire and Land Management Symposium, No. 14. Tall Timbers Res. Sta., Tallahassee, FL.
- Slaughter, C.W., F.J. Barney and G.M. Hansen (eds.). 1971. Fire in the northern environment—a symposium. USDA Forest Serv., Portland, OR. 275 pp.
- Smith, C.C. 1970. The coevolution of pine squirrels (*Tamiasciurus*) and conifers. Ecol. Monogr. 40:349-371.
- Smithers, L.A. 1962. Lodgepole pine in Alberta. Canada Dept. Forestry Bull. No. 127. 153 pp.
- Troup, R.S. 1966. Silvicultural systems. 2nd ed. Oxford Univ. Press, London. 300 pp.
- U.S. Congress. 1976. National Forest Management Act. U.S. Statutes at Large, 94th Congress. Public Law 588. Vol. 90:2949-2963. U.S. Govt. Print. Off., Washington, D.C.
- USDA Forest Service. 1972. Proc. Fire in the environment symposium, May 1-5, Denver, CO. U.S. Forest Serv., Washington, D.C. 151 pp.
- Wellner, C.A. 1970. Fire history in the northern Rocky Mountains. Pages 42-64 in The role of fire in the intermountain West. Intermtn. Fire Research Council.

Potential Impacts of Mountain Pine Beetle and Their Mitigation in Lodgepole Pine Forests

S. William Carter, Jr.

ABSTRACT

The results of a project to prepare guidelines and prescribe treatment for infested lodgepole pine (*Pinus contorta* Douglas var. *latifolia* Engelm.) stands in the Umatilla and Wallowa-Whitman National Forests in northeastern Oregon are used to illustrate the potential impacts of a mountain pine beetle (*Dendroctonus ponderosae* Hopkins) outbreak on all forest resources. Resources considered are timber, fisheries and wildlife, water, soils, recreation and esthetic value. Guidelines to mitigate the effects on these were developed with respect to the treatment selected, a three-phase harvest program over a 21-year period. This management plan was selected over no action, a two-phase harvest program over a 14-year period, and a two-phase harvest program over a 22-year period as best meeting the overall management objectives.

INTRODUCTION

The mountain pine beetle, *Dendroctonus ponderosae* Hopkins, is a periodic forest pest in most lodgepole pine (*Pinus contorta* Douglas var. *latifolia* Engelm.) stands. Extensive areas of lodgepole pine have been destroyed at various times in the past by this insect (Amman et al. 1977, Safranyik et al. 1974). It has been active in the ecosystem as long as there have been lodgepole pine trees.

Other than effects on timber and bulk wood production, little is known of the impact of mountain pine beetle infestations on forest resources such as soils, water, fish and wildlife, recreation and esthetic values. The National Forest Management Act of 1976 demands that equal attention be given to all forest resources in planning and management of public lands. This paper describes a recent attempt to address the mitigation of effects of a severe mountain pine beetle outbreak on all forest resource values.

The mountain pine beetle is currently causing serious timber losses in lodgepole pine stands on the national forests of northeast Oregon. The present outbreak started in 1968 in the Grande Ronde River drainage and covered approximately 972 ha (2400 acres) at the end of that year. The outbreak has expanded during the past 10 years and now encompasses over 405,000 ha (1 million acres) in the Blue Mountains of Oregon (Fig. 1). Ground surveys indicate that in many of the areas where the insect has been epidemic for 7 or more years, there is an almost total loss of all lodgepole pine over 10 cm (4 inches) in diameter (Gregg et al. 1976). Total lodgepole volume loss to date is over 1 billion board feet. The insect has also moved into ponderosa pine stands and is epidemic on approximately 254,000 ha (628,000 acres) in the Blue Mountains. Both old growth and second growth stands are being attacked. Ponderosa pine mortality to date totals 582 million board feet. Salvage logging operations have begun in the accessible portions of the outbreak area. The fire hazard is extreme and will persist until the dead wood is removed, treated or consumed by decay or wildfire.

A Mountain Pine Beetle Interdisciplinary Team consisting of silviculturist, soil scientist, wildlife biologists, fisheries biologists, forester, hydrologist, logging specialist and landscape architects was organized in October 1974 to prepare guidelines and prescribe treatment for the infested lodgepole pine stands of the Umatilla and Wallowa-Whitman National Forests in northeast Oregon (Umatilla National Forest 1974). This was a special coordination effort involving four ranger districts and was designed to ensure that all resources were adequately considered in meeting the following management objectives developed by the two forests:

1. Clean up the mess and reduce the fire hazard.
2. Mitigate adverse effects on soil, water and wildlife.

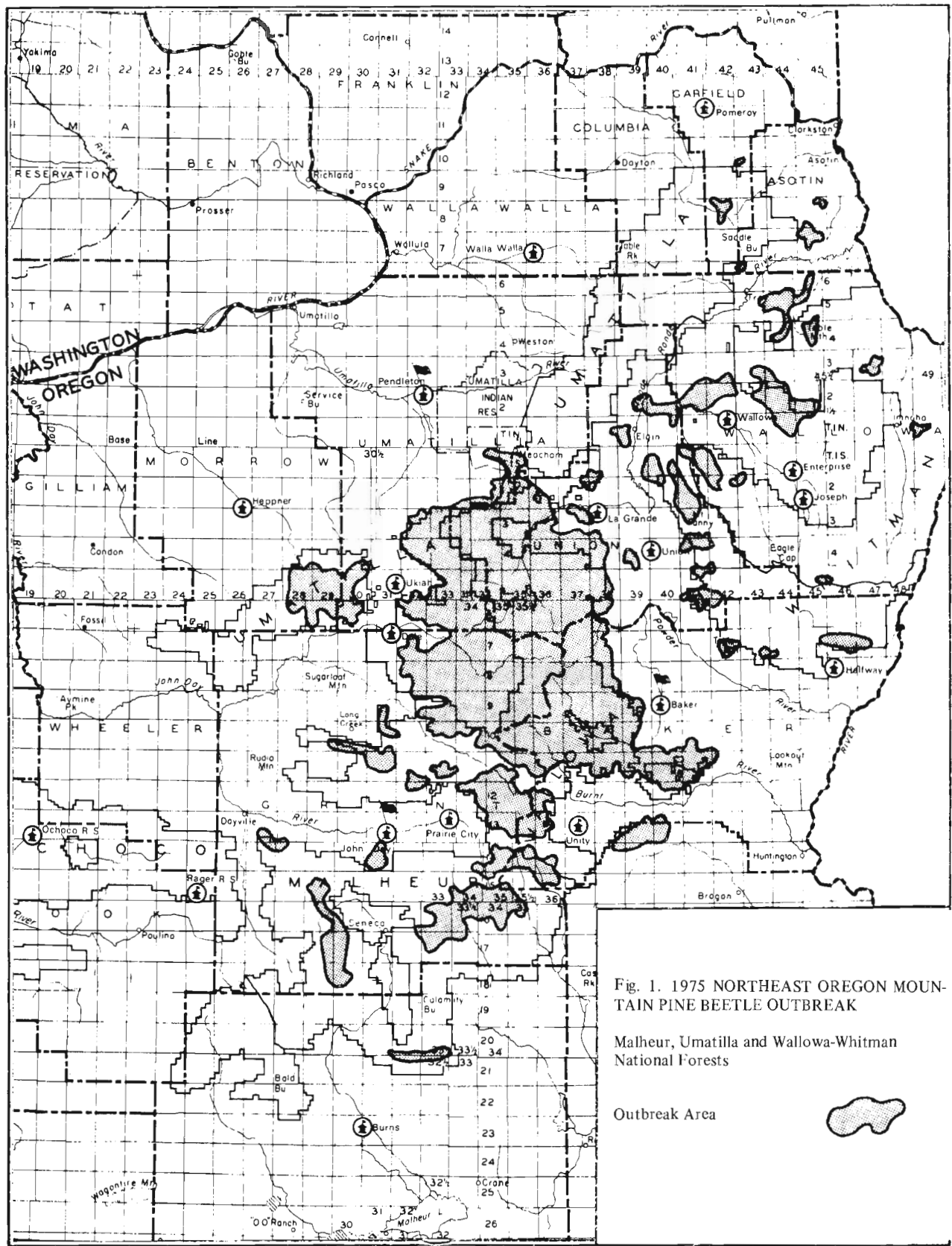


Fig. 1. 1975 NORTHEAST OREGON MOUNTAIN PINE BEETLE OUTBREAK

Malheur, Umatilla and Wallowa-Whitman National Forests

Outbreak Area

3. Regenerate the timber stands as quickly as possible.
4. Utilize the wood fiber to accomplish objectives 1, 2 and 3 above.

A 30,600-ha (75,700-acre) area referred to as Lane-Peet was selected for the initial intensive study by the team. Four plans, including A) no action, B) a two-phase harvest program over a 14-year period, C) a two-phase harvest program over a 22-year period and D) a three-phase harvest program over a 21-year period, were carefully considered.

Each plan was evaluated and ranked from the most to the least desirable for each resource (Table 1). On this basis, Plan D, the three-phase 21-year harvest program, was selected. It was determined that this plan would utilize the wood fiber, meet all three of the other prescribed management objectives, and be applicable to all infested areas. A complete description of this analysis procedure is contained in the report cited.

The following are highlights of the Lane-Peet study.

Table 1. Alternative treatment preference.

Resource	Management Plan			
	A	B	C	D
Timber	4	1	3	2
Wildlife	1	4	3	2
Fisheries	1	4	3	2
Water	1	4	3	2
Soil	1	4	3	2
Grazing	4	1	3	2
Utilization	4	1	3	2
Recreation	4	1	3	2
Hunting	1	4	3	2
Fire	4	1	3	2
Visual	4	3	2	1

First preference = 1; second preference = 2; third preference = 3; last preference = 4.

RESOURCE CONSIDERATIONS AND RECOMMENDED MANAGEMENT PRACTICES

Timber

The lodgepole pine stands in this area originated from fires that swept through the Blue Mountains between 1870 and 1910. These stands are typically overmature, small-diameter, overstocked and stagnated. Ages range from 80 to 110 years; sizes range from 5 to 15 cm (2 to 6 inches) dbh, with 2500 to 12,500+ stems per ha (100 to 5000+ stems per acre), to 15 to 25 cm (6 to 10 inches) dbh with 750 to 1500 stems per ha (300 to 600 stems per acre). The stands are heavily infected with dwarf mistletoe, atropellis canker

and western gall rust. In some areas stands are breaking up due to natural causes (snow, wind, maturity, etc.). White fir, grand fir, Douglas-fir, western larch and lodgepole pine regeneration are commonly found under lodgepole stands where the canopy is beginning to deteriorate. In the past, harvesting has been mostly on a selective basis for sawlogs, poles or posts.

The silvicultural objectives for the outbreak area are to harvest and promptly regenerate the lodgepole pine stands while complying with guidelines developed to meet the objectives for other resources managed in this area.

Lodgepole pine in the Blue Mountains is a prolific seed producer from serotinous and non-serotinous cones. Juvenile growth is rapid in the dense new stands until stagnation occurs. Growth then becomes very limited. Without management, stands similar to those already existing will develop and eventually become susceptible to mountain pine beetle attack.

Table 2 contains specific guidelines to meet the silvicultural objectives for the lodgepole pine plant communities found in the Blue Mountains (Hall 1973). It is for field use with timber-typed maps and aerial photographs available on the forests. Site factors, harvest method alternatives, constraints, and post-sale work are discussed for each lodgepole timber type. It is an aid for prescribing treatment for individual sites, whereas other guidelines in Lane-Peet are developed on an area basis because of the nature of the resources (wildlife, water, visual, etc.).

Wildlife

All forms of wildlife within the lodgepole pine habitat type will be affected to some extent—some will benefit to the detriment of others. Based on animal numbers and recreation use, Rocky Mountain elk are the most important big game animal in the outbreak area. Other wildlife species are also important and maintenance of suitable habitat to sustain all existing species in optimal numbers is considered important.

Four big game management units lie within the outbreak area. These units support 36 percent of Oregon's Rocky Mountain elk hunters (23,130) and generate 135,830 man days of recreation per year in the harvesting of 3542 elk. Mismanagement of cover within the lodgepole type could effectively reduce the elk hunting recreation potential by more than 50 percent, the result of easier harvesting of elk and the consequent overhunting of the population.

The desired situation for maintenance of elk habitat is a scattered, irregular pattern of timber harvest units and dense cover¹ areas. If possible, areas should be interconnected. Timber harvest units and adjacent cover units do not necessarily have to be of equal size, but the amount of dense cover

¹ "Dense cover" is defined as any area where human sight distance is restricted by trees or other vegetation to a point where 50% or more of an elk (or similar-sized object) is hidden from view at a distance of 46 m (150 ft) or less.

Table 2. Silvicultural guidelines.

Lodgepole pine - grouse huckleberry-pinegrass CL-G2-11 (6LS).				
TIMBER TYPES	SITE FACTORS	HARVEST METHOD ALTERNATIVES	CONSTRAINTS	POST-SALE WORK
I. Lp3=, Lp3=, Lp2=, Lp2= and combinations of above with: 1. Other species overstory (< 37 trees per ha). 2. Other species understory (< 750 T.P.H. crop class). 3. Lpp or other species seedlings (< 750 T.P.H. 15-30 cm, good quality).	A. S-SW exposures. 1. Shallow soil (25-60 cm). 2. 0-2.5 cm depth of soil organic matter. 3. Ground vegetation lacks variety and density. 4. Advanced regeneration not usually present. 5. Cold air drainage or pocket. 6. May have slopes 25-45%.	Shelter belt: 1.2 - 1.8 m leave strip between 18 - 36 m harvest strip (HSH Belt). or Shelter group. 10-20 stems 10-cm dbh+, live or dead, left in groups 12-18 m apart (HSH Group).	1. 12-ha size. 2. Shelter belt strips perpendicular to sun. 3. Soil disturbance limited to breaking duff layer; exposure of mineral soil on 20-30% area evenly distributed. 4. Minimize machinery on exposed rocky areas. 5. Logging residue to be left for additional soil cover. 6. No soil compaction on 25 -45% slopes.	1. Clean stand of shelter belts and groups, scattered poles and saplings that are disease infection source within 7 years (SCN). 2. Planting required in 20-40% of area to meet minimum stocking of 250 acceptable seedling/ha at end of 5 years (RPL). Lodgepole pine preferred species.
	B. N-NE exposures. 1. Moderately deep soil (60-100 cm). 2. 2.5-3.8 cm organic matter. 3. Ground vegetation has variety and density. 4. Advanced regeneration usually present. 5. No cold air drainage or pocket.	Clearcut - patch (HCC Patch). Clearcut strip (HCC Strip) in narrow-long strips.	1. 6-8 ha size. 2. Site preparation 30-40% of area. 1. 6-ha size. 2. Less than 0.4 km long. 3. On the contour. 4. Site preparation 30-40% of area.	1. Clean stand of residual disease-infected poles and saplings. 2. Plant 10-20% of area. Lodgepole pine and western larch preferred species.
II. Similar to type I but with at least 750 Lpp seedlings 15-30 cm per ha. Minimum of 250 Lpp seedlings/ha following all activities 1st entry.	I.A. or I.B. above.	Overstory removal (HFR).	1. 16 ha maximum. 2. Minimize machinery on exposed rocky areas. 3. Minimize soil disturbance. Seedbed preparation not needed. 4. Logging residue to be left for additional soil cover. 5. No soil compaction on 25-45% slopes.	1. Clean stand. 2. Release crop trees if needed. 3. Control stocking level through prompt revegetation.

Table 2, continued

Lodgepole pine - grouse huckleberry-pinegrass CL-G2-11 (6LS), Continued				
TIMBER TYPES	SITE FACTORS	HARVEST METHOD ALTERNATIVES	CONSTRAINTS	POST-SALE WORK
III. Lp1-, Lp1=, Lp1≡ Some of this type may be merchantable 10 cm+ dbh.	A. Same as I.A.	No treatment (NTM). Same as I.A.	Same as I.A.	Same as I.A.
	B. Same as I.B.	No treatment (NTM). Same as I.B.	Same as I.B.	Same as I.B.
IV. Lp2 or Lp3 with other species overstory (at least 37 trees per ha) or Other species over- story over Lp2= or Lp3= Example <u>W13-</u> Lp2=	A. Same as I.A.	Shelterwood of other species with shelter belt if needed to modify site.	Same as I.A.	Same as I.A., overstory to be removed when new stand established.
	B. Same as I.B.	Shelterwood of other species.	Same as I.A. except site preparation on 30-40% of area.	Same as I.B., overstory to be removed when new stand established.
V. Lp3-, Lp2-, Lp1- Light stocking may indi- cate extreme site conditions.	Same as I.A.	No treatment. Same as I.A.	Same as I.A.	Same as I.A.
VI. Lp2 or Lp3 Over other species saplings and poles (must have 250 T.P.H. in crop trees class following all activities this entry).	Same as I.B.	Same as II.	Same as II plus log length skidding, pre- located skid trails, stage logging.	Same as II.
Lodgepole pine - big huckleberry CL-S5-11 (7LM).				
Similar to Lpp-grouse huckleberry-pinegrass. Productivity a bit lower - silvicultural guidelines are the same.				
Lodgepole pine - grouse huckleberry CL-S4-11 (7LS). May be a mixture with subalpine fir communities.				
Higher elevations, colder sites. Regeneration and other revegetation limited by temperature and growing season factors. Do not clearcut; maintain shelter over site; protect ground cover; limit site disturbance to minimum.				

should never be less than one-half the 1974 amount. This applies not only to lodgepole, but to all timber stands. It is intended that dense cover areas will remain undisturbed until adjacent harvest units have regenerated and replaced the cover areas lost (at least 12 years).

Around nearly all openings there will be a fringe area. These areas are usually zones of transition, showing complex plant succession different from the three major Blue Mountain lodgepole pine types. Depth of the fringe area will vary and can be determined by examination of ground vegetation. Adjacent to openings, there will often be rocks showing on the surface. These fringe areas are high in value as elk forage and as habitat for a variety of other species of wildlife. At least 50 percent of the fringe areas around meadows, grasslands and other openings should be left undisturbed in the initial entry.

Closure of some roads to motorized vehicles is recommended. This will mean closing certain roads or areas during and after the timber harvest operation for at least the period 25 September through 30 November. As a rule, there should be no more than 1.6 km (1 mi) of road open to vehicle travel during the deer and elk season per 5.2 km² (2 mi²) of land. This will provide sufficient areas of elk sanctuary to help offset the temporary 12- to 15-year loss of escape cover. An exception to this would be during active salvage logging when most roads will be needed for timber sale activities. Clearcuts that will make good elk forage areas should definitely be included in road closure plans.

As much as possible, roads should be located in natural openings, except meadows, or in areas of more open timber that are not considered important for dense escape cover. Special emphasis should be placed on protecting meadows, riparian vegetation, elk travel routes, and on road alignment and sight distances when locating roads.

Grasses palatable to elk should be seeded promptly on all soil disturbed by logging. A rate of 2.3 to 4.6 kg per ha (2 to 4 lb/acre) will not be detrimental to establishment of tree seedlings. A legume should also be seeded if an adaptable species can be found.

Special effort should be made to complete all management activities (road construction, logging, slash treatment and rehabilitation) within a sale unit or cluster of units within two field seasons.

In larger areas of continuous timber (405 ha or more) where natural openings are limited, it is desirable to create or maintain small (2- to 8-ha) blocks of grassland. These would be considered "managed" wildlife forage openings. Location, size and number of these openings will vary according to the natural conditions.

Habitat for those species of wildlife dependent on snags, cull trees, down logs or patches of larger-sized (≥ 50 cm dbh) trees (lodgepole, associated species, ponderosa pine) should be provided in each 12,150- to 16,300-ha (30,000- to 40,000-

acre) harvest block. A snag is any standing dead tree or portion of the stem of a standing dead tree with a minimum of 25 cm (10 inches) dbh and a minimum height of 30 m (100 ft) that still contains at least 10 percent sound wood. Recommendations are to leave

1. Eight existing snags per ha (3/acre) in harvest units;
2. Five live trees (46 cm dbh or over) per ha (2/acre) for future snags in harvest units;
3. Various 0.4- to 4.0-ha (1- to 10-acre) snag patches to total 20 ha per 405 ha (50 acres/1000 acres) of timbered area;
4. Eight cull logs (1.1 m³ or larger) per ha (3/acre) in harvest units.

Availability of the various snag and cull materials will determine what is actually left on specific harvest areas.

Streamside-Fisheries

The beetle epidemic area contains some of the most productive steelhead and salmon spawning streams in the Columbia River system. Maintenance of high quality and quantity of water during low flow periods is essential to maintain desirable levels of these important races of anadromous fish.

The Lane-Peet area has two major stream systems—Camas Creek, which is a tributary of the John Day River, and Meadow Creek, which is a tributary of the Grande Ronde River. Camas Creek and its tributaries support a large run of summer steelhead estimated as high as 2000 fish. As many as 1200 of these fish spawn in the Lane-Peet area. Meadow Creek and its tributaries support a smaller run estimated as high as 289 fish. Nearly all of the tributaries within the Lane-Peet area are important for providing spawning and rearing habitat. Steelhead spawn in the months of May and June. Most of the fry are out of the gravel by 15 July. Many of these spawning streams dry up in August and September; the fry in these cases migrate downstream until a perennial flow is found to sustain them. Because of this trait, a tremendous number of kilometers of stream qualify as spawning habitat in the Lane-Peet area.

Streamside trees and vegetation, duff and organic matter are important for providing shade and for filtering and trapping sediment during surface runoff, preventing this sediment from reaching the stream. Higher-than-normal amounts of sediment can be expected to reach stream courses from overland flows during the lodgepole logging operation.

Maintenance of stream shade is an important part of the State Water Quality Standards. Even dead trees without needles and branches provide valuable shade. Therefore, dead lodgepole from the infestation should be allowed to stand near streams where they can provide stream protection for a number of years. Understory vegetation and reproduction will fill in shade voids as dead trees fall.

To avoid stream and streamside environmental degradation, a buffer strip is needed along all Class I through IV streams.² Within this buffer, a reduction in stream sedimentation can be achieved by providing an undisturbed layer of duff, organic matter, soil and understory vegetation on both sides of the stream. Wood fiber can be removed from part of the buffer zone if it is not needed for shade—provided the soil, duff and ground vegetative layers are left undisturbed.

Streamside buffers needed for shade and sedimentation purposes are

Class I, II and III Streams

1. Forty-six meters (150 ft) of undisturbed ground, measured horizontally from the edge of the flood plain due to meandering;
2. On each side of streams having north-south exposures, a 30-m (100-ft) strip of dead lodgepole next to the stream for shade;
3. A 15-m (50-ft) strip next to the stream left uncut for shade requirements on each side of streams having east-west exposures;
4. Where other species are present within the strip and are providing shade, harvest of lodgepole within the strip with careful logging, on a case-by-case basis.

Establishment of these buffers will withdraw about 6 percent of the total lodgepole pine volume from the timber salvage program in the Lane-Peet unit.

Class IV Streams, Including Spring Seeps

Fifteen meters (50 ft) of undisturbed ground measured horizontally from the edge of the flood plain; 30 m (100 ft) measured horizontally when the stream is in very shallow silt loam soils overlying basalts on south exposures.

To minimize stream sedimentation sources away from buffer strips, landings and skid trails should not be located in ephemeral³ drainways and should be water-barred before the fall rains.

²	Class I stream:	Perennial or intermittent stream used as a direct source of water for domestic use and by large numbers of anadromous fish.
	Class II stream:	Perennial or intermittent stream used by large numbers of anadromous fish.
	Class III stream:	All other perennial streams not meeting higher class criteria.
	Class IV stream:	All other intermittent streams or segments thereof not meeting higher class criteria.

Water

The Lane-Peet area averages 63 to 76 cm (25 to 30 inches) of annual precipitation, with over half the amount occurring as snowfall. Mean monthly temperatures range from the low -10s in December and January to the high +10s in July and August. Temperature extremes range from -46° to over +38°C (-50° to +100°F). The frost-free season is very short and frost can occur in every month of the year.

Streams are the main source of flows for the lower drainage systems, with very high quality water being provided.

Water yield from the sale areas has been or will be affected by the beetle epidemic, with or without any salvage operations. The degree of water yield depends largely on the amount of lodgepole pine in the stand, the soil type and mantle, the amount of snow that was intercepted by the original stand, and how rapidly the understory vegetation consumes the increased soil water.

Melt rates in a pure green lodgepole stand within these sales average 0.3 cm (0.1 inch) per day, while an open area melt rate averages 0.7 cm (0.3 inch) per day during the peak melt season.

The degree of increase in the peak runoff will depend largely on the number of small openings added in the timber type. Summer base flows will be higher until roots of the understory vegetation re-occupy the soil mantle.

Soils

Generally, in the Lane-Peet area, the soils of lodgepole pine stands are shallow to moderately deep, and are developed from volcanic ash over basalts. They have thin (0 to 2.5 cm) organic horizons, exhibit low moisture storage capacity, and exist along cold air drainages.

Under these lodgepole types, there is a lack of organic matter which is related to the tree species and ground vegetation. A thin organic horizon limits the site fertility and the chemical interactions (weathering) that break down the mineral soil and release nutrients. The organic horizon also provides soft mat to break up rainfall impact and permits rapid infiltration. Without duff, the direct impact of raindrops on disturbed ash soils results in soil erosion. In addition, this organic layer holds the soil moisture and reduces the soil evaporation rate. On lodgepole sites, this layer then is especially important to protect the soil's limited moisture reservoir.

³ Ephemeral streams carry only surface runoff and hence flow only during and immediately after periods of precipitation or the melting of snow. They form in slight depressions in the natural contour of the ground surface, but do not normally develop sufficient flow to wash or scour their channels; they can usually be identified by the presence of needles or other litter in the depressions.

Slash should be utilized for soil site and regeneration protection. Slash on logged areas should be lopped and scattered on site, with chips from landing residues scattered across disturbed trails and landings. This will provide additional organic matter, shade and protection to these sites. In clearcuts, the slash should be utilized and scattered evenly over the unit. Burning of the slash is not an acceptable solution from the soil resource standpoint because it could destroy all the organic layers within the lodgepole community types.

Frost heave is present in the fall and spring, affecting seedlings on the protected northern sites and soil resources on the shallow southern exposures. These latter sites have pedestalled soils and suffer severe rill and sheet erosion annually. Site disturbance will further degrade the sites and add to stream siltation. These silts are also generally shallow and thus have low moisture storage capacity. This, plus exposure, leads to overland flow and mostly peak runoff discharge. Slash can entrap silts and thus retard the surface flows and contribute to fertility in these areas.

Recreation

The primary detrimental effects of beetle-killed trees on a recreation site are the hazard to life and limb and the loss of shade. Secondary negative effects can be many, including diminished attractiveness of site, reduced protection from weather, etc. All of the above could contribute to lower or, in some cases, no use of the recreation site. Therefore, the objective for developed recreation sites is to provide young shade at the earliest time possible with the least visual evidence of man's management activity to rehabilitate the site.

The phrase "least visual evidence" refers to such items as minimum mineral soil and sod disturbance, low stumps or removal of stumps, protection of shrubs and young trees, and minimum disturbance to campground roads during salvage logging to rehabilitate the recreation site.

The following recommendations are offered to provide recreation sites within timber stands with young shade at the earliest time possible:

1. Close campgrounds or portions of campgrounds to facilitate rehabilitation work.
2. Develop alternative sites in young shaded areas when available.
3. Thin stands in recreation sites to improve their vigor.
4. Replant lodgepole pine or other conifers with fast juvenile growth. Plant fast-growing deciduous trees, such as willow or alder, adjacent to streams or meadows.

Visual

The outbreak of the mountain pine beetle will leave many acres of lodgepole pine dead or dying within the next

few years, which will have a negative visual effect on the forests involved. This will be true even though there are stands of mixed conifers and ponderosa pine in the area which will not be affected by the beetle. Visually speaking, the sooner the dead lodgepole is replaced with regenerated vegetation, the better. However, if those cutting methods selected for regeneration are visually more undesirable than the effect of standing and fallen dead timber, the visual discontinuity of the landscape will have been aggravated or even magnified instead of lessened.

The following recommendations are offered to reduce visual impairment of landscapes in the outbreak area:

1. Insect kill lines should be followed and sharp-edged rectangles or other geometric patterns should be avoided when laying out cutting units. Units should also vary in size, thus repeating the variety of meadow and opening sizes that occur in nature. (Three general size groups would accomplish this: ± 4 ha, ± 8 ha, ± 12 ha.)
2. Leave-trees in shelter-belt units should be in groupings instead of rows, to eliminate the straight line effect.
3. The location of roads should be as well planned as in green sales, with thought given to such things as minimum clearing widths.
4. Fill slopes and ditches of system roads, especially in light-colored soil areas, should be seeded immediately to grasses. Temporary spurs should be seeded as soon as salvage operations cease.
5. A "dead screen" may be useful in slowing down or stopping the eye as it travels over or through large open spaces created by the salvage activities. It is understood that the dead trees will need to be managed as they begin to fall.
6. Existing regeneration groupings should be used as screens wherever possible. Landings may be screened from a major travel route, even though most of the sale area is not.

DISCUSSION AND CONCLUSIONS

Timber

Plan D comes closest of the four plans to meeting the silvicultural objectives: harvesting and prompt regeneration while meeting the guidelines for other resource objectives for the areas.

Utilization of the volume available for harvesting within the other resource guidelines in Plan D is about 10 percent less than in Plan B, which maximizes utilization.

Regeneration processes are lengthened over 21 years instead of 14. The extra time allows additional discretion in choosing stands for treatment and for refinement of regeneration techniques. It is anticipated that in the first entry into

this area stands with the highest site qualities and potential for regeneration or overstory removal (leaving a quality understory) will be selected. The overall result will be a better distribution of age classes within the managed forest.

Plan D has factors that mitigate the harvest and regeneration effects on other resources. While this alternative is not optimum for fiber production, it best meets the multiple-use objectives for this area.

Wildlife

Plan A would have the least impact on big game habitat because it involves no activity with resultant cover losses.

Plan D is the second choice over B and C because it is believed to best meet the stated goal for maintenance of big game habitat. This is primarily the result of spreading the removal of the timber over three entries rather than two. This plan will result in the most diversification and maintenance of dense cover. Plan B would have a significant adverse impact on Rocky Mountain elk. Plan C would also meet the overall goal, but not as well as D.

Hydrology - Fisheries

Plan A would alter the flow regime the least and have the least impact on water quality because it involves no activity.

Plan D is the second choice over B and C because

1. Less country will have activity on it with each entry, so peak flow will be kept at a minimum level.
2. There will be fewer bare soil areas as sources of sediment.
3. More of the acres have a chance to recover hydrologically before other areas are disturbed, thus reducing the peak flow and other hydrologic impacts.

Soils

Generally, this area is composed of discontinuous timber cover separated by natural drainways and shallow scabland side slopes. Timber occurs in fringe units adjacent to drainways, along side slopes, between shallow rocklands and within closed canopy areas of undisturbed cover.

Because this unit is of open nature, with generally shallow soils, fringe timber stands and dissected rainways, the three-phase harvest plan appears to produce the least impact on the soil resource. By operating in only 30 percent of the area at one time, instead of 50 percent, there will be less area exposed at any one time. Three stages will also allow one more evaluation period in which to assess the results of the guideline decisions. The opportunity to alter the guidelines at 30 percent will give a better chance to adjust prescriptions to reach soils management objectives.

Recreation

Management is forced to treat beetle kill sites immediately because of the hazard to life and limb, especially in developed campgrounds. Therefore, the safety hazard is removed under every plan but that of "no action."

Basically, the faster the site is rehabilitated, the sooner new shade is established to replace that lost. Plan B produces relatively rapid rehabilitation with new shade. Plan D offers less evidence of man's management activity in the surrounding environment because of its three-stage entry with moderate delay in rehabilitation time.

Visual

From the standpoint of the visual resource, Plan D is the most desirable because it spreads out the treatment activity over a longer period of time, it returns the visual landscape to its original condition in a moderate amount of time, and it treats only one-third of the total affected area at one time, thus creating more visual variety.

The Forest Supervisors of the Umatilla and Wallowa-Whitman Forests have elected to use the Lane-Peet guidelines to treat the current mountain pine beetle outbreak area. Salvage efforts are under way in the accessible portions of the area as funding becomes available. The National Forest Management Act of 1976 (PL 94-588) has been helpful by setting up the Salvage Sale Fund under Section 14h.

QUESTIONS AND ANSWERS

- Q. Are you applying protective sprays on green trees in campgrounds now (to protect them from mountain pine beetle)?
- A. We are not applying protective sprays on green trees. This method is recommended in the Lane-Peet report, but no funding has been available to actually do it.
- Q. You seem to be proposing lodgepole pine reproduction. Why not species conversion to some other seral species?
- A. Lodgepole pine will naturally regenerate on most of our sites in the Blue Mountains. A species conversion would be very costly. Lodgepole pine can be managed with stocking control after we clean up the existing mess.
- Q. What is the method of regenerating lodgepole to be used with Plan D?
- A. We are relying mainly on natural regeneration, but have provided for supplemental planting where needed (see Table 2 - Silvicultural guidelines, Post-sale work).

- Q. Do you think sale of special products—in this case, small-diameter lodgepole—can be “forced” on the market in order to achieve faster and more complete utilization?
- A. I do not think we can force this large amount of small-diameter lodgepole on the market. The current “soft” chip market must improve before we can sell a significant amount of dead lodgepole.
- Q. Where are the chips shipped to and processed? What percent is being chipped?
- A. The current local chip market is U.S. Gypsum Co. in Pilot Rock, Oregon. Approximately 20 million board feet of lodgepole pine is chipped in the woods annually and trucked to Pilot Rock for processing. Over 1 billion board feet of lodgepole pine has been beetle-killed in the Blue Mountains to date.
- Q. When you say “deficit lodgepole sales,” do you mean negative stumpage rates? If so, how is it financed?
- A. Lodgepole pine chip material appraises at a negative value, but is sold for base rates (\$0.50 per thousand board feet, plus essential sale area betterment needs). Therefore, we sell chip material in combination with lodgepole and ponderosa pine sawlog material.
- Q. What efforts have been made to develop interest in a house log market?
- A. We have had several inquiries concerning house logs. The size specifications for house logs are so specific that only 5 to 8 trees per ha (2 to 3 trees/acre) in our lodgepole stands are acceptable; therefore this market has not developed. A continuing search for additional markets is being carried on by the Oregon State Department of Forestry through their marketing specialist at Fossil, Oregon.
- Q. What are your recommendations for management of the “jack-straw” stage (e.g., residual volumes too low for harvest)?
- A. This unmanageable stage can only be treated by chipping or burning the mess and regenerating the site.

- Q. What management activities are allowed in RARE II areas?
- A. No management activities which would alter wilderness characteristics are allowed in RARE II areas until the land uses are determined for these areas.
- Q. Would you elaborate on your procedure for broadcast burning lodgepole slash? Specifically, what fuel loading was necessary to carry the burn, and how often did it result from your prescribed cutting methods?
- A. On units harvested as saw logs in the past, we have broadcast burned the slash (40-87 tons/ha). Saw log utilization specifications have changed from 22.5 cm dbh and 15 cm top a few years ago to the current 17.5 cm dbh and 12.5 cm top. Therefore, we have had various rates of fuel loading. Most of the lodgepole pine in the Blue Mountains is now dead and only suitable for chips. We are therefore requiring utilization to a 10 cm dbh and 5 cm top where a chip market exists. It is not necessary to burn the remaining fuel (generally less than 7.5 tons/ha). We also retain the light slash for site protection.

REFERENCES

- Amman, G.D., M.D. McGregor, D.B. Cahill and W.H. Klein. 1977. Guidelines for reducing losses of lodgepole pine to the mountain pine beetle in unmanaged stands in the Rocky Mountains. USDA Forest Serv. Gen. Tech. Rep. INT-36. Intermt. Forest and Range Exp. Sta., Ogden, UT. 19 pp.
- Gregg, T.F., R.E. Dolph and J.S. Hadfield. 1976. Important forest pest outbreaks in Oregon and Washington in 1976. USDA Forest Serv. Region 6 yearly rept. Portland, OR. 11 pp.
- Hall, F.C. 1973. Plant communities of the Blue Mountains in eastern Oregon and southeastern Washington. USDA Forest Serv. R6 Area Guide 3-1. Pac. NW Region. Portland, OR. 62 pp.
- Safranyik, L., D.M. Shrimpton and H.S. Whitney. 1974. Management of lodgepole pine to reduce losses from the mountain pine beetle. Forest. Tech. Rep. 1. Northern Forest Research Centre. Edmonton, Alberta, Canada. 24 pp.
- Umatilla National Forest. 1974. Lane-Peet study area, mountain pine beetle outbreak. Interdisciplinary Team Report. Pendleton, OR. 63 pp.

CAUSES OF THE PROBLEM

Biology, Ecology, and Causes of Outbreaks of the Mountain Pine Beetle in Lodgepole Pine Forests

Gene D. Amman

ABSTRACT

The mountain pine beetle (*Dendroctonus ponderosae* Hopkins) typically produces one generation per year. The year begins with adults infesting trees and introducing blue-stain fungi into them in July and early August. Eggs are laid singly in niches on alternate sides of the vertical egg galleries. Larvae hatch and feed in the phloem, usually at right angles to the egg gallery. Larvae overwinter, then complete development in the spring. Pupation occurs in chambers made in the bark and outer sapwood. During endemic periods, beetles infest weakened and injured trees and those infested by other species of bark beetles. Epidemics appear to start when enough such trees are in proximity and emerging brood adults converge and infest a common tree or group of trees of medium to large diameter and medium to thick phloem. The beetle shows a strong preference for such trees, and its survival usually is best in them. Tree stress is not necessary for the start of epidemics. Stand characteristics associated with epidemics are 1) trees more than 80 years old, 2) average tree diameter more than 20 cm (8 inches), 3) a substantial number of trees in the stand with diameter at breast height of 30 cm (12 inches) or more and phloem 0.25 cm (0.10 inch) thick or more, and 4) stand site at an elevation where temperatures are optimum for brood development.

INTRODUCTION

The mountain pine beetle, *Dendroctonus ponderosae* Hopkins, is the most important insect infesting lodgepole pine, *Pinus contorta* Douglas var. *latifolia* Engelm. During endemic periods, only an occasional tree is infested by the beetle. Then, within a period of 6 to 10 years, from 25 to 50 percent of the stand 10 cm (4 inches) diameter at breast height (dbh) and larger will be killed by a beetle epidemic.

The epidemiology of the beetle from the start of the population build-up through the epidemic has been studied and described in considerable detail. This is the period primarily covered by this symposium. The endemic period is yet to be studied in depth. Factors that keep the beetle population low could lead to development of methods for preventing losses to the mountain pine beetle. The endemic period, particularly the endemic-epidemic interface, is the next research area to be emphasized by the Population Dynamics of Primary Bark Beetle research work unit of the Intermountain Forest and Range Experiment Station in Ogden, Utah.

Abundance of suitable breeding material is of prime importance if bark beetle outbreaks are to occur (Rudinsky 1962). The way in which this material becomes available to the beetles differs according to species of beetle and of host tree. Two main theories have to do with the causes of beetle infestations: 1) the classical theory holds that some stress factor, such as drought or pathogen, weakens the trees, making possible successful infestation by the beetles and associated fungi; and 2) the alternative theory proposes that physiological maturity of the trees (regardless of stress) is required for build-up of beetle populations. The purpose of my paper is to present an overview of the biology and the ecology of the mountain pine beetle and to explore the causes of epidemics.

BIOLOGY AND ECOLOGY

Distribution and Host Trees

The mountain pine beetle can be found throughout the range of lodgepole pine up to about 56° north latitude and about 1220 m (4000 ft) elevation in British Columbia (Safranyik et al. 1974). Although infestations occur to higher elevations farther south (to about 3354 m in Colorado), these are usually light, resulting in low tree mortality (Amman and

Baker 1972, Amman et al. 1973, Amman et al. 1977). The most important hosts of the mountain pine beetle on the basis of commercial value and intensity of beetle epidemics are lodgepole pine (*Pinus contorta* Douglas var. *latifolia* Engelm.), ponderosa pine (*P. ponderosa* Lawson), western white pine (*P. monticola* Douglas), and sugar pine (*P. lambertiana* Douglas). In addition, whitebark pine (*P. albicaulis* Engelm.), limber pine (*P. flexilis* James), pinyon pine (*P. edulis* Engelm.), bristlecone pine (*P. aristata* Engelm.), and foxtail pine (*P. balfouriana* Greville & Balfour) may be infested (McCambridge and Trostle 1972). Some infestations, at high elevations where whitebark pine is commonly found, have caused heavy losses in whitebark stands during weather favorable for the beetle. Occasionally, native non-host trees such as Engelmann spruce (*Picea engelmannii* Parry), grand fir (*Abies grandis* (Douglas) Lindley), and incense cedar (*Libocedrus decurrens* Torrey) are infested, but no brood is produced (Evenden et al. 1943), although a small brood was produced in Norway spruce (*Picea abies* (Linnaeus) Karsten) in a University of Idaho arboretum (Furniss and Schenk 1969).

Life Cycle

The mountain pine beetle usually completes a single generation per year. Beetles mature in July. Adults average about 0.5 cm (0.2 inch) in length and are dark brown to black in color. Prior to emergence, the new adults feed within the bark to complete maturation. During this feeding period, flight muscles increase in size (McCambridge and Mata 1969, Reid 1958) and about 2 percent of the new brood mate (McCambridge 1970). Feeding adults obtain and store fungus and yeast spores and probably bacteria in a special structure for transporting spores, the maxillary mycangium (Whitney and Farris 1970). When the density of brood adults is high, their feeding chambers may coalesce. Then, when one beetle chews an exit hole through the bark, all beetles within the common chamber emerge through the single hole (Amman 1969, Reid 1963).

Emergence and flight of new adults usually begin after several days of relatively high temperatures and abundant sunshine (Rasmussen 1974, Reid 1962). Beetles emerge only during the warm part of the day, starting when temperatures reach about 19°C (66°F) and ceasing in the afternoon when temperatures drop to about the same level (Rasmussen 1974, Reid 1962). Maximum flight activity generally occurs from 4:00 p.m. to 6:00 p.m. (mountain daylight time) in the mountains of Arizona, Colorado, Idaho and Utah in both lodgepole and ponderosa pine forests (Blackman 1931, McCambridge 1971, Rasmussen 1974). Farther north in Washington and British Columbia, maximum flight activity takes place from 11:00 a.m. to 4:00 p.m. in both ponderosa and lodgepole pine forests (Gray et al. 1972, Reid 1962). Data presented by Powell (1967) suggest that the threshold temperature for flight probably occurs earlier in the day in Washington and British Columbia.

Although emergence may continue for a month or more, usually about 80 percent of the beetles emerge within 1 week. In southeastern Idaho and northern Utah, most emergence and

attacks occurred during 7 days in 1970, 9 days in 1971 and 7 days in 1972. Light thunderstorms may have caused the slightly longer period of peak emergence in 1971; beetles remain in the trees during such weather (Rasmussen 1974).

Emerging adults select and infest living trees. The beetles are strongly oriented to trees of large diameter, and vision is believed to play a strong role in final tree selection (Schonherr 1976, Shepherd 1966). Once the female starts boring into a tree, she produces a pheromone that attracts other beetles to the tree (Pitman et al. 1968). When attacks reach a certain density, an antiaggregative pheromone signals the newly arriving beetles not to attack the tree; so they infest another (Rudinsky et al. 1974). Attacks on successfully infested trees are usually completed within 48 hours (Rasmussen 1974). Differences in attack density observed among trees suggest that the beetles are able to adjust density to the vigor of the tree, generally, with greatest attack density occurring on the largest, most vigorous trees (Cole et al. 1976). Others have related attack density to bark texture (Safranyik and Vithayasai 1971, Shepherd 1965). There is some evidence that the sex ratio of the attacking population may affect attack density toward the end of an epidemic; density appears to increase with the proportion of females in the population (Cole et al. 1976). Changes in sex ratio would affect pheromone production and hence the rate at which attacks would stop.

Evidence of beetle infestation usually consists of pitch tubes where beetles have entered the tree and boring dust in cracks and at the base of the tree. In dry years like 1977, few pitch tubes may be present. Beetle entries that leave no pitch tubes are called "blind attacks" and may be difficult to detect. Although pitch tubes may be absent, orangish-brown boring dust around the base of the tree is a sure sign that the tree has been killed.

Adult beetles bore through the outer bark into the phloem/cambium layer, constructing vertical egg galleries. The late July attack period corresponds well with the beginning of a seasonal decline in tree resistance as determined by tree response to inoculations of blue-stain fungi (Reid and Shrimpton 1971). The greatest resistance, however, occurred in the lowest part of the stem (Reid and Shrimpton 1971), the portion of the tree first infested by the beetles (Rasmussen 1974).

Fungus and yeast spores and bacteria carried by the beetle commence growth in the living phloem and xylem tissues soon after the beetle starts its gallery. Although the role of many of these is unknown, the blue-stain fungi help to kill the tree by interrupting water conduction and causing a rapid reduction in moisture of the sapwood (Amman 1977, Reid 1961). The zone of drying is larger than could be expected from the beetle alone, because of the action of the blue-stain fungi (Reid et al. 1967). This initial reduction in moisture the autumn immediately following attack probably benefits larval survival during the winter. Blue-stain fungi have also been considered to be nutritionally beneficial to the beetle larvae; however, Whitney (1971) found beetles to be in contact with

blue-stain fungi only during the first instar and again after pupation, so the nutritional relationship is not well supported.

Eggs are laid singly in niches along the sides of the gallery. They hatch within a week or so, and the larvae feed in the phloem, usually at right angles to the gallery. Most larvae overwinter in the second or third instar. A few reach the fourth instar before the cold weather of late October and November when they become dormant for the winter. Large larvae survive the winter better than small larvae (Amman 1973). The survivors begin to feed again in April, completing development in June after four instars. Larvae pupate within cells excavated in the bark and the sapwood. Pupae transform into adults from late June to mid-July.

The usual 1-year life cycle can have exceptions that are primarily dependent upon weather and climate. Parent beetles can produce two broods in some years (Reid 1962). After infesting one tree, adults emerge and attack a second. This phenomenon is relatively uncommon in lodgepole pine forests south of Montana. However, in Montana, for example, trees along Hellroaring Creek in the Gallatin Canyon showed a high rate of parent reemergence in 1973. Reemerging parents then attacked and killed additional trees, thus causing a spectacular increase in damage. It is doubtful that the second attacks produced much brood, because they came so late in the fall that few eggs hatched. Heat units are insufficient for all eggs to hatch when beetles infest trees in late August (Reid and Gates 1970). All eggs and many small larvae are killed by cold winter temperatures (Amman 1973).

Two years may be required for the beetle to complete a generation at high elevations in eastern Montana and central Idaho (Evenden et al. 1943, Gibson 1943) and in northwest Wyoming at elevations above about 2438 m (8000 ft) (Amman 1973). Cool temperatures delay development and emergence of beetles (McCambridge 1974). Reid (1962) found that the beetle required 2 years to complete a generation in Banff National Park, Alberta, in 1956, although previously he had noted that a generation was completed in a single year in the Park. Thus, the life cycle of the beetle will vary because of weather differences from year to year and place to place, because of elevation and latitude.

Infested trees can be detected by aerial surveys after the foliage has dried and changed color (Klein 1973). As the foliage dries it turns from green to pale green in the spring, then to light orange, and finally to a bright orange by July. Emergence holes in late summer signify that the brood has left the tree to infest green trees.

Factors Affecting Brood Survival

Factors affecting beetle survival within trees have been studied in many infestations. Some individual causes of beetle mortality have been studied in considerable depth. For example, DeLeon (1935a, 1935b) studied the small wasp,

Coeloides dendroctoni Cushman, and the fly, *Medetera aldrichii* Wheeler, respectively the most important insect parasite and insect predator of the mountain pine beetle. DeLeon concluded that *Coeloides* was the mountain pine beetle's most important natural enemy because it parasitizes larvae that are almost mature and ready to pupate. These larvae have a high probability of becoming adults, emerging and attacking other trees if they are not parasitized by *Coeloides*. On the other hand, *Medetera* consumes most beetle larvae in the fall. Many of these larvae would be killed by other causes, such as cold winter temperatures and drying, even if *Medetera* did not kill them.

Reid (1963) reported a comprehensive study of the beetle and its mortality factors in south-central British Columbia. He concluded that beetle survival was more closely correlated with tree diameter than with any other factor he studied. Reid (1963) also found a low degree of association between beetle survival and other factors, including predators, parasites, resinosis, egg gallery density and moisture content of the tree. Factors limiting outbreaks in the study area were thought to be the high resistance of most trees and their generally small size (Reid 1963).

Amman (1969) related beetle production to bark thickness and later to phloem thickness (Amman 1972, Amman and Pace 1976). Phloem is generally thicker in trees of large diameter (Amman 1969, 1975) and is more closely related to diameter growth than to any other factor (Cole 1973). The generally thinner phloem in trees of small diameter, coupled with excessive drying, results in low brood survival in such trees (Cole et al. 1976). The greater amount of drying in trees of small diameter is probably related to the thinner sapwood in small mature trees (Fig. 1).

Berryman (1976) evaluated the effects of phloem thickness, cortical resin canals, predation by woodpeckers, intra-specific competition, parasitism and resinosis in the egg gallery on brood survival. His study corroborated the importance of phloem thickness to beetle survival and showed the negative effect of phloem resin canals on brood production. In the laboratory, larvae avoided areas in the phloem that had many pitch pockets (Amman 1972).

Cole (1974, 1975) evaluated the effects of the following mortality factors on a beetle population in southeast Idaho: crowding, temperature, drying, pitch, pathogens, woodpeckers, parasites and predators. He concluded that none of these mortality factors offered regulatory influence on the beetle population. Cole (1975) found that a beetle has a better chance to survive in trees of large diameter, even when phloem is thin, than in trees of small diameter. Greater survival in large trees with thin phloem is probably related to the slower rate of drying in such trees.

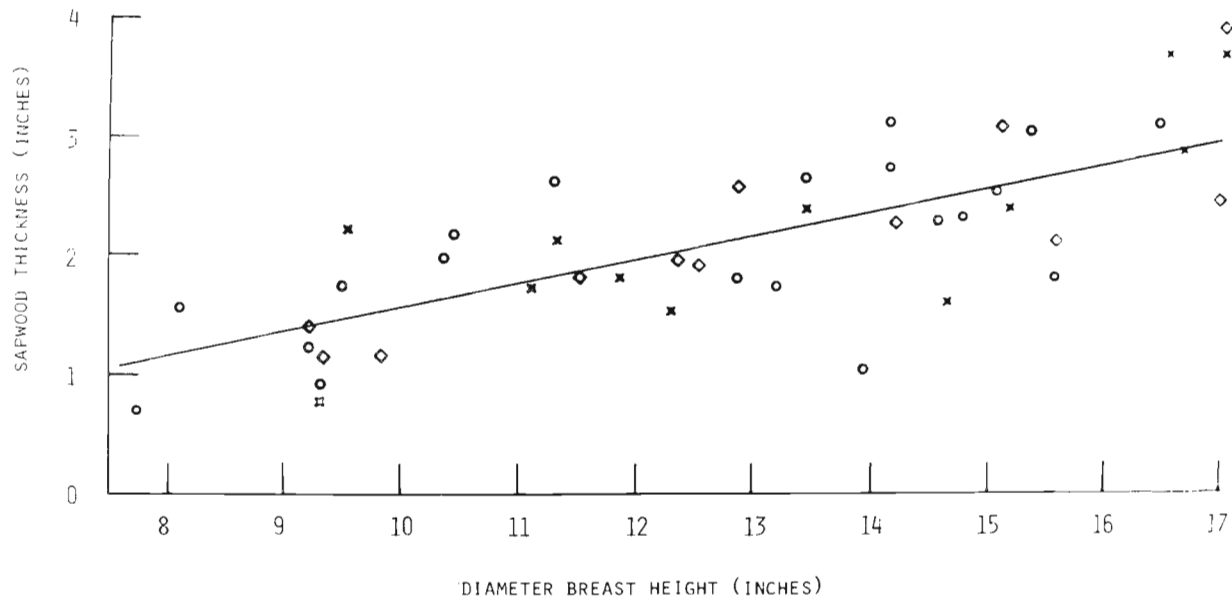


Fig. 1. Sapwood thickness (1 inch = 2.54 cm) at breast height for lodgepole pine trees killed by mountain pine beetles in 1971 (◊), 1972 (x), and 1973 (O), Bear River, Wasatch National Forest, Utah.

CAUSES OF BEETLE OUTBREAKS

Behavior of the mountain pine beetle differs between endemic and epidemic population levels. Hopkins (1909) stated that the mountain pine beetle prefers to attack injured and felled trees. We know from our observations and those of others that he was referring primarily to endemic beetle populations attacking injured trees and that infestation of felled trees is rare in lodgepole pine. Within the same paragraph, Hopkins also wrote, "As a rule, the largest and best trees are attacked first . . ." Again, from many observations, we know that this statement applies to epidemic populations. Craighead et al. (1931) stated that the mountain pine beetle is usually found in lodgepole pines that have been weakened by fire, by lightning or by other causes during endemic periods. However, during epidemics "... it is the larger, thick-barked trees that are first attacked . . ."

During endemic periods, we have found the mountain pine beetle associated with *Pityophthorus* and *Ips* spp. in trees that clearly were infested first by the last two bark beetle species. These trees were usually well below average in growth, had thin phloem and produced few beetles. In addition, we found mountain pine beetles attacking trees severely injured by porcupines.

The undersides of trees blown over but still attached by some roots are occasionally infested. In one case, a few beetles were found in bark on the underside of a log—the tree had been cut during powerline construction. Because they occasionally observed mountain pine beetles in logs or windthrown trees, entomologists thought this behavior could be exploited by using trap trees to attract the beetles. Trap trees have been successful in dealing with the spruce beetle, *Dendroctonus rufipennis* (Kirby) (Nagel et al. 1957); however, attempts to attract the mountain pine beetle in lodgepole pine have failed in the Rocky Mountains.

Shrimpton and Reid (1973), who used inoculation of blue-stain fungus as a measure of tree resistance to mountain pine beetle infestation, suggested that endemic populations maintain themselves by infesting trees that are least resistant.

During endemic periods, the behavior of infesting injured or weakened trees or those of low resistance apparently enables the beetles to maintain their populations at low levels while the stand is growing into conditions that will support an epidemic.

The change from endemic to epidemic beetle infestation is a period of prime importance. Generally, when few beetles

infest a vigorous tree, they are pitched out or eggs laid during gallery construction and fungi introduced by the beetles are killed by resin (Reid and Gates 1970, Reid et al. 1967). We believe that the change from endemic to epidemic populations occurs when subpopulations within scattered trees are close enough to converge on a common tree or group of trees of medium to large diameter and moderate to thick phloem. In such trees, beetle production is greatly increased. The epidemic can start then. If weather conditions are unfavorable, however, the population may decline, in which case, several years may again be required before an epidemic gets under way.

Berryman (1976) theorized that sudden tree stress would allow beetles to infest recently vigorous trees that still have thick phloem for greatly increased beetle production. A long-term decline in tree vigor, such as might occur because of tree disease, would result in a reduction in growth and in phloem thickness. Such trees would produce small numbers of beetles (Amman 1972).

Under epidemic conditions, the beetles most certainly are dependent upon the best trees in the stands for population build-up. As a result, tree losses are usually intensive and extensive. It is therefore essential that we understand the behavior and the dynamics of the beetle under both endemic and epidemic conditions, particularly at the interface of the two.

Theory Based on Weakened or Stressed Trees

Factors that could contribute to bark beetle outbreaks, such as tree injuries or stress, were reviewed by Rudinsky (1962). The classical theory for bark beetle outbreaks emphasizes some form of tree stress or decline in vigor. Stress factors that have been mentioned as possible causes for mountain pine beetle epidemics are insect defoliation, tree disease and drought. Because of the importance of phloem thickness to epidemics of mountain pine beetle (Amman 1972) and the direct relation of phloem thickness to radial growth of lodgepole pine (Cole 1973), Berryman (1976) suggested that the effects of stress may not be immediately apparent in phloem thickness because the tree retains an accumulation of several years of phloem growth (Cabrera these proc.). However, an examination of xylem for recent stress would be easier and just as reliable.

Insect Defoliation/Mountain Pine Beetle Associations

Defoliation would provide one of the most rapid stresses to which a tree could be subjected. Lodgepole pines in Yosemite National Park defoliated by the lodgepole pine needle miner (*Coleotechnites milleri* Busch) were later killed by the mountain pine beetle (Patterson 1921). However, Patterson also reported beetle infestations in that area before defoliations by needle miners. According to Stark and Cook (1957), an outbreak of a needle miner (*C. starki* (Freeman)) in southeastern British Columbia severely weakened and killed some lodgepole pines, but did not result in increased bark beetle activity; however,

there was little bark beetle activity anywhere in that region at that time (R.W. Stark, pers. comm.,¹ 2 June 1978).

Mountain pine beetle infestations occurred in lodgepole pine defoliated by the pandora moth (*Coloradia pandora* Blake) in Utah; however, it was believed that these were extensions of an older beetle infestation adjacent to the defoliated area and were not specifically related to defoliation (Carolyn and Knopf 1968). Nor were infestations of pandora moth in Colorado and Wyoming followed by bark beetle outbreaks.

Tree Disease/Mountain Pine Beetle Associations

Partridge and Miller (1972) examined root rot/beetle associations in several species of conifers in Idaho, including lodgepole, ponderosa and western white pines. Among the pines, they found a significant association between only *Armillaria mellea* (Vahl ex Franco) Kummer and beetles in ponderosa pine. Of a total of 32 trees, 3 contained both beetles and fungi, 2 had beetles only and 2 had fungi only. The authors did not mention the species of bark beetles found.

Another almost ubiquitous disease of lodgepole pine, dwarf mistletoe (*Arceuthobium americanum* Nuttall ex Engelman), has been suspected of contributing to the large infestations of mountain pine beetle within the Intermountain area. Parker and Stipe (1974) attempted to evaluate the association of mountain pine beetle and mistletoe in lodgepole pine. They concluded that the beetle shows some preference for the trees most heavily infected with mistletoe. Few trees with a dbh of less than 25 cm (10 inches), even though heavily infected by mistletoe, were attacked by the mountain pine beetle in the stands examined by Parker and Stipe (1974). The beetle's strong preference for trees of large diameter makes it difficult to separate the influence of mistletoe from that of diameter. McGregor (these proc.), however, was able to achieve a separation of these effects. He observed that the proportion of trees killed in heavily mistletoed stands was less than in stands that had little or no mistletoe.

During early dwarf mistletoe infection of lodgepole pine, growth is stimulated at the site of infection and results in localized thick phloem. Our observations show that when beetles infest trees that have infection sites of mistletoe on the main bole these sites produce significantly more beetles per unit area than the remainder of the tree. In trees with medium to heavy mistletoe infections in the crown, however, phloem is significantly thinner than in uninfected trees (Roe and Amman 1970).

If the mountain pine beetle infested heavily diseased trees in which tree growth was drastically affected, it is doubtful that a surplus of brood adults would be produced. A surplus is the number over and above the number of parents that

¹ R.W. Stark is currently at the College of Forestry, Wildlife and Range Sciences, University of Idaho, Moscow, ID 83843.

attacked and killed the tree. Consequently, the population of beetles would be expected to decline.

Drought/Mountain Pine Beetle Associations

Drought has long been considered a major contributing factor to outbreaks of the mountain pine beetle.

Hopping and Mathers (1945) reported that two outbreaks (Kootenay and Banff, Canada) of the mountain pine beetle in lodgepole pine occurred during a period of deficient moisture. Although Powell (1969) found no strong relation between weather and beetle infestations in western Canada for a 60-year period, infestations were more likely to occur when spring and summer temperatures were above normal and precipitation was below average during the growing season.

Growth data from lodgepole pine in the Bear River drainage on the north slope of the Uinta Mountains in Utah showed that the present infestation increased sharply about 1969, during moist years, and continued to spread under average to better-than-average precipitation. The few trees that were infested in 1968 were widely distributed in the stands. These trees had shown increased growth starting about 1959 (Fig. 2). Non-infested trees in the stand showed a 28 percent

increase in growth in 1969, and trees infested that year (average dbh 27.5 cm) showed an average emergence of 0.03 beetles/cm² (28 beetles/ft²) of bark surface. Moisture content of infested trees averaged 16 percent (range 0 to 26%) as determined by an electrical resistance meter about 3 weeks before beetle emergence. Beetle production during this period of favorable moisture conditions was compared with beetle production that occurred during the dry 1976-1977 generation year. Trees that were infested in 1976 (average dbh 25 cm) showed the same growth as in 1975, the result of precipitation coming as snow the winter of 1975-1976 and rainfall early in the summer of 1976. However, lack of precipitation during late summer, fall and winter of 1976-1977 resulted in excessive drying of infested trees. Average moisture content was 11 percent (range 7 to 18%) on a fresh oven-dry weight basis about 3 weeks before beetle emergence in 1977. These trees yielded an average of only 0.0015 beetles/cm² (1.4 beetles/ft²). Tree mortality declined following this drastic reduction in the beetle population.

Our observations in lodgepole pine are in general agreement with those of Blackman (1931) in ponderosa pine in northern Arizona. He suggested that an increase in the moisture available to the tree during average or better-than-average precipitation results in increased brood survival of the beetle.

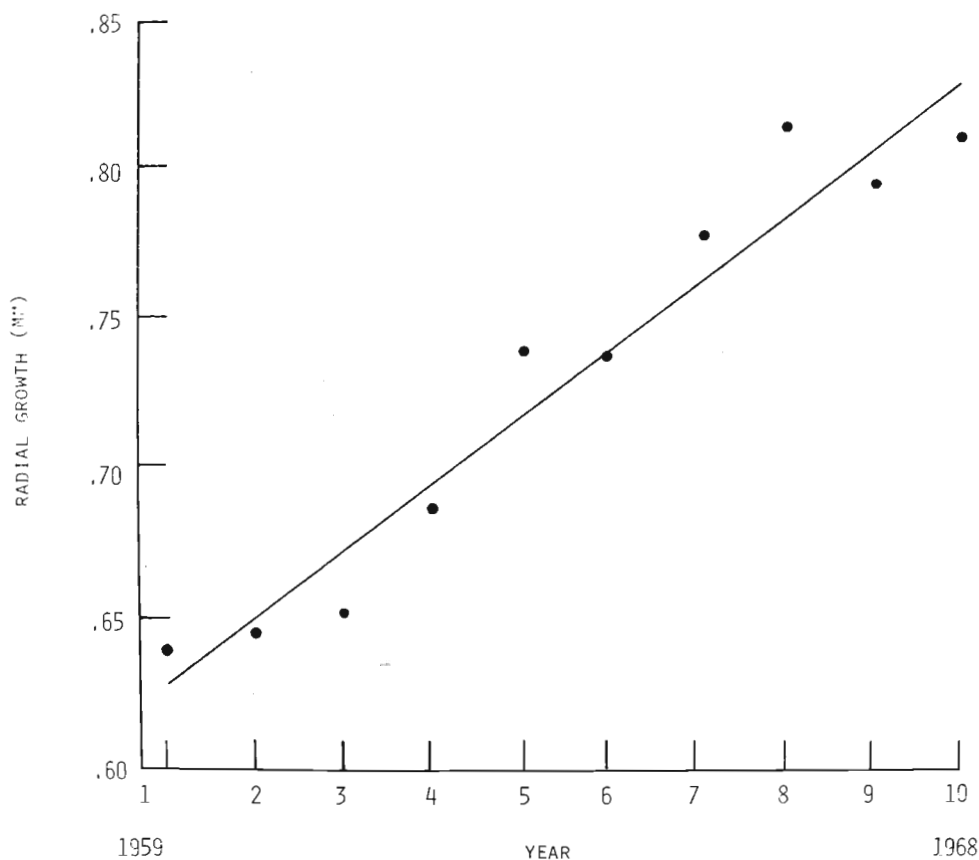


Fig. 2. Average growth of lodgepole pine trees (N = 45) before infestation by mountain pine beetle in 1968. Level of infestation was about 1 tree per 39 ha (100 acres); average diameter breast height of infested trees was 33 cm (13 inches). Bear River, Wasatch National Forest, Utah.

A marked deficiency in available moisture associated with drought results in decreased brood survival.

From this examination of tree stress/mountain pine beetle associations, it can be seen that none of the factors has been studied in depth. Specific studies are needed to establish conclusively the significance of stress factors in mountain pine beetle epidemiology.

Theory Based on Maturation of Lodgepole Pine Trees

I propose that the cause of mountain pine beetle infestations is based on physiological changes of the tree associated with good vigor, not stress. There are four main conditions that must be met for epidemics of the beetle to occur. These are 1) sufficient numbers of trees of large diameter, 2) thick phloem in many large trees, 3) optimal age of trees, and 4) optimal temperature for beetle development.

Effect of Tree Diameter

The mountain pine beetle usually selects the largest trees in the stand to infest, at least during a major epidemic and the few years that precede it (Cole and Amman 1969, Evenden and Gibson 1940, Hopping and Beall 1948). These are the most vigorous trees in the stand (Roe and Amman 1970).

The preference of the beetle for trees of large diameter is apparent when the proportional loss for each diameter class is calculated for an entire infestation. Trees killed by the beetles ranged from 1 percent of the trees with a dbh of 10 cm (4 inches) to 87 percent of the trees with a dbh of 41 cm (16 inches) and larger in two stands in northwest Wyoming (Cole and Amman 1969). Losses reported by other authors (Evenden and Gibson 1940, Hopping and Beall 1948, Parker 1973, Reid 1963, Roe and Amman 1970, Safranyik et al. 1974) show a similar relation of mortality to tree diameter. In addition, the preference of the beetle for large-diameter trees is apparent each year of a major infestation (Cole and Amman 1969).

Safranyik et al. (1975) showed tree mortality to be proportional to the basal area that the diameter class represented in the stand, and suggested that the beetles attack trees according to the surface area that each diameter class represents. Burnell (1977) then presented a dispersal/aggregation model for the beetle in lodgepole pine stands based on a random attack pattern and surface area relations of the trees.

Washburn and Knopf (1959) reported that 3 years of aerial surveys showed the beetle's preference for large open-grown or edge trees during the early stages of infestation to be similar for all epidemic centers. They stated, "Invariably, the epidemics have gotten their start in full-crowned trees, but not necessarily the oldest or biggest, usually located on the outer edge of the timber bordering open rangeland, or lake and stream shores." In the more open portions of stands (Fig. 3), the proportional losses of lodgepole pine are much greater.

Effect of Phloem Thickness

Trees on edges or in the more open stands are usually growing faster than those within stands, and consequently have thicker phloem. The evolutionary basis for the beetle's behavior of selecting trees of large diameter and in more open stands is probably related to the high probability of encountering thick phloem (Amman 1975) that results in high beetle production (Amman 1972, Amman and Pace 1976). Estimates of beetle production from trees in northwest Wyoming ranged from 300 for trees 20 to 23 cm (8 to 9 inches) in diameter to over 15,000 for trees 46 cm (18 inches) in diameter (Cole and Amman 1969). Klein et al.² sampled emergence holes over the entire bole of infested trees and obtained results of even greater magnitude. They reported a range of emergence holes from 152 for a 20-cm (8-inch) tree to over 18,000 for a 46-cm (18-inch) tree. On the average, the number of beetles produced in small trees is less than the number of parent beetles that killed the tree. In contrast, a large surplus of beetles is usually produced in large trees. When the evolutionary strategy of the beetle is viewed over many generations of lodgepole pine, the killing of the largest trees as they become mature or slightly before they reach maturity in persistent and climax lodgepole pine stands provides a continuous supply of food, helps maintain the vigor of the stand, and keeps the stand at maximum productivity (Amman 1977).

Phloem thickness usually increases as diameter increases, yielding coefficients of determination ranging from 0.69 to 0.95 for stands in Montana, Idaho and Utah (Table 1). Although this relation exists for all stands we have measured, the phloem thickness for any given diameter will differ among stands because of differences in stocking level and site quality. For example, Cole and Cahill (1976) predicted that beetles in a stand in Colorado would not build up and cause heavy losses because the stand contained few trees having either large diameter or thick phloem. That prediction has held to date (Cahill, pers. comm.,³ 3 April 1978). Conversely, on good sites, phloem for any given diameter is generally thick—for example, the findings of McGregor et al. (1975) in the Lazier-Meadow Creek area of western Montana. Losses in these stands now have exceeded 750 trees per hectare (300 trees per acre) and are some of the heaviest ever attributed to the mountain pine beetle (McGregor et al. 1977).

The effect of stand density on beetle production was noted by Amman (1969) and is probably related to phloem thickness, which declines with increased stand density (Amman et al. 1977). Brood production (measured as emergence holes) from trees having thick bark in the least dense stands was 0.13 per cm² (125 per ft²) of bark surface, over 4 times

² Klein, W.H., D.L. Parker and C.E. Jensen. (In preparation). Attack, emergence and stand depletion trends of the mountain pine beetle, *Dendroctonus ponderosae* Hopkins, during an epidemic (Coleoptera: Scolytidae).

³ D.B. Cahill is currently at Forest Insect and Disease Management Division, USDA Forest Service, Lakewood, CO.

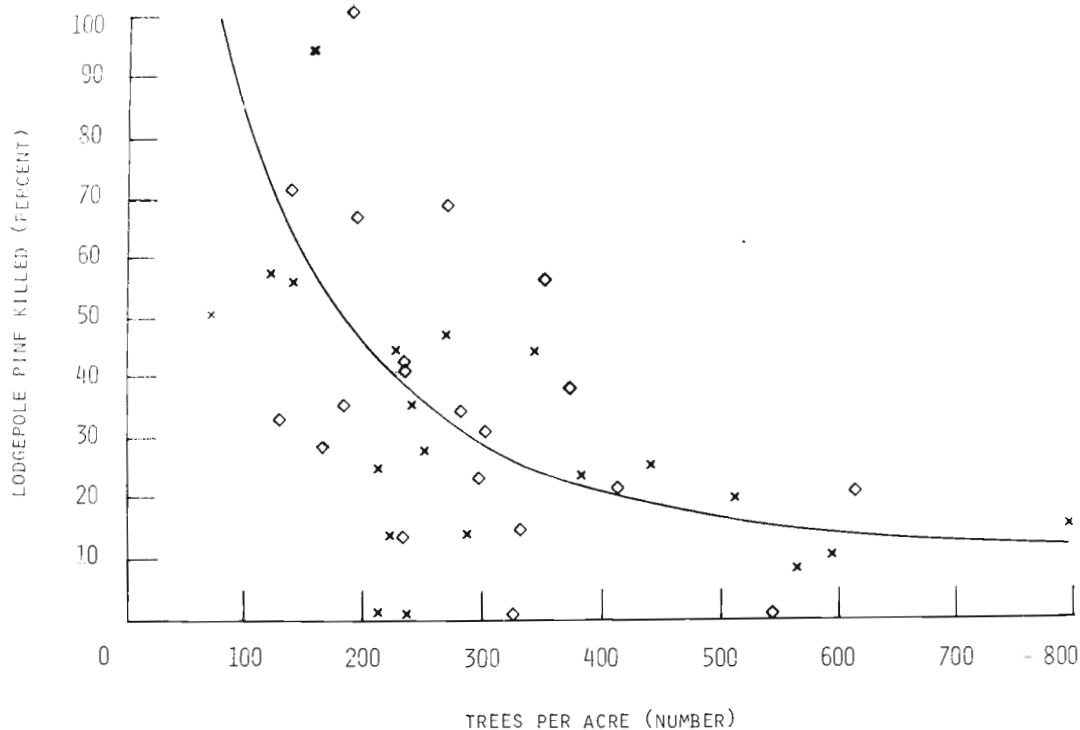


Fig. 3. Percent of lodgepole pine trees killed in relation to tree density of all species 10 cm (4 inches) diameter breast height and larger on Pilgrim Mountain, Grand Teton National Park, Wyoming (◇) and Pacific Creek, Teton National Forest, Wyoming (x). Multiply numbers of trees/acre by 2.5 to obtain approximate numbers/hectare.

greater than in the most dense stands, which had 0.03 per cm^2 (30 per ft^2).

Tree losses also have been related to habitat type (Roe and Amman 1970). A habitat type includes all sites with the potential of supporting the same climax plant association (Daubenmire and Daubenmire 1968) and reflects a difference in environment from other habitat types. Both lodgepole pine and the mountain pine beetle react to a given environment in certain ways, as evidenced by differences in growth and phloem thickness of lodgepole pine (Cole 1973) and in intensity of infestations by the mountain pine beetle (Roe and Amman 1970, McGregor these proc.).

After radial growth, habitat type was the second most important variable explaining variance in phloem thickness in all higher ranking regressions of from two to six independent variables (Cole 1973). Consequently, infestations of mountain pine beetle probably can be expected more frequently on sites providing for the best growth of lodgepole pine.

Effect of Age

Age of host trees is a commonly considered variable in mountain pine beetle infestations. Infestations seldom occur in

lodgepole pine stands less than 60 years of age and there is only moderate probability of infestation in stands 60 to 80 years of age (Safranyik et al. 1974). The age of host trees points clearly to the necessity of a change from juvenile to mature tree for successful brood production by the beetle.

Although part of this age difference may be associated with the generally smaller diameters of trees less than 60 years old, other elements also are involved. Phloem in young trees tends to be more spongy and resinous. Shrimpton (1973) found that blue-stain fungi artificially inoculated into such trees did not establish well because of the greater resinous response of young trees. Tree resistance was found to be highest in the 41- to 60-year age class, where about 90 percent of the trees showed resistance to inoculations. After that age, resistance to blue stain dropped rapidly, with only 30 percent of the trees 111 to 140 years old showing resistance to blue-stain infection. Occasionally, we have found young trees that have been infested and killed, but such trees tend to dry rapidly and few if any brood complete development. Shrimpton and Reid (1973) found fungal inoculation useful in categorizing trees that were resistant and those that were non-resistant to beetle infestation. Peterman (1977), however, obtained poor results when he used the method.

Table 1. Relation of phloem thickness to diameter at breast height of lodgepole pine trees.

Plot location	Coefficient of determination (r^2)	Y intercept	Regression coefficient
Camas Creek, Glacier National Park, MT ¹	.69	.036	.0031
Lazier Creek, Lolo National Forest, MT	.86	.023	.0067
Calyx Creek, Kootenai National Forest, MT	.81	.034	.0038
Solo Joe, Kootenai National Forest, MT	.88	.012	.0052
West Yellowstone, Gallatin National Forest, MT	.95	.043	.0050
Pineview, Targhee National Forest, ID	.77	.057	.0033
Warm River, Targhee National Forest, ID	.88	.027	.0066
Signal Mountain, Grand Teton National Park, WY	.91	.038	.0059
Black Rock Creek, Teton National Forest, WY	.77	.028	.0058
Bear River, Wasatch National Forest, UT	.70	.060	.0042

¹ Mark D. McGregor, Entomologist, Forest Service, Forest Insect and Disease Management, Missoula, MT, kindly furnished data from Camas, Lazier, Calyx and Solo Joe areas.

Shrimpton (1973) reported that resistant trees generally had faster radial growth and thicker phloem than non-resistant trees. When these resistant trees are successfully infested, they usually yield large numbers of beetles and are therefore important to epidemics.

Observations by Roe and Amman (1970) revealed that, in two stands in the Teton and Targhee National Forests that were undergoing beetle infestations, the ages of live trees ranged from 54 to 106 years (average 87) and from 33 to 113 years (average 76) respectively, for trees 10 to 41 cm (4 to 16 inches) dbh. In a third stand in northern Utah where an infestation had started to change from endemic to epidemic, ages ranged from 39 to 220 years (average 97) for trees 15 to 51 cm (6 to 20 inches) dbh. Of the 124 trees measured in this stand, 85 percent would be classed as immature (40 to 120 years) and only 6 percent as overmature, according to silvicultural ages specified by Tackle (1955). Within the stand, the average tree age was 104 years and the average tree size was 33 cm (13 inches) dbh for trees infested by the mountain pine beetle. This apparent age requirement for beetle epidemics points to silviculture as a means of reducing losses to the beetle. Trees probably can be grown to fairly large size under intensive management and be harvested at about 80 years of age without significant loss to the mountain pine beetle.

Effect of Climate

Although diameter and phloem thickness are major items involved in the dynamics of mountain pine beetle populations, epidemics can develop only in stands where temperatures are optimum for beetle development (Amman 1973, Safranyik et al. 1975). Climate becomes an overriding factor at extreme northern latitudes and at high elevations. At these extremes, beetle development is out of phase with winter conditions. Consequently, stages of the beetle that are particularly vulnerable to cold temperatures enter the winter and are killed.

Because of reduced brood survival, infestations are not as intense and fewer trees are killed as elevation and latitude increase (Amman and Baker 1972; Amman et al. 1973, 1977; Safranyik et al. 1974). Tree mortality is low even though an ample food supply (trees of large diameter with thick phloem) exists (Amman et al. 1973).

CONCLUSIONS

Lack of in-depth studies and conflicting evidence that proposes that tree stress contributes to mountain pine beetle epidemics make a clear-cut judgment impossible. Tree weakening occurring over several years will slow growth and result in thin phloem and, subsequently, in low beetle production. However, rapid decline in stand vigor may contribute to the start of an epidemic, as proposed by Berryman (1976), provided enough beetles are present in a stand to take advantage of sudden stress.

On the other hand, evidence that mountain pine beetle epidemics are related to physiological maturity of the trees, irrespective of stress, has considerable support. Epidemics are associated with 1) trees of large diameter, 2) thick phloem that is less spongy and resinous than that found in young trees, and 3) trees about 80 years old, at which age the resinous response is not as great as in younger trees.

The philosophy to which one subscribes will dictate the treatment to be used to reduce tree losses. If stress is considered the primary factor, then one would ignore age. Maintenance of good growth would be the treatment of choice and cutting would take place whenever the stand reaches the desired size. On the other hand, if maturity (as related to tree size, phloem thickness and consistency, and tree age) is considered to be the primary factor, then an upper limit is placed on how long trees can be grown before harvest, regardless of treatment. Emphasis must be placed on intensive management and harvesting of trees at about 80 years of age.

QUESTIONS AND ANSWERS

Q. Is there any intrinsic relationship between tree age and outbreak occurrence, or is age merely confounded with tree size?

A. Age and diameter are related to some extent. There seems to be a maturing of the phloem with age, however, which is important to brood survival of the beetle and probably determines the earliest age that an infestation can occur in a stand. Young trees of large diameter have phloem that is spongy and contains many pitch pockets that phloem of older trees of similar diameter does not have. However, following an epidemic many smaller trees usually survive, frequently of the same age as those killed. These trees must grow to sizes and phloem thicknesses conducive to beetle build-up before the next infestation can occur. These later infestations would not be age dependent.

Q. If temperature is critical for beetle survival, why did the population in West Yellowstone and Yellowstone Park survive?

A. Winter temperatures that occur in these areas are not consistently cold enough to kill most mountain pine beetle brood. The other temperature relation, associated with high elevations, does not seem to apply to most of the stands in these areas. Elevations are low enough for the beetle to complete a generation in a single year, emerge and attack trees early enough that the new brood gets a good start before fall temperatures stop beetle development. At high elevations, however, the beetles may require 2 years to complete a generation, or may complete development but be prevented from emerging by cold fall temperatures. The advanced brood then is killed by winter temperatures.

Q. Is it suspected that drought years affect the blue stain's ability to spread and thus indirectly affect the beetle, or is it a direct effect of drought on the beetle?

A. We don't know enough about the role of blue-stain fungi, except that they appear initially to dry the bark and wood rapidly, but may possibly affect moisture retention in the long run. In the latter case, if the tree dried rapidly before blue stain penetrated most of the sapwood, the beetle would be affected indirectly. Whether this is the case or whether the beetle-infested tree dries only as a direct result of drought, excessive drying of the tree reduces brood survival.

Q. You mentioned that beetles are oriented toward the larger trees in an epidemic. Is this a visual orientation or a matter of greater surface area of larger trees in the stand? Is there a primary attractant or a random selection of the target trees?

A. Evidence is fairly strong that a visual response, but not a strict response to surface area, is involved in final tree selection by the beetle. When the surface area of all trees in the stands 10 cm dbh and larger is considered, the beetle attacks proportionately less surface area in diameters 22.5 cm (9 inches) dbh and less than their representation in the stand. The mountain pine beetle attacks proportionately greater amounts of surface area in diameters 25 cm (10 inches) dbh and larger than their representation in the stand. Consequently, the tree-attack pattern of the beetle cannot be random. Primary attraction involving quantitative differences in terpenes or other host constituents has not been demonstrated.

Q. If phloem thickness is a measure of food for the beetles, then I presume that the nutritional quality of the phloem will be at least as important as phloem thickness per se. One could imagine thick phloem that is nutritionally poor and thin phloem that is nutritionally rich. Apart from the obvious implications of such factors as defoliators and/or leaf and root diseases—all of which would affect the nutritional value of the phloem—what effect do you think the associated blue-stain fungi and particularly yeasts may have on beetle productivity (that is, the course of outbreaks) in thin- and thick-phloemed trees?

A. Most of our work with phloem thickness and beetle production shows a direct relationship between the two, but some of the variance could be caused by differences in phloem quality, and in turn might influence some of the microorganisms. Our work (Amman and Pace 1976) showed that beetles reared from thin phloem were smaller than those from thick phloem, and the sex ratio of beetles from thin phloem was more in favor of females than that of beetles from thick phloem. There seems to have been little work done on yeasts in relation to mountain pine beetle that would answer your question. However, I see no reason to think that quality of the microorganisms associated with the beetle would not change depending upon phloem quality and available moisture. It seems very likely that the quality of microorganisms could receive a big boost when beetles start invading the larger trees. The improved quality of microorganisms when inoculated into small-diameter trees may enable beetles to produce more brood when they eventually must infest small-diameter trees after most large ones are killed. The benefit probably would be short lived, however—one or two generations at best.

Q. How far will beetles travel during flight period (average)?

A. I know of no study that has researched this question. However, I suspect that they fly no farther than is necessary to find a tree that meets their specifications—during early years of epidemics this probably would be no farther than 0.4 to 0.8 km ($\frac{1}{4}$ to $\frac{1}{2}$ mile). However, as most desirable trees are killed the beetle would need to fly farther in search of suitable host trees. During

endemic periods, flight may be no farther than to find a tree that has been severely injured or infested by other species of bark beetles. What we see so far would suggest that beetles from the larger trees having thick phloem on the average are larger, and would be able to fly farther because of greater fat content. Studies on Douglas-fir beetles indicate that beetles can fly over 48 km (not continuously). Collections of beetles from snow fields suggest that beetles are often caught in updrafts and deposited many miles away.

Q. How big were the trees in the British Columbia needle miner outbreak? Could the reason that the beetles did not come into the stand be related to food supply?

A. Not knowing more about the stands, I cannot answer your question. Several possibilities exist in addition to food supply—weather conditions, no beetles in immediate area, or simply that they did not respond to the defoliated trees.

Q. Based on your theory, how do you explain the existence of thick-phloemed, large-diameter stands of 120 years plus at low elevations in Montana and Idaho?

A. Over the past 20 years we have seen most such stands infested and the large-diameter component killed by the beetles. Some stands have not been infested (yet), but, except for those at high elevations, history would indicate that it is going to happen. Factors that might account for the stands' escape up to now are adverse weather conditions such as cold drainages and no beetles in or near the stands.

Q. If phloem thickness is one key to brood development and phloem thickness is correlated with dbh, how do we account for the high mortality in eastern Oregon?

A. I have not seen the infestations in eastern Oregon, but my colleagues have told me that phloem is thicker for any given diameter than what we have seen in the drier Rockies. Even in the Oregon stands, beetle production in these small-diameter trees probably is not great enough to produce surpluses (numbers in excess of those attacking the tree and those lost during flight). The population increase comes from production in the large trees.

Q. At the time of death, most mountain pine beetle-killed trees show decreased growth and are very slow growing—i.e., 8 to 12 rings per cm (20 to 30 rings to the inch). How can you define these trees as fast-growing and vigorous? If this isn't considered as a stress period, what is it?

A. Most measurements of growth are taken at breast height, and then usually only the width of the ring is measured. I don't think radial increment at breast height is necessarily a good measure of current vigor. Most of these trees, certainly the dominants and co-dominants in which beetle production is high, have only 3 to 4 rings per cm (8 to 10 rings to the inch) in the tops. Vigor should be based on volume of growth to account for the much greater surface area of the older, larger trees.

I have seen beetle infestations increase and do very well during periods of increasing tree growth; therefore, I don't believe that stress is a necessary ingredient for epidemics to start or to continue.

Q. If stress on individual trees is necessary to sustain endemic populations, would not stress on stands create epidemics?

A. During endemic periods, beetle numbers are low, and therefore they would be unable to kill vigorous trees. Consequently, they infest injured trees or those attacked by other species of beetles. When mountain pine beetle from a number of such trees are in close proximity, they have the capability of infesting and killing the most vigorous trees in the stand. My position with respect to tree stress is that it is not necessary for beetle epidemics to occur. I have arrived at this position by seeing infestations develop during periods of good tree growth.

Q. Do you believe that physiological maturity is in fact stress due to limitations of various vital elements necessary for continued vigorous growth?

A. No, I don't think a shortage is involved. I believe that changes occur in the phloem, such as those indicated in Cabrera's examination of phloem—a greater compression of phloem and a reduction in resin canals in the phloem. The trees are still growing well, and certainly if the beetle is oriented to poor-vigor trees, it would have taken those left in the stand rather than the dominant and co-dominant trees that it infested and killed.

Q. Why do you consider stress and age as mutually exclusive explanations—can't both be operative?

A. Age per se cannot be a stress factor as long as the tree is growing well. Stress can occur at any age of the tree's life, and is not limited to one time period such as when it reaches maturity. Maturity and thickness of phloem are the essential items. Consequently, epidemics can occur with or without stress.

Q. How do you define maturity? Is your term "physiological maturity" not surely synonymous to undefined stress?

A. I find it difficult to compare my definition of physiological maturity as stated above to something that is undefined. I suspect that many items that people like to toss in the "stress basket" really are not stress at all—for example, age. The problem with the stress theory is that it has been taken for granted and never examined critically, especially in view of new information on the mountain pine beetle/lodgepole pine interaction. To have credibility, any stress theory is going to need consistency with observed beetle epidemics rather than a long listing of possible stresses without hard data to back them up.

Q. Relief of stress by thinning has been successful in preventing beetle epidemics in young ponderosa pine. Has this been tested in young lodgepole, and if not, do you think it will work?

A. We suspect that thinning changes the microclimate in thinned ponderosa pine stands, and that success may not be solely due to relief from stress. The change in beetle response is usually so dramatic that one could not associate it with a change in tree vigor alone.

Mountain pine beetle is not usually much of a problem in lodgepole pine under 80 years of age. Thinning stands when they are approaching this age, or even well before, may make a difference. It needs to be tested. However, lodgepole pine grows in cooler climates and the beetle may not avoid these stands as it does in ponderosa pine. The beetle shows a preference for the more open lodgepole pine stands throughout most of the type. Just the opposite appears to be the case in ponderosa pine, where the beetles show a preference for the dense stands over much of the type.

Q. Do you speculate that there is any advantage in prescribing a mixed species stand (Douglas-fir and lodgepole pine) for beetle control in lodgepole pine? If yes, what percent of the stand would you prescribe to be lodgepole pine at stand age 60 years?

A. The advantage of a mixed species stand is that when a beetle epidemic occurs, considerable volume will remain after most of the lodgepole pine are killed. The beetle appears to kill proportionately as much lodgepole pine in mixed species stands as in pure lodgepole stands. Whether or not an epidemic is as likely to start in mixed species stands is yet to be determined.

Q. What general similarities or differences exist between ponderosa pine and lodgepole pine as regards mountain pine beetle attraction (infestation)?

A. Behavior of the mountain pine beetle in ponderosa pine seems to be more variable over the range of ponderosa. For example, the beetle seems to prefer the small-

diameter trees in dense clumps in eastern Oregon and in parts of Idaho, Montana and South Dakota. In Colorado, the beetle shows a preference for a greater range in diameters. In southern Utah and northern Arizona the beetle appears to prefer the large-diameter trees. No work has explained these differences in beetle behavior.

In lodgepole pine, the beetle shows a strong preference for large-diameter trees over the entire range, but kills trees even in the small-diameter classes, particularly toward the end of an epidemic (for example, in eastern Oregon and parts of western Montana). In these stands the phloem was thicker for any given diameter class than in stands south of Montana. In general, for population build-up to occur, the beetle must infest the large-diameter lodgepole pines where food (phloem) and moisture (throughout beetle development) are more abundant than in small trees.

Q. To what extent can land managers expect the mountain pine beetle to affect ponderosa pine in areas of associated lodgepole pine?

A. I have not worked in areas where these two species were associated, but I have been told that beetles produced in lodgepole pine are now infesting ponderosa pine in eastern Oregon. At low to moderate population levels of mountain pine beetle, Hopkins' host selection principle (beetles infest the species of plant on which they developed) appears to be operative. We have seen this in white bark pine/lodgepole pine associations. Losses in one host type did not result in corresponding losses in the adjacent host type. However, when epidemics occur, the host selection principle does not appear to hold.

Q. What stand densities would you prescribe for a stand 60 years of age on a habitat type that has a potential growth capacity of 60 cu ft per year?

A. Thinning to basal area of 16.5 m²/ha (80 ft²/acre) probably would result in substantial growth over the next 20 to 40 years. However, keep in mind that the risk of loss to the mountain pine beetle increases considerably with each year after tree age 80.

Q. This morning we saw a picture of an area near a campground where one lodgepole apparently was not hit by bark beetles. Would you speculate on why this has occurred?

A. The tree was located on one end of the group. Therefore, I suspect wind direction, hence direction of beetle flight when the other trees were infested, may have been involved; or there may have been only enough beetles to kill all the trees except that one. I have seen similar occurrences, only to have the beetles return in a year or so to kill the remaining large-diameter trees.

REFERENCES

- Amman, G.D. 1969. Mountain pine beetle emergence in relation to depth of lodgepole pine bark. USDA Forest Serv. Res. Note INT-96. Intermt. Forest and Range Exp. Sta., Ogden, UT. 8 pp.
- _____. 1972. Mountain pine beetle brood production in relation to thickness of lodgepole pine phloem. J. Econ. Entomol. 65:138-140.
- _____. 1973. Population changes of the mountain pine beetle in relation to elevation. Environ. Entomol. 2:541-547.
- _____. 1975. Insects affecting lodgepole pine productivity. Pages 310-341 in D.M. Baumgartner (ed.). Management of lodgepole pine ecosystems. Washington State Univ. Coop. Ext. Serv., Pullman.
- _____. 1977. The role of the mountain pine beetle in lodgepole pine ecosystems: impact on succession. Pages 3-18 in W.J. Mattson (ed.). Arthropods in forest ecosystems. Proc. in the Life Sciences. Springer-Verlag, New York.
- Amman, G.D., and Bruce H. Baker. 1972. Mountain pine beetle influence on lodgepole pine stand structure. J. Forest. 70:204-209.
- Amman, G.D., and V.E. Pace. 1976. Optimum egg gallery densities for the mountain pine beetle in relation to lodgepole pine phloem thickness. USDA Forest Serv. Res. Note INT-209. Intermt. Forest and Range Exp. Sta., Ogden, UT. 8 pp.
- Amman, G.D., B.H. Baker and L.E. Stipe. 1973. Lodgepole pine losses to mountain pine beetle related to elevation. USDA Forest Serv. Res. Note INT-171. Intermt. Forest and Range Exp. Sta., Ogden, UT. 8 pp.
- Amman, G.D., M.D. McGregor, D.B. Cahill and W.H. Klein. 1977. Guidelines for reducing losses of lodgepole pine to the mountain pine beetle in unmanaged stands in the Rocky Mountains. USDA Forest Serv. Gen. Tech. Rep. INT-36. Intermt. Forest and Range Exp. Sta., Ogden, UT. 19 pp.
- Berryman, A.A. 1976. Theoretical explanation of mountain pine beetle dynamics in lodgepole pine forests. Environ. Entomol. 5:1225-1233.
- Blackman, M.W. 1931. The Black Hills beetle (*Dendroctonus ponderosae* Hopkins). New York State College Forest. Tech. Publ. 36, Vol. 4. Syracuse. 97 pp.
- Burnell, D.G. 1977. A dispersal-aggregation model for mountain pine beetle in lodgepole pine stands. Res. Popul. Ecol. 19:99-106.
- Carolin, V.M., Jr., and J.A.E. Knopf. 1968. The pandora moth. USDA Forest Serv. Pest Leaflet. 114. Washington, D.C. 7 pp.
- Cole, D.M. 1973. Estimation of phloem thickness in lodgepole pine. USDA Forest Serv. Res. Pap. INT-148. Intermt. Forest and Range Exp. Sta., Ogden, UT. 10 pp.
- Cole, W.E. 1974. Competing risks analysis in mountain pine beetle dynamics. Res. Popul. Ecol. 15:183-192.
- _____. 1975. Interpreting some mortality factor interactions within mountain pine beetle broods. Environ. Entomol. 4:97-102.
- Cole, W.E., and G.D. Amman. 1969. Mountain pine beetle infestations in relation to lodgepole pine diameters. USDA Forest Serv. Res. Note INT-95. Intermt. Forest and Range Exp. Sta., Ogden, UT. 7 pp.
- Cole, W.E., G.D. Amman and C.E. Jensen. 1976. Mathematical models for the mountain pine beetle-lodgepole pine interaction. Environ. Entomol. 5:11-19.
- Cole, W.E., and D.B. Cahill. 1976. Cutting strategies can reduce probabilities of mountain pine beetle epidemics in lodgepole pine. J. Forest. 74:294-297.
- Craighead, F.C., J.M. Miller, J.C. Evenden and F.P. Keen. 1931. Control work against bark beetles in western forests and an appraisal of its results. J. Forest. 29:1001-1018.
- Daubenmire, R., and J.B. Daubenmire. 1968. Forest vegetation of eastern Washington and northern Idaho. Washington Agr. Exp. Sta. Tech. Bull. 60. Pullman. 104 pp.
- DeLeon, D. 1935a. The biology of *Coeloides dendroctoni* Cushman (Hymenoptera-Braconidae) an important parasite of the mountain pine beetle (*Dendroctonus monticolae* Hopkins) Ann. Entomol. Soc. Amer. 28:411-424.
- _____. 1935b. A study of *Medetera aldrichi* Wh. (Diptera-Dolichopodidae), a predator of the mountain pine beetle (*Dendroctonus monticolae* Hopkins, Coleoptera: Scolytidae). Entomol. Amer. 15:59-91.
- Evenden, J.C., and A.L. Gibson. 1940. A destructive infestation in lodgepole pine stands by the mountain pine beetle. J. Forest. 38:271-275.
- Evenden, J.C., W.D. Bedard and G.R. Struble. 1943. The mountain pine beetle, an important enemy of western pines. U.S. Dept. Agr. Circ. 664. Washington, D.C. 25 pp.
- Furniss, M.M., and J.A. Schenk. 1969. Sustained natural infestation by the mountain pine beetle in seven new *Pinus* and *Picea* hosts. J. Econ. Entomol. 62:518,519.
- Gibson, A.L. 1943. Penetrating sprays to control the mountain pine beetle. J. Econ. Entomol. 36:396-398.
- Gray, B., R.F. Billings, R.I. Gara and R.J. Johnsey. 1972. On the emergence and initial flight behaviour of the mountain pine beetle, *Dendroctonus ponderosae*, in eastern Washington. Z. ang. Entomol. 71:250-259.
- Hopkins, A.D. 1909. Contributions toward a monograph of the scolytid beetles. I. The genus *Dendroctonus*. U.S. Bureau of Entomology Tech. Ser. 17. Washington, D.C. 164 pp.
- 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). Forest. Chron. 24:141-145.
- Hopping, G.R., and W.G. Mathers. 1945. Observations on outbreaks and control of the mountain pine beetle in the lodgepole pine stands of western Canada. Forest. Chron. 21:98-108.
- Klein, W.H. 1973. Beetle-killed pine estimates. Photogramm. Eng. 39:385-388.
- McCambridge, W.F. 1970. Spermatozoa in unemerged female mountain pine beetles, *Dendroctonus ponderosae* Hopkins. Ann. Entomol. Soc. Ontario 100:168-170.
- _____. 1971. Temperature limits of flight of the mountain pine beetle, *Dendroctonus ponderosae*. Ann. Entomol. Soc. Amer. 64:534-535.
- _____. 1974. Influence of low temperatures on attack, oviposition and larval development of mountain pine beetle, *Dendroctonus ponderosae* (Coleoptera: Scolytidae). Can. Entomol. 106:979-984.

- McCambridge, W.F., and S.A. Mata, Jr. 1969. Flight muscle changes in Black Hills beetles, *Dendroctonus ponderosae* (Coleoptera: Scolytidae), during emergence and egg laying. Can. Entomol. 101:507-512.
- McCambridge, W.F., and G.C. Trostle. 1972. The mountain pine beetle. USDA Forest Serv. Pest Leaflet. 2. Washington, D.C. 6 pp.
- McGregor, M.D., D.R. Hamel and R.D. Oakes. 1977. Evaluation of mountain pine beetle infestations, Thompson River Drainage, Plains District, Lolo National Forest, Montana, 1976. USDA Forest Serv., Northern Region Rep. 77-5. Missoula, MT. 8 pp.
- McGregor, M.D., D.R. Hamel, R.C. Lood, H.E. Meyer and S. Kohler. 1975. Evaluation of mountain pine beetle infestations, Lazier and Meadow Creek drainages, Plains District, Lolo National Forest, Montana. USDA Forest Serv., Northern Region Rep. 75-17. Missoula, MT. 11 pp.
- Nagel, R.H., D. McComb and F.B. Knight. 1957. Trap tree method for controlling the Engelmann spruce beetle in Colorado. J. Forest. 55:894-898.
- Parker, D.L. 1973. Trend of a mountain pine beetle outbreak. J. Forest. 71:698-700.
- Parker, D.L., and L.E. Stipe. 1974. Does the mountain pine beetle select and kill dwarf mistletoe-infected lodgepole pine? USDA Forest Serv. Insect and Disease Contr., State and Private Forest. Region 4. 5 pp. + append. (unpublished).
- Partridge, A.D., and D.L. Miller. 1972. Bark beetles and root rots related in Idaho conifers. USDA Plant Disease Rep. 56:498-500.
- Patterson, J.E. 1921. Life history of *Recurvaria*, the lodgepole pine needle miner in Yosemite National Park, California. J. Agr. Res. 21:127-143.
- Peterman, R.M. 1977. An evaluation of the fungal inoculation method of determining the resistance of lodgepole pine to mountain pine beetle (Coleoptera: Scolytidae) attacks. Can. Entomol. 109:443-448.
- Pitman, G.B., J.P. Vité, G.W. Kinzer and A.F. Fentiman, Jr. 1968. Bark beetle attractants: *trans-verbenol* isolated from *Dendroctonus*. Nature 218:168-169.
- Powell, J.M. 1967. A study of habitat temperatures of the bark beetle *Dendroctonus ponderosae* Hopkins in lodgepole pine. Agr. Meteorol. 4:189-201.
- _____. 1969. Historical study of the relation of major mountain pine beetle outbreaks in western Canada to seasonal weather. Forest. Res. Lab., Info. Rep. A-X-23. Calgary, Alberta. 11 pp.
- Rasmussen, L.A. 1974. Flight and attack behavior of mountain pine beetles in lodgepole pine of northern Utah and southern Idaho. USDA Forest Serv. Res. Note INT-180. Intermtn. Forest and Range Exp. Sta., Ogden, UT. 7 pp.
- Reid, R.W. 1958. Internal changes in the female mountain pine beetle, *Dendroctonus monticolae* Hopkins, associated with egg laying and flight. Can. Entomol. 110:464-468.
- _____. 1961. Moisture changes in lodgepole pine before and after attack by the mountain pine beetle. Forest. Chron. 37:368-375.
- _____. 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.
- Reid, R.W., and H. Gates. 1970. Effect of temperature and resin on hatch of eggs of the mountain pine beetle (*Dendroctonus ponderosae*). Can. Entomol. 102:617-622.
- Reid, R.W., and D.M. Shrimpton. 1971. Resistant response of lodgepole pine to inoculation with *Europhium clavigerum* in different months and at different heights on stem. Can. J. Bot. 49:349-351.
- 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. J. Bot. 45:1115-1126.
- Roe, A.L., and G.D. Amman. 1970. The mountain pine beetle in lodgepole pine forests. USDA Forest Serv. Res. Pap. INT-71. Intermtn. Forest and Range Exp. Sta., Ogden, UT. 23 pp.
- Rudinsky, J.A. 1962. Ecology of Scolytidae. Annu. Rev. Entomol. 7:327-348.
- Rudinsky, J.A., M.E. Morgan, L.M. Libbey and T.B. Putnam. 1974. Antiaggregative rivalry pheromone of the mountain pine beetle, and a new arrestant of the southern pine beetle. Environ. Entomol. 3:90-98.
- Safranyik, L., and C. Vithayasai. 1971. Some characteristics of the spatial arrangement of attacks by the mountain pine beetle, *Dendroctonus ponderosae* (Coleoptera: Scolytidae), on lodgepole pine. Can. Entomol. 103:1607-1625.
- Safranyik, L., D.M. Shrimpton and H.S. Whitney. 1974. Management of lodgepole pine to reduce losses from the mountain pine beetle. Can. Dept. Environ., Forest Serv., Pac. Forest Res. Cent. Tech. Rep. 1. Victoria, B.C. 24 pp.
- _____. 1975. An interpretation of the interaction between lodgepole pine, the mountain pine beetle and its associated blue-stain fungi in western Canada. Pages 406-428 in D.M. Baumgartner (ed.). Management of lodgepole pine ecosystems. Washington State Univ. Coop. Ext. Serv., Pullman.
- Schönherr, J. 1976. Mountain pine beetle: visual behavior related to integrated control. Pages 449-452 in Proc. XVIth IUFRO World Congr., Div. II. Oslo, Norway.
- Shepherd, R.F. 1965. Distribution of attacks by *Dendroctonus ponderosae* Hopkins on *Pinus contorta* Douglas var. *latifolia* Engelm. Can. Entomol. 97:207-215.
- _____. 1966. Factors influencing the orientation and rates of activity of *Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae). Can. Entomol. 98:507-518.
- Shrimpton, D.M. 1973. Age- and size-related response of lodgepole pine to inoculation with *Europhium clavigerum*. Can. J. Bot. 51:1155-1160.
- Shrimpton, D.M., and R.W. Reid. 1973. Change in resistance of lodgepole pine to mountain pine beetle between 1965 and 1972. Can. J. Forest. Res. 3:430-432.
- Stark, R.W., and J.A. Cook. 1957. The effects of defoliation by the lodgepole needle miner. Forest Sci. 3:376-396.
- Tackle, D. 1955. A preliminary stand classification for lodgepole pine in the Intermtain Region. J. Forest. 53:566-569.

Washburn, R.I., and J.A.E. Knopf. 1959. Mountain pine beetle conditions in the lodgepole pine stands of Forest Service Region 4. USDA Forest Serv., Div. Forest. Insect Res., Intermtn. Forest and Range Exp. Sta., Ogden, UT. 8 pp. + 9 maps (unpublished).

Whitney, H.S. 1971. Association of *Dendroctonus ponderosae* (Coleoptera: Scolytidae) with blue-stain fungi and yeasts during brood development in lodgepole pine. Can. Entomol. 103:1495-1503.

Whitney, H.S., and S.H. Farris. 1970. Maxillary mycangium in the mountain pine beetle. Science 167:54-55.

Phloem Structure and Development in Lodgepole Pine

Homero Cabrera

ABSTRACT

Thickness of phloem and presence of resin canals in lodgepole pine (*Pinus contorta* Douglas var. *latifolia* Engelm.) are important factors in the successful development of mountain pine beetle (*Dendroctonus ponderosae* Hopkins) broods. Thick phloem is closely related to tree vigor, and contains three components: phloem increment, phloem compression and phloem retention. Individual annual phloem increments make a relatively small contribution to total phloem thickness (usually less than 10%). Compression of old phloem tissue, resulting from increases in tree diameter, reduces the contribution of individual increments to phloem thickness to approximately half their original amount. Retention is the major factor affecting both the ultimate phloem thickness and the rate of change of phloem thickness. For the trees used in this study, the overall average period of phloem retention was 21.7 years, but for individual trees it may be in excess of 40 years in the lower bole. Resin canal density is a highly variable characteristic in lodgepole pine, but overall, densities are usually higher in the upper parts of the tree. Resin canal density may be a useful indicator of relative tree resistance to bark beetle attack; however, research on other pine species indicates that even short-term environmental stress may result in a substantial temporary reduction in resistance.

INTRODUCTION

Amman (1972) and Amman and Pace (1976) have shown, in laboratory experiments, that mountain pine beetle (*Dendroctonus ponderosae* Hopkins) emergence from bolts is related to phloem thickness, which Berryman (1976) demonstrated is the single most important variable affecting brood production in the field (Fig. 1). Phloem thickness influences the number of beetles produced, the sex ratio and the size of individuals (Amman and Pace 1976). Trees with thin phloem tend to produce fewer beetles, fewer males relative to females, and smaller individuals of both sexes than do trees with thick phloem. Smaller beetles are believed to have a more limited flight capability and, therefore, a more limited dispersal capacity.

Berryman (1976) reported that resinosis in response to mountain pine beetle attack is correlated with the density of resin pockets in the phloem of lodgepole pine (*Pinus contorta* Douglas var. *latifolia* Engelm.), and that brood survival is very low when phloem resin pocket density is high.

The important role of phloem in the development of mountain pine beetle larvae makes it imperative that we understand the structure and development of lodgepole pine phloem. It is a transient tissue, and its characteristics may be expected to change during the life of the tree. In this paper we will examine the general characteristics of the phloem tissues of the genus *Pinus* and present some preliminary results of studies investigating the structure and development of lodgepole pine phloem.

Growth and Structure of Phloem in Pines

Phloem in the genus *Pinus* consists largely of non-conducting sieve elements. Conducting elements occur only in

Scientific Paper No. SP5137, College of Agric. Res. Center, Washington State University. Work conducted under Projects 0102 and 4102, supported in part by the National Science Foundation and Environmental Protection Agency through contract SC0024 with the University of California (Integrated Pest Management Project). The opinions and findings expressed herein are those of the author and not necessarily those of the University of California, the National Science Foundation or the Environmental Protection Agency.

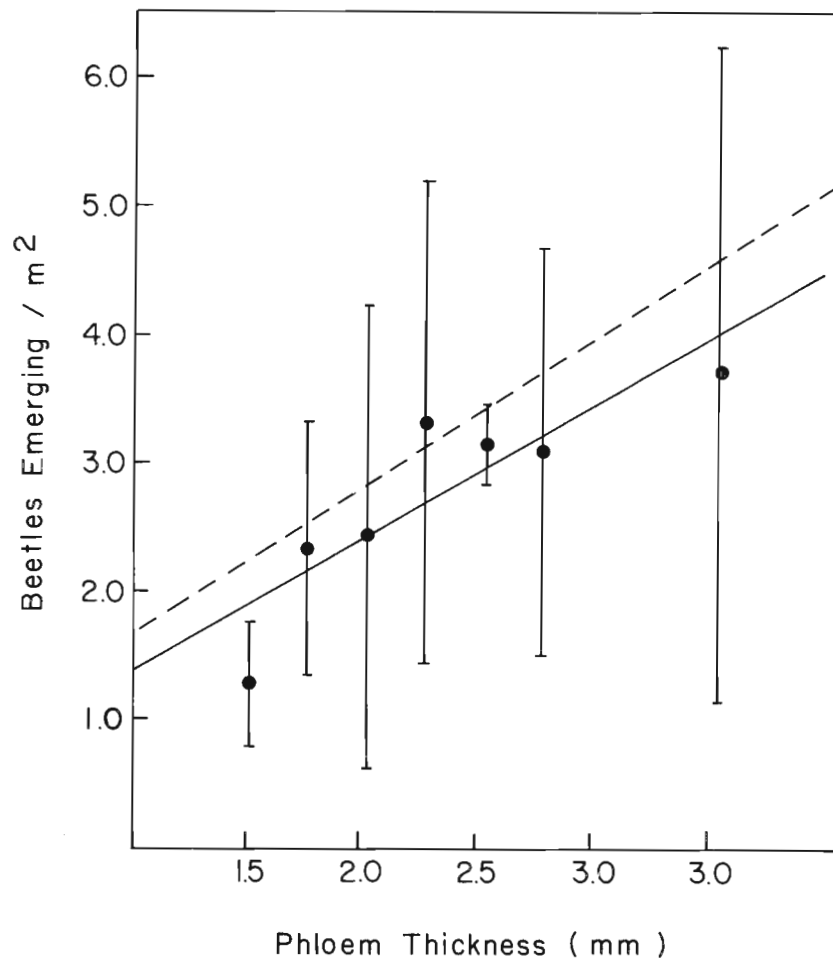


Fig. 1. Effect of lodgepole pine phloem thickness on mountain pine beetles emerging per cm^2 of bark surface. ● = compressed data from 35 trees (vertical lines represent one standard deviation about the mean) sampled on the Gallatin National Forest (Berryman 1976), with linear regression fit (solid line), and regression reported by Amman (1972) from laboratory experiments (dashed line).

the current year's phloem. This tissue also contains phloem parenchymal cells (starch- and tannin-containing cells), albuminous cells and ray cells. Resin canals are often scattered throughout the phloem (Srivastava 1963, Alfieri and Evert 1968).

Like xylem, phloem displays a pattern of annual rings discernible by microscopic examination and, in a few cases, by the unaided eye. Phloem parenchymal cells are arranged in concentric rings among the rings of sieve elements, and have been used to locate the transition between sieve elements formed in the early part of the growing season and those formed in the later part (Alfieri and Evert 1968). Sieve cells that develop early are characteristically larger in diameter and thinner walled than those of late season origin. As tree diameter increases and the old phloem is pushed outward, early season sieve elements usually undergo a greater degree of lateral compression, often making it possible to determine where each year's growth begins and ends (Srivastava 1963, Alfieri and Evert 1968). As growth continues, increments in xylem and phloem continue to push the older phloem outward, further distorting the dead sieve cells. Phloem parenchymal cells enlarge, and rays become distorted. Ultimately, the oldest

portions of the phloem are lost through the repeated formation of phellogen, or cork cambium (Srivastava 1963).

With the exception of a few late-formed sieve elements that overwinter, the sieve elements in *Pinus* are functional for only one season (Alfieri and Evert 1968).

Resin canals (or pockets) are formed in the fusiform phloem rays and expand as the annual rings of phloem are pushed outward (Srivastava 1963). This suggests that resin canal size and density will be influenced by a number of factors, including the magnitude of phloem increments, period of phloem retention and the density of fusiform phloem rays.

METHODS

A total of 10 lodgepole pine stands were selected for tree sampling. These were located in northeastern Oregon, northern Idaho and western Montana, and were about 20

to 120 years of age. In each stand, two dominant or co-dominant trees were felled and total height, dbh, length of crown and age at stump height were recorded. At each fifth year whorl, two disks were removed. On one of these phloem thickness was measured to the nearest .04 cm (1/64 inch) in the four cardinal directions, and the inner boundary of the sapwood was marked. This disk was then stored for stem analysis. From the other disk four samples of phloem tissue and cork (each approximately 4 cm x 9 cm) were removed from the north-facing and south-facing sides of the bole. One sample of each pair was placed in cupric acetic solution to stain the resin (Gray 1954), and the other in formalin-aceto-alcohol (Sass 1951).

The total number of needle-bearing branches was recorded, and two sample branches were collected (north and south) from the centers of the upper, middle and lower thirds of the crown. Total branch length and total length of the needle-bearing portions were recorded, and the branches were stored for needle length and needle count studies.

South aspect phloem samples stored in cupric acetic solution were used for microscopic examination. Transverse sections approximately 0.1 mm thick were made, using a hand microtome, and four to six sections from each sample were mounted, unstained, in a glucose solution (J.D. Rogers, pers. comm.¹). The sections were examined with a light field microscope equipped with an ocular grid.

Two measurements were taken of the widths of the phloem annual rings, and two counts made of the number of cells in the radial rows of each ring. A count was also made of the number of phloem annual rings retained.

Resin pockets were counted under a dissecting scope, using the unused portion of the tissue samples cut in a tangential plane.

Phloem increments for the most recent 5 years were calculated on the basis of microscopic examination of samples. Average cell diameters were determined for the current and preceding years' growth and were multiplied by the number of cells on the radius of each annual ring, to obtain an estimate of the original width of the ring. It should be recognized that the size of sieve cells varies, not only during the season but also from year to year, so that this procedure is only approximate.

Data for phloem thickness, average annual phloem increment, number of annual phloem rings retained, and number of resin canals/cm² of bole surface were plotted against normalized tree height, for which values were computed as follows.

Data for each tree were separated into 10 groups, each group consisting of those samples which occurred in an interval along the bole equal to 10 percent of the height of the tree.

The interval nearest the roots was designated 0 to 0.1, that nearest the top 0.9 to 1.0. Values within each interval for all trees were then used to compute the mean and standard deviation for that interval. It should be noted that this tends to magnify the importance of data from older, taller trees, since these often had several samples within each interval, while in the younger, smaller trees, some intervals are not represented.

Data from the two youngest trees are not presented here because the number of samples taken from these trees was extremely small.

RESULTS

Phloem of lodgepole pine conforms to the characteristic pattern of the genus *Pinus*. Sieve elements, rays, phloem parenchyma, and resin canals (when present) are easily discernible. Phloem parenchyma occurs in more or less complete concentric rings (Srivastava 1963). The arrangement of parenchyma cells in individual rings may show some discontinuity, so that parenchyma cells in adjoining cell tiers are not always adjacent to one another. This suggests that differentiation of the cells of the concentric parenchyma rings may not occur simultaneously throughout the circumference of the tree.

Cole (1973) has shown that the trees with the most rapid growth rates and the largest diameters tend to have the thickest phloem. Phloem thickness can be estimated from a number of variables, such as dbh, total tree height, tree age at breast height, last 5 years' basal area increment, habitat type and elevation. Cole, however, found that basal area increment was the best predictor of phloem thickness in lodgepole pine.

Variation in the thickness of phloem with height in individual trees shows two distinct patterns. Both patterns are characterized by increasing phloem thickness with increasing distance from the tree top, with a maximum at the base of the crown. Below the crown, the phloem thickness may either remain relatively constant (Fig. 2) along the length of the bole, or decline with increasing distance from the base of the crown (Fig. 3). Unfortunately, the data in this study do not indicate how these within-tree variations in phloem thickness are related to other tree characteristics such as dbh, bottom of live crown, age, diameter increment rates, etc.

Figure 4 illustrates the average phloem thicknesses and variations with tree height, in a sample of 18 lodgepole pines. The general increase in phloem thickness from the top downward, to a maximum near the middle of the tree, is apparent. Below this, phloem thickness remains fairly constant or declines slightly.

Phloem thickness at any time in the life of a tree may be expected to reflect the interplay of three factors: annual phloem accretion, which will depend upon the number of cells produced and their diameters; the number of years the phloem is retained; and the degree of compression which the old phloem undergoes as the tree increases in diameter.

¹ J.D. Rogers is currently at the Department of Forestry and Range Management, Washington State University, Pullman, WA 99164.

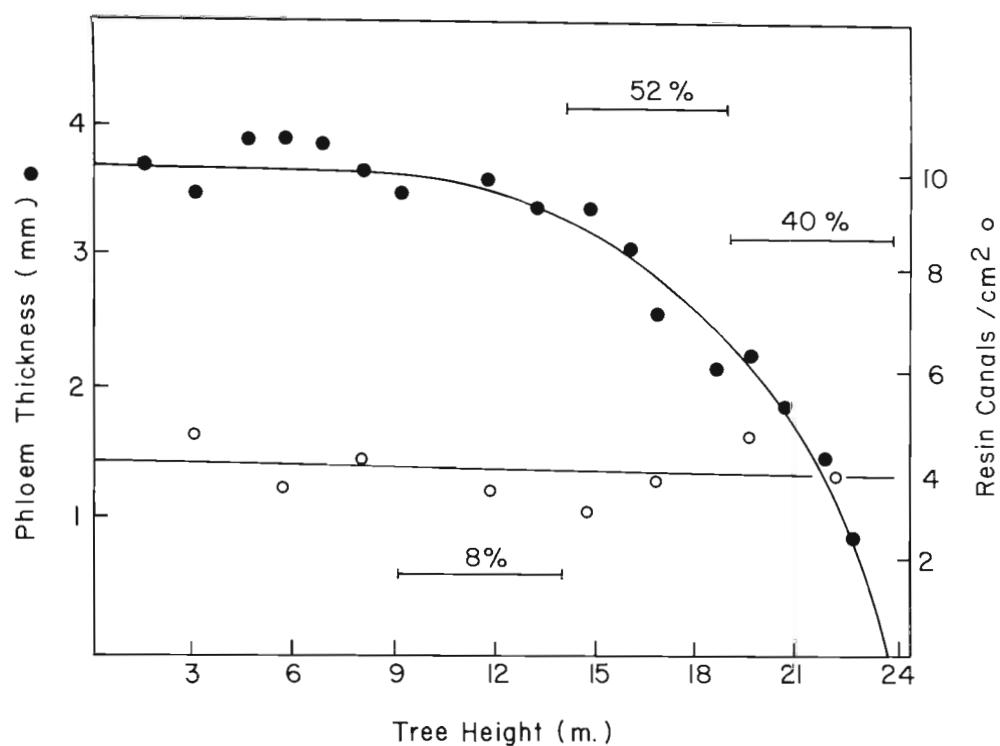


Fig. 2. Changes in phloem thickness (●) and phloem resin canal density (○) with height in the tree. Crown structure is indicated by length of needle-bearing branches in the upper, middle and lower thirds of the crown, expressed as a percentage of the total length of needle-bearing branches.

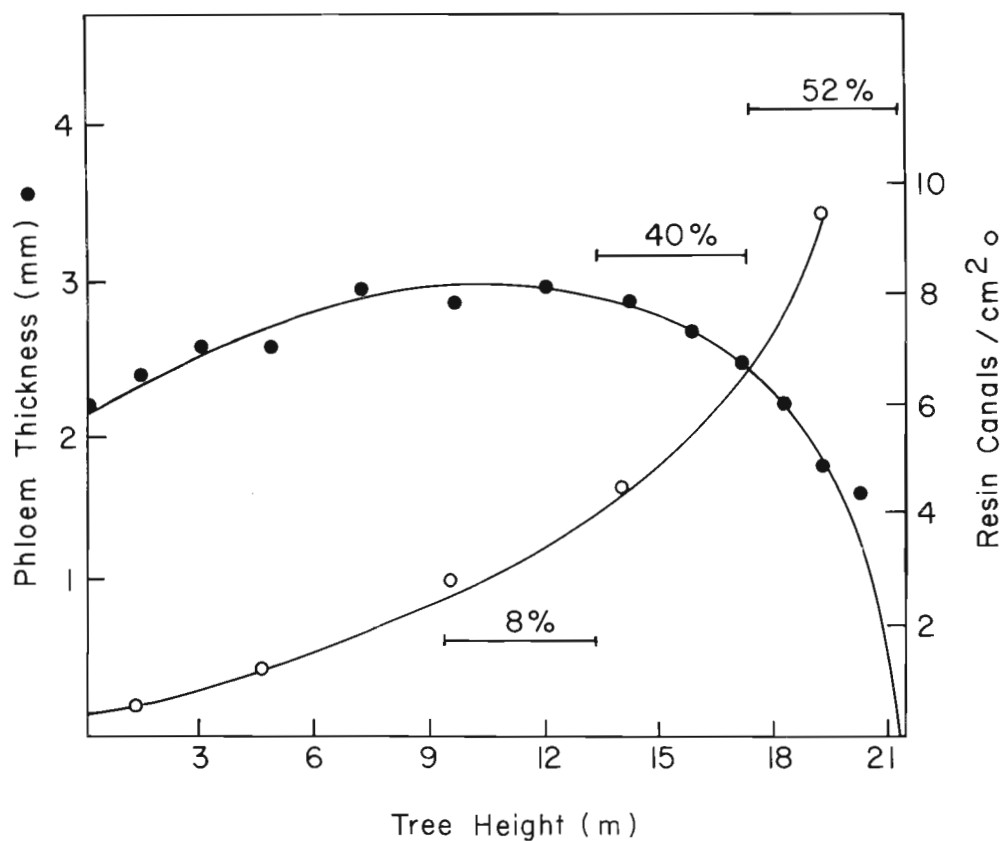


Fig. 3. Same as Fig. 2 but showing a different pattern of phloem thickness and resin canal density distribution with tree height.

That is, where phloem was thick, retention was long, and where phloem was thin, retention was short. This was by no means a universal pattern, however, so the contributions of phloem increment and of compression must also be considered.

The magnitude of the influence of retention upon phloem thickness may be judged from the fact that, even in the tree with greatest average annual phloem increment for the most recent 5 years, the increment was equal to only 10.8 percent of the total thickness of the phloem. For all trees, the average annual phloem increment was equal to only 8.5 percent of the total thickness of the phloem.

Figure 7 shows the average phloem annual ring retention for all trees plotted against normalized tree height. With increasing distance from the tree top, the number of phloem annual rings initially increases, reflecting increasing age of the bole at these heights. After reaching a maximum at the middle of the tree, phloem ring retention seems to decline slightly, although examination of retention patterns for individual trees indicates that phloem retention remains fairly constant in many cases.

Phloem Resin Canals

The cortical resin canals of lodgepole pine, with the outer bark removed, are illustrated in Fig. 8. In this particular sample, resin pocket density is four pockets per cm^2 of surface area.

Resin canal density is a highly variable characteristic, both within the same tree and among different trees. In 10 of the 20 trees examined, resin pocket density was greatest in the upper crown and declined rapidly to a low level in the lower bole (Fig. 3). The remainder of the trees showed either the reverse trend, with resin canal density increasing toward the base of the tree, or little variation in resin canal density throughout the tree (Fig. 2). Figure 9 shows the average number of resin canals per cm^2 of phloem surface in all trees, and the tremendous variability of this characteristic, particularly in the uppermost parts of the crown, is illustrated by the size of the standard deviations from the mean.

Resin pocket density, as noted earlier, may be regarded as an indicator of tree resistance to mountain pine beetle attack. However, with the high degree of variation observed in this study, it would seem doubtful that resin pocket counts at any single point on the tree could readily be used to ascertain resin pocket density for the entire tree. Additionally, Lorio and Hodges (1977), working with loblolly pine (*Pinus taeda* Linnaeus) and southern pine beetle (*Dendroctonus frontalis* Zimmerman), have observed that artificially induced moisture stress reduced oleoresin exudation pressure and associated resistance to successful attack by the southern pine beetle. A similar response to environmental stress by lodgepole pine would suggest that resin canal development, while it may indicate the relative potential for resistance to bark beetle attack, may not be a fool-proof indicator of whether a particular tree will successfully repel a bark beetle attack, if the tree is subjected to environmental stress or if the attack is particularly heavy.

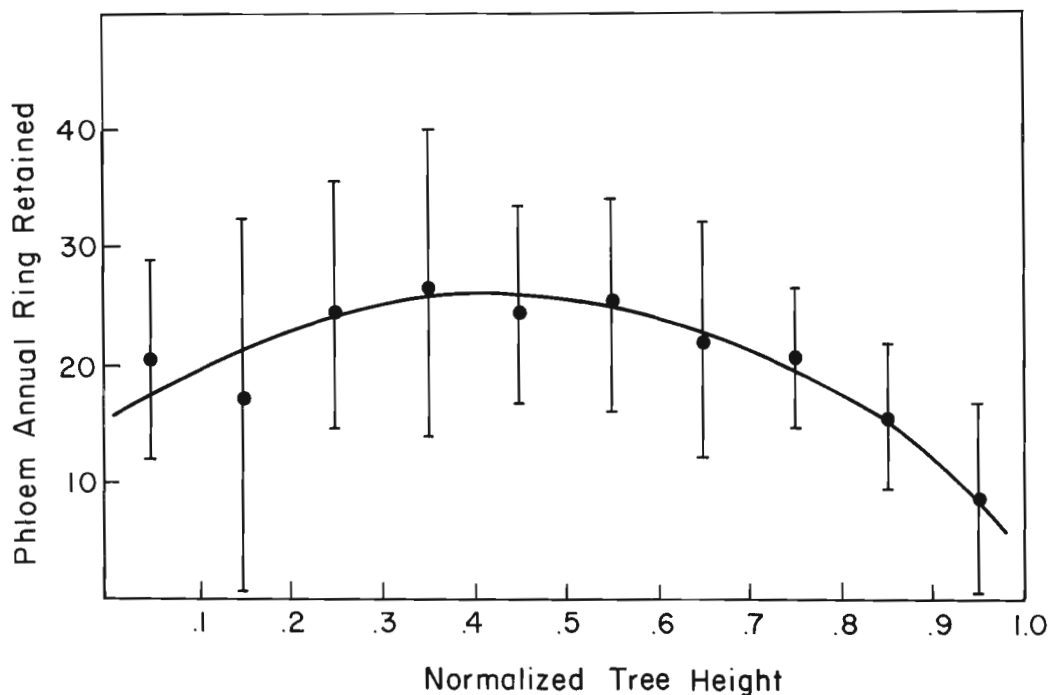


Fig. 7. Retention of phloem annual rings by normalized tree height intervals. Vertical lines represent one standard deviation about the mean.

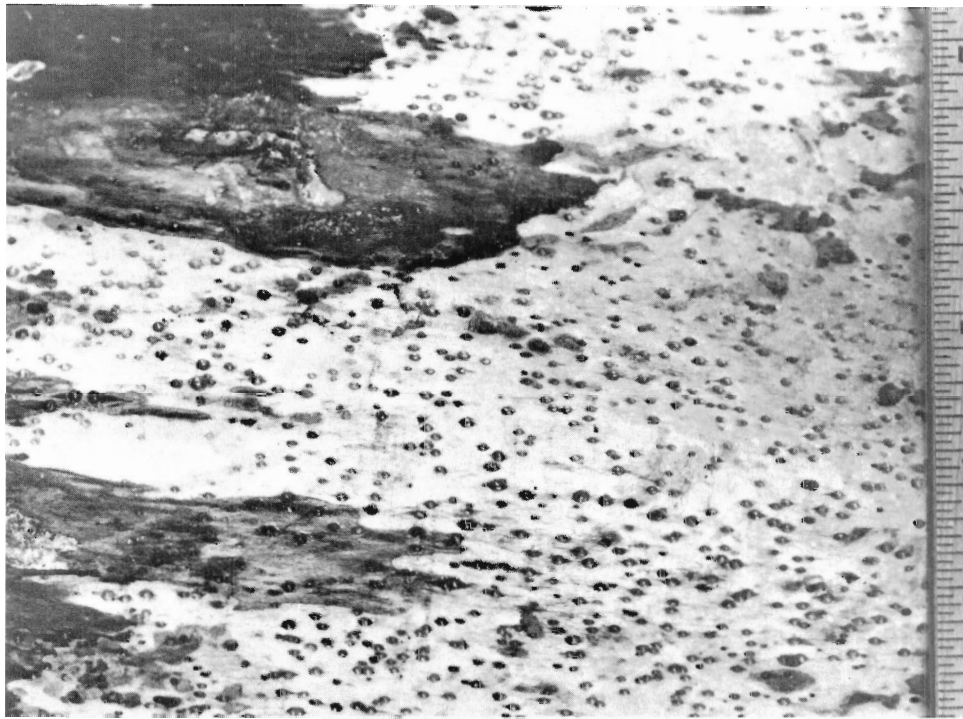


Fig. 8. Resin canals in the phloem of a lodgepole pine. The 2 large necrotic resinous areas are resistant responses to mountain pine beetle attack (after Berryman 1976).

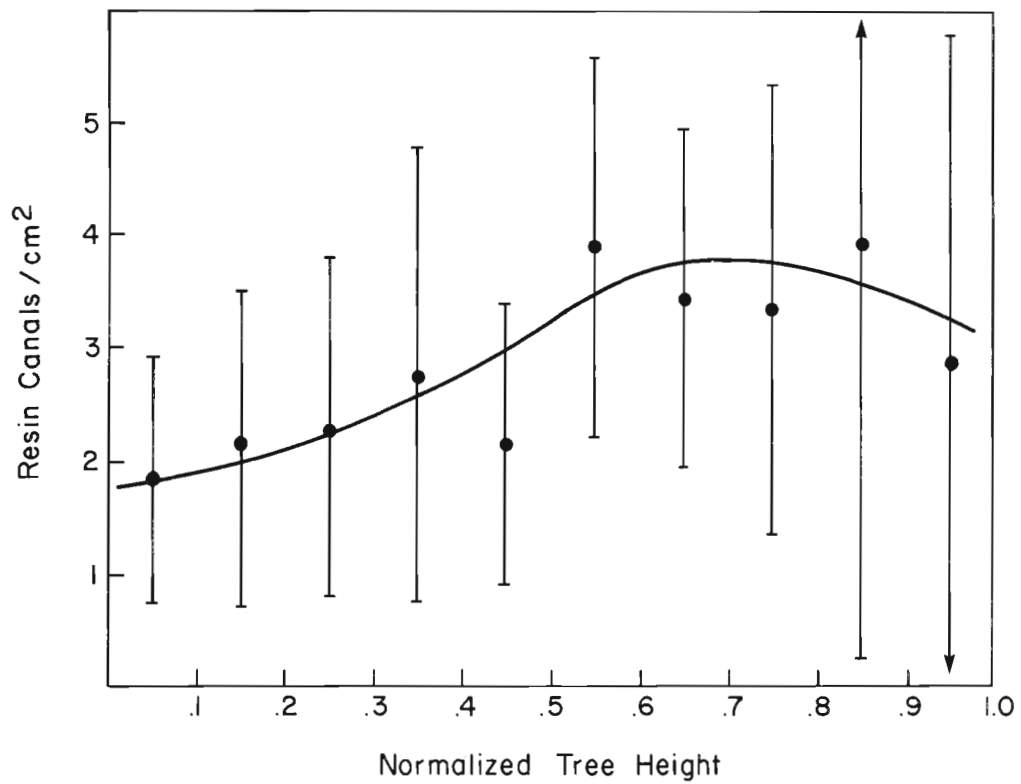


Fig. 9. Changes in the average phloem resin canal density with normalized tree height. Vertical lines represent one standard deviation about the mean.

DISCUSSION

The results of this preliminary study indicate that the contribution of phloem increment of any particular year to total phloem thickness is apt to be a small fraction (less than 10 percent) of that thickness. This contribution is further reduced in subsequent years to approximately one-half its original thickness by compression resulting from growth. Both these factors point to the importance of phloem retention as a determinant of phloem thickness.

Thick phloem usually reflects long periods of accumulation and changes in phloem thickness may be expected to occur slowly. Vigorous trees should be expected to develop thick phloem as a result of both large increments and long accumulation. When undergoing a decline in vigor, these thick-phloemed trees doubtless undergo a reduction in phloem thickness but, with long phloem retention periods, it may be several years before phloem thickness decreases below the minimum necessary for successful beetle reproduction. It has been hypothesized that such trees could provide conditions favorable for beetle brood development and, at the same time, have little resistance to beetle attack (Berryman 1976). This is in agreement with the ideas presented by Mahoney (these proc.), who found that outbreaks were associated with declining growth rates measured as dbh.

ACKNOWLEDGMENTS

I am greatly indebted to Dr. Alan A. Berryman, Washington State University, for his invaluable suggestions pertinent to the preparation of this manuscript. I would also like to express my appreciation to Dr. Donald G. Burnell, Washington State University, and to Dr. Berryman for their assistance and advice on the collection and handling of data upon which this manuscript is based. My thanks to Dr. Jack D. Rogers, Washington State University, for his helpful recommendations on the preparation of tissue samples for microscopic examination.

QUESTIONS AND ANSWERS

- Q. From your graphs on phloem increment, phloem ring compression and phloem retention, is it true that phloem is thickest midway up the bole (lower part of crown)? Can you relate this to why beetles enter trees mainly in the lower 1.8 m (6 ft) of bole?
- A. It seems that beetles select host trees on the basis of diameter—that is, they are attracted to large, dark objects. Under these circumstances, although phloem on a particular tree may be thicker midway up the bole, the bole diameter would be greater at the lower portion, and the larger diameter would likely provide a stronger attractive visual stimulus.
- Q. Because auxin relations are known to mediate cambial activity, wouldn't phloem variations with tree height

also depend on the proximity to the live crown base? Where is maximum phloem thickness in relation to the base of the live crown?

- A. I would expect that maximum phloem thickness would be related to structure of the live crown component, although not necessarily with the live crown base. Our data do not clearly indicate what the situation is. I believe this results primarily from the small number of trees examined, and perhaps also from an inadequate description of live crown structure. Examination of more sample trees and a more complete description of the distribution of needles in the crown should clarify the situation. Additionally, we should not ignore the importance of accumulation, which is greatly influenced by age. Those parts which, by their relationship to the crown, would be expected to be the most rapidly growing may not have achieved maximum phloem thickness because of a short period of accumulation.
- Q. Is there evidence to suggest that phloem retention time becomes shorter after the tree loses its vigor?
- A. I don't know of any evidence to show how phloem retention time is affected by declining vigor. Since one function of phloem is storage, it might be possible for the cells of old phloem to continue to live for an extended period even though the tree is no longer vigorous. This is an important question because it will affect the number of years that a formerly vigorous tree will maintain a thick phloem suitable for beetle brood development.

REFERENCES

- Alfieri, F.J., and R.F. Evert. 1968. Seasonal development of the secondary phloem in *Pinus*. Amer. J. Bot. 55:518-528.
- Amman, G.D. 1972. Mountain pine beetle brood production in relation to thickness of lodgepole pine phloem. J. Econ. Entomol. 65: 138-140.
- . 1975. Insects affecting lodgepole pine productivity. Pages 310-342 in D.M. Baumgartner (ed.), Management of lodgepole pine ecosystems. Washington State Univ. Coop. Ext. Serv., Pullman.
- Amman, G.D., and V.E. Pace. 1976. Optimum egg gallery densities for the mountain pine beetle in relation to lodgepole pine phloem thickness. USDA Forest Serv. Res. Note INT-209. Intermtn. Forest and Range Exp. Sta., Ogden, UT. 8 pp.
- Berryman, A.A. 1976. Theoretical explanation of mountain pine beetle dynamics in lodgepole pine forests. Environ. Entomol. 5:1225-1233.
- Cole, D.M. 1973. Estimation of phloem thickness in lodgepole pine. USDA Forest Serv. Res. Pap. INT-148. Intermtn. Forest and Range Exp. Sta., Ogden, UT. 10 pp.

- Gray, P. 1954. The microtome's formulary and guide. Blakiston Co., Inc. New York. 794 pp.
- Lorio, P.L., Jr. and J.D. Hodges. 1977. Tree water status affects induced southern pine beetle attack and brood production. USDA Forest Serv. Res. Pap. SO-135. Southern Forest Exp. Sta., New Orleans, LA. 7 pp.
- Sass, J.E. 1951. Botanical microtechnique. Iowa College Press, Ames. 228 pp.
- Srivastava, L.M. 1963. Secondary phloem in the Pinaceae. University of California Press, Berkeley. 141 pp.

Resistance of Lodgepole Pine to Mountain Pine Beetle Infestation

D. Malcolm Shrimpton

ABSTRACT

This paper discusses the possible relationships between the mountain pine beetle (*Dendroctonus ponderosae* Hopkins) and the physiological processes of the lodgepole pine (*Pinus contorta* Douglas var. *latifolia* Engelm.) stem that act to heal wounds of the type caused by bark beetles. The resin canal system of lodgepole pine and production of secondary resins are described. The effects of moisture stress and the relationship of each resin system to maturation of the tree are also described. The interaction between tree response and the attacking beetle/blue-stain complex and the relationship between mountain pine beetle outbreak and physiological maturity of lodgepole pine are discussed.

INTRODUCTION

This paper is directed toward definition of the lodgepole pine (*Pinus contorta* Douglas var. *latifolia* Engelm.) tree response to the mountain pine beetle (*Dendroctonus ponderosae* Hopkins) and the effect that this response has upon attacking beetle populations. Many forest entomologists consider that the response of the tree has little effect upon the attacking bark beetle and the death of the tree. They believe that if sufficient numbers of beetles are present any tree will be killed, and that trees come under attack when they are of sufficient size to provide adequate nutrition and suitable habitat for the beetle broods. It remains only for the trees to be situated in a geographic zone suitable for beetle survival and development.

Outbreaks can develop only in stands where many of the stems exceed, by a considerable margin, the minimum size requirements for beetle development. Therefore, a mechanism must exist which ensures survival of numbers of trees beyond the point of minimum size requirements for beetle development. It is my thesis that an integral part of this mechanism is

a strong resinous response by the tree. Within a stand that, on the average, exceeds the beetle's minimum size requirements, one of the factors contributing to the onset of an epidemic is a decrease in tree response due to senescence or stress. This decreased tree response permits colonization by beetles and yields an increase in beetle population to levels necessary to perpetuate an outbreak.

Resin secretion, the most obvious part of the tree response, is only one of a series of physiological processes that act to heal wounds, regardless of cause. Physiological processes, such as photosynthesis, respiration, translocation, growth, etc., are highly sensitive to environmental changes above a certain threshold level. Among the many physiological processes whose expression is adversely influenced by the gradual changes that accompany aging are chlorophyll synthesis, photosynthesis, stomatal control of transpiration, tissue sugar and nitrogen concentration, respiratory sugar consumption, mineral uptake, cone production and growth rate (Kramer and Kozlowski 1969). Since it is also a physiological process, the tree wound response also probably decreases in reaction to environmental stresses, especially as trees age. When a decreased response occurs in trees that exceed the minimum size requirements for beetle development, an increasing beetle population, with its attendant threat to surrounding trees, is possible.

Resin flow is the means by which attacking beetles can be repelled and, because of this, is generally equated with resistance. It is, however, not absolute in its effect upon the beetle/fungus complex. As a physiological process, it varies through time and space and is dependent upon other physiological processes within the tree. Not enough is known of the variability to determine the form of gene control or the relative importance of the underlying genetic system as opposed to environmental influences.

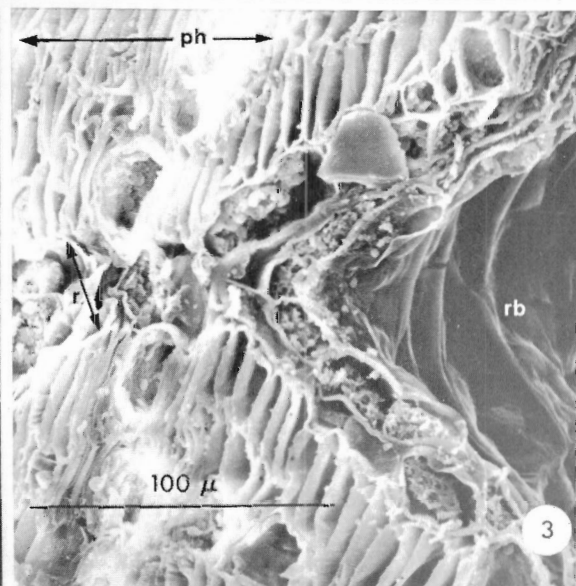
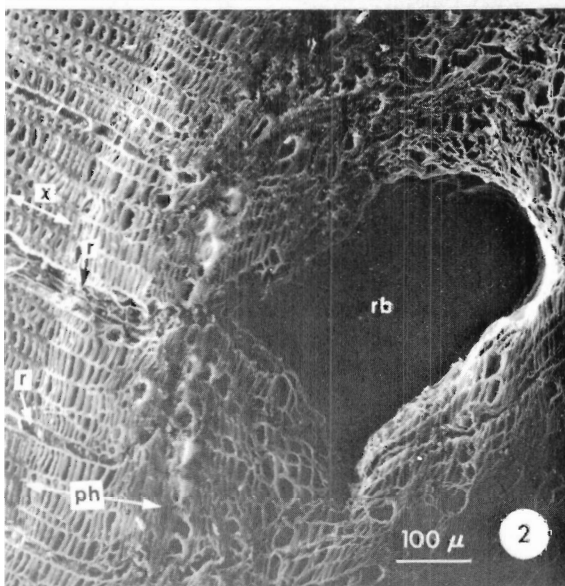
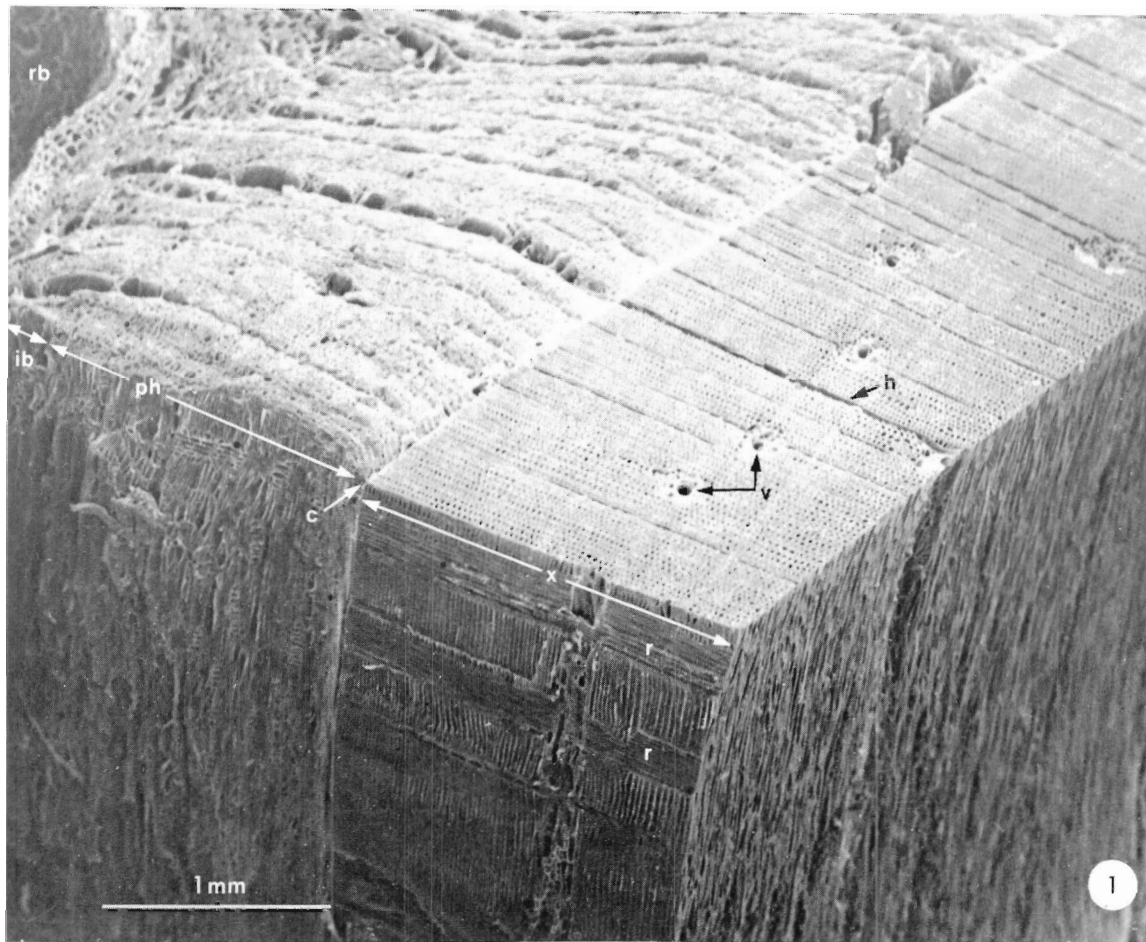


Fig. 1. Scanning electron micrograph of a block of lodgepole pine wood, showing xylem (x) with vertical (v) and horizontal (h) resin ducts and rays (r), cambium (c), phloem (ph) and inner bark (ib) with resin blisters (rb).

Fig. 2. Scanning electron micrograph of resin blister (rb) in the inner bark, showing its relationship to the xylem (x), phloem (ph) and rays (r).

Fig. 3. Scanning electron micrograph showing the junction between a ray (r) and the epithelium of a bark resin blister (rb).

Many theories on bark beetle dynamics center upon a single cause for epidemics. If, however, our theory that an equilibrium exists among beetles, blue-stain fungi and the tree is correct (Safranyik et al. 1975), an epidemic can be the result of a change in any or all of the organisms involved. This paper will be restricted to the possible role of the tree in this interaction. It will review current knowledge of the response of the tree to wounds of the type caused by bark beetles and the resultant effect of this tree response upon the attacking beetle/blue-stain complex.

THE RESIN DUCT SYSTEM IN LODGEPOLE PINE

Literature on the resin duct system of lodgepole pine is limited. Much is known, however, about the resin ducts of pines in general. As a group, pines have a fully developed resin duct system present in needles, stem and roots throughout the lifetime of the tree. Each of these resin synthesizing systems is independent of the others. This section presents a review of literature on resin ducts within the stems of pines and a series of illustrations to show the structure and relationship between the systems in lodgepole pine. The overall distribution of ducts within the stem tissues can be seen in Fig. 1.

The outer bark tissues of lodgepole pine consistently contain discrete resin-filled cysts or blisters (Fig. 2) that are associated with the termination of a ray containing a horizontal resin duct (Fahn 1967) (Fig. 3). Density of bark resin blisters may be greater in younger parts of the tree (Cabrera these proc.). Stem wounds cause a large increase in the number of bark resin blisters. For instance, observations on the bark of a tree undergoing pitch moth (*Vespamima* sp.) attack have shown a large increase in the number of these blisters adjacent to the lesion. With continuing growth of the stem, the blisters are eventually sloughed in the bark scales.

Resin ducts are formed within rays by the secretion of oleoresin into the spaces between cells. Continued secretion enlarges these spaces and the mature duct is formed (Fahn and Benayoun 1976). Horizontal ducts in the bark are very irregular in size, with cyst-like enlargements along their length (Fig. 1). There are no vertical ducts in the bark. The horizontal duct continues within the wood along the same ray, but the intact cambial zone separates the duct in the bark from the continuation of the duct in the wood. In lodgepole pine, it can take several months for the horizontal duct to become fully functional. Therefore, the horizontal resin ducts often do not have a lumen in the outer annual ring (Fig. 4). The functional horizontal ducts in the wood are about 50 microns in diameter (Figs. 5 and 6) (Hudson 1960), but this diameter decreases as the density of ducts increases (Mergen et al. 1958). As the duct ages it becomes progressively more blocked by tylosoids (Fig. 7), the bulbous enlargements of surrounding cells (Bannan 1936). Each horizontal duct is connected to a vertical duct at their point of common origin (Chattaway 1951) (Fig. 7). Other points of interconnection are rare even when the two ducts are physically adjacent

(Fahn 1967) (Fig. 8). My observations indicate that about 5 percent of horizontal ducts are physically adjacent to a vertical duct at some point along their length. The exception is when the horizontal duct passes through a field of ducts formed in response to a wound. Interconnections cannot occur in the outer annual ring because the horizontal duct is non-functional.

Vertical ducts are elongated canals up to 20 cm in length and about 90 microns in diameter (Reid and Watson 1966) (Figs. 9 and 10). They are associated with living ray tissues (Fig. 11) over much of their length. Adjacent to wounds they become not so much elongate ducts (Fig. 12) as spongy, resin-filled tissue (Fig. 13). Tylosoids frequently block the vertical ducts, especially in older ducts and ducts adjacent to wounds, particularly after the wound has stabilized (Bannan 1936).

THE WOUND RESPONSE IN LODGEPOLE PINE

Wounds of the type caused by bark beetles on the stems of lodgepole pine cut into the resin duct system within the bark and sometimes score the wood deeply enough to cut into the functional horizontal ducts within the wood. However, because the ducts do not form a completely interconnected system and because older ducts are frequently blocked, resin flow ceases after 1 to 3 days. There is considerable variation among individual trees in the duration of oleoresin flow. Resin secreted from the cut ducts flows over the damaged wood surface, usually soaks into a few cells at the surface and gradually hardens. This hardened resin, a coat of natural varnish, seals the surface, accelerates the formation of phenolic substances by the ray parenchyma and reduces the possibility of infection by decay fungi (Lyr 1967).

Long before the resins have sealed the exposed wood surface, additional resinous substances begin to accumulate in the ray parenchyma (Reid et al. 1967) (Fig. 14). These resins are secreted into the adjacent tracheids, where they first block the pits (Fig. 15) and then gradually fill the tracheid lumina (Fig. 16). As ray parenchyma progressively further from the wound synthesize resins (Fig. 17), an elliptical zone of resin-soaked wood is formed that completely surrounds each wound and extends to the heartwood.

From the edges of the wound, the live cambium produces parenchyma cells which appear as callus (Fig. 18). The file of parenchyma extends for a varying distance into the undamaged tissues surrounding the wound and the wound resin ducts arise within this file, completely surrounding the wound. Near to the wound, these ducts are a spongy, resin-filled tissue (Fig. 13) that is interconnected with the typical long narrow duct several millimeters above and below the wound (Fig. 12).

Within the bark and surrounding the wound, phloem and ray parenchyma synthesize resin and the inner bark tissues become resin soaked and die. Periderm is formed, surrounding the resin-soaked zone. This soaking in bark and wood lessens

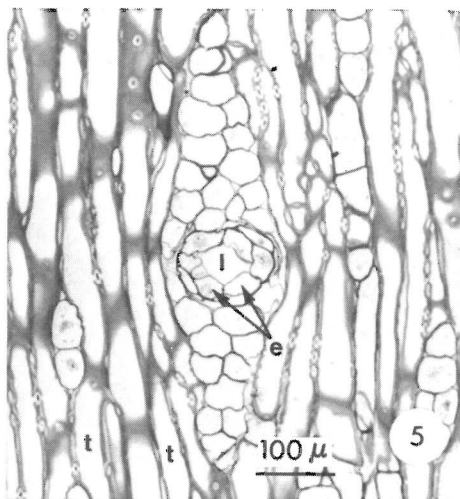
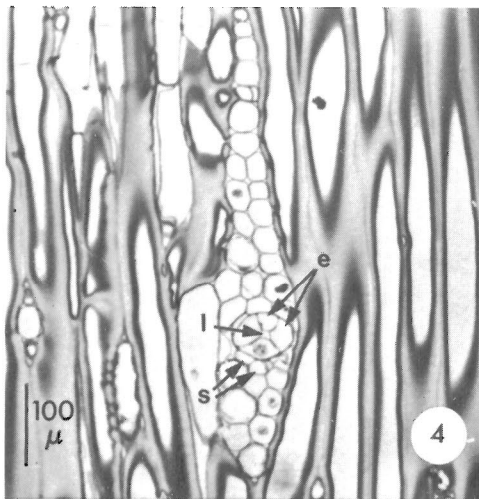


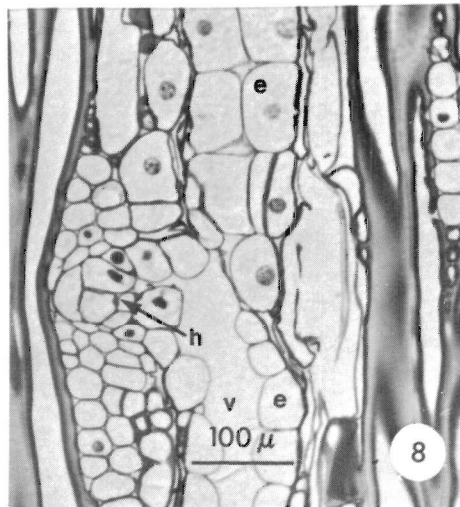
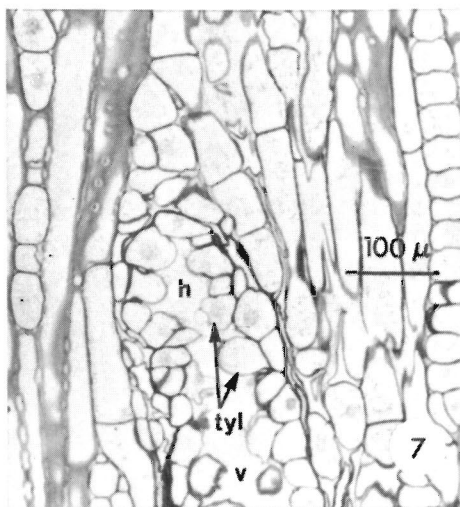
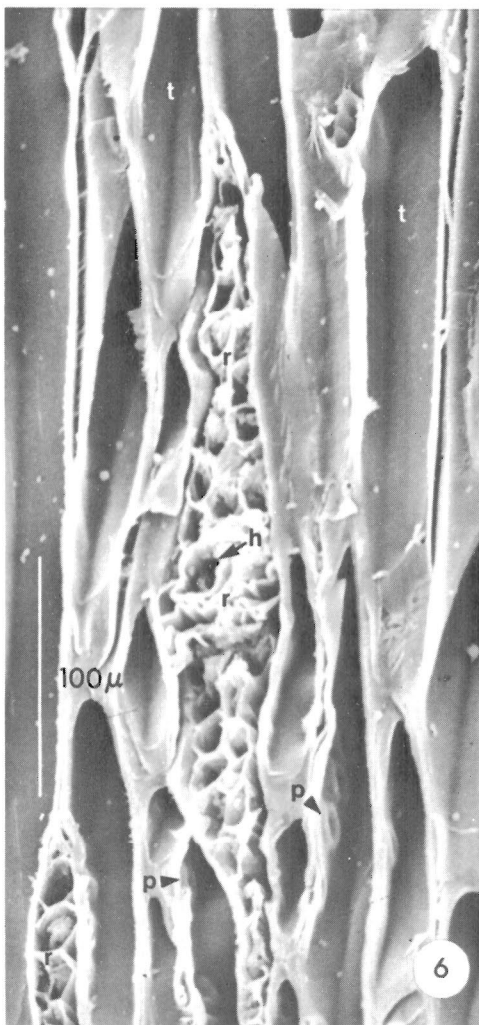
Fig. 4. Horizontal resin duct in the outer annual ring of lodgepole pine, showing partially formed duct lumen (l) and fully developed epithelial cells (e) and sheath cells (s). (tangential section)

Fig. 5. Horizontal resin duct of lodgepole pine (3 years old) showing the duct lumen (l), epithelial cells (e) and tracheids (t). (tangential section)

Fig. 6. Scanning electron micrograph of a horizontal resin duct (h) in tangential section, showing the adjacent tracheids (t) with interconnecting bordered pits (p) and rays (r).

Fig. 7. The point of origin of a vertical (v) and a horizontal (h) duct in a 3-year-old ring; tylosoids (tyl) are present in the vertical duct. (tangential section)

Fig. 8. Horizontal resin ducts (h) are occasionally physically adjacent to vertical ducts (v) lined with epithelial cells (e). (tangential section)



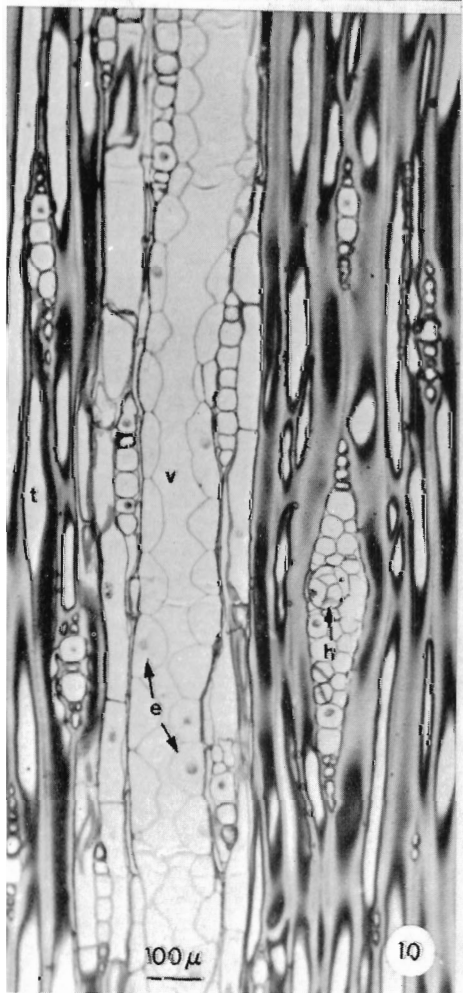
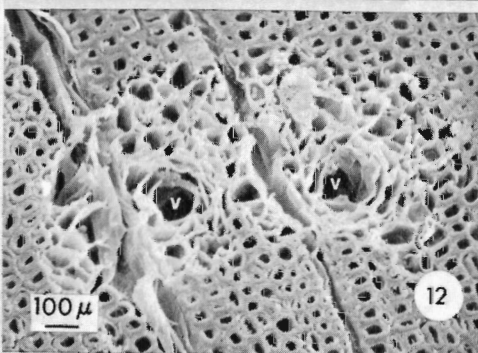
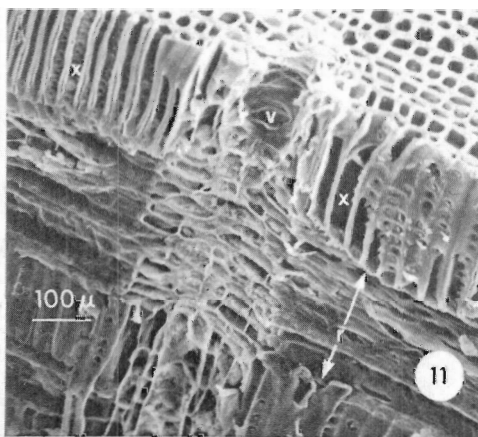
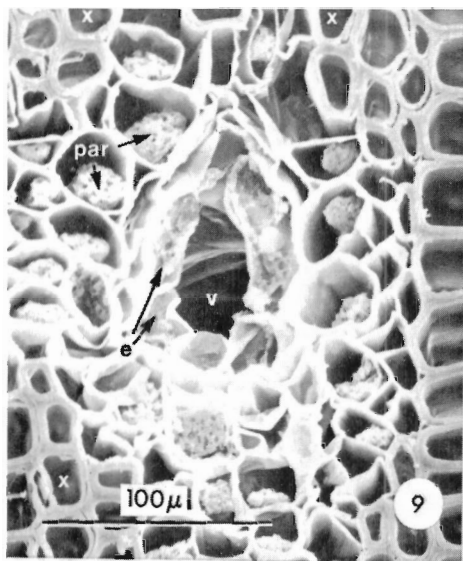


Fig. 9. Scanning electron micrograph of vertical resin duct (v), surrounding parenchyma (par) and adjacent xylem (x). (cross-section)

Fig. 10. Vertical duct (3 years old) showing lumen (l), epithelial cells (e) and adjacent tracheids (t); a horizontal duct (h) is in the field. (tangential section)

Fig. 11. Scanning electron micrograph of a vertical duct (v), showing a ray (r) touching the duct and adjacent xylem. (radial plane)

Fig. 12. Scanning electron micrograph of a group of vertical resin ducts (v) a few millimeters above a wound. (cross-section)

Fig. 13. Vertical ducts formed in response to a wound showing extensive parenchyma (par), duct lumens (l) and epithelial cells (e).

the possibility of secondary infection through the wound and, in turn, permits the wood and bark tissues to heal over the wounded area.

Even though there are many changes in stem tissues that act to heal a wound, the only change that has observable effects upon beetles and blue-stain fungi is the secretion of resin and its accumulation within the wood and bark. There are a number of microorganisms associated with the mountain pine beetle, but only the two blue-stain fungi (*Ceratocystis montia* (Rumbold) Hunt) and *Euophium clavigerum* Robinson and Davidson) have been studied for their interaction with the tree.

RESIN EFFECTS UPON BEETLES AND BLUE-STAIN FUNGI

The physical effects of oleoresin flow as an impediment to gallery construction by the mountain pine beetle have been recognized for many years. Anesthetic and toxic effects of the volatile components of oleoresin against bark beetles have also been proposed, but the greatest effects have been observed with volatiles from non-host species. A major effect of these volatiles, therefore, may be in determining host specificity, because of the general low-level attractance of many of these compounds (Smith 1972).

The mountain pine beetle is very tolerant to oleoresin from any of its host species; however, when oleoresin flow is sufficient, the beetles are less successful in gallery construction and may even leave (Amman 1975). Even on successfully killed trees, as many as one-third of the galleries can have varying portions of their length soaked with oleoresin (Peterman 1974, Berryman 1976). A high density of resin blisters in the bark has been associated with gallery failure (Berryman 1976); since these blisters are associated with horizontal ducts, it is probable that they indicate a copious initial resin flow. This resin soaking will have an effect upon the number of progeny through loss of nutritionally adequate habitat for the larvae (Shrimpton 1973a), and also because any eggs laid in areas soaked by oleoresin are unlikely to hatch (Reid and Gates 1970).

Oleoresin also affects the blue-stain fungi. Spores of these fungi are carried by the adult mountain pine beetles. These spores are dispersed by oleoresin and thus are more easily flushed out of the wound by the flow (Whitney and Blauel 1972). Furthermore, mycelial growth of these blue-stain fungi is inhibited by the volatile substances in oleoresin (Shrimpton and Whitney 1968). The non-volatile resinous components will not, of themselves, support growth of the blue-stain fungi; however, when sugars are added, growth will occur on resinous substances (Shrimpton and Whitney, unpublished data). The tree prevents invasion by the blue stains by producing volatile growth retardants early in the response and by progressively converting contents of the living cells into resinous and phenolic substances that will not support fungal growth.

EFFECTS OF THE BARK BEETLE/BLUE-STAIN COMPLEX ON TREE RESPONSE

The effect of the beetle as it mines a gallery is to cut the phloem and sometimes score the wood surface. It has frequently been suggested that the girdling action is completed when eggs begin to hatch, about 2 weeks after attack, and this eventually causes the death of the tree.

There are two inconsistencies in this point of view. In the first place, girdling the phloem with a knife does not cause crown death (Noel 1970) as rapidly as happens following mountain pine beetle attack. Second, because each horizontal resin duct is connected to a separate vertical duct, the action of the beetle in mining a gallery does not prevent continued resin flow, which is a major impediment to egg hatch.

These inconsistencies arise because the speed at which the blue-stain fungi colonize the stem tissues is not fully appreciated. The blue color develops only late in the life of the fungus. The blue-stain fungi grow rapidly throughout the live tissues in the stem, i.e., rays, resin ducts and cambium. The fungal growth kills the cells and prevents further resin formation in each of these tissues, thereby providing a resin-free environment for the eggs. It also causes a breakdown of the water conducting capacity of the stem, which eventually leads to death of the crown. The tree killing technique of the beetle is to spread a large number of fungus-infected centers over the tree stem in a short space of time and progressively enlarge the size of each infection by continued gallery construction (Safranyik et al. 1975).

Observation of mountain pine beetle attacks supports the idea that early beetle attacks reduce the response of the tree to subsequent attacks. Beetle attack starts toward the base of the tree and moves progressively upward. The final density of attack over the bole, with its maximum about breast height (Safranyik 1971), parallels the variation in resinous response, which also is strongest at this height (Reid and Shrimpton 1971). It is often stated that, given sufficient numbers of beetles, their mass attack behavior can overcome almost any tree's resistance even though brood production from very resistant trees may be low. However, there is no direct experimental evidence for this idea.

An indication that wounds can diminish a later resinous response from nearby tissues was seen from partial girdling of the sapwood (H.S. Whitney, pers. comm.¹). Successful development of blue-stain fungi and beetle galleries was seen above the girdle, whereas on the ungirdled portion of the stem, fungi and beetles were unsuccessful and the wounds were sealed with resin. To determine whether early wounds decrease the capability of the stem to respond to subsequent attack, inoculations of blue-stain fungi were placed on the stems of lodgepole pines in July. Six trees were inoculated on four

¹ H.S. Whitney is located at the Pacific Forest Research Centre, Victoria, B.C.

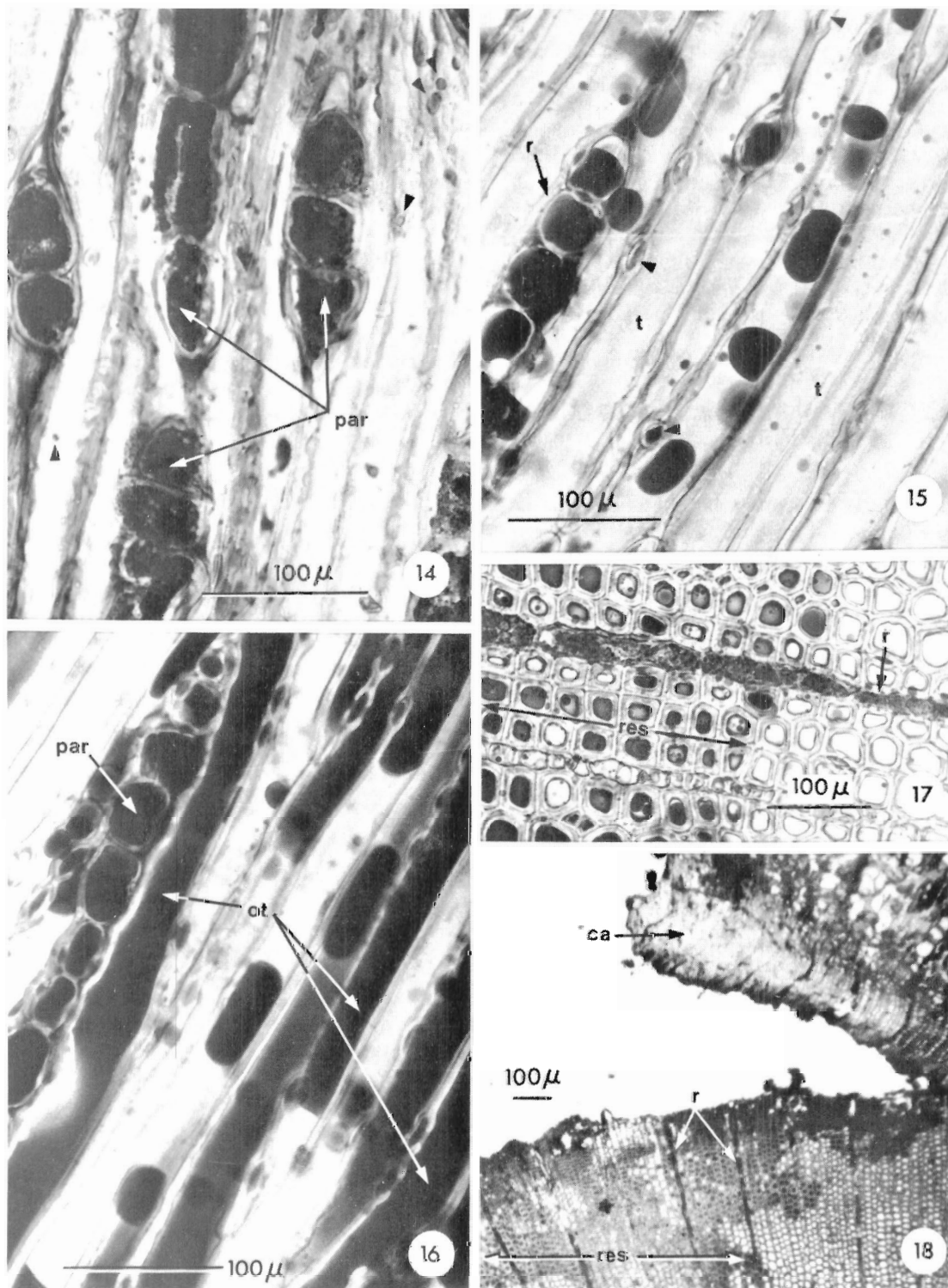


Fig. 14. Accumulation of oil droplets (arrows) in cells of ray parenchyma (par) and in tracheids (t) 24 hours after wounding. (tangential section)

Fig. 15. One week after wounding, cells of ray parenchyma (r) are filled with oil, bordered pits are blocked by oil (arrows) and tracheids (t) contain oil droplets. (tangential section)

Fig. 16. Three weeks after wounding, ray parenchyma is filled with oil, pits are blocked with oil (arrows), and tracheids (t) are mostly filled. (tangential section)

Fig. 17. Oil in ray parenchyma (r) in advance of resin filled wood (res). (cross-section)

Fig. 18. Resin-soaked wood (res) and callus (ca) growing over the wound; note the oil-filled rays (r) external to the resin-soaked wood. (cross-section)

Table 1. The effect of early wounds upon subsequent wounds on the stem of lodgepole pine.

Inoculation Height	Horse Thief Creek		Steamboat Mountain		
	<i>a</i>	<i>b</i>	<i>c</i>	<i>d</i>	<i>e</i>
2.4 m	† 1.2 ± 0.4	1.3 ± 0.5	2.9 ± 0.2	3.0 ± 0	2.7 ± 0.5
2.2 m	1.7 ± 0.5	1.5 ± 0.5	2.8 ± 0.4	3.0 ± 0	2.6 ± 0.5
2.0 m	1.7 ± 0.5	1.8 ± 0.5	2.8 ± 0.4	3.0 ± 0	2.4 ± 0.6
1.8 m	1.8 ± 0.4	1.7 ± 0.5	2.6 ± 0.6	2.7 ± 0.5	2.6 ± 0.5
1.6 m	2.0 ± 0.0	1.8 ± 0.4	2.3 ± 0.8	2.7 ± 0.5	2.5 ± 0.5
1.4 m	2.2 ± 0.4	2.2 ± 0.4	2.4 ± 0.4	2.2 ± 0.5	2.6 ± 0.6
1.2 m	2.5 ± 0.5	2.5 ± 0.5	2.1 ± 0.4	2.2 ± 0.5	2.4 ± 0.6
1.0 m	2.8 ± 0.4	2.7 ± 0.5	1.9 ± 0.6	2.2 ± 0.5	2.3 ± 0.7

*a and c: first wounds were at 1.0 m and later wounds at 2-day intervals progressively higher; b and d: all wounds at the same time; e: sequentially lower wounds every 2 days.

† average of 24 wounds: 4 wounds on each of 6 trees; 3 = resinous response, 2 = intermediate response, 1 = non-resinous response.

faces starting at 1 m above the ground, and later inoculations were made every 2 days, progressively higher at 0.2 m intervals. A second series of six trees were inoculated on each of four faces starting at 2.4 m height on the stem; later inoculations were progressively lower. A third series of six trees received all eight vertically aligned inoculations on each of four faces at the same time.

The expected result, that earlier wounds at the base of the stem would diminish the response to later wounds at higher levels, is shown in Table 1, series a and b. In these two series, the lower inoculations were resin soaked and did not develop any blue stain. The highest inoculations showed some blue stain development. On the other hand, in series c, d and e, wounds higher on the stem diminished the response of later wounds below them, both in comparisons within the series and in comparison with inoculations at each level at the same time. There was a definite reduction in sequential wound response in all treatments, but evidently no single cause for this.

The gradual reduction in response to sequentially higher wounds is usually considered to be due to increasing moisture stress by disruption of the water conducting system by the lower wounds. This is possible in view of the finding, reported below, that moisture stress does reduce the wound response. If, on the other hand, moisture is not limiting and the stem can redistribute available moisture, the continued supply of energy-rich metabolites moving from the crown may become limiting for the response to later wounds, lower on the stem.

Another important factor influencing the successful establishment of beetles is the timing of the attack. Beetles attack about the third week of July in southeastern British Columbia, and this is synchronized to the period when spring wood production is well advanced, before the lumina in the current year's horizontal ducts have developed. Therefore, the horizontal ducts are non-functional close to the cambial surface. In addition, the current year's vertical ducts have not

been produced and there is also a seasonal decline in capacity of the tree to produce secondary resins at this time (Reid and Shrimpton 1971).

THE EFFECT OF MOISTURE STRESS UPON WOUND RESPONSE

The idea that stress, and particularly moisture stress, increases the vulnerability of trees to bark beetle attack has been an intuitive part of thinking about bark beetles for many years. Typically, the physiological functions of the tree are little affected by moisture stress up to a certain threshold level; above this threshold, there is a rapid and significant reduction in the function (Puritch 1973). The levels of moisture stress found to depress physiological functions under experimental conditions are of the order commonly experienced by trees during a dry summer (Brix 1972).

Interestingly, some of the changes that occur within living cells of the tree in response to moisture stress result in an increase in soluble nitrogenous compounds and soluble sugars (Parker 1968). Both of these materials are essential for the beetles and their associated fungi and lack of nitrogenous compounds often limits fungal development in woody tissues (Merrill and Cowling 1966).

Whereas the idea of drought-induced susceptibility has been widely accepted, there has been no definite field proof in lodgepole pine (Hopping and Mathers 1945). Both positive and negative evidence have been gathered (Beal 1943). However, a general relationship has been observed between periods of warmer- and drier-than-normal weather and increased beetle activity over large areas (Powell 1969). Recently, Puritch and Mullick (1975) showed that moisture stress reduces the wound healing process of the bark of *Abies*, and I have used the blue-stain inoculation techniques to study effects of moisture stress upon the wound response in lodgepole pine seedlings.

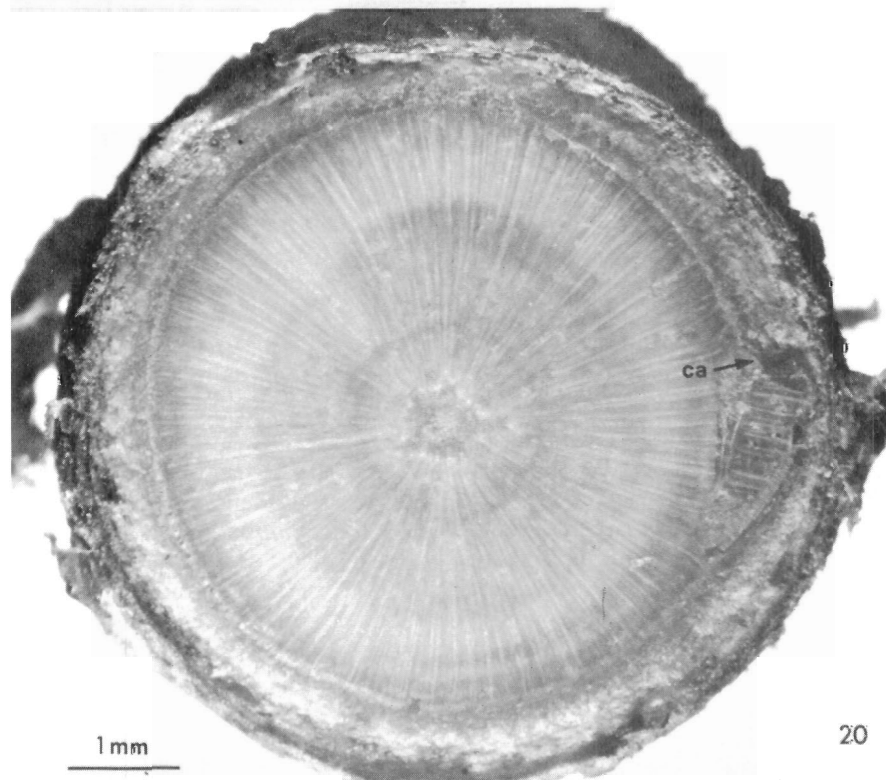
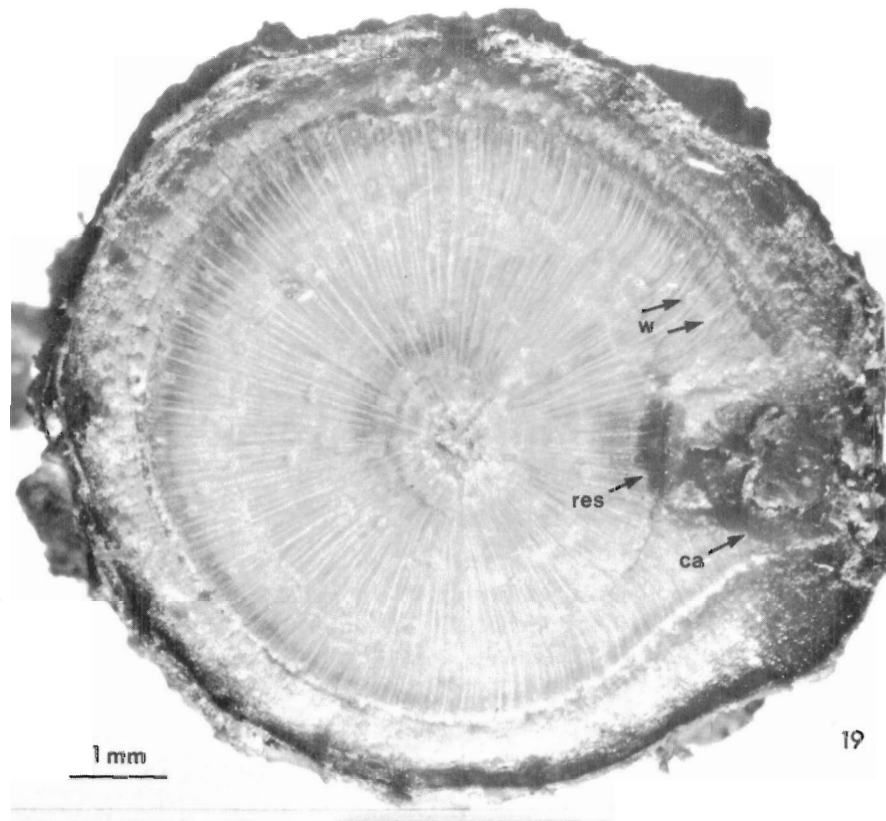


Fig. 19. Cross-section of a well-watered seedling, showing resin soaking (res) and callus (ca) overgrowing the wound.

Fig. 20. Cross-section of a stressed seedling, showing slight callusing (ca) and complete lack of resinous wound response.

Well watered seedlings healed the wound, as previously described (Shrimpton and Watson 1971) (Fig. 19). Seedlings stressed to -18 BARRs, as measured by pressure bomb (Puritch and Turner 1973), developed a small amount of callus at the margin of the wound, but no further healing response occurred (Fig. 20). Seedlings that were rewatered after an exposure to -18 BARR moisture stress produced normal wound responses after watering was resumed.

It is apparent that moisture stress can prevent the wound healing process and that this is reversible when the stress is removed. It is also known that moisture stress reduces resin flow from ducts (Munch 1921).

THE RELATIONSHIP BETWEEN RESISTANCE AND TREE MATURATION

The frequency of both horizontal (Mergen and Echols 1955) and vertical resin ducts (Reid and Watson 1966) remains quite constant in each individual pine after it reaches the sapling stage. The numbers fluctuate in response to environment; temperatures in late summer appear to have the greatest effect (Reid and Watson 1966). In the wood of young stems, the number of resin ducts per unit area gradually increases with age until the mature number of ducts is reached. The length of vertical ducts increases progressively toward the bark. Younger portions of branches also have fewer resin ducts (Bannan 1936).

The chemical composition of the oleoresin of mature trees shows only slight fluctuations with age; however, marked changes in the composition of the oleoresin have been observed as trees emerge from the juvenile stage (Squilace 1976).

The ability to form secondary resin is positively correlated with incremental growth rate (Shrimpton 1973b). For example, it has been shown in Europe that the application of fertilizer successfully increased both increment and resistance to bark beetles (Merker 1967). As trees age, the change in current annual increment parallels the ability of trees to produce a strong resinous response to attack (Safranyik et al. 1974). Pacific Forest Research Centre survey records for British Columbia show that mountain pine beetle outbreaks have originated, and have been maintained, in stands at or beyond physiological maturity as predicted from age of trees and site class.

The beginnings of many outbreaks have been assigned to colonization of the largest-diameter trees, with a progressive decrease in average stand diameter as the outbreak progresses (McGregor et al. 1976). This suggests that there was an increase in vulnerability of the large trees coincident with beetle attack. Other recent data show that this sequence, although common, is by no means universal (McGregor et al. 1975). Mahoney (these proc.) has shown that susceptibility of stands is correlated with declining incremental growth as measured from increments taken at breast height.

Since outbreaks can only be generated and sustained when the majority of stems in the stand are large enough to produce adequate numbers of beetles, the vulnerability of the large-diameter component of the stand must be one of the critical factors in generating an outbreak.

To examine this question, I collected growth data for a group of lodgepole pines in a lodgepole/aspen parkland near Riske Creek, British Columbia. Mountain pine beetles first killed three trees in this stand in 1975. This stand was compared to a stand near Kelowna, B.C., at the head of the Terrace Creek Valley, that has sustained a large outbreak starting about 1969. The average cumulative incremental growth rate for 25 attacked and 25 non-attacked trees is given in Fig. 21 and the average current annual increment in Fig. 22. Phloem thickness as a function of age for all trees sampled is shown in Fig. 23.

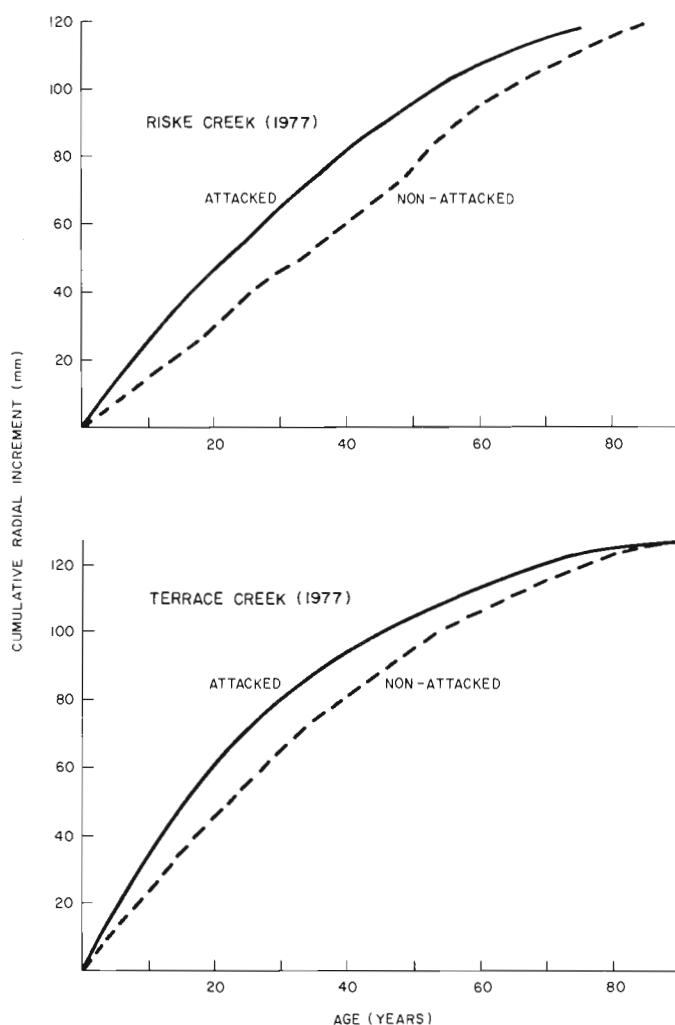


Fig. 21. The relationship between cumulative radial increment and age for infested lodgepole pine stands at two locations in British Columbia.

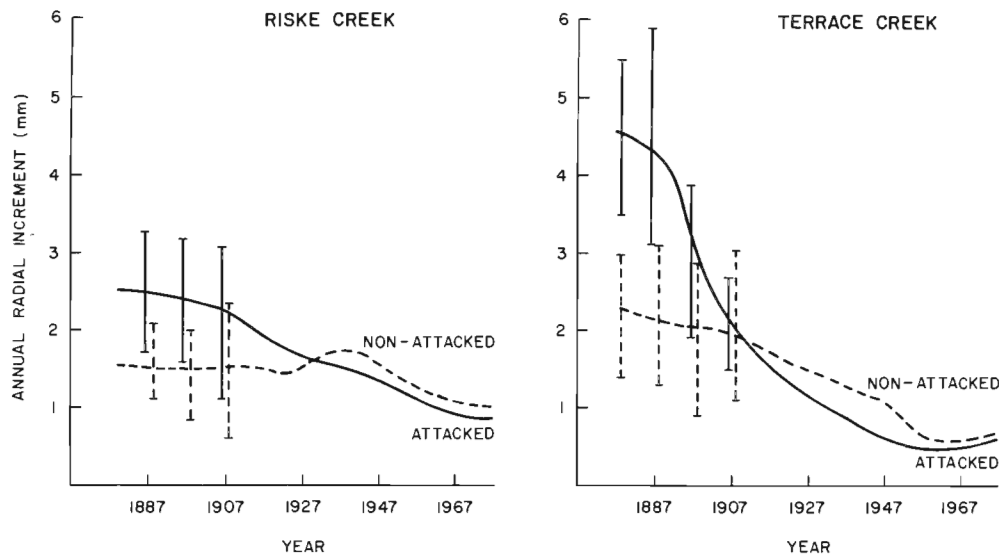


Fig. 22. Relationship between annual radial increment and age for infested lodgepole pine stands at two locations in British Columbia.

The difference between the sites at Riske Creek and Terrace Creek is very apparent. The trees at Terrace Creek grew much faster in radial increment until 20 years ago. In the past two decades, however, all trees on both sites have grown at about the same rate, just under 1 mm per year (Fig. 22). Even though the geographic areas are different, the beetles show an apparent preference for trees that have grown at a faster rate over most of their lifetime but which are now growing at a slower than average rate (Fig. 21).

The low current rate of incremental growth (Fig. 22), together with the tendency for phloem thickness to decrease with advancing age (Fig. 23), suggests that both stands have attained physiological maturity. Also, if a stand should escape attack, phloem may become too thin and the stand may survive for many years. These suggestions should be extended by evaluating past and current volume growth for stands under

attack to determine whether beetle epidemics are truly associated with physiological maturity, as previously suggested (Safranyik et al. 1974).

CONCLUSIONS

Resin ducts are a constant factor throughout that part of the lodgepole pine's life span in which mountain pine beetles are a factor. However, for most trees, the overall process of resin secretion, including secondary resin formation, declines after the culmination of current annual increment.

Within the relationship between the tree and the beetle/blue-stain complex, a critical factor for the beetle may be the seasonal timing of attack. For the tree, moisture stress may be a critical influence. The daily period of beetle flight (Reid 1962) is tuned to the onset of maximal daily moisture stress in trees (Kramer and Kozlowski 1960).

Resistance is a costly process energetically. Resins have more stored energy than sugar (Francis 1971). The cost may be too great for older trees. The possible relationship between physiological maturity of lodgepole pine and successful attack by the mountain pine beetle has been raised (Safranyik et al. 1975, Mahoney these proc., Peterman these proc.) or alluded to (Amman et al. 1977). It is my belief that if this relationship were studied from the point of view of volume growth, both the impact and the function of the beetle within pine stands would become more apparent.

ACKNOWLEDGMENTS

The skilled technical assistance of Mrs. L.E. Manning and Mr. G.A. Kapaniuk is gratefully acknowledged. Thanks are also extended to my colleagues, Mr. S.H. Farris and Drs. H.S. Whitney and L. Safranyik, for many helpful discussions during the course of the studies reported here.

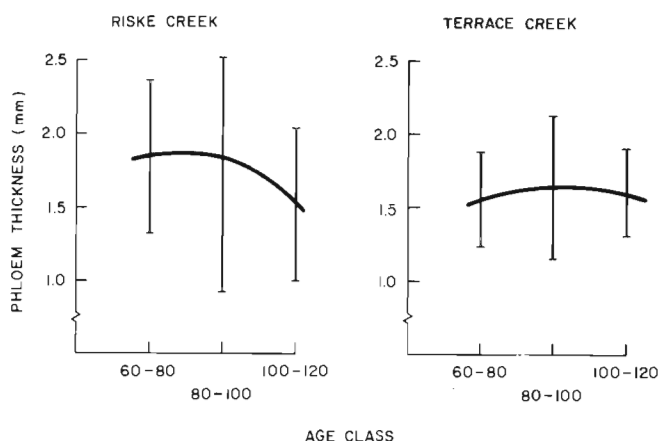


Fig. 23. Relationship between phloem thickness and tree age for infested lodgepole pine stands at two locations in British Columbia.

- Fahn, A., and J. Benayoun. 1976. Ultrastructure of resin ducts in *Pinus halepensis*. Development, possible sites of resin synthesis and mode of its elimination from the protoplast. *Ann. Bot.* 40: 857-863.
- Francis, M.J.O. 1971. Monoterpene biosynthesis. Pages 29-51 in T.W. Goodwin (ed.) *Aspects of terpenoid chemistry and biochemistry*. Academic Press, New York.
- * Hopping, G.R., and W.G. Mathers. 1945. Observations on outbreaks and control of the mountain pine beetle in the lodgepole pine stands of Western Canada. *Forest. Chron.* 11:98-108.
- Hudson, R.H. 1960. The anatomy of the genus *Pinus* in relation to its classification. *J. Inst. Wood Sci.* 6:26-46.
- Kramer, P.J., and T.T. Kozlowski. 1960. *Physiology of trees*. McGraw-Hill, Inc., New York. 642 pp.
- Lyr, H. 1967. The seasonal course of protection-wood formation in *Pinus sylvestris* after wounding. *German. Arch. Forstw.* 16:51-57.
- McGregor, M.D., D.R. Hamel and R.C. Lood. 1976. Evaluation of mountain pine beetle infestation, Gallatin Ranger District. Gallatin Nat. Forest., Montana, 1975. USDA Forest Serv. Forest Environ. Prot. Rep. 76-5, Missoula, MT. 11 pp.
- McGregor, M.D., D.R. Hamel, R.C. Lood, and H.E. Meyer. 1975. Status of mountain pine beetle infestations, Glacier Natl. Park, 1974. USDA Forest Serv. Rep. NR-75-10. Northern Region, Missoula, MT. 7 pp.
- Merker, E. 1967. Inducing increased resistance against bark beetle. *Allg. Forst-u. Jagdztg.* 138:13-24.
- Mergen, F., and R.M. Echols. 1955. Number and size of radial resin ducts in slash pine. *Science* 121:306-307.
- Mergen, F., P.E. Hoekstra and R.M. Echols. 1958. Genetic control of oleoresin yield and viscosity in slash pine. *Forest Sci.* 1:19-30.
- Merrill, W., and E.E. Cowling. 1966. Role of nitrogen in wood deterioration: Amounts and distribution of nitrogen in tree stems. *Can. J. Bot.* 44:1555-1580.
- Munch, E. 1921. *Naturwissenschaftliche Grundlagen der Kiefernharznutzung*. Arb. Biol. Reichsanst. Land-Forstw. 10:1-140.
- Noel, A.R.A. 1970. The girdled tree. *Botanical Review* 36:162-196.
- Parker, J. 1968. Drought resistance mechanisms. Pages 195-234 in T.T. Kozlowski (ed.) *Water deficits and plant growth*, Vol. I. Academic Press, New York. 390 pp.
- Peterman, R.M. 1974. Some aspects of the population dynamics of the mountain pine beetle, *Dendroctonus ponderosae*, in lodgepole pine forests of British Columbia. Ph.D. diss. Univ. of British Columbia, Vancouver. 208 pp.
- * Powell, J.M. 1969. Historical study of the relation of major mountain pine beetle outbreaks in Western Canada to seasonal weather. *Forest. Res. Lab. Info. Rep. A-X-23*. Calgary, Alberta. 11 pp.
- Puritch, G.S. 1973. Effect of water stress on photosynthesis, respiration, and transpiration of four *Abies* species. *Can. J. Forest Res.* 3:293-298.
- Puritch, G.S., and D.B. Mullick. 1975. Effect of water stress on the rate of non-suberized impervious tissue formation following wounding in *Abies grandis*. *J. Exp. Bot.* 26:903-910.
- Puritch, G.S., and J.A. Turner. 1973. Effects of pressure increase and release on temperature within a pressure chamber used to estimate plant water potential. *J. Exp. Bot.* 24:342-348.
- Reid, R.W. 1962. Biology of the mountain pine beetle, *Dendroctonus monticolae* Hopkins, in the east Kootenay region of British Columbia. I. Life cycle, brood development and flight periods. *Can. Entomol.* 94:531-538.
- Reid, R.W., and H.S. Gates. 1970. Effect of temperature and resin on hatch of eggs of the mountain pine beetle (*Dendroctonus ponderosae*). *Can. Entomol.* 102:617-622.
- Reid, R.W., and D.M. Shrimpton. 1971. Resistant response of lodgepole pine to inoculation with *Euophium clavigerum* in different months and at different heights of the stem. *Can. J. Bot.* 49:349-351.
- Reid, R.W., and J.A. Watson. 1966. Sizes, distributions and numbers of vertical resin ducts in lodgepole pine. *Can. J. Bot.* 44:519-525.
- 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. J. Bot.* 45:1115-1126.
- Safranyik, L. 1971. Some characteristics of the spatial arrangement of attacks by the mountain pine beetle, *Dendroctonus ponderosae* (Coleoptera: Scolytidae), on lodgepole pine. *Can. Entomol.* 103:1607-1625.
- Safranyik, L., D.M. Shrimpton and H.S. Whitney. 1974. Management of lodgepole pine to reduce losses from the mountain pine beetle. *Can. Forest. Serv. For. Tech. Rep. 1*. Victoria, B.C. 24 pp.
- _____. 1975. An interpretation of the interaction between lodgepole pine, the mountain pine beetle and its associated blue-stain fungi in Western Canada. Pages 406-428 in D.M. Baumgartner (ed.) *Management of lodgepole pine ecosystems*. Washington State Univ. Coop. Ext. Serv., Pullman.
- Shrimpton, D.M. 1973a. Extractives associated with the wound response of lodgepole pine attacked by the mountain pine beetle and associated microorganisms. *Can. J. Bot.* 51:527-534.
- _____. 1973b. Age- and size-related response of lodgepole pine to inoculation with *Euophium clavigerum*. *Can. J. Bot.* 51:1155-1160.
- Shrimpton, D.M., and J.A. Watson. 1971. Response of lodgepole pine seedlings to inoculation with *Euophium clavigerum*, a blue-stain fungus. *Can. J. Bot.* 49:373-375.
- Shrimpton, D.M., and H.S. Whitney. 1968. Inhibition of growth of blue-stain fungi by wood extractives. *Can. J. Bot.* 46:737-761.
- Smith, R.H. 1972. Xylem resin in the resistance of the Pinaceae to bark beetles. USDA Forest Serv. Res. Note PSW-1. Pac. SW Forest and Range Exp. Sta., Berkeley, CA. 7 pp.
- Squillace, A.E. 1976. Analysis of monoterpenes of conifers by gas-liquid chromatography. Pages 120-157 in J. P. Miksche (ed.) *Modern methods of forest genetics*. Springer-Verlag, Berlin.
- Whitney, H.S., and R.A. Blauel. 1972. Spore dispersion in *Ceratocystis* spp. and *Euophium clavigerum* in conifer resin. *Mycologia* 64: 410-414.

QUESTIONS AND ANSWERS

- Q. Concerning the virulence of attack by bark beetle/fungal associates, can you make an estimate as to the relative importance of the blue-staining vs. non-blue-staining microorganisms?
- A. Blue staining is the result of pigment production in certain fungi as they mature. There are circumstances when pigment is slow to develop or may not develop at all. In general, blue stain is caused by filamentous fungi (*Europhium* and *Ceratocystis*) that aggressively kill the tissues of the tree stem. The non-staining microorganisms, yeasts, bacteria and other filamentous fungi have a different, but I expect important, role in maintaining a suitable "under the bark" habitat for the beetles.
- Q. Crown-produced auxins are known to mediate formation of xylem. If phloem structure is similarly mediated, would not crown descriptions be a better indicator than age of "maturity"?
- A. I think volume growth is the best indicator of physiological maturity; however, this is hard to determine and requires destructive sampling. The crown is the major source of carbohydrate and growth hormones for the tree and as such has a major regulating effect upon total tree growth. If changes in crown form can be accurately diagnosed, I expect them to be good indicators of physiological maturity.
- Q. How much time is involved in the production of wound resin ducts and the soaking of sapwood with resin after wounding (as from the entrance of bark beetles)?
- A. Resin flow from cut ducts occurs instantaneously and lasts for a day or two. This flow affects the beetle as it cuts resin ducts, and flushes fungal spores from the gallery. Secondary resins accumulate in ray cells within 24 hours of wounding and act against the blue-stain fungi as they attempt to invade these ray cells. These secondary resins also increase the resin content of the beetle gallery. Wound resin ducts take about 2 weeks to form. They are situated at the margin of the wound and completely surround it. Resin from these ducts serves to complete the sealing coat of resin over the wound.
- Q. Would unsuccessful beetle attacks produce enough secondary resin ducts to increase tree resistance?
- A. Wound resin ducts can be a major source of resin before they are blocked by tylosoids, some 3 to 5 years after they are formed. In that these wound ducts are always fully interconnected to the horizontal ducts, surface damage such as bark beetle gallery construction will release this resin. If this increased early resin flow allows additional time for the secondary resins and wound resin ducts to form, it could increase resistance.

- Q. You identified a correlation in increased resin duct formation with drought periods. Presumably this will also be a period of relatively greater physiological stress. On balance, which response do you think is more important in a tree's resistance to mountain pine beetle attack during drought periods?

- A. Vertical resin ducts are laid down in early August in lodgepole pine. This is usually later than beetle flight and, therefore, the current year ducts have not been formed at the time of attack, and any change in their numbers has no relation to beetle attack in the year of duct formation.

The increased formation of ducts during hot summers is a response by the tree to a physiological stress. The reasons for this response are not clear.

- Q. What blue-stain fungus did you use, and what was the distribution of this organism on the bole?

- A. *Europhium clavigerum* Robinson and Davidson is used for all my inoculation experiments on the mountain pine beetle question. This fungus is used because it is the most aggressive tree tissue killing fungus carried by the mountain pine beetle. In the mature tree experiment reported here, 8 inoculations, vertically spaced at 0.2 m intervals, were put on each of four faces for a total of 32 inoculations per tree. Six trees were used in each treatment.

REFERENCES

- Amman, G.D. 1975. Abandoned mountain pine beetle galleries in lodgepole pine. USDA Forest Serv. Res. Note INT-197. Intermtn. Forest and Range Exp. Sta., Ogden, UT. 6 pp.
- Amman, G.D., M.D. McGregor, D.B. Cahill and W.H. Klein. 1977. Guidelines for reducing losses of lodgepole pine to the mountain pine beetle in unmanaged stands in the Rocky Mountains. USDA Forest Serv. Gen. Tech. Rep. INT-36. Intermtn. Forest and Range Exp. Sta., Ogden, UT. 19 pp.
- Bannan, M.W. 1936. Vertical resin ducts in the secondary wood of Abietineae. New Phytologist 35:11-47.
- Beal, J.A. 1943. Relation between tree growth and outbreaks of the Black Hills beetle. J. Forest. 41:359-366.
- Berryman, A.A. 1976. Theoretical explanations of mountain pine beetle dynamics in lodgepole pine forests. Environ. Entomol. 5:1225-1233.
- Brix, H. 1972. Nitrogen fertilization and water effects on photosynthesis and earlywood-latewood production in Douglas fir. Can. J. Forest. Res. 2:467-478.
- Chattaway, M.M. 1951. The development of horizontal canals in rays. Austr. J. Sci. Res. 4:1-11.
- Fahn, A. 1967. Plant anatomy. Pergamon Press, Elmsford, NY. 611 pp.

Effects of Climate and Weather on Mountain Pine Beetle Populations

Les Safranyik

ABSTRACT

The literature on the direct effects of climate and weather on the biology and dynamics of mountain pine beetle (*Dendroctonus ponderosae* Hopkins) populations is reviewed and discussed, with emphasis on the development of epidemics. Of the climatic effects, temperature is the most important. Typically, in the optimum range of the beetle's distribution on lodgepole pine (*Pinus contorta* Douglas var. *latifolia* Engelm.), there is enough heat accumulation each year to produce one or more generations and the frequency of adverse weather conditions is not high enough to prevent population build-up or to reduce infestations to endemic levels. In some years, however, adverse weather can cause a decline in population and damage levels, but this reversal is usually temporary and the course of outbreak is largely determined by factors other than climate. In this optimum habitat, the beetle poses a continuous threat to lodgepole pine of susceptible age and size. At high elevation and at northern latitudes, climate becomes the dominant factor controlling the distribution and abundance of mountain pine beetle populations and infestations in space and time. Beetle development is out of phase with the cold season; consequently, the least cold-hardy life stages (eggs, pupae) may enter the winter and suffer heavy mortality. Epidemics tend to be less frequent and intense, and stand depletion decreases, toward the limits of the distributional range. The northern limit of the beetle's range is bounded by the isotherm for -40°C (-40°F) mean annual minimum temperature and a zone where, on the average, heat accumulation during the growing season is less than the estimated minimum (833 degree-days C) for brood development on a 1-year cycle. The upper altitudinal limit, which ranges from about 750 m (2460 ft) near the northern limit (latitude 56°N) to about 3650 m (11,972 ft) near the southern limit (latitude 31°N), is probably delimited by similar temperature conditions.

INTRODUCTION

The mountain pine beetle (*Dendroctonus ponderosae* Hopkins) has been referred to as the most destructive bark beetle (Wood 1963). The average annual loss of timber attributed to this bark beetle since 1895 is about 2 billion board feet. Outbreaks range from less than 1 ha (2.5 acres) to hundreds of square kilometers in size, last from 3 to 20 years, and invariably destroy the large-diameter component of affected stands (Safranyik et al. 1974).

When mountain pine beetle populations are low, a number of abiotic and biotic factors interact to restrict the potential of such populations to increase. Among the most important abiotic factors are climatic effects. Climate affects mountain pine beetle populations in two important ways:

1. Directly, through effects on the behavior and physiology of individual insects. The magnitude of these effects is modified by certain physical characteristics of host trees, especially those of the outer bark and phloem.
2. Indirectly, through the interrelations between climatic factors and the physiology of the host tree and between climatic factors and the associated organisms of the beetle.

There is considerable literature on the effects of climate on beetle behavior, survival and development, especially on laboratory experiments dealing with the effects of temperature. This literature has been reviewed briefly in Safranyik et al. (1974) and Safranyik (1976). Amman's paper (these proc.) described the main effects of climate and weather in relation to the ecology of the beetle. There is much less information concerning the nature and effects of climatic factors on the distribution and abundance of this insect, and concerning

methods to assess the relative suitability of the total climate for development and survival of the beetle. Also, in spite of the voluminous literature on the subject, there is considerable disagreement among entomologists on the role of climate in the control of insect populations.

The objective of this paper is to review the state of knowledge with respect to 1) the role of climate in insect control, 2) the effects of climate and weather on the general biology and population dynamics of the mountain pine beetle, and 3) the practical significance of this knowledge in determining outbreak hazard. Only the direct effects of climate on the beetle and the indirect effects through its associated microorganisms will be reviewed here. The indirect effects of climate manifested through the physiology of the host tree are described in Shrimpton's paper (these proc.).

THE ROLE OF CLIMATE IN THE CONTROL OF INSECT POPULATIONS

Weather and climate are ever-present factors of insect life. The dominant roles of these factors on insect behavior and physiology are commonly accepted by entomologists. Weather defines the changing state of the atmosphere and it is a composite condition of which light, temperature, relative humidity, precipitation and wind are the most important to insect life. Climate is the long-term average condition with respect to the weather factors. Weather is known to determine population change in many insects and certainly plays a dominant role in their population dynamics. These population changes result from the effects of annual, seasonal and diurnal changes of weather on the activity of the endocrine system, on survival and on development and reproduction of the insect. Climate, on the other hand, has an important role in delimiting the geographical range, as well as the abundance of insect species. Generally, as an insect species reaches the edge of its area of distribution, it reproduces more slowly, immigration and extinction tend to balance, and the species tends to become rarer, until its temporal and spatial distribution are irregular and patchy.

Can insect populations be controlled by climate? Attempts to answer this question have generated much controversy among entomologists, especially during the past 3 decades. This relates partly to inconsistency in defining the term "control." In economic entomology, the rather loose, but nevertheless widely used, definition of control is "reduction of the numbers of an insect pest to levels at which the damage to the resource would be acceptable by the managing agency." In the context of this definition, insect populations can indeed be controlled by climatic factors since, as was pointed out in the preceding paragraph, these factors are known to determine population change in many insects. For example, a sequence of years with unseasonably low temperatures may reduce a bark beetle population below injurious levels. This "climate control" is apt to be only temporary, however, within the optimum range of the beetle because in this range the likeli-

hood of long sequences of years unfavorable for beetle reproduction, development and survival is usually very low. At the extreme edges of the range, provided that this range is limited to climate alone, the beetle would tend to be less abundant and could be controlled by climate more or less permanently.

The statement that insect populations can be controlled by climate, in the sense discussed above, is not equivalent to the statement that climate can "regulate" insect populations. Regulation, an alternate meaning of the word control, is a stabilizing process whose intensity of action is related to population density, like that implied by negative-feedback in cybernetics (Varley et al. 1973). Since the intensity of action of climatic factors is independent of population density, insect populations cannot be regulated by climatic factors alone.

CLIMATIC EFFECTS ON THE BIOLOGY OF THE MOUNTAIN PINE BEETLE

Emergence, Flight, Dispersal

Ambient temperatures are instrumental in determining the onset and duration of the emergence period and in delimiting thresholds of diurnal emergence activity. Emergence and flight periods are preceded by warm, dry weather, but apparently no relationship exists between the duration of such periods and the onset of emergence. Essentially, no emergence occurs at temperatures below ca 16°C (60.8°F) (Reid 1962a, Schmid 1972, Billings and Gara 1975), and there is evidence that both hourly and diurnal emergence are reduced when air temperature exceeds 30°C (86°F) (Gray et al. 1972, Rasmussen 1974). Emergence usually begins in the morning when temperatures exceed 16°C and ceases in the afternoon at the same temperature. Peak daily emergence, however, is usually confined to a 2- to 3-hour period from early to mid-afternoon when air temperatures exceed 20°C (68°F). Emergence in the field and the laboratory exhibit distinct diel periodicities in lodgepole pine (*Pinus contorta* Douglas var. *latifolia* Engelman) (Reid 1962b, Watson 1970), as well as other host species (Billings and Gara 1975), which prevail even under conditions of constant temperature and light. Therefore, it appears that daily emergence is controlled by an endogenous rhythm. Thus, observed correlations between the rate of hourly emergence in the field and ambient temperatures may be more coincidental than causal. In addition, the rate of hourly emergence in the optimum temperature range is affected more by other factors, such as cloud cover and precipitation, than by small changes in daily maximum temperature (Schmid 1972).

Beetles of both sexes tend to emerge at greater relative rates from the south sides of the lower boles of lodgepole pines throughout the emergence period in southern British Columbia (Safranyik and Jähren 1970). This emergence pattern is probably related to a combination of differences in rates of development and of maturation of adults on the two aspects—

i.e., because of differential subcortical heat accumulation—as well as to differences on the two aspects in the length of time during which temperatures remain favorable for emergence.

The time of emergence appears to be related to temperatures during the period of brood development (McCambridge 1964), especially during the spring months (Reid 1962a). The median emergence time after exceptionally warm weather during the development period can occur as much as 1 month earlier than after abnormally cool weather. In most years, however, the median dates of emergence will differ by less than 10 days. The period of peak emergence is strongly affected by temperature and precipitation. Peak emergence normally lasts from 7 to 10 days, but can vary from 3 or 4 days to 3 weeks. The occurrence of cool or rainy weather during the flight period will extend the period of emergence. Late emergence and an unusually extended emergence period are thought to be detrimental to the establishment and survival of new broods in the northern part of the beetle's range (Safranyik et al. 1975).

Newly emerged beetles are attracted by high light intensity and utilize spot sources of light rather than diffused light for orientation. The optimum temperature range for spontaneous flight response is from about 22 to near 32°C (71.6 to 89.6°F), but the estimated temperature limits of flight are 19 and 41°C (66.2 and 105.8°F). Flight has been observed in the field at temperatures lower than 19°C, but this resulted from the warming effect of the sun, either directly on the emerged insects or on the bark near the insects' bodies. Once bark beetles start to fly they can generally maintain their flight at suboptimal temperatures (Atkins 1961). At the other extreme, beetles become negatively phototactic at temperatures above 35°C (95°F) (Shepherd 1966), and flight is severely restricted above 38°C (100.4°F) (McCambridge 1971). Flight response in the optimum temperature range is increased by light intensity as well as by humidity up to a point close to saturation. Beetles are able to fly at low light intensities (such as in bright moonlight); therefore, the daily initiation and termination of flight are probably controlled more by temperature than by light intensity.

Although they have not been investigated in the mountain pine beetle, temperature, light intensity and relative humidity have major effects on the duration of initial flight, as well as on flight velocity of other bark beetle species (Atkins 1959, 1960, 1961).

There is a general lack of knowledge on the dispersive behavior of the mountain pine beetle in relation to weather factors. The beetles typically fly during warm, fair-weather periods. These periods are generally characterized by air inversions near the ground and by upward convection currents (Chapman 1967). Furniss and Furniss (1972) suggest that some bark beetles are caught in, and directed by, these warm convection currents and could easily be carried 20 km (12.5 miles) or more. Their thesis is supported by collections of scolytid beetles, including mountain pine beetles, from snowfields above

timberlines in the northwestern United States. We have no information on the frequency of these wind-directed flights or on their importance in the population dynamics of the mountain pine beetle. There is circumstantial evidence to indicate that mountain pine beetles have crossed timberless terrain from 20 to 30 km (12.5 to 18.8 miles) in width (Evenden et al. 1943). However, it is not known whether the beetles spanned these distances mainly through free flight or carried by air currents. The mountain pine beetle is a good flier, and its flight capacity is probably comparable to that of the Douglas-fir beetle, which is capable of sustained flight for up to 4 hours or more at speeds of 3.0 to 6.0 km (1.9 to 3.8 miles) per hour (Atkins 1961).

Host Colonization and Multiplication

The process of host colonization involves establishment of initial attacks on host trees by pioneer beetles and aggregation of both sexes at, and establishment of mass attacks on, these trees in response to a combination of volatiles produced by the host tree and the beetle. There has been very little work done on the role of weather factors on this important aspect of the population dynamics of the mountain pine beetle. The process of multiplication consists of three components: gallery mining, mating and egg laying. The most important weather factor affecting multiplication is temperature, acting directly on the beetle and indirectly through its effect on the rate of drying of the subcortical habitat.

Air movement near the ground is considered to be one of the most important meteorological factors in relation to the searching efficiency of scolytid beetles (Chapman 1967). The searching beetles apparently find the sources of attractive odors by flying upwind to them (Wright 1964). The beetle's ability to encounter and track odors is greater under stable air conditions when high concentrations of odors will persist far from the source. These stable air conditions are most frequently encountered in late afternoons and evenings, during the flight period of the mountain pine beetle. Indeed, peak response to pheromone baits usually occurs in late afternoon when solar radiation is decreased and the wind has subsided (Pitman and Vité 1969). Also, McCambridge (1967) found, in ponderosa pine (*P. ponderosa* Lawson) stands, that peak penetration of trees occurred in the period from late afternoon to early morning. Beetles arriving at dusk, when the temperature and/or light conditions are suboptimal for boring activity, usually stay overnight in crevices or under bark scales and make no attempt at boring into the bark. The next morning, when air temperatures reach about 17°C (62.6°F), many of these beetles will bore into the bark and some take flight (Rasmussen 1974).

Even though beetles may land with roughly equal frequency on all aspects of the bole, attack density will usually be highest on the north aspect. At the time of attack, both light intensity and surface temperature can be quite high, especially on the exposed, sunny sides of the boles. Shepherd (1966) showed that both high light intensity and high temperature stimulate beetles to fly. Since the north sides of the

boles are usually in shade and bark surface temperatures are about 1°C (1.8°F) cooler than on the south side during the attack period (Powell 1967), temperature and light conditions are probably responsible for the differences in attack density among aspects.

Egg gallery excavation and egg deposition are determined in large part by the suitability of temperature and moisture regimes. The lower temperature threshold of boring and oviposition activity is between 2 and 7°C (35.6 and 44.6°F), depending on the vigor of the individual beetle (Reid 1962b). The upper temperature limits of boring and oviposition activity have not been investigated. Rudinsky and Vité (1956) found that the Douglas-fir beetle continued gallery excavation at 32°C (89.6°F), but excessive activity or restlessness hindered organized boring activity at this temperature. Both length of egg gallery and number of eggs laid per day tend to increase curvilinearly with temperature within the temperature range normally encountered by the beetle during the attack period (Amman 1972).

The rate at which infested trees deteriorate in terms of inner bark and outer sapwood moisture determines, in part, the time available to the female for gallery construction, and hence affects the number of eggs laid per individual. Successfully attacked trees dry at different rates, depending in part on their degree of exposure.

Oviposition in lodgepole pine ceases when the moisture contents of the inner bark and outer sapwood drop below ca 105 and 60 percent oven dry weight, respectively (Reid 1962b). Under drier conditions than these, the female will re-emerge to make a second flight and attack. Thus, significant differences in egg gallery lengths and number of eggs per gallery between trees in the same or different infestations may result from differences in the rate at which trees deteriorate after attack. Second flight has a high survival value to the population in the northern parts of its range because the progeny will constitute the bulk of the next generation of beetles (Reid 1963). Such is not the case in the more southerly regions of western white pine, where second-flight progeny supplement a high surviving population from the earlier flight (De Leon et al. 1934).

Development and Survival

Temperature and moisture are the two most important weather factors affecting development and survival. As with other cold-blooded animals, growth, development and survival of the mountain pine beetle depend upon the temperature of its environment. The physiological effects of temperature are important in 1) delimiting growth and development, 2) setting the rates of growth and development, 3) regulating cold hardiness and 4) determining survival. Moisture has importance both as a weather factor that determines survival and as a physiological factor affecting beetle nutrition. Moisture is also known to modify the physiological effect of temperature on the rate of larval development in bark beetles (Rudinsky

1962). However, this aspect of larval development has not been investigated for the mountain pine beetle.

Egg hatching and growth and development of larvae occur between 4.4 and 37.8°C (39.9 and 100°F) (Reid and Gates 1970, Patterson 1930) and optimum development at constant temperatures is near 24°C (75.2°F) (Safranyik unpublished). The rates of development of the various brood stages and, thus, the length of the life cycle are dependent upon heat accumulation (in terms of degree-days) between the minimum and maximum temperature thresholds for development. Safranyik (1975) estimated that the minimum heat requirement for brood development on a 1-year cycle is 833 degree-days within the growing season from 1 August to 31 July the following year. When heat accumulation in an area is less than this, the beetle population is forced into a 2-year cycle. With this extended life cycle the immature stages are exposed to mortality factors for longer periods and survival is usually low. Such low heat accumulation occurs frequently near the northern limit of the beetle's distribution and at high elevations. In these extreme habitats, and also in more favorable locations during unusually cool summers, brood development may become out of synchrony, and, as a consequence, the least cold-hardy stages of the beetle may enter the winter and suffer heavy mortality.

Survival of all stages of the mountain pine beetle is reduced by unseasonably cold weather and extremely high summer temperatures. Eggs have the least tolerance to freezing, followed by pupae, adults and larvae (Safranyik et al. 1974). The lethal low temperature threshold for eggs is near -18°C (-0.4°F) and for larvae it is between -34 and -38°C (-29.2 and -36.4°F) (Wygant 1940, Somme 1964). The cold-hardiness of larvae increases upon exposure to freezing temperatures because of accumulation of glycerol in the blood. Thus, their cold-hardiness is greatest in the period from December to February. The effects of cold are usually seen within the first 2 to 4 hours of direct exposure. The insulating properties of bark and snow modify subcortical temperatures; also, winter kill apparently will be higher in small-diameter trees than in large-diameter trees (Wygant 1940) because the amount of stored heat is greater in the latter, and stored heat affects subcortical temperatures.

Low winter temperatures and unseasonably cold temperatures frequently cause heavy mortality of broods at the northern edge of the distributional range and at high elevation. Because of this, and because there is often inadequate heat for growth and development, epidemics are not as frequent and are less intense in these areas. In the optimum part of the distributional range of the beetle, winter temperatures are seldom severe enough to reduce an infestation to endemic levels.

The order of susceptibility of various brood stages to high temperatures is the same as that to low temperatures (Safranyik et al. 1974). Prolonged exposure to temperatures near 38.0°C (100.4°F) will cause death of all stages, but the lethal high temperature with short exposure is above 43.3°C

(110.0°F) (Patterson 1930). These high subcortical temperatures seldom occur in standing trees in the northwestern United States and Canada, but may occur quite frequently at more southerly latitudes and lower elevations.

Mountain pine beetle eggs will not develop and hatch in atmospheres of less than 90 percent relative humidity (Reid 1969). However, since oviposition occurs only in inner bark having a moisture content higher than 105 percent by oven dry weight, this factor does not significantly affect the population dynamics of the beetle. After the tree has been successfully attacked, the moisture content of the inner bark and sapwood declines at rates partly related to air temperature and humidity conditions. Generally, brood survival is directly related to the final moisture content of the outer sapwood up to about 35 percent (Reid 1963). Reid believed that reduced survival at higher moisture levels was due to extensive resinosis and at very low moisture levels, to the deterioration of the nutritional value of the inner bark. Also, the broods are more subject to desiccation during cold weather in bark that becomes dry prior to the onset of winter than are broods in moist bark (Amman 1973). Since the average diameter of the infested trees decreases during the course of epidemics, and since small-diameter trees tend to dry at faster rates than larger-diameter trees, the moisture factor during brood development plays an important role in the population dynamics of the mountain pine beetle.

Associated blue-stain fungi of the mountain pine beetle have important roles in host colonization and beetle nutrition (Safranyik et al. 1975). The growth, development and reproduction of these blue-stain fungi and the numerous other microbial associates of the beetle are strongly affected by temperature, moisture and light conditions, and by oxygen/carbon dioxide concentration of their environment. The magnitudes and rates of change of these variables are directly affected by weather factors, especially ambient temperature.

Spatial Distribution and Life Cycle

The known geographical range of the mountain pine beetle generally follows the ranges of its principal host trees and extends from central British Columbia (latitude 56°N) to South Dakota, and south to northern Mexico (latitude 31°N). In western Canada, the beetle occurs only over the southern part of the range of lodgepole pine. Extreme cold winter temperatures are the limiting factors (Swaine 1925). The northern and northeastern limits of the beetle's distribution are approximately bounded by the isotherm for -40°C (-40°F) mean annual minimum temperature and a zone where, on average, heat accumulation during the effective growing season is less than the minimum required for development on a 1-year cycle. In areas located between the mean annual minimum temperature isotherms of -34.4°C (-30°F) and -40°C, where heat accumulation during the growing season is frequently insufficient for 1-year cycle development, infestations occur infrequently at all elevations and are generally of low

intensity, even though an ample food supply may exist. In these areas, temperature is the most important limiting factor in the population dynamics of the beetle.

The beetle is distributed throughout the southern part of the range of lodgepole pine, and weather factors play a less important role in its epidemiology in the elevational zone where beetle infestations occur most frequently.

The altitudinal range of the beetle is from about 750 m (2460 ft) above sea level near the northern limit of the geographical range to about 3650 m (11,972 ft) near the southern limit (Struble and Johnson 1955). This difference represents roughly a 120-m (394-ft) decrease in the altitudinal range with each 1°N latitude. Interestingly, this rate of decrease in the altitudinal limit is about the same as the adjustment called for by Hopkins' Bioclimatic Law (Hopkins 1919). This finding appears to indicate that the innate capacities of individuals and populations to survive and multiply in the adverse weather conditions that prevail at higher elevations are about the same throughout the geographical range.

In spite of the wide geographical distribution, a 1-year life cycle is normal in the lower altitudinal zone, where the beetle most commonly occurs. An exception is in areas below 2000 m (6560 ft) south of about latitude 40°N, where two generations per year, and often the beginning of a third generation, will develop (Struble and Johnson 1955).

In the lower altitudinal zone, ranging from 1500 m (4920 ft) at latitude 49°N to about 2600 m (8528 ft) at latitude 39°N, temperatures are generally favorable for survival and multiplication (Amman et al. 1977, Safranyik et al. 1975), and the beetle poses a continuous threat to lodgepole pine of susceptible age and size. This is the zone in which the heaviest losses will usually occur. Above this zone the climate becomes progressively adverse to brood development and survival; broods tend to undergo a 2-year cycle and become poorly synchronized with the cold season (Amman 1973). At these high elevations, as near the northern limit of its range, climate becomes the dominant factor in the population dynamics of the beetle. Because of reduced survival, infestations are not as intense and fewer trees are killed as elevation increases, though an ample food supply may exist (Amman and Baker 1972, Amman et al. 1973).

THE ROLE OF CLIMATE AND WEATHER IN THE DYNAMICS OF MOUNTAIN PINE BEETLE POPULATIONS

Climatic factors play an important role in determining the distribution and abundance of mountain pine beetle populations in space and time. Of the climatic variables, temperature is the most important because adult emergence and dispersal, brood establishment, development and survival are temperature-limited.

Over most of the distributional range of lodgepole pine, where the mountain pine beetle is most abundant and damaging, the beetle has a 1-year life cycle. In this optimum habitat, the characteristic weather conditions during the development period are a moderately warm fall, a mild winter and moderate weather during spring and early summer, followed by a period of hot, dry weather in July and August (Reid 1963). The beetle's life cycle is synchronized with the cold season and the broods usually enter the winter as large larvae, the most cold-hardy stage. Infestations are persistent and intense, and invariably deplete most of the large-diameter components of stands. Winter temperatures are rarely severe enough to reduce infestations to endemic levels.

Temperature effects on spatial and temporal distribution of the beetle increase with latitude and altitude. In the northern part of the distributional range of the beetle, and at high elevations (Amman 1973, Safranyik 1975), there is often insufficient heat during the growing season for brood development on a 1-year cycle. Beetle development becomes poorly synchronized with winter conditions. Consequently, stages of the beetle that are particularly susceptible to cold (such as eggs or young larvae) may enter the winter and suffer heavy mortality. Infestations in these areas usually develop slowly, are low in intensity, and deplete the large-diameter component of the affected stands lightly. They may be reduced to endemic levels by unseasonably cold winter temperatures or unusually cool weather during the summer.

Near the northern limit of its range, beetle survival is very low; immigration probably balances extinction and the distribution of infestations is irregular and patchy. There is rarely economically important damage done in these areas. Although it has not been investigated, it seems logical to assume that this limit is rather dynamic and changes intermittently in response to winter and growing season temperatures. Distribution and abundance are probably characterized by the same pattern near the altitudinal limits.

Climate and Outbreak Hazard

Recognizing that a suitable climate for the beetle must prevail before it can become a continuous threat to lodgepole pine of susceptible age and size, Safranyik et al. (1975) attempted to define areas in western Canada according to climatic suitability within the elevational range where the greatest damage usually occurs. This approach to defining outbreak hazard was supported by survey records which indicated that during outbreak years high-level beetle activity often prevails over extensive areas that presumably contain a variety of stand conditions. Outbreak chance was defined in terms of six climatic factors. Three of these were temperature variables relating to thresholds for emergence and dispersal, survival and development. The others were the moisture variables: spring precipitation, precipitation variability and annual water deficit. High-hazard areas, as defined by an index based on these six variables, are essentially the hotter, drier areas with

mild winters, where climate favorable to the beetles frequently occurs. Areas with a frequent occurrence of one or more of the climatic conditions detrimental to the beetle have a low rating. Therefore, it is the relative frequency of periods favorable for an increase in the beetle population that is expressed by the index of outbreak probability.

The outbreak hazard map based on this work gives a reasonable representation of outbreak potential in western Canada when compared with the distribution and frequency of past outbreaks. Thus, it is useful for long-term management planning to reduce losses from the mountain pine beetle. An attempt at extending the British Columbia hazard map into the United States has not been successful (Crookston 1977), apparently because, at the lower elevations over most of its geographical area, climatic conditions are rarely severe enough to restrict establishment and survival of the beetle.

QUESTIONS AND ANSWERS

- Q. How did you determine base temperature of 5.6°C (42.1°F)?
- A. The base temperature for development was based on the work of Dr. R.W. Reid (Can. Entomol. 102:617-622), who computed a threshold temperature of 3.9°C (39.1°F) for eggs from field data. He also found that development of eggs near the threshold temperature was very slow and only 13 percent of eggs hatched at a constant temperature of 5°C (41°F) in a 90-day period. Therefore, we felt that brood development is not affected appreciably by heat accumulation below 5°C and, quite arbitrarily, selected a base temperature of 5.6°C for all brood stages. We recognize, however, that if any of the other brood stages have significantly different development thresholds than that for the egg stage, heat accumulation above 5.6°C may not be an accurate index of development for those brood stages.

REFERENCES

- Amman, G.D. 1972. Some factors affecting oviposition behavior of the mountain pine beetle. *Environ. Entomol.* 1:691-695.
- . 1973. Population changes of mountain pine beetle in relation to elevation. *Environ. Entomol.* 2:541-547.
- Amman, G.D., and B.H. Baker, 1972. Mountain pine beetle influence on lodgepole pine stand structure. *J. Forest.* 70:204-209.
- Amman, G.D., B.H. Baker and L.E. Stipe. 1973. Lodgepole pine losses related to elevation. USDA Forest Serv. Res. Note INT-171. Intermtn. Forest and Range Exp. Sta., Ogden, UT. 8 pp.

- Amman, G.D., M.D. McGregor, D.B. Cahill and W.H. Klein. 1977. Guidelines for reducing losses of lodgepole pine to the mountain pine beetle in unmanaged stands in the Rocky Mountains. USDA Forest Serv. Gen. Tech. Rep. INT-36. Intermtn. Forest and Range Exp. Sta., Ogden, UT. 19 pp.
- Atkins, M.D. 1959. A study of the flight of the Douglas-fir beetle *Dendroctonus pseudotsugae* Hopkins (Coleoptera: Scolytidae). I. Flight preparation and response. Can. Entomol. 91:283-291.
- . 1960. A study of the flight of the Douglas-fir beetle *Dendroctonus pseudotsugae* Hopkins (Coleoptera: Scolytidae). II. Flight movements. Can. Entomol. 92:941-954.
- . 1961. A study of the flight of the Douglas-fir beetle *Dendroctonus pseudotsugae* Hopkins (Coleoptera: Scolytidae). III. Flight capacity. Can. Entomol. 93:467-474.
- Billings, R.F., and R.I. Gara. 1975. Rhythmic emergence of *Dendroctonus ponderosae* (Coleoptera: Scolytidae) from two host species. Ann. Entomol. Soc. Amer. 68:1033-1036.
- Chapman, J.A. 1967. Response behavior of scolytid beetles and odour meteorology. Can. Entomol. 99:1132-1137.
- Crookston, N.L. 1977. Mountain pine beetle (*Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae)) outbreaks in lodgepole pine (*Pinus contorta* Dougl.) and application of a climatic hazard rating to the Pacific Northwest. M.S. thesis, Univ. of Idaho, Moscow. 91 pp.
- De Leon, D., W.D. Bedard and T.T. Terrel. 1934. Recent discoveries concerning the biology of the mountain pine beetle and their effect on control in western white pine. J. Forest. 32:430-436.
- Evenden, J.C., W.D. Bedard and G.R. Struble. 1943. The mountain pine beetle, an important enemy of western pines. USDA Circ. No. 664. Washington, D.C. 25 pp.
- Furniss, M.M., and R.L. Furniss. 1972. Scolytids (Coleoptera) on snowfields above timberline in Oregon and Washington. Can. Entomol. 104:1471-1477.
- Gray, G., R.F. Billings, R.I. Gara and R.L. Johnsey. 1972. On the emergence and initial flight behaviour of the mountain pine beetle, *Dendroctonus ponderosae*, in eastern Washington. Z. ang. Entomol. 3:250-259.
- Hopkins, A.D. 1919. The bioclimatic law as applied to entomological research and farm practice. Sci. Monogr. 8:496-513.
- McCambridge, W.F. 1964. Emergence period of Black Hills beetle from ponderosa pine in the central Rocky Mountains. USDA Forest Serv. Res. Note RM-32. Rocky Mtn. Forest and Range Exp. Sta., Ft. Collins, CO. 4 pp.
- . 1967. Nature of induced attacks by the Black Hills beetle, *Dendroctonus ponderosae* (Coleoptera: Scolytidae). Ann. Entomol. Soc. Amer. 60:920-928.
- . 1971. Temperature limits of flight of the mountain pine beetle, *Dendroctonus ponderosae*. Ann. Entomol. Soc. Amer. 64:534-535.
- Patterson, J.E. 1930. Control of the mountain pine beetle in lodgepole pine by the use of solar heat. USDA Tech. Bull. No. 195. Washington, D.C. 19 pp.
- Pitman, G.B., and J.P. Vité. 1969. Aggregation behaviour of *Dendroctonus ponderosae* (Coleoptera: Scolytidae) in response to chemical messengers. Can. Entomol. 101:143-149.
- Powell, J.M. 1967. A study of habitat temperatures of the bark beetle *Dendroctonus ponderosae* Hopkins in lodgepole pine. Agric. Meteorol. 4:189-201.
- Rasmussen, L.A. 1974. Flight and attack behaviour of mountain pine beetles in lodgepole pine of northern Utah and southern Idaho. USDA Forest Serv. Res. Note INT-180. Intermtn. Forest and Range Exp. Sta., Ogden, UT. 7 pp.
- Reid, R.W. 1962a. Biology of the mountain pine beetle, *Dendroctonus monticolae* Hopkins, in the East Kootenay Region of British Columbia. I. Life cycle, brood development and flight periods. Can. Entomol. 94:531-538.
- . 1962b. Biology of the mountain pine beetle, *Dendroctonus monticolae* Hopkins, in the East Kootenay region of British Columbia. II. Behaviour in the host, fecundity, and internal changes in the female. Can. Entomol. 94:605-613.
- . 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.
- . 1969. The influence of humidity on incubating bark beetle eggs. Can. Entomol. 101:182-183.
- Reid, R.W., and H. Gates. 1970. Effect of temperature and resin on hatch of eggs of the mountain pine beetle (*Dendroctonus ponderosae*). Can. Entomol. 102:617-622.
- Rudinsky, J.A. 1962. Ecology of Scolytidae. Annu. Rev. Entomol. 7:327-348.
- Rudinsky, J.A., and J.P. Vité. 1956. Effects of temperature upon the activity and behaviour of the Douglas-fir beetle. Forest Sci. 2:258-267.
- Safranyik, L. 1976. Climatic barriers and influences on integrated control of *Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae) in western Canada. Pages 429-438 in R.Z. Callahan and A. Bakke (eds.). Proc. XVIth IUFRO Conf., Oslo, Norway.
- Safranyik, L., and R. Jähren. 1970. Emergence patterns of the mountain pine beetle from lodgepole pine. Bi-Monthly Res. Notes 26:11, 19.
- Safranyik, L., D.M. Shrimpton and H.S. Whitney. 1974. Management of lodgepole pine to reduce losses from the mountain pine beetle. Environ. Can. Forest Serv. Tech. Rep. 1. Victoria, B.C. 24 pp.
- . 1975. An interpretation of the interaction between lodgepole pine, the mountain pine beetle and its associated blue stain fungi in western Canada. Pages 406-428 in D.M. Baumgartner (ed.). Management of lodgepole pine ecosystems. Washington State Univ. Coop. Ext. Serv., Pullman.
- Schmid, J.M. 1972. Emergence, attack densities and seasonal trends of mountain pine beetle (*Dendroctonus ponderosae*) in the Black Hills. USDA Forest Serv. Res. Note RM-211. Rocky Mtn. Forest and Range Exp. Sta., Ft. Collins, CO. 7 pp.
- Shepherd, R.F. 1966. Factors influencing the orientation and rates of activity of *Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae) Can. Entomol. 98:507-518.
- Somme, L. 1964. Effects of glycerol on cold hardiness in insects. Can. J. Zool. 42:87-101.

- Struble, G.R., and P.C. Johnson. 1955. The mountain pine beetle. USDA Forest Serv. Forest Pest Leaflet 2, Washington, D.C. 4 pp.
- Swaine, J.M. 1925. Factors determining the distribution of Canadian bark beetles. Can. Entomol. 57:182-183.
- Varley, G.C., G.R. Gradwell and M.P. Hassell. 1973. Insect-population ecology. Blackwell Scientific Publ., Oxford. 212 pp.
- Watson, J.A. 1970. Rhythmic emergence patterns of the mountain pine beetle *Dendroctonus ponderosae* (Coleoptera: Scolytidae). Can. Entomol. 102:1054-1056.
- Wood, S.L. 1963. Revision of the bark beetle genus *Dendroctonus* Erichson (Coleoptera: Scolytidae). Great Basin Naturalist 23:1-117.
- Wright, R.H. 1964. The science of smell. G. Allen and Unwin, Ltd., London. 164 pp.
- Wygant, N.D. 1940. Effects of low temperature on the Black Hills beetle (*Dendroctonus ponderosae*) Hopkins. Summary, Ph.D. diss., State Univ. of New York, Coll. of Environ. Sci. and Forestry, Syracuse. 57 pp.

INTEGRATION AND ANALYSIS

Management Strategies for Preventing Mountain Pine Beetle Epidemics in Lodgepole Pine Stands: Based on Empirical Models

Walter E. Cole

ABSTRACT

Empirical models have been prepared describing the interaction between mountain pine beetle (*Dendroctonus ponderosae* Hopkins) and lodgepole pine (*Pinus contorta* Douglas var. *latifolia* Engelman). These models show the relationship between losses of lodgepole pine and survival of mountain pine beetle by life stages. Further, they identify stand characteristics conducive to mountain pine beetle epidemics and provide the basis for determining probabilities of infestation and resultant tree losses. This probability of infestation and tree loss can be determined for stands of varying diameter/phloem structure and can be further refined as additional information is gained. Harvesting techniques based on this probability can be applied strategically to prevent mountain pine beetle epidemics.

INTRODUCTION

Historically, the mountain pine beetle (*Dendroctonus ponderosae* Hopkins) has depleted stands of lodgepole pine (*Pinus contorta* Douglas var. *latifolia* Engelman) by periodically killing the largest, most vigorous trees in the infested stand. This relation between tree diameter and beetle attack is well documented. Evenden and Gibson (1940) reported losses of 84 percent of trees 22.8 cm (9 inches) dbh and greater in the Big Hole Basin of Montana; Hopping and Beall (1948) accorded an increase of 5 percent loss for each 2.5-cm (1-inch) increase in tree diameter near Banff, Alberta; Roe and Amman (1970) found an increase of 8.8 percent for each 2.5-cm (1-inch) diameter increase in southeast Idaho and Wyoming; Reid (1963), Shepherd (1966), Cole and Amman (1969) and D.M. Cole (1973) all have shown that this relationship exists between large trees (and thick phloem) and beetles.

Models describing losses of lodgepole pine and mountain pine beetle survival by life stages were prepared from data accumulated during 13 years of research on the beetle/stand interaction (Cole et al. 1976)—representing the most comprehensive assemblage of information now available on mountain pine beetle epidemiology. The models provide estimates of beetle populations and tree losses critical to land management decisions, particularly within areas where temperatures are optimum for beetle development and survival. This paper summarizes these models and suggests some management strategies for preventing mountain pine beetle epidemics in lodgepole pine stands.

OBJECTIVES OF THE EMPIRICAL MODELS

The analytical objective of the models was to characterize the course of a mountain pine beetle infestation in lodgepole pine from endemic through epidemic and post-epidemic stages, linking beetle dynamics, by life stage, to stand characteristics and stand mortality.

The following series of models accomplished this:

1. Green stand structure when the infestation was at an endemic level (number of trees per acre expressed as a function of tree diameter and year of infestation).
2. Annual tree mortality observed over the 6-year epidemic portion of the infestation (annual loss as percent of original stand expressed as a function of tree diameter and year of infestation).
3. Cumulative tree mortality of the above stand over the 6-year epidemic portion of the infestation.

4. Brood density for each of the four life stages of the beetle (expressed as a function of tree diameter and year of infestation).

5. Brood density by life stage superimposed on the residual stand structure at critical times in an infestation (residual stand structure obtained from reduction of the original green stand model by cumulative mortality for specified years).

Descriptions of endemic and epidemic periods, causes of infestation and data sources are found in Cole et al. (1976). Graphic and descriptor development procedures follow those specified in Matchacurves 1, 2 and 3 (Jensen and Homeyer 1970, 1971; Jensen 1973).

THE BEETLE/LODGEPOLE PINE INTERACTION

Green Stand Structure

The green stand model (Fig. 1) is typical for a stand in which a beetle epidemic might occur. A relatively large proportion (22 percent) of the stand (trees over 10 cm dbh) is in trees over 30 cm (12 inch) dbh—a condition regarded as necessary for an epidemic (Cole and Amman 1969, Amman 1969).

Annual and Cumulative Tree Mortality

Losses of lodgepole pine over the main epidemic years are proportionately greater in the large-diameter classes. The epidemic period is considered to occur between the sixth and eleventh years of the infestation—or between the sharp rise and fall of the annual mortality, including the greatest

loss period (Figs. 2A and 2B). Peak annual tree loss occurs in the third year of an epidemic or in approximately the eighth year of the infestation. This peak annual loss amounts to around 35 percent of the large-diameter trees and about 5 percent to 10 percent of the small-diameter trees. Cumulative mortality, over the life of the epidemic, amounts to about 85 percent or more of the large-diameter trees (the bulk of the volume) and about 3 percent of the small-diameter trees (Figs. 3A and 3B). Loss can vary by elevation, habitat and stand structure, but these losses are typical for stands of similar characteristics and habitats, which comprise the majority of lodgepole pine stand conditions.

Brood Density by Life Stage

Beetle density by life stage was modeled for the infestation period (Fig. 4). Egg density increased with tree diameter within any 1 year. This can be attributed to the increases in length of egg galleries and eggs/2.54 cm of gallery in the large trees, which generally have thick phloem that provides the food source for beetles (Amman 1969, D.M. Cole 1973) (Fig. 5). Egg density peaked in the twelfth year of the infestation. Survival of small larvae through winter also increased with tree diameter and peaked in the tenth year—2 years before peak egg deposition. The decline in survival of small larvae after the tenth year is probably due to intraspecific competition among larvae, which continues to intensify as egg gallery starts and size increase with time.

Survival of the large larvae peaked in the eighth year—again 2 years before the small larvae. Survival of large larvae was relatively steady from year to year within all diameter classes during endemic years. Low density of large larvae is

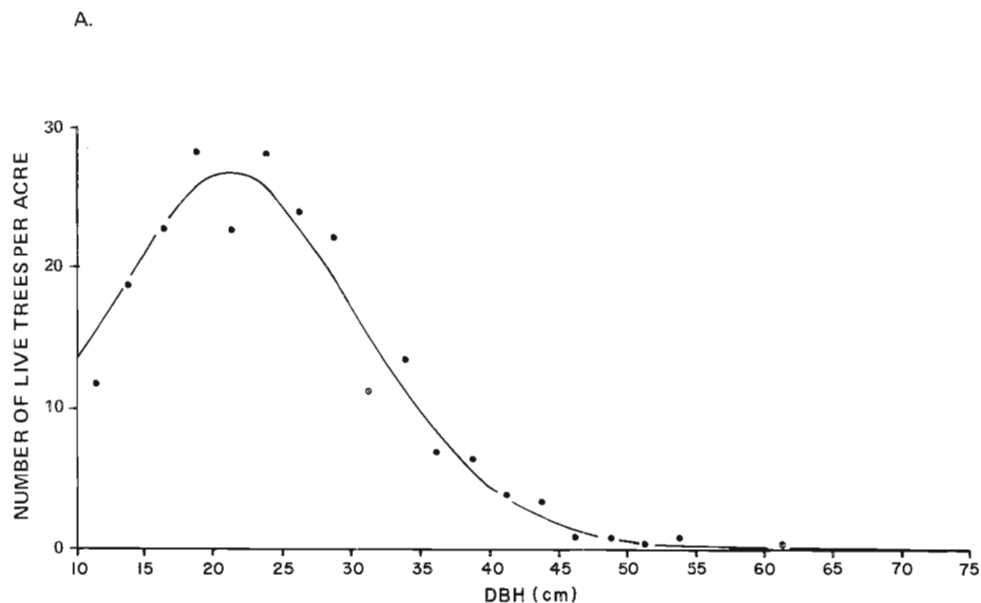


Fig. 1. Green stand structure at the beginning of the mountain pine beetle infestation.

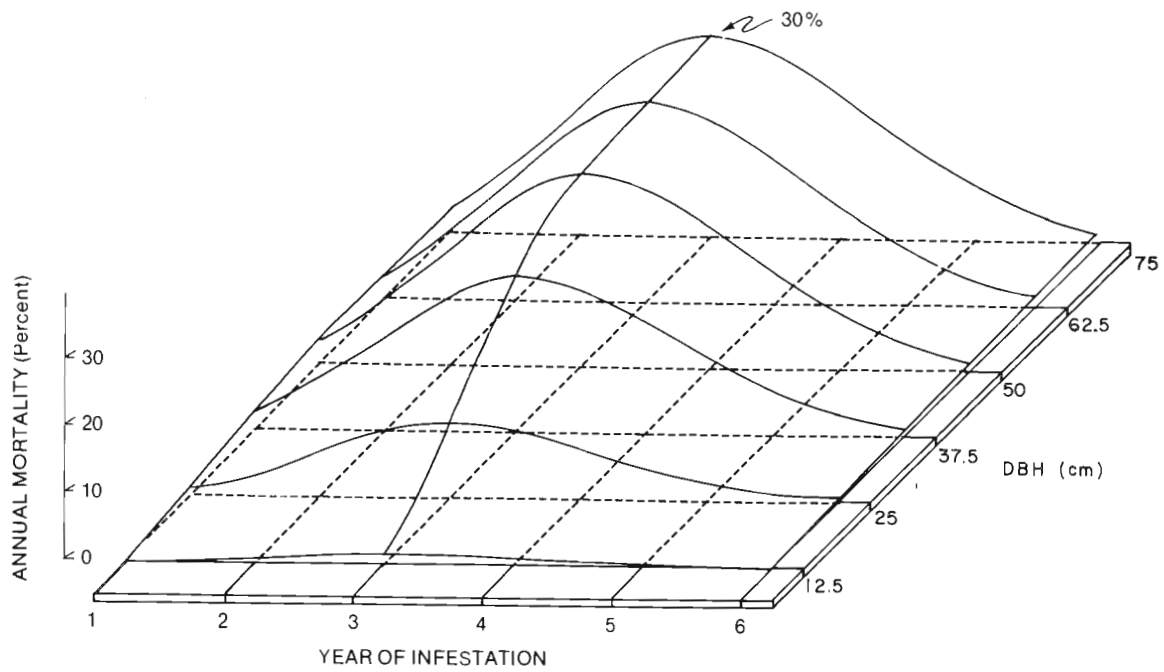


Fig. 2A. Annual mortality (percent) by diameter and year of infestation (Cole et al. 1976).

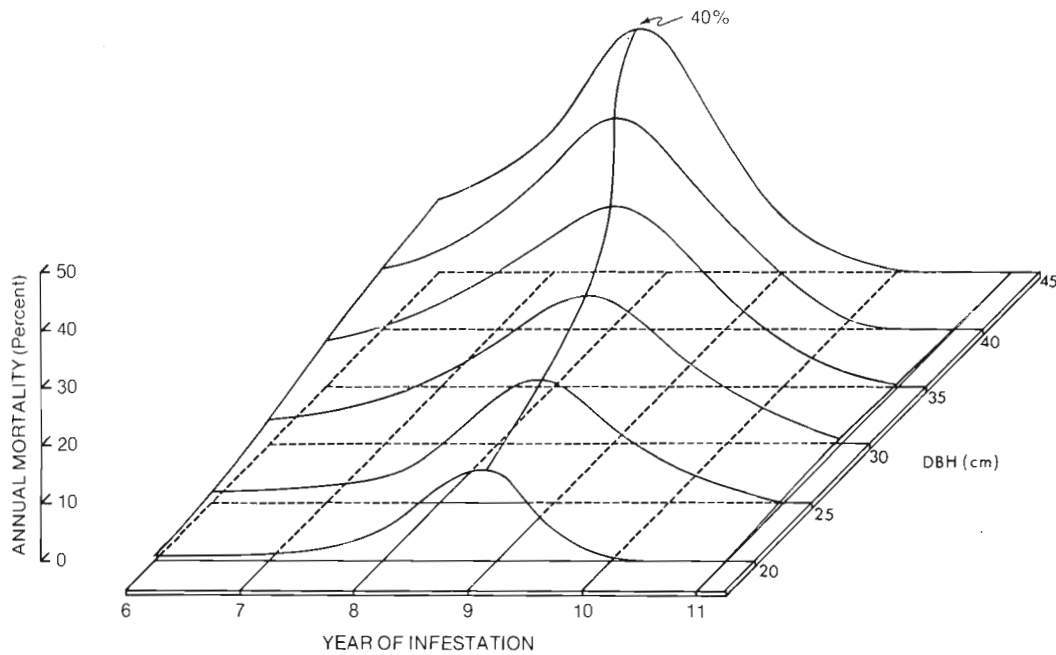


Fig. 2B. Annual mortality (percent) by diameter and year of infestation (Klein et al. in prep.).

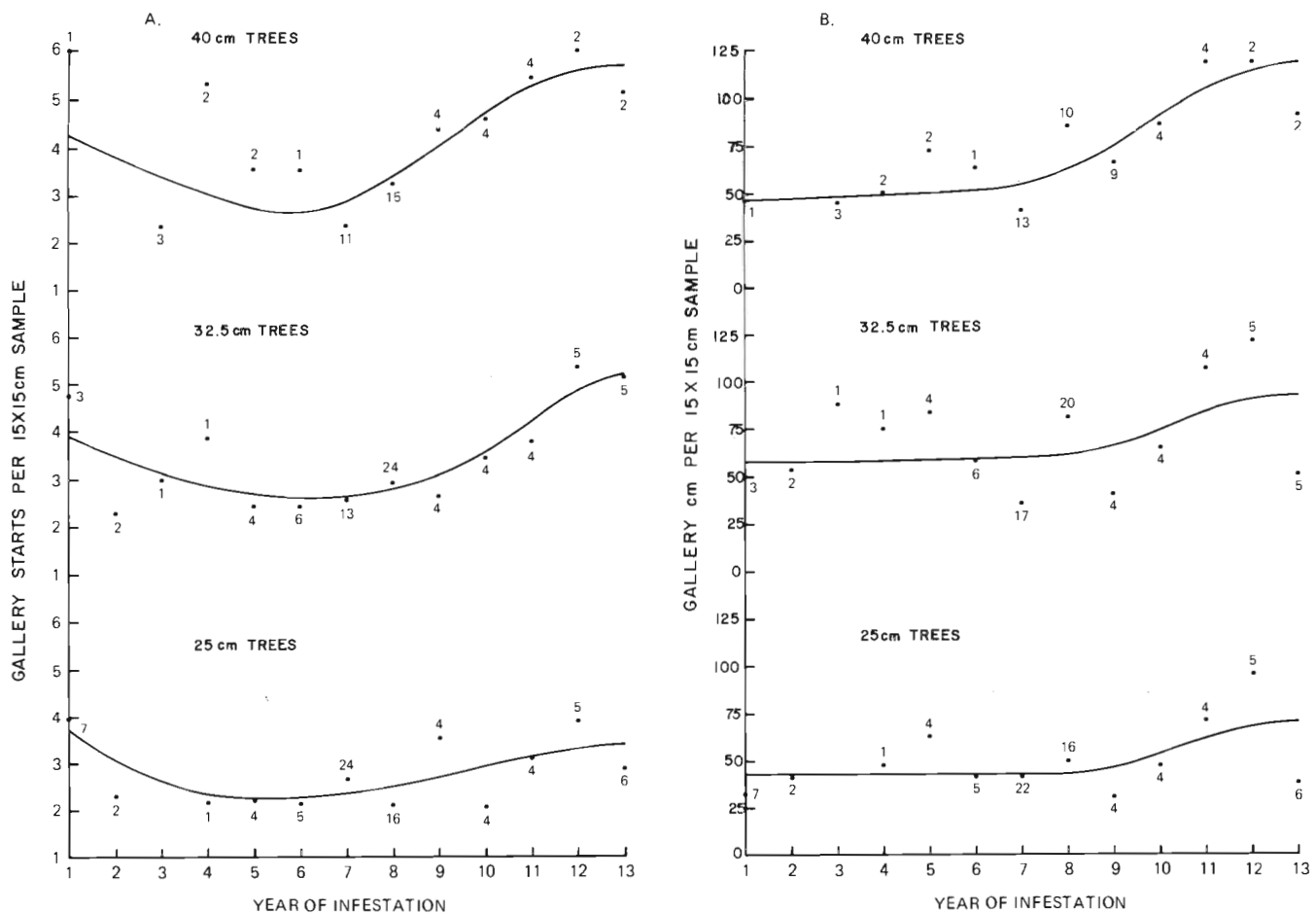


Fig. 5. Mountain pine beetle egg gallery starts and egg gallery length by diameter for a 13-year period. A = egg gallery starts; B = egg gallery length. Number at each data point indicates number of trees sampled.

The fact remains that epidemics develop in stands of diameter and phloem distributions conducive to successful brood survival. In lodgepole pine stands of the Forest Service's Rocky Mountain and Intermountain Regions, the general criterion for evaluating epidemic potential is that a stand can support an epidemic when 20 percent or more trees of 20 cm (8 inch) dbh or greater contain phloem of 0.28 cm (0.11 inch) or thicker. This criterion may vary in other areas, e.g., eastern Oregon and northern Montana, where trees of 18 cm (7 inches) dbh having phloem greater than 0.28 cm, 100 years of age or older and growing in site 3+ conditions, are subject to epidemics.

Stand and beetle models were merged for selected years to show the close association of beetle dynamics with numbers and sizes of trees that are infested at certain times in the infestation cycle (Fig. 6). Figure 6A, for a year of endemic populations (year 1), shows expected beetle survival in a tree of any specified diameter—if the tree becomes infested. Such beetle survival is quite low, as are tree losses (less than 2.5 trees/ha).

Both emergence and tree losses peaked in year 8 (Fig. 6B). Egg density and adult emergence had doubled since

year 1. Galleries and egg density continued to increase in subsequent years, while emergence declined—thus indicating that optimum gallery density and larval populations occurred around year 8 (Figs. 4 and 5). About half of all trees lost are killed by year 8. While the apparent numerical loss is similar for all diameter classes, proportionately the loss is much greater for the large-diameter class.

The continued increase in eggs and galleries by year 10 (Figs. 4 and 5) is reflected in the leveling of small larvae survival and reduced large larvae survival due to increased competition for food and habitat. Thus emergence at year 10 approximates that of the endemic (year 1) emergence (Fig. 6C). From year 8 to year 10, cumulative tree loss doubled.

This trend of high egg densities resulting in high larval mortality continued to be reflected in year 12 (Fig. 6D). Adult emergence, as would be expected, dropped to below the pre-epidemic level. As a result of this low emergence, cumulative tree loss leveled off and annual tree loss dropped to an endemic level (Figs. 2 and 3). By year 12, total tree loss ranged from approximately 4 percent of 10-cm (4-inch) diameter trees, to 49 percent of 30-cm (12-inch) trees, to over 80 percent of trees 48 cm (19 inches) or greater.

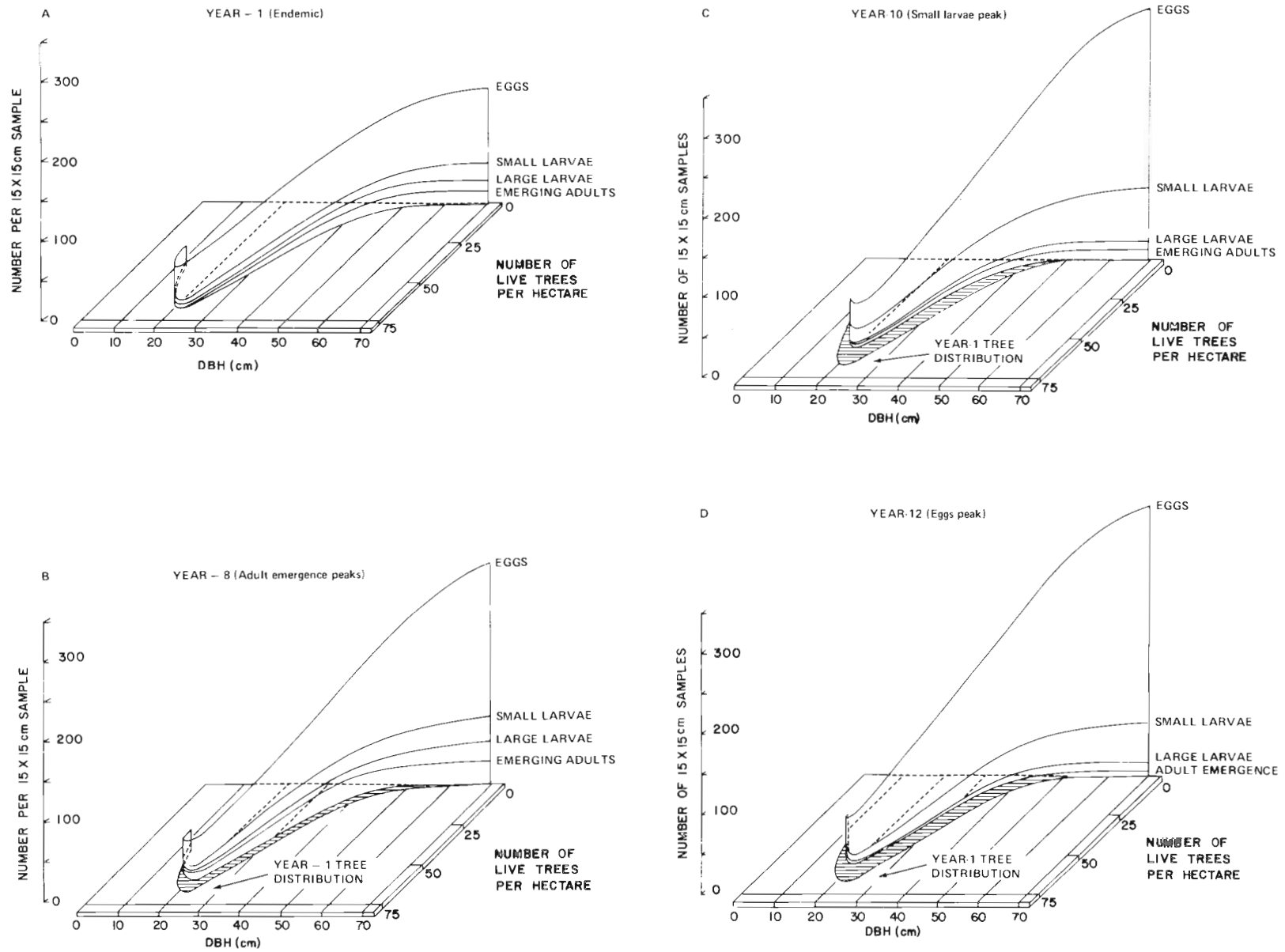


Fig. 6. Interaction models of beetle survival and lodgepole pine losses. A = year 1 (endemic beetle population level); B = year 8 (peak adult emergence); C = year 10 (peak small larvae density); D = year 12 (peak egg density). Shaded area shows cumulative tree mortality (Cole et al. 1976).

Beetle Survival and Thickness of Phloem

Of the evaluated mortality factors acting on mountain pine beetle populations, phloem thickness of host trees remains the most important factor accounting for differential beetle survival (Cole 1974). Because there is a high correlation between phloem thickness and dbh, a pronounced dbh effect is expected when considering tree mortality and brood density.

Brood in small trees with thin phloem tend to have higher proportions of females than those in large trees with thick phloem. Females survive better under stress than males. Cole (1973) demonstrated that females survived in greater proportion than males when crowding of larvae increased, and Amman and Rasmussen (1974) found that female survival was greater than that of males when drying of bark increased.

There is evidence that the increases in density of gallery starts and in subsequent gallery length are related to a changing sex ratio in the beetle population (unpublished data, Intermountain Forest and Range Experiment Station, Ogden, UT). From about the time of peak emergence (year 8), there appear to be insufficient males to mate most females in a short span of time. Unmated females probably continue to produce the aggregative pheromone, *trans*-verbenol (Pitman et al. 1968), which attracts additional females as well as males, and females probably continue to attack the host tree until sufficient males are present, or sufficient females have been mated, that the male's anti-aggregative pheromone masks the aggregative pheromone (Rudinsky et al. 1974).

Thus, after most large-diameter trees are killed and the beetle infests primarily trees of small diameter (Cole and Amman 1969), stress on the beetle increases and the sex ratio shifts even further in favor of females. The attack density, and hence gallery length, then increase. Subsequent larval populations suffer heavy mortality from competition and from the drying of phloem, and emergence declines. When these remaining small trees are attacked (usually successfully), brood production is low as a result of excessive drying of the phloem (which is usually thin), sex ratio shifts in favor of the female, and populations decline—not because of the so-called resistance of trees. The infestation then returns to the endemic level and does not become epidemic again until the stand of lodgepole pine has grown into diameter and phloem distributions conducive to increased beetle survival and increased survival of males. Thus, again, the beetle dynamics are closely tied to the dynamics of lodgepole pine, and epidemics are strongly dependent upon the presence of large-diameter trees having thick phloem.

Klein's studies (N.D.) show the same trends as these models, even though data were obtained from two different stands, in different locations. Thus, these models can be generally applied to all beetle-infested lodgepole pine stands.

Table 1. Percentage distribution of attacking and emerging populations of mountain pine beetle among lodgepole pine by tree diameter and phloem thickness; data based on the number of attack and emergence holes (Cole and Cahill 1976).

Diameter at Breast Height (cm)					
Phloem thickness (cm)	17.8	20-22.5	2.5-2.8	30	Total
Percent Attacking Population					
<0.28	7	15	18	20	60
≥0.28	1	3	7	29	40
Total	8	18	25	49	100
Percent Emerging Population					
<0.28	1	5	10	15	31
≥0.28	1	4	10	54	69
Total	2	9	20	69	100

MANAGEMENT STRATEGIES

The basic problem facing the manager is that of lowering the probability of beetle epidemics within a particular stand of lodgepole pine. At the same time, any attempt to prevent or reduce lodgepole pine losses to the mountain pine beetle must consider overall management objectives; any harvest method or timber management practice must be compatible with lodgepole pine silvicultural systems; and measures taken to reduce losses to the mountain pine beetle must be initiated prior to the epidemic phase. Once the beetle has reached this stage, it is too late—neither chemicals (insecticides or pheromones) nor cutting practices can keep pace logistically or physically with the infestation.

Epidemics are definitely correlated with the abundance of large, thick-phloem trees, particularly in stands at elevations below 1950 m (6500 ft), where beetle development is not continually inhibited by low temperatures. Decline of an epidemic is directly correlated with the loss of these large trees. Roe and Amman (1970) found that 44 percent of lodgepole pine stands in the *Abies lasiocarpa/Vaccinium scoparium* habitat type (1965-2535 m) had active mountain pine beetle infestations, as did 92 percent of stands in the *Abies lasiocarpa/Pachistima myrsinites* habitat type (2010-2340 m) and 64 percent in the *Pseudotsuga menziesii/Calamagrostis rubescens* habitat type (1800-2325 m). The manager must evaluate the risk for each situation. Using the probabilities of infestation of 92 percent and 44 percent within habitat types *Abla/Pamy* and *Abla/Vasc*, respectively, and the percent expected loss of trees (in this case 40 cm dbh and greater) as 85 within either habitat type, we find the expected loss is 78 percent and 37 percent for *Abla/Pamy* and *Abla/Vasc*, respectively. Reciprocally, there is a 25 percent or lower survival expectation for trees 40 cm dbh or greater in the *Abla/Pamy* habitat type and 64 percent in

Wasatch National Forest the infestation finally spread from the eastern to the western part of the North Slope, more or less subsided to endemic levels, and now is building back to epidemic levels in certain areas. This has been more or less correlated to stand growth and recovery after the epidemics.

Q. You say you can tell the forest manager where mountain pine beetle is likely to act and what it is likely to do—but not *when*. Do you think one could approach the “when” by stating that it is at that point in time when the manager can no longer afford to do annual detection surveys and apply direct control measures to keep the situation endemic—or from exceeding Berryman’s critical threshold?

A. Yes, it’s a viable approach if organization is geared to “react” to such situations. For long-term planning, however, one must predict 5 to 10 years in advance of an epidemic. Possibly using “probability of attack” we could schedule stands for sales or management, etc., far enough in advance to prevent large-scale outbreaks.

Q. How would you apply your tree mortality percentages to a stand having different diameter distributions than the one represented in your data (i.e., to estimate losses should an epidemic occur)?

A. I would refer you to Cole and Cahill (1976) for probabilities of loss by diameter/phloem distributions.

Q. How much variation in insect survival, attack pattern, duration of outbreak and stand diameter distribution have you observed from outbreak to outbreak? Does your model provide options for users to alter model parameters to more closely reflect on-the-ground conditions observed in different parts of the insect’s range?

A. The configuration is the same, with exceptions geared to diameter/phloem distributions: the greater diameter and thicker phloem, the shorter and “sweeter” the epidemic; the smaller and thinner, the longer the epidemic. Variation in most cases is minimal, both in insect survival and in attack patterns that normally change over the life of the infestation—a general tendency to concentrate during the waning stages of the outbreaks, thus causing greater brood mortality. Our model is empirical, which is descriptive in nature and not predictive as such.

Q. If mountain pine beetle epidemics are related to physiological maturity of lodgepole pine, what is the relationship of stagnant stands to mountain pine beetle attacks? Does a stagnant stand reduce the age at which physiological maturity is reached?

A. First, what is the definition of stagnant stands? If by stagnant you mean anything from dog hair stands to stands of small diameter, no growth, etc., then the relationship of these stands to mountain pine beetle

attacks is either nil or negative. Remember attacks depend upon large diameters; brood survival depends upon thick phloem.

Second, I doubt that a stagnant stand reduces the age at which physiological maturity is reached. A stand can become stagnant at an early age without affecting the physiological maturity (or age) of phloem. The phloem will undoubtedly be thin, but not necessarily mature. In any case, and repeating—phloem is primarily related to brood production; first we have to have a reason for beetle attack, which is diameter-related, whatever the primary attraction for the adult beetle (size response, odor response, etc.). An attacking adult beetle is a sophisticated organization of systems instinctively geared to seek 1) a place in which to live, 2) food and 3) reproduction. Randomness has no place in these processes.

Q. If diameter size is positively related to brood survival and therefore directly related to epidemic conditions, are stagnant lodgepole pine stands with small average diameter high risk areas? If so, why?

A. No, it is just the opposite because of the absence of trees with large diameters and thick phloem.

Q. If I have a lodgepole pine stand of large diameter, how do I set year 0 to initialize your model and predict the epidemic trajectory?

A. Year 0 would be when mortality of lodgepole pine reaches about 5 trees per hectare (2 trees/acre).

Q. What factor correlated positively with phloem thickness that could be related to soil, site, stocking, etc.?

A. Basal area is positively correlated to phloem thickness. I would refer you to D.M. Cole’s 1973 paper for other related factors.

Q. Your model includes only tree diameter as a factor determining likelihood of outbreaks. How would you incorporate the additional effect of tree resistance?

A. First, we would have to know how to measure resistance. I will agree that a tree is resistant (to mountain pine beetle attack) right up to the day it’s killed.

Q. If 25 cm dbh trees are coming under stress, and we then manage the stand to reduce stress (i.e., thinning and other techniques), then we could grow large trees without a beetle problem. Do you agree?

A. Yes, but first consider your management objectives. I believe we can manage for large diameters. With each increase in growth toward larger diameters, however, the probability of infestation increases and options decrease.

the *Abla/Vasc* habitat type. A choice has to be made as to where to grow lodgepole pine and what other alternatives are available.

Beetle brood production is correlated positively with phloem thickness and phloem thickness is correlated positively with tree diameter. The distributions of phloem thickness and tree diameter within a stand then become effective measurements for evaluating infestation potential. An example of the importance of these measurements is presented in Table 1.

Disregarding phloem thickness classes, only trees 30 cm dbh produced more beetles than attacked the host tree. When phloem is considered by diameter class, only those trees with phloem 0.28 cm or greater produced more beetles than attacked those trees.

A direct accounting of the insect population focuses specifically on trees equal to or greater than 25 cm (10 inch) dbh. An estimated 69 percent of the emerging adults came from trees equal to or greater than 30 cm dbh and 89 percent from 25 cm dbh or greater trees (Table 1). Maintaining stands so that trees grow no larger than 25 cm in diameter would restrict brood production to a level below that needed for a beetle epidemic in most stands. Harvesting techniques based upon diameter and phloem distribution can reduce the food supply before the beetle becomes excessively active within the stands.

The concerned manager can predict the probability of infestation from the structure of the stand (i.e., the diameter distribution within the stand and the phloem distribution within diameters) and the expected adult beetle production by diameter class. A simple cruise-type survey can be conducted to account for the percentage of trees equal to or greater than 30 cm dbh and the percentage of these trees containing phloem 0.28 cm or more thick. If the probability that any 30 cm tree in a stand will contain 0.28 cm or thicker phloem is 0.20 or greater, then that stand will support a mountain pine beetle infestation that may become epidemic (unpublished data, Intermountain Forest and Range Experiment Station, Ogden, UT). Such a stand is ready for at least a management plan that will reduce the food supply of the beetle (trees over 20 cm dbh) and lessen the probability of an infestation (Cole and Cahill 1976).

The manager must now either decide how much risk he is willing to accept if he desires large diameters, or be willing to accept and manage for smaller-diameter stands. If the risks are too high to accept, the manager then has the options of type conversion, shorter rotation, species and age class mixtures or development of the best phenotypes in relation to beetle behavior. Cuttings compatible with silvicultural systems and situations such as pure even-aged lodgepole pine stands, mixed species stands, uneven-aged stands, current and future stocking, habitat types and elevations must all be considered.

The roles of fire, disease and succession will also dictate the type of cutting method to be employed. Considering all these factors, the manager can

- ✓ 1. clearcut and start anew.
- ✓ 2. partial-cut and convert to younger stands, considering all ramifications of the risks involved.
- ✓ 3. restrict lodgepole pine management to the higher elevations, accepting slower growth and longer rotation.
4. restrict the growing and harvesting of lodgepole pine to young, smaller-diameter trees—grow fast and cut early.
5. increase the growing rate to grow larger-diameter lodgepole pine faster, under management, and harvest before or upon the first signs of beetle activity. This has the highest risk factor, but current indications show that cutting prior to phloem maturation (about age 60 in the case of fast-growing trees) is possible to prevent large outbreaks.

As more is learned about the role and influence of other ecological factors such as habitat type, soil, aspect, slope and elevation, then our ability to appraise these risks will become more reliable and accurate.

QUESTIONS AND ANSWERS

- Q. Under intensive management practices, do you think it would be possible to grow lodgepole for a longer time and reach larger diameters before it becomes susceptible?
- A. Yes, faster growth and large diameters could well result before the maturation of phloem ("aging") that would be conducive to brood survival. I also believe, however, that the beetle will eventually adapt to this rotation and tree or stand structure.
- Q. Calculating infestation risk, stand condition, phloem thickness, etc., have been covered quite extensively, but is there any way to ascertain infestation probability of stands that are not infested and not adjacent to infested stands, but neighbor districts or forests that are known to have infested stands? There are probably many parameters included (topography, climatologic factors, etc.), but, for instance, what is the flying distance of the beetle and what is known about spread rates?
- A. The beetle probably flies as far as needed to infest a tree. For instance, on the Targhee National Forest the infestation is still spreading after 10 years. On the

- Q. Do you know of any natural or managed stands that have grown into "normal" stocking level at age 70 to 90 and then have been attacked and reduced below minimum stocking level?
- A. What is normal stocking? The usual stem loss was 30 percent and there was stocking left. In the Hot Sulphur Springs, Colorado, infestation, however, there were no trees left over 25 cm dbh.
- Q. How much time variance did you observe in the duration and the peak of epidemics in the Intermountain Region? Is there a tendency for epidemics to last longer at high latitudes and altitudes?
- A. I observed 6 to 10 years in time variance. Epidemics do not necessarily last longer at high latitudes and altitudes. The epidemic at Togwotee Pass, Wyoming, was over in about 3 years; that at Pitch Stone Plateau (Yellowstone Park) was over in about 8 years. These high elevation infestations seem to be influenced by beetle pressure from below (lower elevations).

REFERENCES

- Amman, G.D. 1969. Mountain pine beetle emergence in relation to depth of lodgepole pine bark. USDA Forest Serv. Res. Note INT-96. Intermtn. Forest and Range Exp. Sta., Ogden, UT. 8 pp.
- _____. 1972. Some factors affecting oviposition behavior of the mountain pine beetle. Environ. Entomol. 1:691-695.
- Amman, G.D., and L.A. Rasmussen. 1974. A comparison of radiographic and bark-removal methods for sampling of mountain pine beetle populations. USDA Forest Serv. Res. Pap. INT-151. Intermtn. Forest and Range Exp. Sta., Ogden, UT. 11 pp.
- Cole, D.M. 1973. Estimation of phloem thickness in lodgepole pine. USDA Forest Serv. Res. Pap. INT-148. Intermtn. Forest and Range Exp. Sta., Ogden, UT. 10 pp.
- Cole, W.E. 1973. Crowding effects among single-age larvae of the mountain pine beetle, *Dendroctonus ponderosae* (Coleoptera: Scolytidae). Environ. Entomol. 2:286-293.
- _____. 1974. Competing risks analysis in mountain pine beetle dynamics. Res. Popul. Ecol. 15:183-192.
- Cole, W.E., and G.D. Amman. 1969. Mountain pine beetle infestations in relation to lodgepole pine diameters. USDA Forest Serv. Res. Note INT-95. Intermtn. Forest and Range Exp. Sta., Ogden, UT. 7 pp.
- Cole, W.E., and D.B. Cahill. 1976. Cutting strategies can reduce probabilities of mountain pine beetle epidemics in lodgepole pine. J. Forest. 74:294-297.
- Cole, W.E., G.D. Amman, and C.E. Jensen. 1976. Mathematical models for the mountain pine beetle-lodgepole pine interaction. Environ. Entomol. 5:11-19.
- Evenden, J.C., and A.L. Gibson. 1940. A destructive infestation in lodgepole pine stands by the mountain pine beetle. J. Forest 38:271-275.
- Hopping, G.R., and G. Beall. 1948. The relation of diameter of lodgepole pine to incidence of attack by the bark beetle. (*Dendroctonus monticolae* Hopk.) Forest. Chron. 24:141-145.
- Jensen, C.E. 1973. Matchacurve-3: multiple-component and multi-dimensional mathematical models for natural resource models. USDA Forest Serv. Res. Pap. INT-146. Intermtn. Forest and Range Exp. Sta., Ogden, UT. 42 pp.
- Jensen, C.E., and J.W. Homeyer. 1970. Matchacurve-1 for algebraic transforms to describe sigmoid- or bell-shaped curves. USDA Forest Serv., Intermtn. Forest and Range Exp. Sta., Ogden, UT. 22 pp.
- _____. 1971. Matchacurve-2 for algebraic transforms to describe curves of the class X^n . USDA Forest Serv. Res. Pap. INT-106. Intermtn. Forest and Range Exp. Sta., Ogden, UT. 39 pp.
- Klein, W.H., D.L. Parker and C.E. Jensen. (N.D.) Attack, emergence and stand depletion trends of the mountain pine beetle, *Dendroctonus ponderosae* Hopkins, during an epidemic (Coleoptera: Scolytidae). Methods Application Group, USDA Forest Service, Davis, CA (in prep.).
- Pitman, G.B., J.P. Vité, G.W. Kinzer and A.F. Fentiman, Jr. 1968. Bark beetle attractants: *trans-verbenol* isolated from *Dendroctonus*. Nature 218:168-169.
- 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.
- Roe, A.L., and G.D. Amman. 1970. The mountain pine beetle in lodgepole pine forests. USDA Forest Serv. Res. Pap. INT-71, Intermtn. Forest and Range Exp. Sta., Ogden, UT. 23 pp.
- Rudinsky, J.A., M.E. Morgan, L.M. Libbey and T.B. Putnam. 1974. Antiaggregative-rivalry pheromone of the mountain pine beetle, and a new arrestant of the southern pine beetle. Environ. Entomol. 3:90-98.
- Shepherd, R.F. 1966. Factors influencing the orientation and rates of activity of *Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae). Can. Entomol. 98:507-518.

A Synoptic Model of the Lodgepole Pine/Mountain Pine Beetle Interaction and Its Potential Application in Forest Management

Alan A. Berryman

ABSTRACT

A simple graphical model is presented which displays the risk and intensity of mountain pine beetle (*Dendroctonus ponderosae* Hopkins)-caused timber mortality in terms of average stand phloem thickness, stand resistance to attack, and climate. The model provides a tool to help the forest manager understand the interaction between the beetle and the stand and, when fit to data from lodgepole pine (*Pinus contorta* Douglas var. *latifolia* Engelman) stands, can be used to predict the likelihood of mountain pine beetle epidemics in real or simulated stands and to evaluate management alternatives.

INTRODUCTION

There are many ways of describing our understanding of how a complex system works. However, they all involve the construction of some kind of model, which may take the form of an oral or written statement, a diagram or graph, a scaled-down replica, or a mathematical equation. Whatever method is used, the model represents a particular conception of how the system works and, thus, contains the misconceptions of the builder. The validity of a model can be objectively determined only by evaluating its predictions against observed events.

Previous speakers in this symposium have identified the major forces which govern the population dynamics of the mountain pine beetle (*Dendroctonus ponderosae* Hopkins). It

now becomes important to develop an understanding of how these forces interact, or act together. In other words, our previous speakers have dissected the system and identified its major parts. My job, and that of other speakers on this panel, is to put the parts back together again and examine the behavior of the system as a whole.

In the following discussion I will develop a simple model representing a synopsis, or general overview, of the interaction between lodgepole pine (*Pinus contorta* Douglas var. *latifolia* Engelman) forests and mountain pine beetle populations. This model is based on the work of many researchers, but the way in which the information is put together represents my particular conception of the system. I have attempted to assemble this model in a highly simplified form so that it is digestible, and can be used by those involved in the management of lodgepole pine stands. For this reason mathematical arguments have been strictly avoided and, hopefully, what the model lacks in rigor it makes up for in comprehensibility.

DERIVATION OF A MODEL

A model which proposes to explain the epidemiology of the mountain pine beetle must consider how the beetle and lodgepole pine interact with each other and with their environment. Previous papers have alluded to the many factors involved in the dynamics of mountain pine beetle populations, but there seems to be a consensus that three variables—host resistance, phloem thickness and climate—are the most significant. There remains, however, considerable controversy concerning the roles and relative importance of these three variables in the epidemiology of the bark beetle.

Rather than pursuing our differences, let us first examine the common ground. For example, most researchers

Scientific Paper No. 5068, College of Agriculture Research Center, Washington State University. Work conducted under Projects 0102 and 4102, supported in part by the National Science Foundation and Environmental Protection Agency through contract SC0024 with the University of California (Integrated Pest Management Project). The opinions and findings expressed herein are those of the author and not necessarily those of the University of California, the National Science Foundation or the Environmental Protection Agency.

will probably agree that endemic (low level) beetle populations persist in individual trees which have been weakened by lightning strike, disease, ice and wind storms, etc. (Craighead et al. 1931, Shrimpton and Reid 1973). From this we can deduce that **the infestation of healthy trees by small bark beetle populations is prevented by host resistance**. On the other hand, epidemic mountain pine beetle populations appear to be able to overcome the resistance of quite healthy trees by rapid and massive attack (Roe and Amman 1970, Safranyik et al. 1975, Berryman 1976). Thus, most of us would probably accept the statement that **relatively healthy trees can be successfully invaded during beetle epidemics**. Our major differences, then, revolve around the explanation of how mountain pine beetle populations transcend their endemic condition to attain epidemic status. We will attempt to resolve this problem later on in this paper.

Model Assumptions

Let us consider a lodgepole pine stand to be a homogeneous group of dominant and co-dominant trees which have roughly equal attributes—e.g., phloem thickness and resistance. This is not such an unreasonable assumption, as intermediate and suppressed trees contribute little to mountain pine beetle epidemics, and many lodgepole pine stands are quite uniform in age and genetic make-up. Let us further suppose that a few trees in the stand will be weakened each year by various stress agents so that some trees of very low resistance are always present to support an endemic beetle population. In addition, we will assume that mountain pine beetle reproduction and survival are completely determined by the three variables, host resistance, phloem thickness and climate, and that the effect of each variable is independent of the others.

We will now construct a model from the above assumptions by considering first the interaction between the beetle population and stand resistance when phloem thickness and climate are constant, and then adding the effects of the other two variables.

Host Resistance/Beetle Interaction

We define host resistance as the ability of a lodgepole pine to defend itself against mountain pine beetle attack. This definition implies that a resistant tree, although it can fend off the attack of a large number of beetles, can also be killed if the attack is heavy enough. Thus, the fate of a tree, whether it lives or dies, depends on its intrinsic resistance and the size of the bark beetle population. In other words, if we have a stand of given resistance, there exists a **critical beetle population** which, once attained, can overcome the resistance of the average tree (Thalenhorst 1958, Berryman 1976).

Consider a stand of rather high resistance containing a small beetle population, for example, the point A in Fig. 1. Somewhere above A is a critical beetle population, C_1 , at which the average healthy tree in the stand can be successfully invaded. If the beetle population can reach this critical level, then an epidemic will erupt. We may now ask, "How can a

beetle population increase from A to C_1 ?" The most obvious answers to this question are 1) that large numbers of beetles invade the stand from nearby epidemic populations, or 2) that larger than usual amounts of weakened host material become available, enabling the resident population to increase in size.

Alternatively, an outbreak may be caused if the overall resistance of the stand is lowered by old age, competition, insect defoliation, drought, etc. As the resistance of the stand declines the critical population level will fall from C_1 towards C_2 , while the endemic population remains the same (Fig. 1). An epidemic will be triggered when the critical population level is reduced to the size of the endemic beetle population.

We can now draw a line describing the relationship between the critical beetle population level and stand resistance (Fig. 2). This line, in effect, separates endemic from epidemic beetle population behaviors. For intuitive reasons I have assumed that the line is geometric, rather than linear, because I suspect that outbreaks cannot be maintained in extremely resistant stands. However, assuming the relationship to be linear will not seriously alter the behavior of the model. As mentioned earlier, the beetle population may move into the epidemic zone by immigration of beetles from adjacent stands, an increase in the supply of severely weakened trees or a general decline of stand resistance. It is also important to realize that permanent stress or the stand is not required to generate a bark beetle outbreak. Stands may recover quite quickly from the effects of drought or insect defoliation. However, if the beetle population increases sufficiently during the period of stress so that it exceeds the critical level after the trees recover, then the outbreak will proceed unhindered.

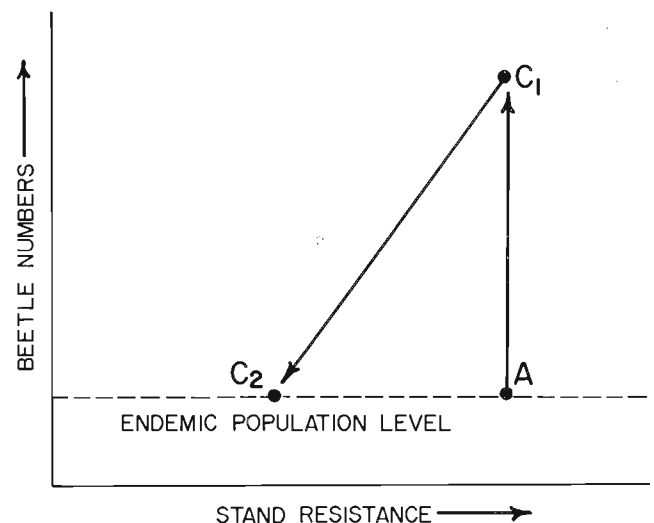


Fig. 1. Theoretical interaction between stand resistance and bark beetle population size. Given an endemic population in a fairly resistant stand, A, an epidemic can be generated if the population is increased to the critical level, C_1 , or if stand resistance declines, causing the critical level to drop from C_1 to C_2 .

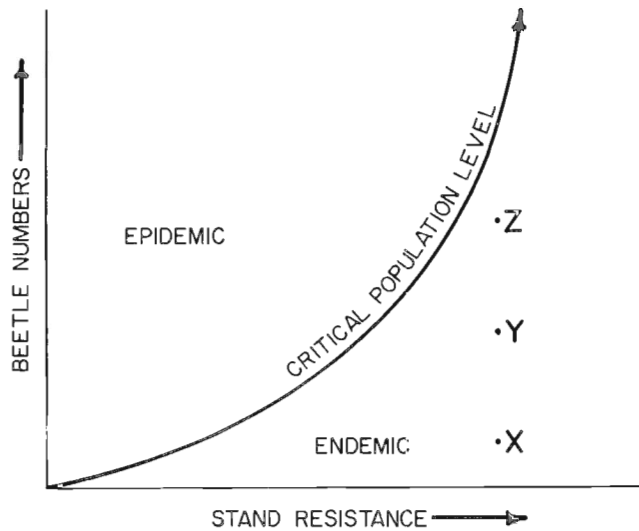


Fig. 2. The critical beetle population level which separates endemic from epidemic behavior is considered a continuous function of stand resistance. The risk of an epidemic depends on the distance that an actual stand is from this critical level; e.g., stand Z is at greater risk than stands X and Y, even though resistance is identical, because it is closer to the epidemic threshold.

The Phloem Effect

Phloem is the tissue on which the beetle larvae feed, so, given equal conditions of resistance and climate, more beetles will usually emerge from the thicker-phloemed trees and stands (Amman 1972, Berryman 1976). Thus, we expect endemic populations to be greater in thick-phloemed stands, given that equal numbers of trees are weakened each year. For example, in Fig. 2 the points X, Y and Z represent the endemic beetle populations in stands of increasing phloem thickness, everything else being equal. Obviously the stand with thick phloem, Z, is at greatest risk of developing an outbreak because it is closest to the critical level, and a very small increase in the beetle population will precipitate an epidemic.

The theoretical interaction between stand resistance and phloem thickness in determining the risk of mountain pine beetle outbreaks is depicted in Fig. 3. Note that phloem thickness affects not only the risk of outbreak but also its intensity. That is, the rate of timber mortality will be much higher in the thick-phloemed stands because beetle production will be greater.

The Climate Effect

Climate can be incorporated into our model as a third dimension (Fig. 4). This effect may be more conveniently represented by latitude (Safranyik et al. 1974), elevation (Amman 1973) or habitat type (Roe and Amman 1973), and may be modified by variables such as slope and aspect (Safranyik these proc. discusses the effect of climate in detail). The general rule is that cooler climates lead to decreased beetle survival, smaller populations, lower risk of epidemic and, if an outbreak should occur, smaller timber losses.

APPLICATION OF THE MODEL

There are two ways in which the synoptic model may be used to aid the manager of lodgepole pine forests. First, we can examine the behavior of the model itself under a series of hypothetical conditions to get a feel for the dynamic behavior of the modeled system. If we have confidence in the model, this systems analysis procedure will provide us with an understanding of the range of expected behavior of the real system and a feel for its sensitivity to environmental disturbances and management prescriptions. Second, the model may be fit to actual data from lodgepole pine stands and then be used to predict the risk of mountain pine beetle outbreak in other stands; that is, it can be used as a risk, or hazard, decision model.

Systems Analysis

The forest manager is concerned with the growth, yield and persistence of lodgepole pine stands in terms of certain management goals, be they timber, water or wildlife production, or recreational usage. He is, therefore, more interested in the dynamics of lodgepole pine stands than in the dynamics of bark beetle populations. We can analyze lodgepole pine stand dynamics by setting up hypothetical conditions for stand growth and then projecting the imaginary stand through time, using the model to evaluate the risk of beetle outbreak. For example, let us start with a well-spaced lodgepole pine plantation on a good site, and imagine its growth and development under constant climatic conditions (Fig. 5). As seedlings and saplings the lodgepoles' phloem is too thin to support moun-

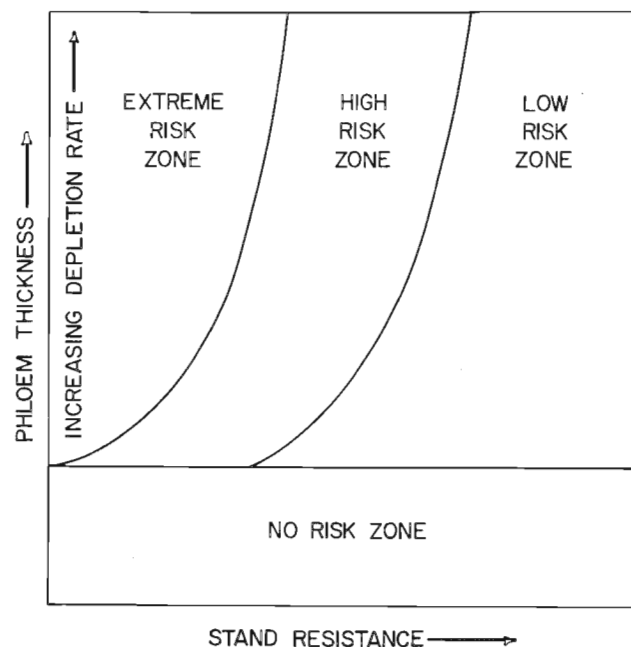


Fig. 3. Theoretical interaction between lodgepole pine stand resistance and phloem thickness in determining the risk of mountain pine beetle epidemic.

tain pine beetle reproduction, and vigor (resistance) should improve as the young trees become established. The trajectory in phloem/resistance phase space should resemble the 0 to 20 arrow of Fig. 5. From age 20 to 60 we would expect phloem to thicken in direct relationship to diameter growth (Cole 1973), and resistance to remain high as long as the stand suffers no severe stress. However, suppose that the crowns begin to close at age 60, causing a decline in growth and vigor. What will happen to the stand trajectory under these conditions? If phloem thickness and resistance are both related to vigor, as Shrimpton (1973) suggests, then the stand might move in the direction of the broken arrow in Fig. 5. This pathway avoids the high-risk zones and the chance of an outbreak is slight. However, the evidence indicates that phloem thickness changes rather slowly in response to changes in growth rate (Cole 1973, Cabrera these proc.). Logic supports this conclusion because it is difficult to imagine a physical attribute, such as phloem thickness, changing rapidly as trees come under stress. On the contrary, I have argued that resistance, being a reflection of the immediate health of the stand, will change very rapidly with change in vigor (Berryman 1976). Under these conditions the stand trajectory will deflect towards the high-risk zones in a manner similar to that illustrated by the solid line in Fig. 5. If a mountain pine beetle

outbreak should not occur in this stand, then phloem may eventually become so thin that the probability of an epidemic recedes, in which case the stand may survive to a ripe old age; for example, the 80- to 150-year trajectory (Fig. 5) carries the stand into the zone where phloem is too thin to support mountain pine beetle population growth.

Earlier we assumed that climate remained constant over the growth of our imaginary stand. This assumption is, of course, untrue. Climatic variability, or changes in weather from year to year, will cause fluctuations around the trajectory shown in Fig. 5. However, because phloem dimensions change relatively slowly in comparison to resistance, we can reasonably assume that the fluctuations around the mean stand trajectory are largely in the horizontal resistance plane. Thus, changes in weather will be extremely important in moving stands into higher or lower risk categories. For example, a drought occurring at age 80 in the trajectory shown in Fig. 5 may deflect the stand, temporarily, into the extreme-risk zone (see the dotted line in Fig. 5).

We can, of course, play an infinite variety of management "games" on this model. We could examine the effect of thinning from below to promote resistance, or from above to

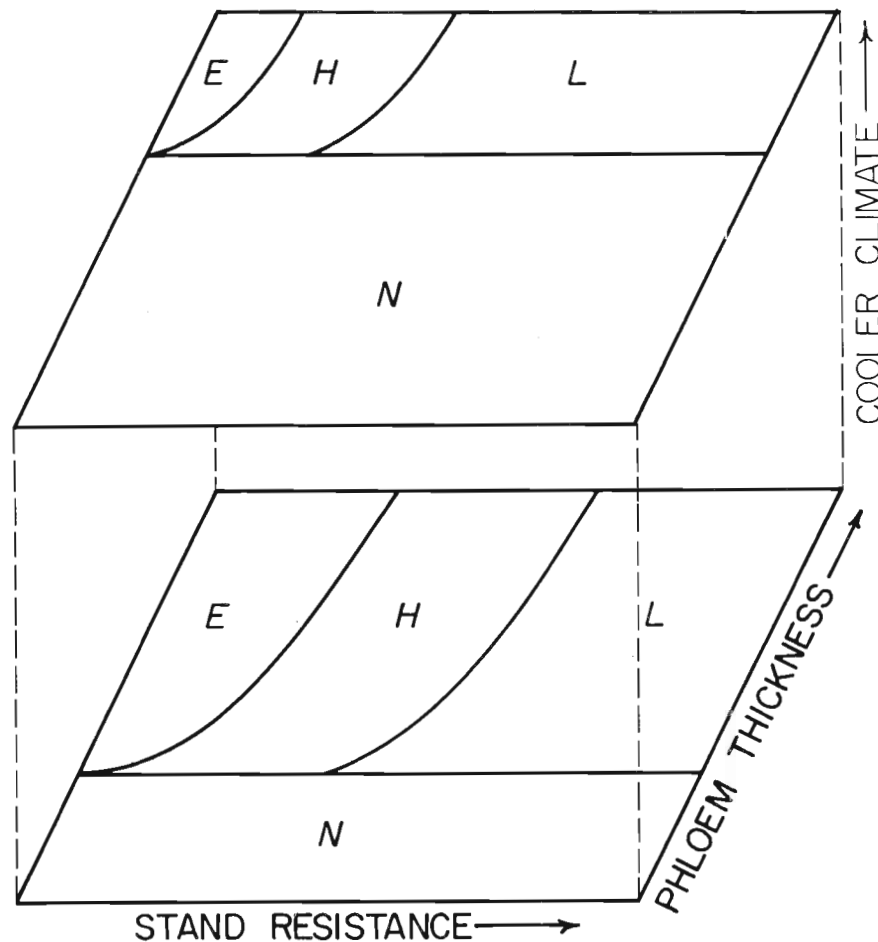


Fig. 4. Theoretical interaction between lodgepole pine stand resistance, phloem thickness and climate in determining the risk of mountain pine beetle epidemic. E = extreme risk; H = high risk; L = low risk; N = no risk.

reduce phloem thickness. We could grow the stand on different sites and at various stocking densities. Through this process of analysis the manager should end up with a general understanding of the system and a feel for the power of management prescriptions in avoiding outbreaks of the mountain pine beetle. Such an analysis may lead him to some of the following conclusions:

1. Slow-growing stands, overstocked or growing on poor sites, will have thinner phloem at the time resistance begins to decline and, consequently, the risk and intensity of epidemics will be lower.
2. Fast-growing stands may remain at low risk for long periods of time but, because of their thick phloem, the risk may become extreme when their resistance declines.
3. Temporary stress from drought, insect defoliation, etc. may be very important in the initial phases of mountain pine beetle epidemics, acting as a trigger which sets off the population explosion.
4. Direct control aimed at killing bark beetles seems a futile activity in **permanently** weakened stands. However, outbreaks may be avoided if endemic beetle populations can be kept below the critical level during periods of **temporary** stress.
5. It is important that forest management be coordinated across political or other land boundaries, because beetle populations can be raised above the critical level by immigration from surrounding areas. This is extremely important, because even if you are practicing sound forestry, your stands may be at risk because of your neighbor's carelessness.
6. Silvicultural practices aimed at maintaining stand vigor seem to offer the most promise for reducing the risk of mountain pine beetle outbreaks. True, vigorous stands have thick phloem, and if their vigor ever declines, explosive epidemics may erupt. However, the alternative—managing for non-vigorous, small-diameter stands with thin phloem—has some undesirable economic and genetic ramifications.

Prediction

Although the synoptic model has enabled us to investigate some important theoretical problems, the forest manager is particularly interested in predicting the likelihood of mountain pine beetle outbreaks in his "real life" lodgepole pine stands. To apply the model to these ends we must define the control variables in terms of measurable stand characteristics, and then fit the model to real stand data.

Phloem thickness is probably the most easily quantified variable, as it can be measured directly from a sample of trees, or predicted from more standard mensurational data; for

example, Cole (1973) provides us with empirical equations for predicting phloem thickness from basal area increment, diameter, elevation, habitat type, etc. The climatic variable is also easily quantified using relationships to latitude, elevation or both (Amman 1973, Safranyik et al. 1975, Amman et al. 1977). The estimation of resistance, however, poses some difficult problems.

Safranyik et al. (1974) demonstrated that resistance declines rapidly after stands reach 60 years of age, and Amman et al. (1977) used stand age as one of the three main variables in their risk classification model. However, research at the University of Idaho indicates that crown competition and periodic growth rate should also be considered as predictors of stand resistance. These variables may modify the rate of decline in resistance or the age at which the decline begins. For example, densely stocked stands may decline at a greater rate than similar, but more open-grown, stands. This subject is dealt with in more detail in the next paper of this symposium, where Mahoney presents some procedures for estimating stand resistance.

Given methods to measure the three key variables, we can proceed to construct a risk decision model. First, the observed stand data must be sorted according to elevational classes. Then, for each elevation, the resistance/phloem thickness coordinates are plotted for each stand, and the observed mortality rates inserted at the coordinates (Fig. 6). The first risk transition line is drawn to include all epidemic stands and then lower risk categories are drawn to management specifications. A fitted model, such as that presented in Fig. 6, will only form a preliminary risk decision system. Its credibility will be subject to question as its predictions are evaluated.

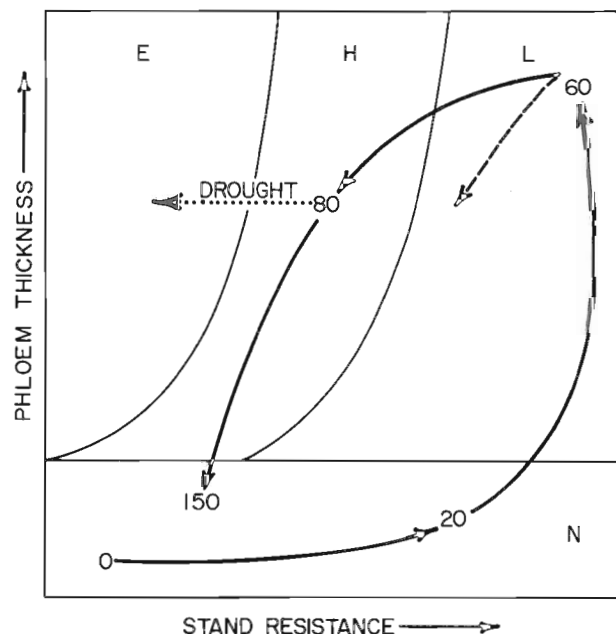


Fig. 5. Hypothetical time trajectory of a lodgepole pine stand through resistance/phloem thickness phase space.

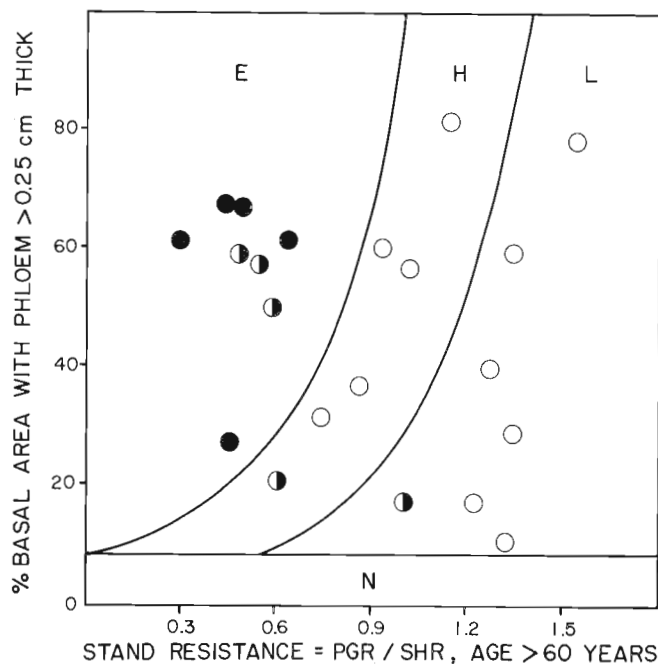


Fig. 6. A fit of the synoptic model to data from lodgepole pine stands in Montana and Idaho at elevations < 2100 m; ○ = < 10% basal area killed over 7 years, ◐ = 11-40% basal area killed, ● = > 40% basal area killed. Phloem thickness was measured directly at breast height, and stand resistance was estimated using Mahoney's methods (these proc.).

However, the model must be subjected to a fair evaluation. In particular, it is geared to evaluating the risk of an epidemic starting **within** a stand under evaluation. As we know, the risk of a stand being destroyed by mountain pine beetles is increased by immigration of beetles from adjacent stands. The risk estimates must, therefore, be interpreted in this light.

A valid risk decision model can be an extremely useful tool for the forest manager. Not only can he evaluate the present risk of mountain pine beetle outbreaks but also he can use the model as an adjunct to a stand prognosis model to evaluate future risks. Stage (1973) has implemented a prognosis system which projects the expected structure of lodgepole pine stands from inventory into the future. Stand mensurational data are generated at 10-year intervals over the projection period. These data can be used to estimate phloem thickness and stand resistance, which can then be plotted on the synoptic model as a stand trajectory (Fig. 7). The manager can then identify periods during the growth of the stand where mountain pine beetle problems are non-existent, where low-level timber losses should be expected, and where the risk of catastrophic losses is high. For example, the manager of the stand shown in Fig. 7 should be most concerned with the possibility of a mountain pine beetle outbreak during the time when the stand is between 80 and 110 years of age. He should also expect outbreaks at the end of this period to be more devastating because a greater proportion of the trees have thick phloem.

The stand prognosis model can also be used to evaluate management practices. For instance, the stand may be thinned at various times during the projection period. The trajectories

for the stand under different thinning regimes can be compared on the risk model, and the manager can choose the thinning program which best suits his particular plan. Thus, the synoptic model provides us with a method for displaying the trajectory of a stand through time, in an unmanaged state or under a set of management alternatives, and relating it to the expected intensity of mountain pine beetle activity.

ACKNOWLEDGMENTS

I would like to thank the following for their critical comments which were most helpful to me in writing this paper: Randall Peterman, University of British Columbia; Clarence DeMars, Jr., USDA Forest Service (Berkeley); Walter Cole and Gene Amman, USDA Forest Service (Ogden). The concepts developed in this paper arose out of discussion, and at times vigorous argument, with many of my colleagues. However, the expression of these ideas is entirely mine and the above acknowledgments do not imply agreement with my views.

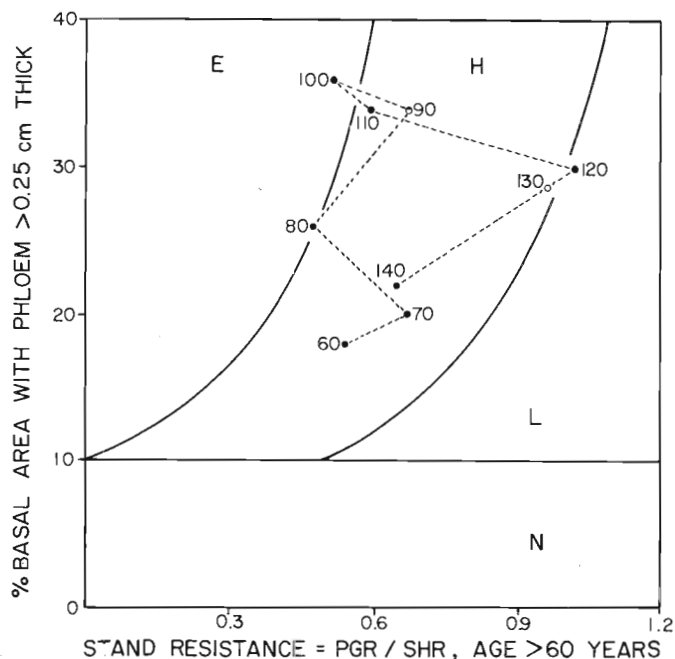


Fig. 7. A stand trajectory produced by Stage's prognosis model (Stand ID = FL 405104) superimposed on the fitted synoptic model; phloem thickness estimated from D.M. Cole's model ($\ln Y = .63143 \ln DBH - .00432 \text{ AGE} - 3.3843$) and resistance estimated using Mahoney's methods (these proc.).

QUESTIONS AND ANSWERS

- Q. What is a resistant stand?
- A. As used in this paper, stand resistance is a measure of the capability of the average dominant or co-dominant tree in the stand to defend itself against beetle attack. This quality is largely determined by the ability of the trees to produce sustained and copious resin flow in a short period of time. Alternatively, from the beetle's standpoint, a highly resistant stand will require a larger beetle population to kill the average thick-phloemed tree than a less resistant stand.

- Q. How do you account for epidemics in areas where beetles have not immigrated? You refer quite often to immigrating populations as “triggering” or aiding epidemic starts. How does your model explain epidemics in those stands from which the beetles emigrated?
- A. The resistance of the average dominant and co-dominant tree in the stand must be lowered to such an extent that the **resident** beetle population is able to attack and overcome these thick-phloemed trees.
- Q. What was your measure of stand resistance when plotting observed values on your graphs of phloem thickness/stand resistance? On your graphs you defined stand resistance as PGR/SHR. Please elaborate.
- A. We used a combination of Schenk et al.’s stand hazard rating (SHR), Mahoney’s periodic growth ratio (PGR), and the constraint that age must exceed 60 years, to measure resistance. Basically the resistance variable says that as crown competition and lodgepole composition increase in stands more than 60 years old, and as the periodic growth ratio decreases, then stand resistance will decline proportionally. This subject is covered in more detail by Mahoney in these proceedings.
- Q. If the resistance changes as **fast** as Shrimpton reported, how can we assay for resistance?
- A. An extremely difficult problem. There seems to be no adequate way to assay for current resistance, which may change from month to month or even day to day. Mahoney will present methods for assaying average stand resistance based on crown competition, lodgepole pine composition and periodic growth ratio. Beyond that, the manager should be observant of departures from the normal situation that would increase the stress on his marginally resistant stands. For example, the risk of an epidemic would be expected to intensify during drought years, or perhaps even excessively moist years (Kulhavy et al., later in this symposium show root flooding to be linked with mountain pine beetle infestations).
- Q. Why did the lodgepole stand shown in Fig. 7 decrease to low hazard level at age 120 compared with age 100?
- A. According to data generated by Stage’s prognosis model, crown competition declined due to natural thinning from age 100 to 120, and the growth rate remained stable or even increased slightly. This resulted in a general improvement in our measure of stand resistance.
- Q. What forest manager is going to manage lodgepole pine stands beyond 80 years in the future?
- A. Undoubtedly the safest rotation, from the standpoint of mountain pine beetle epidemics, is less than 80 years.
- However, those managers willing to take the risk for the benefits of old growth, large-diameter stands may well set longer rotations. I believe that, by careful stand manipulation (density control) and sanitation practices, particularly during periods of temporary stress (droughts, etc.), the risk can be substantially reduced.
- Q. If we can maintain a stand in a non-stressed condition, can we grow trees to 120+ years?
- A. Yes. There are many examples of stands which have lived to more than 120 years with only minor losses to mountain pine beetle. Some of these stands are thin-phloemed and often mistletoe infected (McGregor these proc.). Others are thick-phloemed but are in a more vigorous condition (e.g., Appendix I, Mahoney these proc.).
- Q. At what point does an endemic population become epidemic?
- A. An endemic population will become epidemic when that population gains access to the average co-dominant or dominant trees in the stand, provided the phloem of these trees is thick enough to generate a lot of beetles. This may occur if the endemic population gets help from immigrant beetles in overcoming these trees, when the amount of severely weakened trees raises the endemic population level, or when the overall resistance of the stand declines.
- Q. How thick must the phloem layer be in order to sustain beetle attack?
- A. There seems to be a general opinion that trees with phloem greater than 0.25 cm (0.10 inch) thick usually produce more beetles than they absorb, while those with thinner phloem have a net production of less than unity and, therefore, cannot sustain an infestation.
- Q. You didn’t mention the role of dwarf mistletoe. Would this wide-spread parasite always provide a weak tree source that could “trigger” mountain pine beetle outbreaks?
- A. Although I am not well versed in the effect of dwarf mistletoe on the physiology of lodgepole pine, I believe it produces a slowly debilitating disease. If so, then vigor is reduced gradually, perhaps at a similar rate to the reduction in phloem thickness. Under these conditions, I would not expect the pathogen to trigger epidemics. You might reach similar conclusions by imagining the vigor/phloem trajectory of a mistletoe-infected stand and plotting it on the phase diagram shown in Fig. 5.
- Q. What factors have you observed that you believe place sufficient stress on a lodgepole pine stand to make it susceptible to mountain pine beetle attack?

- A. Schenk and his associates maintain that crown competition is a critical factor. Kulhavy et al. (these proc.) found that root flooding predisposes trees to attack. Although it is difficult to prove empirically, I believe droughts are frequently responsible for triggering outbreaks in marginally resistant stands. Whenever I am viewing a mountain pine beetle outbreak with a local forester I ask him when the beetle population increase was first noticed. I then inquire whether there was a high fire danger rating (dry summer) at that time, or in the preceding year. These two events frequently coincide.
- Q. Can your model accommodate a population of beetles that is capable of adaptive change to tree resistance, phloem thickness and climatic effects? Suppose, for example, that a population of beetles has been sick or parasitized and was recovering at the time you ran your model.
- A. Genotypic, phenotypic and physiological variations in the beetle population are not intrinsically accounted for by the model described in my paper. However, if you can provide me with the information to measure these conditions, and to determine their effects on host resistance, then the model can be adjusted to account for them by altering the critical population threshold curve (Fig. 2); i.e., a vigorous population will have a lower critical threshold than a sick one.
- Q. Do you advocate direct control during stress periods?
- A. Yes. It is particularly important to keep the beetles below their critical population threshold (Fig. 2) during periods of temporary stress. Even though infested trees may be few and far between and the cost of removal high, the benefits in timber protection warrant sanitation practices. Fire crews might be used during their inactive periods, particularly during years when the fire danger is also high.
- Q. Two apparent theories have been advanced to explain the occurrence of mountain pine beetle outbreaks: tree age (maturity) and vigor. I suspect it is a problem of semantics, and differences between these theories are more apparent than real. Would you comment on these theories?
- A. I agree and I believe Ciesla reaches the same conclusion in his summary of the symposium. Lodgepole pines may become susceptible to attack by mountain pine beetles through the interaction of many stress agents. Some of these may be intrinsic (e.g., genetics, age, development) and others extrinsic (e.g., drought, disease, competition). The sum of all processes acting on a tree determines its

innate vigor, or physiological vitality, which in turn governs its ability to defend itself. Thus, age (maturity) and environmental stress will often act in concert to determine the resistance of lodgepole pine trees and stands.

REFERENCES

- Amman, G.D. 1972. Mountain pine beetle brood production in relation to thickness of lodgepole pine phloem. *J. Econ. Entomol.* 65: 138-140.
- . 1973. Population changes of the mountain pine beetle in relation to elevation. *Environ. Entomol.* 2:541-547.
- Amman, G.D., M.D. McGregor, D.B. Cahill and W.H. Klein. 1977. Guidelines for reducing losses of lodgepole pine to the mountain pine beetle in unmanaged stands in the Rocky Mountains. USDA Forest Serv. Gen. Tech. Rep. INT-36. Intermtn. Forest and Range Exp. Sta., Ogden, UT. 19 pp.
- Berryman, A.A. 1976. Theoretical explanation of mountain pine beetle dynamics in lodgepole pine forests. *Environ. Entomol.* 5:1225-1233.
- Cole, D.M. 1973. Estimation of phloem thickness in lodgepole pines. USDA Forest Serv. Res. Pap. INT-148. Intermtn. Forest and Range Exp. Sta., Ogden, UT. 10 pp.
- Craighead, F.C., J.M. Miller, J.C. Evenden and F.P. Keen. 1931. Control work against bark beetles in western forests and an appraisal of its results. *J. Forest.* 29:1001-1018.
- Roe, A.L., and G.D. Amman. 1970. The mountain pine beetle in lodgepole pine forests. USDA Forest Serv. Res. Pap. INT-71. Intermtn. Forest and Range Exp. Sta., Ogden, UT. 23 pp.
- Safranyik, L., D.M. Shrimpton and H.S. Whitney. 1974. Management of lodgepole pine to reduce losses from the mountain pine beetle. Can. Forest Serv. Forest Tech. Rep. 1, Victoria, B.C. 24 pp.
- . 1975. An interpretation of the interaction between lodgepole pine, the mountain pine beetle and its associated blue stain fungi in Western Canada. Pages 406-428 in D.M. Baumgartner (ed.). Management of lodgepole pine ecosystems, Washington State Univ. Coop. Ext. Serv., Pullman.
- Shrimpton, D.M. 1973. Age- and size-related response of lodgepole pine to inoculation with *Euophium clavigerum*. *Can. J. Bot.* 51:1155-1160.
- Shrimpton, D.M., and R.W. Reid. 1973. Change in resistance of lodgepole pine to mountain pine beetle between 1965 and 1972. *Can. J. Forest Res.* 3:430-432.
- Stage, A.R. 1973. Prognosis model for stand development. USDA Forest Serv. Res. Paper INT-137. Intermtn. Forest and Range Exp. Sta., Ogden, UT. 32 pp.
- Thalenhorst, W. 1958. Grundzüge der Populationsdynamik des grossen Fichtenborkenkäfers. *Ips typographus* L. Schriftenreihe Forstl. Fak. Univ. Göttingen, Band 21. 126 pp.

lodgepole pine stands tested in the method described above. The PGR is calculated by dividing the current 5-year radial increment by the past adjacent 5-year radial increment of dominant and co-dominant lodgepole pine trees. The PGR of individual sample trees is averaged to provide a PGR for the stand. If this value is equal to 1.0, then stand growth and vigor have remained stable for the past 10 years; a PGR above 1.0 indicates increasing growth and vigor for the 10-year period. Thus, stands with a PGR value equal to or greater than 1.0 should have relatively high resistance to successful mountain pine beetle attacks (a successful attack in this context is one where the tree is killed as a result of attack). When PGR falls below 1.0, a decline in vigor and resistance is indicated, and a substantial decline (i.e., $PGR < .90$) indicates a lodgepole pine stand that will generate an increasing mountain pine beetle population and sustain an epidemic.

Earlier in this symposium, Cabera discussed the growth characteristics of lodgepole pine phloem. He noted that the thickness of the phloem is a function of many years (avg. 26) of growth increment, modified by compression and depletion. Thus, lodgepole pine stands that are growing relatively well, but suffer a decline in growth rate, should provide trees with thick phloem, but lowered resistance due to decline in PGR.

Table 2 shows that PGR is indeed a valuable indicator of the resistance or susceptibility of lodgepole pine stands to mountain pine beetle infestation (data from Appendix I). Of the 21 stands, only 1 was misclassified. The 9 stands classified as resistant had PGR values ranging from .94 to 1.21, and sustained 0 to 9 percent mortality over the 7-year observation period. The 11 stands classified as susceptible had PGR values ranging from 0.52 to 0.88 and sustained 18 to 62 percent mortality during the observation period.

The management implication of this risk classification method is that the resistance of lodgepole pine stands to infestation by mountain pine beetle can be sustained by maintaining diameter growth rates. This may be done by planned thinnings at appropriate intervals to avoid growth-reducing competition among trees. Resistance might also be improved if trees in

Table 2. A test of periodic growth ratio (Mahoney 1977) as a stand risk classification method for 21 lodgepole pine stands.

Observed Mortality	Number of Stands by Risk Class	
	Periodic Growth Ratio	
	≤ .90 (Susceptible)	> .90 (Resistant)
<10%	1	9
≥ 10%	11	0
Correct Classification (%)	92	100

overcrowded stands with declining PGR are provided additional growing space by thinning or selective harvest (see D.M. Cole these proc.).

Because none of the 21 test stands used in the development of this classification method exceeds the thresholds of climate, age and diameter specified by Amman et al. (1977) as the limits for beetle survival, it should be applied only to stands with favorable climate, average dbh of at least 17.5 cm, and older than 60 years.

Method 3 (Schenk et al. 1978)

This method is based on an equation that predicts the level of mortality to be expected, as well as providing a continuous measure of relative stand resistance. The concepts, procedures and management implications described here, as well as the data in Appendix I, are summaries from a manuscript in preparation for publication elsewhere.

The regression equation uses crown competition factor (CCF), a measure of average stand competitive stress, and the proportion of stand basal area occupied by lodgepole pine (PLPP), a measure of host availability, as independent variables. Lodgepole pine mortality by mountain pine beetle is predicted in terms of the percent of the lodgepole pine basal area killed (% BAK). The CCF and PLPP were mathematically related so that their interaction would provide a single predictor variable called stand hazard rating ($SHR = CCF \times PLPP/100$). Thus, stands with nearly pure lodgepole pine and high CCF values will have the highest SHR values, the lowest resistance, and the highest predicted (and presumably observed) mortality levels. A regression equation (Fig. 1) was fit to data from the 11 central Idaho stands (Appendix III). The exponential form of the equation provided a better statistical fit to these data than linear or other mathematical forms, which implies that the level of mortality increases at a faster rate for each equal increment of SHR. Nearly 90 percent of the observed variation in mortality relative to SHR was explained by the equation. Thus, the fit of the equation to the data is remarkably good, in a statistical sense. Figure 2, which shows the observed data points for the 10 western Montana stands (Appendix III) plotted about the predicted line from the equation, provides an independent test of the predictive ability of the equation. Figures 1 and 2 show good agreement, regardless of statistical significance, in the relationship between SHR (resistance) and % BAK (mortality).

The management implication is that by reducing SHR, one increases resistance. This can be accomplished by thinning existing stands or increasing diversity of tree species. Young stands can be established to contain a diversity of tree species and can be scheduled for periodic thinning to ensure adequate growing space and to avoid competitive stress.

The variables required to use the equation can be computed from data gathered in normal timber inventories. The CCF is computed from the dbh and species of each tree, or from a sample of trees on a per-acre basis, in each lodgepole

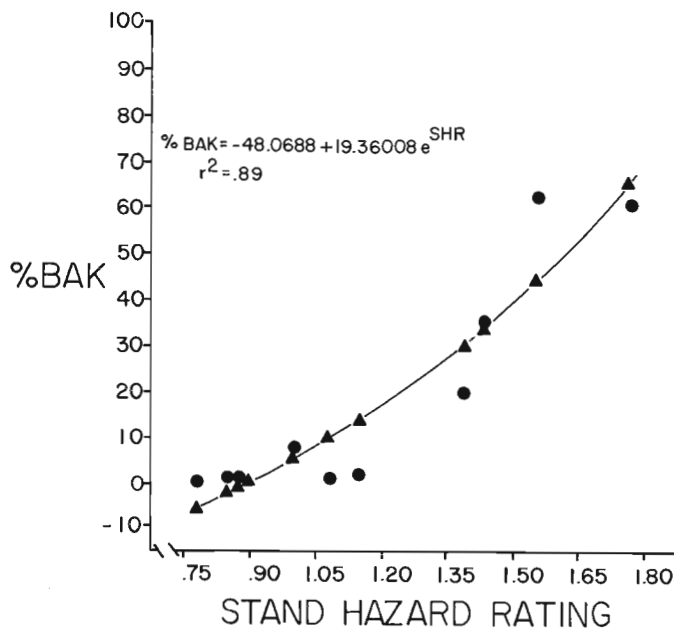


Fig. 1. The relationship of stand hazard rating and percent of lodgepole pine basal area killed by the mountain pine beetle for 11 central Idaho stands. (Schenk et al. 1978)

pine stand according to the method of Krajicek et al. (1961). The data required to calculate CCF will include what is needed to calculate PLPP. As noted earlier, the product of CCF and PLPP, divided by 100, will provide the SHR for insertion into the equation. This method is also applicable only within the limitations of climate, average dbh, and age thresholds specified by Amman et al.'s (1977) classification system.

Method 4 (Berryman, these proc.)

This method is similar in concept to that of Amman et al. (1977), but uses variables which Berryman proposes are more sensitive to the interaction between lodgepole pine and the mountain pine beetle. He suggests that average dbh be replaced by an actual measure of phloem thickness, which is equivalent to beetle productivity. The measure I chose to use is the percent of lodgepole pine basal area with phloem thickness greater than or equal to 0.25 cm (0.1 inch). This weights the phloem thickness of sample trees by their respective diameters, thus combining the important beetle production variables of diameter and phloem thickness. Age is replaced with a variable called resistance, which refers to the active tree resistance, or the ability of lodgepole pine trees to render mountain pine beetle attacks unsuccessful. The resistant reaction in lodgepole pine was discussed previously in this symposium by Shrimpton, and is related to the vigor of the attacked tree relative to the intensity of the attacking beetle population. I have used an interaction between two stand variables of methods 2 and 3 to provide a measure of resis-

tance. Because resistance (vigor) increases with PGR and decreases with SHR, the two variables were mathematically so related that resistance = PGR/SHR.

Berryman's synoptic model, using the above measures of phloem thickness and stand resistance, predicts that 1) all stands with relatively high mortality will be clustered in the graphed space where resistance is low and the percentage of lodgepole with thick phloem is high; 2) stands with high resistance and thick phloem should have low mortality levels, as would high-resistance stands with thin phloem; 3) stands with low resistance and thin phloem will have low (i.e., 10 to 20%) mortality levels; and 4) there is a phloem threshold below which mortality will not occur. This latter category of stands would contain low-resistance lodgepole pine stands in a stagnant (over-dense) condition that is commonly referred to as "dog haired." Figure 3 shows the results of an application of Berryman's model to the test stand data (Appendix I). The test data show good agreement with the fundamental predictions of the synoptic model. In particular, the stands generally cluster, with respect to their observed mortality, into their predicted graphical spaces. There are, however, some noteworthy exceptions. Two relatively thin-phloemed stands with low resistance had observed mortality of over 30 percent. These stands were adjacent to a creek bottom where beetle productivity was high; therefore, beetle immigration was a complicating factor (see Berryman these proc.). Two additional test stands had thin phloem, were rated high in resistance, and had observed mortalities of 18 and 32 percent. These two stands were adjacent to clearcuts, which may have subjected them to stress in addition to that caused by competition. Although such explanations do not improve prediction, I believe they justify exempting such stands when discussing the management implications of the relationships within the risk classification method. The results suggest that measures of the potential immigrating beetle population and of the effects of adjacent open areas and abrupt or unusual environmental changes (such as drought or high water tables) on resistance might provide improved predictions. These variables have not been successfully quantified, however, and, in the case of immigrating beetle populations, may not be necessary if stands which are capable of producing increasing populations are identified and managed.

Another important aspect of the fit of these data is the nearly vertical slope of the line representing the threshold between endemic and epidemic beetle infestations. This indicates that the resistance axis has a much greater effect in differentiating beetle-endemic from beetle-epidemic lodgepole pine stands. Thus, management of lodgepole pine stands to maintain resistance throughout the rotation should maintain the mountain pine beetle at endemic levels, even if stands are grown to large diameters with thick phloem. There is, however, a risk associated with any large-diameter lodgepole pine stand with thick phloems if extremely adverse weather (drought or inundation) or other vigor-reducing agents are encountered. Such phenomena are generally of short duration and could be countered by management techniques. The concepts and mechanics of measuring and maintaining the resistance of

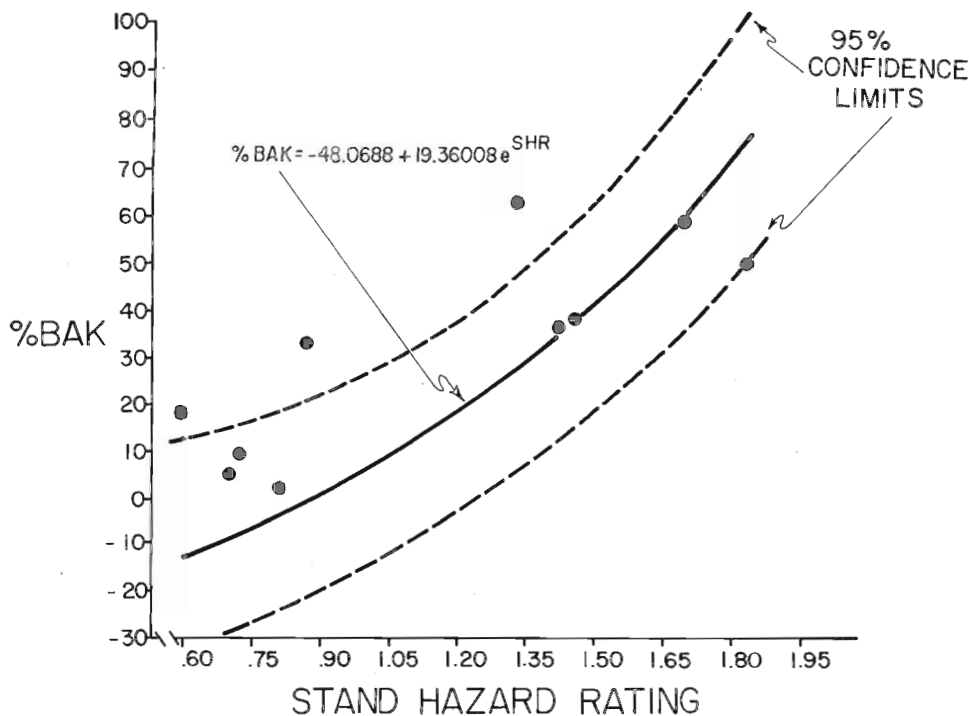


Fig. 2. Observed values for 10 western Montana lodgepole pine stands; a test of the risk classification method of Schenk et al. (1978).

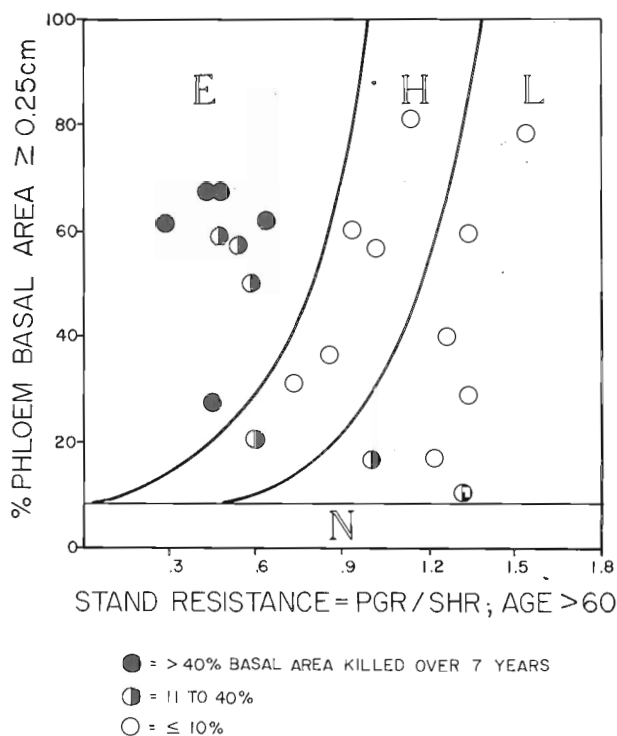


Fig. 3. A fit of the synoptic model to data from 21 lodgepole pine stands (see Berryman these proc.). E, H, L = extreme, high, low hazard.

lodgepole pine stands to mountain pine beetle have been discussed under the above risk classification methods which provided the resistance variables for the synoptic model.

SUMMARY

These recently developed stand risk classification methods add significantly to the understanding, prediction and assessment of management alternatives in mountain pine beetle infestations of lodgepole pine forests. The low-risk class of stands identified by Amman et al. (Method 1) indicates lodgepole pine stands where conditions are unfavorable for mountain pine beetle survival. Stands identified as moderate or high risk for beetle survival should be further classified by either the periodic growth ratio (Mahoney, Method 2), the stand hazard rating (Schenk et al., Method 3), or a combination of methods 2 and 3 with phloem thickness data (Berryman, Method 4). The synoptic model (Berryman these proc.) can be used as a vehicle for understanding lodgepole pine/mountain pine beetle interactions in managed and unmanaged stands.

Management of lodgepole pine stands to maintain conditions unfavorable to mountain pine beetle populations by reducing diameter alone can sometimes have undesirable effects on stand genetics and productivity. If competitive stress is avoided by stocking and growing space control, and stand diversity is encouraged, the above methods suggest that resistant lodgepole pine stands can be maintained, and that lodgepole pine can be grown to large diameters with longer rotations without serious threat of mountain pine beetle infestation.

QUESTIONS AND ANSWERS

- Q. How can you relate risk prediction in true fir/fir engraver, ponderosa pine/western pine beetle and southern pine beetle ecosystems with mountain pine beetle in lodgepole pine when the mountain pine beetle does not operate the same way in lodgepole pine and ponderosa pine in the same area?
- A. I made no claims for mountain pine beetle behavior in ponderosa pine. Researchers studying each of these other beetle/host ecosystems have independently provided strong evidence of mutually similar biological relationships that can be expressed in terms of total host mortality as a function of host competitive stress. The variables most closely associated with stress and the magnitude of their influence on host mortality will certainly differ for each host/beetle interaction, but their functions are similar.
- Q. In your test stands, how did you determine that lodgepole pine mortality by mountain pine beetle was complete? Did the infestation begin in the test stands or elsewhere?
- A. Lodgepole pine stands selected for this test were in the early stages of infestation or exhibited symptoms of having maintained an endemic population of beetles for at least 3 years past. Lodgepole pine mortality on permanent variable (25 BAF) and fixed (strip) plots was recorded initially and at annual intervals. Each of the 21 stands included in the above tests either sustained an epidemic infestation for about 5 years and returned to an endemic infestation ($< 1\%$ /year) for at least 2 years, or maintained mortality at or below this endemic level throughout the 7-year mortality assessment period.
- Q. Your goal was stated as describing capacity to generate and sustain mountain pine beetle populations. Do you believe the same factors that control **generation** also control the **sustaining** of a population?
- A. I do, although the extent of control (i.e., the coefficients associated with controlling variables) will vary with numerical and qualitative changes in host and beetle populations.
- Q. Since you multiply CCF by PLPP to get SHR, why not use only the CCF of LPP in the first place? Since CCF is calculated differently for different tree species, the SHR attributes more CCF to lodgepole pine than the contribution of lodgepole pine to total stand CCF.
- A. All trees in a stand, regardless of species, contribute to stand competition for growing space (CCF). Hence, all trees in the test stands were included in the calculation

of CCF. This value was then applied to PLPP to provide the SHR. This latter variable reflects the fact that only lodgepole pine (with rare exception) contributed to available host material.

- Q. Does the Schenk et al. method forecast total mortality during the life of an outbreak or annual mortality?
- A. Total mortality is forecast by their method.
- Q. If growth rate is an important factor of a stand, the PGR fails to distinguish between fast- and slow-growing trees. Comment?
- A. My research shows that change in growth rate (PGR) is more important than actual growth rate. Because the key function of phloem thickness depends on many years (avg. 26) of growth rate (see Cabrera these proc.), it seems logical that a function that expresses change in growth rate over time would be more influential than the actual current growth rate. Also, a tree with an historically fast growth rate will have thick phloem, regardless of recent (i.e., 5 years) growth rate. Lodgepole pine with a declining PGR (i.e., less than 0.90) must have been growing fast for a significant decline in growth rate to occur. Thus, such trees would provide low-vigor, susceptible hosts with thick phloem that could produce a high input/output ratio of mountain pine beetle.

REFERENCES

- Amman, G.D., M.D. McGregor, D.B. Cahill and W.H. Klein. 1977. Guidelines for reducing losses of lodgepole pine to the mountain pine beetle in unmanaged stands in the Rocky Mountains. USDA Forest Serv. Gen. Tech. Rep. INT-36. Intermt. Forest and Range Exp. Sta., Ogden, UT. 19 pp.
- Cole, W.E., and D.B. Cahill. 1976. Cutting strategies can reduce probabilities of mountain pine beetle epidemics in lodgepole pine. *J. Forest.* 74:294-297.
- Crookston, N.L., R.W. Stark and D.L. Adams. 1977. Outbreaks of mountain pine beetle in northwestern lodgepole pine forests—1945 to 1975. *Forest, Wildl. and Range Exp. Sta. Bull. No. 22.* Univ. of Idaho, Moscow, 7 pp. + map.
- Krajicek, J.E., K.A. Brinkman and S.F. Gingrick. 1961. Crown competition—A measure of density. *Forest Sci.* 7:35-42.
- Mahoney, R.L. 1977. Classifying lodgepole pine stands as resistant or susceptible to mountain pine beetle. M.S. thesis, Univ. of Idaho. Moscow. 28 pp.
- Safranyik, L., D.M. Shrimpton and H.S. Whitney. 1974. Management of lodgepole pine to reduce losses from the mountain pine beetle. *Can. Forest Serv. Forest Tech. Rep. 1.* Victoria. B.C. 24 pp.
- Schenk, J.A., R.L. Mahoney, J.A. Moore and D.L. Adams. 1978. A preliminary model for hazard rating lodgepole pine stands for mortality by mountain pine beetle. Univ. of Idaho, Moscow. (unpublished).

APPENDICES

Appendix I. Data summary for 11 central Idaho and 10 western Montana lodgepole pine stands over a 7-year period, ranked by mortality.

Elevation (100')†	Latitude (°)	Avg. LPP Age (yrs)	Avg. LPP dbh (inches)	% Phloem > 0.1 inch	CCF ^a	PLPP ^b	SHR ^c	PGR ^d	PGR/SHR	% LPP Killed by MPB
<i>Central Idaho</i>										
51	44	76	9.8	67	156	1.00	1.56	.68	.44	62
50	44	93	10.2	60	179	.99	1.77	.52	.29	61
53	44	89	9.4	58	148	.97	1.44	.67	.47	35
48	44	79	9.7	57	190	.73	1.39	.73	.53	20
53	44	124	11.6	32	205	.49	1.00	.74	.74	7
67	44	93	13.9	37	158	.73	1.15	.98	.85	2
66	44	168	13.7	60	138	.78	1.08	1.00	.93	1
64	44	122	10.9	59	138	.65	.90	1.21	1.34	1
65	44	121	12.2	82	144	.62	.89	1.00	1.12	1
52	44	84	11.5	57	92	.94	.86	.94	1.09	1
50	44	100	10.9	40	83	.94	.78	.99	1.27	0
<i>Western Montana</i>										
42	48	107	10.7	62	174	.78	1.36	.86	.63	61
43	48	108	10.8	67	204	.85	1.73	.80	.46	60
38	47	105	7.3	27	204	.91	1.86	.86	.46	49
57	42	81	8.6	50	209	.71	1.48	.86	.58	37
38	47	102	7.1	21	189	.76	1.44	.86	.60	35
41	48	136	9.6	18	164	.55	.90	.90	1.00	32
30	48	122	10.7	11	170	.39	.66	.88	1.33	18
64	42	79	12.6	78	136	.55	.75	1.14	1.52	9
63	42	129	13.9	28	129	.57	.73	.97	1.33	5
32	48	142	11.1	17	174	.48	.84	1.02	1.21	2

^a CCF = Crown competition factor (Krajicek et al. 1961).

^b PLPP = Proportion of total stand basal area in lodgepole pine.

^c SHR = Stand hazard rating (CCF × PLPP/100) (Schenk et al. 1978).

^d PGR = Periodic growth ratio (Mahoney 1977).

† Original data use standard units. 1 inch = 2.54 cm; 1 ft = 0.305 m.

Appendix II. Test of the stand risk classification method of Amman et al. (1977) for 11 central Idaho and 10 western Montana lodgepole pine stands.

Latitude (°)	Elevation (100')†	Risk Factor	Avg. LPP Age (yrs)	Risk Factor	Avg. LPP dbh (inches)	Risk Factor	Stand Risk	Predicted Mortality (%)	Observed Mortality (%)
<i>Central Idaho</i>									
44	51	(3)	76	(2)	9.8	(3)	18	25-50	62
44	50	(3)	93	(3)	10.2	(3)	27	> 50	61
44	53	(3)	89	(3)	9.4	(3)	27	> 50	35
44	48	(3)	79	(3)	9.7	(3)	18	25-50	20
44	53	(3)	124	(3)	11.6	(3)	27	> 50	7
44	67	(3)	93	(3)	13.9	(3)	27	> 50	2
44	66	(3)	168	(3)	13.7	(3)	27	> 50	1
44	64	(3)	122	(3)	10.9	(3)	27	> 50	1
44	65	(3)	121	(3)	12.2	(3)	27	> 50	1
44	52	(3)	84	(3)	11.5	(3)	27	> 50	1
44	50	(3)	100	(3)	10.9	(3)	27	> 50	0
<i>Western Montana</i>									
48	42	(3)	107	(3)	10.7	(3)	27	> 50	61
48	43	(3)	108	(3)	10.8	(3)	27	> 50	60
47	38	(3)	105	(3)	7.3	(2)	18	25-50	49
42	57	(3)	81	(3)	8.6	(3)	27	> 50	37
47	38	(3)	102	(3)	7.1	(2)	18	25-50	35
48	41	(3)	136	(3)	9.6	(3)	27	> 50	32
48	30	(3)	122	(3)	10.7	(3)	27	> 50	18
42	64	(3)	79	(2)	12.6	(3)	18	25-50	9
42	63	(3)	129	(3)	13.9	(3)	27	> 50	5
48	32	(3)	142	(3)	11.1	(3)	27	> 50	2

† Original data use standard units. 1 inch = 2.54 cm.

Appendix III. Data summary for prediction of lodgepole pine mortality by mountain pine beetle (Schenk, et al., in prep.) for 11 central Idaho and 10 western Montana lodgepole pine stands.

Stand Hazard Rating (SHR)	Observed Mortality (%BAK)	Predicted Mortality (%BAK)	Confidence Limits ($\alpha = .95$)
<i>Central Idaho</i>			
1.56	62	44	
1.77	61	66	
1.44	35	34	
1.39	20	30	
1.00	7	5	
1.15	2	13	
1.08	1	9	
.90	1	0	
.89	1	-1	
.86	1	-2	
.78	0	-6	
<i>Western Montana</i>			
1.36	61	27	± 20.69
1.73	60	61	± 23.68
1.86	49	76	± 25.97
1.48	37	37	± 21.19
1.44	35	34	± 20.98
.90	32	0	± 21.06
.66	18	-11	± 21.85
.75	9	-7	± 21.54
.73	5	-8	± 21.60
.84	2	-3	± 21.24

Evaluation of Management Alternatives for Lodgepole Pine Stands Using a Stand Projection Model

Nicholas L. Crookston, Robert C. Roelke, Donald G. Burnell and Albert R. Stage

ABSTRACT

Silvicultural planning requires reliable estimates of stand growth, species and tree size composition, and mortality levels. Mountain pine beetle (*Dendroctonus ponderosae* Hopkins) infestations are inherent events in the development of many lodgepole pine (*Pinus contorta* Douglas var. *latifolia* Engelman) stands. Therefore, tree mortality expected from future infestations must be considered when planning for the use of stands which may sustain appreciable beetle-caused mortality. The mountain pine beetle population dynamics simulation program (MPBMOD) has been coupled to a prognosis model for stand development (TREMOS). Together these models form a unified program (TREINS1) which can be used by forest managers and research workers to explore management alternatives designed to reduce beetle-caused losses of lodgepole pine. This paper describes how the information produced by TREINS1 can be used by timber managers. The program design, limitations, data requirements and operation are discussed.

INTRODUCTION

Management of lodgepole pine (*Pinus contorta* Douglas var. *latifolia* Engelman) forests is strongly influenced by mountain pine beetle (*Dendroctonus ponderosae* Hopkins)

The work reported herein is the result of cooperation among scientists at Washington State University, the University of Idaho and the USDA Forest Service and was supported by the National Science Foundation and the Environmental Protection Agency (Grant No. GB-341728) through contract SC0024 with the University of California at Berkeley. The opinions expressed herein are not necessarily those of the University of California, the NSF or the EPA.

populations. Prospects of beetle-caused losses influence the way silvicultural activities—for example, regeneration cutting, thinning, salvage cutting—are scheduled by the manager. In turn, these activities change the way the forest develops and interacts with future populations of the beetle. To plan a schedule of activities that meets the goals of forest management requires the ability to foretell how the outcome of one activity schedule differs from another, both with respect to the growth of the forest and with respect to the future losses that can be expected.

Where, how much and how often beetles will damage stands are items of information needed for rational silvicultural decisions. To supply this information to the manager, we have developed procedures for showing how existing stands can be expected to develop under alternative silvicultural regimes. Potential losses to mountain pine beetle are given particular emphasis. With these procedures, long-range implications of proposed silvicultural activities can be displayed. The manager who evaluates the alternatives is left to decide which one best meets his needs.

Use of these procedures requires 1) an inventory of the present forest including the status of mountain pine beetle populations, 2) access to a computer system where the programs that represent our models can be run, and 3) specification of the alternative activities to be evaluated.

From the initial inventory, we produce a prognosis for each stand showing growth, mortality, removals, and the number, sizes and volumes of surviving trees as they are expected to change in the future. The time spans of these prognoses extend for the life of the existing trees.

The prognosis model for stand development (Stage 1973)¹ is currently being used by timber managers to predict growth of stands under various management regimes. Various causes of mortality are not identified and catastrophic mortality factors are not accounted for, other than being part of the regional averages. The addition of catastrophic mortality models will greatly improve the realism of the projections for use in planning forest management.

The mountain pine beetle population dynamics simulation program (MPBMOD) is a catastrophic mortality model for lodgepole pine. Coupled to the stand prognosis model (TREMODO), it provides the ingredient necessary to make predictions of lodgepole pine stand growth which allow for the effects of mountain pine beetle on stand development (Stage 1975).

INFORMATION PRODUCED

The stand prognosis model shows expected stand development from time of inventory until the end of the rotation. Standard mensurational data needed by timber managers to evaluate management alternatives are displayed. These data include diameter distributions of stand volume, growth and mortality, and species composition of the entire stand. Representative records of individual trees show their predicted growth in diameter, height, crown ratio, past growth and number of trees per acre represented by the tree records. The stand age, mean diameter, total trees and basal area per acre, and the relative density or crown competition factor (CCF) (Krajicek 1961) are listed for the entire stand. When a beetle epidemic is simulated, MPBMOD prints detailed information about the expected dynamics of the interaction between mountain pine beetle and lodgepole pine. Cumulative tree mortality and numbers of surviving and dead trees per acre are printed by diameter class for each year of the epidemic. The number of beetles per acre emerging from previously attacked trees, those leaving the stand, and those dying from unidentified causes are also printed for each year. At the end of the infestation the cumulative mortality levels are summarized. This information also appears in the displays produced by the stand prognosis model. A graph of the dynamic variables which describe the infestation may also be printed.

Example: Management of a 40-year-old Lodgepole Pine Stand

As an example of a use of this system, consider the development of a young lodgepole pine stand (40 to 50 years old) on the Flathead National Forest, Montana. At the time the inventory was taken (1974) this homogeneous stand (all sample trees were lodgepole pine) consisted of trees too small to support a mountain pine beetle outbreak. The diameter distribution is typical of a stand of this age, with 10 percent of the trees greater than 15.5 cm (6.2 inches) dbh. There are

2018 cu ft volume per acre and 391 bd ft per acre. The predicted growth rate over the next 10 years is 122 cu ft per year. The stand habitat type is Douglas-fir/snowberry (*Pseudotsuga menziesii*/*Symphoricarpos albus*).

The evaluation of proposed management alternatives will be illustrated using data taken from this stand. For simplicity, consider only two management alternatives: 1) thinning the stand from below during the initial projection cycle and 2) not thinning the stand. The mountain pine beetle is considered to be part of the system in both cases. However, the probability of an epidemic occurring, and the resulting tree losses, will differ according to the management alternative chosen.

The probability branching diagram (Stage 1975) in Fig. 1 illustrates the different options. The switching probabilities are given by equations² adapted from Mahoney (these proc.). The probability that a particular course will be followed is equal to the product of the probabilities of branching in a given direction at each decision point. For example, the probability of ending at the thin and no-epidemic branch is equal to the product of taking the no-epidemic leg in years 1994, 2014 and 2034.

The expected board foot volume is plotted over time for each of the two management alternatives (Fig. 2). These are plots of the weighted averages of the projected board foot estimates found by simulating the outcome of each leg of the thin and no-thin options (Fig. 1).

The manager may now be in a position to decide which alternatives he wishes to choose, or he may decide that he would like to generate additional alternatives—for example, schedule a commercial thinning. His choice of a management plan would depend upon many factors in addition to those displayed by this model. As we have illustrated, the system can be used to project stand conditions in the future; these conditions can become input to a larger management plan evaluation model such as Timber-RAM (Navon 1971).

THE PROJECTION SYSTEM

The major component of this projection system is the prognosis model for stand development (TREMODO). It acts as the main computer program from which the mountain pine beetle population model (MPBMOD) is called (Fig. 3). Together these programs form a unified computer program called

² The probability of an epidemic occurring is determined using the following equation:

$$P(\text{outbreak}) = 1 / (1 + e^{(9.583 - 0.08967 * \text{SHR})})$$

where SHR is the product of the stand crown competition factor and the proportion of the stand basal area in lodgepole pine. The only constraint is that the proportion of lodgepole pine basal area is assumed to be always less than 0.8.

¹ The mountain pine beetle population model described herein is different from that described by Stage (1973).

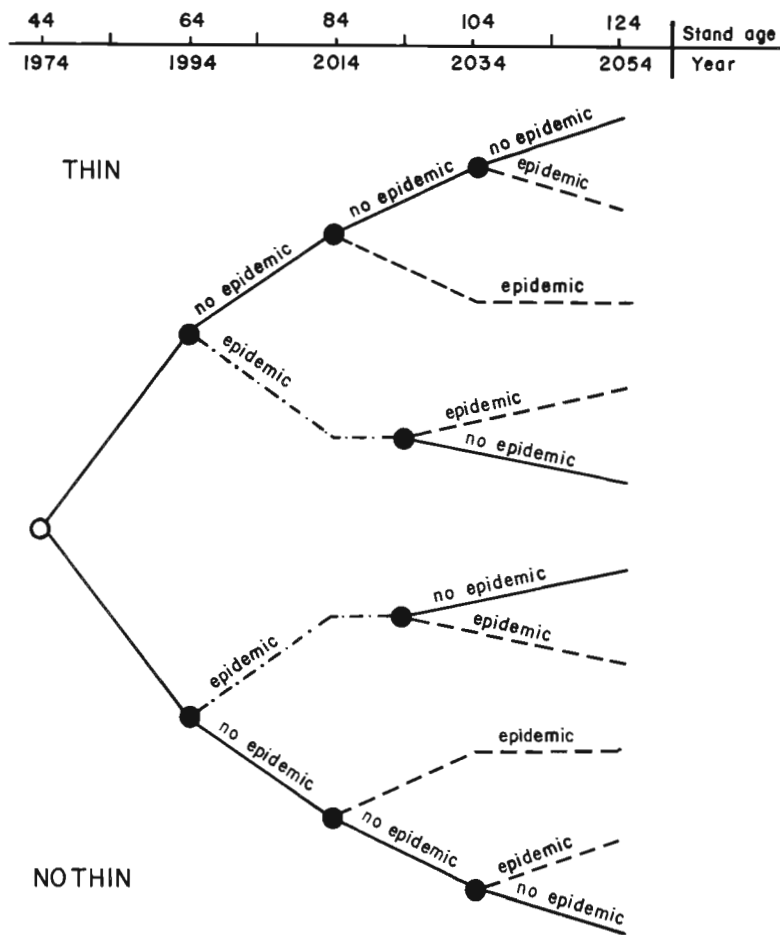


Fig. 1. Branching diagram showing 10 pathways which a young lodgepole pine stand could take during natural (no thinning) or managed (thinned) development. The open circle represents a divergence because of a management decision; the large black circles represent points of divergence which occur as random events.

TREINS1. The stand prognosis model is an individual tree model that does not contain mapped tree locations. The growth equations that form the bases for the stand projection are expressions of basal area increment per tree. The tree growth projections are functional expressions of habitat type, stand elevation and past growth data provided by the user. Although tree age is printed as part of the output, it is not used as an independent variable in the growth equations. Age is represented by variables such as crown ratio, height, diameter and basal area increment. Ten tree species and an "other" category may be represented in the program.

The stand prognosis model is currently being used in the northwest United States for planning, educational and scientific purposes. It has been calibrated for the national forests of central and northern Idaho, western Montana and north-eastern Washington.

THE MOUNTAIN PINE BEETLE POPULATION DYNAMICS SIMULATOR

The mountain pine beetle model has two major components. The first is the flight-and-attack model, which includes submodels representing emergence, emigration, distribution

and flight mortality of the beetles and the effects of aggregation pheromones. The second is the productivity model, which calculates the number of beetles emerging from the attacked trees during the next cycle.

Flight and Attack

Emergence

Mountain pine beetles emerge as adults in mid-summer. We inferred from data published by Safranyik and Jähren (1970) that the emergence pattern can be approximated by a normal distribution. The model mimics this pattern by dividing the emergence distribution into 11 increments. The beetles emerge over these intervals according to the binomial distribution, which is an approximation of the normal distribution.

Emigration

Some of the beetles emerging during a given period leave the stand. These beetles are responsible for the spread of the epidemic to adjacent stands, but from the viewpoint of the stand we are modeling they are lost from the system. Therefore, the mountain pine beetle model removes the emigrating

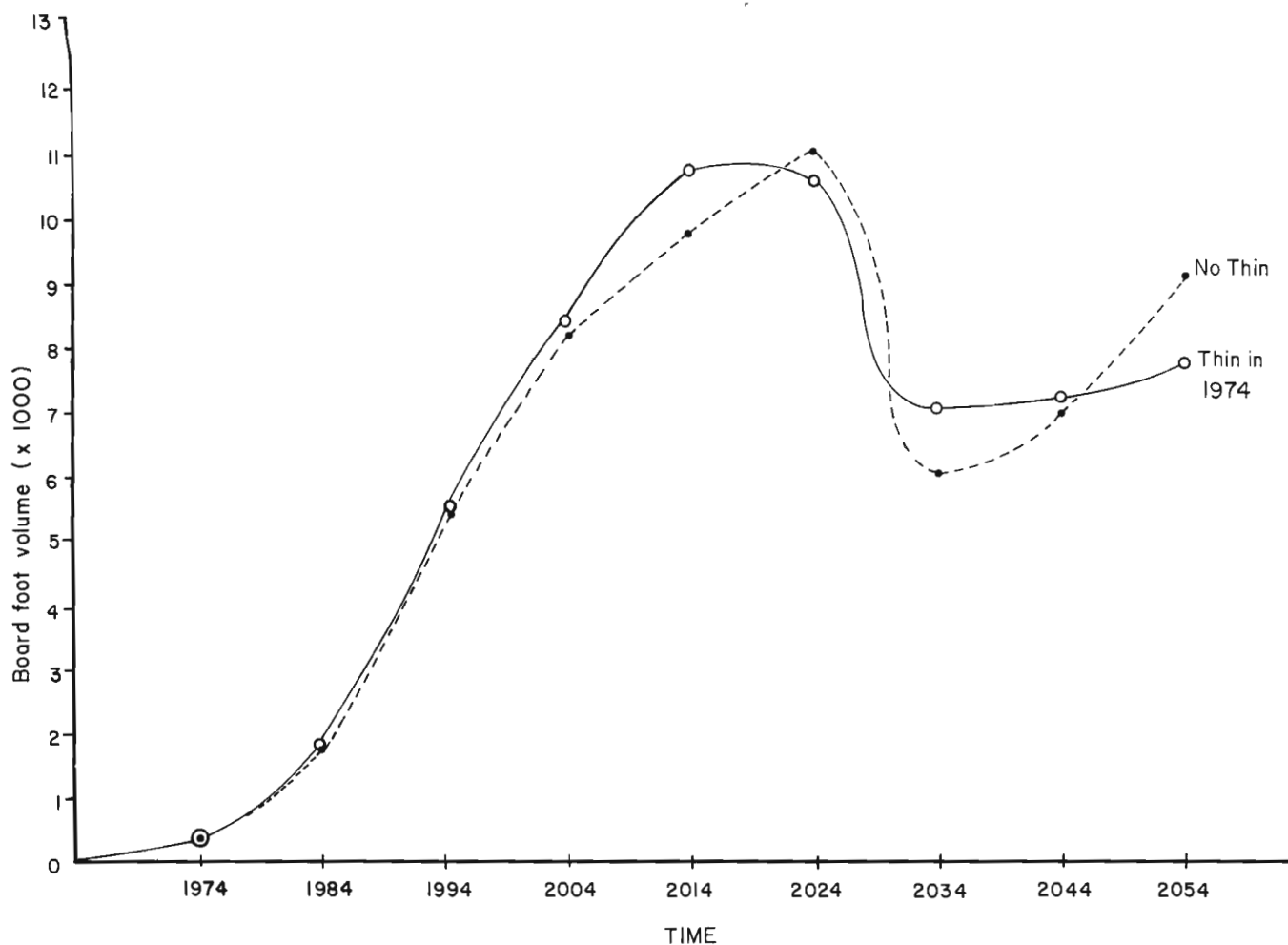


Fig. 2. Expected board foot volume estimates under thinning and no-thinning options.

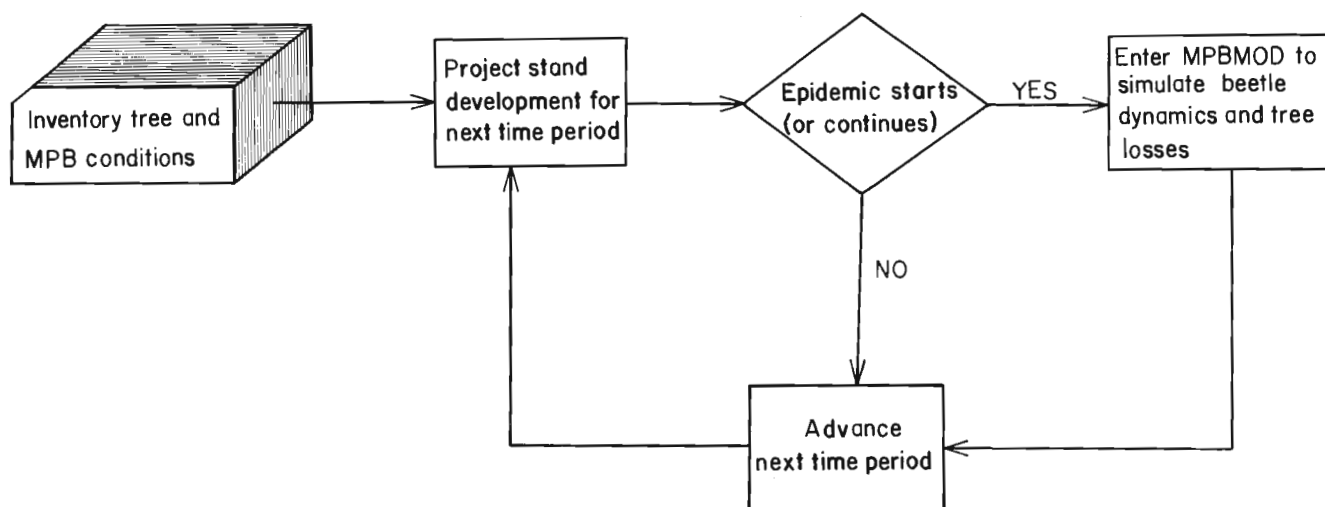


Fig. 3. Conceptual program flow of TREINS1.

stand, regardless of the tree species composition or average diameter, etc., would be correctly evaluated for its susceptibility to attack. An epidemic is assumed to have zero probability of occurring if the average lodgepole dbh is under 15 cm (6 inches) when considering trees greater than 11.25 cm (4.5 inches) dbh. The conditional probability of an epidemic occurring is calculated using a model (Hamilton 1974) that was calibrated from data described by Mahoney (these proc.). Variables that determine the conditional probability are CCF and the proportion of total basal area in lodgepole pine.

Data Transmission

The second major problem, that of data transmission, resulted from the two dissimilar modeling techniques used in the stand prognosis model and the mountain pine beetle model. The prognosis model carries up to 1350 records of trees with differing attributes and the mountain pine beetle operates on a few classes of trees which represent the stand as a whole. The data compression technique quickly groups like trees for input to the mountain pine beetle model. In turn, mortality results imposed on the groups can be assigned to the tree records in the stand prognosis which made up the groups.

SIMULATING MANAGEMENT STRATEGIES

To simulate a management strategy the user must specify the proper program control option(s). These may be combined to form an integrated strategy of silvicultural and/or insect regulation control. The options are as follows:

1. The user may specify the time thinnings should take place and the stocking levels which should remain. Thinnings may be carried out in any of the following ways:
 - a. thin from below to a specified residual basal area per acre,
 - b. thin from above to a specified residual basal area per acre,
 - c. thin from below to a specified residual number of trees per acre,
 - d. thin from above to a specified residual number of trees per acre,
 - e. thin using an automatic thinning system which mimics USDA Forest Service Northwest Region thinning guidelines,
 - f. remove all trees below a specified diameter,
 - g. remove all trees above a specified diameter,
 - h. remove the individual trees coded for removal by the user.
2. The user may apply direct beetle control to attacked trees. Two effectiveness percentages are required for each year the outbreak control is to occur. The first is the percentage of the attacked trees which are actually treated and the second is the percentage of the beetles in the treated trees

which die as a result of the treatment. Then, given knowledge of the effectiveness of a treatment compound, a user may test various control strategies.

Data Requirements

Four categories of input information are required by the coupled system:

1. The sampling method used to collect mensuration data. This includes the number of plots, fixed plot size, basal area factors and limiting dbh dividing population sampled by fixed plot from population sampled by variable-radius plot.
2. Site characteristics of the sampled stand. This includes site index, elevation, habitat type, aspect and slope.
3. The size of the stand in acres.⁵
4. The characteristics of the trees that make up the stand. This includes the species, dbh, height, live crown ratio, periodic growth rate and management class of each sample tree. All of these data are routinely collected in the course of silvicultural stand examinations. Virtually any sampling design can be accommodated by the model.

FUTURE USES

The prognosis model has been calibrated for use in the habitat types of northern Idaho and western Montana. It is continually being updated, modified and recalibrated for additional areas. We have calibrated MPBMOD on all the data sets which we had available. Whether it will perform acceptably in all situations remains to be tested. However, we believe that it is the best summary of existing knowledge concerning future growth of lodgepole pine in the presence of mountain pine beetle. Therefore, we recommend its use in the evaluation of possible management strategies. As data are accumulated, this new information can be used to improve the fidelity of the mountain pine beetle simulator.

We anticipate making the computer program (TREINS1) available through both the Fort Collins and Washington State University computing centers. This paper serves as an introduction to the program and describes its utility. A separate users' manual, which will contain detailed instructions for program operation and necessary job control statements to use the program within the IBM 360/370 OS computing environment, is being prepared.

⁵ For purposes of representing epidemics of mountain pine beetle, a stand should be defined as an area of about 160 to 240 ha (400 to 600 acres). Although such an area may contain substantial variation in tree conditions, the logic of TREMOD can accommodate and represent some within stand variation.

QUESTIONS AND ANSWERS

- Q. What data would have to be collected to simulate the middle and final years of an epidemic in progress?
- A. In addition to the stand mensurational data described in the paper, you would need to collect the data necessary to estimate the current beetle population per acre. This can be done by sampling several trees for emergence density and multiplying estimated emergence densities times the estimated surface area of the killed trees.
- Q. Would your simulation of the Hellroaring Creek infestation have been affected by the fact that many beetles make two attacks per year in that stand, with the second attacks occurring too late to produce any brood but still kill the trees?
- A. Parameters for the productivity model were developed using data which includes examples of this phenomenon and, hence, it would account for the double-hit trees.
- Q. What must be done to move the mountain pine beetle model to a drastically different geographic area?
- A. The stand variables include latitude and altitude as inputs to the productivity submodel and, therefore, require these minimal inputs. Also, since the major different data sets were located at roughly the same latitude but different altitudes, parameters for the productivity model should be chosen for diverse stands at drastically different latitudes. Development of parameters for the model would require measuring both attack and emergence densities, changing the resulting parameters in the productivity model if necessary.

REFERENCES

- Amman, G.D. 1973. Population changes of the mountain pine beetle in relation to elevation. *Environ. Entomol.* 2:541-547.
- Amman, G.D., and B.H. Baker. 1972. Mountain pine beetle influence on lodgepole pine stand structure. *J. Forest.* 70:204-209.
- Amman, G.D., B.H. Baker and L.E. Stipe. 1973. Lodgepole pine losses to mountain pine beetle related to elevation. USDA Forest Serv. Res. Note INT-171, Intermtn. Forest and Range Exp. Sta., Ogden, UT. 19 pp.
- Amman, G.D., M.D. McGregor, D.B. Cahill, and W.H. Klein. 1977. Guidelines for reducing losses of lodgepole pine to the mountain pine beetle in unmanaged stands in the Rocky Mountains. USDA Forest Serv. Gen. Tech. Rep. INT-36, Intermtn. Forest and Range Exp. Sta., Ogden, UT. 19 pp.
- Berryman, A.A. 1974. Dynamics of bark beetle populations: Towards a general productivity model. *Environ. Entomol.* 4:579-585.
- Berryman, A.A., and L.V. Pienaar. 1973. Simulation of intraspecific competition and survival of *Scolytus ventralis* broods (Coleoptera: Scolytidae). *Environ. Entomol.* 2:447-459.
- Burnell, D.G. 1977. A dispersal-aggression model—pine beetle in lodgepole pine stands. *Res. Pop. Ecol.* 19:11-18.
- Cole, W.E., and G.D. Amman. 1969. Mountain pine beetle infestations in relation to lodgepole pine diameters. USDA Forest Serv. Res. Note INT-95, Intermtn. Forest and Range Exp. Sta., Ogden, UT. 7 pp.
- Crookston, N.L. 1977. Mountain pine beetle (*Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae)) outbreaks in lodgepole pine (*Pinus contorta* Dougl.) and applications of a climatic hazard rating to the Pacific Northwest. M.S. thesis. University of Idaho, Moscow. 92 pp.
- Dudley, C.D. 1971. A sampling design for the egg and first instar larval population of the western pine beetle, *Dendroctonus brevicornis* (Coleoptera: Scolytidae). *Can. Entomol.* 103:1291-1313.
- Hamilton, D.A., Jr. 1974. Event probabilities estimated by regression. USDA Forest Serv. Res. Pap. INT-152, Intermtn. Forest and Range Exp. Sta., Ogden, UT. 18 pp.
- Hopkins, A.D. 1938. Bioclimatics: A science of life and climate relations. USDA Misc. Pub. No. 280. U.S. Govt. Print. Off. Washington, D.C. 188 pp.
- Hopping, G.R., and G. Beall. 1948. The relation of diameter of lodgepole pine to the incidence of attack by the bark beetle *Dendroctonus monticolae* Hopkins. *Forest. Chron.* 24:141-145.
- Klein, W.H., D.L. Parker and C.E. Jensen. 1978. Attack, emergence and stand depletion trends of the mountain pine beetle in a lodgepole pine stand during the outbreak. *Environ. Entomol.* 7:732-737.
- Krajicek, J.E. 1961. Crown competition—a measure of density. *Forest Sci.* 7:35-42.
- McMullen, L.H., and M.D. Atkins. 1961. Intraspecific competition as a factor in the natural control of the Douglas-fir beetle. *Forest Sci.* 7:197-203.
- Navon, D.I. 1971. Timber-RAM, a long-range planning method for commercial timber lands under multiple use management. USDA Forest Serv. Res. Pap. PSW-70, Pac. SW Forest and Range Exp. Sta., Berkeley, CA. 22 pp.
- Parker, D.L. 1973. Trend of a mountain pine beetle outbreak. *J. Forest.* 71:668-670.
- Pitman, G.B., and J.P. Vité. 1967. Aggregation behavior of *Dendroctonus ponderosae* (Coleoptera: Scolytidae) in response to chemical messengers. *Can. Entomol.* 101:143-149.
- Reid, R.W. 1958. The behavior of mountain pine beetle, *Dendroctonus monticolae* Hopkins, during mating, egg laying and gallery construction. *Can. Entomol.* 90:505-509.
- Roe, A.L., and G.D. Amman. 1970. The mountain pine beetle in lodgepole pine forests. USDA Forest Serv. Res. Pap. INT-71. Intermtn. Forest and Range Exp. Sta., Ogden, UT. 23 pp.
- Safranyik, L., and R. Jähren. 1970. Emergence patterns of the mountain pine beetle from lodgepole pine. *Can. Dept. of Fisheries and Forest. Bi-monthly Res. Notes* 26:11-12.

- Safranyik, L., D.M. Shrimpton and H.S. Whitney. 1974. Management of lodgepole pine to reduce losses from the mountain pine beetle. Can. Forest. Serv. Forest. Tech. Rep. 1, Pac. Forest Res. Centre, Victoria, B.C. 24 pp.
- Safranyik, L., D.M. Shrimpton and H.S. Whitney. 1975. An interpretation of the interaction between mountain pine beetle and its associated blue stain fungus in western Canada. Pages 406-428 in D.M. Baumgartner (ed.). Management of lodgepole pine ecosystems. Washington State Univ. Coop. Ext. Serv., Pullman. oop.
- Schenk, J.A., R.L. Mahoney, J.A. Moore and D.L. Adams. 1978. A preliminary model for hazard rating lodgepole pine stands for mortality by mountain pine beetle. Univ. of Idaho, College of Forest, Wildl. and Range Sci., Moscow. 18 pp. (unpublished).
- Schmitz, R.F., and J.A. Rudinsky. 1968. Effects of competition on survival in western Oregon of the Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopkins (Coleoptera: Scolytidae). Res. Pap. 8. School of Forest., Oregon State Univ., Corvallis. 42 pp.
- Stage, A.R. 1973. Prognosis model for stand development. USDA Forest Serv. Res. Pap. INT-137. Intermtn. Forest and Range Exp. Sta., Ogden, UT. 32 pp.
- . 1975. Forest stand prognosis in the presence of pests: Developing the expectations. Pages 233-245 in D.M. Baumgartner (ed.). Management of lodgepole pine ecosystems. Washington State Univ. Coop. Ext. Serv., Pullman.
- Stipe, L.E. 1974. Yearly trend of a mountain pine beetle infestation near Spring Creek Park, Bridger-Teton National Forest. USDA Forest Service, Region 4, Ogden, UT. 4 pp.
- Wood, D.L. 1977. Manipulation of forest insect pests. Chap. 22 in Chemical control of insect behavior: Theory and application. H.H. Shorey and T.T. McKelvey (eds.). John Wiley and Sons, New York.

SOLUTIONS TO THE PROBLEM

Detection and Evaluation Surveys for the Mountain Pine Beetle in Lodgepole Pine Forests

Douglas L. Parker

ABSTRACT

Detection and evaluation surveys are conducted by survey entomologists to gain information for advising resource managers on the need, feasibility and justification for control of damaging insect infestations. This evaluation process involves aerial and ground detection surveys and the following evaluation surveys: estimation of tree damage, determination of the relative abundance of the pest, and estimation of forest susceptibility. The survey techniques commonly used by survey entomologists to detect and evaluate mountain pine beetle (*Dendroctonus ponderosae* Hopkins) infestations are discussed.

INTRODUCTION

The performance of forest insect and disease detection and evaluation surveys must be a major component of forest management programs. Information provided by survey entomologists is particularly important to managers of lodgepole pine (*Pinus contorta* Douglas var. *latifolia* Engelmann) forests because catastrophic mountain pine beetle (*Dendroctonus ponderosae* Hopkins) outbreaks significantly affect immediate and long-range management objectives. Land managers must use the information and recommendations provided by survey entomologists, in addition to inputs from other specialists, in establishing management directions. The purpose of this paper is to briefly explain common survey techniques, to aid land managers who must use insect survey information.

In 1947, Congress enacted the Forest Pest Control Act in recognition of the need for public and private cooperation in combating insects and diseases, and the need for federal leadership and financial aid. The Cooperative Forestry Assistance Act of 1978, P.L. 95-313, 92 Stat. 365, 16 U.S.C. 2101 (Section 5) is the basic statutory authority for forest insect and disease management on all classes of land.

Since single mountain pine beetle outbreaks frequently involve several ownerships, effective forest insect management programs are dependent on cooperation among the USDA Forest Service, other federal agencies, states and private organizations. Entomologists in the Forest Service, and those in states that have their own statutes and also have cooperative agreements with the Forest Service, annually conduct planned, systematic surveys of forested lands. Forest Service entomologists survey all federal and Indian lands in states where there is a state entomologist and forested lands of all ownerships where there is no state entomologist. State entomologists are responsible for surveying lands in their respective states. Also, a few private companies have forest entomologists who give them technical advice.

The detection and evaluation process ultimately leads to the determination of the need, feasibility and justification for control. The following insect survey sequence is used in the evaluation process:

1. **Detection** - This term is used to describe planned aerial and ground survey procedures used by entomologists to systematically discover and delineate outbreaks.
2. **Evaluation** - After an outbreak has been detected, the following surveys are conducted:
 - a. Estimation of damage. Since the mountain pine beetle kills trees, aerial and ground techniques are used to estimate tree losses.
 - b. Relative abundance of pest. Entomologists attempt to measure insect densities in infested trees or use their professional judgment to predict the relative abundance of a pest. Entomologists

also attempt to determine the effect of predators, parasites and other natural controls on beetle broods. This information is used to determine probable infestation trends.

c. Forest susceptibility. In addition to having sufficient abundance of the pest, forest conditions must be favorable to enable an insect population to remain or to increase to damaging levels. Entomologists collect forest susceptibility information to help in determining the probable course of the infestation in the year following the survey.

Detection and evaluation survey information is used by entomologists to attempt to predict the course of an outbreak and estimate the potential for tree losses or damage. Programs for coping with the infestation are presented to the land manager, who decides if the recommended actions are environmentally acceptable, economically feasible and consistent with management objectives and administrative decisions.

To be complete, the detection and evaluation process must include all elements of the insect survey sequence. Each of these elements will be discussed separately in this paper with reference to the mountain pine beetle.

DETECTION

The frequency of outbreaks and their location usually cannot be predicted. Early discovery of outbreaks of destructive insects on lands of all ownerships is a task that no agency can accomplish alone. Thus, discovery of outbreaks has developed into a cooperative undertaking with two distinct phases. The first phase is a program of planned, systematic surveys, called detection surveys. The second and equally important phase is field surveillance undertaken by forest workers in connection with their regularly assigned duties.

Detection Surveys

A primary role of the survey entomologist is to ensure prompt discovery of outbreaks. There are two basic types of detection surveys: aerial and ground.

Aerial Surveys

These are used when insect-caused damage can be seen by an observer in a low-flying aircraft. Generally, these surveys will be organized in a well-planned, systematic manner to ensure that all visible damage is detected. Flat or rolling country can be covered by flying parallel lines, while contour flight patterns are used for rough terrain.

Highly trained aerial observers are needed for this work; they must have the skill to direct the aircraft, know their location at all times, observe and identify causes of tree damages or symptoms of infestation, and record data on maps at the proper locations. All of these tasks must be done in the proper sequence.

There are several means of recording survey data, but most observers use a coding system of black or multi-colored letters and numbers. For example, the color red often is used to denote mountain pine beetle-caused mortality in lodgepole pine. Polygons of various sizes, correlated with the intensity and extent of tree mortality and with geographical features, are used to mark infestation centers. Spots are often used to mark 1 to 10 infested trees at a given location. Also, a number can be placed within or adjacent to a polygon or spot to indicate the approximate number of currently killed trees. Some entomologists use light (L), medium (M) and heavy (H) categories for indicating the relative intensity of fatal attacks on beetle-killed trees.

There are three points that land managers should realize when using mountain pine beetle aerial survey information:

1. Usually, by the time managers receive aerial survey maps, the beetle has flown from currently faded trees and has attacked green trees. Therefore, the survey information is 1 year behind the infestation trend. This is one reason why ground surveys are needed.
2. Estimates of the number of dead trees are notoriously inaccurate, especially when infestations have been in progress for several years and cover large forested areas. Estimates of losses should be used mostly to indicate relative intensities of tree losses. Ground survey techniques should be used to get estimates of the actual damage.
3. Placements of some infestation centers on maps may not conform exactly to ground locations. This is especially a problem in flat areas where there are no distinct geographical or man-made features to enable surveyors to place polygons or spots at the right location.

Ground Surveys

These are used to detect destructive forest insects that can be found only by a search of forest stands or by close inspection of host trees. They usually are designed to discover the occurrence of a particular pest. A ground survey would be needed in the fall to locate lodgepole pines that had recently been infested by the mountain pine beetle.

Surveillance

All forest workers should be on the alert for forest insect and disease outbreaks in conjunction with their normal field activities. Timber cruising, stand improvement, trail maintenance, fire reconnaissance and other such activities afford excellent opportunities for forest workers to discover outbreaks before they become visible from the air. Land managers or owners share the responsibility for discovery of outbreaks on forested lands they manage. There are too few survey entomologists to discover all outbreaks on a timely basis.

Prompt reporting of new outbreaks is of the utmost importance to ensure early follow-up by entomologists. Any form of communication is acceptable, but most Forest Service regions and states have sent detection kits and forms to land managers to speed the reporting of newly discovered outbreaks. The kits can be used to send in specimens of insects and damage.

EVALUATION

After an outbreak has been detected, evaluation surveys are used to assess current conditions and predict the probable future trend of an outbreak. The specific emphasis of an evaluation survey is determined by the type of information needed by the survey entomologist or the resource manager.

Estimation of Damage

Estimation of tree mortality caused by the mountain pine beetle is a major element of the evaluation process. Ground surveys are used to determine tree losses on small tracts of land or when estimates of green infested trees are needed. When estimates of visual damage over large forested areas are required, aerial photographic techniques have proven to be the most efficient and precise approach. Each of these approaches is discussed separately.

Ground surveys

There have been only a few evaluations of the precision and efficiency of sampling techniques used for estimating tree losses caused by insects. Although I did not conduct an in-depth review of the literature, only three papers are commonly cited in the literature and in unpublished reports comparing ground survey techniques (Knight et al. 1956, Knight 1958, Parker 1973). Due to this limited information, entomologists and foresters have been forced to use techniques developed for cruising timber. However, several different problems are encountered in estimating beetle-caused losses versus cruising for timber. The relatively low density of dead or attacked trees and the tendency of the beetle to attack trees in groups are two major difficulties. The precision of estimates is affected considerably by these two situations. For example, zero counts always occur at some sample points and 20 or more infested trees can be counted at other locations. The variation between these extremes, using .04-ha (0.1-acre) fixed radius plots, would be zero to 494 trees per ha (200 trees/acre). Little confidence could be placed on the estimates obtained from a survey with this amount of variation.

Today, entomologists are in no better position to provide more precise loss estimates from on-the-ground surveys than they were 10 years ago. Most often the number of personnel and the amount of time available to conduct a survey, not the level of statistical precision desired, determine the sample size. Even with all of the difficulties discussed, land managers need estimates of current infestation levels and other tree

loss data. Resource managers should insist that entomologists provide them with statistical estimates to assist them in determining the confidence they can place on survey data.

Aerial photography surveys

Even though little progress has been made with ground sampling methods, considerable progress has been made in the use of aerial photography in estimating tree losses. Klein (1970, 1973a) has shown that 35-mm aerial photography at a scale of about 1:5000 will give precise estimates of current and past lodgepole pine losses. This approach has proven to be inexpensive as well as effective under operational conditions (Klein 1973b). Similar results also have been obtained by using other formats and various film types. Aerial photography is particularly useful in estimating tree losses over large forested areas. Several points are photographed along flight lines in the survey area, and interpreters count dead trees on each photographic plot. Stereoscopic coverage is needed to maximize interpretation. After this phase is completed, a subsample of plots is ground-checked to determine the accuracy of the photographic interpretation.

Aerial photographic techniques for estimating lodgepole pine losses have been adequately developed and most survey entomologists have or can obtain access to the equipment they need to conduct aerial photographic damage surveys. Some survey entomologists, however, still use visual estimates to determine tree losses.

Relative Abundance of Pest

There is neither an efficient nor an effective method for estimating the relative abundance of mountain pine beetle by counting insects. An unpublished sequential sampling plan has been used by survey entomologists, but most have found it to be time-consuming and ineffective for their work. It is not generally used today.

At present, survey entomologists must use their professional judgment to predict the relative abundance of a beetle population in an infested area. They do this by counting the number of infested trees, measuring the diameters of infested trees, subjectively determining the vigor of beetle broods, and estimating the influence of natural enemies of the mountain pine beetle. It is fairly easy to estimate heavy and low-level populations in a small area by determining the density and size of infested trees and having records on the history of the outbreak. However, the overall population level of a large outbreak is difficult to determine because there are always increasing, static and decreasing centers in a single contiguous infestation. Even with this difficulty, not to mention the unscientific aspects of the approach, entomologists have been quite accurate in estimating population trends.

Many survey entomologists are uncomfortable with subjectively determining beetle population levels and they would like to have a better approach. As Knight (1968) indicated,

evaluation techniques must be practical and economically feasible, and if counting trees will give satisfactory results in *estimating beetle populations, then it should be used*. I believe it is possible, using current information, to develop a survey technique to estimate potential population levels using data on numbers and sizes of infested trees. Only the absence or presence and the relative density of beetle broods would be noted. Infested trees would be given a numerical rating, depending on their size—the larger the tree, the higher the rating. The ratings would be multiplied by the number of trees in each category to yield a stand rating. This approach is basically what is being done by some entomologists, but there would be less subjectivity if a standard tree-rating technique were developed.

Forest Susceptibility

Considerable information has been collected to show that sawtimber-sized stands of lodgepole pine favor mountain pine beetle outbreaks (Cole and Amman 1969). Generally, the largest trees are killed at the beginning of an infestation and smaller-diameter trees at the end of an outbreak cycle. Entomologists can predict probable outbreak trends in subsequent years by knowing the stand structure.

Timber cruising techniques are used to obtain forest susceptibility data. These surveys usually are done at the same time as damage surveys.

PREDICTION OF OUTBREAK TRENDS

In addition to records of past outbreaks, the relative abundance of the pest and the susceptibility of the forest, one other technique is used by survey entomologists to get information to help in predicting tree losses for the succeeding year. This involves counting both recently faded and newly attacked green trees to give a build-up ratio. An entomologist will use aerial survey information to select several sites in an infestation to get build-up ratios. He visits these sites and walks through the forest for a period of time, counting “faders” and green infested trees. Data collected during these stand examinations show the relative density of infested trees and the infestation trend in a stand.

Resource managers can use build-up ratio information to decide upon action programs for specific areas. For example, if the Two Springs survey location (Table 1) were within a planned timber sale, the manager might decide to start a harvesting program early because of the high density of attacks, as well as an increasing trend. However, he probably would take no action if the Pole Canyon site were in a sale area.

COORDINATION

Close coordination between the resource manager and the survey entomologist is needed for making management

Table 1. Simulated results of a stand examination to get build-up ratios for the mountain pine beetle.

Area	1978 attacks	1977 attacks	Build-up ratio	Trend
Turkey Flat	38	39	1:1	Static
Two Springs	130	101	1.3:1	Increasing
Pole Canyon	5	11	0.5:1	Decreasing
Clear Creek	58	35	1.7:1	Increasing

decisions to cope with an outbreak or making long-term management plans for lodgepole pine forests. The resource manager should request a meeting with the entomologist and all other interested parties to discuss all entomological aspects, management alternatives and recommended courses of action. Many misunderstandings can be avoided by having these discussions, and more effective resource management programs will result through a team effort. The role of the survey entomologist is to advise the resource manager, who makes the management decisions.

ACKNOWLEDGMENTS

Thanks are due J.W.E. Harris, Pacific Forest Research Centre, Victoria, B.C.; LeRoy N. Kline, Office of the Oregon State Forester, Salem, OR; and C. Kendal Lister, USDA Forest Service, Lakewood, CO, for their review of this paper.

REFERENCES

- Cole, W.E., and G.D. Amman. 1969. Mountain pine beetle infestations. Note INT-95. Intermtn. Forest and Range Exp. Sta., Ogden, UT. 7 pp.
- Klein, W.H. 1970. Mini-aerial photography. J. Forest. 68:475-478.
- _____. 1973a. Beetle-killed pine estimates. Photogram. Eng. 39: 385-388.
- _____. 1973b. Evaluating a mountain pine beetle infestation with the aid of 35-mm aerial photography. USDA Forest Serv. Region 4, Ogden, UT. 7 pp.
- Knight, F.B. 1958. Methods of surveying infestations of the Black Hills beetle in ponderosa pine. Forest Sci. 4:35-41.
- _____. 1968. Evaluation of forest insect infestations. Annu. Rev. Entomol. 12:207-228.
- Knight, F.B., W.F. McCambridge and B.H. Wilford. 1956. Estimating Engelmann spruce beetle infestations in the central Rocky Mountains. USDA Forest Serv. Pap. No. 95. Rocky Mtn. Forest and Range Exp. Sta., Ft. Collins, CO. 12 pp.
- Parker, D.L. 1973. Evaluation of plots used during mountain pine beetle surveys. USDA Forest Serv. Region 4, Ogden, UT. 9 pp.
- U.S. Congress. 1947. Forest Pest Control Act of 25 June 1947 (61 Stat. 177), as amended by the act of 20 June 1975 (89 Stat. 224; 16 USC 594-1 through 594-5).

Management of Mountain Pine Beetle in Lodgepole Pine Stands in the Rocky Mountain Area

Mark D. McGregor

ABSTRACT

Mountain pine beetle (*Dendroctonus ponderosae* Hopkins) is the primary bark beetle influencing management of lodgepole pine (*Pinus contorta* Douglas var. *latifolia* Engelm.). Management by chemical treatment and by felling and burning of infested trees or salvage logging are rearguard techniques and do not prevent or reduce anticipated tree mortality. Methods are available for risk rating susceptible stands so management can be directed toward highest hazard stands. Characteristics such as slope, aspect, elevation, tree diameter, percent of lodgepole pine basal area with mistletoe infection, percent of lodgepole pine basal area in the stand and habitat type should be considered when risk rating stands. Suggested management strategies are discussed for areas designated for timber production, for individual trees of high value and for non-timber values.

INTRODUCTION

Lodgepole pine (*Pinus contorta* Douglas var. *latifolia* Engelm.) is one of the most important timber species in the area from northern Colorado to the west coast of the United States, north to southern British Columbia. It is a dominant component of western coniferous forests, forming the major cover type on more than 6 million ha (15 million acres) in 11 western states, as well as extensive areas in two Canadian provinces. In these cases, it comprises 30 to 92 percent of the total commercial timber stand (Berryman 1975).

Timber production, however, is only one of the key uses of lodgepole pine forests in the central Rocky Mountains. Lodgepole pine occupies areas that are also important for water yield, wildlife habitat, recreation and scenic beauty (Alexander 1975).

One of the primary problems of managing lodgepole pine is the ever-present pressure of recurring epidemics of mountain pine beetle (*Dendroctonus ponderosae* Hopkins). Because of the frequency and severity of infestations, past managers were inclined to implement chemical control, fell and burn infested trees or salvage log to halt an infestation in lodgepole pine stands. These efforts were futile, however. Management by chemical treatment of infested trees or by felling and burning is only temporary (Hopping 1951), and salvage logging is only a means of recovering some of the mortality already incurred. Salvage logging is, even under favorable conditions, a "rearguard" action limited to a few of the most accessible damaged stands (Prebble 1951); only a small fraction of the total volume of insect-killed timber has ever been recovered in such operations.

Because these management methods are only temporary, they do not reduce anticipated mortality. Many of the endeavors of forest entomologists have been devoted to finding facts and relationships that could be used advantageously in pre-salvage cuttings—that is, to make it possible to employ foresight in attempting to manage, reduce or prevent anticipated mortality.

Practical measures proposed for the reduction of tree mortality caused by insects, such as early harvest, pre-salvage, or salvage cuttings, may differ very little from some silvicultural measures proposed for prevention of damage. Nevertheless, there is an important distinction between the two concepts. The first is an emergency action to recover existing or immediate mortality; the second implies long-term planning as a part of a program of silvicultural management to prevent or reduce the risk of future damage.

Forest managers operating under multiple-use policies would benefit from techniques that would allow them to pre-determine which stands are susceptible to mountain pine

beetle infestation. Preventive or suppressive treatments are not practical for all lodgepole pine stands. Prescribed management must vary according to differences in stand characteristics and management objectives. Risk-rating systems based on characteristics of the biological interaction between mountain pine beetle and lodgepole pine will enable forest managers to prescribe management regimes that may possibly prevent outbreaks from developing.

HAZARD-RATING SYSTEMS

Several hazard-rating systems for lodgepole pine forests have been proposed prior to and during this symposium.

Safranyik et al. (1974) described the influence of climate and weather on risk of mountain pine beetle population increase and developed a risk-rating system for lodgepole pine in British Columbia. Climatic regions conducive to mountain pine beetle population increase were mapped and also designated as areas where more intensive risk ratings should be applied.

A similar map, using stand age, density, size and, to a degree, habitat type, was prepared for areas on the Kootenai (Hamel and McGregor 1976) and Gallatin National Forests, Montana (McGregor et al. 1976), supporting a significant lodgepole pine component ≥ 60 years of age. These were not stand-specific, but applied to extensive areas of lodgepole.

Crookston et al. (1977) plotted historical infestations on a map covering the range of lodgepole pine in the western United States. This method directs land managers to areas of past repeated mountain pine beetle infestations where stand level risk ratings and subsequent treatment prescriptions should be made.

Amman et al. (1977) used average stand dbh, average stand age, elevation and latitude to hazard rate lodgepole pine areas for susceptibility to mountain pine beetle outbreak. This method provides a broad classification of the low-, moderate- and high-risk lodgepole pine areas.

Berryman (these proc.) proposes a method using variables he believes are more sensitive to the interaction between lodgepole pine and mountain pine beetle. Berryman's method would replace average dbh with a measure of phloem or of beetle productivity; age is replaced with a variable called resistance, and provides a conceptual framework for understanding lodgepole pine/mountain pine beetle interactions in managed and unmanaged stands. The synoptic model provides the manager with a method for displaying the trajectory of a stand through time, in an unmanaged state or under a set of management alternatives, then relating it to the expected intensity of mountain pine beetle activity.

Schenk et al. (1978) propose a stand hazard rating (SHR) to rate lodgepole pine stands for tree mortality due to the mountain pine beetle. This SHR is a function of crown competition factor (CCF) and percent lodgepole pine basal area

(%BALPP). This information would be of value to managers in establishing priorities for prescribed cuttings by simulating various strategies to obtain maximum production and minimum beetle-caused mortality. Using standard inventory data, a hazard-rating model and simulation techniques, managers could perform stocking regulation with a forecast of how management actions are likely to affect mountain pine beetle-caused tree mortality.

Mahoney (these proc.) used various vigor-related stand measurements including crown ratio, sapwood ratio, 10-year radial increment and periodic growth ratio (PGR) and developed an equation to classify stands in northwestern Idaho and western Montana as resistant or susceptible to mountain pine beetle infestation.

Mahoney rated stands as resistant or susceptible to mountain pine beetle by measuring PGR, a measure of current vigor and trend of a lodgepole pine stand. The PGR is calculated by dividing the current 5-year radial increment by the previous 5-year radial increment taken from co-dominant and dominant lodgepole pine trees.

The CCF and %BALPP/100 were described in a single interaction variable, SHR. We applied this equation to 30 Montana stands and 9 Idaho and Wyoming stands; the results were generally just the opposite of those found by Mahoney (McGregor and Amman, unpublished data). Stands with the highest SHR usually had the lowest mortality and vice versa. The SHR method appears to be applicable to stands from which the method was derived but does not fit the data from those lodgepole pine stands that we examined in Idaho, Wyoming and Montana.

These hazard-rating systems are not proposed as a panacea, but do provide the land manager with some guidelines as to which stands may suffer greatest mortality. Most of the hazard-rating systems consist of broad categories applied to large areas of lodgepole pine, but some are intended to apply to specific stands as delineated by the National Forest Timber Inventory System. This inventory is designed to catalog stand characteristics that occur under a given set of conditions, and how these factors interact to alter potential yield.

Regardless of which hazard rating managers choose, they must determine which variables affect gross mountain pine beetle-caused tree mortality and measure them. Variables and combinations of variables that may influence amount of tree mortality can differ by region, area, forest and stand.

THE GALLATIN NATIONAL FOREST— AN EXAMPLE

On the Gallatin National Forest in 1977, 109 stands were inventoried to determine which stand characteristics or combinations of characteristics influenced the amount of mountain pine beetle-caused tree mortality.

Methods

A stand was defined by forest inventory planners as a homogeneous unit 2 ha (5 acres) or more, with characteristics (i.e., habitat type, land classification and photo interpretation) that separate it from adjacent stands. From 2 to 30 variable plots (10 BAF) were established in each stand. Stands ranged from 2 to 84 ha (average 52 ha) and number of plots varied depending on stand size. Stand characters were measured using conventional forest measurement devices and techniques. In addition, mistletoe infection in each tree was rated using Hawksworth's (1977) 6-point system.

Analyses

Each of the 13 dependent variables was screened via computer, using a stepwise regression routine, for strength of relation to the simple linear additive effects of the 24 independent variables. Several of the stronger relations isolated were then studied in greater detail for the presence of interaction, expectation for which was reasonably finite. The data were explored graphically within the constraints of expectation, and specific graphic hypotheses were developed for each relation following techniques outlined in Matchacurve-3 (Jensen 1973). Mathematical specification of these interactions is deferred to the future. Expected interactions were quite evident in the data, and the three- and four-dimensional graphic portrayals of these are used as a basis for discussion here.

Results and Discussion

Although 13 dependent variables relating to mortality were tested, in only four of these were combinations of independent variables found that explained over 40 percent of the variation. These were 1) trees > 30 cm dbh killed/ha, 2) total basal area > 30 cm dbh killed, 3) percent of trees killed per ha and 4) percent basal area > 30 cm dbh killed (Tables 1, 2, 3 and 4).

All of these indicators of lodgepole pine mortality are of interest, but perhaps the one most pertinent to the forest manager and most versatile in application is number 4, selected here for further analysis.

The associated independent variables include three with strong biological ties to beetle production capacity in the lodgepole pine stand and for which the expected interaction is strong: percent lodgepole pine > 30 cm dbh, percent basal area with mistletoe infection and percent lodgepole pine > 20 cm dbh. Exploration of the data under the constraints of this expectation resulted in the hypothesized relation shown in Fig. 1.

The percent of lodgepole pine basal area killed in the > 30 cm dbh size classes was

1. **negatively** related to percent of the basal area infected with mistletoe.

2. **positively** related to percent of lodgepole pine ≥ 30 cm dbh.
3. **positively** related to percent of lodgepole pine ≥ 20 cm dbh.

The percent of lodgepole pine basal area killed in the 20 to 30 cm dbh and in the > 30 cm dbh size classes was found to be

1. **negatively** related to percent of the basal area infected with mistletoe.
2. **positively** related to percent of lodgepole pine ≥ 30 cm dbh.
3. **positively** related to percent of lodgepole pine ≥ 20 cm dbh.

Procedures like those just described were also applied in modeling percent basal area 20 to 27 cm dbh killed. The effect of the independent variable, percent of lodgepole pine stand > 20 cm dbh, was not discernible in the data in this case, and the final relationship included only the remaining two independent variables. As can be seen, the effect of mistletoe is still negative, but that for percent of lodgepole pine stand ≥ 30 cm dbh now reaches an optimum in accord with expectation for this new dependent variable.

Effect of Mistletoe. The expected effect of mistletoe was negative in the interaction and was strongly expressed in the data (Fig. 1). Failure to include interactive effects in the original screening effort resulted in the misleading positive effect for mistletoe specified in Table 1. The linear additive model was inappropriate.

Stands that had the least mistletoe infection suffered the greatest mortality from mountain pine beetle infestations (Fig. 1). Because of the beetle's strong propensity for the large-diameter trees, the proportions of such trees in the stands had to be considered in the analysis. This permitted sorting out the effect of mistletoe from that of diameter. As the proportions of the trees in the stands that were 20 cm dbh or larger increased (3 classes were used—0-35%, 36-70%, and 71% or more) and as the proportions of trees 30 cm dbh and larger increased from 0 to 100 percent, percent mortality increased, thus demonstrating the strong relation of beetles to lodgepole pine diameter and the necessity of accounting for this effect before trying to evaluate the beetle-mistletoe interaction.

I interpret this interaction as being related to reduced phloem thickness caused by mistletoe infection, and as a result reduced brood production by the beetle when mistletoe-infected trees were infested. Trees having medium to heavy mistletoe infection have thinner phloem than uninfected trees (Roe and Amman 1970). Slow growth results in thin phloem (Cole 1973) and consequently in reduced beetle production (Amman 1972). This is in contrast to the usual interpretation of beetle/tree disease interactions—that losses to beetles will increase with disease incidence.

Table 1. Analysis of variance for numbers of lodgepole pine 30 cm dbh and larger killed per acre¹ by mountain pine beetle.

Multiple R	.6759			
Multiple R-square	.4569			
Std. error of est.	7.7681			
<i>Analysis of variance</i>				
	<i>Sum of squares</i>	<i>DF</i>	<i>Mean square</i>	<i>F ratio</i>
Regression	5228.4651	3	1742.882	28.882
Residual	6215.3524	103	60.34323	
<i>Variables in Equation</i>				
<i>Variable</i>	<i>Coefficient</i>	<i>Std. error of coeff.</i>	<i>Std. reg. coeff.</i>	<i>F to remove level</i>
(Y-Intercept	-6.698)			
CFVTOT*	.001	.000	.167	4.436
LPBA 30**	.276	.037	.575	54.226
YEARINFS†	1.251	.382	.242	10.719

*CFVTOT = Total cubic foot volume/acre.

**LPBA 30 = Basal area lodgepole pine > 30 cm dbh.

†YEARINFS = Years stands have been infested.

¹ Multiply by 2.471 to convert to hectares.

Table 2. Analysis of variance for basal area of lodgepole pine trees 30 cm dbh and larger killed per acre¹ by mountain pine beetle.

Multiple R	.6875			
Multiple R-square	.4727			
Std. error of est.	9.3056			
<i>Analysis of variance</i>				
	<i>Sum of squares</i>	<i>DF</i>	<i>Mean square</i>	<i>F ratio</i>
Regression	7917.1827	4	1979.296	22.857
Residual	8832.5284	102	86.59342	
<i>Variables in Equation</i>				
<i>Variable</i>	<i>Coefficient</i>	<i>Std. error of coeff.</i>	<i>Std. reg. coeff.</i>	<i>F to remove level</i>
(Y-Intercept	-6.077)			
LPBA 30*	.361	.042	.623	72.478
YEARINFS**	1.388	.453	.222	9.376
LETELV†	-1.715	.896	-.139	3.661
PERTAMST††	20.894	11.769	.130	3.152

*LPBA 30 = Basal area lodgepole pine > 30 cm dbh.

**YEARINFS = Years stands have been infested.

†LETELV = Cosine analysis for elevation.

††PERTAMST = Percent lodgepole pine/acre with mistletoe infection.

¹ Multiply by 2.471 to convert to hectares.

Table 3. Analysis of variance for percent of all lodgepole pine per acre¹ killed by mountain pine beetle.

Multiple R	.7427
Multiple R-square	.5517
Std. error of est.	.0735

Analysis of variance

	<i>Sum of squares</i>	<i>DF</i>	<i>Mean square</i>	<i>F ratio</i>
Regression	.66493816	6	.1108230	20.507
Residual	.54040673	100	.5404067	

Variables in Equation

<i>Variable</i>	<i>Coefficient</i>	<i>Std. error of coeff.</i>	<i>Std. reg. coeff.</i>	<i>F to remove level</i>
(Y-Intercept	-.032)			
MISTBA 12-30*	-.015	.005	-1.833	10.254
MISTTA 30**	-.022	.006	-1.945	12.765
YEARINFS†	.021	.004	.389	32.247
MISTBAT 12††	.011	.005	2.271	5.929
PERBAMST‡	2.479	.261	1.074	90.291
LPBA 20§§	.001	.000	.231	10.272

*MISTBA 12-30 = Lodgepole pine basal 12-30 cm dbh/acre with mistletoe infection.

**MISTTA 30 = Lodgepole pine > 30 cm dbh/acre with mistletoe infection.

†YEARINFS = Years stands have been infested.

††MISTBAT 30 = Total basal area > 30 cm dbh/acre with mistletoe infection.

‡PERBAMST = Percent basal area/acre with mistletoe infection.

§§LPBA 20 = Lodgepole pine basal area > 20 cm dbh/acre.

¹ Multiply by 2.471 to convert to hectares.Table 4. Analysis of variance for percent of basal area for lodgepole pine trees 30 cm dbh and larger per acre¹ killed by mountain pine beetle.

Multiple R	.6537
Multiple R-square	.4274
Std. error of est.	.1088

Analysis of Variance

	<i>Sum of squares</i>	<i>DF</i>	<i>Mean square</i>	<i>F ratio</i>
Regression	.89256687	5	.1785134	15.076
Residual	1.1959258	101	.1184085	

Variables in Equation

<i>Variable</i>	<i>Coefficient</i>	<i>Std. error of coeff.</i>	<i>Std. reg. coeff.</i>	<i>F to remove level</i>
(Y-Intercept	-.034)			
CFVTOT*	.000	.000	.164	4.184
YEARINFS**	.018	.005	.254	11.002
PERLP 30 †	.602	.099	.767	37.164
PERBAMST††	.648	.245	.218	7.008
PERLP 20‡	-.228	.069	-.423	10.924

*CFVTOT = Total cubic foot volume/acre.

**YEARINFS = Years stands have been infested.

†PERLP 30 = Percent lodgepole pine > 30 cm dbh.

††PERBAMST = Percent basal area/acre with mistletoe infection.

‡PERLP 20 = Percent lodgepole pine > 20 cm dbh.

¹ Multiply by 2.471 to convert to hectares.

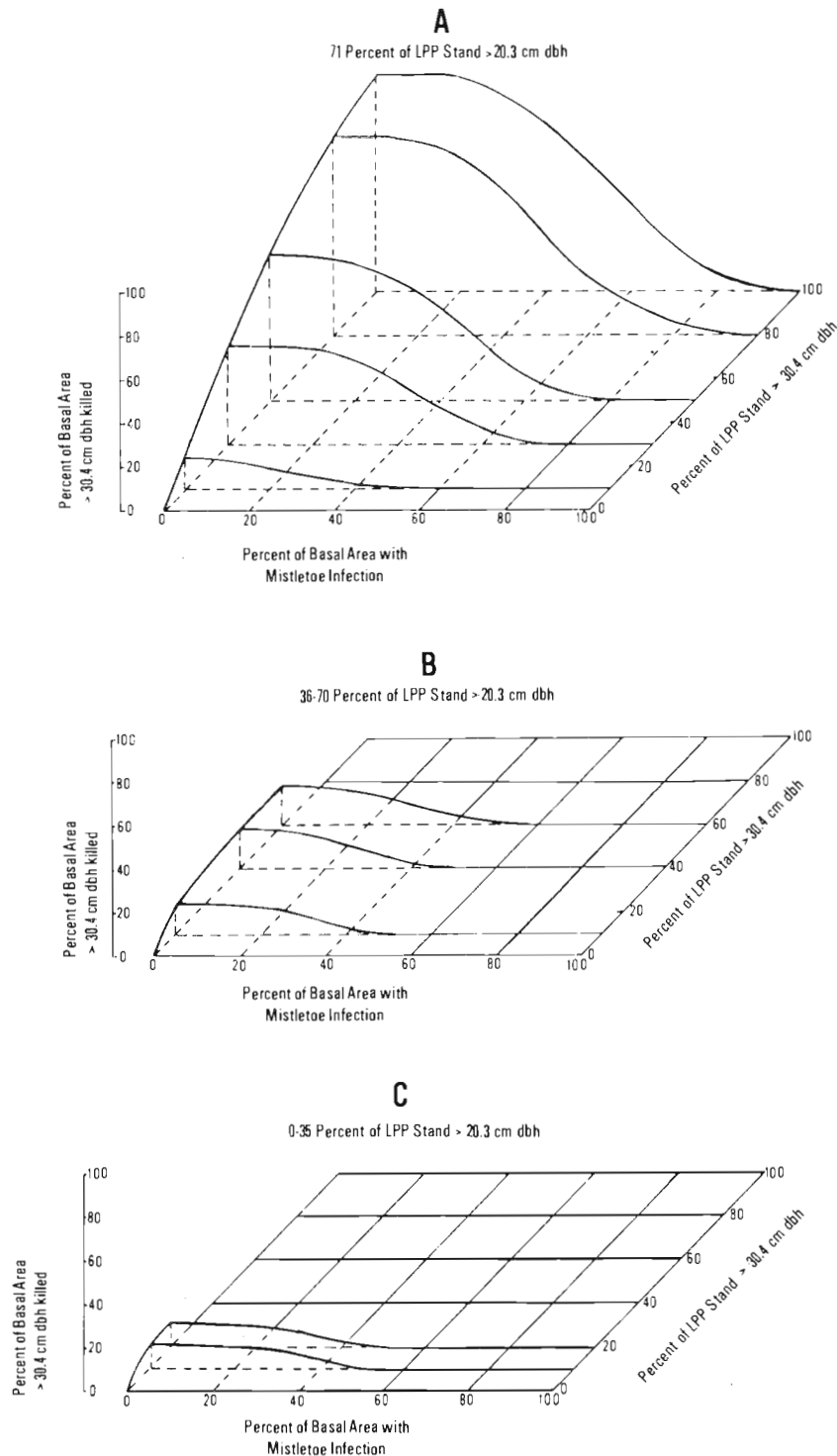


Fig. 1. Percent of basal area of trees 30.4 cm dbh and larger killed by mountain pine beetle as affected by percent of lodgepole pine (LPP) 30 cm dbh or larger in the stand and the percent of basal area with mistletoe infection where:

- A. 71 percent of the lodgepole pine ≥ 20.3 cm dbh; habitats = spruce, subalpine fir, Douglas-fir; av. stand age = 145 yrs.; av. total BA = $28.6 \text{ m}^2/\text{ha}$ (128.7 sq ft/ac); av. years infested = 3.0.
- B. 36 to 70 percent of the lodgepole pine ≥ 20.3 cm dbh; habitats = spruce, subalpine fir, Douglas-fir, lodgepole pine; av. stand age = 121.9 yrs.; av. total BA = $29.5 \text{ m}^2/\text{ha}$ (132.7 sq ft/ac); av. years infested = 3.4.
- C. 0 to 35 percent of the lodgepole pine ≥ 20.3 cm dbh (Gallatin National Forest, Montana); habitats = subalpine fir, Douglas-fir, lodgepole pine; av. stand age = 108.4 yrs.; av. total BA = $30.4 \text{ m}^2/\text{ha}$ (133.7 sq ft/ac); av. years infested = 3.8.

Effect of Habitat Type. Tree mortality caused by the mountain pine beetle was strongly related to habitat types as defined by Pfister et al. (1977). Habitat types were grouped into 4 classes (on the advice of S. Arno, pers. comm.¹). In decreasing order, mountain pine beetle-caused tree mortality by habitat type group was associated with Douglas-fir, spruce, subalpine fir and lodgepole pine climax. Roe and Amman (1970) also noted that heaviest mortality occurred in one of the true fir habitat types.

Beetle-caused tree mortality declined as elevation increased within habitat types. For example, in the xeric fir types 42 percent of the trees 20 cm dbh and larger were killed at 1828 m (6000 ft) elevation (Psme/Caru habitat type), whereas 25 percent were killed at 2438 m (8000 ft) elevation (Abla/Vasc habitat type) (Fig. 2).

In the mesic spruce types, 40 percent of the trees 20 cm dbh and larger were killed at 1767 m (5800 ft) elevation (Picea/Libo habitat type), whereas in the mesic fir types

(Abla/Als habitat type) 13 percent were killed at 2377 m (7800 ft) elevation (Fig. 3).

Lodgepole pine mortality varied only slightly in relation to the proportion of other species of trees in the stands. For example, in the spruce habitat types, where lodgepole pine basal area did not exceed 43 percent of the total in the stand, the beetles killed an average of 40 percent of the lodgepole pine basal area for lodgepole pine 30 cm dbh and larger. Mortality averaged only 2 percent more of the lodgepole basal area in the Douglas-fir habitat types where lodgepole pine basal area was 15 percent greater (58% total).

As the lodgepole pine basal area decreased with decreasing elevation, the percent of the basal area killed by the beetles increased. As elevation decreased, sites were more moist and better for tree growth. Consequently, one would expect trees to produce thicker phloem, resulting in more beetles being produced and a greater percent of the lodgepole pine basal area being killed.

Cole (1973) found that habitat type was the second most important variable explaining variance in phloem thickness in all higher ranking regressions of from two to six independent

¹ S. Arno is currently at the Intermountain Forest and Range Exp. Sta., Missoula, MT.

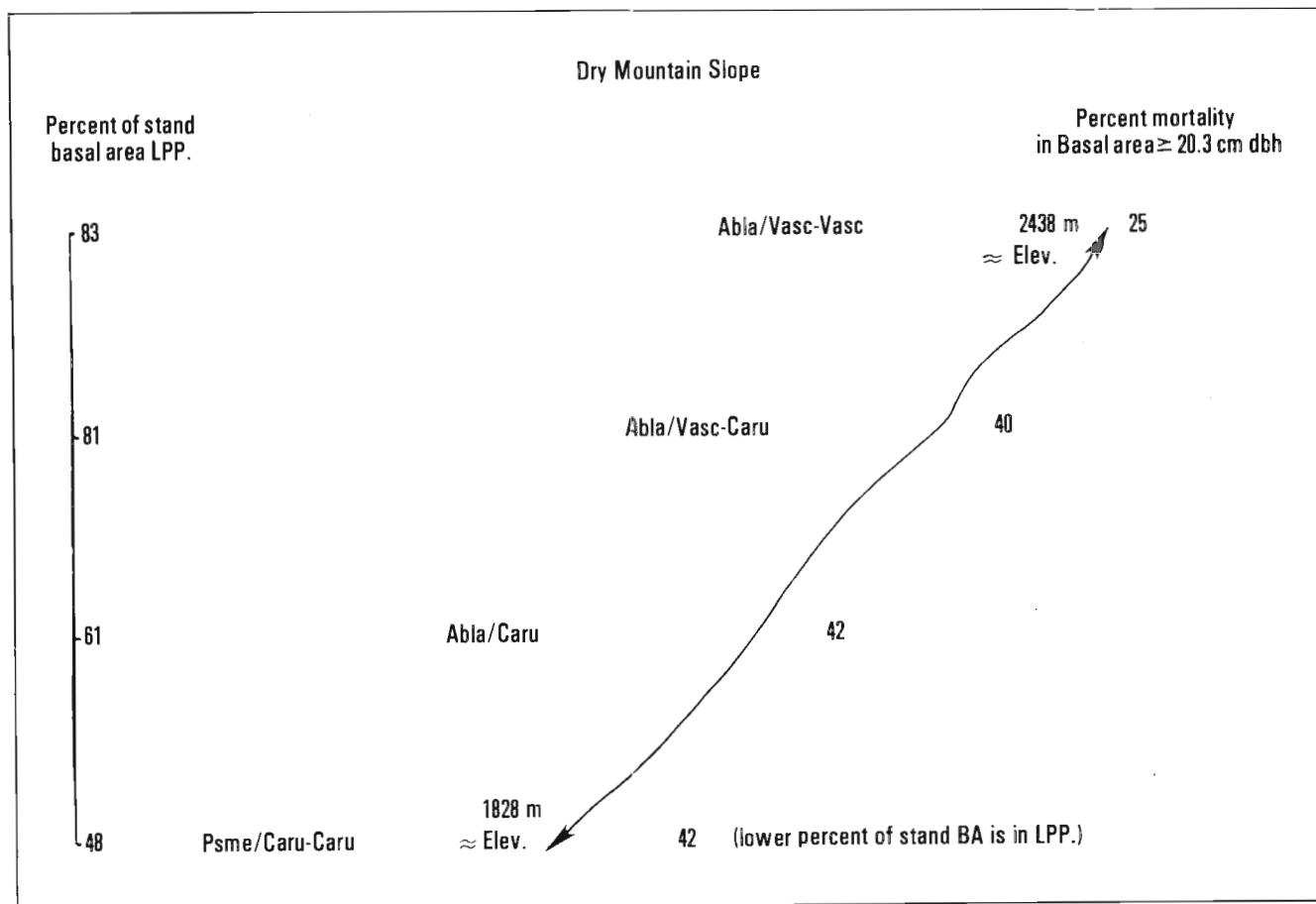


Fig. 2. Percent lodgepole pine (LPP) basal area for trees 20.3 cm dbh and larger killed by mountain pine beetle in relation to elevation, habitat type and percent lodgepole basal area in the stands on dry aspects.

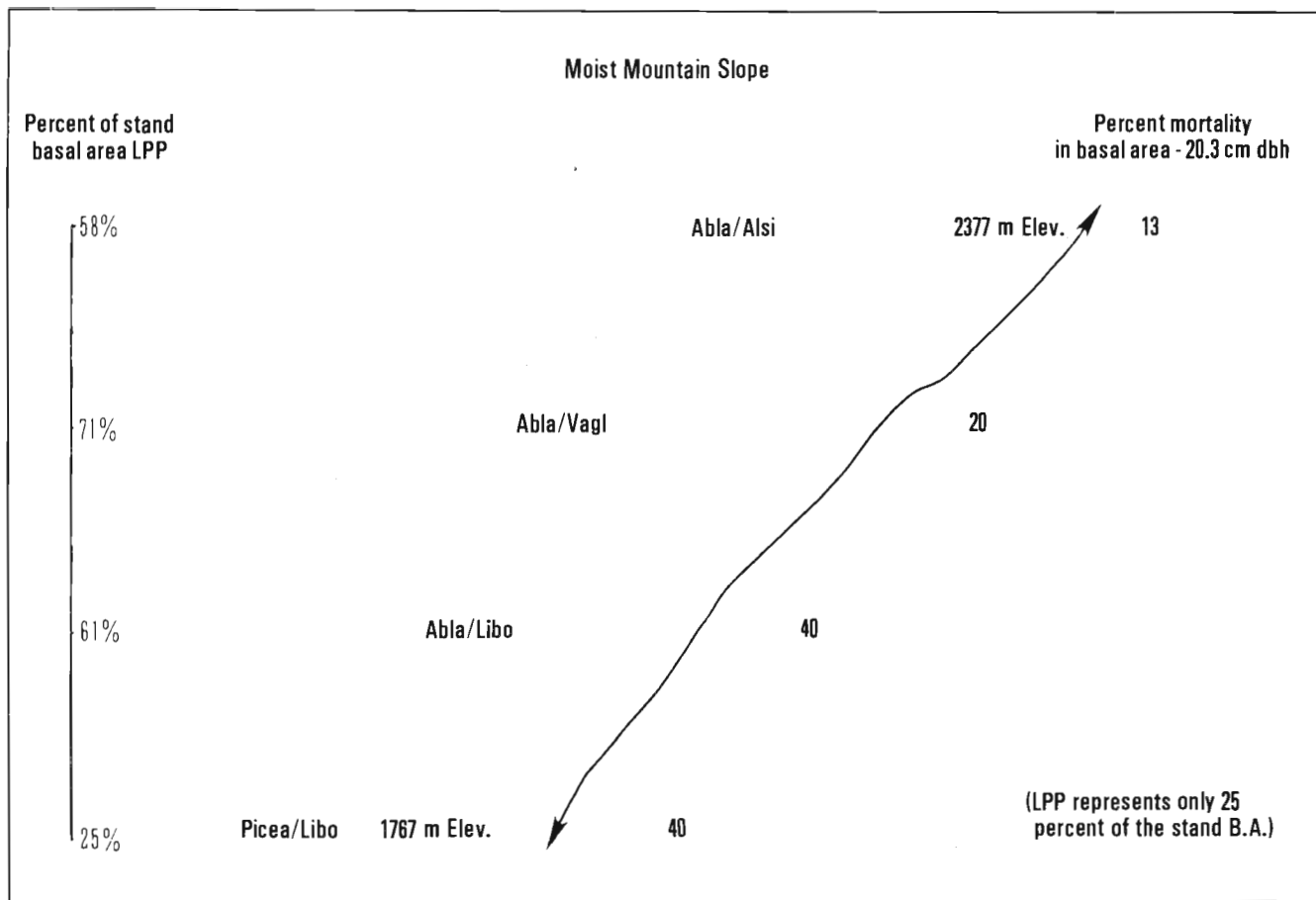


Fig. 3. Percent lodgepole pine (LPP) basal area for trees 20.3 cm and larger killed by mountain pine beetle in relation to elevation, habitat type and percent lodgepole pine basal area in the stands on wet aspects.

variables. Amman (these proc.) concluded that mountain pine beetle infestations could be expected more frequently on sites providing for the best growth of lodgepole pine, and more intense infestations could be expected because phloem will be thicker for any given tree diameter on good than on poor fully stocked sites.

Effect of Infestation Age. The expected cumulative effect of age of beetle infestation on tree mortality within individual stands was completely absent. I postulate that since the beginning of the present epidemic infestation in the Gallatin Canyon in 1969, severity had increased to the point that recently infested stands experienced as much mortality in 2 to 4 years as older infested stands had experienced in 6 to 8 years (Table 5). Although the data may be too limited to verify a related thesis, I think that as the severity of the epidemic intensified, beetles were less discriminating and killed higher proportions of small trees. Also, I speculate that when beetle populations developed to epidemic levels in 1969, build-up occurred in stands conducive to high beetle brood production. Whether these were the most susceptible stands isn't known, but combinations of stand characteristics were favorable for rapid beetle population build-up.

SUGGESTED MANAGEMENT STRATEGIES

The choice of management strategies depends on the capability to predict beetle population behavior and the infestation trend over a wide range of stand conditions with a known probability of success. Therefore site, stand and indi-

Table 5. Percent of lodgepole pine basal area killed by mountain pine beetle in stands infested for different numbers of years.

Years infested	Total basal area ¹ all species (m ²)	Lodgepole pine	
		Basal area killed ¹ (m ²)	Percent basal area killed
1	2968	240	8
2	1013	274	27
3	1493	300	20
4	1420	268	19
5	2137	454	21
6	1586	457	29
8	625	156	25

¹ Multiply by 2.471 to obtain basal area/hectare.

vidual tree characteristics that affect beetle incidence should become a regular part of pest management surveys to provide regionwide data to predict beetle hazard in specific stands. As stands are hazard rated, it is possible, using a growth prognosis model (Stage 1973) and growth data for lodgepole pine (D.M. Cole and Stage 1972), to predict several years in advance when existing lodgepole pine stands will become susceptible to a beetle outbreak. Management alternatives that best fit given stands can be compared using a stand projection model (Crookston et al., these proc.).

Management Strategies for Timber Production

Several alternatives are available for use in commercial forests to minimize mortality caused by the beetle. In stands where the probability of loss is low, the manager can grow trees to saw log size. Where the probability of loss is high, trees should be grown on a short rotation that will yield sizes to meet product requirements—for example, poles or house logs. Safranyik et al. (1975) state that rotation on good to medium sites at about 80 years and reduction of diameters in the stand to around 20 cm will probably prevent or reduce the incidence of outbreaks.

Because the beetle prefers and selects large-diameter trees, continuous old growth lodgepole forests could be broken up into small blocks of different age and size classes, thereby reducing the area likely to be infested at any one time. This mosaic would not only reduce incidence of mountain pine beetle over large continuous areas, but would permit sustained cutting and provide benefits for non-timber uses such as openings beneficial to wildlife.

Clearcutting, well done, is one of the best means to convert mature and overmature stands to younger age classes because it simulates the natural disturbances that create conditions favorable for lodgepole pine establishment (Berntsen 1975).

Even-aged stands can be developed from shelterwood and seed tree methods, as well as by clearcutting. Stands not infested with mountain pine beetle and without serious dwarf mistletoe infections are usually suitable for shelterwood or seed tree silvicultural prescriptions (Lotan 1975). A shelterwood system may be used to manage dwarf mistletoe if seed trees are carefully selected and if the overwood is promptly removed following seedling establishment. Seed tree, shelterwood and selection systems of cutting may not be applicable to some stands for the following reasons (Alexander 1954, Hatch 1967): 1) dense lodgepole pine stands are seldom wind firm and many trees blow down when these stands are opened up by partial cutting; 2) leave trees have short crowns, and their vigor and growth are poor; 3) partial cutting encourages the spread and intensification of dwarf mistletoe; 4) disposal of logging slash and unmerchantable material is difficult; and 5) reserve trees are damaged by partial cutting.

In spite of the many disadvantages of seed tree, shelterwood and selection cutting systems, they should be considered where visual and environmental impacts of clearcutting are unacceptable. These systems also should be considered in lodgepole pine stands that are open grown or have been opened up by fire, wind, disease or beetle attacks, and where the more shade-tolerant climax species have become established as an understory (Tackle 1955). Overstory lodgepole pine could be removed in these stands to release the understory and reduce chances of infection by mistletoe.

Partial cutting of the larger lodgepole pines has been found to reduce mountain pine beetle infestation potential of susceptible stands (Hamel and McGregor 1976, Hamel these proc., Cole and Cahill 1976). This, of course, is accomplished by removing trees the beetles prefer. Amman (1976) discusses the use of partial cuts for management of mountain pine beetle where timber values are primary, as applicable only where 1) a small proportion of the trees is in lodgepole pine of the larger diameter and phloem thickness categories conducive to beetle build-up, and 2) residual trees would be numerically adequate and vigorous enough to maintain productivity of the stand. Only those tree sizes that have high probability of being killed by the mountain pine beetle should be removed. Guidelines for estimating this have been developed (Cole and Cahill 1976, Amman et al. 1977).

D.M. Cole (1975) showed that, except for stands experiencing stagnation, repeated thinnings only redistributed growth to larger stems but did not increase total basal area growth. Most repeated thinning treatments resulted in lower total volume production. Although repeated thinning of stands experiencing stagnation results in increased total volume production far above the untreated state, results were not as great as for the best early stocking control thinnings. Cole further concludes that the major growth-increasing effect of repeated thinning in stagnating stands probably comes from the first thinning that secures or retrieves growth potential of the stand. Cole (1973) also found that thick phloem is functionally related to high tree vigor; hence, thinnings that produce diameter growth and vigor will also result in trees having thicker phloem for their size. Repeated thinning would seem to increase the probability of beetle infestation, making attainment of the rotation objectives of the thinnings increasingly uncertain.

Management Strategies for Individual Trees of High Value

Trees in picnic areas, campgrounds, around visitor centers and summer and permanent homesites have a much higher value than trees in a forest situation. Protective chemical sprays can be applied to high-value trees before beetle flight and attack. Sprays have prevented attack for 1 year and in some instances through a second year (Gibson 1978). Managers of high-use recreation areas should also consider planting trees of different species where lodgepole pine are likely to be killed. Thus, shade and esthetics will be preserved as larger lodgepole pine are killed.

Management Strategies for Non-timber Values

Forested areas selected for recreation purposes, such as national and state parks, wilderness areas and land not included in the timber-growing base, can be managed by other means than cutting. In these areas, the proportion of other tree species will increase with each beetle infestation until succession is completed and both lodgepole pine and the mountain pine beetle are eliminated from the stand (Amman 1976). While this is happening, for several years following an infestation, managers will be faced with a number of related problems. Large numbers of dead trees may fall across trails, fences, powerlines and recreational facilities unless trees are felled and removed. There is potential hazard from falling trees to hikers, campers and others using the forest. Large numbers of dead trees also will result in increased fuel loads, resulting in hotter, more destructive fires (Amman et al. 1977).

The mountain pine beetle's strong preference for large trees gears heavy fuel build-up to a time when stands are mature or overmature. Evenden and Gibson (1940) calculated that 54,431 to 81,646 kg of beetle-killed boles and crowns per ha are possible on medium sites, which increases fuel build-up and intensifies fire hazard. Brown (1975) states that fire provides diversity by creating a mosaic of age classes, life forms and species. Proper management of lodgepole pine requires that we manage fire completely, with full awareness of its biological effects. D.M. Cole (these proc.) suggests that a conscious program of fire management and prescribed burning should be instituted in some areas.

In considering the welfare of wild and domestic ungulates, management prescriptions should heed points made by Dealy (1975):

1. Large-scale clearcutting reduces wild ungulate use because hiding cover is too far from most feeding sites.
2. Human harassment is an important factor in causing wild ungulates to shun large clearcuts.
3. Foraging by wild ungulates occurs throughout clearcuts that are 16 ha (40 acres) or less in diameter; domestic livestock will forage over openings of any size.
4. Alternate-strip clearcutting 6 km (3 chains) wide with equal width leave strips is favored by deer in Colorado. This width is optimum for natural regeneration of lodgepole pine in central Oregon.
5. Exact cover requirements for wild ungulates are not known; however, Dealy proposed the following technique for enhancing use of large clearcuts: develop adequate-sized cover patches by determining the distance at which an animal or human disappears into a stand and then use this as the radius of each cover patch.
6. If harvest is in strips, care should be taken to prevent development of "shooting lanes" by interrupting the strips at reasonable distances.
7. If clearcut is block-shaped, rectangular leave patches should be arranged to minimize the open areas that can be seen from any one point.

8. Thinning and clearcutting can dramatically increase forage production for ungulates. Production increases have lasted for as long as 20 years in some stands.

9. Where wild and domestic ungulates compete for forage, manipulation of livestock use periods may be necessary to insure forage for winter deer use.

10. Cattle can be used to remove cured grass and enhance wild ungulate use of resulting new grass regrowth during fall, winter and spring periods.

In Montana, the 40 percent cover: 60 percent open area ratio should be considered when laying out cutting blocks in relation to elk habitat. Although this is not a "magical" ratio—it can be varied 10 percent in either direction—it has been found to be a satisfactory ratio for elk habitat in Montana (E. Schneegas, pers. comm.²).

Probably the most critical consideration is the necessity for a well-coordinated management approach to ensure that actions taken provide maximum benefit (or at least minimal adverse impact) on timber, wildlife and range resources. Direct treatments for enhancement of wildlife and range resources on timbered sites are generally impractical. Such treatments "piggybacked" on a carefully coordinated timber management plan can provide many of the same benefits at much less cost.

² E. Schneegas is currently Director, Wildlife and Fisheries, USDA Forest Service, Missoula, MT.

QUESTIONS AND ANSWERS

- Q. Please state in one sentence the relationship you found between dwarf mistletoe susceptibility of trees and successful attack by bark beetles.
- A. In our studies, percent of basal area infected with dwarf mistletoe was negatively correlated to percent basal area killed in the 20 to 29.75 cm (8 to 11.9 inch) dbh and the > 30 cm (12 inch) dbh size classes.
- Q. How would spraying with Sevimol-4 be performed to give adequate protection of a forest stand? Please comment on what coverage of stem is necessary and hazard for personnel.
- A. Spraying Sevimol-4 (Union Carbide, Jacksonville, FL) is not recommended to protect a forest stand, only to protect high-value trees in campgrounds, administrative sites, etc. The infested bole should be sprayed to a 10-cm (4-inch) top, and spray should be applied to run off on the bark. A 2 percent (2 parts Sevimol-4 to 100 parts water) solution is mixed for application. The material is registered by the EPA, considered safe, but applicators and mixers must use protective clothing and goggles.

- Q. Is the negative correlation between percent basal area of lodgepole pine killed by mountain pine beetle and percent basal area infected by dwarf mistletoe an effect of thinner phloem in trees infected by dwarf mistletoe?
- A. We assume so, particularly in older lodgepole pine.

REFERENCES

- Alexander, R.R. 1954. Mortality following partial cutting in virgin lodgepole pine. USDA Forest Serv. Sta. Pap. 16, Rocky Mtn. Forest and Range Exp. Sta., Ft. Collins, CO. 9 pp.
- . 1975. Partial cutting in old-growth lodgepole pine. USDA Forest Serv. Res. Pap. RM-136, Rocky Mtn. Forest and Range Exp. Sta., Ft. Collins, CO. 17 pp.
- Amman, G.D. 1976. Integrated control of the mountain pine beetle in lodgepole pine forests. Pages 439-446 in Proc. XVIth IUFRO World Cong., Div. II. Oslo, Norway.
- Amman, G.D., M.D. McGregor, D.B. Cahill and W.H. Klein. 1977. Guidelines for reducing losses of lodgepole pine to the mountain pine beetle in unmanaged stands in the Rocky Mountains. USDA Forest Serv. Gen. Tech. Rep. INT-36, Intermtn. Forest and Range Exp. Sta., Ogden, UT. 19 pp.
- Berntsen, C.M. 1975. Management conflicts in lodgepole pine. Management of lodgepole pine ecosystems. Pages 503-515 in D.M. Baumgartner (ed.). Management of lodgepole pine ecosystems. Washington State Univ. Coop. Ext. Serv., Pullman.
- Berryman, A.A. 1975. Management of mountain pine beetle in lodgepole pine ecosystems. Pages 527-650 in D.M. Baumgartner (ed.). Management of lodgepole pine ecosystems. Washington State Univ. Coop. Ext. Serv., Pullman.
- Brown, J.K. 1975. Fire cycles and community dynamics in lodgepole pine forests. In D.M. Baumgartner (ed.). Management of lodgepole pine ecosystems, Washington State Univ. Coop. Ext. Serv., Pullman.
- Cole, D.M. 1973. Estimation of phloem thickness in lodgepole pine. USDA Forest Serv. Res. Pap. INT-148. Intermtn. Forest and Range Exp. Sta., Ogden, UT. 10 pp.
- . 1975. Culture of immature lodgepole pine stands for timber objectives. Pages 536-555 in D.M. Baumgartner (ed.). Management of lodgepole pine ecosystems, Washington State Univ. Coop. Ext. Serv., Pullman.
- Cole, D.M., and A.R. Stage. 1972. Estimating future diameters of lodgepole pine trees. USDA Forest Serv. Res. Pap. INT-31. Intermtn. Forest & Range Exp. Sta., Ogden, UT. 20 pp.
- Cole, W.E., and D.B. Cahill. 1976. Cutting strategies can reduce probabilities of mountain pine beetle epidemics in lodgepole pine. J. Forest. 74:294-297.
- Crookston, N.L., R.W. Stark and D.L. Adams. 1977. Outbreaks of mountain pine beetle in northwestern lodgepole pine forests—1945 to 1975. Forest, Wildl. and Range Exp. Sta. Bull. No. 22, Univ. of Idaho, Moscow. 8 pp.
- Dealy, J.E. 1975. Management of lodgepole pine ecosystems for range and wildlife. Pages 556-568 in D.M. Baumgartner (ed.). Management of lodgepole pine ecosystems. Washington State Univ. Coop. Ext. Serv., Pullman.
- Evenden, J.C., and A.L. Gibson. 1940. A destructive infestation in lodgepole pine stands by the mountain pine beetle. J. Forest. 38:271-275.
- Gibson, K.E. 1978. Results of a 1977 pilot project to evaluate the effectiveness of Sevin insecticide in preventing attacks by the mountain pine beetle in lodgepole pine on the Targhee National Forest, Idaho. USDA Forest Serv., Forest Insect and Disease Manage., Ogden, UT. 22 pp.
- Hamel, D.H., and M.D. McGregor. 1976. Evaluation of mountain pine beetle infestations—Lap, Cool, Lang and Caribou Creek Drainages, Yaak Ranger District, Kootenai National Forest, Montana. USDA Forest Serv., State and Priv. Forest. Rep. 76-6. Missoula, MT. 10 pp.
- Hatch, C.R. 1967. Effect of partial cutting in overmature lodgepole pine. USDA Forest Serv., Res. Note INT-66, Intermtn. Forest and Range Exp. Sta., Ogden, UT. 7 pp.
- Hawksworth, F.G. 1977. The 6-class dwarf mistletoe rating system. USDA Forest Serv. Gen. Tech. Rep. RM-48, Rocky Mtn. Forest and Range Exp. Sta., Ft. Collins, CO. 7 pp.
- Hopping, G.R. 1951. Forest entomology in Canada in relation to silviculture in Canada. Part V. The mountain pine beetle. Forest. Chron. 27:21-24.
- Jensen, C.E. 1973. Matchacurve-3: Multiple-component and multi-dimensional mathematical models for natural resource models. USDA Forest Serv. Res. Pap. INT-146, Intermtn. Forest and Range Exp. Sta., Ogden, UT. 42 pp.
- Lotan, J.E. 1975. Regeneration of lodgepole pine forests in the Northern Rocky Mtns. Pages 516-535 in D.M. Baumgartner (ed.). Management of lodgepole pine ecosystems. Washington State Univ. Coop. Ext. Serv., Pullman.
- McGregor, M.D., D.R. Hamel and R.D. Oakes. 1976. Status of mountain pine beetle infestations, Gallatin National Forest—1975. USDA Forest Serv., State and Priv. Forest. Rep. 76-5. Missoula, MT. 11 pp.
- Pfister, R., B.L. Kovalchik and S.F. Arno. 1977. Forest habitat types of Montana. USDA Forest Serv. Gen. Tech. Rep. INT-34, Intermtn. Forest and Range Exp. Sta., Ogden, UT. 174 pp.
- Prebble, M.L. 1951. Forest entomology in relation to silviculture in Canada. Part I. Review of general principles. Forest. Chron. 27:1-9.
- Roe, A.L., and G.D. Amman. 1970. The mountain pine beetle in lodgepole pine forests. USDA Forest Serv. Res. Pap. INT-71. Intermtn. Forest & Range Exp. Sta., Ogden, UT. 23 pp.
- Safranyik, L., D.M. Shrimpton and H.S. Whitney. 1975. An interpretation of the interaction between lodgepole pine, the mountain pine beetle and its associated blue-stain fungi in western Canada. Pages 406-428 in D.M. Baumgartner (ed.). Management of lodgepole pine ecosystems. Washington State Univ. Coop. Ext. Serv., Pullman.
- . 1974. Management of lodgepole pine to reduce losses from the mountain pine beetle. Canadian Dept. of Environ., Forestry Serv., Pac. Forest Res. Centre Tech. Rep. 1. Victoria, B.C. 24 pp.
- Schenk, J.A., R.L. Mahoney, J.A. Moore and L.L. Adams. 1978. A preliminary model for hazard rating lodgepole pine stands for mortality by mountain pine beetle. Univ. of Idaho, Moscow. (in prep.).
- Stage, A.R. 1973. Prognosis model for stand development. USDA Forest Serv. Res. Pap. INT-137. Intermtn. Forest & Range Exp. Sta., Ogden, UT. 32 pp.
- Tackle, D. 1955. A preliminary classification for lodgepole pine in the Intermountain Region. J. Forest. 53:566-569.

Feasibility of Silvicultural Practices for Reducing Losses to the Mountain Pine Beetle in Lodgepole Pine Forests

Dennis M. Cole

ABSTRACT

A variety of standard silvicultural practices, and variations of them, have been proposed for reducing the losses caused by the mountain pine beetle (*Dendroctonus ponderosae* Hopkins) in lodgepole pine (*Pinus contorta* Douglas var. *latifolia* Engelman) forests. This paper outlines silvicultural practices deemed applicable for a variety of lodgepole pine stand descriptions and management situations; it also discusses factors that limit application and some consequences of misapplication. The necessity that silvicultural practices be compatible with the requirements of forest growth regulation and with management for other resource values is stressed, and an example is given of the role of silvicultural practices in an integrated long-range program for reducing losses.

INTRODUCTION

As one reviews the mountain pine beetle (*Dendroctonus ponderosae* Hopkins) literature, one is struck by the consistent conclusion that **silvicultural** practices seem to offer the most promise for reducing damage (Craighead 1925, Hopping and Beall 1948, Hopping 1951, Roe and Amman 1970, Safranyik et al. 1974, Amman 1976). In the latter three of the preceding references, this generalized conclusion has been extended to fairly specific recommendations for controlling losses through applied silviculture.

Recent references demonstrate the growing awareness that control tactics aimed at specific (usually narrow) aspects of either beetle or host vulnerability are not likely to be effective unless they are viewed as component tools in an integrated approach to controlling losses. A similar awareness has evolved among those working on the southern pine beetle (*Dendroctonus frontalis* Zimmerman) problem (Coster 1977).

This paper discusses some of the more frequently proposed silvicultural practices for reducing losses from the mountain pine beetle in lodgepole pine (*Pinus contorta* Douglas var. *latifolia* Engelman) forests and the compatibility of these practices with some of the major requirements of lodgepole pine silvicultural management systems. Such compatibility is a prerequisite for any control tactic or silvicultural practice to be a truly useful component of an integrated strategy for permanently reducing losses.

Another prerequisite for proper silvicultural prescriptions is a risk classification system that accurately identifies both absolute and relative susceptibility of individual lodgepole pine stands. The system needs to be applicable over a wide geographic area and for a wide range of stand development, stand condition and species composition situations. When keyed to basic land units—for example, through ecological habitat types—the relative risk potential of a specific land unit could be determined with such a system, regardless of the stand now occupying the site. This capability would provide an extremely valuable planning and management tool.

The subject of stand risk classification is a specific topic assigned elsewhere in this symposium, and in addition has been discussed in several other papers in these proceedings. It is a controversial and crucial issue, because forest entomologists have split generally into two groups over factors controlling the susceptibility of lodgepole pine trees and stands to successful attack by the mountain pine beetle. This presents the silviculturist with a serious dilemma in determining the actual consequences (hence the applicability and feasibility) of specific practices for controlling losses.

One group contends that phloem thickness and associated parameters of age and diameter, as well as elevation and latitude, are the controlling factors in the susceptibility of

unmanaged stands, and infers these are likely to be the same for managed stands.

The second group agrees that losses are related to diameter distributions and that phloem thickness is an important regulator of beetle productivity in unmanaged stands, but contends that the most important factor in susceptibility is reduction of tree vigor and associated resistance. Thus, they contend, larger trees are successfully attacked because they are low in vigor at the time of attack, not just because they are generally larger in diameter and have thick phloem.

The difference between the viewpoints is quite important because of the differences in constraints on management that are implied. For example, the large-diameter/thick phloem viewpoint implies such management recommendations as:

1. Liquidate present growing stock of large-diameter trees as rapidly as possible.
2. In the future, harvest stands or portions of them before they attain "susceptible" large-tree diameters.
3. Reduce probability of attack by removing thick-phloemed trees from the stand by partial cutting.
4. Convert to other species where possible.

On the other hand, the tree vigor/resistance viewpoint suggests that tree size and value goals are not constrained by threat of mountain pine beetle attack if high vigor is maintained throughout the life of the stand because:

1. Early stocking control can raise the vigor level of trees and stands enough above the historical condition of unmanaged stands that they are resistant to attack for much longer periods.
2. Intensive management practices for increasing rate of growth (such as intermittent thinnings, fertilization and genetic improvement) can also raise and maintain vigor levels enough that present size and age limits are not as restrictive.

In my opinion, both of the groups have included a certain amount of circumstantial evidence in their conclusions, and neither has proved its case, especially as to whether managed stands will be more or less susceptible to attack than unmanaged stands, and whether they will be susceptible sooner or later than unmanaged stands.

Most of the silvicultural practices covered in the following sections appear workable with either entomological position; however, we must carefully evaluate stand and insect conditions and the requirements of silvicultural systems, forest regulation and other resources before specific silvicultural practices are prescribed for reducing losses from the mountain pine beetle. To do this properly, the factors controlling susceptibility of

trees and stands must be clarified. Hopefully, this symposium will do this or at least expose the knowledge gaps that prevent clarification.

REDUCING LOSSES IN COMMERCIAL FORESTS

The species composition, the form and the condition of stands greatly influence the compatibility of objectives for controlling losses from the mountain pine beetle with other silvicultural and management objectives. Composition and condition of stands are reasonably obvious. The form (or age distribution) of lodgepole pine stands is less obvious; in fact, lodgepole pine stands are often taken for granted as being even-aged. This stand characteristic must not be guessed at, for errors in identifying stand form can lead to improper silvicultural prescriptions. A good classification for describing lodgepole pine stands was developed by Tackle (1955) (Fig. 1). It incorporates proper recognition of form and composition into descriptive classes based on the number of recognizable crown stories in the stand. Although not all of the stand classes described by Tackle are discussed as they might relate to mountain pine beetle effects, the stand situations described in this paper are identifiable in Tackle's classification.

Pure, Even-Aged Lodgepole Pine Stands

Where composition is pure lodgepole pine and form is even-aged, valid practices are generally limited to: 1) stocking control in young stands, 2) organized clearcutting in blocks to create age, size and species mosaics from mature stands, 3) salvage cutting to mitigate losses in stands under attack, and 4) sanitation cutting in some situations.

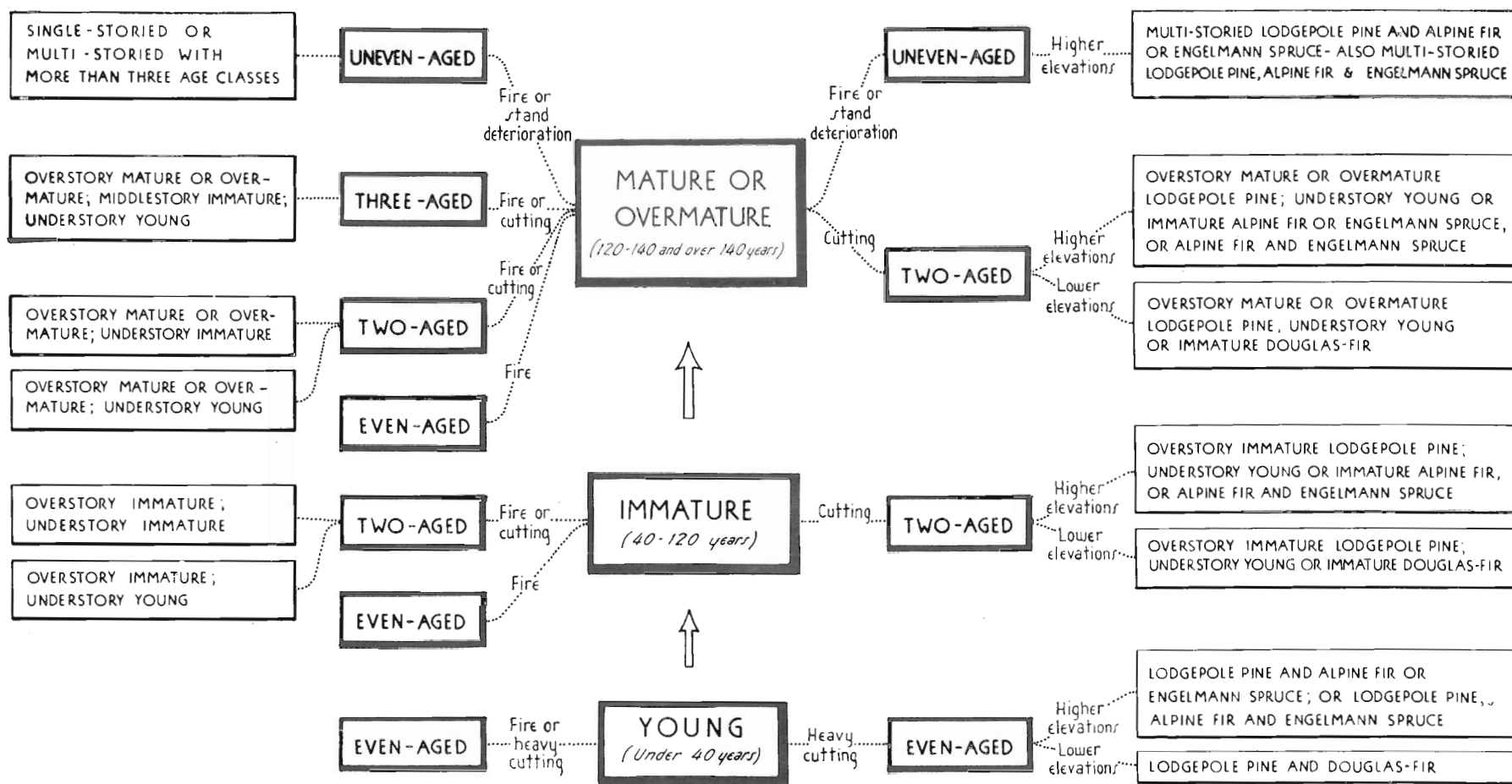
Stocking Control

This is an extremely important preventive practice in pure, even-aged lodgepole pine. It allows the sustenance of good stand vigor and the direction of stand growth toward moderate tree size and rotation objectives.

Specifically, stocking control by age 25 (preferably by age 15) to spacing of about 3.05 by 3.05 m (10 by 10 ft) results in culmination of mean annual cubic volume increment on medium-to-good sites at about age 80—with average stand diameters of about 25 cm (10 inches) (Cole 1973). Projected diameter distributions for this kind of stand indicate that the largest diameter class (36 cm, 14 inches) represents less than 1 percent of the trees, while all trees over 30 cm (12 inches) dbh comprise only about 8 to 10 percent of the stand (Lee 1967). For a large proportion of the lodgepole pine type, these rotation and size limits do not appear to be very susceptible to mountain pine beetle epidemics (Safranyik et al. 1974, Cole and Cahill 1976). Exceptions can occur on good sites at low elevations (Amman et al. 1977). Another exception is noted in eastern Oregon, where an extensive epidemic is occurring in stands having trees generally thought to be too small for epidemics to develop. The age of these stands, however, is over 80 years.

(PRELIMINARY)

M I X E D



Prepared by D. Tackle.

Fig. 1. Lodgepole pine stand classification (after Tackle 1955).

Still, it is possible that the improved vigor of trees in managed stands will work against the welfare of *Ips* sp., *Pityogenes* sp., and other bark beetles that seem to assist endemic mountain pine beetle populations in building to epidemic levels in overmature stands. Thus, even though suitable sized trees may be present, overall high vigor in the managed stand might postpone the conditions that allow the beetle to shift its behavioral mode from endemic to mass attack. The oft-observed situation of mass attacks beginning on the apparently highest vigor trees in the stand—those found on meadow edges and in bottoms—does not necessarily refute this possibility, since the overall lower vigor of the general unmanaged stand might have provided the opportunities for the population to build to the point where it can successfully attack the kinds of trees that are capable of producing large broods. If overall high stand vigor of managed forests is found to, in fact, keep the mountain pine beetle in an endemic state, management targets of tree size and rotation lengths can be increased. Until this possibility is clearly demonstrated, however, it would seem safest to aim for the stocking and product goals mentioned above, which at present are limited only by the economics of harvesting and conversion. Economic limitations related to product size are likely to be far less important than they now are by the time stands treated to these stocking recommendations reach rotation age.

Block Clearcutting

Organized clearcutting in small- to moderate-sized blocks creates age and hence size mosaics from extensive, pure, even-aged stands and is a highly recommended practice (Roe and Amman 1970, Amman 1976). The emphasis here needs to be on the word "organized." Organization begins with good surveys and maps of stand growth and volume, site quality and other risk-related data such as phloem thickness, elevation, stand structure and form, composition and ecological habitat type. Then, long-term harvesting patterns can be planned to create less favorable conditions for the beetle and more favorable conditions for reducing losses where smaller infestations do occur. Such a plan, of course, will need to meet the requirements of forest regulation.

Planning alone is not enough—the plan has to be applied, and here the existence of a stable forest products industry to provide continuity of harvests is quite important. Largely because of historically poor markets for lodgepole pine relative to other western species, the planning and execution of organized block cutting has had little chance to reduce losses to the mountain pine beetle. This is unfortunate, because the severe losses suffered in our commercial lodgepole pine forests in the past 20 years could have been significantly reduced by properly planned and executed block clearcutting, had it been started 20 to 35 years ago. It appears, then, that at least 15 years lead time is necessary in planning and executing block cutting for controlling losses.

Still, organizing block clearcutting as a preventive measure presumes that differences in stand susceptibility can

be related to differences in site and stand characteristics. Forest entomologists and silviculturists generally agree that such relationships exist, but as mentioned earlier, there is considerable disagreement on how relationships are best measured and interpreted.

Whatever susceptibility explanation and risk classification are finally agreed upon, objectives of multiple use need to be considered by managers of federal lands in the process of developing schedules for block cutting as a loss-control practice. Models for predicting stand development for a variety of management assumptions (Stage 1973, Myers et al. 1971) are quite helpful for such purposes. Upon starting a schedule of block cutting on sites where probability of loss is high, further safeguards against future losses can be achieved by directing regeneration of sites to patterns of alternating species among blocks or to an overall pattern of mixed species within blocks.

Salvage and Sanitation Cutting

In stands under attack, where it is too late for preventive practices, salvage cutting can reduce wood losses. Salvage cutting should be carefully planned and administered as a conscious silvicultural practice because of the need to protect other resource values. How much salvage cutting can reduce losses is mostly a function of harvesting economics and the length of time between tree killing and salvage operations, so that wood deterioration is minimized. Due to limited salvage volume per unit area, costly access, distant processing facilities and environmental constraints, only a very small percentage of mortality from the mountain pine beetle in commercial forests is now economically recoverable. Improvements in this situation must probably await increased demand for wood and changes in forest use policy. Should it seem worthwhile to slow the attack on susceptible stands, salvage can be anticipated by **sanitation cutting** to remove highly susceptible trees before they are attacked. But sanitation cutting is expensive and must be carefully coordinated to prevent spread of beetles; also, benefits can be expected to be only temporary.

In short, **sanitation** and **salvage** cutting must be justified either directly by timber economics or indirectly through protection of other resources, in order for them to qualify as actual loss-reduction practices.

Pure, Uneven-Aged Lodgepole Pine Stands and Mixed Species Stands

An appreciable percentage of pure lodgepole pine stands contain from two to several age classes, mainly because of the mountain pine beetle/fire history, and severe site conditions that excluded other species and required many years to reach full stand stocking. Most of these stands occur near and east of the Continental Divide (S. Arno, pers. comm.¹).

¹ S. Arno is located at USDA Forestry Sciences Laboratory, Missoula, MT.

Many uneven-aged lodgepole pine stands are mixed species stands. A very common situation is a mature or over-mature lodgepole pine overstory, with a mixture of smaller shade-tolerant species and some younger lodgepole pine in the understory, the size and mixture of the understory depending largely on the pattern of openings created in the overstory by insects, diseases and climatic factors.

Another common mixed stand situation involves one or more other species in the overstory alongside lodgepole pine, with an understory of one or more climax species. This situation is quite common west of the Continental Divide in the ranges of other seral or relatively intolerant species such as western larch (*Larix occidentalis* Nuttall), white pine (*Pinus monticola* Douglas) and Rocky Mountain Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Beissner) Franco). Near and east of the Continental Divide mixed overstory stands are usually well advanced toward succession to subalpine fir (*Abies lasiocarpa* (Hooker) Nuttall), Engelmann spruce (*Picea engelmannii* Parry) or Douglas-fir, with the lodgepole pine in a decadent condition.

Stocking Control, Clearcutting and Salvage Cutting

For the uneven-aged stands just discussed and for similarly described stands (Tackle 1955), the loss-control practices mentioned earlier for pure, even-aged lodgepole pine stands are also feasible. For example, mature uneven-aged or mixed stands with a significant component of large lodgepole pines in the overstory can be treated by **block clearcutting** as a preventive, and if they are already under attack, losses can perhaps be reduced by **salvage cutting** practices. If immature, both uneven-aged and mixed species stands are candidates for **stocking control**, with **species discrimination** possible in mixed species stands.

Discrimination against lodgepole pine is possible in older mixed species stands by partially cutting only the larger lodgepole pine. This is a valid practice in regulated forests only if the residual stand is sufficient in vigor and stocking to maintain stand growth near the yield capability level of the site. Even then, value of volume removed must exceed costs of removal for the practice to be feasible, unless indirect benefits of beetle control warrant subsidization.

Partial Cutting Practices

Partial cutting of the larger lodgepole pines reduces the beetle infestation potential of susceptible stands (Hamel and McGregor 1976, Cole and Cahill 1976). It accomplishes this by removing the trees the beetles want. Amman (1976) concluded that partial cuts, for control of mountain pine beetle where timber values are primary, applied only where: 1) a small portion of the trees is in lodgepole pine having the larger diameter and phloem thickness categories conducive to beetle build-up, and 2) residual trees would be numerically adequate and vigorous enough to maintain productivity of the stand.

Stands meeting these conditions, however, will involve **only a small percentage of the stands susceptible to beetle infestation**. Usually, only stands having a healthy component of other species can provide a residual component capable of maintaining volume productivity near required levels. Discriminating against the susceptible lodgepole pines in such stands can be silviculturally acceptable, but the low volume involved is often not economical to remove. Conversely, removal of sufficient additional volume to be economical will usually overcut the stand. Further, the volume in susceptible trees is usually not enough to pay for the road system necessary to utilize the material unless roads are already in place. Thus, maintaining adequate growing stock for forest growth regulation must be considered important enough to subsidize development costs if losses are to be reduced in inaccessible stands where only a small proportion of the volume is susceptible at any one infestation cycle.

There are, nevertheless, a couple of other risk situations where partial cutting **might** be useful. For example, partial cuts might be justified in mixed species stands just coming under attack, if there were extensive lodgepole pine stands nearby that would benefit if expected attacks on them could be delayed until they could be silviculturally treated. This would be accomplished if the build-up of the beetle population in the mixed species stand were postponed or effectively slowed by removing the larger lodgepole pines. This use of partial cutting, which is actually a form of sanitation cutting, should never be carried out without the involvement of a qualified forest entomologist because it is possible for partial cutting to accelerate the attack on nearby stands. This can occur if the susceptibility of the stands or the status of the beetle population is misinterpreted or ignored.

A case can also be made for reducing losses by harvesting the susceptible portion of stands in partial cuts before the beetle attacks, hence recovering significantly greater value than is possible from salvage of dead material.

In both of these justifications for partial cutting, two additional factors need to be considered to ensure that the partial cutting does not reduce long-term timber productivity **more** than would the mountain pine beetle:

1. Only those trees that have high probability of being killed by the beetle should be removed. Preliminary guidelines for estimating this have been developed (Cole and Cahill 1976, Amman et al. 1977), but these guidelines should be refined to individual tree characteristics within susceptible size classes.
2. The faster-growing genotypes in unmanaged lodgepole pine stands appear to be selected for attack (Roe and Amman 1970); consequently, these genotypes will also be the ones selected for partial cutting. In the natural state, we can expect at least some of the fast-growing genotypes to be maintained despite the beetle because they are represented in stored seed of serotinous cones where for

decades they are available for natural regeneration. Therefore, in partially cut lodgepole pine stands, seed should be collected from the most vigorous large trees and saved for regeneration on the site at an appropriate time.

Susceptible multi-storied stands that are predominately lodgepole pine cannot be expected to maintain adequate productivity when the overstory is partially cut or attacked by the beetle, unless the residual stand is 50 or more years younger than the overstory—and then only if competitive effects of the overstory have not been too severe. Even with a young, non-stagnated understory, the complete removal of the overstory would usually be more appropriate for future growth of the understory than partial cutting. Whether complete overstory removal or partial cutting is used, future productivity is likely to be further impaired by logging damage, dwarf mistletoe (*Arceuthobium americanum* Nuttall ex Engelman) infection and windthrow (Hatch 1967, Alexander 1975). The yield-reducing effect of dwarf mistletoe infection, in itself a serious management problem, becomes even more serious in multi-storied stands where lodgepole pine understories are infected. It is extremely doubtful if yield capability of the site can be attained if such understories are featured in management through partially cutting the overstory, unless costly mistletoe control programs are carried out. Thus, the dwarf mistletoe factor needs very careful consideration when partial cuts are contemplated for beetle control purposes.

For all of the above reasons managers should be extremely cautious in the use of partial cutting, for any purpose, in lodgepole pine stands where sustained timber productivity is important. Where partial cutting is used for controlling beetle-caused losses, serious and long-lasting mistakes can be made if partial cutting is extensively applied to stands that are not in fact under serious or imminent threat, and particularly if more volume is removed than the beetle would take.

REDUCING LOSSES IN NON-COMMERCIAL FORESTS

In national parks, wilderness areas and the like, high value is placed on maintaining a natural ecosystem. Therefore, one viable management alternative for coping with mountain pine beetle infestations on these lands is to do nothing (Amman et al. 1977).

Timber, as a commodity, is not a recognized value on such recreational lands. Therefore, loss of wood products and its related economics are not relevant. Losses are generally determined in terms of impairment of the visual resource and increased costs to maintain convenience and safety for the users of these areas. Most of the management activities required to correct or ameliorate these situations are better described as groundskeeping practices than as silvicultural practices. One exception is fire management.

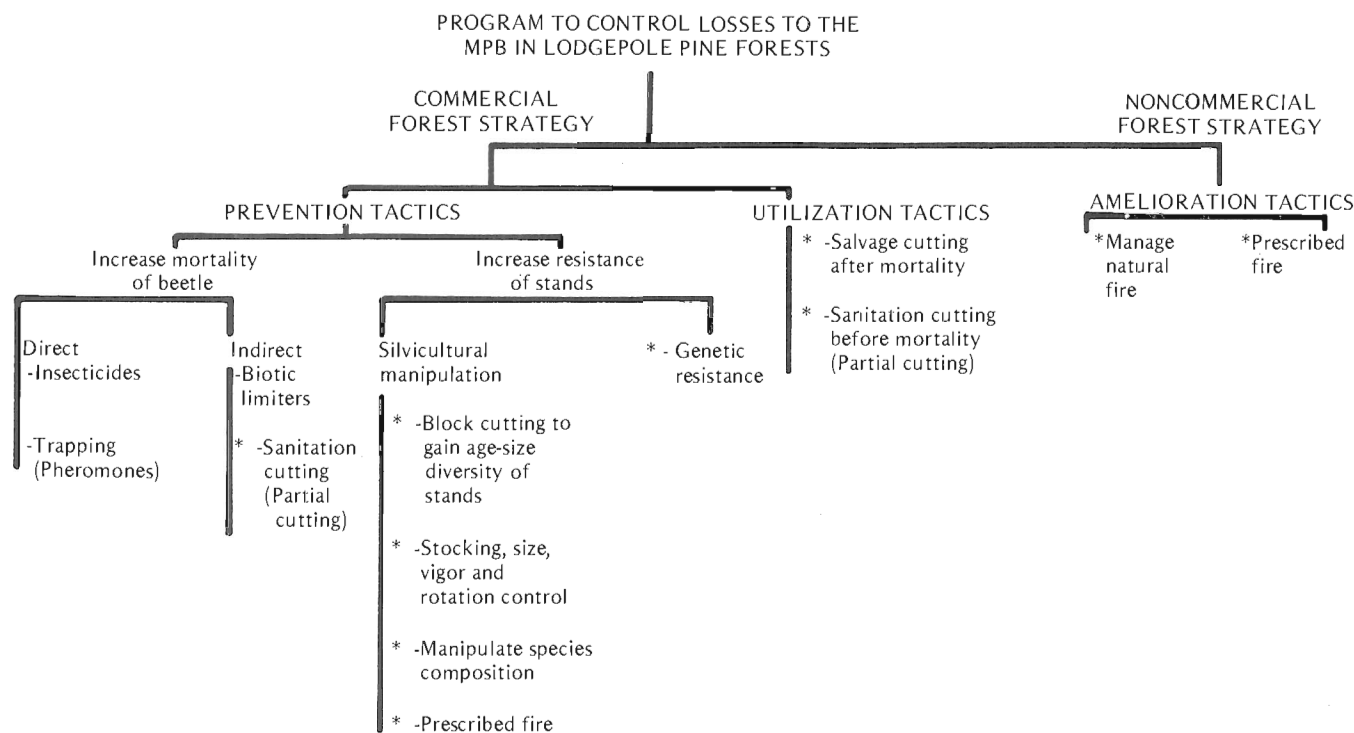
Fire has been an integral part of the ecology of lodgepole pine forests and, along with the mountain pine beetle, has been largely responsible for the maintenance of lodgepole pine as a widespread forest type. When extent and intensity of fire are moderate, lodgepole pine ecosystems can be renewed with less severe disturbance of the life forms and values involved with the ecosystems than is the case with large infernos. In many park and wilderness areas natural fires have been suppressed so that dead wood resulting from beetle epidemics accumulates until large and hot fires occur. Such fires are normally more destructive than ones that would have otherwise occurred if fires had not been suppressed, and they tend to perpetuate future extremes in the mountain pine beetle/lodgepole pine/fire interaction.

To moderate this cycle, a deliberate program of fire management and prescribed burning can be instituted. It should involve reliable surveys and maps of stand age and size, and fuel structure. With such data, plans can be developed to allow some fires, once started, to burn under supervision to create a mosaic of regenerated stands within the extensive areas of large timber that have developed. However, prescribed fire can create these ecosystem mosaics more effectively. Prescribed burning offers real silvicultural advantages over trying to manage naturally occurring fires in such high hazard situations as beetle-infested areas. It allows taking advantage of optimum conditions for managing size of burns and achieving fuel reduction and regeneration objectives.

INCORPORATING PRACTICES INTO MANAGEMENT

As stated before, feasible silvicultural practices for reducing losses to the mountain pine beetle should be subject to incorporation into integrated programs for controlling such losses. One way of viewing the role of such practices in an integrated program is to arrange them into a schematic showing their potential application relative to tactics, strategies and forest value situations as shown in Fig. 2.

Notice that **prescribed fire** is included as a silvicultural practice for controlling losses in commercial forests, yet this practice was discussed only for non-commercial forests as a tactic to ameliorate beetle effects. It definitely can be a valid practice for commercial forests and should be considered an important long-range management alternative in integrated programs for controlling losses. In commercial forests, it is, however, somewhat of a last resort alternative. It is obvious that all natural stands will never be put under management by stand tending practices—for example, a large proportion of stagnated stands that are past the point of responding adequately to stand culture will eventually become susceptible to the beetle. In these kinds of stands, **prescribed fire** can be a valuable silvicultural practice for bringing the stands under management by “starting over.” This strategy must, of course, be carried out within the framework of forest regulation planning and must be executed with due regard for maintenance, protection and enhancement of other resource values.



* Indicates silvicultural practice is involved.

Fig. 2. Role of silvicultural practices in an integrated program for controlling losses to the mountain pine beetle in lodgepole pine forests.

Figure 2 includes other tactics and practices not discussed in this paper; however, their relationships to silvicultural practices are obvious in the schematic. Details on other practices are covered elsewhere in this symposium.

Finally, all persons who must cope with the mountain pine beetle should remember that it is the forest which must be the **primary** focus of lodgepole pine management, and not the beetle. If we are to stop the cycle of just cleaning up after the beetle, we must emphasize reduction of losses through managing the forest with sound, renewable-resource silviculture, which includes attention to the beetle as just one of the factors. Without this broad awareness, silvicultural recommendations may evolve which are too narrow in scope—perhaps solving some immediate problem, but creating greater long-term forest management problems.

QUESTIONS AND ANSWERS

- Q. Would there ever be a justification for, or in what cases could you recommend, a thinning from below—from the standpoint of either the beetle or silvics?
- A. One of the major advantages of low thinnings is that they allow recovery of most volume otherwise lost to suppression mortality. When we consider the cost of

each thinning, however, we often find the costs exceed the value produced—this is particularly so for lodgepole pine. Purely from the standpoint of growth and yield, the major case I can see for low thinning in pure even-aged lodgepole pine stands is when management is directed toward a board-foot objective. In this case low thinnings can provide that all of the stand will considerably exceed the minimum merchantable size at rotation age. These sizes and rotations, however, are of real concern from the standpoint of the mountain pine beetle threat—**unless** the increased vigor from thinning is found to make the stand non-susceptible to mountain pine beetle infestation throughout the extended rotation. Though this possibility has been raised in this symposium, it is yet to be confirmed, and it will necessarily take many years for the question to be answered conclusively. In the meantime (as I mentioned earlier) the thinning recommendation I feel safest with, in relation to the mountain pine beetle, is a stocking control thinning at an early age, aimed at culminating total cubic volume at 80 to 90 years, with modest tree sizes.

- Q. Does your suggested 3 x 3 m (10 x 10 ft) thinning at 15 to 25 years, to develop 25 cm (10 inch) dbh trees at 80 years, include a commercial thinning? At 60 years perhaps? Either way it's encouraging.

- A. No, the suggested thinning does not include a commercial thinning. It could, but this would only be justified under a board-foot objective, which, as I mentioned in the previous question, is suspect for susceptibility to the mountain pine beetle. Although I've emphasized the 3 x 3 m (10 x 10 ft) thinning at an early age as the one that provides optimum cubic volume culmination at an early enough age to be low-risk from the beetle standpoint, I would not quibble much with any spacings from 3 x 3 m to 3.7 x 3.7 m (10 x 10 ft to 12 x 12 ft).
- Q. Does the beetle have to go through an epidemic stage in order to survive as a species? If so, silviculture as a long-term solution will not work because it puts selection pressure on the beetle.
- A. This is an interesting question, but one I am not qualified to answer. Hopefully, the coming entomological emphasis on investigating the endemic and epidemic phases of the mountain pine beetle will provide an answer to this. As far as your conclusion that silviculture is not a long-term solution if the beetle has to go through an epidemic stage to survive as a species—I do have an opinion. If my understanding of the theory of evolution is correct, selection pressure can be so great as to cause a species to either change or become extinct. Although I'm not suggesting that silviculture is going to eliminate the mountain pine beetle, I think it's plausible that silviculture, if intensive and widespread in application, can influence the beetle to exist in its endemic state.

REFERENCES

- Alexander, R.A. 1975. Partial cutting in old-growth lodgepole pine. USDA Forest Serv. Res. Pap. RM-136. Rocky Mtn. Forest and Range Exp. Sta., Ft. Collins, CO. 17 pp.
- Amman, G.D. 1976. Integrated control of the mountain pine beetle in lodgepole pine forests. Pages 439-447 in Proc. XVIth IUFRO World Congr., Div. II, June 1976, Norway.
- Amman, G.D., M.D. McGregor, D.B. Cahill and W.H. Klein. 1977. Guidelines for reducing losses of lodgepole pine to the mountain pine beetle in unmanaged stands in the Rocky Mountains. USDA Forest Serv. Gen. Tech. Rep. INT-36. Intermtn. Forest and Range Exp. Sta., Ogden, UT. 19 pp.
- Cole, D.M. 1973. Culture of immature lodgepole pine stands for timber objectives. Pages 536-555 in D.M. Baumgartner (ed.). Management of lodgepole pine ecosystems. Washington State Univ. Coop. Ext. Serv., Pullman.
- Cole, W.E., and D.B. Cahill. 1976. Cutting strategies can reduce probabilities of mountain pine beetle epidemics in lodgepole pine. J. Forest. 74:294-297.
- Coster, J.E. 1977. Towards integrated protection from the southern pine beetle. J. Forest. 75:481-484.
- Craighead, F.C. 1925. The *Dendroctonus* problem. J. Forest. 23:340-354.
- Hamel, D.R., and M.D. McGregor. 1976. Harvesting strategies for management of mountain pine beetle infestations in lodgepole pine, Montana. USDA Forest Serv. Northern Region, Forest Insect and Disease Prog. Rep. Missoula, MT. 11 pp.
- Hatch, C.R. 1967. Effect of partial cutting in overmature lodgepole pine. USDA Forest Serv. Res. Note INT-66, Intermtn. Forest and Range Exp. Sta., Ogden, UT. 7 pp.
- Hopping, G.R. 1951. Forest entomology in relation to silviculture. Part V. The mountain pine beetle. Forest. Chron. 27:21-24.
- 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). Forest. Chron. 24:141-145.
- Lee, Y. 1967. Stand models for lodgepole pine and limits to their application. Ph.D. diss., Univ. of British Columbia, Vancouver. 332 pp.
- Myers, C.A., F.G. Hawksworth and L. Stewart. 1971. Simulating yields of managed dwarf mistletoe-infested lodgepole pine stands. USDA Forest Serv. Res. Pap. RM-72, Rocky Mtn. Forest and Range Exp. Sta., Ft. Collins, CO. 15 pp.
- Roc, A., and G.D. Amman. 1970. The role of the mountain pine beetle in lodgepole pine forests. USDA Forest Serv. Res. Pap. INT-71, Intermtn. Forest and Range Exp. Sta., Ogden, UT. 23 pp.
- Safranyik, L., D.M. Shrimpton and H.S. Whitney. 1974. Management of lodgepole pine to reduce losses from the mountain pine beetle. Can. Dept. Environ. Forest Serv. Forest Tech. Rep. 1. Victoria, B.C. 24 pp.
- Stage, A.R. 1973. Prognosis model for stand development. USDA Forest Serv. Res. Pap. INT-137, Intermtn. Forest and Range Exp. Sta., Ogden, UT. 32 pp.
- Tackle, D. 1955. A preliminary stand classification for lodgepole pine in the Intermountain Region. J. Forest. 53:566-569.

Strategies and Tactics for Reducing Losses in Lodgepole Pine to the Mountain Pine Beetle by Chemical and Mechanical Means

William H. Klein

ABSTRACT

The mountain pine beetle (*Dendroctonus ponderosae* Hopkins), easily the most destructive bark beetle in the West, has ravaged the lodgepole pine (*Pinus contorta* Douglas var. *latifolia* Engelm.) forests of the northern Rockies since the turn of the century. The progress of mountain pine beetle epidemics in lodgepole pine is traced from a beginning in northern Montana in 1909 to full-scale outbreaks that progressed southward through the lodgepole pine forests of southern Idaho, western Wyoming and northern Utah. During the past two decades, the infestation pattern has reversed itself, with outbreaks recurring in parts of northern Utah, southern Idaho, western Wyoming, and back into Montana. Various control strategies employing a variety of methods, practically all of which entailed treatment of individual trees, were attempted but at best only a few were touted as successful. The large-scale and costly control programs that were aimed at portions of large outbreaks and undertaken during the late 1950s and early 1960s in the Intermountain area failed to stop the infestations. During the 1970s, emphasis changed from individual tree control to individual tree protection. Methods are available for protecting high-value trees from beetle attacks, but they may be relatively costly and are impractical on a forest-wide basis. Individual tree treatment continues to be a management option, but a poor one. Long-lasting control can best be achieved by application of preventive techniques. In some instances, a do-nothing policy could be a viable alternative.

INTRODUCTION

For more than half a century entomologists and foresters, when describing the mountain pine beetle (*Dendroctonus ponderosae* Hopkins) and its effect on lodgepole pine (*Pinus contorta* Douglas var. *latifolia* Engelm.), have adopted a rather extensive vocabulary that is egregious in the extreme.

It has been described in such terms as aggressive, deadly, threatening, debilitating, menacing, devastating and catastrophic, to name some. Popularized versions of mountain pine beetle outbreaks read like an introduction to a pulp magazine horror story. In fact, one highly respected entomologist, in describing the outbreak on the Beaverhead National Forest in Montana during the late 1920s, compared the infestation and the attempts to control it to a famous military battle (Evenden 1928). Certainly these descriptions and comparisons were justified, considering the magnitude and intensity of these outbreaks and the sincere and diligent, but futile, attempts at stopping them.

Now I would like to add a few disquieting and somewhat subjective personal assumptions of my own. During this century, the mountain pine beetle has probably killed more timber in the western United States and Canada than all other forest insects combined. Going one step further, though admittedly lacking specific data, it is probably safe to say that more money has been spent on mountain pine beetle control than on control of all other western bark beetles combined and, in the overall race for forest insect control moneys, the mountain pine beetle probably was a close third to the gypsy moth and western spruce budworm. For example, during the period 1958 to 1970, upwards of 16 million dollars were spent for control of the insect in lodgepole pine in the Intermountain Region. Unfortunately, these efforts, for the most part, were ineffective (Klein and McGregor 1966, Amman and Baker 1972).

HISTORY OF CONTROL

In an attempt to comprehend the mountain pine beetle/lodgepole pine problem, the numerous and legendary attempts at control, and the assorted control methods and techniques, it would be appropriate to discuss recent control history. By

recent history, I mean the status of the most significant outbreaks in this century, their movements and trends, the damage caused and the various control attempts and control philosophies.

The mountain pine beetle has caused serious tree losses throughout the range of suitable host type, but the most widespread, enduring and damaging outbreaks occurred throughout the lodgepole stands of the Rocky Mountain region early in this century. One of the earliest recorded observations of mountain pine beetle activity was made by H.B. Ayers in 1898, in western white pine (*P. monticola* Douglas) in the North Fork of the Flathead River, Montana (Evenden 1944). The first record of the mountain pine beetle in lodgepole pine in the northern Rockies may have been in 1909, when entomologist Brunner reported the loss of some 500 million board feet of timber (assumed to be lodgepole pine) destroyed in Flathead County, Montana, during the previous 10-year period. Additional lodgepole pine losses were reported on the Flathead National Forest in 1910 and 1911. During 1912, two widely separated control projects were undertaken in Montana, one involving 28,000 trees near Swan Lake on the Flathead National Forest, the other entailing 2326 trees in the Big Hole Basin, Beaverhead National Forest. In 1913, an additional 23,393 infested trees were treated in the Big Hole Basin. The Swan Lake effort was declared successful, for no follow-up treatment was required. However, Evenden (1944) postulated that the apparent "success" was due to the fact that most of the larger trees had already been killed and the infestation was subsiding. During the next several years, widely scattered tree killing continued throughout the lodgepole pine stands of western Montana and southern Canada, with damaging outbreaks occurring in localized areas. Small control projects were undertaken in 1923 in the Big Belt Mountains and in 1924 on the Deerlodge (then Missoula) National Forest in an attempt to halt the apparent southward advance of the infestations. The strategy was to halt the infestation movement by locating and treating all infested trees along the infestation "front," thus creating a beetle-free barrier which was termed "No Bugs Land" (Evenden 1944). This tactic was promptly discontinued with the discovery of a new infestation to the south near the head of the Bitterroot River and in the Big Hole Basin (Fig. 1).

Control was undertaken in 1925 and 1926 in the Bitterroot National Forest in a desperate attempt to retard the southern spread of the outbreak over the Continental Divide into the Big Hole Basin on the Beaverhead National Forest. It was also hoped that the large timber-free area of the Basin would provide an effective barrier to the flying beetles. By this time, however, the infestation was firmly established in the Big Hole Basin. Although control continued through 1928, it too was discontinued because of the apparent failure to significantly reduce the number of newly attacked trees and the discovery of additional outbreaks to the south on the Salmon and Targhee National Forests, Idaho.

Beginning in 1928, control efforts were extended to the Deerlodge National Forest and southward to the Targhee National Forest in Idaho. In 1929, the infestations increased in

size and intensity, and additional projects were initiated on the Caribou and Cache National Forests, Idaho, and the Teton and Bridger (now Bridger-Teton) National Forests, Wyoming. Suppression efforts continued in these forests for the next 2 years. During 1931, new projects were started in Yellowstone National Park, Wyoming; the Beaverhead National Forest, Montana; and the Wasatch National Forest, Utah. Although some areas were reported to show a reduction in attack rates—notably parts of the Targhee, Teton and Cache National Forests—the overall infestation continued to expand. The futility of these efforts was soon realized, and by 1932 most of the major control projects were terminated. Reports of significant tree killing in Utah, on the Ashley and Wasatch National Forests, only added to the frustration and discouragement.

This story has yet to end. During the next 20 years localized, widely scattered outbreaks erupted throughout Rocky Mountain lodgepole pine ecosystems, followed by sporadic, relatively small-scale control projects. In the Targhee National Forest, for example, control was attempted during the late 1940s, and in 1950 more than 40,000 trees were treated (J. Kinchloe, pers. comm.¹). For the most part, however, mountain pine beetle populations throughout the Rocky Mountains during the late 1940s and early 1950s were at a relatively low level.

This respite was short-lived, for in 1953 a small infestation was discovered on the north slope of the Uinta Mountains, Utah, and by 1958 it had developed into a full-scale outbreak. Control was again undertaken in 1958, continued for 8 consecutive years, and then stopped.

During this period, many of the small existing infestation centers throughout the Intermountain Region began to expand, while others developed anew, and by 1965 most of the lodgepole forests in northern Utah, southern Idaho and western Wyoming were experiencing massive outbreaks. In addition to the large control project on the Wasatch National Forest (north slope), projects were also undertaken at one time or another on the Ashley National Forest, Utah; Cache (now Wasatch) National Forest, Utah and Idaho; Caribou, Sawtooth and Payette National Forests, Idaho; Targhee National Forest, Idaho and Wyoming; and Teton National Forest and Grand Teton National Park, Wyoming. The largest and most intense projects, in addition to the Wasatch project, were in the Teton and Targhee National Forests and Grand Teton National Park. The Teton park and forest projects were terminated in 1967 and 1968, respectively. The Targhee project was started in 1964 and continued each year until 1970. In this period, more than 1,605,000 trees were treated in the Targhee at a cost of \$8,375,105. Although these efforts reduced tree killing in some areas, and slowed infestation movement in others, they had little overall control impact.

¹ J. Kinchloe is currently at Toiyabe National Forest. Mr. Kinchloe was Project Director of the Targhee Control Project from 1964 to 1969.

The infestation continued its generally northward movement, sweeping through Yellowstone National Park and into the Gallatin National Forest in Montana. By 1975 epidemic conditions prevailed in lodgepole stands in portions of the Beaverhead, Lolo and Kootenai National Forests and in Glacier National Park (Tuunock and Dooling 1976).

Now, almost 70 years after Brunner's first record of mountain pine beetle damage in Flathead County, the infestation has come full circle. It is just a matter of time before the undisturbed and once depleted but now rejuvenated stands in Montana experience another damaging mountain pine beetle cycle.

REVIEW OF CONTROL METHODS AND STRATEGIES

A brief review of the history of these outbreaks, their progress, and attempts at control is extremely important, for it is only in this context that we can hope to understand the various methods used, the strategies involved and the philosophies behind them.

The first recorded research effort for control of the mountain pine beetle was in ponderosa pine (*P. ponderosa* Lawson) during 1902-1903 in the Black Hills. These studies involved felling or girdling more than 200 "trap trees" to "determine their attractive influence on the Black Hills beetle [mountain pine beetle] and other forest-tree insects" (Hopkins 1905). The first attempt at control on an operational basis was near Colorado Springs, Colorado, in 1905, when some 600 to 800 ponderosa pines were felled, peeled and burned (Hopkins 1905).

In lodgepole pine, the first effort at control was in a mixed ponderosa/lodgepole pine infestation in 1910 and 1911 on the Whitman (now Wallowa-Whitman) National Forest in northeastern Oregon (Craighead et al. 1931). More than 30,000 infested ponderosa pines and 20,000 lodgepole pines were treated using three methods: felling and peeling, felling and scoring on top, and felling and burning (Burke 1946). In the northern Rockies, as mentioned earlier, control was started in 1912 near Swan Lake and in Big Hole Basin. In the Swan Lake project the treatment method is thought to have been felling, skidding into decks and burning. In the Big Hole Basin, at first the trees were felled and peeled, but later, in an attempt to expedite efforts, the trees were left standing and peeled to a height of 12 feet, using long-handled spuds (Evenden 1927). During subsequent years, however, the most commonly used method was felling, skidding into decks and burning (Fig. 2).

Although this "tried and true" method of control was common practice and is in some instances still in use today,² its shortcomings were evident, and efforts were made to make individual tree treatment a more effective and efficient operation. Adams (1926), for example, in an original experiment, tried to kill mountain pine beetle broods in lodgepole pine by use of explosives. He wrapped a hollow lead cable filled with TNT around the lower bole and ignited it. Unfortunately, after the smoke and debris cleared, it was found that the only dead insects were those directly beneath the cable. During the Big

² In 1973, in the Wildhorse Campground, Sawtooth National Forest, infested trees were felled, cut into bolts, and hand-carried to central pyres. A survey conducted the following year showed a reduction in the number of attacks.



Fig. 1. Mountain pine beetle-infested lodgepole pine stand in 1927 on the East Fork of the Bitterroot River, Montana. The light colored trees are the "red tops," resulting from 1926 attacks (from Evenden 1927).

Hole Basin control project of 1927, 5 percent of the infested trees were burned standing by piling brush around the trees and igniting it (Fig. 3) (Evenden 1927). In most instances the fire was not hot enough to kill the brood. Evenden (1929) then sprayed the boles with fuel oil before ignition, but brood destruction was achieved only in the lower bole where heat was intense. It was recommended that brush be stacked around the base of the larger trees before ignition to allow them to "crown out." This was probably the forerunner for more sophisticated burning methods, including the pressurized flame throwers that had limited use during the late 1950s and early 1960s in the Intermountain Region (Fig. 4).

Lodgepole pine's thin bark and its relatively low insulating properties qualified it as a test subject for solar heat. In a controlled field experiment, Patterson (1930) felled and limbed several infested pines and exposed them to the sun. He found that bark temperatures of less than 43°C (110°F) were not effective, while temperatures in the range of 43 to 49°C (110-120°F) were critical if maintained 2 to 3 hours. It was recommended that, in order for this method to be effective, the trees must be limbed, completely exposed, oriented in a north-south direction, and rolled at midday for periods of 2 to 5 days.

It was not until the 1930s that chemicals were used to kill the mountain pine beetle in individual trees. From then to the present it was simply a matter of finding the right chemical, the most suitable carrier, and the most efficient method of application. Salman (1938), citing an accumulation of tests that began in 1931 against several western bark beetles, concluded that the most effective formulation was 340 g (0.75 lb) of crude flake naphthalene dissolved in 3.8 liters (1 gal) of a light distillate type of oil. Although no specific data were available for the mountain pine beetle in lodgepole pine, mortality was stated as satisfactory and considerably greater than that obtained with the same material in thick-barked sugar pine. Whether or not this formulation was used operationally is unknown.

Taking a slightly different approach, Bedard (1938) resorted to tree injection rather than bark surface application. Some 600 lodgepole pine were girdled and injected with six chemical compounds. The most effective material was a copper sulfate solution which killed 90 percent of the brood. This technique was used operationally against the mountain pine beetle in western white pine on the Kaniksu and Coeur d'Alene National Forests, Idaho, in 1933-1936 and found to be less expensive than the fell, deck and burn method. However,

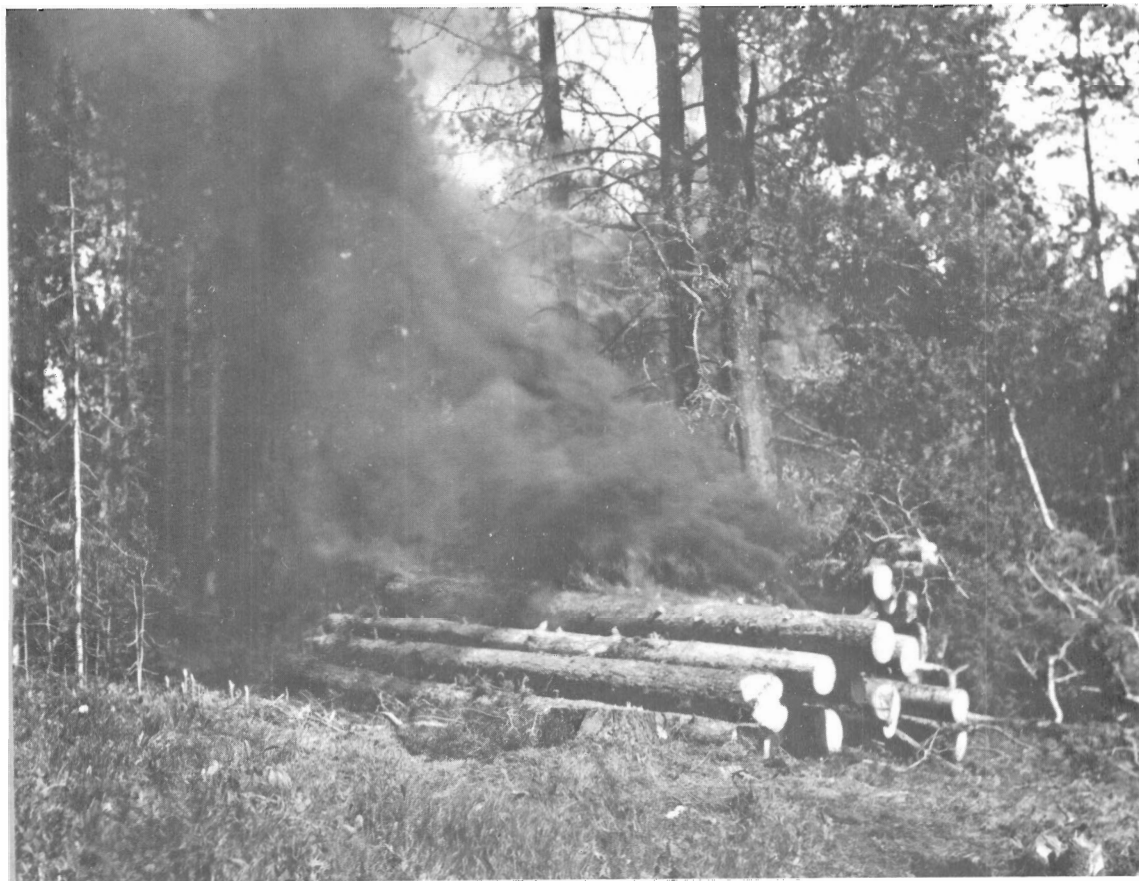


Fig. 2. Burning a deck of mountain pine beetle-infested lodgepole pine (from Evenden 1928).

Fig. 3. Burning a standing infested lodgepole pine. The fire was carried by brush—dry limbs, sticks and slash—piled around the base of the tree (from Evenden 1927). Later, the tree's bole was sprayed with fuel oil and then ignited.

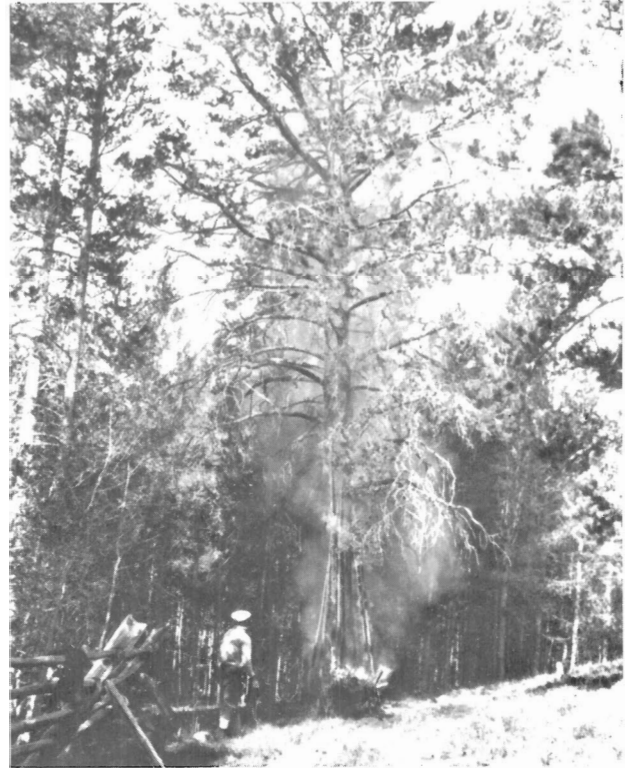


Fig. 4. A portable flamethrower scorches an infested lodgepole pine, Wasatch National Forest, circa 1961.



Fig. 5. Spraying a mountain pine beetle-infested lodgepole pine with a garden-type sprayer, circa 1930s.

the many problems associated with tree injection, such as precise timing and time-consuming injection techniques, were serious drawbacks to this method. In a later experiment Kinghorn (1955) applied two systemic insecticides, schraden and Systox,³ to freshly attacked lodgepole pine, but they were ineffective. He felt that the rapid penetration of the xylem by blue-stain fungi impaired the movement of the chemicals, and reduced the effective treatment period to such an extent as to make the technique impractical.

Studies to determine the efficacy of penetrating sprays were conducted from 1934 to 1938 (Gibson 1943). Naphthalene flakes dissolved in various densities of oil gave excel-

lent kill of the brood, but were difficult to use because of their relative insolubility, especially at low temperatures. The most effective combination, which gave excellent brood mortality at low cost, was orthodichlorobenzene mixed at a ratio of 1 part to 8 or 9 parts diesel fuel, and applied at the rate of 3.8 liters of mixed spray to 8.4 m² (1 gal/90 ft²) of bark surface. This formulation was used to treat infested standing trees in Grand Teton National Park in 1939, but the overall project was unsuccessful because many trees could not be treated in time and the taller trees were not sprayed to their full infested length. An experimental project, conducted the previous year on the Wasatch National Forest, showed that adequate beetle kill was obtained by felling the trees and spraying them on the ground (Gibson 1941).

Spraying standing trees, rather than felling the trees first, was easier and certainly more cost effective. In the early years, spraying was done with small garden-type sprayers (Fig. 5) that were eventually replaced with stirrup pumps mounted in 19-liter (5-gal) jeep cans and directed upwards with a long extension rod (Fig. 6). The maximum height which could be reached using this apparatus was 6 to 7.5 m (20 to 25 ft) at the very best. In 1948, Terrell developed a gasoline-powered portable pump drafting from a 19-liter jeep can that could reach 10.5 m (34.4 ft). However, the apparatus was heavy and required at least two men to transport it. Later, a gasoline-driven pump was used in the successful treatment of more than 2000 trees in Yosemite National Park. Although the working spray height was 12 m (39.4 ft), dead brood were found in two trees infested to a height of 16.5 m (54.1 ft), thought to be the result of upward drift (Sharp and Stevens 1962). Various other mechanical pumping devices have been tried, including lightweight gear pumps driven by 2-cycle engines, but they were undependable.

Throughout the 1940s and early 1950s, fuel oil solutions of orthodichlorobenzene were used to control the mountain pine beetle in both lodgepole and ponderosa pine. Oil solutions, although effective, were expensive, unpleasant to use, and caused skin ailments. Massey et al. (1953) tested several chemicals and solvents and an emulsifier mixed with water for control of the mountain pine beetle in ponderosa pine. Four hundred fifty-four grams (1 lb) of ethylene dibromide (EDB) in 19 liters (5 gal) of fuel oil emulsion was effective against all stages, but 907 g (2 lb) of EDB was recommended to ensure success. Kinghorn (1955) tested several fumigants and residual insecticides against the mountain pine beetle in lodgepole pine in Canada. Aldrin, EDB, heptachlor, lindane, and dieldrin, each formulated at a rate of 1.4 kg (3.1 lb) of active ingredient in 19 liters of emulsion, gave good control, but EDB caused the most rapid mortality. In a separate pilot experiment, EDB formulated at a rate of 907 g in 19 liters of emulsion containing 20 percent fuel oil also gave excellent results, which was consistent with the recommendation of Massey et al. (1953). Stevens (1957, 1959) recommended use of a water emulsion spray of EDB and gave specific instructions as to its formulation and use.

³ Mobay Chemical Co., Kansas City, MO.



Fig. 8. Aerial view of Operation Pushover on the north slope of the Uinta Mountains, Utah and Wyoming. At left center, the windrows of lodgepole pine are being burned. Some areas had to be reburned a second and third time. At right center, the burned material was bulldozed into individual piles and reburned.

these findings were stated as being inconclusive, it was hypothesized that this trap-bait method, under the right conditions, would be an effective and adequate control method.

As a further extension of this theory, Cole et al. (1975) integrated the use of chemical and natural attractants with a preventive spray to protect high-value lodgepole pine in an operational setting. High-value trees in a recreational complex (Big Sky, Montana) were treated with a 2-percent Dursban⁵/water solution. Surrounding this protective zone in a circular pattern were ten 2-chain radius circular plots. The design involved paired plots containing single trees baited with *trans*-verbenol or infested billets, surrounded by several non-bait trees and check plots. With the exception of the trees in the peripheral check plots, all other trees, including the baited ones, were sprayed with a 2-percent Dursban/water mixture.

In the final analysis, there were no significant differences between plots, treatments or areas. Dursban failed to prevent attacks and the peripheral attractants did not appear to draw beetles from the protective zone (W.E. Cole and M.D. McGregor, pers. comm.⁶).

⁵ Chlorpyrifos. Doro Chemical Co., Midland, MI.

⁶ W.E. Cole is currently located at the Intermountain Forest and Range Experiment Station, Ogden, UT, and M.D. McGregor is located at State and Private Forestry, USDA Forest Service, Missoula, MT.

Prior to and concurrent with this setback, tests to determine the efficacy of preventive sprays continued. In a series of west-wide field tests involving the mountain pine beetle in lodgepole and ponderosa pine, Smith et al. (1977) tested the effectiveness of 2-percent oil solutions and water emulsions of lindane and Dursban, or water suspensions of carbaryl (Sevin⁷). Control effectiveness was measured in two ways: by the incidence of attacks in treated trees compared to checks, and by the reduction in egg gallery length from forced attacks on caged bolts. With the exception of Dursban applied as a 2-percent water emulsion to ponderosa pine, all treatments were successful. An additional observation was that the oil formulations were phytotoxic to some of the thin-barked trees of both species.

A pilot study was undertaken in 1975 to determine the effectiveness of 2-percent oil mixtures of lindane, Sevin and Dursban in protecting 600 lodgepole pine in an operational setting on the Targhee National Forest. No supplemental attractants were used, since the area was known to be under extreme pressure from natural beetle populations. Practically all of the check trees were attacked, while over 98 percent of the treated trees remained unattacked. The cure was worse than the disease, however, for most of the treated trees died. An analysis showed the phytotoxic agent to be fuel oil (Rogers 1976 a,b).

⁷ Union Carbide, Jacksonville, FL.

In a follow-up field test, Gibson (1977) treated three 100-lodgepole pine groups with 2-percent water mixtures of Sevimol,⁸ lindane and Dursban. As in the previous test, no supplemental attractants were used, for the area had been monitored and found to have heavy beetle population pressure. The results bore this out, for in the post-spray analysis, 61 percent of the more than 1600 check trees were successfully attacked. Of the three treatments, Sevimol gave 98.9 percent protection, lindane 79.2 percent and Dursban only 29.3 percent. Due to the heavy population pressure, however, many of the "protected trees" were attacked above the 7.6-m (25-ft) spray height.

DISCUSSIONS AND RECOMMENDATIONS

We still continue to ask the inevitable question: "Why doesn't control in individual trees work?" After all, whether we spray the tree, burn it, or remove it by logging, don't we kill all of the insects or at least a large proportion of them? Certainly, but whether we kill all, part, or just a few of them, the issue is somewhat academic. It is not a matter of what we do, or how we do it; it is what we do not do. What we do not accomplish by individual tree treatment is to change the condition which was responsible for the outbreak in the first place. In the propagation and protection of the lodgepole pine ecosystem, we are perpetuating a highly vulnerable monotype. This monotype consists of biologically mature and overmature forests, in an almost continuous band stretching from northern Utah into Canada. To quote a well-used cliché, "What we really have is not so much an epidemic of mountain pine beetle, but rather an epidemic of lodgepole pine."

Hopefully, we are now experiencing the renaissance of mountain pine beetle management, or the transition from what was formerly a preservative ethic, to a far more realistic, practical and biologically sound concept of fundamental forest management. For some of us this concept will be difficult to accept.

What are some management alternatives for lodgepole pine in respect to the mountain pine beetle? Several of these alternatives will be covered in considerable detail by other symposium contributors; however, very briefly, here are some major options.

1. **Control in individual trees**, at the very best, is no more than a delaying action. Once control is terminated, the infestation will run its course and tree mortality will be essentially the same as that in the uncontrolled areas (Amman and Baker 1972). There may be instances where it is the only acceptable option. Examples may be in small, high-value, isolated stands, or in a large infestation that poses an immediate threat to nearby high-value timber. In the Targhee

outbreak during the 1960s, for example, intensive and sustained control efforts were successful in maintaining the infestation at the pre-control level, but not in reducing it. The purpose of this project was to protect a high-value timber sale (250 MM bd ft) that was sold, but never cut. Control was terminated following an unfavorable benefit/cost evaluation.

2. **Individual tree protection** is not practical under forest conditions, but is feasible with high-value trees such as those found in recreation areas, administrative sites and around individual homes. Treatment will have to be repeated for several years until the surrounding infestation subsides. Costs may vary considerably, depending on the size and number of trees involved, their location, the number of times treatment is required, and the efficiency of the applicator.
3. **Preventive measures.** Guidelines are now available for rating lodgepole stands as to degree of risk based on readily measured physical factors (Amman et al. 1977, Mahoney these proc.). Clearcutting offers the best option, but in stands where dwarf mistletoe is not serious, selective cutting can be done.
4. **To do nothing** may be a viable option, particularly in reserved areas and in other areas where timber values are not primary. In some infestations, mountain pine beetle has the potential of killing upwards of 62 percent of the trees 23 cm (9 inches) dbh and greater and 65 percent of the volume of lodgepole pine, and 56 percent of the trees and 55 percent of the volume for the entire stand (Klein 1976). In the absence of fire and following several outbreaks, the stands will be converted to more tolerant species (Roe and Amman 1970).

QUESTIONS AND ANSWERS

- Q. In peeling either standing or felled lodgepole pine, is any further treatment required to kill the insects (e.g., burning of bark)?
- A. If peeling is done in the fall, probably not. The brood and bark will have been dessicated sufficiently by early summer emergence. However, if peeling is not done until late spring or early summer, burning or spraying may be necessary to kill the potentially emerging brood.

REFERENCES

- Adams, A.C. 1926. Memorandum for the files: Beaverhead-Bitterroot project-season of 1926. USDA Forest Insect Lab., Bur. Entomol. and Plant Quarantine, Coeur d'Alene, ID. 4 pp.
- Amman, G.D., and B.H. Baker. 1972. Mountain pine beetle influence on lodgepole pine stand structure. *J. Forest.* 70:204-209.

⁸ Union Carbide, Jacksonville, FL.

- Amman, G.D., M.D. McGregor, D.B. Cahill, and W.H. Klein. 1977. Guidelines for reducing losses of lodgepole pine to the mountain pine beetle in unmanaged stands in the Rocky Mountains. USDA Forest Serv. Gen. Tech. Rep. INT-36, Intermt. Forest and Range Exp. Sta., Ogden, UT. 19pp.
- Bedard, W.D. 1938. Control of the mountain pine beetle by means of chemicals. J. Forest. 36:35-40.
- Burke, H.E. 1946. My recall of the first years in forest entomology. Internal Rep., Pac. SW Forest and Range Exp. Sta., Berkeley, CA. Mimeo. 37 pp.
- Cole, W.E., M.D. McGregor, G.D. Amman, L.A. Rassmussen and G.C. Trostle. 1975. Plans for a field test on mountain pine beetle population manipulation through attraction-preventive management strategies. Intermt. Forest and Range Exp. Sta., Ogden, UT. 9 pp.
- Craighead, F.C., J.M. Miller, J.C. Evenden, and F.P. Keen. 1931. Control work against bark beetles in western forests and an appraisal of results. J. Forest. 29:1001-1017.
- Evenden, J.C. 1927. Big Hole Basin insect control project, Beaverhead National Forest. Progress report for the season of 1927. USDA Forest Insect Lab., Bur. Entomol. and Plant Quarantine, Coeur d'Alene, ID. 22 pp.
- _____. 1928. The second battle of the Big Hole Basin. USDA Forest Insect Lab., Bur. Entomol. and Plant Quarantine, Coeur d'Alene, ID. 6 pp.
- _____. 1929. Plan of operation for control of the mountain pine beetle in lodgepole pine by burning standing tress. USDA Forest Insect Lab., Bur. Entomol. and Plant Quarantine, Coeur d'Alene, ID. 23 pp.
- _____. 1944. Montana's thirty-year mountain pine beetle infestation. USDA Forest Insect Lab., Bur. Entomol. and Plant Quarantine, Coeur d'Alene, ID. 23 pp.
- Gibson, A.L. 1941. Status of the mountain pine beetle infestation in lodgepole pine on the Grand Teton National Park, 1940. USDA Forest Insect Lab., Bur. Entomol. and Plant Quarantine, Coeur d'Alene, ID. 4 pp.
- _____. 1943. Penetrating sprays to control the mountain pine beetle. J. Econ. Entomol. 36:396-398.
- Gibson, K.E. 1977. Results of a pilot study to test the efficacy of three insecticides in preventing attacks by the mountain pine beetle in lodgepole pine. USDA Forest Serv., Intermt. Region, Ogden, UT. 7 pp.
- Hopkins, A.D. 1905. The Black Hills beetle. USDA Bur. Entomol. Bull. 56. U.S. Govt. Print. Off., Washington, D.C. 22 pp.
- Hosley, N.W., and L. Adams. 1947. Special report: The effects on mammals of DDT used in experiment efforts to control bark beetles in northwestern Wyoming. Wildlife Investigators on Public Lands, Chicago, IL; Missoula, MT. 6 pp.
- Kinghorn, J.M. 1955. Chemical control of the mountain pine beetle and the Douglas-fir beetle. J. Econ. Entomol. 48:501-504.
- Klein, W.H., and M.D. McGregor. 1966. Forest insect conditions in the intermountain states during 1965. USDA Forest Serv., Intermt. Region, Ogden, UT. 13 pp.
- Klein, W.H. 1969. Forest insect control in Utah's north slopes. Pages 45-46 in Proc., 16th annu. Field Conf. of Intermt. Geologists, Salt Lake City, UT.
- _____. 1976. Preliminary report of a survey to measure the impact of the mountain pine beetle in a lodgepole pine forest. USDA Forest Serv., Intermt. Region, Ogden, UT. 7 pp.
- Lyon, R.L. 1959. Toxicity of several residual-type insecticides to selected western bark beetles. J. Econ. Entomol. 52:323-327.
- _____. 1965. Structure and toxicity of insecticide deposits for control of bark beetles. USDA Forest Serv. Tech. Bull. 1343. U.S. Govt. Print. Off., Washington, D.C. 59 pp.
- Massey, C.L., R.D. Chisholm and N.D. Wygant. 1953. Ethylene dibromide for control of Black Hills beetle. J. Econ. Entomol. 46:601-604.
- Patterson, J.E. 1930. Control of the mountain pine beetle by solar heat. USDA Forest Serv. Tech. Bull. 195. U.S. Govt. Print. Off., Washington, D.C. 19 pp.
- Roe, A.L., and G.D. Amman. 1970. The mountain pine beetle in lodgepole pine forests. USDA Forest Serv. Res. Pap. INT-71. Intermt. Forest and Range Exp. Sta., Ogden, UT. 23 pp.
- Rogers, S.W. 1976a. A preliminary anatomical study of the outer tissue of lodgepole pine boles following treatment with fuel oil-formulated insecticides. USDA Forest Serv., Intermt. Region, Ogden, UT. 5 pp.
- _____. 1976b. An analysis of the phytotoxic reaction of lodgepole pine following treatment with fuel oil-formulated insecticides. USDA Forest Serv., Intermt. Region, Ogden, UT. 7 pp.
- Salman, K.A. 1938. Recent experiments with penetrating oil spray for the control of bark beetles. J. Econ. Entomol. 31:119-123.
- Sharp, R.H., and R.E. Stevens. 1962. New techniques for spraying standing trees infested with bark beetles. J. Forest. 60:584-650.
- Smith, R.H. 1970. Length of effectiveness of lindane against attacks by *Dendroctonus brevicornis* and *D. ponderosae* in California. J. Econ. Entomol. 63:1180-1184.
- _____. 1976. Low concentrations of lindane plus induced attraction traps mountain pine beetle. USDA Forest Serv. Res. Note PSW-361. Pacific SW Forest and Range Exp. Sta., Berkeley, CA.
- Smith, R.H., G.C. Trostle, and W.F. McCambridge. 1977. Protective spray tests on three species of bark beetles in the western United States. J. Econ. Entomol. 70:119-125.
- Stevens, R.E. 1957. Ethylene dibromide emulsion spray for control of the mountain pine beetle in lodgepole pine. USDA Forest Serv. Res. Note 122. Pac. SW Forest and Range Exp. Sta., Berkeley, CA. 4 pp.
- _____. 1959. Ethylene dibromide sprays for controlling bark beetles in California. USDA Forest Serv. Res. Note 147. Pac. SW Forest and Range Exp. Sta., Berkeley, CA. 6 pp.
- Terrell, T.T. 1948. A portable power sprayer for the treatment of trees infested with the Black Hills beetle. USDA Forest Insect Lab., Bur. Entomol. and Plant Quarantine, Coeur d'Alene, ID. 8 pp.
- Tunnock, S., and O.J. Dooling. 1976. Forest insect and disease conditions—1975. USDA Forest Serv., Forest Environ. Protect. Rep. 76-01. Missoula, MT. 14 pp.
- USDA Forest Service (N.D.). Operation pushover. Intermt. Region, Ogden, UT. 8 pp.
- Wickman, B.E., and R.L. Lyon. 1962. Experimental control of the mountain pine beetle in lodgepole pine with lindane. J. Forest. 60:395-399.

In Defense of the Concept of Direct Control of Mountain Pine Beetle Populations in Lodgepole Pine: Some Modern Approaches

Harvey S. Whitney, Les Safranyik, S. John Muraro and E. David A. Dyer

ABSTRACT

The strategy and tactics of direct control of the mountain pine beetle (*Dendroctonus ponderosae* Hopkins) are reviewed and the absolute requirement for detection of incipient infestations and diligence in treatment application is reiterated. Modern approaches to the use of explosives, the entomopathogenic fungus *Beauveria bassiana* (Balsam) Vuillemin, improvements in standing single tree burning, a mechanical debarker and microwave power are described. The current and future needs for direct control are discussed.

INTRODUCTION

Considerable information and numerous recommendations have been published on how to reduce or prevent damage to lodgepole pine (*Pinus contorta* Douglas var. *latifolia* Engelman) caused by epidemics of the mountain pine beetle (*Dendroctonus ponderosae* Hopkins) (Amman et al. 1977, Craighead et al. 1931, Hopping 1946, Keen 1952, McCambridge and Trostle 1972, Safranyik et al. 1974, Wygant 1959). The question remains, however, what to do when this beetle is in low numbers in a stand and, although there may be no current economic damage, the potential for devastating losses increases with each passing year. This problem is most acute in large, even-aged, mature stands of lodgepole pine that are not about to be logged, but also in other situations, as discussed by D.M. Cole (these proc.). In many of these stands, the temporal and spatial extent of harvesting will be dictated by beetle activity and market conditions. Eventually the problem will diminish, as lodgepole pine comes under more intensive management and opportunities are realized for the avoidance of mountain pine beetle losses through silvicultural practices. In the meantime, must we stand idly by and do nothing while whole hill-sides and valleys are turning red with dead and dying trees? Is there no way that valuable trees and stands can be preserved on the stump for at least a few years?

Berryman (these proc.) described the concept of a critical beetle population sufficient to overcome resistance of the average tree in a given stand. We believe that mountain pine beetle damage could be maintained at an acceptably low level if prompt, thorough, **direct** control action is taken when beetle populations are near or below such a critical threshold level. Damage might even decline if there were sufficient suppression pressure and little or no migration into the area. Aggregation behavior of the mountain pine beetle results in the critical population being together in time and space, thus making them vulnerable to annihilation. The possibility of finding "hot spots" of infested trees is realistic because the beetles spend most of their lives in their host trees and are not widely and uniformly dispersed throughout the stand. This line of reasoning has led to several well-known recommendations for direct control: sanitation salvage logging, felling and peeling, felling and burning, standing tree burning, application of insecticidal chemicals either onto or into standing or felled trees and, more recently, attracting attacking beetles into traps using the beetle's natural pheromone or *trans*-verbenol (Dyer 1978, Smith 1976). The statement appears often that direct control measures applied promptly and diligently will prevent serious epidemics.

There are very few documented examples of successful direct control operations. The work of Hopping (1946) in Banff National Park, Canada, perhaps approached it. There are also a few file reports by the British Columbia Forest Service describing local extermination of the mountain pine beetle that resulted in a new lease on life to the adjacent mature pine. Their recent film, "One Jump Ahead,"¹ documents an attempt at direct control that appears to have been successful.

¹ Produced by the Prince Rupert Forest District and the Information Division, Victoria; available on loan and for sale from British Columbia Forest Service, Information Division, Victoria, B.C.

But judging by the extent and persistence of mountain pine beetle infestations over the last 50 or 60 years in western North America, one is forced to conclude that direct control either does not work or is not being properly applied (for example, at the right time, on large enough areas, or before a critical population density is reached).

Recommendations for direct control of the mountain pine beetle have always emphasized that the effectiveness of the action taken would be directly proportional to the thoroughness and completeness of the treatment and that, at best, the results would be temporary. It has been stated repeatedly that for such action to really work there must be annual detection surveys, prompt and thorough application of one or more direct control measures, and a persistent follow-up. The follow-up is possibly the most important but the most neglected aspect of direct control of the mountain pine beetle. It cannot be too strongly emphasized that once a stand of lodgepole pine reaches maturity it contains a large proportion of trees that are highly susceptible to mountain pine beetle attack. Furthermore, these trees have a high potential for favoring rapid beetle population growth (Amman et al. 1977, Safranyik et al. 1974). Therefore, where lodgepole pine stands susceptible to mountain pine beetle are to be retained for future harvesting, it is imperative that they be subject to annual detection surveys and direct control treatments for as many years as they are to be preserved. Obviously, these stands may eventually become depleted because of the direct control treatments, but, during the intervening years, forest managers will have had the option of harvesting the stand according to their own plan without having to gamble with the beetle.

Another essential ingredient of direct control that has not always been taken into account is the need to ascertain that the undertaking will not exceed the resources available for it. There would have been no point in attempting to douse the Chicago fire on the second day with only one pail of water—but one could hardly fault the method of using water to put out the fire. Several reported attempts at direct control have suffered this defeat (Alexander et al. 1976, Amman and Baker 1972, Keen 1952). The fault was with the tactics, not the strategy.

Evaluation of direct control strategy is complex and perhaps it is impossible to measure all aspects of it. The strategy contains a negative feedback in that the better it works the less we need it, and the less opportunity there is to obtain positive data on its effectiveness.

Recently we began investigating new alternatives and approaches for use in direct control of the mountain pine beetle in the interior of British Columbia. We are convinced that prevention of population build-up of this beetle in susceptible high-value stands is a useful strategy and that tactics can be developed to achieve it. There is no proof that it does not work. Moreover, there is new evidence from two unreplicated 16-ha (64-acre) plots of infested lodgepole pine that a combination of a pheromone with an insecticide and an arboricide can be used sequentially to reduce the spread of an infes-

tation by as much as sixfold (Dyer 1978). Supporting this approach is the improved outlook for intensive management of lodgepole pine. Depletion of large contiguous even-aged stands resulting from harvesting by man or beetle, better methods of fire suppression, plus changing values for lodgepole pine in multiple land-use programs, have important implications for mountain pine beetle management, especially in the matter of reduced migration of beetles from unmanaged reservoirs of pine. Our objective is to provide management the best possible direct control technology as an aid in deciding on the control alternative to be used in incipient pre-epidemic infestations. This search for new and better ways is guided by the need for biological effectiveness, environmental safety and economy. The latter means low cost, because of the long times involved, and portability, to facilitate prompt action in remote or wilderness areas with little or no access. In this paper, we will describe only the rationale of the approaches and some of the progress toward their development. The details of methods have been omitted.

SOME MODERN APPROACHES

Bark Disruption with Detonating Cord

Detonating cord was reported by Taylor in 1973 to simulate lightning strikes on standing pine trees in the forest. We hypothesized that an explosive of this type could be useful for destroying mountain pine beetle broods, not so much by direct heat and concussion as by disruption of the bark, which exposes the beetle broods to the elements. Some possibilities are being explored on the rationale that beetle broods produced above 8 to 10 m (26 to 33 ft) in standing lodgepole pine trees are not sufficient to sustain a growing population, and that ways and means can be devised for applying detonating cord up to this height without climbing the trees. In addition to meeting the general criteria for direct control, the versatility of this unique source of energy is attractive.

Preliminary experiments in collaboration with the Fleet Driving Unit (Pacific), Canadian Department of Defense, using infested bolts on a firing range, confirmed that proper placement of a sufficient charge would indeed remove all the bark (Figs. 1 and 2). For example, firing a 50-grain cord wrapped in a 6- to 10-cm (2.4- to 4-inch) spiral left no bark on bolts containing advanced brood. Further tests and consultation with the military explosives experts showed that virtually any degree of bark disruption desired could be achieved. There is a fire hazard in firing ordinary detonating cord but this can be reduced by using cord with no-flash properties. The main disadvantage of using explosives is the hazard in connection with accidental firing.

To ascertain the minimum treatment necessary for a significant reduction of an overwintering beetle population, a field test was set up in October 1977. The lower 3 m (10 ft) of 40 beetle-infested trees were treated with three spacings of

Further demonstration, field testing and population sampling were conducted in May and June of 1976, using a British Columbia Forest Service suppression crew and their standard initial fire-attack equipment. The areas treated were pine/grassland interfaces readily accessible to 4-wheel drive vehicles fitted with standard 568-liter (125-gal) porta-tankers, one filled with water and a second trailer-mounted unit filled with the 90 percent/10 percent diesel/gas fuel mix. Changing the standard and Echo pumps that have diesel-sensitive impellers to an all-metal Monarch pump, and the use of a No. 4 nozzle tip were the only equipment modifications required. A delivery rate of about 3.6 liters (0.96 gal) per minute at 689.4 k Pa (10 psi) nozzle pressure allowed a two-man crew to treat a tree in about 5 minutes, using from 3.4 to 6.8 liters (0.9 to 1.8 gal) of fuel per tree. Treatment height was limited by the ability of the equipment to apply the fuel and generally did not exceed 10 m unless the tree was crowned. Dispersal of the fuel stream severely limits the use of this technique in windy conditions.

Pre- and post-burn sampling of treated areas showed the treatment to be 99 percent effective on adults and 87 percent effective on larvae. As expected, areas of obviously light scorch, indicated by only slight discoloration of the surface bark, maintained living beetles. Treated trees that had been only partially attacked or trees that had pitched out previous attacks survived the scorching but were invariably heavily attacked during subsequent flights, thus corroborating the attractiveness of fire-scorched trees, either as a result of stress or as a result of immediate effects such as those cited by Rust (1933).

Limited field use of single tree burning was implemented in the west Chilcotin in the winter of 1976 and extensively in the Riske Creek District during the early summer of 1977.

In early winter of 1977, a total of 1246 trees were fire treated in the Gaspard Creek area of Riske Creek District, British Columbia; 601 trees were felled, bucked, piled and burned, and 645 were treated by standing burning. A three-man crew working out of a trailer did the job. An average of 20.3 trees per day were felled and burned at a cost of \$16.50 per tree. The daily average for standing burning was 43 trees at a cost of \$9.40 per tree. Currently, more compact and efficient pumping equipment is being fabricated to facilitate winter use.

Additional Alternatives for Direct Control

The self-climbing mechanical tree pruning device known as the "tree monkey" could be modified to remove or possibly mangle bark, as well as cut off branches, as it travels up and down a tree stem. Such a machine, although fairly complex, perhaps heavy and useless on forked or very crooked trees, would do a thorough job in a matter of a few minutes on trees it could climb. There would be no need for men to climb or fell trees and no environmentally undesirable side effects.

Recent advances in application of microwave power and in portable electric generators suggest the possibility of microwave-treating bark beetle broods in situ. An 8- to 10-m hand-held antenna that could be moved in and among branches, where necessary, would suffice to apply microwave power directly to the infested bole. Unfortunately this method is impractical in remote areas because of electrical power limitations. However, experiments should be done to find out what effect lesser doses of microwave energy might have on growth, development and function of bark beetles in the brood habitat, especially in the immature stages. In any case, microwave heating could be considered for direct control treatment of brood logs from salvage logging operations arriving at millsites where there is adequate electricity for generating microwave power.

CONCLUDING REMARKS

We believe there are both current and potential lodgepole pine management problems where direct control of endemic mountain pine beetle populations is clearly indicated. In these cases it is of utmost importance that the forest manager not be intimidated into a do-nothing position because of past mistakes in attempts at mountain pine beetle control. Many so-called failures to control this beetle have been failures to conceive rather than to achieve. A combination of ignorance about the dynamics of the beetle interaction with the host, inadequate technological capability and misinterpretation of the reasons for failure of most direct control attempts has resulted in an undeserved bad reputation for direct control. If we ignore the possibilities and opportunities available through well chosen direct control applied at the right time and in the right way, we will continue to be at the mercy of the mountain pine beetle. This will certainly be the case until the new "silviculturally managed" stands reach maturity, and, in all probability, direct control will be an essential adjunct to the planned harvesting of these stands as they become susceptible to beetle epidemics. It is for these reasons that we have begun developing modern direct control methods for keeping mountain pine beetle populations below critical threshold levels necessary for epidemics to get started. The threat from the endemic beetles can be reduced.

Pest control systems are not automatic or self-activating and no technology, however new or innovative, is going to work all by itself. Eventually someone, or some agency, is going to have to take some action. Experience in direct control of mountain pine beetle in merchantable lodgepole pine has shown that control must be undertaken with determination. The problem will not just go away. Direct control treatment is not a once-over-lightly affair. It requires diligent, repetitious activity representing an investment in the future availability of wood. Clearly it involves intensive, intelligent management of real values.

The idea of preventive maintenance is not new or unique, and although some of the approaches we have described may be considered innovative, the most significant approach

of all would perhaps be for forest managers to in fact take up the challenge of preserving high-risk trees and stands of lodgepole pine by using present-day knowledge and technology for direct control of the mountain pine beetle.

QUESTIONS AND ANSWERS

- Q. Did burning standing trees to control mountain pine beetle brood increase the activity of secondary insect pests or other pathogens?
- A. We did not sample these particular burns. I expect secondary insect pests and fire-related fungus infections would be similar to those following any small fire.
- Q. Have you calculated cost/benefit ratios for any of your methods of insect control?
- A. No; however, one would expect a very favorable result compared with certain do-nothing or salvage logging alternatives that have been followed.
- Q. What would be the cost of using detonating cord?
- A. The cord we used 3 weeks ago cost 26.8¢ / meter (8.2¢ / ft). The costs of applying it will be worked out after we verify its biological effectiveness.
- Q. How does one economically justify the control measures conducted to the extent shown in film yesterday and slides today, if your average stand diameter is only 20 to 25 cm (8 to 10 inches) and relatively inaccessible, as is the case in many areas in eastern Oregon?
- A. I don't know. I suspect that values other than the current wood value of these small, inaccessible trees would have to weigh heavily in such a justification. As mentioned, our intention is that the cost of treatment not be higher than is absolutely necessary for biological effectiveness.

REFERENCES

- Alexander, N.E., J.H. Borden and J.M. Vakenti. 1976. A pest management study of a mountain pine beetle outbreak in tree farm license number 9. Pest Management Paper No. 8, Simon Fraser Univ., Burnaby, B.C. 95 pp.
- Amman, G.D., M.D. McGregor, D.B. Cahill and W.H. Klein. 1977. Guidelines for reducing losses of lodgepole pine to the mountain pine beetle in unmanaged stands in the Rocky Mountains. USDA Forest Serv. Gen. Tech. Rep. INT-36, Intermtn. Forest and Range Exp. Sta., Ogden, UT. 19 pp.
- Amman, G.D., and B.H. Baker. 1972. Mountain pine beetle influence on lodgepole pine stand structure. J. Forest. 70:204-209.
- Bell, J.V. 1974. Mycoses. Pages 185-236 in G.E. Cantwell (ed.). Insect diseases, Vol. 1. Marcel Dekker, New York.
- Craighead, F.C., J.M. Miller, J.C. Evenden and F.P. Keen. 1931. Control work against bark beetles in western forests and an appraisal of its results. J. Forest. 29:1001-1018.
- Dyer, E.D.A. 1978. Mountain pine beetle management trials in small infestations in lodgepole pine. Unpublished file report. Pacific Forest Research Centre, Victoria, B.C.
- Hopping, G.R. 1946. Control of the more injurious bark beetles of the Canadian Rocky Mountain Region. Can. Dept. Agri., Div. Entomol., Proc. Publ. 49. Ottawa. 8 pp.
- Keen, F.P. 1952. Insect enemies of western forests. USDA Misc. Pub. No. 273, Washington, D.C. 280 pp.
- McCambridge, W.F., and G.C. Trostle. 1972. The mountain pine beetle. USDA Forest Serv. Forest Pest Leaflet 2, Washington, D.C. 6 pp.
- McLaughlin, R.E. 1971. Use of protozoans for microbial control of insects. Pages 151-172 in H.D. Burgess and N.W. Hussey (eds.). Microbial control of insects and mites. Academic Press, New York.
- Moore, C.E. 1971. Mortality factors caused by pathogenic bacteria and fungi of the southern pine beetle in North Carolina. J. Invert. Path. 17:28-37.
- _____. 1973. Pathogenicity of three entomogenous fungi to the southern pine beetle at various temperatures and humidities. Environ. Entomol. 2:54-57.
- Nuorteva, M., and M. Salonen. 1968. Versuche mit *Beauveria bassiana* (Bals.) Vuill. gegen *Blastophagus piniperda* L. (Col., Scol.). Ann. Entomol. Fennici 34:49-55.
- Roberts, D.W., and W.C. Yendol. 1971. Use of fungi for microbial control of insects. Pages 125-149 in H.D. Burgess and N.W. Hussey (eds.). Microbial control of insects and mites. Academic Press, New York.
- Rust, H.J. 1933. Final report on the study of the relation of fire injury to bark beetle attack in ponderosa pine, Tubbs Hill burn. Coeur d'Alene, Idaho. Unpublished report cited by Miller and Keen (1960). Biology and control of the western pine beetle, a summary of the first fifty years of research. USDA Misc. Pub. 800. Pac. SW Forest and Range Exp. Sta., Berkeley, CA.
- Safranyik, L., D.M. Shrimpton and H.S. Whitney. 1974. Management of lodgepole pine to reduce losses from the mountain pine beetle. Can. Forest Serv. Forest Tech. Rep. 1. Ottawa. 26 pp.
- Smith, R.H. 1976. Low concentration of lindane plus induced attraction traps mountain pine beetle. USDA Forest Serv. Res. Note PSW-316. Pac. SW Forest and Range Exp. Sta., Berkeley, CA. 5 pp.
- Taylor, A.R. 1973. Ecological aspects of lightning in forests. Proc. Annu. Tall Timbers Fire Ecol. Conf., Mar. 22-23, Tallahassee, FL.
- Wygant, N.D. 1959. Bark beetle control. J. Forest 57:274-277.

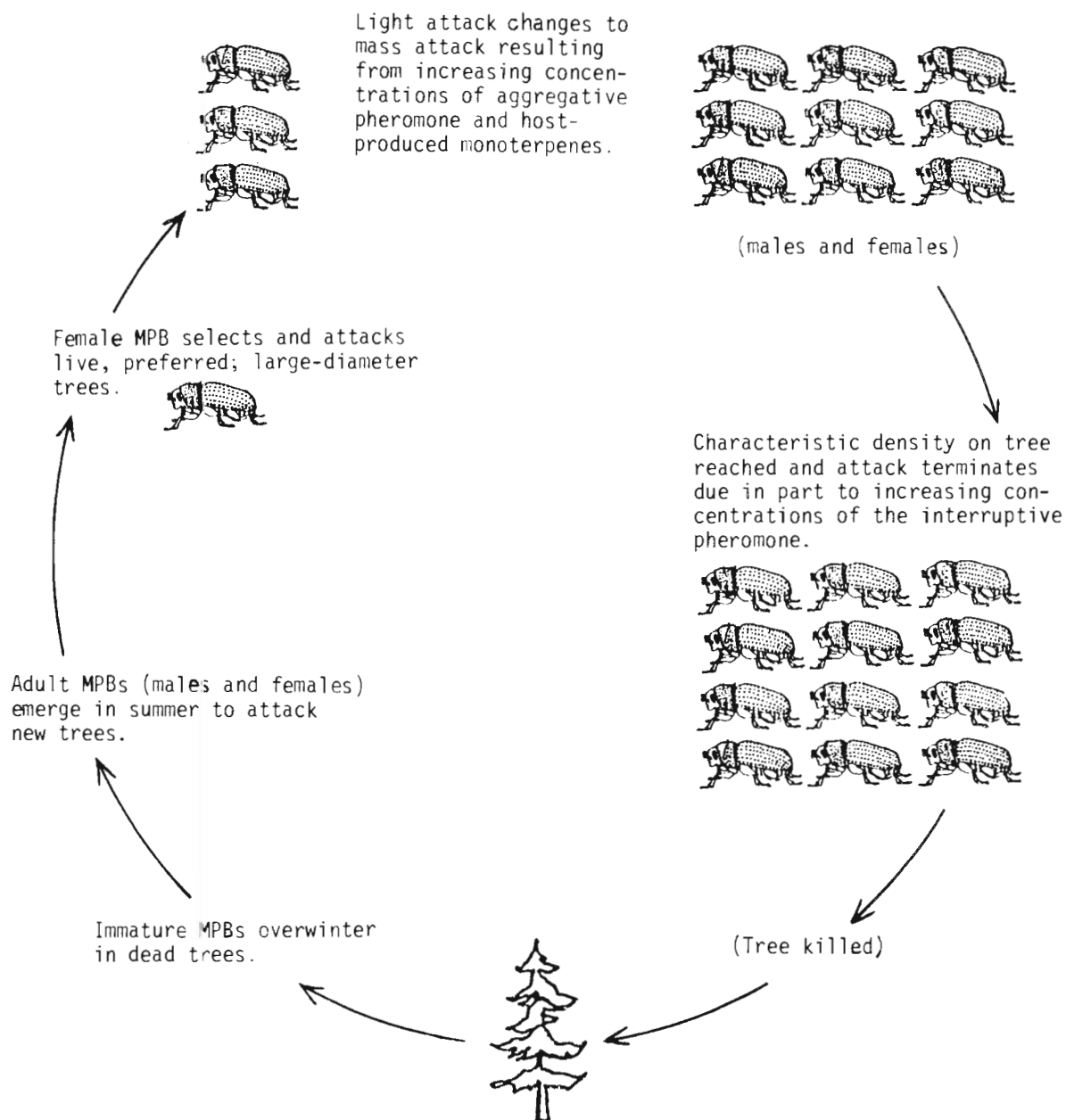


Fig. 1. Diagrammatic illustration of typical mountain pine beetle (MPB) life cycle.

Vité et al. (1976) carried out the first study designed to disrupt host selection and colonization by the southern pine beetle by aerial broadcasting of aggregative pheromone at extremely high concentrations. In an effort to confuse the southern pine beetle and prevent host selection at an epidemic level area in southeast Texas, rice was soaked with the attractive mixture frontalure (frontalin [Kinzer et al. 1969] and α -pinene, 2:1) and applied twice to a 10-ha (25-acre) section of infested pine. Although the results clearly showed the effectiveness of the treatment in concentrating beetles within the treated areas, they did not show disruption of the process whereby this bark beetle is able to select its host and signal aggregation.

In another experiment, Knopf and Pitman (1972) treated live trees in several areas in a southern Idaho drainage that had an extensive outbreak of the Douglas-fir beetle (*D. pseudotsugae* Hopkins) with the aggregative pheromone douglure (2:3:0.7 frontalin and the host cofactors α -pinene and camphene). All treatment blocks were designated for clearcutting. Mature Douglas-fir were marked as check trees or baited with pheromone in a slow-release device. All 157 baited trees were mass-attacked, and an additional 520 adjacent trees were mass-attacked and killed within the clearcut areas. All mass-attacked trees were harvested. The following year, this outbreak became inactive, which suggests that removal of the mass-attacked trees effectively reduced population numbers.

In northern Oregon and southern Idaho, Furniss et al. (1972) treated Douglas-fir trees with various combinations of the aggregative pheromone frontalin, the interruptive pheromone MCH, and *trans*-verbenol plus certain monoterpenes. The interruptive pheromone MCH effectively blocked the response of Douglas-fir beetle to frontalin-baited trees, and the authors proposed that MCH could be used to exclude beetles and prevent population build-ups in susceptible trees.

Furniss et al. (1974) established that the optimum rate of MCH release for maximum protection of felled Douglas-fir was 1 g/0.4 ha/day (0.09 oz/acre/day). To further test the effect of MCH on interrupting the colonization of susceptible hosts, MCH was formulated in various controlled-release granular systems to obtain the optimum controlled-release rate (Furniss et al. 1977). Subsequently, 35 Douglas-fir were felled before beetle flight, and MCH was released from granular formulations spread by hand or perforated film cans. In addition, liquid MCH was delivered in 0.5-dram vials inside perforated cans set on stakes 3 m (10 ft) apart. The most effective treatments were the liquid standard and a formulation consisting of a molecular sieve impregnated with MCH and coated with wax.

Hedden and Pitman (1978) conducted a study over a 2-year period in northern Idaho where Douglas-fir stands in drainages of the North Fork of the Clearwater River have been sustaining heavy mortality from the Douglas-fir beetle since 1970. Both the attractive pheromone douglure (Pitman et al. 1975)

and the interruptive pheromone MCH were placed simultaneously at varying concentrations on and near Douglas-fir trees. The two pheromones markedly altered the attack pattern of the Douglas-fir beetle. At a release rate of 1 mg/hr/tree of attractant and 2 to 2.5 mg/hr/tree of interruptive pheromone MCH, the attack density was reduced below the critical level for successful attack and colonization (4 to 6 female attacks/0.1 m² of bark surface).

In these areas, we recently concluded a 3-year study on the effectiveness of an aerial application of MCH and *trans*-verbenol in suppressing active infestation centers of Douglas-fir beetle (Table 1). In all areas, the percent tree mortality expressed as number and volume was significantly less than in untreated check plots. Aerial infrared photographs of the 1976 and 1977 plots proved what earlier cruise data had suggested. Spread of beetles from the treated infestation centers into adjacent uninfested stands was not detectable. Tree mortality was reduced markedly after treatment, and the infestation centers became inactive (no new mortality) the following year. Preliminary cost/benefit analyses appear favorable. The technique is now ready for large-scale testing to determine efficacy and safety, a requirement for government registration.

MOUNTAIN PINE BEETLE PHEROMONES

Like many of the bark beetles described, the mountain pine beetle (*D. ponderosae* Hopkins) uses at least two types of pheromones, aggregative and interruptive, to successfully attack and colonize host trees. At present, this communication is best understood in mountain pine beetle populations infesting white pine (*P. monticola* Douglas). The aggregative pheromone is composed of at least one female-produced compound, the terpene alcohol *trans*-verbenol (Pitman et al. 1968), which in association with a host volatile such as α -pinene or myrcene (Pitman 1971, Billings et al. 1976) signals population aggregation (Pitman et al. 1968, 1969). This aggregation and subsequent mass attack (8 to 14 attacks per 0.1 m² of bark surface) is essential to successfully overcome the trees' natural resistance (pitch exudation) to the boring beetles.

The pheromone *exo*-brevicomin, produced predominately by the male mountain pine beetle (Pitman et al. 1969), interrupts aggregation of mountain pine beetles in white pine (McKnight 1979). During the 1976-1977 flight periods, we baited 9 mature trees with the pheromone pondelure (*trans*-verbenol and α -pinene 9:1 [Pitman, 1971]) plus *exo*-brevicomin, and 9 trees with pondelure alone. In both years, no successful attacks occurred on trees baited with the two pheromones in combination. All trees baited with pondelure alone were successfully mass-attacked and killed. Thus, the function of *exo*-brevicomin, when released by the male at low concentrations, could be to signal females, responding to the aggregative pheromone, to initiate new attacks at discrete distances from previous attacks.

Table 1. Potential methods of using aggregative and interruptive pheromones to manage mountain pine beetle in lodgepole pine.

Pheromone type	Objective	Method of pheromone use	Comments
Aggregative	Survey and detection	Sticky traps (lethal)	Counting trapped beetles can aid estimation and prediction of population trends.
		Olfactometer ¹	Live beetles are necessary for pheromone analyses, systematic studies and genetic comparison of populations.
	Control	Sticky traps (lethal)	Traps are used in high-risk stands and are most effective at low mountain pine beetle densities.
	Control	Individual trees	Beetles are induced to attack baited trees unsuitable for brood development (such as trees with thin phloem).
		Groups of trees	Aerial broadcasting of pheromone can focus beetle attacks in specific areas. The method requires associated follow-up logging and increased efficiency of salvage harvesting.
Interruptive	Tree protection	Individual trees	High-value trees in parks, rest areas and campsites, watersheds, and areas of forest development can be protected from beetle attack.
	Control	Groups of trees	
Aggregative plus Interruptive	Control	Groups of trees	

¹ Any device from which beetles can be collected. An olfactometer can be a passive device such as a flight barrier or a powered device using electrically-driven fans.

When the density of attack by mountain pine beetle reaches a critical level on lodgepole pine (*Pinus contorta* Douglas var. *latifolia* Engelman), the attack abruptly terminates and switches to nearby trees (Geiszler and Gara these proc.). Male mountain pine beetles feeding in lodgepole pine also produce *exo*-brevicomin but, when released in a controlled system, this pheromone did not interrupt the response of beetles to large-diameter trees baited with pondelure (McKnight 1979). Therefore, the function of *exo*-brevicomin may be totally different between populations of mountain pine beetle that infest white pine and those that infest lodgepole pine.

In 1973, we undertook a study to determine if sticky traps baited with pondelure could reduce mortality of white pine by mountain pine beetle. In a section of virgin white pine in northern Idaho that was heavily infested with mountain pine beetle, approximately 65 ha (162 acres) were treated with plastic-coated sticky traps, 6.4 x 13.6 cm (2.5 x 5.4 inches), mounted on wooden stakes approximately 40 m (133 ft) apart. Traps were baited with the attractive pheromone pondelure. After the principal early summer flight, the treated plot and an additional 65-ha check plot were given 100 percent cruises. Large numbers of mountain pine beetle were trapped

and killed, but no significant reduction in total tree mortality occurred in the plot containing the sticky traps. Mortality expressed by volume of dead trees was reduced significantly, however, in plots with the attractive sticky traps. This reduction in total volume of trees killed was a result of the beetle population attacking small-diameter white pine near the attractive traps. Small-diameter white pine are not usually preferred hosts.

In another study (Pitman 1971), we sought to control mountain pine beetles by spraying mature white pine with a contact insecticide and then baiting the trees with the aggregative pheromone pondelure. In a mature stand of white pine in northern Idaho, several 16-ha (40-acre) plots were selected and approximately 100 trees per plot were baited with the pondelure contained in a slow-release system. Each tree was then sprayed with a 2.3 percent solution of the insecticide lindane to a height of nearly 6 m (20 ft). A large number (18 percent) of the 725 sprayed and baited trees were killed. This technique has considerable potential, however, where a light selective harvest is scheduled. Other studies (Cox 1972) in which mature white pine were baited with pondelure and logged after beetle flight indicated that white pine mortality

was reduced in the areas where the aggregative pheromone was used and the mass-attacked trees were harvested.

Mountain pine beetle produce few brood in small-diameter, thin-phloem trees (Amman 1971). To see if mountain pine beetle could be lured to this type of tree, Rasmussen (1972) baited 95 trees of small diameter (2.8 to 3.6 cm) and thin phloem (0.004 cm) with the aggregative pheromone pondelure in a slow-release system. Only 31.5 percent of the baited trees were attacked and many of these attacks were unsuccessful. Rasmussen concluded that pondelure will not efficiently induce mass attacks on small-diameter, thin-phloem lodgepole pine. It will, however, focus the attack on nearby large-diameter pines.

PRACTICAL ASPECTS OF PHEROMONE USE IN MOUNTAIN PINE BEETLE CONTROL

Obviously, the practical problems in implementing techniques using pheromones to suppress mountain pine beetle populations are many. Mountain pine beetle outbreaks are characteristically found in undermanaged lodgepole pine stands. Many of these undermanaged stands occur on sites that are overstocked and frequently the proportion of overmature, susceptible trees is high (Amman et al. 1977). Lodgepole pine management has consisted, to a great extent, of periodic harvesting, irrespective of prescribed rotation schedules, and salvage of dead and dying trees. At the present level of beetle activity in areas such as south central British Columbia, the Targhee National Forest in southeastern Idaho and the Blue Mountains in northeastern Oregon, current control techniques, regardless of tested effectiveness, would not significantly alter the population status of the beetles. In the absence of rigorous stand management, little control can be accomplished with an almost limitless supply of beetles and high-risk hosts, except when dead and dying timber is salvaged, and at times even this practice is not possible due to economic constraints. Some evidence shows, however, that more intensive and systematic management of lodgepole pine forests will be practiced in the future (Cahms 1971, Baumgartner 1973, Cochran 1975).

In addition to the extensive nature of the problem of mountain pine beetle outbreaks in lodgepole pine, we must deal with the lack of information concerning their key behavior-modifying chemicals. Our current ability to manipulate mountain pine beetle in lodgepole pine is restricted to baiting of large-diameter trees with pondelure in areas of low beetle density. As previously noted, this lure is effective in inducing a mass attack on baited trees. Thus, this pheromone has considerable potential value in stands with low beetle populations and high-risk trees, where a partial cut of large-diameter trees is scheduled. Under these conditions, trees that are going to be cut are baited with pheromone before beetle flight and attack (the time of which varies with latitude and elevation). The pheromone can thus decrease stand mortality as high-risk trees infested with mountain pine beetle are removed. In areas of high beetle density, however, this practice would have

little effect on tree mortality, as attacks would spill over from baited trees onto adjacent large-diameter trees (Rasmussen 1972).

USE OF PHEROMONES IN MOUNTAIN PINE BEETLE CONTROL: FUTURE DIRECTION

A summary of tactics for mountain pine beetle management incorporating pheromones and some comments on implementation and effects, as described above, are given in Table 1. We believe that the three basic objectives—survey and detection, pest control and tree protection—have the highest probability of being attained in the near future through more intensive research. To reach these three objectives, we must be able to convey chemical messages that signal a point source of attraction (exploited in detection and survey and in lethal trapping, either with sticky traps or with physiologically unsuitable trees), an area source of attraction (exploited in mass aggregation on trees designated for harvesting), or disruption of the response to point sources (exploited in protection of individual trees) and to area sources (exploited in reducing attack densities resulting in trees becoming pest population “sinks”).

CONCLUSIONS

Bark beetle pheromones hold much promise as one of several techniques for use in integrated control of the mountain pine beetle. Current limitations stem primarily from the lack of precise identification of the behavior regulators involved and information concerning the type of behavior they elicit. For example, we know that *trans*-verbenol is only one component of the mountain pine beetle aggregative pheromone complex, but, at present, we do not know the other essential ingredients. For this reason, mountain pine beetle in lodgepole pine forests do not respond to traps, although we have baited many different types of traps with many different combinations of pheromones (active for other bark beetle species) and host terpenes. Only one record exists of mountain pine beetle responding to a trap in a lodgepole pine stand (Rudinsky et al. 1974a). Virtually nothing is known of the chemically mediated system whereby attraction to a mass-attacked tree is terminated and the attack switches to a new host, despite considerable research on this pattern of behavior (Geiszler and Gara these proc.).

Research on mountain pine beetle is under way in our laboratory and others to identify additional chemical messengers that mediate behavior during host selection and colonization of lodgepole pine. When the principal mountain pine beetle pheromones are identified and synthesized, most of the tactics in Table 1 will become practical. However, increased information about mountain pine beetle pheromones and techniques for their use will only be effective towards our goal of long-term mountain pine beetle control when they are incorporated into other contemporary pest and host management strategies (Waters 1974, Stark 1975).

ACKNOWLEDGMENTS

We sincerely appreciate the time and effort contributed by D.L. Wood, J.H. Borden, R.W. Stark, G.D. Amman and L.A. Rasmussen in the development of ideas and constructive criticism during the writing of this paper.

We also thank Royce G. Cox and the many other people, too numerous to mention, of the Potlatch Corporation, Lewiston, Idaho, for their untiring encouragement and help during the many phases of our work on mountain pine beetle. This work was also supported in part by Boyce Thompson Institute for Plant Research, Yonkers, NY.

QUESTIONS AND ANSWERS

- Q. Could the inhibitor pheromone *exo-brevicomin* be used in a liquid form and sprayed on like a tree paint?
- A. Technically this is possible if the inhibitor pheromone were formulated in a type of stabilized liquid-crystal. The technology for producing this type of slow-release system is available; however, I know of no work currently under way to produce such a device.
- Q. Is there any effect on predatory beetles (such as clerids) caused by using aggregative pheromones in combination with sticky traps, etc.?
- A. Several predator species use the aggregative pheromones produced by bark beetles to locate their prey. For example, the clerid *Enoclerus sphageus* readily responds to *trans*-verbenol with α -pinene. By using sticky traps baited with the mountain pine beetle aggregative pheromone, we caught *E. sphageus* at a ratio of about 1:5 to its prey. The impact of high predator mortality could be reduced in a bark beetle survey or control program by timing the trapping period to coincide with the main mountain pine beetle flight. This clerid emerges several weeks prior to beetle flight.
- Q. What is the effect of the aggregative pheromone on immigration rate of mountain pine beetle from adjacent infestations?
- A. The effect on immigration of beetles from adjacent infestations into areas where aggregative pheromones are being used is unknown. A complicating element in assessing this phenomenon is that we do not know what effect we are having on beetles that would have left the area if pheromones had not been used. We speculate that immigration is increased and migration is reduced but, until we know the attraction distance of these chemical messengers, this subject will remain speculative.
- Q. Could you give an example of a control program we could do now with pheromones in a lodgepole pine stand?
- A. At present, the best use we see for pheromones in lodgepole pine stands is baiting of large-diameter trees marked for a selective harvest on sites where mountain pine beetles have not yet reached outbreak status.
- Q. Are pheromones effective in inducing attacks by mountain pine beetle on, say, 10-12.5-cm lodgepole pine? If so, what do you think of the possibility of such a scheme to cause the beetle to run its course in this size class in stands ready for thinning?
- A. This is an intriguing possibility and one that has been tried, so far unsuccessfully, by the USDA Forest Service. There are probably several explanations why mountain pine beetle cannot be enticed to attack small-diameter lodgepole pine baited with aggregative pheromone. First, we are not sure if the current attractive mixture, *trans*-verbenol and α -pinene (pondelure) is complete. In other words, additional compounds may be needed to obtain maximum attractiveness. Second, responding beetles show a very strong preference for large-diameter trees. If we can overcome this preference, via a more potent aggregation lure or in some other fashion, then baiting small-diameter trees scheduled for thinning could be effective as a beetle control technique.
- Q. Since the aggregative pheromone works in combination with the terpene of individual lodgepole pine trees and Lotan showed that variation in terpene composition of individual genotypes exists, is there any on-going research into the development of resistant genotypes?
- A. I know of none. However, we have a study planned for the near future which will be the initial step in determining if certain types of monoterpenes occur in lodgepole pine which would limit the aggregation pheromone produced by the beetle.

REFERENCES

- Amman, G.D. 1971. Mountain pine beetle brood production in relation to thickness of lodgepole pine phloem. J. Econ. Entomol. 65: 138-140.
- Amman, G.D., M.D. McGregor, D.B. Cahill and W.H. Klein. 1977. Guidelines for reducing losses of lodgepole pine to the mountain pine beetle in unmanaged stands in the Rocky Mountains. USDA Forest Serv. Gen. Tech. Rep. INT-36. Intermtn. Forest and Range Exp. Sta., Ogden, UT. 19 pp.

- Bakke, A. 1973. Bark beetle pheromones and their potential use in forestry. IEPP/EPPA Bull. 9:5-15.
- Baumgartner, D.M., ed. 1973. Management of lodgepole pine ecosystems, Vol. I and II. Washington State Univ. Coop. Ext. Serv., Pullman. 825 pp.
- Bedard, W.D., and D.L. Wood. 1974. Bark beetles—the western pine beetle. Pages 441-449 in M.C. Birch (ed.). Pheromones. North-Holland, Amsterdam.
- Beroza, M. 1970. Chemicals controlling insect behavior. Academic Press, New York. 170 pp.
- Beroza, M., B.A. Bierl, J.G.R. Tardif, D.A. Cook and E.C. Paszek. 1971. Activity and persistence of synthetic and natural sex attractants of the gypsy moth in laboratory and field trials. J. Econ. Entomol. 64:1499-1508.
- Billings, R.F., R.I. Gara, and B.F. Hrutfiord. 1976. Influence of ponderosa pine resin volatiles on the response of *Dendroctonus ponderosae* to synthetic *trans*-verbenol. Environ. Entomol. 5:171-179.
- Birch, M.C., ed. 1974. Pheromones. Frontiers of biology, Vol. 32. North-Holland Research Monographs. North-Holland, Amsterdam. 495 pp.
- Borden, J.H. 1977. Behavioral responses of Coleoptera to pheromones, allomones and kairomones. Pages 169-198 in H.H. Shorey and J.J. McKelvey, Jr. (eds.). Chemical control of insect behavior: theory and application. John Wiley & Sons, Inc. New York.
- Burkholder, W.E. 1977. Stored products pests. Pages 449 ff in M. Birch (ed.). Pheromones. North-Holland, Amsterdam.
- Cahms, W.G. 1971. Fifty-five-year-old lodgepole pine response to thinning. USDA Forest Serv. Res. Note PNW-47. Pac. NW Forest and Range Exp. Sta., Portland, OR. 11 pp.
- Cochran, P.H. 1975. Response of polesize lodgepole pine to fertilization. USDA Forest Serv. Res. Note PNW-206. Pac. NW Forest and Range Exp. Sta., Portland, OR. 15 pp.
- Copony, J.A., and C.L. Morris. 1972. Southern pine beetle suppression with frontalure and cacodylic acid treatments. J. Econ. Entomol. 65:754-777.
- Coulson, R.N., J.L. Foltz, A.M. Mayyasi and F.P. Hain. 1975. Quantitative evaluation of frontalure and cacodylic acid treatment effects on within-tree populations of the southern pine beetle. J. Econ. Entomol. 68:671-678.
- Coulson, R.N., F.L. Oliveria, T.L. Payne and M.W. Houseweart. 1973a. Variables associated with use of frontalure and cacodylic acid in the suppression of the southern pine beetle. I. Factors influencing manipulation to prescribed trees. J. Econ. Entomol. 66:893-896.
- . 1973b. Variables associated with the use of frontalure and cacodylic acid in the suppression of the southern pine beetle. II. Brood production in trees treated with cacodylic acid. J. Econ. Entomol. 66:897-899.
- Cox, R.G. 1972. Cooperative research on control of the mountain pine beetle in western white pine. Progress Rep. No. 8. Bark beetle committee. Montana-Northern Idaho Forest Pest Action Council. Lewiston, ID. 28 pp.
- Daterman, G.E. 1974. Synthetic sex pheromone for detection of the European pine shoot moth. USDA Forest Serv. Res. Pap. PNW-180. Pac. NW Forest and Range Exp. Sta., Corvallis, OR.
- Dyer, E.D.A. 1975. Frontalin attractant in stands infested by the spruce beetle, *Dendroctonus rufipennis* (Coleoptera: Scolytidae). Can. Entomol. 107:979-988.
- Furniss, M.M., L.K. Kline, R.F. Schmitz and J.A. Rudinsky. 1972. Test of three pheromones to induce or disrupt aggregation of Douglas-fir beetles (Coleoptera: Scolytidae) on live trees. Ann. Entomol. Soc. Amer. 65:1227-1232.
- Furniss, M.M., J.W. Young, M.D. McGregor, R.L. Livingston and D.R. Hamel. 1977. Effectiveness of controlled-release formulations of MCH for preventing Douglas-fir beetle (Coleoptera: Scolytidae) infestations in felled trees. Can. Entomol. 109:1063-1069.
- Furniss, M.M., G.E. Daterman, L.N. Kline, M.D. McGregor, G.C. Trostle, L.F. Pettinger and J.A. Rudinsky. 1974. Effectiveness of the Douglas-fir beetle antiaggregative pheromone methylcyclohexenone at three concentrations and spacing around felled host trees. Can. Entomol. 106:381-392.
- Graham, S.A., and F.B. Knight. 1965. Principles of forest entomology. McGraw-Hill, San Francisco. 417 pp.
- Hadden, R.L., and G.B. Pitman. 1978. Attack density regulation: a new approach to the use of pheromones in Douglas-fir beetle population management. J. Econ. Entomol. In press.
- Jacobson, M. 1972. Insect sex pheromones. Academic Press, New York. 382 pp.
- Kaissling, K.F., and F. Priesner. 1970. The olfactory threshold of the silk moth. Naturwiss. 57:19-58.
- Karlson, P., and A. Butenandt. 1959. Pheromones (ectohormones) in insects. Annu. Rev. Entomol. 4:39-58.
- Kilgore, W.W., and R.L. Doutt, eds. 1967. Pest control. Biological, physical and selected chemical methods. Academic Press, New York. 477 pp.
- Kinzer, G.W., A.F. Fentiman, Jr., T.F. Page, Jr., R.L. Foltz, J.P. Vité and G.B. Pitman. 1969. Bark beetle attractants: Identification, synthesis and field bioassays of a new compound isolated from *Dendroctonus*. Nature (London) 221:477-478.
- Knopf, J.A.E., and G.B. Pitman. 1972. Aggregation pheromone for manipulation of the Douglas-fir beetle. J. Econ. Entomol. 65:723-726.
- Lainer, G.N., R.M. Silverstein and J.W. Peacock. 1976. Attractant pheromone of the European elm bark beetle (*Scolytus multi-striatus*): Isolation, identification, synthesis and fertilization studies. Pages 149-175 in J.F. Anderson and H.K. Kaya (eds.). Perspectives in forest entomology. Academic Press, New York.
- McKnight, R.C. 1979. Differences in response among populations of *Dendroctonus ponderosae* Hopkins to its pheromone complex. Master's thesis. Univ. of Washington, Seattle. In prep.
- McLean, J.A., and J.H. Borden. 1977a. Suppression of *Gnathotrichus sulcatus* with sulcatol-baited traps in a commercial sawmill and notes on the occurrence of *G. retusus* and *Trypodendron lineatum*. Can. J. For. Res. 7:348-356.
- . 1977b. Attack by *Gnathotrichus sulcatus* (Coleoptera: Scolytidae) on stumps and felled trees baited with sulcatol and ethanol. Can. Entomol. 109:675-686.
- Mitchell, E.B., and D.D. Hardee. 1974. In field traps: A new concept in survey and suppression of low populations of boll weevils. J. Econ. Entomol. 67:506-508.

- Mitchell, E.B., E.P. Lloyd, D.D. Hardee, W.H. Cross and T.B. Davich. 1976. In field traps and insecticides for suppression and elimination of populations of boll weevils. *J. Econ. Entomol.* 69:83-88.
- Payne, T.L., J.E. Coster and P.C. Johnson. 1977. Effects of slow-release formulation of synthetic *endo*- and *exo*-brevicomin on southern pine beetle flight and landing behavior. *J. Chem. Ecol.* 3:133-141.
- Pitman, G.B. 1971. *trans*-Verbenol and α -pinene: Their utility in manipulation of the mountain pine beetle. *J. Econ. Entomol.* 64:427-430.
- Pitman, G.B., R.L. Hedden and R.I. Gara. 1975. Synergistic effect of ethyl alcohol on the aggregation of *Dendroctonus pseudotsugae* (Col.: Scolytidae) in response to pheromones. *Z. ang. Entomol.* 78:203-208.
- Pitman, G.B., J.P. Vité, G.W. Kinzer and A.F. Fentiman, Jr. 1968. Bark beetle attractants: *trans*-verbenol isolated from *Dendroctonus*. *Nature* (London) 218:168-169.
- . 1969. Specificity of population-aggregating pheromones in *Dendroctonus*. *J. Insect Physiol.* 15:363-366.
- Rasmussen, L.A. 1972. Attraction of mountain pine beetles to small-diameter pines baited with *trans*-verbenol and α -pinene. *J. Econ. Entomol.* 63:1396-1399.
- Rudinsky, J.A., M.E. Morgan, L.M. Libby and T.B. Putnam. 1974a. Anti-aggregative-rivalry pheromone of the mountain pine beetle, and a new arrestant of the southern pine beetle. *Environ. Entomol.* 3:90-98.
- Rudinsky, J.A., C. Sartwell, Jr., T.M. Graves, and M.E. Morgan. 1974b. Granular formulation of methylcyclohexenone: An antiaggregative pheromone of the Douglas-fir and spruce bark beetles (Coleoptera: Scolytidae). *Z. ang. Entomol.* 75:254-263.
- Shorey, H.H. 1973. Behavioral responses to insect pheromones. *Annu. Rev. Entomol.* 18:349-380.
- Shorey, H.H., and J.J. McKelvey (eds.). 1977. Chemical control of insect behavior: Theory and application. John Wiley & Sons, Inc., New York. 414 pp.
- Shorey, H.H., L.K. Gatson and R.S. Kaac. 1976. Air-permeation with gossypure for control of the pink bollworm. *In* M. Beroza (ed.). Pest management with insect sex attractants. *Ann. Chem. Soc. Symposium* 23.
- Silverstein, R.M., R.G. Brownlee, T.E. Bellas, D.L. Wood and L.E. Browne. 1968. Brevicomin: Principal sex attractant in the frass of the female western pine beetle. *Science* 159:889-891.
- Stark, R.W. 1975. Forest insect pest management. Pages 509-528 *in* W.H. Luckmann and R.H. Metcalf (eds.). Introduction to insect pest management. John Wiley & Sons, Inc., New York.
- Taschenberg, E.F., and W.L. Roelofs. 1976. Pheromone communication disruption of the grape berry moth with micro-encapsulated and hollow fiber systems. *Environ. Entomol.* 5:688-691.
- Vité, J.P. 1970. Pest management systems using synthetic pheromones. *Contrib. Boyce Thompson Inst.* 24:343-350.
- . 1975. Möglichkeiten und Grenzen der Pheromonsueve-ndung in der Borken Käfer-bekämpfung. *Z. ang. Entomol.* 4:171-174.
- Vité, J.P., P.R. Hughes and J.A.A. Renwick. 1976. Southern pine beetle: Effect of aerial pheromone saturation on orientation. *Naturwiss.* 63:44.
- Waters, W.E. 1974. Systems approach to managing pine bark beetles. Pages 12-14 *in* T.L. Payne, R.L. Coulson and R.C. Thatcher (eds.). Proc. Southern pine beetle symposium. Texas A&M Univ. and USDA Forest Serv., College Station, TX.
- Wood, D.L. 1974. Progress Rep. Pine bark beetle subprojects. Pages 692-697 *in* The principles, strategies and tactics of pest population regulation and control in major crop ecosystems, Vol. 2. Integrated Pest Management Coordinating Committee for the western pine beetle subprogram. Internatl. Center for Integrated and Biological Control, Univ. of California, Berkeley.
- . 1977. Manipulation of forest insect pests. Pages 371-384. *in* H.H. Shorey and J.J. McKelvey, Jr. (eds.). Chemical control of insect behavior: Theory and application. John Wiley & Sons, Inc., New York.
- Wood, D.L., R.M. Silverstein and M. Nakajima. 1970. Control of insect behavior by natural products. Academic Press, New York. 345 pp.
- Young, J.C., and R.M. Silverstein. 1975. Biological and chemical methodology in the study of insect communication systems. Pages 75-161 *in* D.G. Moulton, A. Turk and J.W. Johnson (eds.). Methods in olfactory research. Academic Press, New York.

NEW INFORMATION AND APPROACHES

Mountain Pine Beetle and Disease Management in Lodgepole Pine Stands: Inseparable

David L. Kulhavy, Arthur D. Partridge and Ronald W. Stark

ABSTRACT

Pest management strategies addressing only the mountain pine beetle (*Dendroctonus ponderosae* Hopkins) may lead to recurrence of mountain pine beetle, occurrence of associated insects and expansion of disease problems. The roles of diseased lodgepole pine (*Pinus contorta* Douglas var. *latifolia* Engelm.) and of lodgepole pine with flooded root zones acting as triggers of mountain pine and associated bark beetle population build-ups are presented. Silvicultural treatments for dwarf mistletoe, and to a lesser extent for the rusts and root disturbances, are presented in the context of mountain pine beetle management. We conclude that the forest manager must consider the consequences of any silvicultural prescriptions on diseases and insects.

INTRODUCTION

Effective integrated pest management is based upon a thorough knowledge of the ecology of the insect pest and its host(s) and the resultant effects of any management prescriptions on the host/pest ecosystem (Stark 1977).

The work reported here was funded in part by the National Science Foundation and the Environmental Protection Agency through a grant to the University of California. The findings, opinions and recommendations expressed herein are those of the authors and not necessarily of the National Science Foundation, the Environmental Protection Agency or the University of California.

Evidence that diseases and site quality are intimately involved in population fluctuations of the mountain pine beetle, *Dendroctonus ponderosae* Hopkins, is mounting (Cobb et al. 1974, Hawksworth 1975, Alexander et al. 1976, Berryman 1976, Goheen 1976, Kulhavy 1977). Management practices, climate and site quality also affect both insect and disease fluctuations in forest stands (Safranyik et al. 1974, Amman et al. 1973, Amman et al. 1977). Partial cuttings to promote vigorously growing stands may increase the incidence and spread of dwarf mistletoe (*Arceuthobium americanum* Nuttall ex Engelm.) (Baranyay 1975) and root diseases (Partridge et al. 1977). This interaction of biological systems is generally ignored in forest practices.

Collection of survey data on stem and branch diseases, mountain pine beetle and other insects is simple if planned in advance of and then implemented as part of forest management (Alexander et al. 1976). On the other hand, surveys for root-inhabiting insects and diseases are more difficult. These require sampling of root crowns (Ehrlich 1939, Cobb et al. 1974, Goheen 1976) or other techniques that allow direct examination of the root systems (Hertert et al. 1975, Goheen 1976, Kulhavy 1977). Cultural isolations must be combined with field identifications, as many of the pathogens act together and produce the same disease symptoms.

This paper examines the management implications of treating lodgepole pine stands infested with mountain pine beetle without proper consideration of other stand-debilitating factors such as diseases and excessive ground water.

METHODS

Study Areas

We examined 16 lodgepole pine (*Pinus contorta* Douglas var. *latifolia* Engelman) stands in central Idaho in 1976 and 1977. These stands ranged from 40 to 80 years of age and were at least 80 percent lodgepole pine in stocking and basal area (60 percent in one stand). Site indices ranged from 74 to 110 (Alexander 1966), and elevation from 1525 to 1700 m (5002 to 5576 ft).

In each of 11 stands in the McCall, Idaho area, 10 plots were established at 1-chain intervals. A plot consisted of all trees acceptable by a 20-factor prism. In the Dixie, Idaho area only one prism plot was established in each of 5 stands. Stand structure and mistletoe incidence were recorded for these plots. On each lodgepole pine in these prism cruises crown infections of dwarf mistletoe were rated using the 6-point system of Hawksworth and Lusher (1956). Stem infections by dwarf mistletoe, stalactiform rust (*Peridermium stalactiforme* Arthur and Kern) and western gall rust (*P. harknessii* J.P. Moore) were also recorded for each tree. Basal area, stems per hectare and mortality from the mountain pine beetle were reconstructed from the cruise data for the years 1972 through 1977.

Root Excavations

In each of the 16 sample stands, from 4 to 8 root systems were excavated with explosives (a total of 92 trees) in order to examine them for diseases and bark beetles. Infestations of secondary bark beetles, including *Ips* spp., *Dendroctonus valens* LeConte, *Hylurgops* spp. and *Hylastes* spp., were noted. Samples of diseased wood from the roots and stems were collected and cultured on malt agar following the procedures of Nobles (1948). The resulting fungi were then identified using descriptions of Nobles (1948), Kendrick (1962) and Partridge and Miller (1974). Both symptomatic (fading crowns, mountain pine beetle-attacked trees) and apparently healthy trees were examined.

RESULTS AND DISCUSSION

In central Idaho, major losses from the mountain pine beetle occurred from 1971 through 1975, declined precipitously in 1976, then increased slightly in 1977. The mountain pine beetle is presently most active in those stands with a dwarf mistletoe infection rating of 3 or higher, in stems infected with dwarf mistletoe, western gall rust or stalactiform rust, and in stands with water-saturated soils or standing water. The beetles are now colonizing disease-weakened portions of host trees, and tree mortality and attacked trees increased in 1977. Lodgepole pine strip-attacked by the mountain pine beetle, with root diseases, or with the root systems submerged are serving as reservoirs for secondary bark beetles (Table 1) including *Hylurgops porosus* LeConte, *D. valens*, *Ips* spp.,

and *Hylastes longicollis* Swaine, some of which may be carrying root-stain fungi, including species of *Verticicladiella*, *Graphium*, *Leptographium*, *Europhium*, and *Ceratocystis* (Wagner 1977, Kulhavy and Partridge, unpublished data).

Although mortality from mountain pine beetle is currently low (1 to 5 stems per hectare or 0.3 to 2 per acre), high incidence of stem pathogens, periodic water table fluctuations and the increase of root diseases provide ample opportunities (triggers) for the resurgence of the beetle population.

Mountain Pine Beetle and Dwarf Mistletoe

Lodgepole pines with bole infections of dwarf mistletoe are targets for localized mountain pine beetle infestations. Hawksworth (1975) recognized that mountain pine beetles attack lodgepole pines which are heavily infested with dwarf mistletoe. McGregor (these proc.), however, demonstrated that losses to beetles are much reduced in heavily mistletoed stands. Mistletoe infections stimulate different kinds of tree growth, one of which is swelling in the area of infection. These swollen sites, because of thicker phloem, can provide a substrate for bark beetle reproduction (Amman these proc.) and may be sources of bark beetle build-ups. The opportunity to reduce bark beetle populations exists here because the resource manager can substantially reduce the incidence of dwarf mistletoe by silvicultural manipulations of stands (Hawksworth 1977).

Table 1. Bark beetles and fungi found together in root systems of lodgepole pine (*Pinus contorta* var. *latifolia*), central Idaho, 1976-1977.

Fungus	Frequency ^a (N = 92)	Associated Bark Beetles
<i>Armillaria mellea</i>	occasional	none
<i>Europhium clavigerum</i>	abundant	<i>Dendroctonus ponderosae</i> ; <i>Hylurgops porosus</i>
<i>Graphium</i> spp.	abundant	<i>D. ponderosae</i> ; <i>H. porosus</i>
<i>Leptographium</i> spp.	abundant	<i>D. ponderosae</i> ; <i>H. porosus</i>
<i>Ceratocystis</i> spp.	abundant	<i>D. ponderosae</i> ; <i>H. porosus</i>
<i>Verticicladiella wagnerii</i>	rare	<i>H. porosus</i>
<i>V. procera</i>	occasional	<i>H. porosus</i>
<i>V. abietina</i>	abundant	<i>H. porosus</i>
<i>V. antibiotica</i>	rare	?
<i>V. penicillata</i>	abundant	<i>D. ponderosae</i> , <i>Ips mexicanus</i> ; <i>H. porosus</i> ; <i>Hylastes longicollis</i>

^a Rare, less than 5 occurrences in all trees sampled; occasional, more than 5 and less than 20 occurrences; abundant, more than 20 occurrences.

When large-scale salvage or pest management operations are required (Baranyay and Smith 1972), or during commercial and precommercial thinnings, the resource manager has an opportunity to incorporate prescriptions that discriminate against pest problems (Hawksworth 1977). Although this potential has been recognized for many years, resource managers have been slow in utilizing the existing knowledge to improve the vigor and subsequent productivity of diseased stands (Alexander et al. 1976). Reasons for this include higher priority for other timber species over lodgepole pine, cost of treatment and insufficient knowledge of how to manage a host/insect/disease system.

Schwandt (1977) reviewed the literature and found 6 alternatives for dwarf mistletoe treatment. These are 1) do nothing, 2) convert to non-host species, 3) clearcut, 4) seed-tree cut with removal of overstory after regeneration is established, 5) completely sanitation cut and 6) partially sanitation cut, which reduces but does not eliminate dwarf mistletoe. Land managers can achieve one or more of the above in prescribing regeneration cuts, pruning, salvage and commercial and precommercial thinnings (Baranyay and Smith 1972, Baranyay 1975).

The first alternative should be employed if stands are already within 10 years of harvesting, undergoing natural conversion to a desirable host species, or the manager rejects the remaining alternatives for economic or other reasons.

A conversion of stands to a non-host species for a specific dwarf mistletoe problem can both decrease the incidence of the disease and eliminate the potential of bole-infected trees serving as host for the local build-up of mountain pine beetle populations.

Clearcutting is an excellent method of eliminating dwarf mistletoe and also the mountain pine beetle, if brood trees are removed from the site. Against the pathogens, clearcutting is best used in young stands when infection levels are 4 or greater (Hawksworth and Lusher 1956) and commercial harvest will not be realized in a normal stand rotation. Such heavily infected stands deteriorate rapidly from the effects of diseases and beetles (Hatch 1967).

Regeneration using seed-tree cuts, a selection cut on a species preference basis, or a shelterwood cut may be the best alternative when heavily infected stands are to be harvested and clearcuts are unacceptable, or when a local seed source is preferred for regeneration. Diseased trees should not be left as seed sources because of their potential as mountain pine beetle host trees.

Complete sanitation requires the removal of all infected and infested material and is usually prohibitively expensive. It is practical only in unusual circumstances, such as at campgrounds or similar areas where esthetics are of primary concern.

Partial sanitation for mistletoe-infested stands is aimed at long-range reduction of this pathogen and is generally com-

patible with proposed mountain pine beetle treatments if planned in advance (e.g., diameter-phloem cuts; Hamel and McGregor 1976, Cole and Cahill 1976, Amman et al. 1977). Following guidelines for reducing mistletoe and eliminating potential host trees for the mountain pine beetle may result in less than optimal stocking of desirable diameter classes, however, because mistletoe infects all size classes. Partial sanitation is not recommended for stands over 40 years of age if over 40 percent of the stand is infected (Hawksworth 1977).

Mountain Pine Beetle and Rusts

Mountain pine beetles can successfully attack boles of lodgepole pine with rust cankers on the main bole. These attacks are concentrated at the edge of cankers and produce less than 0.6 m (2 ft) of galleries. Recommendations for treatment of stands having mountain pine beetle infestations and western gall rust and stalactiform rust include the removal of all stem-infected trees during silvicultural operations (even if this results in less than desirable stocking), conversion to non-host species, and promotion of non-infected trees. Ignoring rust-infected trees in these stands will provide diseased host trees for the mountain pine beetle.

Mountain Pine Beetle and Root Diseases

Incidence of root diseases and mountain pine beetle infestation did not correlate well in the studies of mature lodgepole pine (Partridge and Miller 1972). Gara and Geiszler (pers. comm.¹), however, found an association between root disease and the beetle in old growth lodgepole pine stands. In post-outbreak areas of the mountain pine beetle we found an increase in the number of infections of *Armillaria mellea* (Vahlgren) Kummer on lodgepole pine roots and an increase in incidence of root-stain fungi (*Verticicladiella*, *Graphium*, *Leptographium*, *Europhium* and *Ceratocystis*) and associated secondary bark beetles (Table 1).

Although root diseases have not been implicated in predisposing lodgepole pine to attack by the mountain pine beetle, we feel that evidence from studies of other pines (*Pinus ponderosa* Lawson, Cobb et al. 1974, Goheen 1976; *Pinus monticola* Douglas, Kulhavy 1977) indicate there is a real possibility of bark beetle and root disease interactions. Ignoring these root-diseased trees (stands) may result in 1) a resurgence of the mountain pine beetle, 2) an increase in the incidence of secondary beetles that carry root-stain fungi, and 3) spread of root diseases and root-stain fungi.

Integration of mountain pine beetle management with root disease management is difficult because of certain characteristics of root-diseased lodgepole pine: 1) they are difficult to identify; 2) the dynamics of the diseases are virtually

¹ R.I. Gara and D.R. Gieszler are located at the University of Washington, College of Forest Resources, Seattle, WA.

unknown; and 3) root diseases have not been positively correlated with mountain pine beetle build-ups in lodgepole pine. *In a post-outbreak area an interrelationship does occur between bark beetles and diseases.* We are currently conducting research on the bark beetles associated with root disease complexes.

We believe that management recommendations in post-outbreak areas should include 1) monitoring populations of bark beetles and diseases in these areas, 2) encouraging conversion to a non-host species and 3) treatment of diseased stumps of salvaged trees and of dead-standing trees. Neglecting these post-outbreak areas may lead to 1) resurgence of the mountain pine beetle populations, 2) an increase in secondary pests (insects and diseases) and 3) a delay in effecting conversion to a vigorous, productive stand.

Mountain Pine Beetle and Root Flooding

The most severe root disturbances we found during our excavations of the root systems of lodgepole pines were the complete or partial submergence of the roots of trees in marshy areas, along stream banks and adjacent to creeks. These lodgepole pines are thick-phloemed and can produce a large residual mountain pine beetle population. These trees appear to be the focal point of bark beetle build-ups in the Paddy Flat and Kennally Creek areas near McCall.

This complete or partial submergence of the root systems results in rapid killing of large-diameter, thick-phloemed lodgepole pine and an increase in the formation of succulent root tissue, susceptible to root diseases (Boyce 1966).

The only management alternative for lodgepole pine growing in these areas that are subject to severe water table fluctuations is to treat them as **high-risk areas**. Management guidelines include: 1) manage lodgepole pine on a shortened rotation; 2) encourage stand conversion to other species adapted to these habitats; 3) discourage lodgepole pine reproduction to convert area to non-timber use; 4) border plant with other tree species to protect lodgepole pine trees within the stand (Amman 1975); and 5) give stands having increasing mountain pine beetle populations top priority in management. If these areas are ignored, regardless of the number of trees in them, mountain pine beetle may build up rapidly and move into economically valuable stands.

CONCLUSIONS

It is becoming increasingly clear that disease management and bark beetle management are inseparable. Ineffective or inaccurate insect and disease surveys may cause the land manager to evaluate the situation erroneously. It is important that no part of the insect/disease system be ignored, as is so often the case with "target"-type controls. A single pest cannot be effectively managed over the length of the stand rotation if other interactive agents are ignored. Management guidelines for pest control must integrate silvicultural systems with other biotic and abiotic systems. Ineffective or partially

effective control measures may magnify the pest problems, deplete the usefulness of a stand and prevent regeneration of future forests.

QUESTIONS AND ANSWERS

- Q. What is the phloem thickness of trees with root disease? What is the mountain pine beetle brood production from root-diseased trees?
- A. Phloem thicknesses of lodgepole pine with root-stain fungi were 0.25 cm (0.10 inch) or greater. We did not measure brood production. Lodgepole pine with root-stain fungi or with root systems submerged or partially submerged in water had up to 77.5 m (250 ft) of mountain pine beetle brood gallery.
- Q. Many investigators have referred to mountain pine beetle infestations starting in open-grown trees along stream courses and meadow edges. Why do you think this happens? Also, does disease or mountain pine beetle come first?
- A. There is no single cause or single effect setting off bark beetle population build-ups. The entire biotic and abiotic system should be examined before assigning a "cause" to a mortality center. In our examination of root systems of lodgepole pine, we found submerged and partially submerged root zones a contributing factor to the decline of large-diameter lodgepole pine.

It is not important to know which came first—the mountain pine beetle, or disease. What is important is that resource managers must manage the system and not just the pest. In our examination of lodgepole pine stands, we found that managing for the mountain pine beetle without due consideration for diseases and site condition will lead to perpetuation of similar disease/insect problems over the length of the stand rotation.

REFERENCES

- Alexander, N.E., J.H. Borden and J.M. Vakenti. 1976. A pest management study of a mountain pine beetle outbreak in tree license number 9. Pest Management Pap. No. 8, Pest. Cen., Dept. Bio. Sci., Simon Fraser Univ., Burnaby, B.C. 95 pp.
- Alexander, R.R. 1966. Site indexes for lodgepole pine, with corrections for stand density: Instructions for field use. USDA Forest Serv. Res. Pap. RM-24. Rocky Mtn. Forest and Range Exp. Sta., Ft. Collins, CO. 7 pp.
- Amman, G.D. 1975. Insects affecting lodgepole pine productivity. Pages 310-341 in D.M. Baumgartner (ed.). Management of lodgepole pine ecosystems. Washington State Univ. Coop. Ext. Serv., Pullman.

- Amman, G.D., B.H. Baker and L.E. Stipe. 1973. Lodgepole pine losses to mountain pine beetle related to elevation. USDA Forest Serv. Res. Note INT-171. Intermtn. Forest and Range Exp. Sta., Ogden, UT. 8 pp.
- Amman, G.D., M.D. McGregor, D.B. Cahill, and W.H. Klein. 1977. Guidelines for reducing losses to mountain pine beetle in unmanaged stands in the Rocky Mountains. USDA Forest Serv. Gen. Tech. Rept. INT-36. Intermtn. Forest and Range Exp. Sta., Ogden, UT. 19 pp.
- Baranyay, J.A. 1975. Dwarf mistletoe as a factor in western Canada. Pages 359-376 in D.M. Baumgartner (ed.). Management of lodgepole pine ecosystems. Washington State Univ. Coop. Ext. Serv., Pullman.
- Baranyay, J.A., and R.B. Smith. 1972. Dwarf mistletoe in British Columbia and recommendations for their controls. Environ. Can. Forest Serv., Pac. Forest Res. Cen., Victoria, B.C. 18 pp.
- Berryman, A.A. 1976. Theoretical explanation of mountain pine beetle dynamics in lodgepole pine forests. Environ. Entomol. 5:1225-1233.
- Boyce, J.S. 1966. Forest pathology. McGraw-Hill Book Co., New York. 572 pp.
- Cobb, F.W., Jr., J.R. Parmeter, Jr., D.L. Wood and R.W. Stark. 1974. Root pathogens as agents predisposing ponderosa pine and white fir to bark beetles. Pages 8-15 in Proc. Fourth Internat. Conf. on *Fomes annosus*, IUFRO Sect. 24: Forest Prot., Athens, GA.
- Cole, W.E., and D.B. Cahill. 1976. Cutting strategies can reduce probabilities of mountain pine beetle epidemics in lodgepole pine. J. Forest. 74:294-297.
- Ehrlich, J. 1939. A preliminary study of root diseases in western white pine. USDA Forest Serv., Northern Rocky Mtn. Forest and Range Exp. Sta. Pap. No. 1. Missoula, MT. 11 pp.
- Goheen, D.J. 1976. *Verticicladiella wagnerii* on *Pinus ponderosa* Epidemiology and interrelationships with insects. Ph.D. diss. Univ. of California, Berkeley. 129 pp.
- Hamel, D.R., and M.D. McGregor. 1976. Harvesting strategies for management of mountain pine beetle infestations in lodgepole pine, Montana. USDA Forest Serv., Forest Environ. Prot. Rep. 76-3, Missoula, MT. 7 pp.
- Hatch, C.R. 1967. Effects of partial cutting in overmature lodgepole pine. USDA Forest Serv. Res. Note INT-66. Intermtn. Forest and Range Exp. Sta., Ogden, UT. 7 pp.
- Hawksworth, F.W. 1975. Dwarf mistletoe and its role in lodgepole pine ecosystems. Pages 342-358 in D.M. Baumgartner (ed.). Management of lodgepole pine ecosystems. Washington State Univ. Coop. Ext. Serv., Pullman.
- _____. 1977. Silvicultural control of dwarf mistletoe in young lodgepole pine stands. USDA Forest Serv., Forest Insect and Dis. Manage. Tech. Rep. R2-10, Lakewood, CO. 13 pp.
- Hawksworth, F.W., and A.A. Luscher. 1956. Dwarf mistletoe survey and control on the Mescalero-Apache reservation, New Mexico. J. Forest. 54:384-390.
- Hertert, H.D., D.L. Miller and A.D. Partridge. 1975. Interaction of bark beetles (Coleoptera: Scolytidae) and root-rot pathogens in grand fir in northern Idaho. Can. Entomol. 107:899-904.
- Kendrick, W.B. 1962. The *Leptographium* complex, *Verticicladiella* Hughes. Can. J. Bot. 40:771-797.
- Kulhavy, D.L. 1977. The root and stem diseases, bark beetle complex, and their interactions in standing western white pine in Idaho. Ph.D. diss., Univ. of Idaho, Moscow. 69 pp.
- Nobles, M.K. 1948. Studies in forest pathology. VI. Identification of cultures of wood-rotting fungi. Can. J. Bot. (C) 26:281-431.
- Partridge, A.D., and D.L. Miller. 1972. Bark beetles and root rots related in Idaho conifers. Plant Dis. Repr. 56:498-500.
- _____. 1974. Major wood decays in the Inland Northwest. Idaho Res. Foundation Natur. Res. Ser. No. 3, Univ. of Idaho, Moscow. 125 pp.
- Partridge, A.D., E.R. Canfield and R.J. Chacko. 1977. Forest pathology outline. Forest, Wildl. and Range Exp. Sta. Contrib. No. 49. Univ. of Idaho, Moscow. 236 pp.
- Safranyik, L., D.M. Shrimpton, and H.S. Whitney. 1974. Management of lodgepole pine to reduce losses from the mountain pine beetle. For. Tech. Rep. No. 1, Pacific For. Res. Cen., Victoria, B.C. 24 pp.
- Schwandt, J.W. 1977. Dwarf mistletoe control guidelines for Idaho forests. Forest Insect and Disease Control, Idaho Dept. of Lands, Coeur d'Alene. 13 pp.
- Stark, R.W. 1977. Integrated pest management in forest practice. J. Forest. 75:251-254.
- Wagner, R.L. 1977. *Verticicladiella* species associated with *Hylurgops porosus* LeConte (Coleoptera: Scolytidae) in lodgepole pine. M.S. thesis, Univ. of Idaho, Moscow. 15 pp.

Mountain Pine Beetle Attack Dynamics in Lodgepole Pine

Daniel R. Geiszler and Robert I. Gara

ABSTRACT

The "switching mechanism" by which mountain pine beetles (*Dendroctonus ponderosae* Hopkins) will kill lodgepole pine (*Pinus contorta* Douglas var. *murrayana* (Greville and Balfour) Engelman) in groups during outbreaks was investigated. The agents causing beetles to switch from attacking a "focus" tree to attacking a "recipient" tree appear to be the sequential effects of aggregative and anti-aggregative pheromones. Analysis of the attack rates shows that recipient trees are initially attacked more quickly than trees baited with *trans*-verbenol and α -pinene. Regression analysis shows that beetles select recipient trees on the basis of tree diameter and distance from the focus tree. Thinning prescriptions based on a tolerance interval about a regression line relating diameters of recipient trees to distance from the focus tree might be used to reduce beetle kill.

INTRODUCTION

During outbreaks, the mountain pine beetle (*Dendroctonus ponderosae* Hopkins) kills millions of cubic meters of timber annually (Powell 1966, Shrimpton 1975). Although the beetles primarily invade weakened trees during periods of

low population density, attacks on healthy trees are common during outbreaks, when beetles kill trees in groups (Graham and Knight 1965, Rudinsky 1962).

Group killing of trees occurs as follows. After initial host selection, the attacking female beetles release an aggregative pheromone, *trans*-verbenol (Pitman et al. 1968), which stimulates beetles to fly to the selected focus tree. As the focus tree is mass-attacked, incoming beetles switch from attacking this focus tree to attacking adjacent trees (recipient trees) (McCambridge 1967, Billings 1974). A mass-attacked recipient tree then becomes a focus tree and again incoming beetles may switch from attacking this new focus tree to attacking new recipient trees. We term the change in the focus of attacks "switching."

The principal causal agents of switching are likely to be the sequential effects of aggregative and anti-aggregative pheromones. While the aggregative pheromone serves to attract beetles to the focus tree (Pitman et al. 1968), it may also, at high concentrations, stimulate incoming beetles to land on and attack several adjacent trees simultaneously. In contrast, an anti-aggregative pheromone prevents incoming beetles from attacking an already fully attacked tree (Renwick and Vité 1970, Furniss et al. 1973, Rudinsky et al. 1974). The repelled beetles may then attack nearby trees at a quick rate, which may aid beetles in killing trees (Miller and Keen 1960, Rasmussen 1974, Reid et al. 1967, Smith 1975).

This work was supported according to Cooperative Agreement 16 USC 581: 581a-581i between the University of Washington and the Pacific Northwest Forest and Range Experiment Station. Based on a thesis submitted in partial fulfillment of the requirement for the M.S. degree in the Biomathematics Group at the University of Washington.

During switching, beetles seem to select a recipient tree by virtue of its diameter and distance from the focus tree. The largest-diameter trees suffer the greatest mortality (Cole and Amman 1969, Roe and Amman 1970) and the distance over which switching may occur is limited. Studies on the southern pine beetle (*D. frontalis* Zimmerman) indicate that the number of beetles landing and attacking decreased with increased distance from the attractant source (Coster and Gara 1968, Gara and Coster 1968). This observation presumably involves a decrease in the pheromone concentration as distance increases (Sutton 1947). During switching, a threshold level in pheromone concentration is assumed to exist such that beetles only attack an adjacent tree that has a pheromone concentration above the threshold. Therefore, if trees are spaced far enough apart, the pheromone concentration will be lower than the threshold and beetles will not attack (Gara and Coster 1968).

If indeed tree spacing is important to the switching mechanism, then judicious thinning regimes could reduce bark beetle damage (Sartwell and Stevens 1975). Sartwell and Dolph (1976), for example, found that there was less *D. ponderosae* damage in thinned ponderosa pine (*Pinus ponderosa* Lawson) stands than in controls.

We wished to determine how distance between trees, tree diameters, and pheromone concentration related to the dynamics of a *D. ponderosae* outbreak in lodgepole pine, *Pinus contorta* var. *murrayana* (Greville and Balfour) Engelman (Little 1971).

MATERIALS AND METHODS

We conducted our studies in the northern part of the Fremont National Forest in south central Oregon. The study site is characterized by an infertile pumice soil (Youngberg and Dyrness 1964) deposited about 6600 years ago when Mt. Mazama erupted and formed Crater Lake. Our site lies 1980 m (6500 ft) above sea level and rainfall is less than 63.5 cm (25 inches) per year. Consequently, the lodgepole pine/bitterbrush community grows sparsely. The range of observed tree diameters extends up to 50.8 cm (20 inches) with a mean dbh of 19.7 cm (7.8 inches) and with ages of about 135 years for a 20.3-cm (8-inch) tree. Over 6 years (1970-1975) an extensive mountain pine beetle outbreak has killed about 58 percent of the trees greater than 15.2 cm (6 inches) dbh in 20.2 ha (50 acres) that we surveyed.

Plots of lodgepole pine were chosen so that the distance between a center tree and the nearest tree ranged from 4.3 to 15.2 m (14 to 50 ft) and the diameter of the nearest tree in the plots ranged from 10.2 to 38.1 cm (4 to 15 inches). The plots, which encompassed all of the attacked trees in a group, were mapped using a planar table and a 30.5-m (100-ft) tape measure. The distances between trees and the planar table were measured to the nearest 0.3 m (foot) and dbh was measured to the nearest 2.5 cm (inch) on all trees.

Mountain pine beetles were induced to attack the center tree of each plot by temporarily baiting the tree with 3 cc of *trans*-verbenol and α -pinene mixed in a ratio of 9:1 (i.e., pondelure, Pitman 1971). The bait was removed after 30 attacks had occurred on the center tree. In most cases the arbitrary standard of 30 attacks was found to be indicative of an attraction sufficient to induce a mass attack (Billings 1974).

Five out of 17 plots were baited 14 July 1975, 7 on 2 August and 5 on 12 August. The plots were monitored daily from 14 July to 26 August 1975. A daily count of fresh beetle attacks was taken each morning by marking all the entrance holes below 2.4 m (8 ft) with staples on each tree. A recipient tree and the nearest focus tree were designated as paired trees where switching had occurred. Trees that were "successfully" switched to and mass-attacked were of the most interest; thus those trees with less than 30 total attacks on the lower 2.4 m of the bole were considered to be "unsuccessful" and were separated from the "successfully" colonized recipient trees. Pairs of trees where switching had occurred while the center tree was still baited were eliminated from the analyses, as the bait may have stimulated incoming beetles to attack the recipient trees prematurely.

Since the amount of *trans*-verbenol emitted from a focus tree was suspected to cause beetles to switch (Rasmussen 1972), an equation was developed, in reference to the work of Pitman and Vite' (1969), to estimate the relative amount emitted over time (Appendix).

The initial attack rates for those trees attacked by switching were compared with those for trees attacked due to the synthetic attractant, pondelure, since we thought that a quick rate of beetle attacks aided beetles in killing healthy trees (Rasmussen 1974). By this comparison we could determine whether switching was instrumental in beetles' killing trees.

Regression analysis was performed between the distance over which switching occurred and the diameter of recipient trees. The distance between the focus tree and the recipient tree was chosen as the independent variable. The dependent variable was the diameter of the recipient tree. The statistical analysis consisted of testing, at the .05 significance level, whether the coefficient of the independent variable was equal to zero (i.e., if the slope was equal to zero).¹ For predictive purposes a tolerance interval was constructed about the regression line (Miller 1966, Wallis 1951).

¹ Before the statistical analysis was made, the assumptions of having the correct model, normality, constant variance (homoscedasticity) and no outliers were checked (Neter and Wasserman 1974:113-121, 282; Draper and Smith 1966:26-32; Shapiro and Wilk 1965, Grubbs 1969, Tietjen and Moore 1972).

RESULTS AND DISCUSSION

Beetles began attacking on 25 July 1975 and ended their attacks by 26 August 1975. In nine of the plots the incoming beetles switched their attack from focus to recipient trees, so that a total of 47 trees were attacked. Ten trees were omitted from the regression analysis because they were considered "unsuccessfully" attacked (i.e., less than 30 attacks) and six trees were eliminated because the bait was on the center tree when switching occurred. The remaining 31 trees were paired as recipient and focus trees and formed the observation units for the analysis.

The cumulative number of attacks and the relative amount of *trans*-verbenol emitted (see Appendix) were graphed with respect to time for each pair of focus and recipient trees (Fig. 1 is one example). Examination of the 24 graphs showed that only five pair of trees had switching before the peak emission of *trans*-verbenol from the focus tree.

The initial attack rates, analyzed by comparing the number of attacks on each tree's first day of attack, had a mean of 23 attacks (below 2.4 m) for those trees baited with pondelure and a significantly greater mean of 44 attacks for those trees attacked by switching ($t(35) = 1.81, p < .05$).

The regression analysis indicated that beetles selected recipient trees according to the regression equation:

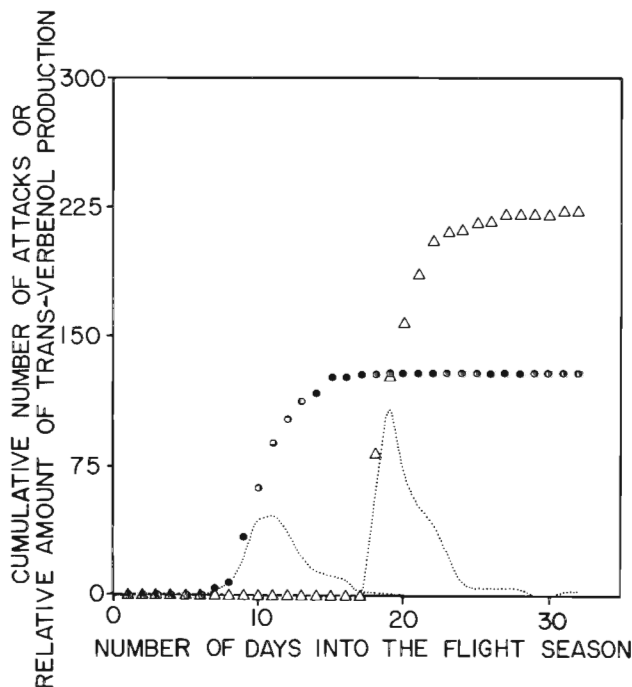


Fig. 1. One example of the cumulative number of attacks on a focus tree (points) and a recipient tree (triangles) and their estimated relative amount of *trans*-verbenol emission (curves) as related to the number of days into the flight season.

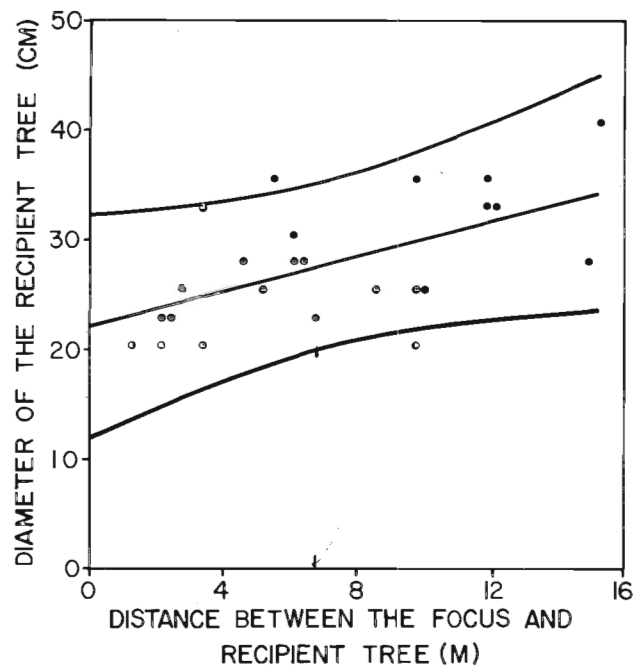


Fig. 2. The observed values and the regression line for the relationship between the diameter of the recipient tree and the distance between the recipient tree and the focus tree. A tolerance interval is plotted about the regression line.

tree diam. = $22.05 + (0.83)(\text{distance from focus tree})$
where diameter is in centimeters and distance in meters,
with a correlation coefficient of $r = .57$.

The slope of 0.83 was significantly greater than zero ($p = .003$). Figure 2 is a graph of the observations, the regression line and a tolerance interval which contains 90 percent of all future observations with a 90 percent probability.

The graphs of the cumulative number of attacks and of the relative amount of *trans*-verbenol emitted indicate that *trans*-verbenol alone does not stimulate incoming beetles to switch attacks from a focus to a recipient tree (Fig. 1). If *trans*-verbenol alone were to stimulate incoming beetles to land on and attack a recipient tree, we would expect beetles to attack before or at peak *trans*-verbenol emission. On the contrary, beetles switched only 5 times out of 24 times before or at the estimated peak of *trans*-verbenol emission. This interpretation rests on the provision that the equation given in the Appendix is correct.

Even though a repelling pheromone may slow the attack rate on a focus tree, *trans*-verbenol emission appears to continue to attract beetles to the vicinity so that recipient trees are quickly attacked. Evidence for this hypothesis is that beetles must feed for about 12 hours before they produce large quantities of *trans*-verbenol (Pitman and Vité 1969). Thus *trans*-verbenol emission from the recipient tree would be low and could not stimulate a quick attack rate. The fact that the initial attack rates for recipient trees are significantly

greater than those for baited trees suggests that the focus tree plays an important role in switching the attack to adjacent trees.

The results suggest that beetles are stimulated to attack a recipient tree during switching by a combination of chemicals emanating from the focus tree and the size of the recipient tree. That is, during switching, beetles attack big trees rather than small ones, but if the stimulants from a focus are too weak, then beetles do not attack at all. These results correspond with Rasmussen's (1972) observations where small-diameter trees were baited with pondelure, but not attacked, while nearby larger-diameter trees were attacked.

Thinning procedures to reduce switching might be based on the tolerance interval about the regression line (Fig. 2). For example, if the distances between the trees are 7.2 m (24 ft), then 90 percent of the recipient tree diameters would be greater than 20.3 cm and less than 35.6 cm (14 inches), with a 90 percent probability. Thus, if trees were no larger than 20.3 cm with 7.2 m spacing, then the likelihood of switching would be small.

Actual thinning prescriptions might be based on empirical results from a variety of stand cuttings and beetle population densities or from a model of biological factors affecting switching. Although the causal agents of switching are not fully understood, our results indicate that when switching occurs there is a quick rate of beetle attacks on recipient trees which aids successful tree colonization (Rasmussen 1974).

QUESTIONS AND ANSWERS

- Q. Your graph of the distance switched vs. tree diameter seems to imply that the closer the recipient tree is to the focus tree, the smaller the diameter of the recipient tree has to be in order to be mass attacked. Could you elaborate on this?
- A. I don't think this implication is true, since I would expect large trees to be readily attacked when they are close to a focus tree. The reason our observations show no large recipient trees near a focus tree is that there were no large trees near a focus tree, only smaller trees. Part of the reason for two large trees not becoming a focus and a recipient tree is that both would be attacked simultaneously (i.e., both would become recipient trees at the same time); hence, one of them could not be considered a focus tree.
- Q. Does the distance vs. dbh relationship change with the population level of mountain pine beetle?
- A. Yes, I believe the relationship would change with population level. We suspect that incoming beetles are stimulated in part by pheromones to attack adjacent trees, so that at low concentrations beetles will not attack, but at high concentrations they will. The pheromone concentration at an adjacent tree is dependent upon the distance from the focus tree and the rate of attacks on a focus tree, which is a function of population level. At a low population level the pheromone concentration would be low and switching would be restricted to short distances, and at the same time the number of incoming beetles would be small so that likelihood of successful switching would be small.
- I would like to add at this time that the regression equation and the prediction based on the tolerance interval will hold only when the causal conditions are similar to those of our study. Exactly what the causal agents are and how they relate to population level is not fully known.
- Q. Do you think mountain pine beetles react differently in lodgepole pine in the pumice soil area of central Oregon compared with non-pumice soil areas in eastern Oregon and the Rockies? Central Oregon lodgepole pine is often climax, often uneven-aged, and has non-serotinous cones.
- A. I would expect beetles to select larger-diameter trees in eastern Oregon and in the Rockies, since the diameters are generally greater than those of our study area. I suspect that the switching phenomenon is similar for many types of stands, since we think that the primary causal agents are pheromones, which are a common factor for all mountain pine beetles (as well as for other *Dendroctonus* beetles).
- Q. What stimulates the change in production from attracting pheromone to repellent pheromone? (How do the beetles know the tree has been attacked to its capacity?)
- A. Females, which initiate attacks on a tree, emit the attracting pheromone, which attracts both male and female beetles to the focus tree. While the females continue to emit the attracting pheromone, the males emit a repelling pheromone. The attracting pheromone may act over a long range, whereas the repelling pheromone may act over a short range, so that beetles continue to fly to the focus tree but are repelled at close distances, where the concentration is high.
- Q. How did you determine that a tree that you termed a "recipient tree" was not in fact an initially attacked "focus tree," rather than one "switched" to?
- A. The answer lies within the methods and materials section.
- Q. Would stand density and mean stand dbh affect the diameter vs. distance regression you derived to describe the switching phenomenon?

- A. Our results suggest that pheromones and visual cues are causal agents in switching. I suspect that the pheromone quality or quantity will not change much with a change in stand density or dbh. However, the visual cues that a beetle uses may depend upon the relative size of trees rather than absolute size, in which case the regression line would probably change.
- Q. Do you believe that pondelure is an effective chemical for aggregating mountain pine beetle?
- A. Yes. All of the trees I baited were killed when the population of flying beetles was sufficient and if the baited tree was greater than 12.5 cm dbh.
- Q. Did attacks occur on "recipient" trees before the "focus" tree was fully attacked? Does the visual response (to large trees) operate only after switching, or does the attraction pheromone bring the beetles to the vicinity of suitable hosts where the beetles then select a host tree by visual cues?
- A. Nearly all of the focus trees had three-fourths of their total number of attacks when switching occurred. I believe the answer to the second question lies within the discussion section.
- Q. How does intensive management of lodgepole pine relate to attack by mountain pine beetle, if we manage at 370 to 500 stems per hectare (150 to 200 stems/acre) above 762 m (2500 ft) elevation in Washington? Is this feasible?
- A. At 7.2 m (24 ft) spacing, the number of stems per hectare would be about 175 (70/acre). This type of thinning would reduce switching by quite a bit, according to our results, providing the causal agents are similar to those in our study. I suspect that thinning need not be as far as 7.2 m, since tree vigor should increase when released from competition so that successful beetle colonization is deterred. Also, since the source of attractant will be from trees widely separated rather than from several focus trees close together, the beetles will be divided and less effective at killing. As a guide one might use Sartwell and Dolph's (1976) results in ponderosa pine. They found that 4.6 m (15 ft) spacing (i.e., 375 to 500 stems/ha) produced the greatest net growth during a 5-year period.

REFERENCES

- Billings, R.F. 1974. Host selection and attack behavior of *Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae) in ponderosa pine of eastern Washington. Ph.D. diss. Dept. of Forest Resources, Univ. of Washington, Seattle. 229 pp.
- Cole, W.E., and G.D. Amman. 1969. Mountain pine beetle infestations in relation to lodgepole pine diameters. USDA Forest Serv. Res. Note INT-95. Intermt. Forest and Range Exp. Sta., Ogden, UT. 7 pp.
- Coster, J.E., and R.I. Gara. 1968. Studies on the attack behavior of the southern pine beetle. II. Response to attractive host material. Contrib. Boyce Thompson Inst. 24:69-76.
- Draper, N.R., and H. Smith. 1966. Applied regression analysis. John Wiley and Sons, Inc., New York. 407 pp.
- Furniss, M.M., L.N. Kline, R.F. Schmitz and J.A. Rudinsky. 1973. Tests of three pheromones to induce or disrupt aggregation of douglas-fir beetle (Coleoptera: Scolytidae) on live trees. Ann. Entomol. Soc. Amer. 65:1227-1232.
- Gara, R.I., and J.E. Coster. 1968. Studies on the attack behavior of the southern pine beetle. III. Sequence of tree infestation within stands. Contrib. Boyce Thompson Inst. 24:77-86.
- Graham, S.A., and F.B. Knight. 1965. Principles of forest entomology. McGraw-Hill Book Co., New York. 417 pp.
- Grubbs, F.E. 1969. Procedures for detecting outlying observations in samples. Technometrics 11 (1):1-21.
- Little, E.L., Jr. 1971. Atlas of United States trees. vol. 1 - conifers and important hardwoods. USDA Forest Serv. Misc. Publ. 1146, U.S. Govt. Print. Off., Washington, D.C. 196 pp.
- McCambridge, W.F. 1967. Nature of induced attacks by the black hills beetles, *Dendroctonus ponderosae* (Coleoptera: Scolytidae). Ann. Entomol. Soc. Amer. 60:920-928.
- Miller, J.M., and F.P. Keen. 1960. Biology and control of the western pine beetle. USDA Forest Serv. Pac. SW Forest and Range Exp. Sta., Berkeley, CA. 381 pp.
- Miller, R.G. Jr. 1966. Simultaneous statistical inference. McGraw-Hill Book Co., New York. 272 pp.
- Neter, J., and W. Wasserman. 1974. Applied linear statistical models. Richard D. Irwin, Inc., Homewood, IL. 842 pp.
- Pitman, G.B. 1971. *trans*-Verbenol and alpha-pinene: their utility in manipulation of the mountain pine beetle. J. Econ. Entomol. 64:427-430.
- Pitman, G.B., and J.P. Vité. 1969. Aggregation behavior of *Dendroctonus ponderosae* (Coleoptera: Scolytidae) in response to chemical messengers. Can. Entomol. 101:143-149.
- Pitman, G.B., J.P. Vité, G.W. Kinzer, and A.F. Fentiman. 1968. Bark beetle attractants: *trans*-verbenol isolated from *Dendroctonus*. Nature 218:168-169.
- Powell, J.M. 1966. Distribution and outbreaks of *Dendroctonus ponderosae* Hopk. in Forests of western Canada. Inform. Rep. A-X-2, Forest Res. Lab., Calgary, Alberta. 19 pp.
- Rasmussen, L.A. 1972. Attraction of mountain pine beetles to small-diameter lodgepole pine baited with *trans*-verbenol and α -pinene. J. Econ. Entomol. 65:1396-1399.
- _____. 1974. Flight and attack behavior of mountain pine beetles in lodgepole pine of northern Utah and southern Idaho. USDA Forest Serv. Res. Note INT-18. Intermt. Forest and Range Exp. Sta., Ogden, UT. 7 pp.
- 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. J. Bot. 45:1115-1126.

- Renwick, J.A.A., and J.P. Vité. 1970. Systems of chemical communication in *Dendroctonus*. Contrib. Boyce Thompson Inst. 24:283-292.
- Roe, A.L., and G.D. Amman. 1970. The mountain pine beetle in lodgepole pine forest. USDA Forest Serv. Res. Pap. INT-71. Intermtn. Forest and Range Exp. Sta., Ogden, UT. 23 pp.
- Rudinsky, J.A. 1962. Ecology of Scolytidae. Annu. Rev. Entomol. 7:327-348.
- Rudinsky, J.A., M.E. Morgan, L.M. Libbey and T.B. Putnam. 1974. Antiaggregative-rivalry pheromone of the mountain pine beetle and a new arrestant of the southern pine beetle. Environ. Entomol. 3:90-98.
- Sartwell, C., and R. E. Dolph, Jr. 1976. Silvicultural and direct control of mountain pine beetle in second-growth ponderosa pine. USDA Forest Serv. Res. Note PNW-268. Pac. NW Forest and Range Exp. Sta., Portland, OR. 8 pp.
- Sartwell, C., and R.E. Stevens. 1975. Mountain pine beetle in ponderosa pine—prospects for silvicultural control in second-growth stands. J. Forest. 73:136-140.
- Shapiro, S.S., and M.B. Wilk. 1965. An analysis of variance test for normality (complete samples). Biometrika 52:591-611.
- Shrimpton, D.M. 1975. History of infestation in British Columbia and principles of detection. Pages 51-52 in Permanent Association Committee Proceedings. Western Forestry and Conservation Association. Portland, OR.
- Smith, R.H. 1975. Formula for describing effect of insect and host tree factors on resistance to western pine beetle attack. J. Econ. Entomol. 68:841-844.
- Sutton, O.G. 1947. The problem of diffusion in the lower atmosphere. Q. J. R. Meteorol. Soc. 73:257-276.
- Tietjen, G.L., and R.H. Moore. 1972. Some Grubbs-type statistics for the detection of several outliers. Technometrics 14:583-597.
- Wallis, W.A. 1951. Tolerance intervals for linear regression. Pages 43-51 in Proc. Second Berkeley Symposium on Mathematical Statistics and Probability, Statistics Lab., Dept. of Mathematics, Univ. of California, 31 July and 12 August, 1950. Univ. of California Press, Berkeley, CA.
- Youngberg, C.T., and C.T. Dyrness. 1964. Some physical and chemical properties of pumice in Oregon. Soil Sci. 97:391-399.

APPENDIX

Since the amount of *trans*-verbenol emitted from a focus tree was suspected to cause beetles to switch (Rasmussen 1972), an equation was developed, in reference to the work of Pitman and Vité (1969), to estimate the relative amount emitted over time. Pitman and Vité determined the relative amounts of *trans*-verbenol present in the feces of 50 female mountain pine beetles that had fed in ponderosa pine billets for various periods of time. In making the estimation we assumed that the amount of *trans*-verbenol in the feces reflects the amount emitted and that the amount emitted is similar for beetles in ponderosa pine and lodgepole pine.

The first step was to graph the relative amount of *trans*-verbenol in the feces as related to feeding time. Since beetles respond to *trans*-verbenol during the day, estimates of daytime averages of *trans*-verbenol production were used. These estimates, which were taken over the time intervals 0 to 10 and 24 to 34 hours of feeding, were calculated by averaging the amount present at the beginning and end of each interval. The averages for 0 to 10 and 24 to 34 hours were 7 and 10. Although measurements by Pitman and Vité did not extend beyond 36 hours, beetles are believed to produce *trans*-

verbenol during 48 to 58 hours of feeding as they are exposed to its precursor, α -pinene; accordingly, the average was set arbitrarily at 1.

The total relative amount of *trans*-verbenol emitted from a tree was calculated and graphed according to the equation

$$q(t) = V_0 * N_0(t) + V_1 * N_1(t) + V_2 * N_2(t)$$

where

	units	meaning
$q(t)$	—	relative amount of <i>trans</i> -verbenol emitted on day t.
t	days	number of days into the flight season.
V_i	1/attack	estimated relative amount of <i>trans</i> -verbenol emitted by a single <i>i</i> th-day-old beetle attack. (The estimates used are $V_0=7$, $V_1=10$, and $V_2=1$.)
$N_i(t)$	attacks	the number of the <i>i</i> th-day-old female beetle attacks on day t.

Cutting Strategies as Control Measures of the Mountain Pine Beetle in Lodgepole Pine in Colorado

Donn B. Cahill

ABSTRACT

Efforts to suppress mountain pine beetle (*Dendroctonus ponderosae* Hopkins) epidemics in Colorado have been carried out since the early 1900s using various methods of treating or removing beetle populations. These methods have slowed the rate of annual tree losses, but have done little to reduce total tree mortality over the course of an infestation, or to reduce the susceptibility of the stands to additional beetle attack. Based on recent research findings that demonstrated the importance of lodgepole pine (*Pinus contorta* Douglas var. *latifolia* Englemann) phloem thickness and diameter in mountain pine beetle epidemics, stands in the Middle Park area of Colorado were cut using strategies to reduce stand susceptibility to beetle attack. Partial cutting and clearcutting, combined with the logging of infested trees, were used to reduce the inventory of larger-diameter trees. Other factors considered were dwarf mistletoe, comandra rust and visual management concerns. Losses in partial-cut areas have been reduced to 1 to 2 percent of the residual trees, whereas in unmanaged stands 39 percent of the trees have been lost.

INTRODUCTION

Mountain pine beetle (*Dendroctonus ponderosae* Hopkins) epidemics in lodgepole pine (*Pinus contorta* Douglas var. *latifolia* Englemann) stands throughout much of the Rocky Mountains usually last between 5 and 7 years. During this period, tree mortality increases from about 1.25 trees per ha (0.5/acre) to a peak of over 62.5 trees per ha (25/acre)

in 3 to 4 years, then declines to less than 1.25 per ha during the next 2 to 3 years. The cumulative effect on the stand is drastic. Tree losses range from 60 percent of the 30 cm (12 inch) dbh class to about 90 percent of the trees 40 cm (16 inch) dbh and larger. Total stand mortality may average 33 percent or greater (trees 15 cm dbh and larger).

Lodgepole pine stands in the Middle Park of central Colorado are no different from those in other areas in that they have been "blessed" with mountain pine beetle infestations since at least 1910, the date of the first reported infestation. From 1915 to 1921, "cut and peel" was the most common treatment and was accomplished at the forest district level on a day-by-day basis. From 1933 to 1937, large-scale treatments were applied by the Civilian Conservation Corps. Infestations continued on a somewhat regular basis, with the current infestation beginning about 1963. Some effort was made to "control" the mountain pine beetle in 1964 and 1965; the effort was limited to clearcut sales and ethylene dibromide chemical treatments (see Klein these proc.).

The question that remained throughout these years was, "Do effective control measures exist?" Efforts to control populations of mountain pine beetle in lodgepole pine by chemical spraying, salvage logging or combinations of both treatments were evaluated recently (Amman and Baker 1972). Beetle populations declined in about the same number of years, whether or not control was attempted, and tree losses were similar for lodgepole pine stands having similar characteristics.

Techniques such as chemical spray, either preventive or insecticidal, salvage logging and logging of infested trees do not have, to any great extent, a lasting effect on either the course or the duration of an infestation or on the potential for population build-ups. Susceptibility of the stand to beetle epidemics remains because stand characteristics remain essentially the same.

A MANAGEMENT APPROACH

The basic problem facing the land manager is how to reduce the probability of beetle epidemics developing within particular stands of lodgepole pine. As is well documented, both in the literature and as presented at this symposium, epidemics are definitely correlated with the presence of large-diameter, thick-phloemed trees, and beetle brood production is correlated positively with phloem thickness.

Cole and Cahill (1976) stated, after measuring several Colorado stands of lodgepole pine, that epidemics are not as likely to occur in stands where the proportion of 20 cm (8 inch) dbh and larger trees containing phloem 0.28 cm (0.11 inch) thick or thicker is 20 percent or less. Therefore, the distribution of phloem thickness over diameter classes can be an effective measurement for evaluating infestation potential in a lodgepole pine stand. Guidelines for reducing losses of lodgepole pine to the mountain pine beetle have been developed, based on ecological relationships of the beetle to its host (Amman et al. 1977, Safranyik et al. 1974).

A management approach to reduction of lodgepole pine losses to the mountain pine beetle has been used within stands in the Middle Park area of Colorado from 1972 to the present time. During this period, 2600 ha (6500 acres) of lodgepole pine were cut, including 1600 ha (4000 acres) of partial cuts. The total volume removed was 42 million board feet.

Clearcutting to Reduce Losses

Clearcutting is the best silvicultural system for lodgepole pine and was used in the Buffalo Peak area to prevent losses to the beetle. This area had a large number of trees in each diameter class that contained thick phloem. For the stand, one-third of all phloem samples were thicker than 0.28 cm—a high beetle-producing capacity. The probability of 30 cm dbh and larger trees containing phloem 0.28 cm or thicker was 0.72; 25 cm and larger trees had a probability of 0.51; 20 cm and larger trees had a probability of 0.45. Consequently, in such stands, where even small-diameter lodgepole trees have a high potential for maintaining the beetle epidemic, clearcutting is the best strategy.

In another area of low to moderate visual impact, clearcutting was used because of stand size and high mistletoe rating. These clearcut patches were small and generally under 16 ha (40 acres) in size.

Partial Cuts to Reduce Losses

Where clearcutting is restricted, partial cutting can be used effectively. Alexander (1975) modified his recommendations for partial cutting in old-growth lodgepole pine stands to consider dwarf mistletoe, comandra rust and mountain pine beetle. Some recommendations for dealing with mistletoe and comandra (Brown 1977) are compatible with those for mountain pine beetle. These causes of mortality of lodgepole pine, as well as windfall, place rather severe limitations on the management of this species. Economics can also limit choice of activity. As Alexander states, "Cutting to bring old growth under management is likely to be a compromise between what is desirable and what is possible."

Based upon Cole and Cahill's (1976) work, attacked trees and all or most of the trees 30 cm dbh and larger should be cut first within susceptible stands. Then as many of the trees in the 25 to 30 cm dbh class, regardless of vigor, should be removed to make up the remainder of the basal area to be cut. A second cut should follow within 10 years. The susceptibility of a stand can be reduced for a longer period of time by removing all trees 20 cm dbh and larger. However, stocking and stand productivity should be of prime concern when making partial cuts.

Over 1600 ha were partial-cut on Bureau of Land Management and private lands to reduce losses to the beetle. Partial cuts were used in areas of visual concern that possessed high potential for beetle build-up and in stands adjacent to clearcuts in order to avoid having extensive clearcut areas. A do-nothing strategy was adopted for stands on steep hill-sides and for inaccessible areas.

Loss to the mountain pine beetle has been greatly reduced in these cut stands. Surveys showed the trend of loss to be static to decreasing following tree harvest. In the stands where nothing was done, infestations of the beetle continued. Losses to the beetles were expected to be from 35 to 55 percent of the stems 15 cm (6 inch) dbh and larger; however, accumulated losses after partial cuts were only 1 to 2 percent of the residual trees. In the do-nothing area, 39 percent of the trees, or 52 percent of the basal area, was lost to the beetles.

CONCLUSIONS

Cutting practices within lodgepole pine stands should be primarily concerned with maintaining continuity of cover, yet silvicultural systems, stand structure, site, habitat, wind, diseases and insects all limit the available options. Clearcutting is the best silvicultural system for lodgepole pine. Where its use is restricted, however, partial cutting can be used effectively. Partial cutting to remove 50 percent or less of the basal area will provide openings for regeneration, minimize windthrow, help control dwarf mistletoe, remove the majority of the food supply of the mountain pine beetle and, if designed properly, maintain scenic values.

QUESTIONS AND ANSWERS

Q. Where 50 percent cuts were undertaken, what incidence of blowdown was noted within a 5-year period following harvest? In general, do you have a specific percent recommendation to best serve multiple-use objectives?

A. The stands cut to 50 percent of basal area were areas classed in low windfall risk situations by Alexander's "Partial Cutting in Old-Growth Lodgepole Pine." This is heavier than he recommends. In these cuts we had about 2 percent mortality over the 5-year period. In reference to recommendations that best serve multiple-use objectives, the individual land manager has the best understanding of his particular needs and should develop the specifications accordingly.

Q. When partial cutting, what about mistletoe in future regeneration?

A. The publication entitled "Guidelines for Dwarf Mistletoe Control in Lodgepole Pine in the Northern and Central Rocky Mountains," Report No. 76-14, August 1976 (Doolling and Brown, Forest Service Region 1, Missoula, MT), provides detailed guidelines for management of mistletoe-infested stands. In summary, the land manager must use partial cutting practices where the maintenance of a continuous forest cover is required; however, partial cutting generally produces ideal conditions for intensification and subsequent damage by dwarf mistletoe.

When dwarf mistletoe is present in stands where partial cutting is proposed, the following cutting modifications are recommended (Alexander 1975):

Cut only in stands where the average mistletoe rating of the stand, using the six-class system to classify infection, is Class 2 or less. Individual tree infection ratings are averaged to obtain a value for the stand. In single-storied stands where site index is 70 or above, trees in the intermediate and lower crown classes should be removed in preference to dominants and co-dominants. If site index is below 70, trees in all crown classes are about equally susceptible to infection. In two- and three-storied stands, as much of the cut as possible should come from the lower stories because these trees are likely to be more heavily infected. To minimize infection of new reproduction in single-, two- and three-storied stands, the final overstory removal should be made within 20 years of the regeneration cut when the average mistletoe rating is Class 1, or within 10 years when the rating is Class 2. After the final cut, the young stand should be evaluated to determine any need for treatment. In multi-storied stands, the safest procedure is an overwood removal, with a cleaning and thinning from below.

In old-growth stands with an average mistletoe rating greater than Class 2, any partial cutting, thinning or cleaning is likely to intensify the infection. The best procedure, therefore, is to either remove all of the trees and start a new stand or leave the stand uncut. If the manager chooses to make a partial cut for any reason, the initial harvest should be heavy enough to be a regeneration cut. All residual trees must be removed within 10 years after the first to avoid infection of the regeneration.

Weeding and thinning are cultural methods used to release crop trees from competition and accelerate their growth rate. These methods will have varying effects on dwarf mistletoe infection, depending on how and when they are applied and the condition of each stand. Most stands with an average dwarf mistletoe rating of Class 2 or less will benefit from treatment and produce acceptable yields. Tree density and intensity of dwarf mistletoe are two key factors that determine the feasibility of thinning. Stands with heavier stocking levels can tolerate higher levels of dwarf mistletoe and still produce acceptable yields. For infested stands of precommercial age, more favorable management options are available when stand densities exceed 2500 trees per ha (1000/acre). By utilizing RMYLD (a computerized yield program), the land manager can select the appropriate silvicultural treatment for each stand and rank stands by priority.

Q. There appears to be quite a difference in your results as compared with Hamel's from similar treatments. Any explanation? Were there infested areas around your stands?

A. The Middle Park area was cut on a stand-by-stand basis compared with Region 1, where blocks were cut in the middle of stands and the check areas were in several cases adjacent to the same stands, thereby subjecting the treated areas to beetles building up in the check areas. Also, the Colorado area was cut at the beginning of mountain pine beetle build-up in the area, whereas a large beetle population was present in the Montana area. Most of the Colorado area was treated to remove mountain pine beetle host-sized trees, compared with several small blocks in Montana.

Q. Due to the annual occurrence of fires and the resultant species conversion to lodgepole pine stands, would you consider complete stand conversion (from lodgepole pine) as a viable management goal wherever possible? Was lodgepole pine reintroduced to your clearcut blocks?

A. I would consider stand conversion of some sites but not all sites. The decision to make stand conversion is dependent upon your future timber needs and what species is best adapted for a particular site. The threat of insect

and disease losses should also be a consideration. What will be the market needs—studs, lumber or fiber, etc.? Yes, lodgepole pine was reintroduced in most of the sites but other species of trees are present on some sites (spruce, Douglas-fir or white bark pine).

Q. Were your **tree losses** actually reduced in your partial cut areas when you consider the basal area you were forced to remove in the logging operation? Are you just removing trees that would have been hit anyway?

A. Yes! The tree losses were reduced and, yes, we removed most of the trees that would have been hit by mountain pine beetles, thereby preventing a build-up of the beetle population. The cutting system outlined provides a guide to determine which trees are susceptible to attack and the greatest producers of beetle broods. These should be removed from the stand. Most operators prefer green sales rather than salvage sales.

REFERENCES

- Alexander, R. 1975. Partial cutting in old-growth lodgepole pine. USDA Forest Serv. Res. Pap. RM-136. Rocky Mtn. Forest and Range Exp. Sta., Ft. Collins, CO. 17 pp.
- Amman, G.D., and D.H. Baker. 1972. Mountain pine beetle influence on lodgepole pine stand structure. J. Forest. 70:204-209.
- Amman, G.D., M.D. McGregor, D.B. Cahill, and W.H. Klein. 1977. Guidelines for reducing losses of lodgepole pine to the mountain pine beetle in unmanaged stands in the Rocky Mountains. USDA Forest Serv. Gen. Tech. Rep. INT-36. Intermtn. Forest and Range Exp. Sta., Ogden, UT. 19 pp.
- Brown, D.H. 1977. Management guidelines for lodgepole pine stands infected with comandra blister rust and dwarf mistletoe. USDA Forest Serv. Forest Insect and Disease Manage. Tech. Rep. R2-9. Rocky Mtn. Region. 21 pp.
- Cole, W.E., and D.B. Cahill. 1976. Cutting strategies can reduce probabilities of mountain pine beetle epidemics in lodgepole pine. J. Forest. 74:294-297.
- Safranyik, L., D.M. Shrimpton and H.S. Whitney. 1974. Management of lodgepole pine to reduce losses from the mountain pine beetle. Can. Dept. Environ., Forest Serv. Tech. Rep. 1. Pac. Forest Res. Cent., Victoria, B.C. 24 pp.

Results of Harvesting Strategies for Management of Mountain Pine Beetle Infestations in Lodgepole Pine on the Gallatin National Forest, Montana

Dennis R. Hamel

ABSTRACT

Mountain pine beetle (*Dendroctonus ponderosae* Hopkins) epidemics in lodgepole pine (*Pinus contorta* Douglas var. *latifolia* Engelman) are correlated with large-diameter, thick-phloemed trees, and decline of epidemics is associated with loss of these trees. Beetle brood production is directly correlated with phloem thickness, which is directly related to tree diameter. Probabilities of mountain pine beetle-caused losses to lodgepole pine can be developed from phloem thickness/tree diameter distribution data. Based on these probabilities, harvesting strategies were implemented in 1974 on the Gallatin National Forest to reduce average tree diameter and assess the effect on population build-up. Harvesting of four 16-ha (40-acre) blocks within heavily infested areas, based on diameter and phloem distributions, was completed in 1976. A 3-year post-harvest evaluation will determine the efficacy of this management alternative. Preliminary results indicate beetle population reductions in blocks harvested to 25- and 30-cm (10- and 12-inch) diameter limits, but population build-up in the block harvested to an 18-cm (7-inch) limit and in the block harvested on the basis of phloem thickness. Population build-ups were also noted in check blocks.

INTRODUCTION

Epidemics of mountain pine beetle (*Dendroctonus ponderosae* Hopkins) in lodgepole pine (*Pinus contorta* Douglas var. *latifolia* Engelman) have occurred frequently in the Northwest (Crookston et al. 1977), with extensive losses in the northern region (Ciesla 1971, Evenden 1944, McGregor and Dewey 1971, McGregor and Tunnock 1971, McGregor 1973, McGregor et al. 1976). Infestations on the Gallatin National Forest developed in 1969-1970 (Ciesla 1971, McGregor and Tunnock 1971) and currently occur on approximately 90,700 ha (224,000 acres).

Generally these epidemics have been related to such stand characteristics as age, diameter distribution, phloem thickness distribution, elevation and latitude. Of these, food, represented by phloem thickness, is probably the leading limiting factor on survival of mountain pine beetle broods (Amman 1969, Amman 1972, Amman et al. 1977). Phloem serves as food for developing larvae, and the number completing development therefore depends in part on phloem thickness. Although phloem thickness/tree diameter relationships can be variable, large-diameter trees generally contain thicker phloem than small-diameter trees (Amman 1972).

During the course of an infestation, large-diameter trees are usually infested and killed first. Large trees usually produce more beetles per unit area of bark due to their thicker phloem, and more beetles per tree due to their greater surface area (Amman et al. 1977, Cole and Amman 1969).

Past control efforts have focused primarily on direct attempts to reduce beetle populations over large areas. These have included treating felled and standing infested trees either by burning or by chemical spraying, and sanitation salvage logging. These methods have not effectively prevented subsequent tree losses, primarily because stand conditions favoring beetles remained unchanged.

The problem is one of managing lodgepole pine stands in such a way as to reduce or prevent potential build-up of beetle populations by altering the stand conditions which favor them. Cole and Cahill (1976) developed probabilities of loss based on phloem/diameter distribution, and theorized that harvesting strategies could be implemented to eliminate or reduce mountain pine beetle epidemic potential. Based on this work, a study was established in Montana (Hamel et al. 1975, Hamel and McGregor 1976) to determine if silvicultural methods could be used to manage mountain pine beetle in

Table 1. Pre-harvest sampling of mountain pine beetle study plots, Montana, 1974.

Location	Plot elevation (m)	Average stand age (years)	Habitat type	Average tree diameter (cm)	Average number infested trees/ha	% phloem samples ≥ 0.25 cm thick	Mean phloem thickness (cm)	% of stand lodgepole pine
Gallatin National Forest								
<i>Hebgen Lake District</i>								
18-cm cut block	2031	75.0	<i>Pinus contorta</i> / <i>Purshia tridentata</i>	22.5	—	—	—	100.0
25-cm cut block	2031	193.3	<i>Pinus contorta</i> / <i>Purshia tridentata</i>	22.2	5.8	4.46	0.1600	100.0
Phloem cut block	2031	76.3	<i>Pinus contorta</i> / <i>Purshia tridentata</i>	21.7	5.0	12.00	0.1922	100.0
Check block (A)	2031	75.0	<i>Pinus contorta</i> / <i>Purshia tridentata</i>	18.9	5.8	13.80	0.1860	100.0
<i>Gallatin District</i>								
30-cm cut block	2257	162.7	<i>Pseudotsuga menziesii</i> / <i>Linnaea borealis</i>	24.9	10.0	17.40	0.1955	77.0
Check block (B)	2019	97.5	<i>Abies lasiocarpa</i> / <i>Linnaea borealis</i>	17.7	40.0	20.00	0.2210	84.7

lodgepole pine stands. The study is intended to develop more fully the proposed harvesting strategies. The methods and results of the first 4 years of this effort are presented here.

STUDY AREAS AND METHODS

Six 16-ha (40-acre) blocks of lodgepole pine, within a mountain pine beetle infested area, were selected on two districts of the Gallatin National Forest in 1974. Four blocks were established on the Hebgen Lake District, where mountain pine beetle became epidemic in 1970 (Ciesla 1971, McGregor and Tunnock 1971). Two blocks were established on the Gallatin District,¹ where infestations developed in 1969 (McGregor and Dewey 1971). Summaries of pre-harvest stand characteristics are presented in Table 1. Selected blocks received the following silvicultural treatments:

1. Removal of all infested trees and all green trees ≥ 18 cm (7 inches) diameter at breast height (dbh), regardless of phloem thickness;
2. Removal of all infested trees and all green trees ≥ 25 cm (10 inches) dbh, regardless of phloem thickness;
3. Removal of all infested trees and all green trees ≥ 30 cm (12 inches) dbh, regardless of phloem thickness;
4. Removal of all infested trees and all green trees with phloem thickness ≥ 0.25 cm (0.10 inch) (based on an average

of two samples taken at breast height from each tree), minimum diameter 20 cm (8 inches) dbh;

5. Removal of no trees on two check blocks.

Pre-harvest plot sampling and marking for harvest were conducted during October and November 1974. Each block contained 20 equally spaced 0.04-ha (0.1-acre) plots. Hypsometers were used to determine which trees were within plot boundaries. Estimates of phloem thickness for each diameter class were obtained from bark samples removed from opposite sides of two green, uninfested trees in each dbh size class, except in the phloem block, where every tree was sampled. Phloem thickness was measured to the nearest 25 mm (0.01 inch) and tree diameters were measured to the nearest 250 mm (0.1 inch).

To determine infestation intensity, forty 0.1-ha (0.25-acre) plots were taken in each block. Trees 12 cm (5 inches) dbh and larger were recorded by species and dbh and were categorized into one of the following classes:

- 0 = green, uninfested;
- 1 = current attack, green or partially faded foliage, brood present, blue stain present;
- 2 = 1-year-old attack, red foliage, brood emerged;
- 3 = 2-year or older attack, majority of needles dropped;
- 4 = unsuccessful attack or "pitch-out," green foliage and pitch tubes present, brood and blue stain absent.

One hundred percent cruises were conducted in August each year following harvest to determine number of current attacked trees per acre, number of "pitch-out" trees, dbh and phloem thickness of attacked trees.

¹ Forest reorganization in 1976 combined the Gallatin District with the Bozeman District. Current name is Bozeman District.

RESULTS AND DISCUSSION

Harvesting of all blocks was completed in 1976, and a 3-year post-harvest evaluation will determine the efficacy of this forest management alternative. Table 2 summarizes post-harvest data to date.

In the 18-cm block, all infested and those green trees ≥ 18 cm dbh were cut, regardless of phloem thickness. Harvest was completed in 1974. In 1975, only six attacked trees were located. Five of these were ≥ 18 cm dbh and were missed during harvest. In 1976, 85 attacked trees were tallied, representing 5.2 trees per ha (2.1/acre), or a build-up ratio of 1:14. In 1977, there were 230 attacked trees, representing 14.3 trees per ha (5.8/acre). Mean diameter of attacked trees decreased from 18 cm (7.2 inches) dbh in 1975 to 14.3 cm (5.6 inches) and 15.8 cm (6.2 inches) in 1976 and 1977, respectively. Mean phloem thickness of attacked trees decreased from 0.28 cm (0.11 inch) in 1975 to 0.18 cm (0.07 inch) in 1976 and 0.20 cm (0.08 inch) in 1977. Percent of phloem samples ≥ 0.25 cm thick from attacked trees was 83, 16 and 35 in 1975, 1976 and 1977, respectively. Percent of "pitch-outs" increased from < 1.0 in 1975 to 6.0 in 1976 and 26.0 in 1977.

It was predicted (Hamel et al. 1975) that by eliminating the range of host material ≥ 18 cm dbh future infestation levels would be minimal in this block, and that attacked trees would have thicker-than-average phloem for their diameter class. These predictions held true for the first post-harvest survey in 1975; however, infestation increased dramatically in 1976 and 1977. At present we have no definitive explanation for these increases. However, examination of killed trees in 1977 shows low beetle production. Therefore, beetles are probably coming in from surrounding areas—e.g., from the adjacent check plot. Why they are doing this remains unanswered.

Although the number of attacked trees per ha increased in the 18-cm block, there was also an increase in the percentage of "pitch-outs" or unsuccessful attacks. Deletion of the

unsuccessful attack figures from computations reduces the mean number of successfully infested trees to 10.6 per ha (4.3/acre) in 1977, representing a build-up ratio from 1976 to 1977 of 1:2.

Harvest in the 25-cm block removed trees ≥ 25 cm dbh, regardless of phloem thickness, and was completed in mid-July 1976. Post-harvest surveys in 1976 indicated 281 attacked trees in the block or 6.4 infested trees per ha (2.6/acre), a decline in build-up ratio of 1:0.6 from pre-harvest sampling. A further decline was noted in 1977, with 5.7 attacked trees per ha (2.3/acre). Mean diameter of attacked trees decreased from 30 cm (12 inches) in 1975 to 20 cm (8 inches) in 1976 and 1977. Mean phloem thickness of attacked trees decreased from 0.23 cm (0.09 inch) in 1975 to 0.18 cm (0.07 inch) in 1976 and 1977, respectively. Percent of phloem samples ≥ 0.25 cm thick from attacked trees was 60, 17 and 28 in 1975, 1976 and 1977, respectively. Percent of "pitch-outs" increased from < 1.0 in 1975 to 21.3 in 1976 and 49.5 in 1977.

Harvest to a 25-cm minimum theoretically eliminated the majority of preferred host material, i.e., large-diameter trees with thick phloem. As a result, infestation levels decreased from an average of 10.5 successfully infested trees per ha (4.2/acre) in 1975 to 5.2 in 1976 and 3.0 in 1977 (2.1 and 1.2/acre, respectively). Future infestation levels should remain low, since most of the preferred host material has been removed.

Selective harvest of the 30-cm block removed all trees ≥ 30 cm dbh, regardless of phloem thickness. Harvest of all 1974 attacked trees containing brood was completed in 1975; however, the remaining green component was not removed until spring 1976. As a result of this delay, 41 trees marked for removal (i.e., ≥ 30 cm dbh) were attacked in 1975. In addition 12 unmarked (i.e., ≤ 30 cm dbh) trees were attacked, resulting in 3.2 attacked trees per ha (1.3/acre) in 1975. This increased to 4.0 and 6.8 trees per ha (1.6 and 2.7/acre) in 1976 and 1977, respectively. Mean diameter of attacked trees decreased from 32 cm (13 inches) dbh in 1975 to 25 cm (10 inches) in 1976 and 1977. Mean phloem thickness of attacked trees was 0.22 cm (0.09 inch) in 1975, 0.15 cm (0.06 inch) in

Table 2. Sampling of mountain pine beetle attacked trees in study blocks, Gallatin National Forest, Montana, 1974-1977.

Location	Mean no. of attacked trees/ha				% of attacked trees classed "pitch-outs"			Mean no. of successfully infested trees/ha			Mean diameter at breast height (cm)			Mean phloem thickness of attacked trees (cm)			% attacked trees having phloem ≥ 0.25 cm		
	1974	1975	1976	1977	1975	1976	1977	1975	1976	1977	1975	1976	1977	1975	1976	1977	1975	1976	1977
<i>Hebgen Lake District</i>																			
18-cm block	—	0.5*	5.2*	14.5*	< 1.0	5.9	26.5	0.5	5.0	10.7	18.3	14.2	15.7	0.28	0.18	0.20	83.3	16.0	34.8
25-cm block	6.0	10.5	6.5*	5.7*	< 1.0	21.3	49.5	10.5	5.0	3.0	31.0	20.3	19.8	0.23	0.18	0.18	60.1	17.0	27.6
Phloem block	5.1	10.2	28.5*	74.0*	< 1.0	21.8	20.3	10.2	22.2	59.0	28.7	24.6	23.4	0.23	0.18	0.18	48.8	12.5	31.0
Check block (A)	6.0	7.0	20.7	75.5	< 1.0	1.9	11.4	7.0	20.2	67.0	26.7	24.9	25.1	0.23	0.20	0.20	58.4	31.5	49.4
<i>Gallatin District</i>																			
30-cm block	10.0	3.2*	4.0*	6.7*	17.0	28.1	46.2	2.7	1.2	3.5	33.8	25.7	25.4	0.23	0.15	0.18	60.4	0.1	30.2
Check block (B)	40.5	194.5	79.5	25.7	48.4	35.0	62.4	100.2	51.7	9.7	22.1	19.0	18.3	0.23	0.18	0.20	52.6	19.0	47.3

*Post-harvest figures

1976, and 0.18 cm (0.07 inch) in 1977. Percent of phloem samples ≥ 0.25 cm thick from attacked trees was 60, 0.1 and 30 in 1975, 1976 and 1977, respectively. Percent of "pitch-outs" increased from 17 in 1975 to 28 in 1976 and 46 in 1977.

Infestation levels in the 30-cm block have been reduced from 10 successfully attacked trees per ha (4/acre) pre-harvest to 2.5 trees per ha (1/acre) post-harvest.

In the phloem cut block, harvest of all infested trees and those green trees with a phloem thickness ≥ 0.25 cm was completed in mid-July 1976. Post-harvest surveys in 1976 indicated 454 attacked trees in the block, or 28.5 infested trees per ha (11.4/acre), an increase in build-up ratio of 1:2.8 over the previous year (pre-harvest). In 1977 there was a further increase to 74.0 trees per ha (29.6/acre). Mean diameter of attacked trees decreased from 28.5 cm (11.3 inches) in 1975 to 24.2 cm (9.7 inches) in 1976 and 23.0 cm (9.2 inches) in 1977. Mean phloem thickness of attacked trees decreased from 0.22 cm (0.09 inch) in 1975 to 0.18 cm (0.07 inch) in 1976 and 1977, respectively. Percent of phloem samples ≥ 0.25 cm thick from attacked trees was 48, 13 and 31 in 1975, 1976 and 1977, respectively. Percent of "pitch-outs" was < 1.0 in 1975, 22.0 in 1976, and 20.0 in 1977. It was predicted that future infestation levels in this block would decline due to removal of trees having greater phloem thickness and greater brood production capability. This has not been the case. Infested trees increased from 5 to 10 trees per ha (2 to 4/acre) in 1974 and 1975 (pre-harvest) to 22 and 60 per ha (9 and 24/acre) in 1976 and 1977 (post-harvest). These build-up levels nearly parallel those of check block A, where no harvesting was conducted. Examinations of killed trees in the phloem block in November 1977 (Amman, pers. comm.,² 1977) showed that brood production was low.

For example, in a grid pattern survey of attacked trees in the block, it was determined that there was an average of 3.0 attacks per 0.46 m² (0.5 ft²) bark sample, while there were only 2.3 emergence holes per 0.46 m². It can be hypothesized, therefore, that attacking beetles may be coming in from surrounding areas. In addition to these anomalous attack-vs.-emergence densities, it was determined that 42.3 percent of the green trees in the plot had phloem thickness ≥ 0.25 cm. These increases in phloem thickness can only be attributed to tree release following harvest.

Two check blocks were established to monitor mountain pine beetle populations under undisturbed conditions near the study blocks. Check block A was established adjacent to the 18-cm block. Average number of infested trees per ha in this block increased steadily from 6.0 in 1974 to 7.0 in 1975, 20.8 in 1976 and 75.5 in 1977 (2.4, 2.8, 8.3, 30.2/acre, respectively). Mean diameter and phloem thickness of attacked

trees have remained near 25 cm dbh and 0.2 cm, respectively. Percent of phloem samples ≥ 0.25 cm thick from attacked trees was 58, 31 and 49 in 1975, 1976 and 1977, respectively. Percent of "pitch-outs" increased from < 1.0 to 2.0 and 11.0 in 1975, 1976 and 1977, respectively.

Check block B was established along Hellroaring Creek in an area of heavy infestation on the Gallatin District. Average number of infested trees in 1974 was 40.5 per ha (16.2/acre). This increased to 194.5 per ha (77.8/acre) in 1975, decreased to 79.5 per ha (31.8/acre) in 1976 and 25.8 per ha (10.3/acre) in 1977. This decline is attributed to food source depletion. Very few susceptible host trees remain in the area. Mean diameter and phloem thickness of attacked trees have remained near 12 cm dbh and 0.2 cm, respectively. Percent of phloem samples ≥ 0.25 cm thick from attacked trees was 53, 19 and 47 in 1975, 1976 and 1977, respectively. Percent of "pitch-outs" has ranged from 48.0 in 1975 to 62.0 in 1977.

These results suggest that future infestation levels in blocks harvested according to diameter levels will be lower and proportional to the amount of large-diameter timber removed. In contrast, population reductions have not been achieved in the block harvested according to phloem thickness independent of tree diameters. This reintroduces a basic ecological relationship between the beetle and its host. The apparent propensity of beetles to initially attack large, vertical objects based on visual cues (Shepherd 1966) precludes success with a management alternative based on phloem measurements; therefore, harvest of trees based on diameters, with their inherent positive correlation with phloem thickness, appears to be a better management strategy.

Evaluation of these blocks will continue through 1979 to determine the feasibility of these harvesting strategies for management of mountain pine beetle infestations. In addition, it is recommended that this study be replicated in other areas to further evaluate the use of harvesting strategies as a management alternative for mountain pine beetle infestations in lodgepole pine.

ACKNOWLEDGMENTS

The author wishes to express special appreciation to Gene D. Amman, Walt E. Cole and Lynn A. Rasmussen, Intermountain Forest and Range Experiment Station, Ogden, UT, and Mark D. McGregor, Forest Insect and Disease Management, Missoula, MT, for their assistance in study design and implementation, data collection and analysis, and manuscript review. Thanks are also due the staff of Gallatin National Forest for cooperation in obtaining study areas and collecting data. Appreciation is extended to John H. Borden and Max M. Ollieu for manuscript reviews.

² G.D. Amman is located at the USDA Forest Service Intermountain Forest and Range Experiment Station, Ogden, UT.

REFERENCES

- Amman, G.D. 1969. Mountain pine beetle emergence in relation to depth of lodgepole pine bark. USDA Forest Serv. Res. Note INT-96. Intermtn. Forest and Range Exp. Sta., Ogden, UT. 8 pp.
- _____. 1972. Mountain pine beetle brood production in relation to thickness of lodgepole pine phloem. J. Econ. Entomol. 65:138-140.
- Amman, G.D., M.D. McGregor, D.B. Cahill and W.H. Klein. 1977. Guidelines for reducing losses of lodgepole pine to the mountain pine beetle in unmanaged stands in the Rocky Mountains. USDA Forest Serv. Gen. Tech. Rep. INT-36. Intermtn. Forest and Range Exp. Sta., Ogden, UT. 19 pp.
- Ciesla, W.M. 1971. Evaluation of mountain pine beetle infestations on the Hebgen Lake District, Gallatin National Forest, Montana. USDA Forest Serv. Rep. No. 71-38. Northern Region, State and Private Forestry, Missoula, MT. 3 pp.
- Cole, W.E., and G.D. Amman. 1969. Mountain pine beetle infestations in relation to lodgepole pine diameters. USDA Forest Serv. Res. Note INT-95. Intermtn. Forest and Range Exp. Sta., Ogden, UT. 7 pp.
- Cole, W.E., and D.B. Cahill. 1976. Cutting strategies can reduce probabilities of mountain pine beetle epidemics in lodgepole pine. J. Forest. 74:294-297.
- Crookston, N.L., R.W. Stark, and D.L. Adams. 1977. Outbreaks of mountain pine beetle in northwestern lodgepole pine forests—1945-1975. Forest., Wildl. and Range Exp. Sta. Bull. No. 22. Univ. of Idaho, Moscow. 7 pp. + map.
- Evenden, J.C. 1944. Montana's thirty-year mountain pine beetle infestation. USDA Forest Serv. Forest Insect Control Rep., May 6. Northern Region, Missoula, MT.
- Hamel, D.R., and M.D. McGregor. 1976. Harvesting strategies for management of mountain pine beetle infestations in lodgepole pine, Montana. Progress report. USDA Forest Serv. Rep. No. 76-3. Northern Region, State and Private Forestry, Missoula, MT. 7 pp.
- Hamel, D.R., G.D. Amman, M.D. McGregor, W.E. Cole, and L.A. Rasmussen. 1975. Harvesting strategies for management of mountain pine beetle infestations in lodgepole pine, Montana. Establishment report. USDA Forest Serv. Rep. No. 75-12. Northern Region, State and Private Forestry, Missoula, MT. 11 pp.
- McGregor, M.D. 1973. Status of mountain pine beetle, Gallatin Ranger District, Gallatin National Forest. USDA Forest Serv. Rep. No. 73-9. Northern Region, State and Private Forestry, Missoula, MT. 7 pp.
- McGregor, M.D., and J.E. Dewey. 1971. Evaluation of mountain pine beetle infestations on the Squaw Creek Ranger District, Gallatin National Forest, Montana. USDA Forest Serv. Rep. No. 71-14. Northern Region, State and Private Forestry, Missoula, MT. 4 pp.
- McGregor, M.D., and S. Tunnock. 1971. Status of mountain pine beetle infestations on the Hebgen Lake Ranger District, Gallatin National Forest, Montana. USDA Forest Serv. Rep. No. 71-45. Northern Region, State and Private Forestry, Missoula, MT. 3 pp.
- McGregor, M.D., D.R. Hamel, and R.C. Lood. 1976. Evaluation of mountain pine beetle infestations, Gallatin National Forest, Montana. USDA Forest Serv. Rep. No. 76-5. Northern Region, State and Private Forestry, Missoula, MT. 11 pp.
- Shepherd, R.F. 1966. Factors influencing the orientation and rates of activity of *Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae). Can. Entomol. 98:507-518.

Implications of Genetic Differences between Mountain Pine Beetle Populations to Integrated Pest Management

Mary W. Stock, Jerry D. Guenther and Gary B. Pitman

ABSTRACT

Electrophoresis was used to evaluate genetic diversity among mountain pine beetle (*Dendroctonus ponderosae* Hopkins) populations in relation to geographic location and host trees. Populations attacking lodgepole pine (*Pinus contorta* Douglas var. *latifolia* Engelm.) in pure and mixed stands, western white pine (*P. monticola* Douglas) mixed with lodgepole *latifolia*, and lodgepole var. *murrayana* (Greville and Balfour) mixed with ponderosa pine (*P. ponderosa* Lawson) were examined. No genetic differences were detected among populations from stands of pure lodgepole var. *latifolia* or from *latifolia* mixed with ponderosa pine or white pine. In contrast, there was a larger degree of genetic difference observed between mountain pine beetles in lodgepole *murrayana* and all other populations. Further morphological, physiological and behavioral comparisons between mountain pine beetles in lodgepole *latifolia* and *murrayana* may reveal differences which contribute to variations in the insects' response to specific management practices, such as those employing pheromones.

INTRODUCTION

The mountain pine beetle (*Dendroctonus ponderosae* Hopkins) is considered one of the most economically damaging and aggressive insect pests of native pine trees in the western United States and Canada. Documented outbreaks of mountain pine beetle date back to 1847 (Blackman 1931, Crookston et al. 1977). The emphasis of most mountain pine beetle research, as with other large-scale research programs dealing with pest

insects, centers on environmental factors in the insect/tree ecosystem. However, there is an increasing awareness of the need for information on intraspecies diversity and its relation to the population dynamics and associated control strategies used on these insects (Wellington 1977).

Intraspecies diversity within the mountain pine beetle species is manifested by differences in species of host tree attacked, differences in diameters of trees attacked, and differential responses to specific pheromones. While the beetle is known to attack 16 host trees (Morrow 1972), lodgepole pine (*Pinus contorta* Douglas) is among its principal hosts, especially in terms of economic loss to timber resources. Of the four varieties of lodgepole pine, the insect is a major pest in var. *murrayana* (Greville and Balfour) in the Sierras and western Oregon and in var. *latifolia* (Engelmann) in more easterly regions.

The mountain pine beetle is widely and often discontinuously distributed in association with its preferred host trees. For example, long-standing physical barriers such as arid regions and mountain ranges have resulted in the separation of two varieties of lodgepole, *murrayana* and *latifolia*. Consequently, beetles infesting these two tree types also have non-overlapping (allopatric) distributions. Such geographic isolation is an important component of genetic divergence and differentiation within species (Mayr 1970).

In areas where the ranges of preferred host types overlap, emerging adult beetles often appear to attack host trees of the

same species from which they emerged (Craighead 1921). Individual tree preference is expressed in the mountain pine beetle by selection of trees of a certain diameter. Under endemic conditions, beetles infesting lodgepole and white pine (*P. monticola* Douglas) both attack specific size classes within the diameter ranges of these preferred host species. This diameter preference will break down under high-density epidemic conditions when beetles will also attack other host trees if they are available. For example, in the long-term infestation of mountain pine beetle in lodgepole pine near LaGrande, Oregon, the insects are now attacking ponderosa pine (*P. ponderosa* Lawson) and small-diameter lodgepole that, in previous years, they did not attack.

Mountain pine beetle populations also differ in their response to certain pheromones, such as *exo*-brevicomin. Such striking behavioral differences between populations could result from genetic differences between groups and have a significant effect on regional pest management strategies. If genetic divergence is occurring, either in discontinuous or overlapping mountain pine beetle populations or in different host trees, it is critical that we obtain a better understanding of genetic characteristics and relations between the different populations.

We undertook this study to obtain a clearer understanding of intrinsic genetic diversity within the mountain pine beetle species and its relation to the above-described differences in geographic location and host tree preference. This information will permit the results of studies on one mountain pine beetle population to be extrapolated more accurately to other populations upon which such studies have not been made. The work has important implications to managers dealing with this insect in different areas of its distributional range.

METHODS

Live adult mountain pine beetles were obtained from pure and mixed stands of lodgepole pine and a mixed stand of white pine by rearing the insects from billets obtained from sites listed in Table 1 and kept in enclosed broodhouses at Headquarters, Idaho, until adults emerged. Beetles were collected, sexed and frozen until electrophoretic processing.

We used biochemical genetic methods (specifically, starch gel electrophoresis) to examine and quantify genetic features of, and relations among, these populations (Utter et al. 1974, Avise 1974). This technique produces visible banding patterns for individual insects (up to 50 per gel) that can be directly related to specific gene expression. From these banding patterns, direct quantitative statistical comparisons can be made between and among populations. Practical uses of such data include quantitative definition of genetic similarities and distances between groups (useful in taxonomic clarification at the species and population levels) and definition of genetic indicators or markers of specific population characteristics or types. We used methods following or modified

Table 1. Sources of mountain pine beetles acquired for genetic analysis during summer 1977.

Site	Tree and Stand Type	Emergence Dates
Waha, Idaho	LP var. <i>latifolia</i> pure stand	5/23/77 to 8/11/77
McCall, Idaho	LP var. <i>latifolia</i> mixed with PP	7/13/77 to 8/11/77
Headquarters, Idaho	WP mixed with LP var. <i>latifolia</i>	5/20/77 to 7/31/77
Silver Lake, Oregon	LP var. <i>murrayana</i> , mixed with PP	7/11/77 to 8/8/77

LP = lodgepole pine, WP = white pine and PP = ponderosa pine.

from those of Shaw and Prasad (1970), Brewer (1970), Bush and Huettel (1972), and May (1975).

We assayed a total of 24 enzymes and developed routine assays for 13 of these, 6 of which show genetic variation in some or all populations and one of which is distinctly different between males and females. Data were recorded for individual insects for each gene locus in every sample and converted to genotype and allele frequencies for analysis.

Initially, the genetic makeup of each sample for each gene was compared to expected values derived from the Hardy-Weinberg equation. Deviations from expected values provide clues that factors such as selection, non-random mating or population mixtures were affecting the theoretical equilibrium.

Next, populations were compared at individual gene loci to detect differences using contingency tables based on the observed number of each type of variant gene in each population (Table 2). Loci differing significantly between populations with respect to the distribution of particular variant gene types were used to define specific genetic characteristics of mountain pine beetle populations from different geographic locations or attacking different tree types.

Finally, data from several genes in each population were compared, using Rogers' (1972) similarity coefficient, to determine degrees of overall genetic relationships among the populations. These similarity values can be used to quantify genetic relationships among groups and the amount of genetic difference or similarity among them. Values range from 0 to 1, where 1 equals genetic identity. In previous studies with other organisms (including many insects), similarity values of conspecific populations were usually well above .90 on this scale, while separate species commonly had similarity values of .75 or less (Avise 1974).

Table 2. Results of tests for genetic differences at the esterase (EST), aspartate aminotransferase (AAT), and acid phosphatase (AcP) loci in mountain pine beetle populations (sexes combined). Chi-square values were calculated from contingency tables based on the observed number of each allele at each locus between each pair of populations.

EST	LP pure <i>latifolia</i>	LP <i>latifolia</i> with PP	WP with LP <i>latifolia</i>	LP <i>murrayana</i> with PP
LP pure <i>latifolia</i>	—			
LP <i>latifolia</i> with PP	8.8*	—		
WP with LP <i>latifolia</i>	5.0	2.2	—	
LP <i>murrayana</i> with PP	4.6	10.25*	6.0	—
AAT				
LP pure <i>latifolia</i>	—			
LP <i>latifolia</i> with PP	0.3	—		
WP with LP <i>latifolia</i>	0.2	1.1	—	
LP <i>murrayana</i> with PP	16.2**	19.1**	14.7**	—
AcP				
LP pure <i>latifolia</i>	—			
LP <i>latifolia</i> with PP	0.9	—		
WP with LP <i>latifolia</i>	1.7	0.1	—	
LP <i>murrayana</i> with PP	0.6	2.2	3.0	—

Note: Differences significant at the 95% and 99% levels are indicated by * and **, respectively. LP = lodgepole pine, WP = white pine and PP = ponderosa pine.

RESULTS AND DISCUSSION

In a few cases, deviations from expected proportions of certain genes were observed. For example, beetles from white pine in a mixed stand with lodgepole *latifolia* showed a highly significant difference from expected values at the aspartate aminotransferase (AAT) gene locus. Such imbalances may result from selection against specific gene combinations such as might occur by differential survival of the genotypes encountering host trees resistant to colonization.

At the esterase (EST) gene locus, beetles from lodgepole *latifolia* mixed with ponderosa pine showed a significant difference from beetles in lodgepole *murrayana* mixed with ponderosa and pure lodgepole *latifolia*. Marked genetic differences were also seen between populations at the AAT locus. Beetles attacking *murrayana* differed significantly from all other populations. These data strongly suggested that mountain pine beetles from lodgepole var. *murrayana* were genetically different from beetles in either lodgepole var. *latifolia* or white pine mixed with *latifolia*.

We used similarity values, based on information from several gene loci, to determine if beetles from *murrayana* were genetically distinct from the other populations, as was suggested by the single-locus tests (Table 3). Among beetle populations in *latifolia* in pure and mixed stands and in white pine mixed with *latifolia*, similarity levels were very high (i.e., .99), as would be expected for populations within a single species.

However, beetles attacking *murrayana* had a genetic similarity to all other populations at the .84 to .85 level. A dendrogram (Sneath and Sokal 1973) illustrates further the genetic relationships between the mountain pine beetle populations (Fig. 1).

Thus, our data show that there is little, if any, detectable genetic difference between beetles in pure or mixed stands of

Table 3. Similarity coefficients calculated between all pairs of mountain pine beetle populations using information from nine gene loci. The higher the coefficient, the greater the genetic similarity; the lower the coefficient, the greater the genetic distance.

	LP pure <i>latifolia</i>	LP <i>latifolia</i> with PP	WP with LP <i>latifolia</i>	LP <i>murrayana</i> with PP
LP pure <i>latifolia</i>	—			
LP <i>latifolia</i> with PP	.99	—		
WP with LP <i>latifolia</i>	.99	.99	—	
LP <i>murrayana</i> with PP	.85	.84	.84	—

LP = lodgepole pine, WP = white pine and PP = ponderosa pine.

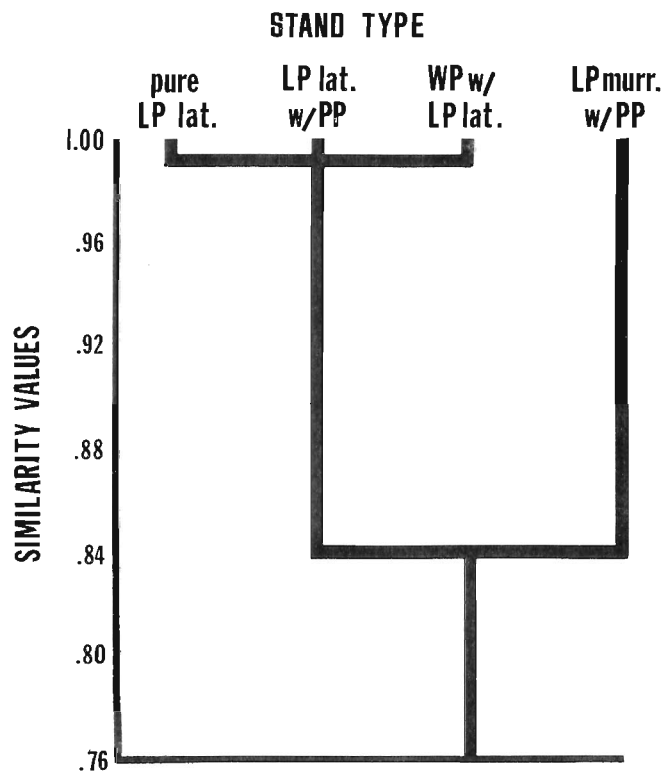


Fig. 1. Dendrogram, based on electrophoretic data, showing genetic relationships among mountain pine beetle populations infesting different stand types. LP = lodgepole pine, lat = *latifolia*, murr. = *murrayana*; WP = white pine; PP = ponderosa pine.

latifolia and white pine with *latifolia*. During outbreaks, mountain pine beetles would be expected to invade associated pine species. Consequently, regular gene flow occurs between sympatric mountain pine beetle populations and high levels of genetic similarity are maintained, if random mating occurs.

In contrast, the larger degree of genetic difference between mountain pine beetles in *latifolia* and *murrayana* is probably a reflection of the long-term geographic separation of these host trees and their associated mountain pine beetle populations. This genetic divergence could be manifested in associated physiological, behavioral or other phenotypic characters contributing to variations in the beetle response to environmental factors. Therefore, tactics used to control mountain pine beetle in one variety of lodgepole pine may be less effective when used on beetles in the other variety. For this reason, further morphological, physiological, behavioral and hybridization comparisons could provide additional information directly applicable to development of regional mountain pine beetle management programs.

ACKNOWLEDGMENTS

We greatly appreciate the advice and reviews of this manuscript provided by R.W. Stark, G.D. Amman, F.M. Utter, G.N. Lanier, R.J. Hoff and A.A. Berryman. We also sincerely thank R.C. McKnight for his assistance in obtaining mountain pine beetles for this study.

QUESTIONS AND ANSWERS

- Q. Are there genetic differences between endemic and epidemic mountain pine beetle populations? Can you detect differences in genetic profiles between beetles from early and later stages of outbreak?
- A. Not yet. We believe we can do this with the Douglas-fir tussock moth, however. We have detected genetic changes associated with different phases of the outbreak episode in the DFTM and expect that, with further work, similar profiles will be detected for the mountain pine beetle.
- Q. Of what use are such descriptive electrophoretic studies unless you can relate the observed differences to ecologically relevant characteristics? Has anyone yet attempted to investigate differences in behavior, physiological response, etc., that parallel the genetic differences you have detected?
- A. That is the aim of our work. We are attempting to associate ecologically relevant (i.e., management-related) characteristics such as pheromone response. In other forest insects, such as the defoliators, we have found genetic indicators of insecticide response and what may be genetic features that can be used for predicting changes in population status (e.g., endemic to outbreak or outbreak to collapse).
- Q. Since mountain pine beetles in mixed stands are genetically identical, do you think this refutes the hypothesis of host specificity or Hopkins' Host Selection Principle?
- A. Not necessarily. Our data are too preliminary to come to any conclusion about this yet. Also, host specificity is most clearly manifested at low population densities and we have been working with populations at high densities.
- Q. Are there genetic differences in mountain pine beetles from one geographic area of North America to another?
- A. I believe that many of the differences described in this paper are a result of geographic separation of the two varieties of lodgepole pine infested by the mountain pine beetle. We would expect to find other such differences, especially when comparing groups from areas similarly subjected to long-term geographic separation, such as the Black Hills beetles vs. populations in more western regions.

- Q. Although they are allopatric, are the two varieties of lodgepole very different? Could you give an indication of differences in the varieties?
- A. In areas where the two varieties come together, they are difficult to tell apart because intermediates of all characters are found. However, where they are more widely separated, differences can be seen in cone characteristics (weight, persistence), in needle width and length, and in the color of small seedlings.
- Q. You say we should not look at or consider the mountain pine beetle as a homogeneous entity, that there are intrinsic differences. I agree, but I believe you have fallen into a trap by using whole beetles for analysis. It is my observation that a whole field-collected or wild mountain pine beetle is more often than not a collection of nematodes, mites, fungi, bacteria, protozoans. Please comment.
- A. In electrophoretic work with whole-insect homogenates, the bands which show the genotype of the insect are much darker than those produced by most associated fauna. In the case of parasitism by a large nematode, however, you are correct. This might not be the case. Faint shadows of bands occur during staining in most insects. These could be indicators of certain types of bacteria, fungi, etc., that are associated with the insect.

REFERENCES

- Avisé, J.C. 1974. Systematic value of electrophoretic data. *Syst. Zool.* 23:465-481.
- Blackman, M.W. 1931. The Black Hills beetle. Tech. Publ. No. 36. Bull. State Univ. of New York, Coll. of Environ. Sci. and Forestry, Syracuse. 77 pp.
- Brewer, G.J. 1970. An introduction to isozyme techniques. Academic Press, New York. 186 pp.
- Bush, G.L., and R.N. Huettel. 1972. Starch gel electrophoresis of tephritid proteins, a manual of techniques. Publ. by Population Genetics Project, Phase I. International Biological Program Working Group on Fruit Flies. 56 pp.
- Craighead, F.C. 1921. Hopkins' host selection principle as related to certain cerambycid beetles. *J. Agric. Res.* 22:189-220.
- Crookston, N.L., R.W. Stark and D.L. Adams. 1977. Outbreaks of mountain pine beetle in lodgepole pine forests—1945 to 1975. Forest, Wildl. and Range Exp. Sta. Bull. No. 22. Univ. of Idaho, Moscow. 7 pp.
- May, B. 1975. Electrophoretic variation in the genus *Oncorhynchus*: the methodology, genetic basis and practical applications to fisheries research and management. Master's thesis, University of Washington, Seattle. 96 pp.
- Mayr, E. 1970. Populations, species and evolution. Belknap Press of Harvard University Press, Cambridge. 453 pp.
- Morrow, R.A. 1972. *Dendroctonus ponderosae*: the mountain pine beetle. Insect and Disease Laboratory, Colorado State Forest Serv., Colorado State Univ., Ft. Collins, CO. 83 pp.
- Rogers, J.S. 1972. Measures of genetic similarity and genetic distance. University of Texas Publication 7213:145-153.
- Shaw, C.R., and R. Prasad. 1970. Starch gel electrophoresis of enzymes—a compilation of recipes. *Biochem. Genet.* 4:297-320.
- Sneath, P.H.A., and R.R. Sokal. 1973. Numerical taxonomy. W.H. Freeman, San Francisco. 573 pp.
- Utter, F.M., H.O. Hodgins and F.W. Allendorf. 1974. Biochemical genetic studies of fishes: Potentialities and limitations. Pages 213-237 in D.C. Malins and J.R. Sargent (eds.). Biochemical and biophysical perspectives in marine biology, Vol. 1. Academic Press, New York.
- Wellington, W.G. 1977. Returning the insect to insect ecology: Some consequences for pest management. *Environ. Entomol.* 6:1-8.

ASSESSMENT OF RESEARCH AND APPLICATION

Comments on the Mountain Pine Beetle/Lodgepole Pine Symposium

Maynard T. Rost

ABSTRACT

The questions of what managers need from researchers and the extent to which this symposium met that need are discussed. The importance of preventive programs is emphasized. Ways in which managers can become more involved in solving the problem of mountain pine beetle (*Dendroctonus ponderosae* Hopkins) in lodgepole pine (*Pinus contorta* Douglas var. *latifolia* Engelman) are suggested.

INTRODUCTION

A little over a year ago, Dr. Stark wrote and asked if I would consider serving on the evaluation panel for this symposium. By golly, I worried about it for a day or two and called him on the phone and asked, "Why me and what could I contribute?" He said, "They have a serious need for representatives from management to evaluate this symposium and express some thoughts on its effectiveness and the applicability of present research to managers' needs." I thought, "Well that's over a year away, I might be dead or he might forget about my commitment," and agreed to participate.

I'm a little bit awed to participate in an evaluation of such an impressive cadre of speakers. However, I'm not awed enough that I won't comment. I intend to orient my remarks to four general areas:

1. What I believe managers need from entomologists.
2. Whether this symposium satisfied this need.
3. What managers should do to obtain more effective use of researchers.
4. Suggestions for your consideration on ways this symposium might be improved.

WHAT DO LAND MANAGERS NEED FROM ENTOMOLOGISTS?

Most forest land managers have peripheral knowledge of mountain pine beetles (*Dendroctonus ponderosae* Hopkins) and only a few have intensive experience. It is increasingly more common for managers to depend upon specialists to identify impacts and develop alternatives. This is especially true in lodgepole pine (*Pinus contorta* Douglas var. *latifolia* Engelman) forests attacked by mountain pine beetles, because of more complex land management objectives.

Insect Information

Land managers need to know species of insects, their relative abundance and population trends. Are the populations increasing or decreasing, endemic or epidemic, parasites present? What is the projected increase or decrease in ratio to existing beetle? Are the insects spread evenly through the area or are they in "clumps"? What insects are present? Are they initial attackers or do they follow after the tree is weakened or dead? What insects, if any, are apt to follow the present population?

Parker and others spoke specifically about this. I believe entomologists know the insect information managers need.

Habitat Information

The species, susceptibility and abundance of the host are obviously critical information for the manager. What tree species is the insect attacking and what is the abundance of the host species? Is the total host population susceptible to attack? Is the host species widespread or isolated? Are other susceptible species present? What are the relative values of the primary and secondary hosts?

Another question I would like to address is, "Are this symposium and the proceedings that will be published the final products of the IPM program and the allied research efforts? Will the symposium proceedings ensure that the research that has been described will be put into practice?" I believe that there are opportunities for informal workshops, pilot projects and demonstrations of new technology that would materially improve chances of transfer of this new knowledge.

A somewhat similar accelerated effort has been under way by the USDA for the past 3 years on two major forest defoliators, the gypsy moth and the Douglas-fir tussock moth. These programs were characterized by three full field seasons of active research, accompanied by a "phase-down year" that was dedicated to summarizing research, preparation of a "state of the art" compendium and development of a series of "how to" user guides. These activities were an integral part of the program, to ensure that research products would find their way to users. Perhaps this is the way the effort should be directed in the final year of the mountain pine beetle program.

One final question is, "When should a research and development effort such as this receive input from users?" Experts in the field of knowledge utilization believe that potential users should be involved early in the program to help guide

the research effort and ensure that results are relevant and applicable. To my knowledge, the IPM portion of the mountain pine beetle research and development program has not actively solicited input from resource managers, until we were asked to provide a management review at this symposium, 6 years into the program. Perhaps this was an oversight on the part of the research community and perhaps some of us in the user category should have been more insistent on participation in the research planning. It is academic to question whether the results presented here would have been measurably different if user input had been solicited and considered in the research planning. It might have made the transfer of technology easier, however, as there would have been some individuals more committed and receptive to using the results.

Finally, I would like to thank the program coordinators for the opportunity to critique this program. With the exception of having had to read about 20 pounds of manuscripts over the past month, it has been a lot of fun. Since I am presently in a position of the "man in the middle," between the research community and those who will ultimately use research products, it has given me a chance to expound on problems I see on both sides of the fence. In addition, having had to synthesize this symposium has kept me awake, alert and sober for a greater portion of this symposium than most others that I have attended!

APPENDIX I

APPENDIX I

SPEAKERS AND MODERATORS

Washington State University, Pullman, WA 99164

A.A. Berryman
Dept. of Entomology

H. Cabrera
Dept. of Forestry and Range Management

D.G. Burnell
Dept. of Entomology

R.C. Roelke
Dept. of Entomology

University of Idaho, Moscow, ID 83843

R.W. Stark
College of Forestry

J.A. Schenk
College of Forestry

D.L. Adams
College of Forestry

R. Mahoney
College of Forestry

N.L. Crookston
College of Forestry

A.D. Partridge
College of Forestry

D.L. Kulhavy
College of Forestry

M.W. Stock
College of Forestry

J. Guenther
College of Agriculture (student)

Canadian Forestry Service, Pacific Forest Research Centre, Victoria, B.C., Canada V8Z 1M5

D.M. Shrimpton
L. Safranyik
S.J. Muraro
H.S. Whitney

Forest Service, USDA, Intermountain Forest and Range Experiment Station, Ogden, UT 84401

G.D. Amman
W.E. Cole
R.F. Schmitz

Forest Service, USDA, Forest Sciences Laboratory, Moscow, ID 83843

A.R. Stage
C.A. Wellner (ret.)

Forest Service, USDA, Rocky Mountain Forest and Range Experiment Station, Ft. Collins, CO 80521

William F. McCambridge

Forest Service, USDA, Box 25127, Lakewood, CO 80225

D.B. Cahill

Forest Service, USDA, 517 Gold Ave. S.W., Albuquerque, NM 87101

D.L. Parker

Forest Service, USDA, Methods Application Group, 2810 Chiles Road, Davis, CA 95616

W.M. Ciesla
W.H. Klein

Forest Service, USDA, Forest Sciences Laboratory, Bozeman, MT 59715

D.M. Cole

Forest Service, USDA, Kootenai National Forest, Libby, MT 59923

M. Rost

Forest Service, USDA, Federal Building, Missoula, MT 59801

M.D. McGregor
D.R. Hamel

Forest Service, USDA, 2517 S.W. Hailey Avenue, Pendleton, OR 97801

S.W. Carter, Jr.

University of British Columbia, Institute of Animal Resource
Ecology, Vancouver, B.C., Canada V6T 1W5

R.M. Peterman

Oregon State University, Corvallis, OR 97331

G.B. Pitman

Bureau of Timber Management, Idaho Department of Lands,
Boise, ID 83720

W. Clark

University of Washington, College of Forest Resources, Seattle,
WA 98105

D. Geiszler (student)

R. Gara

University of California, Department of Entomological
Sciences, Berkeley, CA 94720

W.E. Waters (NSF observer)

University of Georgia, Department of Entomology, Athens,
GA 30602

C. Wayen Berisford (NSF observer)

APPENDIX II

APPENDIX II

PARTICIPANTS

Robert Authier
Star Route - Malheur National Forest
Mt. Vernon, OR 97865

Bill Barber
Washington State Dept. of
Natural Resources
208 E. 11th
Ellensburg, WA 98926

Tim Beebe
Champion Timberlands
P. O. Box 3598
Missoula, MT 59806

Robert Berg
Bureau of Land Management
705 Murray St.
Rawlins, WY 82301

Thomas Bohannon
2815 Eaton
Missoula, MT 59801
(self-employed)

Charles Boldt
USDA Forest Service
2219 Lockwood Drive
Rapid City, SD 57701

John Boro
Oregon State Dept. of Forestry
Rt. 2, Box 357
Prineville, OR 97754

Bob Bosworth
USDA Forest Service
Box 963
Bonners Ferry, ID 83805

David Bridgwater
USDA Forest Service
319 SW Pine St.
P. O. Box 3623
Portland, OR 97208

George Cameron
USDA Forest Service
Box 625
White Sulphur Springs, MT 59645

Jim Carbone
Oregon State Dept. of Forestry
Rt. 2, Box 357
Prineville, OR 97754

J.H. (Howie) Carter
Crown Zellerbach Canada Ltd.
Box 220
Kelowna, B.C.

Dwight Chambers
USDA Forest Service
Sula Ranger Station
Sula, MT 59871

Howard Christensen
USDA Forest Service
P.O. Box 466
Tonasket, WA 98855

Richard Clabaugh
USDA Forest Service
Box 1136
Burney, CA 96013

Ron Circle
Box 201
Nespelem, WA 99155

Dave Clark
Colville Tribe
Timber Stand Improvement Program
Box 328
Nespelem, WA 99155

Ernest Collard
Wallowa-Whitman National Forest
P.O. Box 907
Baker, OR 97814

Gary Collier
USDA Forest Service
P. O. Box 466
Tonasket, WA 98855

Jack Coster
Applications Coordinator, ESPBRAP
Southern Pine Beetle Program
2500 Shreveport Highway
Pineville, LA 71360

W.L. (Bill) Coulter
Crown Zellerbach Canada Ltd.
Box 220
Kelowna, B.C.

Barrie Custance
British Columbia Forest Service
518 Lake Street
Nelson, B.C.

John Cuthbert
British Columbia Forest Service
518 Lake Street
Nelson, B.C.

Walter Deepers
Bureau of Indian Affairs
Warm Springs Agency
Warm Springs, OR 97761

Jed Dency
USDA Forest Service
Federal Bldg.
Missoula, MT 59801

Darrell Dick
Bureau of Indian Affairs
Colville Agency
P.O. Box 111
Nespelem, WA 99155

William Driver
Gallatin National Forest
P.O. Box 130
Bozeman, MT 59715

George Ducharme
Confederated Salish &
Kootenai Tribes
Box 36
Polson, MT 59860

Roy Elmgren
Box 549
Jacksonville, OR 97530

Greg Elstad
Ashton Ranger District
Ashton, ID 83420

Keith Engebretson
Champion Timberlands
P.O. Box 3598
Missoula, MT 59806

Paul Erler
Targhee National Forest
115 Highland
Ashton, ID 83420

Gary Fiddler
USDA Forest Service
Box 1078
Burney, CA 96013

Joe Frost
10524 Landmark Ct.
Boise, ID 83704

Randall Gay
Gallatin National Forest
P.O. Box 130
Bozeman, MT 59715

Gordon George
USDA Forest Service
Umatilla National Forest
2517 S.W. Hailey Ave.
Pendleton, OR 97801

Kenneth Gibson
USDA Forest Service
4746 S. 1900 E.
Ogden, UT 84403

William Gibson
USDA Forest Service
P.O. Box 185
Crescent, OR 97733

Samuel Gilbert
Gallatin National Forest
P.O. Box 130
Bozeman, MT 59715

Robert Gilrein
Bureau of Indian Affairs
Colville Agency
P.O. Box 111
Nespelem, WA 99155

Ralph Goode
Confederated Salish &
Kootenai Tribes
Rt. 1, Box 83CH
Ronan, MT 59864

Alan Grenier
Confederated Salish &
Kootenai Tribes
Rt. 1, Box 12AB
Ronan, MT 59864

David Griffin
Lolo National Forest
Nine Mile Ranger Station
2787 Beilvue Drive
Missoula, MT 59801

Ronald Hamilton
USDA Forest Service
1512 E. 1350 S.
Ogden, UT 84404

Chuck Harris
Swan Lake Ranger Station
Bigfork, MT 59911

John Herbst
Area Extension Forester
Oregon State University Extension Service
P.O. Box 760
La Grande, OR 97850

Darrell Hersley
Idaho Department of Lands
Rt. 1, Box 400
Idaho Falls, ID 83401

Robert Hilliard
USDA Forest Service
P.O. Box 234
John Day, OR 97845

Bert Hockett
Georgia Pacific Corporation
P.O. Box 130
Chemult, OR 97731

Neil Hyde
USDA Forest Service
Flathead National Forest
P.O. Box 147
Kalispell, MT 59901

Steve Jacky
Oregon State Dept. of Forestry
Rt. 2, Box 357
Prineville, OR 97754

Paul Joseph
Oregon State Dept. of Forestry
2600 State Street
Salem, OR 97310

John Joy
USDA Forest Service
Box 528
Whitehall, MT 59759

Wesley Kellie
Lolo National Forest
Bldg. 24, Fort Missoula
Missoula, MT 59801

LeRoy Kline
Insect & Disease Lab.
Oregon State Dept. of Forestry
2600 State Street
Salem, OR 97310

William Kurrle, III
Coeur d'Alene Tribe
P.O. Box 44
Latah, WA 99018

Richard Kusicko
Kootenai National Forest
Libby, MT 59923

Richard Lasko
USDA Forest Service
Murphy Lake Ranger Station
Fortine, MT 59918

Thomas Lawrence
Kootenai National Forest
Rexford Ranger District
Eureka, MT 59917

Dave Leatherman
Colorado State Forest Service
2602 Countryside Ct.
Fort Collins, CO 80521

Amy Lester
University of Montana
School of Forestry
Missoula, MT 59801

W.A. Leuschner
Dept. of Forestry &
Forest Products
VPI & SU
Blacksburg, VA 24060

Chris Liggett
Targhee National Forest
Island Park Ranger Station
Island Park, ID 83429

Staffan Lindgren
Pestology Centre
Biological Sciences Dept.
Simon Fraser University
Burnaby, B.C. V5A 1S6

Larry Lindner
Clearwater Ranger District
Grangeville, ID 83530

Ken Lister
12850 West 6th Place
Golden, CO 80401

Ladd Livingston
Idaho State Dept. of Forestry
P.O. Box 670
Coeur d'Alene, ID 83814

Donald Lougee
Bureau of Land Management
P.O. Box 550
Prineville, OR 97754

Deb Louie
Colville Tribe
Box 328
Nespelem, WA 99155

R. Loveless
School of Forestry
University of Montana
Missoula, MT 59801

J. Lowe
School of Forestry
University of Montana
Missoula, MT 59801

Jon Luibrand
Champion Timberlands
P.O. Box 3598
Missoula, MT 59806

Wayne Maahs
Champion Timberlands
P.O. Box 3598
Missoula, MT 59806

Everett MacDaniels
Crown Zellerbach
416 N.E. Burgess Place
Bend, OR 97701

P.F. (Paul) MacNamara
Crown Zellerbach Canada Ltd.
Box 220
Kelowna, B.C.

Rick Maczocchi
Fernie, B.C.

Carl Marsh
Helena National Forest
616 Helena Ave.
Helena, MT 59601

Rich Mazzacki
Box 4
Elk, B.C.

William McArthur
USDA Forest Service
Box 594
Ashton, ID 83420

James F. McClinton
USDA Soil Conservation Service
Rm. 122, U.S. Courthouse
Spokane, WA 99201

Jim McFarland
Box 14
Rager Ranger Station
Paulina, OR 97751

Bob McKnight
P.O. Box 227
Headquarters, ID 83534

Dr. J.A. McLean
Faculty of Forestry
University of British Columbia
Vancouver, B.C. V6T 1W5

Robert Monserud
USDA Forest Service
Intermountain Forest and Range Experiment Station
1221 S. Main
Moscow, ID 83843

C.R. Moore
Pest Management Officer
425 6th Ave. W.
Prince Rupert, B.C. V8J 1Z5

Paul Oester
Oregon State Dept. of Forestry
Rt. 2, Box 357
Prineville, OR 97754

Max Ollieu
USDA Forest Service
Boise Field Office, FI/DM
1075 Park Blvd.
Boise, ID 83706

Mitchell Panelli
803 S. H
Lakeview, OR 97630

Dave Parminter
British Columbia Forest Service
Nelson, B.C.

Kai Tim Petersen
Bureau of Land Management
4709 Linda Ct.
Cheyenne, WY 82001

Ronald Prichard
Flathead National Forest
Box 147
Kalispell, MT 59901

Iral Ragenovick
125 D Northridge Dr.
Ashville, NC 28804

Lynn Rasmussen
USDA Forest Service
507 - 25th Street
Ogden, UT 84401

John C. Ridungton
27 Hill Street
Prineville, OR 97754

Gary Ringold
Silviculture Operations Supervisor
Potlatch Corporation
P.O. Box 1016
Lewiston, ID 83501

George Rogers
USDA Forest Service
Missoula Ranger District
2801 Russell
Missoula, MT 59801

Jim Runyan
Champion Timberlands
P.O. Box 3598
Missoula, MT 59806

Gary Ryan
Bureau of Land Management
Box 768
Pinedale, WY 82941

Bill Samuels
Targhee National Forest
Island Park, ID 83429

Gordon Sanders
Champion Timberlands
P.O. Box 3598
Missoula, MT 59806

Ollie Scott
USDA Forest Service
Box 961
Cody, WY 82414

Chuck Seeley
Champion Timberlands
P.O. Box 3598
Missoula, MT 59806

Douglas Shaner
USDA Forest Service
Lolo National Forest
Bldg. 24, Fort Missoula
Missoula, MT 59801

Jerry Sheldon
Fernan Ranger District
P.O. Box 1649
Coeur d'Alene, ID 83814

Philip Simonski
USDA Forest Service
Wallowa-Whitman National Forest
P.O. Box 907
Baker, OR 97814

Jim Simpson
Champion Timberlands
P.O. Box 3598
Missoula, MT 59806

Anthony Smith
Fort Rock Ranger District
Deschutes National Forest
211 N.E. Revere
Bend, OR 97701

Lathrop Smith
USDA Forest Service
Jefferson Ranger District
Box F
Whitehall, MT 59759

Sheila Sourer
Colville Tribe
Timber Stand Improvement Program
Box 328
Nespelem, WA 99155

LaVelle Stanger
USDA Forest Service
Timber Management
P.O. Box 3623
Portland, OR 97208

Lawrence Stipe
USDA Forest Service
4746 S. 1900 E.
Ogden, UT 84403

Brian Stone
Targhee National Forest
Island Park, ID 83429

Malcolm Stump
Bureau of Indian Affairs
Colville Agency
P.O. Box 111
Nespelem, WA 99155

Bill Targeersen
Rt. 1, Box 75 W.
Butte, MT 59701

Robert C. Thatcher
USDA Southern Pine Beetle
RD&A Program
2500 Shreveport Highway
Pineville, LA 71360

Bill Timentwa
Colville Tribe
Timber Stand Improvement Program
Box 328
Nespelem, WA 99155

Ross Tozer
British Columbia Forest Service
Nelson, B.C.

Galen Trostle
USDA Forest Service
14395 - 27th Ct.
Beaverton, OR 97005

Scott Tunnock
USDA Forest Service
546 Woodworth
Missoula, MT 59801

David Tupper
USDA Forest Service
Ukiah Ranger Station
Ukiah, OR 97880

Daniel Twardus
USDA Forest Service
S&PF
Forest Insect & Disease Management
2500 Shreveport Highway
Pineville, LA 71360

Stan Underwood
Superior Ranger District
Superior, MT 59872

Jan A. Volney
Dept. of Entomology
University of California, Berkeley
Berkeley, CA 94720

Thomas Ward
Dept. of Biological Sciences
Simon Fraser University
Burnaby, B.C. V3L 3R7

John Wenz
USDA Forest Service
Forest Insect & Disease Management
630 Sansome Street
San Francisco, CA 94111

Richard Wiest
USDA Forest Service
P.O. Box 310
Coeur d'Alene, ID 83814

Carroll Williams, Jr.
USDA Forest Service
1960 Addison
P.O. Box 245
Berkeley, CA 94707

George Wilson
Flathead National Forest
Box 147
Kalispell, MT 59901

Marvin Wolfe
Targhee National Forest
720 N. 5th W.
St. Anthony, ID 83445

Jerry Worley
Beaverhead National Forest
23 Sunrise
Dillon, MT 59725

Leslie Yates
USDA Forest Service
417 S.E. Yew Lane
Bend, OR 97701

Richard Youngs
USDA Forest Service
211 N.E. Revere
Bend, OR 97701