THE HAZARD OF MOUNTAIN PINE BEETLE

OUTBREAK IN LODGEPOLE PINE FORESTS

by

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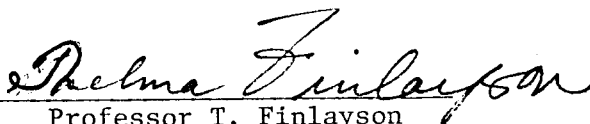Title of Thesis: The Hazard of Mountain Pine Beetle Outbreak
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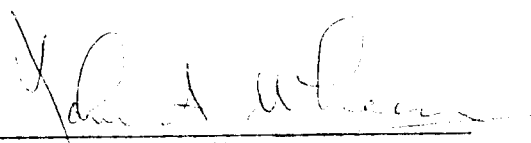Examining Committee:

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ABSTRACT

The factors affecting the hazard of mountain pine beetle outbreak
are examined and discussed as a basis for their potential usefulness in
forest pest management. The main objective is to identify those conditions
that render lodgepole pine forests susceptible to beetle outbreak so
that the forest pest manager may be able to practice preventive forest
management, the only control that is currently feasible.

The most reliable characteristic for assessing individual tree
susceptibility is tree diameter. Highly susceptible trees or high risk
trees are defined as those trees larger than 8 in. diameter at breast
height (d.b.h.) as these are preferred by the beetles during the course
of an outbreak. To assess stand susceptibility it is recommended that
the proportion of high risk trees in the stand and the altitude of the
stand be used. The most susceptible forests are those located at low
elevations, i.e. below 3,700 ft (1,128 m) with more than 32% of trees
larger than 8 in. d.b.h./acre. Such stands located in areas where the
climate is often favourable for the beetle will have a high hazard
rating.

Several other factors are recognized as important in determining
tree and stand susceptibility (e.g. tree resistance) but they are
difficult to measure in a practical appraisal of hazard situation.

It is concluded that when the stand susceptibility is considered
in conjunction with estimates of the size and trend of the insect
population, one can arrive at a good estimate of the degree of risk of

the stand under study. It is proposed that the size and trend of the bark beetle population be determined by studying the trend of past losses through sequential aerial photographic sampling accompanied by some ground checking.

The degree of risk in a stand may be expressed by a numerical hazard index which is an integration of all the factors affecting the degree of risk into one single figure. This integration must be based on experience and trial and error approximation.

The forest manager will be able to make the appropriate corrections in the overall management plan by assessing the degree of hazard of each stand in a management unit.

ACKNOWLEDGEMENTS

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INTRODUCTION

The appraisal of hazard is a part of what has been termed biological evaluation of insect infestations. According to the U.S. Forest Service (1961), biological evaluation is "the determination of the likely course an outbreak will take unchecked and the estimation of the damage and loss expected if the outbreak is not suppressed". In this paper, outbreak hazard is defined as the probability that an insect will develop a population level able to cause significant damage in a forest area.

Correct appraisal of the degree of hazard in a forest area is the key to taking several decisions in forest protection and management. Correct appraisal of risk prevents the consequences of failure to take proper action, reduces wastage from unnecessary and inappropriate action, and provides advance warning of latent outbreaks (Graham 1963). Hazard appraisal is a tool that enables the forester to determine where and when forest insect outbreaks are likely to occur, where and when direct control measures are necessary and where cuttings are needed to prevent excessive losses (Graham 1963).

More than a simple annual assessment of insect numbers and the related damage is necessary to evaluate the degree of bark beetle hazard. The forest entomologist must understand those forces that are operating in bringing about the increase or decrease of insect numbers. It must be fully recognized that two major dependent biological organisms are

involved: the insects and the host trees. The insect will do no serious damage if the host is not susceptible, and a susceptible host will remain practically undamaged if the insect is not present in sufficient numbers (Graham and Knight 1965). The appraisal of hazard must be rooted in an assessment of the insect population and a prediction of its growth, with judgement on the numbers, health and trend of insect populations, as well as on the predisposition of trees and stands (Graham 1963). This means that hazard evaluation must be based on sound knowledge of the insect's population dynamics and forest ecology. One must recognize that scientific knowledge in these areas is far from complete.

This paper deals with the factors affecting the outbreak hazard of mountain pine beetle, *Dendroctonus ponderosae* Hopk., in forests of lodgepole pine, *Pinus contorta* Dougl.. A critical review rather than an encyclopedic one is intended. Two sets of interrelated factors are discussed: those concerned directly with the insects; and those that render lodgepole pine trees and stands susceptible to attack by the beetle, and the lay-out for a hazard rating is given.

1.   MOUNTAIN PINE BEETLE IN LODGEPOLE PINE STANDS

The mountain pine beetle, *D. ponderosae*, is native to many pine forests of western North America, from Canada to Northern Mexico. Its main hosts are lodgepole pine, western white pine (*Pinus monticola* Dougl.), and ponderosa pine (*Pinus ponderosa* Laws). It has been cited also as attacking sugar pine (*Pinus lambertiana* Dougl.), white bark pine (*Pinus albicaulis* Engelm.), limber pine (*Pinus flexilis* James) (Safranyik, Shrimpton and Whitney 1974; Sartwell and Stevens 1975), and Engelmann spruce (*Picea engelmannii* Parry) (Blackman 1931).

In Canada it has been classified as the most serious enemy of mature pines (Safranyik *et al.* 1974), especially lodgepole pine which it depletes by periodically killing the largest and most vigorous trees (Cole 1973b).

The phloem layer of the tree is the feeding and breeding habitat of the beetles. The adult beetle feeds upon and constructs an egg gallery in this layer. The symbiotic fungi, *Ceratocystis montia* Rumb. and *Europhium clavigerum* Robinson and Davison, are carried into the tree by the beetles. The tree dies when living tissue is killed by these micro-organisms (Safranyik, Shrimpton and Whitney 1975). The beetle larva constructs feeding galleries, at right angles to the egg gallery, in the inner bark that is being colonized by the blue stain fungi (Safranyik *et al.* 1975).

The mountain pine beetle has one generation per year at Ivermere, British Columbia. The eggs are laid near mid-summer, broods most commonly over winter in the larval stage, adults appear in late spring of the following year, and they emerge near mid-summer. Depending on weather variations, the life cycle may alter in time within the same region in different years and in different regions in the same year (Reid 1962).

A low endemic mountain pine beetle population may exist in lodgepole pine stands for many years before it develops into outbreak status. At low population levels the beetles infest trees weakened by fire, lightning, or other causes and colonize the least resistant trees of the stand (Shrimpton and Reid 1973). Whether a beetle population is considered of outbreak status is relative. This term generally conveys an impression of economically unacceptable damage, but the level may vary with the outlook and the goals of the individual land manager. Safranyik *et al*. (1974) considered that an outbreak comprises one or more killed trees/acre/year. However, most reports of outbreaks cite tree mortality at considerably higher levels. Blackman (1931) considered that an outbreak situation existed when the beetles were able to kill groups of 7 or more trees.

An outbreak spreads progressively from small groups of infested trees (Safranyik *et al*. 1974; Peterman 1974). At high population levels, the beetle attacks and kills the most vigorous trees of the stand, showing a preference for the largest trees each year (Roe and Amman 1970). As

the large diameter trees are killed, the beetles successively infest the residual smaller diameter trees, and by the end of an outbreak most of the large, dominant trees have been killed (Amman and Baker 1972). The average diameter of the residual stand is usually below 8 inches (Safranyik *et al*. 1974).

An outbreak of mountain pine beetle in lodgepole pine generally lasts about 8 years (Fig. 1), ranging from four to fourteen years, and may reach mortality levels of up to 32 trees/acre (Amman and Baker 1972).

FIGURE 1   Yearly tree mortality in a typical mountain pine beetle

outbreak in lodgepole pine (after Parker 1973).
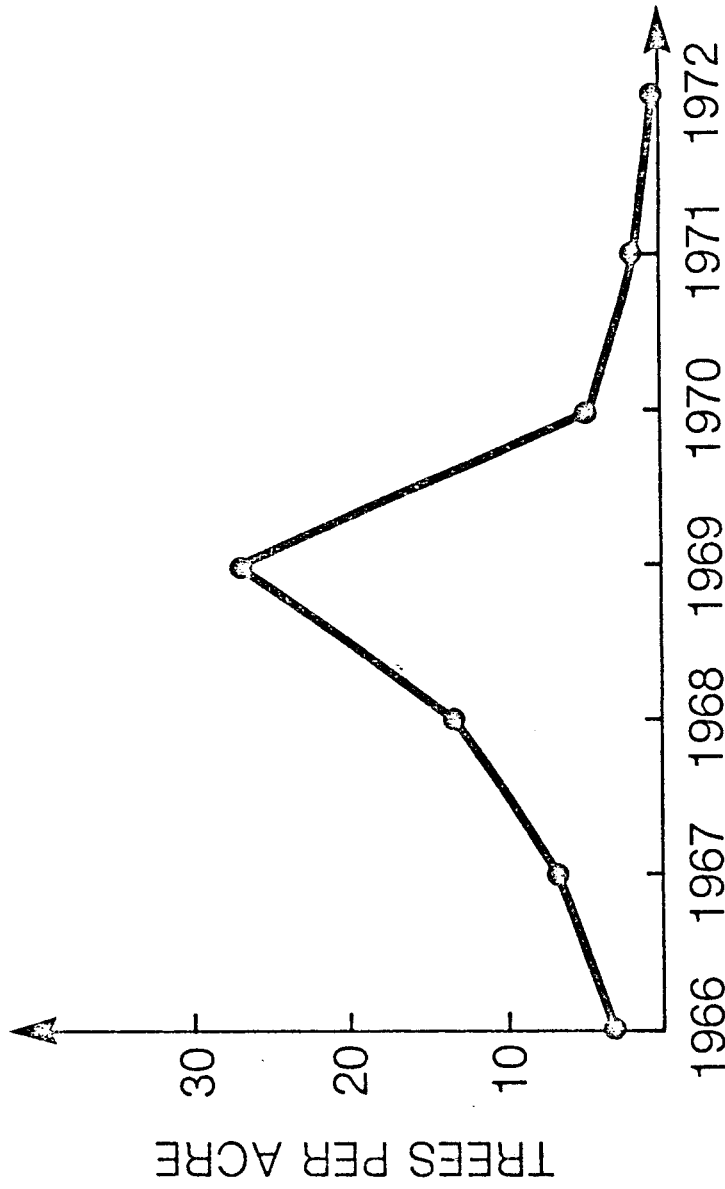
2.　　　FACTORS AFFECTING THE HAZARD OF MOUNTAIN
PINE BEETLE OUTBREAK

The potential destructiveness of an insect population is determined by the single or combined roles of many natural control factors, such as parasites, predators, disease organisms, host density, and climatic factors. It follows that the effects of all these and other factors must be taken into consideration in evaluating the outbreak hazard of an area. Special attention must be given to estimating the possible effect of the key factors i.e. those triggering the outbreak when all remaining conditions are permissive. According to Morris (1963), the population dynamics of an insect are affected by many variables but determined by only a few.

It is generally accepted that both the physiological condition of the host tree and the population level of an insect must be considered in ascertaining the degree of destructiveness of the insect. Most bark beetles prefer dead, dying, or weakened trees as breeding sites and are therefore referred to as secondary pests which can become primary pests under outbreak conditions (Rudinsky 1962). The western pine beetle (*Dendroctonus brevicomis* Leconte) prefers overmature trees in poor health and normally develops outbreaks only when the stand as a whole is weakened from drought, overmaturity, or overstocking (Johnson 1972). The mountain pine beetle easily develops outbreaks in stands of normal vigor (Wygant 1959).

For discussion purposes, the factors influencing mountain pine beetle outbreak hazard have been divided into classes: those related to the insects, those related to the trees and stands, and those related to the climate. It is clear that in natural ecosystems these factors are acting in a highly complex inter-relationship.

2.1   FACTORS RELATED TO THE BEETLES

The threat from a beetle population may be judged as real if there is: abnormal extent of the area of population; an abnormally high population level; an upward trend of the insect numbers. A latent threat will exist in cases of recurrent species of insects or when the stand being studied is in proximity to a large population that may invade (Graham 1963).

2.1.1   Population size and trend

To determine the insect numbers and the size of the infestation requires a survey designed to give results that are statistically acceptable. The survey will vary in accuracy according to sampling intensity, which is usually determined by economic factors. The justification of survey costs depends on which courses of action could arise from the appraisal (Flora 1968). For example, surveys may provide data needed to plan control projects or to make management decisions as to which stands should be harvested first (Orr 1954).

Forest entomologists have long studied methods of population

estimation, and different approaches have been developed. For the scope of this paper it is enough to say that the estimation can be done from surveys in which the beetle numbers are counted directly, or from surveys in which the population is indirectly estimated from population indexes such as measurements of the feeding damage, i.e. numbers of trees attacked and killed. Both methods can be applied to the mountain pine beetle. The direct count of insect numbers is usually done in population dynamics research. When rapid assessment is required as in hazard appraisal, an aerial and terrestrial survey of the number and distribution of the trees killed by the beetle may suffice.

In British Columbia, trees are attacked by the mountain pine beetle in mid-summer and the first noticeable foliage color change usually occurs in spring of the following year (Safranyik *et al.* 1974). Therefore, most aerial surveys in the year following the attack show only the number of trees killed the year before and thus give an estimation of the insect population in that year. An appraisal method based upon aerial color photography and limited ground sampling considerably reduces survey cost and increases precision (Safranyik *et al.* 1974). This combined survey permits the determination of numbers of uninfested trees, green infested trees, and trees killed more than a year earlier for the whole infestation area. The ground survey should be conducted as soon after beetle flight as possible because fresh boring dust and pitch tubes (symptoms in green infested trees) are conspicuous at this time (Safranyik *et al.* 1974).

The trend of an infestation is determined by sequential sampling of the insect population through time. Periodical sampling should indicate the trend of numbers and the incidence and trend of natural controls or mortality factors.

Life tables may be used to summarize the degree of mortality in each generation when insects are counted directly. Although life tables are not a practical evaluation procedure, they can aid in deciding which instar to sample in order to predict the number of emergent adults the next summer.

Knight (1967), working with life tables of *D. ponderosae* in the U.S. Rockies, did not find a clear-cut relationship between the number of eggs laid when the beetle attacks the trees and the likely course of the infestation. However, the quality of the prediction increased when the survival counts were made closer to the emergence period. Knight (1967) concluded that fair predictions can be made in April and almost perfect predictions in July, a period in which the insect is found as last larval instars, pupae or adults.

Cole (1973a, 1974, 1975) has disclosed some of the mortality factors affecting the population dynamics of *D. ponderosae* in Rocky Mountain lodgepole pine forests. The main mortality factors are: crowding of the larvae inside the bark; low temperatures; parasites and predators; the rate of drying of the phloem; resin flow (pitching); and pathogens. The most lethal combination is low temperatures (especially in winter) followed by quick phloem drying. The beetles have a high

probability of survival within larger rather than smaller diameter trees (Cole 1975).

The critical probability of an individual beetle surviving the entire growth period was calculated as little over 0.15 by Cole (1974). An epidemic would be likely if the probability of survival increased to greater than 0.15, but an endemic or static situation would be predicted if it decreased or remained the same.

The use of life tables limits prediction of an infestation trend to 1-2 months before emergence and subsequent attack. This allows very little lead time for planning and implementing control operations. The main limitations of life table data for predicting infestation trends are this time limitation and the fact that some mortality factors may act drastically and unpredictably on the beetle population shortly before or even after emergence. However, this method may be adequate for hazard rating purposes, especially when infestation trends have been followed for several years and availability of food for the beetles is taken into consideration.

Under intensive protection practises, a cheaper but useful approach to estimating the population trend is through recording trees killed each year per unit of forest area. The damage survey can be done by ground sampling or by aerial photo interpretation. Sequential aerial photography techniques can be used when large areas have to be evaluated (Caylor and Thorley 1970). This method should enable a manager to determine when an endemic population is evolving towards an epidemic

stage. Moreover, a good prediction should be possible if the vulnerability of the forest is measured and taken into consideration. Miller and Keen (1960) found that the trend of past losses from *D. brevicomis* was highly correlated with future losses in California ponderosa pine stands when other stand factors were taken into consideration.

Successive direct counts of insect numbers and measurements of beetle damage are not mutually exclusive techniques. It often may be desirable to make a direct count of insect numbers to provide a more precise prediction after tree mortality close to outbreak level is detected, e.g. 1 killed tree/acre/year (Safranyik *et al.* 1974).

Data on the number and trend of insects in a forest area are meaningful only when they are analyzed in conjunction with information on the amount of habitat and food available for the beetles, i.e. vulnerability of trees and stands. Moreover, any trend towards an increase in insect numbers will depend to a certain extent on favourable climatic conditions.

2.1.2   Recurrence of the infestation

An insect species that periodically develops outbreaks in a given locality is said to be recurrent and represents a continuing threat to that area. An understanding of the factors conducive to recurrence will aid in preventing outbreak-associated losses before economic damage levels occur.

The mountain pine beetle evidently is a recurrent species in many lodgepole pine forests. Amman (1969) and Cole and Amman (1969) determined that the size of the beetle population is food regulated. They concluded that each year the beetles strongly prefer largest diameter trees which, as was shown later, usually contain the thickest phloem (Cole 1973c). The phloem is the food of the beetles.

During the course of an infestation the beetles progressively destroy their preferred food supply which, combined with the fact that only trees of large diameter produce enough beetles to maintain the level of the infestation, brings the population numbers down (Cole and Amman 1969). This hypothesis has been reinforced by Cole's observation (1974, 1975) that even though some mortality factors affect beetle survival, none of them exert sufficient influence to be considered true regulatory factors.

Safranyik *et al.* (1975) noted that most mountain pine beetle outbreaks in Canada occurred in tree stands about 80 years old. They claim that at this age the level of tree and stand resistance decreases sharply. Tree resistance is measured by the amount of resinous response of the tree to injury by both the bark beetles and the blue stain fungi.

Beetle outbreaks seem to serve the ecological function of preparing the stand for successive forest types (Safranyik *et al.* 1975). According to Peterman (1974), lodgepole pine may have adjusted its age of increased susceptibility so that the stands are decimated when they

are at the peak of reproductive fitness. This prevents the excessive production of seeds and overcrowding in the next generation.

Thus, the mountain pine beetle may be considered a host-dependent, recurrent species. The length of time between outbreaks in a given area is determined by the time required for the forest to recover from previous outbreaks and to develop once more to a susceptible stage, i.e. to develop enough large diameter trees of low resistance to maintain an outbreak. It follows, then, that a forest pest manager assessing the risk of mountain pine beetles in a lodgepole pine forest must keep in mind that the beetles will develop outbreaks only as the susceptibility of the forest permits it. Long-term management and protection plans should include the possibilities of outbreaks of stand-dependent, recurrent *D. ponderosae* and proper prevention planning should follow.

2.1.3 Proximity of an infestation and the outbreak hazard

Wygant (1959) stated that the Engelmann spruce beetle migrates in large numbers when its food supply is exhausted to establish new outbreaks up to 30 miles distant. This type of statement, well founded or not, does not appear to have been made for the mountain pine beetle.

The degree of hazard in a lodgepole pine stand near an area which is heavily infested by mountain pine beetles is not clear. Conflicting reports exist.

Richmond (1933) reported the spreading of a *D. ponderosae* infestation across a valley from one aspect timbered with lodgepole pine to the opposite aspect timbered with ponderosa pine.

Baker, Amman and Trostle (1971) compared *D. ponderosae*-caused mortalities in adjacent stands of lodgepole pine and white bark pine (*Pinus albicaulus* Engelm.). They concluded that the beetle does not migrate between adjacent stands of the two pine species studied and stated that the beetle shows specificity for the tree species in which it completed its larval development.

So little is known of the flight habits of *D. ponderosae* that the question remains as to whether a population builds up in one stand and then moves to others, or whether certain conditions favour the build-up in a number of stands simultaneously (Amman and Baker 1972). Parker's (1973) statement that a 1966 outbreak in Yellowstone Park (U.S.A.) was a consequence of beetles spreading from the neighbouring Targhee National Forest, starting in the late 1950's, must be considered speculation.

As a measure of security, a lodgepole pine stand located in the vicinity of a mountain pine beetle infested forest should be rated as being at higher risk than a stand which is isolated from infestations, especially if the stand at risk is in a vulnerable stage.

2.2   FACTORS RELATED TO THE TREES

The risk of attack on trees depends not only on the insect population pressures, but also on the presence of factors predisposing

the trees to attack and death. To elucidate these factors it is necessary to know which characteristics of the trees induce differences in feeding behavior when the insect attacks different trees of the same species.

Different trees of a given species vary in susceptibility to attack by insects by reason of inherited factors and environmental influences. Genetic differences influence chemical and physical characteristics which render them more or less attractive to insects. Different trees may have chemical compounds which are toxic to the insect or they may differ in their capability to produce physiological reactions which are deleterious for the insect (e.g. pitching). The environmental influences may provoke a lower state of vigor in the tree by stressing the tree or injuring it.

2.2.1   Risk rating systems

Early observations of forest entomologists led them to believe that certain bark beetles tended to select certain types of trees for feeding. The fact that the western pine beetle, *D. brevicomis* LeConte, attacked mainly slow growing, large diameter, decadent ponderosa pine trees on poor sites (Craighead 1925a) made possible the development of risk rating systems. Dunning (1928) described 7 categories for ponderosa pines which showed different degrees of risk from attack by bark beetle, based on differences of age, dominance, and vigor in individual trees. Keen (1936) expanded Dunning's classification into 16 classes based on

combinations of four age groups: young, immature, mature, and overmature; and 4 degrees of crown vigor: full vigorous crown, fair to moderate vigorous crown, fair to poor crown, and very poor crown. The age division reflected relative maturity or physiological age, rather than chronological age as shown by the number of annual rings, and was based on external characteristics. The division into vigor classes was based on the assumption that the size of the crown and area of leaf surface are generally indicative of growth vigor. The major indicators used were: the size of the crown, its density and its position in the forest canopy. The various combinations of age and crown represented differences in risk of attack by the western pine beetle.

The hypothesized value of these classifications was that if the type of tree most likely to be killed could be recognized with a fair degree of accuracy, it would be possible to make a light cut of the beetle-susceptible trees for the purpose of sanitation and thereby reduce subsequent pine beetle infestations and salvage valuable trees.

Salman and Bongberg (1942) designed another risk rating system based on four categories: low risk, moderate risk, high risk, and very high risk. Their definitions exploit the fact that many dying ponderosa pine trees develop identifiable characteristics prior to final infestation and death. The tree risk is rated by appraising the health of the individuals as indicated by the condition and amount of foliage per twig or branch, dead or dying branches, presence of active insect or pathological infestations, and others. In the field the trees were given

penalty points for each abnormal condition indicative of risk whose total indicated the degree of risk (Miller and Keen 1960).

The risk rating system of Salman and Bongberg (1942) (later known as the California risk rating system) and a modified version of Keen's classification (Keen 1943) proved to be very useful in terms of timber management and they are still used by foresters in sanitation and salvage logging of ponderosa pine (Johnson 1972).

However, these risk rating systems have some shortcomings in that the degree of risk changes with time as the health and vigor of the tree changes, and the method is intrinsically subjective (Miller and Keen 1960). Moreover, the hazard rating systems described apply in practice to the east side of the Sierra Nevada but not to the west (Graham 1963) and only to old growth ponderosa pine (Sartwell and Stevens 1975). Significantly, *D. brevicomis* remains an extremely severe problem, despite the passing of most of the timber stands for which the risk rating systems were developed.

No rating systems have been developed to grade the risk of mountain pine beetle in lodgepole pine. This probably is because *D. ponderosae* does not attack selectively certain trees that show easily recognizable risk rating characteristics. Moreover, *D. ponderosae* is very aggressive and is capable of attacking even thrifty second growth or healthy mature trees under outbreak conditions (Craighead 1925a; Roe and Amman 1970; Amman and Baker 1972).

2.2.2   Effects of the tree diameter

D. ponderosae attacks the largest diameter trees of a stand
each year during the course of an infestation. As the number of
large trees is reduced by mortality, the beetles move into progressively
smaller trees until the epidemic subsides (Craighead 1925a; Hopping
and Beale 1948; Cole and Amman 1969; Parker 1973). Shepherd (1966)
suggested that this beetle has evolved a searching image for large
diameter trees. The preference, whatever reasons underlie it, is of
great value to the beetle. Reid (1963) found that brood production
and survival per ft^2 of bark was much greater in large than in small
diameter trees, and suggested that enforced attack on small diameter
trees may be one of the factors in a population decline.

For risk rating of individual trees it is important to note the
precise diameter classes that are most vulnerable to attack by *D.
ponderosae*. The relation between the diameter of lodgepole pine trees
and the intensity of attack by the beetles has been studied by several
researchers (Table I; Fig. 2); all have found an increase in the intensity
of attack and numbers of trees killed as the diameter of the trees
increased.

Two problems arise when a distinction in risk classes according
to diameter of the tree is to be made: any classification of diameter
classes in grades of risk is subjective; and reported mortalities by
diameter classes differ (Table I), probably due to difference in study
locations, altitude, and forest type.

FIGURE 2   Proportion of lodgepole pine trees killed according

to diameter.   After Cole and Amman (1969).
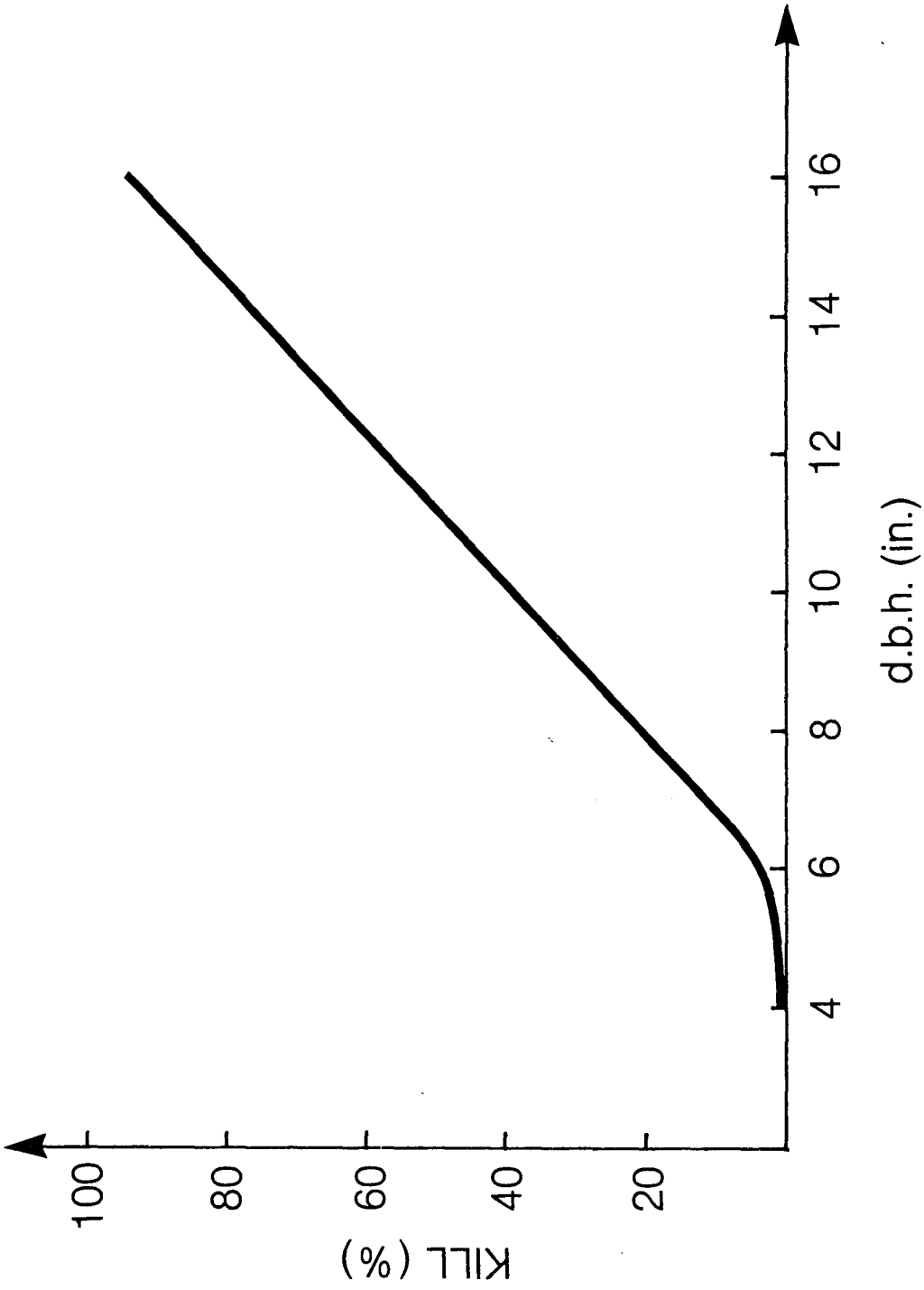
TABLE I   Mortality of lodgepole pine under attack by mountain pine beetle, according to diameter class

Reference	Location	Tree diameters (d.b.h.) (inches)	Percentage of diameter class killed
Craighead (1925a)	N. Idaho and Montana	8	few
Gibson* (1943)	S.W. Montana	6	27
		8	56
		10	87
		12	100
Hopping and Beal (1948)	Alberta, Canada	6	very few
		15	50
Cole and Amman (1969)	W. Wyoming and E. Idaho	4	1
		12	50
		16	87
Roe and Amman (1970)	W. Wyoming and E. Idaho	7	very few
		12	50
		16	82
		18	100
Amman and Baker (1972)	W. Wyoming and E. Idaho	8	30
		10	50
Parker (1973)	W. Wyoming	8	50
		12	71

* Cited by Roe and Amman (1970)

I define diameter classes of high vulnerability as those in which the trees have more than 50% probability of death during an outbreak, and diameter classes of low vulnerability as those in which the trees have 50% or lower probability of death[1]. This fairly rudimentary classification seems realistic in the present state of knowledge.

The diameter class sustaining 50% mortality (or 50% probability of death) varies among various studies (Table I). Since 8 in. d.b.h. is the lowest diameter class with 50% mortality (Parker 1973), it identifies the transition between high and low vulnerability. Thus, trees of 8 in. d.b.h. and less will be considered of low vulnerability and those larger than 8 in.d.b.h. will be considered of high vulnerability.

The choice of 8 in.d.b.h. as the limit diameter in this two-fold classification is reinforced by Safranyik *et al.* (1974), who state that outbreaks usually develop in stands having many trees over 10 in.d.b.h. and that the average diameter of the post-outbreak residual stand is usually below 8 in.. Moreover, areas in which the average diameter is less than 8 in.d.b.h. should be assigned the lowest priority in sanitation salvage cuttings (Safranyik *et al.* 1974).

A more precise study is needed to separate the diameter classes into three or four risk classes (e.g. low, moderate, high, and extreme) according to the intensity of *D. ponderosae* attack. Further research

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[1] Probability of death by diameter class is based on published mortality data (Table I).

on this subject should be encouraged. The critical d.b.h. of 8 in. should be only a general guideline, because critical diameters should be worked out for each managed forest.

As the survival of *D. ponderosae* is high in large diameter trees (Reid 1963), the proportion of the stand that includes diameter classes favouring the beetles is important in determining the course of an infestation.

Cole and Amman (1969) calculated that the production of beetles per tree could vary between 300 from trees 8-9 in.d.b.h. to more than 15,000 from trees 18 in.d.b.h.. Trees 8-9 in.d.b.h. would produce only 1/3 enough beetles to infest and kill a healthy green tree. Thus, *D. ponderosae* are apparently food-limited, because only trees 14 in. d.b.h. and larger can contribute enough beetles to maintain or increase an infestation. The beetle strongly prefers the larger diameter trees each year over the duration of an infestation, and thus progressively destroys its preferred food supply (Cole and Amman 1969).

The presence of many very large, susceptible trees will permit the rapid build-up of a large beetle population and promote a short, devastating outbreak. When a stand has few large trees the development of the outbreak will be slower and its duration longer. However, similar destructiveness may occur.

Amman and Baker (1972) compared tree mortality between stands subjected to sanitation salvage operations and stands that were left untouched. They concluded that removal of infested trees had only

slowed down the rate of tree infestation and mortality and that at the end of the infestation the mortality in both types of stands was about the same.

The susceptibility of a stand can be determined by the percentage of susceptible trees in the stand per unit of area. Therefore, stand susceptibility can be expressed as the percent per unit of area of trees larger than 8 in. d.b.h.. This percentage can be easily calculated from a stand table which expresses the number of trees per diameter class per acre.

It is very likely that a correlation can be found in a particular forest between average d.b.h. of the stand and percent of trees larger than 8 in.. Then one could express the susceptibility of the stand as an average diameter. Similarly, the average age of a stand could be indicative of a certain proportion of susceptible trees, i.e. trees of appropriate physiological age. This hypothesis is supported by the observations of Safraynik *et al.* (1974) that outbreaks usually develop in stands older than 80 years.

The literature has many statements that *D. ponderosae* outbreaks develop in stands with "many" large diameter trees (Amman and Baker 1972; Safranyik *et al.* 1974). The question remains as to what percent of susceptible trees render a stand as a whole more or less vulnerable to the development of an outbreak. Research designed to elucidate this relationship is urgently needed.

Alternatively, a closer observation of the published research may prove useful. From Parker's (1973) data (Table II) one can calculate that at the start of the Yellowstone Park outbreak, in 1965, there were 32% of trees larger than 8 in. d.b.h. (excluding class 8 in.). At the end of the outbreak, in 1972, there were only 19% of trees larger than 8 in. d.b.h.. If there were no mortality factors other than food limitation, i.e. lack of an adequate number of large diameter trees of thick phloem, then a logical hypothesis is that the forest became non-susceptible when the proportion of the stand in trees larger than 8 in. decreased to 19%. These figures may serve as an indicator of the number of susceptible trees necessary in a stand for it to be rated in a particular risk class. If the number of susceptible trees per acre is less than 19%, one may speculate that the forest in question bears low risk. Between 19% and 32%, the risk would be intermediate. But when the percent of susceptible trees per acre rises about 32% the forest becomes susceptible to bark beetle outbreak.

The assumption of the minor role played by mortality factors other than food limitation may prove valid. Cole (1974, 1975) states that some mortality factors affect the beetle survival, but none exerts sufficient influence upon the population dynamics of the beetle to be considered a regulatory factor.

TABLE II   Number of living trees per acre before, during, and after
the mountain pine beetle outbreak in Yellowstone National
Park, Wyoming.   After Parker (1973)

Year	Diameter class, inches							Total/ acre
	6	8	10	12	14	16	>16	
1965*	80	63	39	17	8	2	2	211
1966	79	62	39	16	8	2	2	208
1967	79	61	38	15	6	1	1	203
1968	79	58	34	12	4	1	0	189
1969	77	50	23	8	2	0	0	162
1970	77	50	22	7	2	0	0	159
1971	77	49	21	7	2	0	0	156
1972**	77	49	21	7	2	0	0	156

*
   Pre-outbreak stand structure

**
   End of outbreak

2.2.3   Effects of bark and phloem thickness

Phloem thickness plays a notable role in the population dynamics of *D. ponderosae*. Roe and Amman (1970) observed that the beetles tend to attack and kill trees that have thick phloem and not many trees of similar diameter that have thin phloem. Safranyik (1971) analysed the distribution of *D. ponderosae* entrance holes on the bole and found that a bark thickness greater than 1.5 mm (1/16 inch) is necessary for successful gallery establishment. This places an upper limit on the height to which a stem can be attacked. However, no studies have examined the relationship between the number of trees killed and the thickness of either bark or phloem. A greater understanding of this relationship would aid in assessing the vulnerability of individual trees.

The finding that trees with phloem less than about 3.1 mm (0.12 in.) thick do not produce enough brood per unit area of bark surface to sustain a successful infestation (Roe and Amman (1970)) may be very important in assessing susceptibility of the stand as a whole.

Beetle survival is positively related to depth of bark (Amman 1969), and more properly to the thickness of the phloem (Amman 1972; Cole 1973a, c). The low survival in trees with thin phloem is apparently due to food limitations and a consequent increase in crowding (Cole 1973a). In Cole's (1975) opinion, brood production is directly related to food quantity, i.e. phloem thickness, especially at low elevations where growing conditions are optimal for the beetle. This substantiates the hypothesis

that food is the limiting factor of population size (Cole and Amman 1969).

Determination of the distribution of bark or, preferably, phloem thickness in a stand will give an accurate estimation of its degree of susceptibility. In assessing susceptibility, bark thickness may be easier to measure than phloem thickness, but it may be a less accurate indicator. For example, the phloem thickness may vary between trees with bark of the same thickness. However, Amman (1969) found a correlation between bark and phloem thickness and concluded that bark thickness could still be used as an estimator of phloem thickness. Cole (1973c) developed several equations for estimating the phloem thickness of individual trees. The most useful equation related phloem thickness to the last five years of basal area increment, the d.b.h. outside the bark, the height of the tree, and the number of rings at breast height. The total bark thickness is a measurement which is often taken by timber cruisers so it may be readily available from the forest inventory data.

2.2.4   Effects of tree resistance

Individual lodgepole pines differ in their resistance to attack by *D. ponderosae* and its associated fungi. Complete resistance results in failure of the beetle and the blue stain fungi to complete their life cycles, both ultimately dying in situ; conversely, when no resistance exists, both insect and fungi quickly colonize the stem, and the tree soon dies (Reid, Whitney and Watson 1967).

The resistance response in the tree is primarily a response to the blue stain fungi and consists of an initial resin flow escaping into adjacent tissues from those resin ducts severed by the beetle and a secondary resinosis resulting from synthesis of monoterpenes within parenchyma cells adjacent to the beetle's gallery and the formation in the sapwood surrounding the wound of some extractives typical of heartwood (Reid *et al.* 1967; Reid and Shrimpton 1971; Shrimpton 1973a).

It is possible to identify resistant trees in a stand by artificially inducing the resistance response with blue stain fungi inoculation. In a lodgepole pine stand all gradations between resistant and susceptible trees may exist (Reid *et al.* 1967). The number of resistant trees varies within and between years because the resistant character in a tree seems to be governed by some unknown environmental factors in addition to the genetic potential of the tree (Shrimpton and Reid 1973). The resistance is seasonal: minimal in spring, maximal in mid-summer, and declining during the rest of the season (Reid *et al.* 1967).

Shrimpton (1973b) found that lodgepole pines in the age class 31 to 50 years old had the greatest frequency of resistant individuals, and that the resistance of trees older than 90 years declined faster than that of young trees during the season. Resistant trees have a better diameter growth and thicker phloem than non-resistant ones. Shrimpton (1973b) concluded that the resistance of large diameter trees with thick phloem is critical in maintaining a low level beetle population because

the beetles can maintain an increasing population only by infesting
large trees. The beetles probably have shorter distances to travel to
locate a suitable host, and mortality during flight may be lessened
when the frequency of resistant trees in a stand is low (Safranyik
et al. 1974). A situation conducive to outbreaks is created when
the stand resistance declines due to advanced age or stress, and many
large diameter trees become available for colonization (Safranyik *et al.*
1975).

The proportion of the phloem occupied by pitch pockets is
still another variable affecting brood survival within the tree (Amman
1972). However, its utility as a factor for screening resistant from
susceptible trees is limited because this character changes from year
to year in a single tree apparently due to environmental influences (Reid
and Watson 1966).

2.2.5   Effects of tree vigor

Vigor is a very broad term, related to the health and growth of
a tree. It can be expressed in a number of forms. In assessing tree
vigor one may use symptomatic correlates indicative of the state of vigor
such as external crown characteristics, growth rate of different meristems,
oleoresin exudation pressure, voltage gradients, chronological age, weakness
defined by various criteria, and others (Graham 1963).

Published attempts to identify particular states of vigor
rendering lodgepole pine susceptible to beetle attack are contradictory.

Roe and Amman (1970) state that "mountain pine beetle infestations remove the most vigorous elements of the stand because they prefer the largest and dominant trees usually with thickest phloem". This statement implies a definition of tree vigor based on external characteristics of the tree such as size and position of the crown in the stand canopy but it does not include the physiological health of the tree. It is possible that the preference of the beetle for the most vigorously growing, dominant trees instead of for those of poorer growth may be explained by Blackman's hypothesis that trees accustomed to favourable conditions suffer greater stress from moderate environmental deviations than do trees maintaining smaller crowns.

Low radial growth has been used by some researchers as an index of low vigor, particularly when associated with environmental stresses affecting the trees. Beal (1943) found a positive correlation between most of the 13 *D. ponderosae* outbreaks in the central U.S. Rockies between 1895 and 1939 and reduced growth rates resulting from deficient precipitation. He concluded that increases to epidemic proportions often occur during drought periods when tree growth is poor but he warned that since some of the outbreaks did not follow this pattern, some epidemics are governed by other causes. Hopping and Mathers (1945) reached similar conclusions for western Canada. However, Blackman (1931), studying outbreaks in several areas of U.S.A., between 1846 and 1926, concluded that "all epidemics seem to have started during a period of rapid growth" and that "the ending of the epidemics in all

cases studied except one coincided with a decline in tree growth". He speculated that a period of semi-drought caused the beetles to be in an endemic situation due to mortality produced by rapid drying of the phloem in stressed trees. He claimed that during seasons of plentiful moisture there is a greater brood survival and that a consequence of several wet seasons is a build-up in the number of beetles.

Reid and Gates (1972) found that resistant trees appeared to grow faster than susceptible trees, even though they completed their seasonal growth at approximately the same time, with the same final increment.

Declining tree vigor is also a consequence of ageing. *D. ponderosae* apparently prefers trees of a given physiological age or maturity rather than trees of a particular chronological age. The preferred large diameter trees may have quite different ages. Therefore, the use of age alone to classify individual trees in different risk classes is not enough to obtain accurate results. Nevertheless, a correlation may be found between the age of the entire stand and the attack intensity as a consequence of the general correlation between stand age and average diameter. Peterman (1974) found that trees in epidemic areas were older than those in endemic areas and it seems that most outbreaks occur in stands 80-90 years old (Safranyik *et al.* 1974).

Diseases and injuries may also result in a lower state of tree vigor. However, *D. ponderosae* has not been reported to prefer diseased or injured trees. On the contrary, it is usually cited as attacking

vigorously growing trees in good health (Craighead 1925a; Roe and Amman 1970). Moreover, an inverse relationship has been found between dwarf mistletoe and *D. ponderosae* infestations (Roe and Amman 1970). A heavy infestion with dwarf mistletoe apparently resulted in a reduction in phloem thickness of the infested trees, which reduced the bark beetle population and the intensity of attack.

More research is needed to elucidate the relationship between tree vigor and susceptibility to bark beetle attack. This would aid in clarifying the dynamics of outbreak development. It is known, however, that due to the phenomenon of mass attack, the beetle is able to over-come vigorously growing trees under epidemic conditions (Blackman 1931; Peterman 1974).

2.2.6   Other tree characteristics

The grade of bark roughness and the branching pattern of lodge-pole pine trees affect the intensity of *D. ponderosae* attack on the trunk. However, differences in these characteristics are more important in determining the variation of attack intensity on single trees rather than between trees (Reid 1963; Shepherd 1965).

Differences in plant resistance to insects may depend on the presence or absence of chemical repellents, attractants, or toxicants to the insects. Such chemicals are the basis for breeding resistant varieties of certain agricultural crops (Maxwell, Jenkins and Parrot 1972).

The host finding mechanism of *D. ponderosae* involves the location of suitable trees by the early emerging female beetles (pioneer beetles) (Peterman 1974). Once suitable hosts are found, other individuals in the population are attracted to these sites by a secondary attraction mechanism involving pheromones (Renwick and Vite 1970). There is evidence that *D. ponderosae* uses tree chemicals in the primary host selection and that quantitative variation in those chemical attractants are responsible for the different attractiveness of mature and juvenile trees (Syed 1972). Chemical variation between trees may also explain the selection of large diameter trees of thick phloem.

Bark beetles and the associated fungi derive virtually all their nutritional requirements from the inner bark of their host trees; thus, a variation in the chemical content of the bark is likely to influence their survival. White's (1969) hypothesis that when a plant is subject to stress, especially to water stress, there is a complex change in the quantity, distribution, and composition of its nitrogen content, which affects the insects favourably, should be tested in lodgepole pines.

When trees are grouped in stands they may sustain modifications in their physiological characteristics. The modifications are the result of the interaction between trees and other organisms within a highly complex ecosystem of which *D. ponderosae* also forms a part. The effect of different stand characteristics on the stand-beetle relationship is considered in the following sections.

2.2.7 Effects of forest cover type

Some forest cover types are more susceptible to insect attack than others, apparently because of differences in environment and successional stage. These differences seem to affect *D. ponderosae's* behavior and survival as well as tree susceptibility. Phloem thickness again emerges as a significant factor. Cole (1973c) disclosed significant differences in phloem thickness of lodgepole pine trees growing in different habitat types.

Roe and Amman (1970) studied 42 stands growing in three of the most extensive forest cover types containing lodgepole pine in the U.S. Rocky Mountains and compared the intensity of *D. ponderosae* activity. Four classes of attack intensity were derived based on the number of susceptible trees infested. Susceptible trees were defined as those of 6.6 in. d.b.h. and larger. By far the most intense beetle activity was found in the type *Abies lasiocarpa/Pachistima myrsinites*, ranging from 1/3 to more than 2/3 of the susceptible trees killed. This habitat type exists largely between 6,700 to 7,800 ft, mostly in northwest facing exposures. The cover type *Pseudotsuga menziesii/Calamagrostis rubescens* (6,000-7,750 ft; all exposures) showed moderate beetle activity, expressed in about 1/3 of the trees being killed. Stands located in the type *Abies lasiocarpa/Vaccinium scoparium* (6,550-8,450 ft; all exposures) were in the light damage category with less than 1/3 of the susceptible trees killed by the beetles.

The number of infested stands was also different between the different cover types. Of the stands studied in the *A. lasiocarpa/P. myrcinites*, 92% showed symptoms of active infestations. Those within the *P. menziesii/C. rubescens* type included 64% with active infestations, and 44% of the stands in *A. lasiocarpa/V. scoparium* type were infested. Roe and Amman (1970) used these figures to calculate the risk of growing lodgepole pine to different diameters in the cover types studied.

In practical hazard classification it is likely that risk zones will follow cover type lines. No studies have been conducted in Canada to establish the relative susceptibility of different cover types. Therefore, at present any hazard rating intended should rely on stand altitude which determines forest cover type to a certain extent, with significant variation caused by slope and aspect. Basing risk on habitat type as well as elevation, would permit consideration of slope, aspect and latitude (Amman and Baker 1972).

As the classification of forest cover types is a biological classification, it will change with time as the succession advances and also with interventions of man and natural forces, such as fire. Therefore, a risk classification based on cover types will also change with time.

2.2.8 Effects of elevation

Cole (1975), summarized the research done at the U.S. Forest Service, Intermountain Forest and Range Experiment Station on *D. ponderosae*

population dynamics in lodgepole pine forests at different elevations

(Amman 1969, 1973; Amman and Baker 1972; Amman *et al.* 1973). Brood

production in phloem of a given thickness is inversely related to

elevation, which in turn is associated with temperature, particularly

winter temperature. Brood production is relatively low at elevations

above 2,400 m; consequently beetle-caused mortality in lodgepole pine

is also much lower. Apparently, at higher elevations the beetle is out of

its range for optimal development; its biological activities are poorly

synchronized with the seasonal weather changes so that two year life

cycles and low brood survival frequently result. In the elevation zones

sampled, the probability of lodgepole surviving *D. ponderosae* attack is

a linear function of stand elevation. This relationship holds at high

elevations even in the presence of thick phloem in trees of large diameter.

However, at more optimal, low elevations, brood production is directly

related to food quantity. Thus, in Cole's (1975) opinion, food is limiting

to population growth at low elevations and temperature is limiting at

high elevations.

The increase in tree survival with altitude can be used to define

altitude-based hazard classes. Amman and Baker's (1972) graph

on increase of tree survival with altitude (Fig. 3) to define four classes

of stand hazard for southern British Columbia (Table III). Amman and Baker

(1972) obtained their data from the Teton and Targhee National Parks in

Wyoming and Idaho, at 43° latitude. To make their data valid for southern

B.C. (latitude 50°) 400 ft was subtracted for each degree of latitude

FIGURE 3   Survival of lodgepole pine 9 in.d.b.h., and larger,

from mountain pine beetle attack according to the

elevation of the stand.   After Amman and Baker (1972).

The equivalent altitude for British Columbia is

indicated between brackets.
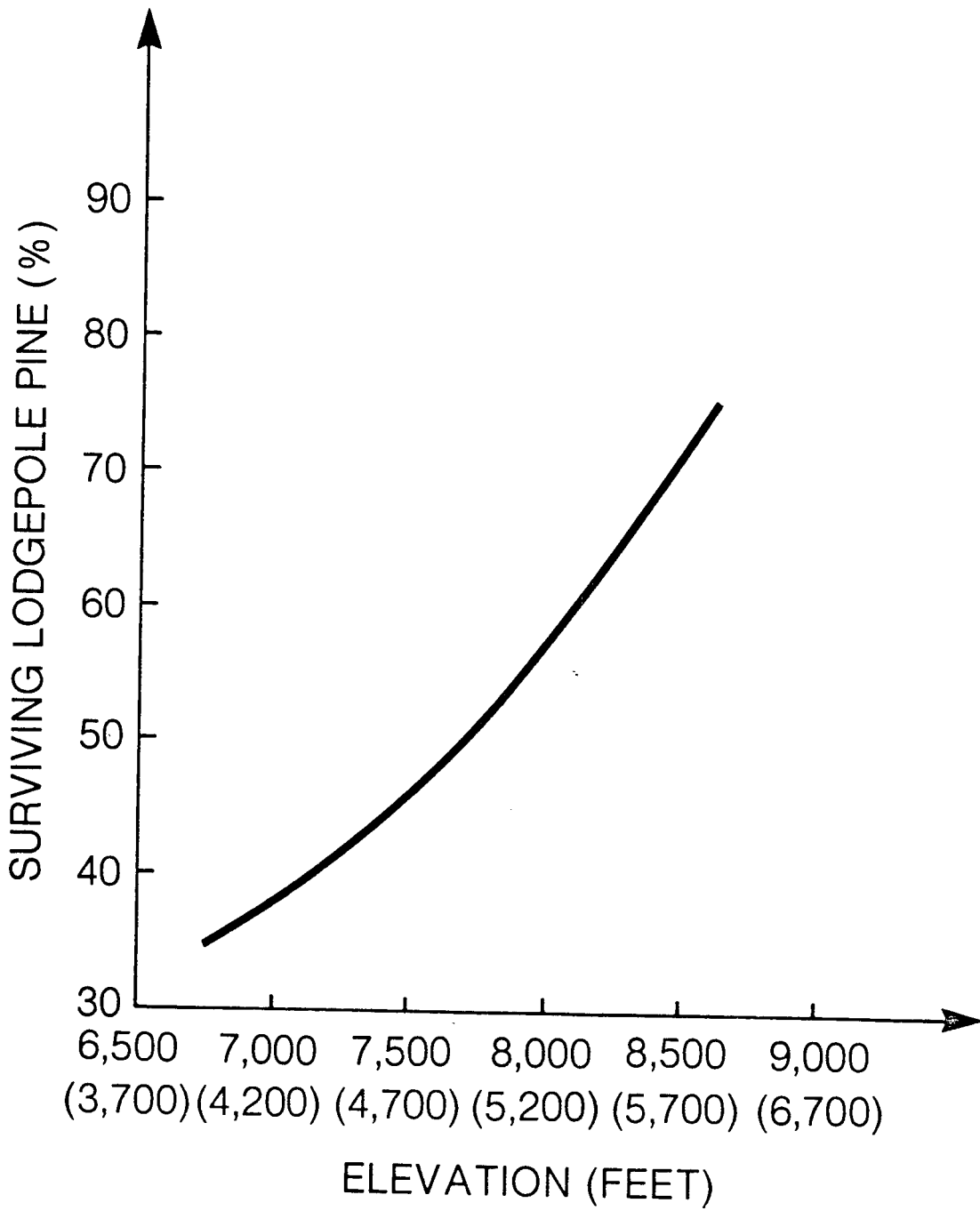
TABLE III   Hazard classes of lodgepole pine stands 9 in.d.b.h.
and larger according to their location in altitude.
Based on data from Amman and Baker (1972).

Hazard class	Survival (%)	Altitude (British Columbia)	
		feet	meters
Low	Above 70	5,700 and above	1,737 and above
Moderate	50 - 70	4,800 - 5,700	1,463 - 1,737
High	30 - 50	3,700 - 4,800	1,128 - 1,463
Extreme	Below 30	Below 3,700	Below 1,128

These classes should be regarded only as guidelines because of the
uncertainties of extrapolating data from one region to another.

difference between localities. This correction is based on Hopkins (1919) bioclimatic law. Amman, Baker and Stipe (1973) arrived at the conclusion that lodgepole pine mortality caused by *D. ponderosae* was the same between two localities when the altitude at which mortality occurred was corrected by the difference in latitude.

2.2.9   Effects of stand density

Stand density indicates the degree of competition between trees which, if excessive, can be expected to reduce growth rate and tree vigor, factors that may influence *D. ponderosae* activity.

Amman (1969) found that the combination of factors which best explained variation in number of emergence holes (an index of brood success), were: bark depth, stand density, and plot elevation. Trees growing in plots with the least stand density had the largest number of emergence holes for a given bark depth and elevation. These findings contradict the general idea that densely stocked stands where tree increment is slowed down by competition will favour bark beetle outbreaks. Amman (1969) speculated that in dense stands the ratio of phloem to dead bark may be reduced, thereby reducing the amount of food available for the beetle.

Sartwell and Stevens (1975) working with *D. ponderosae* in ponderosa pine forests found a completely different relationship from that found by Amman (1969). Severe ponderosa pine mortality occurred predominantly in dense stands where competition had substantially slowed

the growth of even the dominant trees. Sartwell and Stevens (1975) concluded that a stem basal area of 150 ft^2 per acre is a critical maximum above which the stands (assuming a sufficient number of large diameter trees) are liable to become severely infested. Quite possibly, ponderosa pine phloem thickness remains sufficient to sustain outbreak conditions, regardless of stand density.

Further research should be encouraged to clarify this between species difference. Since stand density can be regulated, the determination of critical densities rendering either ponderosa or lodgepole pine stands susceptible, may be a powerful tool in the control and prevention of *D. ponderosae* outbreaks.

2.2.10   Effects of site quality

The term site comprises the combination of biotic, climatic, and soil conditions of an area that determines the existence of a given vegetation type on it. Site quality is determined by the height reached by various tree species at a given age.

The incidence of *D. ponderosae* attack in different lodgepole pine site classes has not been studied. However, data on other host species indicate that some relationship may exist for lodgepole pine. Sartwell and Stevens (1975) indicate that the first *D. ponderosae* outbreak in second growth Pacific Northwest ponderosa pine occurs earlier in the life of a forest growing on a good than on a poor site. Apparently, those stands growing on good sites reach a critical density earlier, and become

more liable to *D. ponderosae* attack.

Another unresearched question is the incidence of *D. ponderosae* attack in relation to soil characteristics affecting tree growth and vigor, e.g. soil fertility, depth of soil to bed rock, soil series and water holding capacity. Such research may, in conjunction with all other factors, help in assessing the bark beetle hazard.

The effect of forestry practices on the soil and its relation to bark beetle outbreak should also be researched. For example, changes in outbreak risk might occur following logging, thinning, or fertilization.

2.2.11   Tree and stand susceptibility

The most reliable characteristic for assessing individual tree susceptibility apparently is diameter. This conclusion supports the definition of highly susceptible or high risk trees as those trees larger than 8 in.d.b.h. which are preferred by the beetles during the course of an outbreak.

Bark thickness can be important in detailed screening of susceptible from non-susceptible trees but, for practical work, the diameter measurement may be sufficient because it is likely that a positive correlation exists between tree diameter and bark thickness.

When accurate risk rating is required, trees should first be divided into broad risk classes according to diameter. Then they can be separated into grades of susceptibility according to their bark

thickness and the amount of resinous response to inoculation with the blue stain fungi. However, the fungal rating system may be difficult to use (Peterman 1974).

The use of other characteristics for risk rating purposes, such as tree growth, is not recommended because their relationship with *D. ponderosae* outbreaks are poorly understood.

The important factors determining the degree of stand susceptibility to *D. ponderosae* are the altitude of the stand and the proportion in the stand of large diameter trees with thick phloem. Other factors such as forest type and site quality may be important, but their relationship to the occurrence of beetle outbreaks is not yet well understood.

All possible combinations of susceptibility factors can be found in nature. Thus, the most highly susceptible forest will be at low altitude, i.e. below 3,700 ft (1,128 m), with many highly susceptible trees per acre (more than 32% of trees larger than 8 in d.b.h., of thick phloem). A stand of lowest susceptibility will contain mostly small diameter trees (e.g. a regeneration stand) and/or be located at high altitude.

When the comparative susceptibility of lodgepole pine in different forest types is known, it is recommended that hazard rating be according to forest cover type instead of altitude because it is a more general indicator that includes altitude in addition to other biotic and abiotic parameters.

The aforementioned risk categories should by no means be considered of universal validity. Rather, they must be considered as general guide-lines or starting points from which local hazard ratings can be developed for each particular forest.

2.3   FACTORS RELATED TO CLIMATE

Climatic factors can affect the susceptibility of a forest to *D. ponderosae* by affecting tree susceptibility or the beetle brood survival, either favourably or adversely. Safranyik *et al.* (1974) contend that a suitable climate for the beetle must prevail before it can become a continuous threat to lodgepole pine. They defined and mapped five grades of outbreak hazard (very low, low, moderate, high, and extreme) in western Canada, according to climatic suitability for the beetle. High hazard rating climatic areas are hot, dry, and have mild winters. Areas with a frequent occurrence of one or more climatic conditions detrimental to the beetle have a low rating. However, in each area there is a mosaic of hazard classes due to local effects of climate.

In my opinion, this type of broad classification of hazard may be of limited practical use. The forest entomologist confronted with the task of hazard rating a local forest area will have to delineate very specific hazard zones according to local climatic records and topographic features. To accomplish this goal it is necessary to know precisely how the beetles are affected by the local climate.

Major outbreaks of many bark beetles have been related to periods of hot, dry weather. This type of weather can render trees more susceptible to successful attack. Once *D. ponderosae* broods are established, however, the most favourable weather is, according to Reid (1963) "...moderately warm, followed by a mild winter and moderate weather the following spring and early summer; then a period of hot dry weather in July and early August for rapid brood maturity and flight...".

2.3.1   Effects of temperature

Provided a host species is available, geographical limits and local distribution of most scolytid species are imposed by the minimum temperature necessary for larval development and by the higher temperatures which are debilitating or lethal. As bark beetles live inside the bark for most of their life, they are more protected from sudden temperature changes than other insects. However, those beetles developing under thin bark are particularly subject to wide temperature fluctuations (Rudinsky 1962). The thickness of the bark is usually related to tree diameter. Therefore, a differential mortality may be expected to occur between trees of different diameter. In fact, *D. ponderosae* brood mortality from low winter temperatures is lower in large than small diameter trees because more insulation is provided by the thicker bark (Cole 1974, 1975).

Egg hatch, growth and development of *D. ponderosae* larvae occur between 2.2 and 37.8° C, the optimum being between 20 and 25.6°C (Safranyik

et al. 1974; McCambridge 1974). The optimum temperatures for flight and

attack range from about 19°C to 32°C; higher and lower temperatures limit

beetle activity (Rasmussen 1974). Adult females establish two egg

galleries in warm summers when the first flight is early (late June, early

July) (Reid 1972), but survival of the first broods is generally less

than 5% by the end of the summer. Since they overwinter as pupae and

young tenerals, which lack cold resistance, most of the remainder are

destroyed by low winter temperatures. The survival of the second brood

is higher at the end of the summer, and the survivors overwinter as

larvae, which is the most cold resistant stage (Reid 1963).

Of all the stages, eggs have the least tolerance to freezing,

being killed near - 17.8°C, followed by pupae, adults, and larvae,

in that order. Temperatures lower than -17°C are common for several

months in all areas of Canada except the southwestern coast and Vancouver

Island, in British Columbia (Safranyik *et al.* 1974). However, snow

covering the lower bole may modify the subcortical temperatures due to

its insulating properties.

Cole (1975) found that the most important mortality factor for

D. ponderosae is low winter temperatures, especially if followed by phloem

drying. The occurrence of deleterious, low temperatures is very common

at high altitudes. In these regions the beetle is out of its range for

optimal development, and it usually has a two year cycle and low brood

survival (Amman and Baker 1972). Cool temperatures at high altitudes delay

development so that the beetle overwinters in stages that are particularly

vulnerable to winter temperatures (Amman 1973). Apparently *D. ponderosae* populations are regulated by weather at high elevations (Amman 1973).

Eggs are also the least resistant to high temperatures. Prolonged exposure to about $38^{o}C$ will cause the death of all stages, but the critical temperature is above $43^{o}C$ for short exposure. Subcortical temperatures of such high levels seldom occur in infested standing trees even at low elevations in British Columbia (Safranyik *et al.* 1974).

2.3.2   Effects of rainfall

The belief that trees and stands are conditioned by drought to bark beetle susceptibility is very longstanding (e.g. Craighead 1925b; St. George 1930). Such deficiency would diminish the available soil moisture and indeed would reduce the growth and vigor of the trees. Hoppings and Mathers (1945) thought that the vigor of the entire stand must be reduced to reach a susceptible stage where an outbreak may develop. They considered 18 in. of rain/year to be the minimum average for reasonable vigor of lodgepole pine stands in Banff, Alberta, and found that severe *D. ponderosae* outbreaks occurred during years of below average precipitation when trees were experiencing subnormal radial increment. Beal (1943) reached the same conclusion but warned that some outbreaks do not follow this rule and may be originated by other causes. Reid and Gates (1972) stated that water tension levels in lodgepole pine trees following dry periods showed a relation with the resistance of non-resistance of trees to *D. ponderosae* attack.

The question of whether or not a period of drought affects tree susceptibility is not yet clear, but it seems to affect favourably the survival of the mature larvae, pupae, and adults. Reid (1963) emphasizes that a period of dry and hot weather in July and August increases beetle survival and accelerates maturation and flight. However, a drought period early in the insect life cycle can cause great mortality due to a rapid drying of the phloem in the attacked trees (Blackman 1931).

2.3.3   Hazard due to climate

Both temperature and rainfall should be considered when considing the hazard zonation of an area. Areas where the climate is often favourable for the beetle will have a high hazard rating. Areas where one or more climatic conditions are often detrimental to the beetle will have a low rating. In delimiting each zone one should use the frequency of occurrence of lethal temperatures for the beetle and the occurrence of drought periods which favourably affect beetle survival and probably diminish tree resistance.

When a beetle population has been detected at dangerously high levels, the temperatures and rainfall (amount and distribution) should be strictly monitored in order to forecast the infestation trend. However, the unpredictability of the weather over long periods may lead to somewhat uncertain forecasts.

When a short range forecast is needed, then extremely cold winter or late spring temperatures will be indicative of a reduction in the emergent, summer beetle population. When important decisions depend upon the forecast, a ground survey should be done to check the stage of the brood.

Climatic release of an outbreak will occur sooner in areas with an otherwise susceptible forest, its destruction being only a matter of time. These areas should be rated as bearing very high risk. In long term planning, the general climate of the area should be considered and the development and eventual susceptibility of the forest should be projected in the future. In this manner one can arrive at future dates of change in the rate of risk of a particular stand.

3.   ASSESSING THE OUTBREAK HAZARD

In practice, all relevant outbreak hazard factors, i.e. those related to the insects, trees, stands and climate, must be integrated and weighed according to their relative importance. A system of hazard rating should then be developed which permits hazard appraisal of any given situation, provided the factors determining the hazard are known. The factors should be integrated into one or more qualitative or numerical indices which provide an objective basis and uniform guidelines for evaluating the danger and possible damage, and serve as a basis for protection decisions.

I have selected six factors as the most reliable in assessing the hazard rating of a forest: 1) the insect population level; 2) the population trend; 3) the susceptibility of the stand as determined by its diameter distribution; 4) the stand elevation; 5) the regional climate; and 6) the local weather characteristics and variation. Some of these outbreak factors are variable in time whereas others are constant. The insect population level and trend and the weather are highly variable between and within years. The diameter distribution varies slowly as a stand ages and succession advances. In short term planning this factor can be considered as constant but not in long term forest management. The area climate and stand altitude are, of course, constant.

In assessing the outbreak hazard of a forest, constant and variable factors must be treated differently. Constant factors can be studied and identified well before outbreak conditions arise. Variable factors (insect population and weather) must be monitored each year and/or projected in the future, considering all possible natural or man-made interferences (e.g. alteration of stand diameter distribution).

Each factor comprises a whole set of possible conditions with gradation between them. Consequently, each factor must be broken down into categories each representing a different degree of hazard. Based on the literature, I have attempted to divide each factor into categories (Table IV).

The categories into which insect population level and trend can be divided depend on the criteria used in the measurement of this factor. I have used an indirect measurement of the insect population through a count of the number of trees killed the previous year and the trend of insect numbers as indicated by the trend of the past losses.

A crucial problem is the integration of all the individual hazard estimates into a single meaningful figure, that is a hazard rating or hazard index for a particular forest. If one were to apply each of the factors to several stands one would obtain readings as follows:

	Factors				
	1	2	3	4	5
Stand No. 1:	1	1	2	2	2
Stand No. 2:	3	1	1	2	2
etc.					

TABLE IV   Hazard classes of lodgepole pine stands according to selected outbreak hazard factors.

Factor	Hazard Class	Hazard Rating	Description of the Class
Percent of trees larger than 8 in.d.b.h./acre	1	low	0 to 19%
	2	moderate	20 to 29%
	3	high	more than 30%
Elevation of the stand (ft)	1	low	5,700 and above
	2	moderate	4,800 to 5,700
	3	high	3,700 to 4,800
	4	extreme	below 3,700
Climate	1	low	frequent occurrence of prolonged weather unfavourable for the insect
	2	high	frequent occurrence of prolonged weather favourable for the insect
Insect population level and trend (indirect estimation)	1	low	less than 1 tree killed/acre; losses declining
	2	moderate	less than 1 tree killed/acre; losses rising
	3	high	more than 1 tree killed/acre; losses declining
	4	extreme	more than 1 tree killed/acre; losses rising
Weather in the previous winter	1	low	extremely cold winter with prolonged periods of lethal temperatures for the beetles
	2	high	mild winter

These types of readings are deficient in that it is very likely that each factor will have a different relative importance. Thus, a reliable weight and the integration of factors must be worked out separately for each particular forest situation.

4.   OPERATION OF THE HAZARD RATING SYSTEM

For practical purposes, integration of the different factors affecting the bark beetle outbreak hazard should be done in two steps.

First, the degree of hazard must be estimated for each of the constant factors, i.e. climate, stand elevation, and in short-term planning, the percent of large diameter trees per acre. Each of these must be evaluated (weighed) and integrated in a single figure which represents the degree of hazard due to the constant hazard factors (constant hazard index). Map plots are recommended to delineate the zones of equal constant hazard. This hazard zonation map will permit an easy visualization of the location and accessibility of each stand, which may be very important if salvage operations are required. This map may also include data on the timber values at risk.

Secondly, each year, the weather and the insect population and trend should be monitored. In Canada this should be done in spring. The occurrence or non-occurrence of lethal temperatures for the beetles, the number of trees killed the previous year (or currently infested), and the trend of the losses indicate grades of hazard (Table 4). These two figures must also be weighed and then integrated with the constant hazard index. The final resultant figure is the "current mountain pine beetle hazard index" (Fig. 4).

In long term planning, it must be considered that the stand

FIGURE 4   Structure of a model of the mountain pine beetle outbreak hazard rating system.
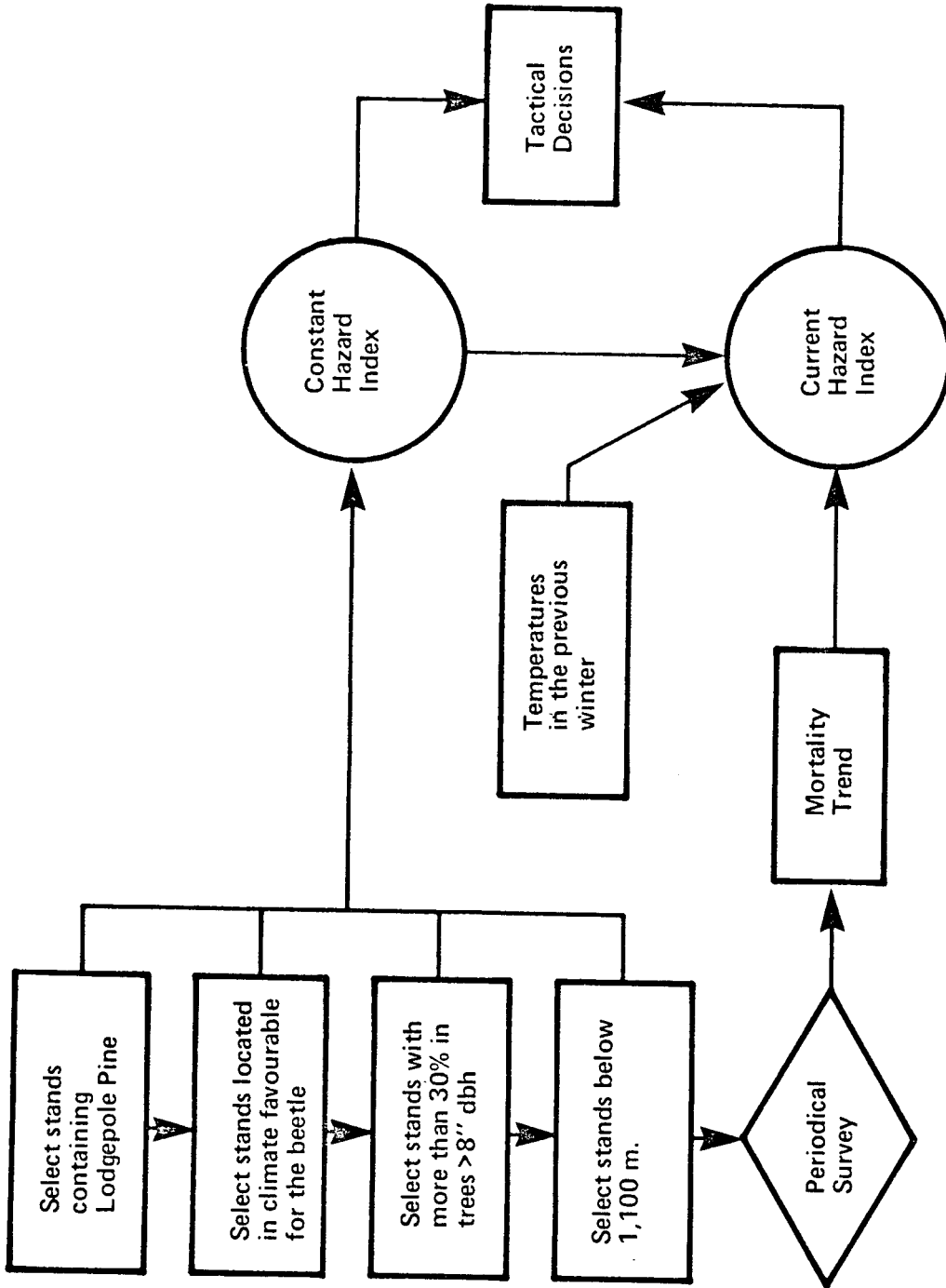
diameter distribution will change with time as the forest ages and as various stand treatments are made. However, by making projections of stand development, figures of constant hazard at any future date can be developed.

Any hazard rating system must be adapted to each forest and management situation. Refinement of the system will depend on the value of the resource to be protected and the importance of forest protection decisions within the greater context of the forest management system in operation.

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