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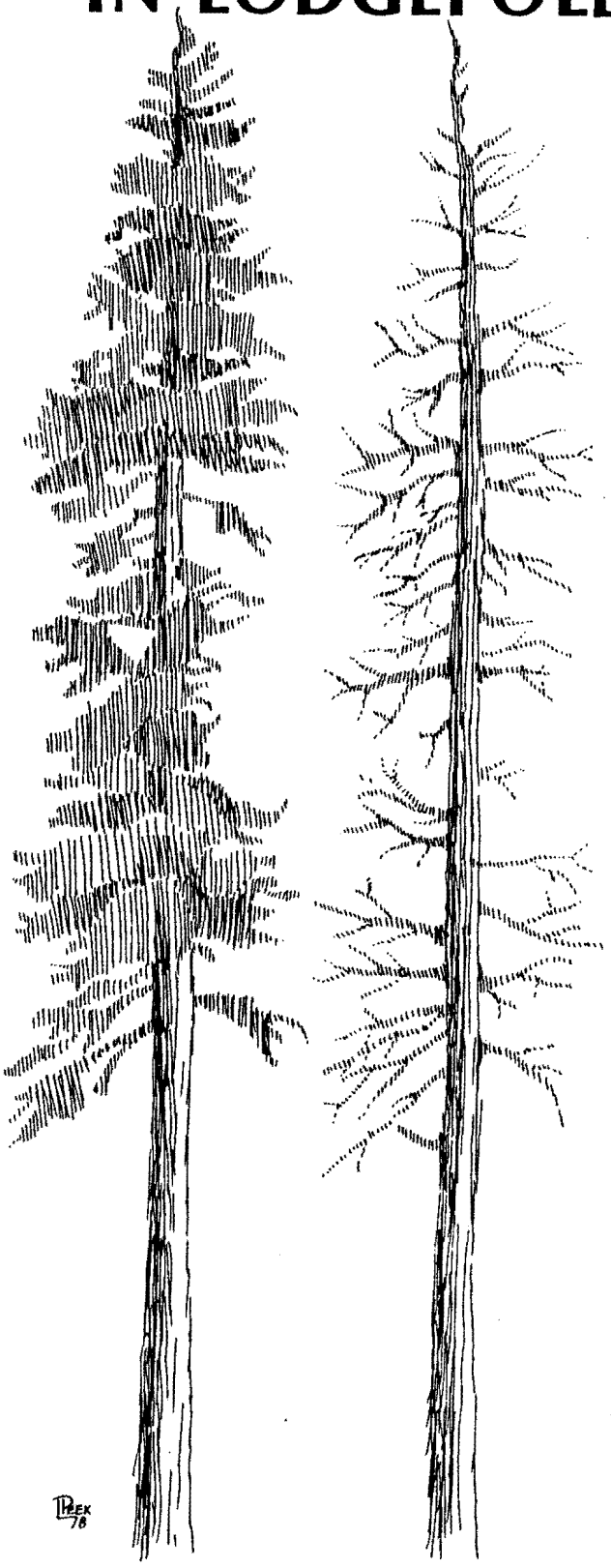
Gene D. Amman

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



SYMPOSIUM PROCEEDINGS

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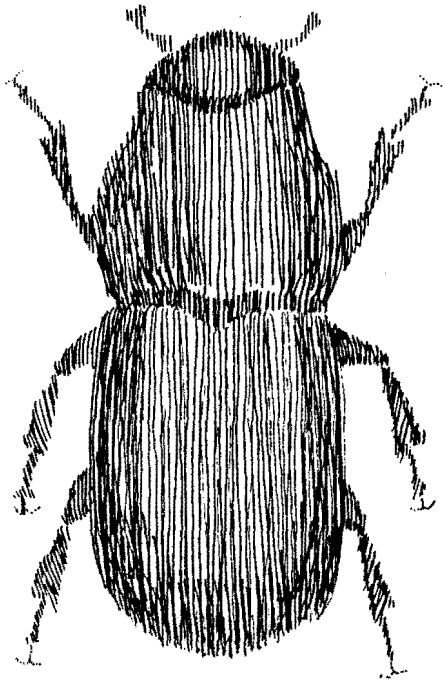

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THEORY AND PRACTICE OF MOUNTAIN PINE BEETLE MANAGEMENT IN LODGEPOLE PINE FORESTS

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December 1978

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* Engelmann). 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* Engelmann) 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

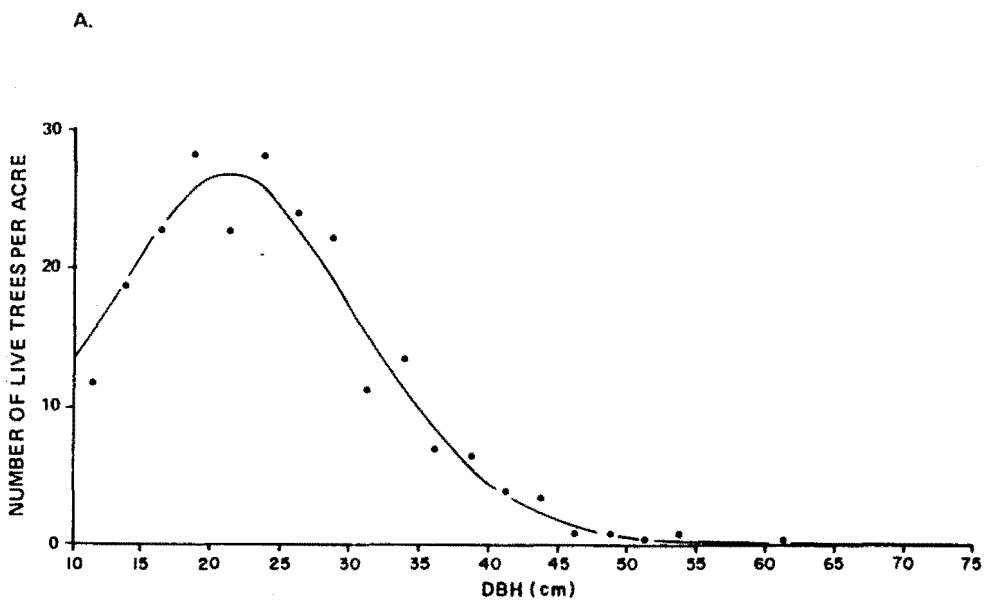

Fig. 1. Green stand structure at the beginning of the mountain pine beetle infestation.

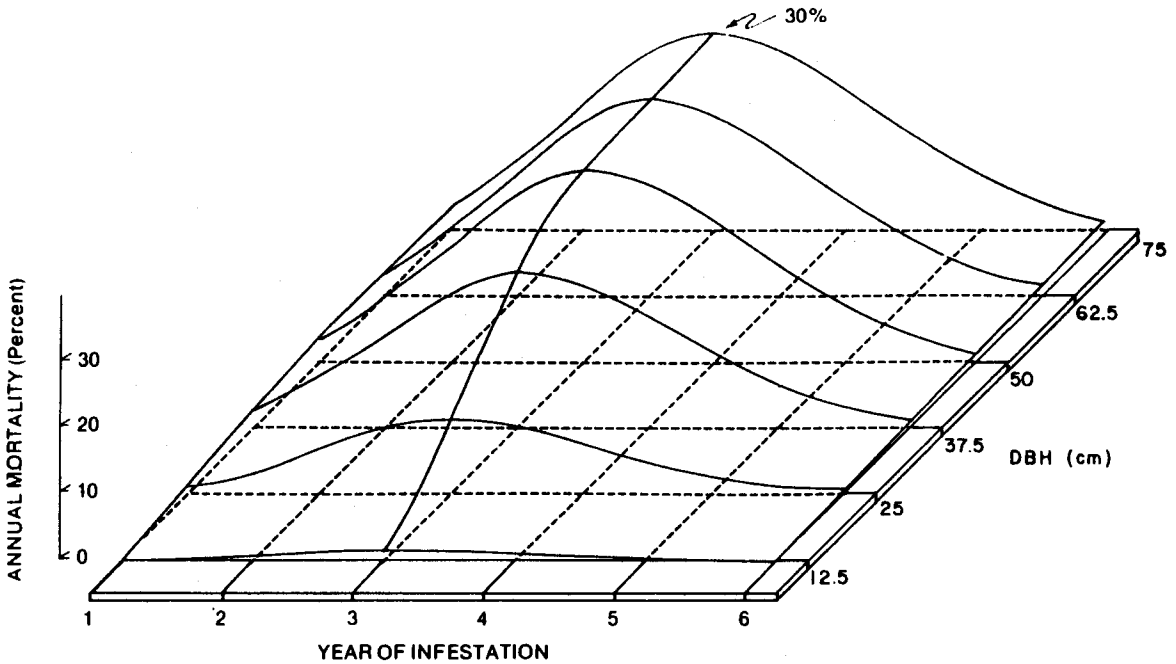

Fig. 2A. Annual mortality (percent) by diameter and year of infestation (Cole et al. 1976).

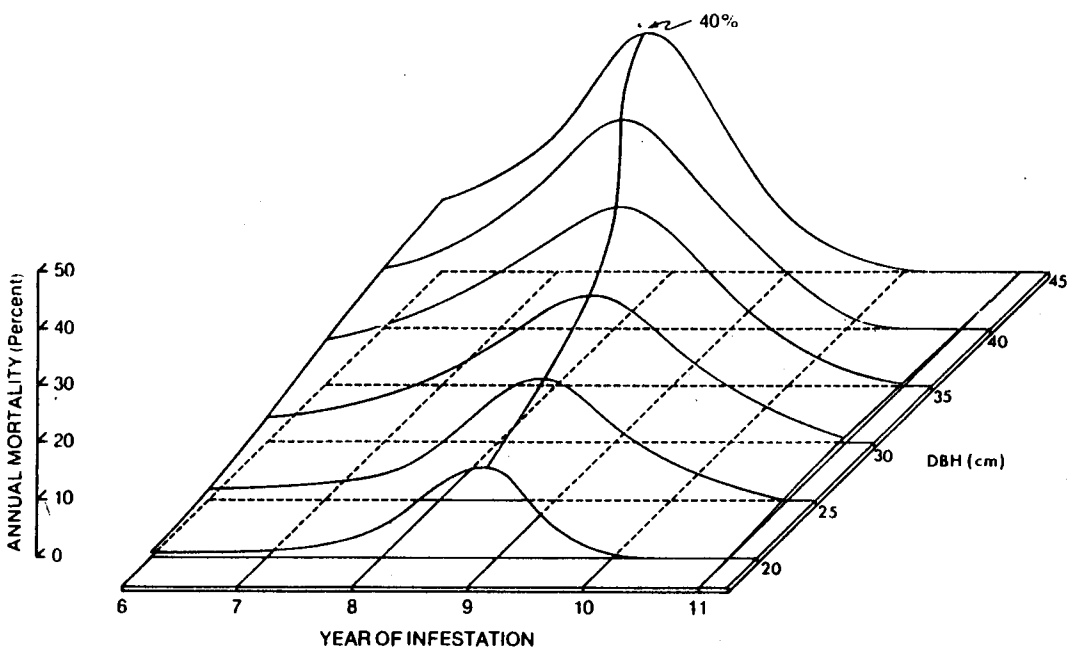

Fig. 2B. Annual mortality (percent) by diameter and year of infestation (Klein et al. in prep.).

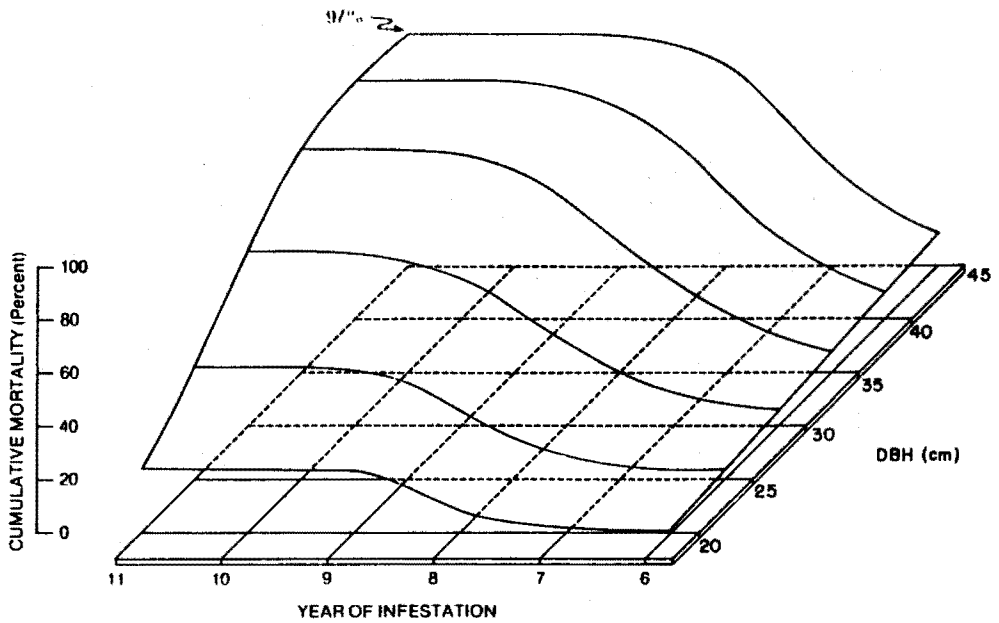

Fig. 3A. Cumulative mortality (percent) by diameter and year of infestation (Cole et al. 1976).

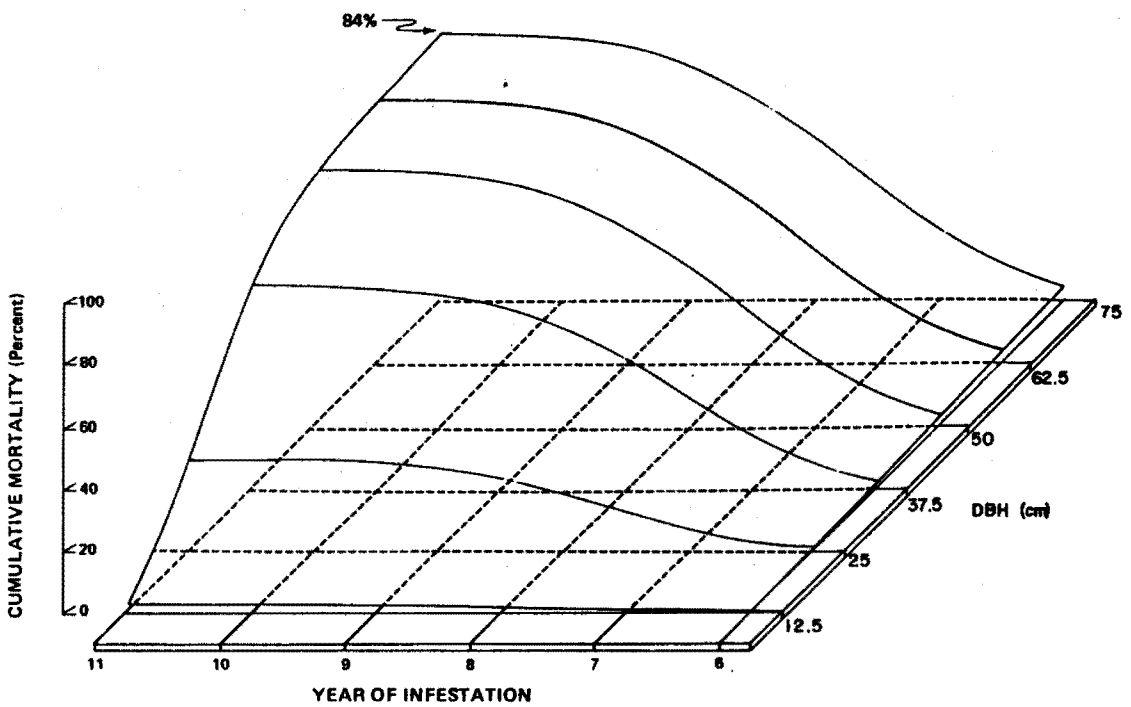

Fig. 3B. Cumulative mortality (percent) by diameter and year of infestation (Klein et al. In prep.).

related to low gallery density, and hence to low egg density. Survival of large larvae increased over time within all diameter classes and increased substantially during years 6 through 8. However, as the infestation progressed, egg galleries increased (and egg density), and an apparent optimum number of large larvae occurred in year 8.

Adult density was similar to that of large larvae, but reduced, the peak occurring in year 8. Emergence within a diameter class was fairly steady, but always greater in the larger trees. Laboratory studies show that adult emergence is directly related to centimeters of egg galleries when attack densities are low, resulting in low larval competition and little crowding (Amman 1972). When gallery densities are high, adult emergence is directly related to phloem thickness.

Brood Density and Stand Structure Interaction

An epidemic is dependent upon successful infestation of large trees. On the average, only large trees can be expected to produce enough brood to keep an infestation going, particularly during the later years of an infestation. By the eleventh to thirteenth year of an infestation, few large-diameter trees remain in a stand—not enough to keep an infestation active. This dependency of outbreaks on the successful infesting of large-diameter trees implies that during endemic periods the beetle could infest mostly small-diameter trees. Not enough is known about beetle behavior during its low population phase to substantiate this implication.

The explanation or description of the transition from endemic to epidemic populations, or even the start of epidemic populations, awaits further research. However, our most recent studies of endemic populations suggest that the beetle does indeed infest small-diameter trees that may be injured by porcupines, lightning, comandra rust or the like. We have seen the number of successfully attacked trees fluctuate from one to six trees in a stand during the endemic periods. When a larger-diameter tree is attacked, the tree may repel the beetles. When a larger-diameter tree is successfully attacked, we can only assume that the few surviving beetles from the nearby small-diameter trees congregated on the large tree in enough numbers to be successful. This situation is covered in detail in Amman's paper (these proc.).

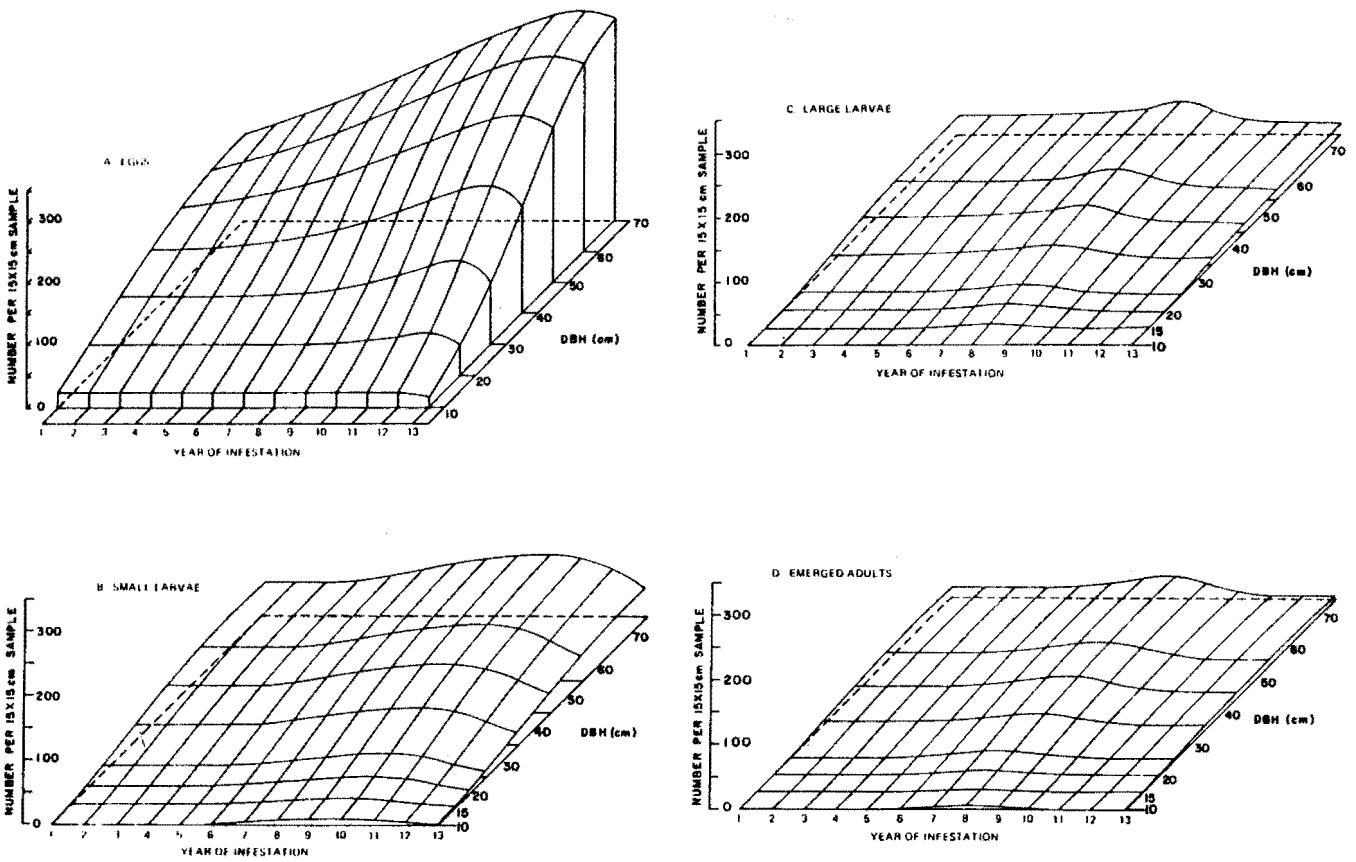

Fig. 4. Densities of four life stages of the mountain pine beetle by tree diameter for a 13-year period. A = eggs; B = small larvae; C = large larvae; D = emerged adults.

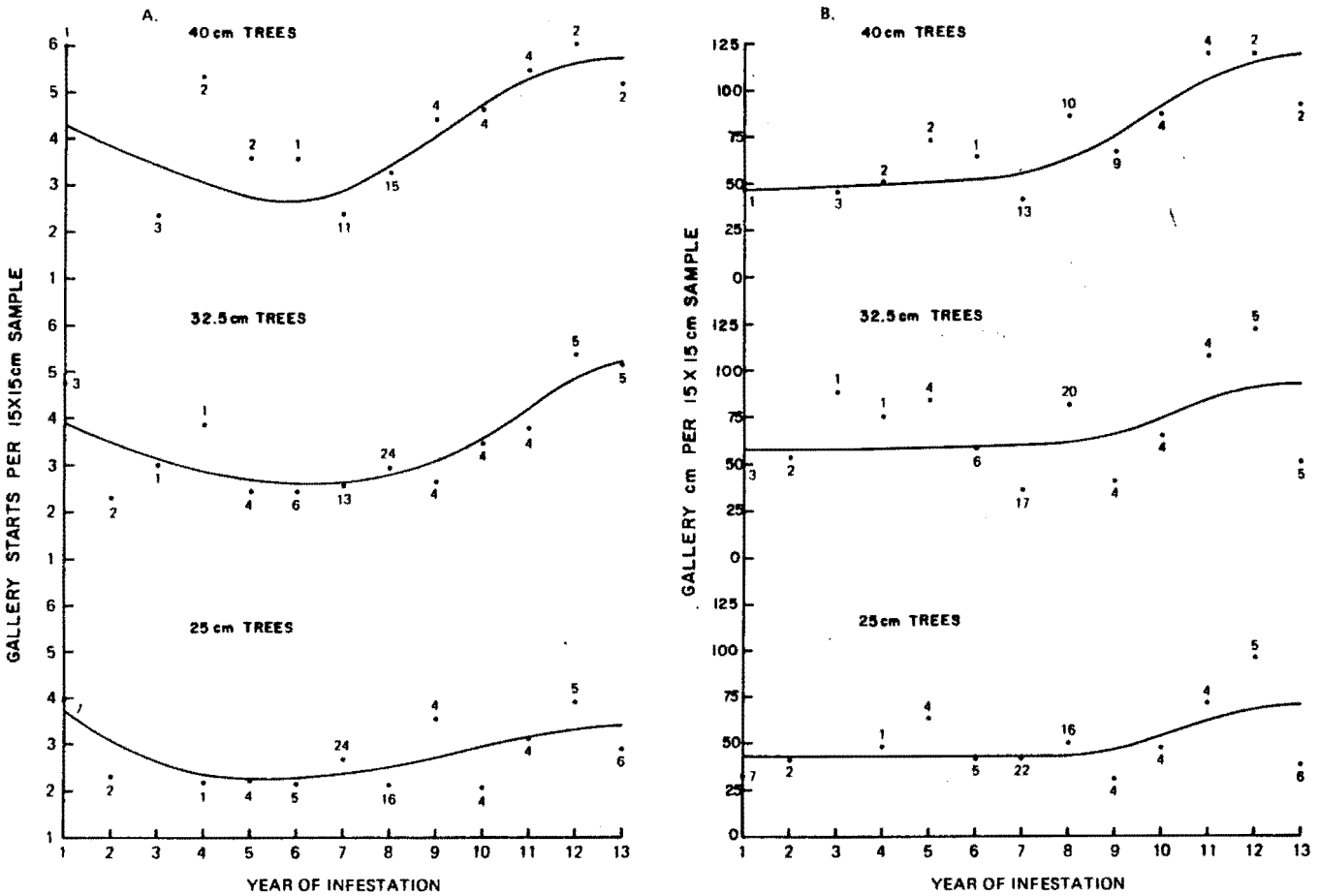

Fig. 5. Mountain pine beetle egg gallery starts and egg gallery length by diameter for a 13-year period. A = egg gallery starts; B = egg gallery length. Number at each data point indicates number of trees sampled.

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.

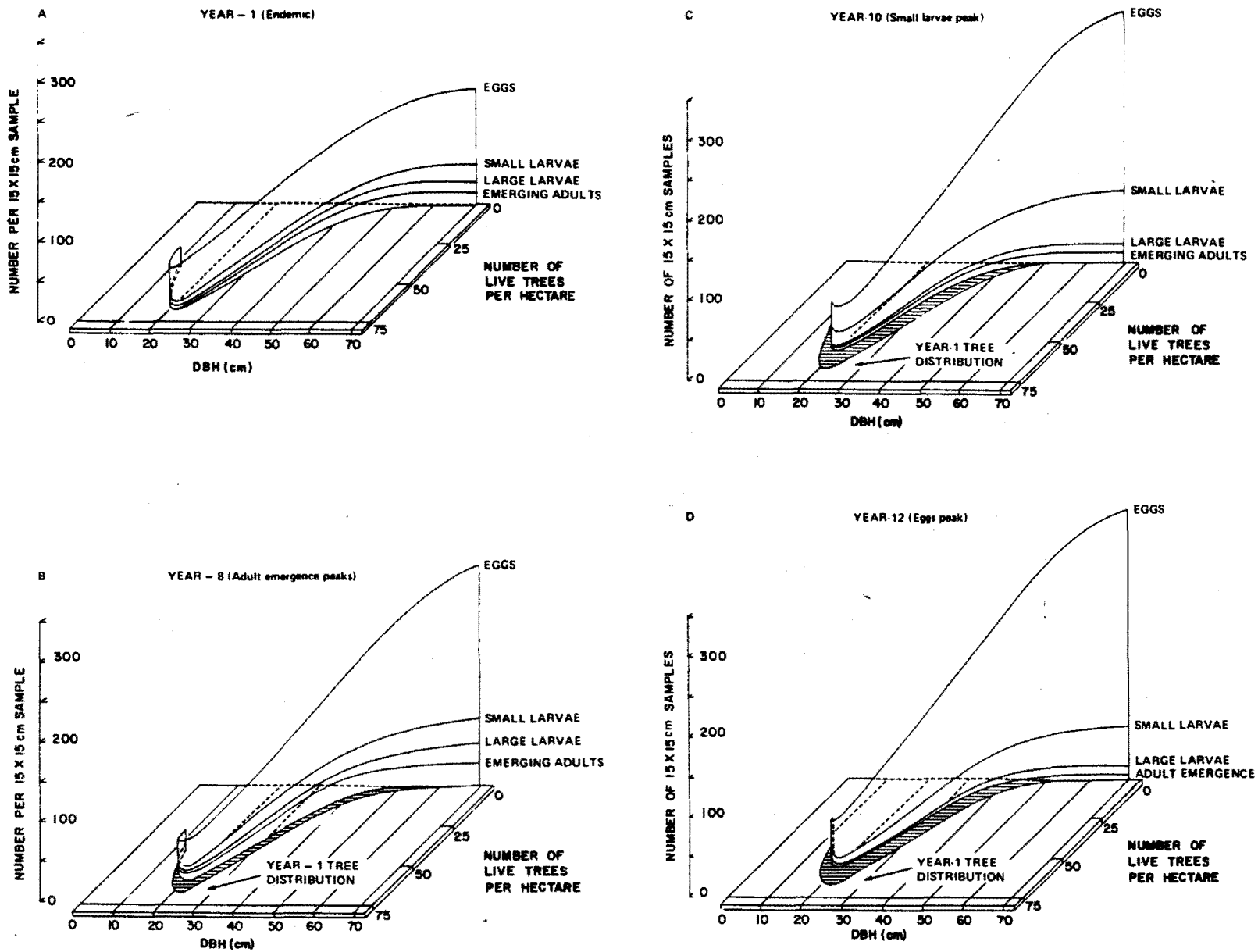

Fig. 6. Interaction models of beetle survival and lodgepole pine losses. A = year 1 (endemic beetle population level); B = year 8 (peak adult emergence); C = year 10 (peak small larvae density); D = year 12 (peak egg density). Shaded area shows cumulative tree mortality (Cole et al. 1976).

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).

Phloem thickness (cm)	Diameter at Breast Height (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

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

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., thinnings 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.

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).

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