

Mathematical Models for the Mountain Pine Beetle–Lodgepole Pine Interaction

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ABSTRACT

Mathematical models describing losses of lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.) and survival of mountain pine beetle (*Dendroctonus ponderosae* Hopkins) by life stage were prepared from data covering a 13-yr period. The greatest survival and emergence of beetles/unit area of bark occurred in trees of large diameter. After most trees of large diam were killed, gallery starts and egg production continued to increase. However, larval survival declined and emergence returned to the endemic level. At high densities of gallery starts and inches, beetle survival was low, probably because of excessive competition among larvae and drying of phloem. Under these conditions of stress, the sex ratio appears to shift further in favor of ♀ after most of the large trees are killed. These observations demonstrate the close association of beetle dynamics with diam structure of lodgepole pine stands, and support the theory that epidemics are strongly dependent upon the presence of large trees having thick phloem.

Currently, there is strong research and management emphasis on the development of computer systems to permit mass storage of information pertinent to a discipline and efficient retrieval of associated facts sought by the user. Some Forest Service examples are: GIM, GELO, TIMBER- and RANGE RAM, FOCUS, INVEST-III, and AFFIRMS. After 13 yr of research on mountain pine beetle activity in lodgepole pine stands, we have reached an appropriate point in time to undertake a summary of this information in mathematical form, for use in such systems, as well as a summary in verbal and graphic form for general reader consumption.

Research entomologists and forest managers alike should find the material incorporated in this overview of an infestation to be of practical interest. The researcher, for example, will see brood-by-life-stage trends over the course of an infestation, characterized from the longest continuous sets of MPB brood records ever assembled. Forest managers have already utilized some of the information included here, to design and apply diameter-phloem-limit cutting systems for lodgepole pine stands.

It is generally recognized that the mountain pine beetle, *Dendroctonus ponderosae* Hopkins, is an extremely destructive insect in pine forests of Western North America (McCambridge and Trostle 1972). Evenden and Gibson (1940) reported some of the heaviest losses ever to occur in lodgepole pine, *Pinus contorta* var. *latifolia* Engelm., during an epidemic of the beetle in the Big Hole Basin of Montana. There, 84% of the trees 9 in. and larger diameter at breast height (DBH) were killed, with the beetle killing proportionately more of the large than small diam trees. Hopping and Beall (1948), in Canada, recorded an increase of 5% in lodgepole pine mortality for each 1-in. increase in diameter. Roe and Amman (1970) found an increase of 8.8% for each 1-in. increase in diam for lodgepole forests of northwest Wyoming and southeast Idaho. Cole and Am-

man (1969) demonstrated that the beetle infests the larger trees in greater proportion each year of an epidemic infestation. Losses in northwest Wyoming ranged from about 1% of trees 4 in. DBH to about 87% of those 16 in. and larger DBH. However, these figures vary considerably with elevation (Amman and Baker 1972, Amman et al. 1973).

Cole and Amman (1969), using emergence holes as a measure of emergence, reported that usually only trees that were greater than 13 in. DBH in 2 stands in northwest Wyoming produced enough beetles to maintain or cause an increase in the infestation rate.

Reid (1963) reported that numbers of emerging beetles were more closely related to tree diam than to any other factor he measured. Attraction of the mountain pine beetle to large diam lodgepole pine was studied in the laboratory by Shepherd (1966). He found that the beetle was attracted to large dark objects against a light background, which simulated the large trees of the forest. His studies indicate visual response by the beetle in selecting trees to infest. Amman (1969) related emergence to bark thickness. Laboratory studies subsequently demonstrated a direct relation between phloem thickness and amount of emergence (Amman 1972a). Phloem, on the average, is thicker in large than in small diam trees (D. M. Cole 1973).

Several mortality factors acting on mountain pine beetle populations were evaluated by W. E. Cole (1974). However, phloem thickness remains the most important factor accounting for differential beetle survival among trees that we have been able to identify.

Then it appears that there is rather strong expectation for a positive DBH effect when considering tree mortality and brood density. This, of course, has an impact on our modeling efforts.

Methods

Our analytical objective for this paper was to characterize the course of a mountain pine beetle infestation in lodgepole pine, from the endemic

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through the epidemic and postepidemic stages, linking beetle activity, by life stage, to stand characteristics and stand mortality. This was accomplished in a series of models:

1. Green stand structure of a lodgepole pine stand just prior to the beginning of the MPB epidemic; i.e., the infestation was at an endemic level. Number of trees/acre is expressed as a function of DBH for yr 1 of the observation period.

2. Annual tree mortality in the above stand, observed over the 7-yr course of the infestation (the epidemic stage was included). Annual loss, percent of the original green stand, is expressed as a function of DBH and year of infestation.

3. Cumulative mortality in the above stand. This is a simple cumulative summary of annual mortality figures from the previous model.

4. Brood density/6×6-in. bark sample (at DBH), by life stage. Density is expressed as a function of DBH and year of infestation. Data are from 2 sources and cover 13 yr of infestation as will be explained shortly.

5. Brood density, by life stage, is superimposed on residual stand structure curves at critical points in an infestation. Residual stand structure is obtained from reduction of the original green stand model by the cumulative mortality for specified years of the infestation. Brood for corresponding years is calculated from the brood models. When comparing the green stand the tree mortality models with the beetle brood models for the main epidemic years, the following years are assumed to correspond: residual stand or annual mortality model yr 1 = beetle model yr 1 through 5; 2 = 6; 3 = 7; 4 = 8 (peak year); 5 = 9; 6 = 10; and 7 = 11 through 13.

Mathematical counterparts of the graphic models displayed in the text are contained in the appendix. FORTRAN statements are used for brevity. Matchcurve components have been left almost unsimplified for the benefit of readers interested in linking Matchcurve methods to the applications here. In the event that highly repetitive use is made of the mathematical forms, as in simulation, some added computer efficiency may be achieved with further simplification.

Data Sources

Data for structure of the original green stand and subsequent losses of lodgepole pine to mountain pine beetles during the epidemic on the Teton National Forest came from Cole and Amman (1969). These data were used to establish the residual green stands upon which beetle survival models have been superimposed.

Beetle survival was determined through life table sampling (density/unit area of bark, over time) on 2 National Forests—the Wasatch in northern Utah and the Teton (now Bridger-Teton) in northwestern Wyoming. At the beginning of the study, the beetle infestation on the Teton National Forest was epidemic and the infestation on the Wasatch National

Forest was endemic, developing to epidemic during the study.

During the endemic period (Wasatch 1965–69) all infested trees (3–12 trees/year) were sampled in an area of several mi² in the upper Bear River drainage. When the beetle population increased so that more than 12 trees/generation yr were found (1970–72), as in the epidemic period (Teton 1961–69), 4 trees in each of 3 diam classes were sampled: 10-in. class (8.0–11.9); 13-in. class (12.0–14.9); and 16-in. class (15.0 and larger). Beetle brood sampling consisted of counting all insects and the number of egg gallery starts, and measuring the number of inches of egg gallery within two 6-in.² areas of bark that were selected at random within ±1 ft of breast height (4½ ft above ground level) as described by Carlson and Cole (1965). Four observations were made during each generation year. The 1st sample (eggs and small larvae) was taken in October after oviposition and egg hatch had stopped because of cold temperatures. The egg density was estimated by multiplying inches of egg gallery/sample by a constant factor for number of eggs laid/in., which was derived from laboratory studies (Amman 1972b). The constants based on oviposition in relation to phloem thickness were 3.5 for trees in the 10-in. DBH class which usually have thin phloem (<0.10 in.); 4.0 for trees in the 13-in. DBH class which usually have phloem of medium thickness (0.10–0.13 in.); and 4.5 for trees in the 16-in. class which generally have thick phloem (>0.13 in.).

The 2nd sample (small larvae) was taken in May, and was used to estimate survival between fall and spring to determine the effect of cold winter temperatures.

The 3rd sample (large larvae) was taken in June, and was used to assess survival up to the peak of large larval development.

The 4th sample (emerged adults) was taken in July and August. Adults that emerged were trapped in 2 plastic screen cages/tree, each stapled over a 6-in.² area of bark. Trapped insects fell into test tubes attached to the cages and were collected from these. Following final emergence of mountain pine beetles, cages were removed and the bark covered by the cages also was removed. Insects found in the bark were counted; these usually consisted of dead mountain pine beetles and insect parasites and predators. During the past 3 yr of our studies, mountain pine beetles that emerged into the cages were sexed.

Data Analysis

Following conventional procedures for each model to be developed, we would normally select potential mathematical model components independently of the data set on which these components were to be evaluated statistically. However, in the absence of finite prior knowledge on the form of the relation, this procedure is likely to be insensitive in isolating real, but unique, curve form and interaction information expressed in a data set.

Therefore, since strong, but algebraically unde-

finer, year-DBH interactions were expected to occur in all except the green stand model (2-dimensional), we elected to sacrifice statistical evaluation in model development, directly exhausting each data set of the interaction information it contained. The models are considered to be interim and validation has been left to subsequent research efforts.

Each model was 1st developed graphically utilizing expectation, known constraints, and apparent data trends in arriving at smoothed curve forms. These were carefully fitted through the data by approximate "least deviations." The resulting graphic forms were described algebraically. These descriptors were given a simple adjustment ($< 5\%$ in all cases) to their respective data sets that consisted of the ratio of the sum of the descriptor values for the observations to the sum of the actual values. The descriptors can also be adjusted to new data sets in the same way.

Graphic and descriptor development procedures follow those specified in Matchacurves 1, 2, and 3 (Jensen and Homeyer 1970 and 1971, Jensen 1973).

All models are shown in graphic as well as mathematical form. Data points are included with the 2-dimensional graphs but this was impractical, by reason of data volume, for the surfaces. In all cases, R^2 has been specified. Also, an approximation of the standard error of the estimate ($s_{y,x}$) is included as a rough index to variability about regression, but is of questionable value in strong unequal variance situations, especially the brood model for eggs.

Added detail for development of the individual models follows.

Green Stand.—Previously outlined methods cover this model fairly well. Matchacurve-1 Standards were used for descriptor development. The right $\frac{3}{4}$ of a bell-shaped curve was expected, asymptoting near zero at higher diameters.

Annual Mortality.—Methods were covered by previous statements. Matchacurves 1 and 3 were used for development. Expected effects consisted of positive DBH and bell-shaped year effects. Responses were expected to asymptote at low and high values of each variable.

Brood Models.—To provide overview brood models for the 1st time, it was necessary to accept subjective input consisting of brood data, end-matched in time, from 2 areas. Data from the Wasatch National Forest were held representative of the endemic period (yr 1–5); the epidemic (6–9) and postepidemic years (10–13) were characterized by data from the Teton National Forest. We feel that this was justified because the beetle operates similarly within stands where temperatures are optimal for development and where diameter distributions are similar (see Amman and Baker 1972 for comparisons of tree losses). In addition, data taken since 1972 indicate that the Wasatch infestation is continuing to increase, and that beetle survival and tree losses are following trends similar to those of the Teton infestation.

Expectations for DBH and year effects, the only 2

variables included in each brood model, have been reasonably well-established by either experimental or field survey work. Brood production has been found to increase with phloem thickness (Amman 1972a). Large trees in a stand are generally faster growing than smaller ones and, on the average, are expected to have thicker phloem. This is especially true where the beetles have not yet decimated the stand. Therefore, the fundamental expectation is for a positive DBH effect on brood production. These effects were further evaluated using the individual tree data within each brood data set. Tree DBH measurements to the nearest in. or $\frac{1}{40}$ in. were available only in yr 3, 4, 6, 7, 8, 9, 12, 13. For eggs, this detail was missing in yr 8 and 9. Within the limits of these data, year effects on brood density were assessed statistically, along with the covariate effect of DBH.

High variability masked significance in some cases. And, within a few years, there were reversals of the expected positive DBH effect. Overall, the general expectations appear to have been met and some insight on years of peaking was provided.

Eggs.—The slope over DBH was positive in all years, weakly displayed in yr 3–6 ($P < 0.17$ to $P < 0.10$, $0.04 \leq r^2 \leq 0.30$), and more strongly displayed in yr 7–13 ($P < 0.10$ to $P < 0.05$, $0.32 \leq r^2 \leq 0.65$). There was no year effect from yr 3–6. A positive but weak effect existed from yr 6–7 ($P < 0.17$ approx.) and from 7–12 ($P < 0.20$ approx.). Year effect was strongly negative from yr 12–13 ($P < 0.005$). From these evaluations we might reasonably expect to find a positive DBH effect in most years, with the trend over years beginning to rise about yr 6 and peaking at the 12th yr. It is also reasonable to expect a smaller year effect with smaller DBH, an interaction.

Small Larvae.—A positive DBH effect existed in all but yr 12 and, in about half of those years, the effect was weak ($P < 0.10$ to $P < 0.20$, $0.09 \leq r^2 \leq 0.26$). The negative effect in yr 12 was strong ($P < 0.05$, $r^2 = 0.36$). There was no significant year effect between 3 and 6, but there was a positive year effect between yr 6 and 7 ($P < 0.05$). Inconsistent year effects appeared between yr 7 and 13, possibly attributable in part to the crude models fitted (linear, with intercept). From these evaluations, a positive DBH effect might be expected to exist in most years, along with a rising year effect beginning about the 6th yr. A peak might be expected to occur some place beyond yr 7, although not apparent with the models fitted here. The imposition of a positive DBH constraint in smoothing across yr 8–13, helped to identify an approximate point of peaking (yr 10).

Large Larvae.—A positive DBH effect existed in yr 3–7 but was only significant ($P < 0.06$, $r^2 = 0.31$) in yr 7. Slopes were inconsistent and nonsignificant in yr 8–13. No year effect was apparent between yr 3 and 4 vs. 6 and 7. A positive year effect appeared to exist between yr 6 and 7 vs. 8 ($P < 0.005$) and a negative effect from yr 8–9 ($P < 0.05$). No effect existed between yr 9 and 12, but yr 13 was substantially lower than 12. From this, a positive

Table 1.—Brood model performance on year-DBH means.

Stage	No. trees	Mean density per 6×6-inch sample	$s_{y,x}$ *	R^2
Eggs	128	111	33	0.57
Small larvae	124	33	16	.38
Large larvae	125	16	9	.52
Emerging adults	143	9	7	.55

* Standard error of the estimate.

DBH effect was assumed to exist prior to peaking, at least, and a peak was assumed to exist in yr 8. Since the drop in yr 13 could only be construed as an unusual year effect, it was averaged with yr 12.

Adult Emergence.—The DBH effect was positive for all years but 7 and 13. However, the effect was only significant for yr 8 ($P < 0.15$, $r^2 = 0.10$) and 12 ($P < 0.05$, $r^2 = 0.21$). The year effect seemed well specified here, there being none from yr 3–7, a well-defined positive effect from yr 6 and 7–8 ($P < 0.005$) and a definite drop from yr 8–9 ($P < 0.025$). We infer from this a positive DBH effect in all years and a sigmoidal year effect, flat in yr 3–7, peaking at 8, and dropping back in yr 9 to an asymptote reaching through yr 13.

Graphic brood models (across years, by 3 DBH groups), supported by the above information, were fitted through unweighted² brood-density means by approximate least deviations. Density was smoothed over year. These smoothed values, by year, were plotted over DBH-group means and resmoothed. The resulting surfaces were described mathematically using techniques specified in Matchacurves 1, 2, and 3 (Jensen and Homeyer 1970 and 1971, and Jensen 1973). The mathematical forms were given a proportional adjustment to the density means by the ratio of transformed to the actual means for each brood. The adjustments ranged from 0.9565–1.0144 for the 4 broods. Performance statistics for the models are shown in Table 1.

Less variability, along with smaller $s_{y,x}$ values and higher R^2 values, might be expected for a single-source data set. All models (green stand, annual tree mortality, and brood) are highly significant. However, such probability evaluations are inappropriate for reasons involving the use of multiple-source data and/or the direct exploitation of data interaction information to develop the fitted forms.

Results and Discussion of Models

The green stand model (Fig. 1A) is typical for a stand in which a beetle epidemic might be expected. A relatively large proportion of the stand (of trees 4 in. DBH and over) is in trees over 12 in. diam (22% here), a condition regarded necessary for an epi-

dem (Cole and Amman 1969, Amman 1969). The epidemic potential exists primarily under optimal temperatures for beetle development (Amman and Baker 1972, Amman et al. 1973, Safranyik et al. 1974).

Losses of lodgepole pine over the main epidemic years are proportionately much greater in the large diam classes (Fig. 1B). Most tree losses occurred

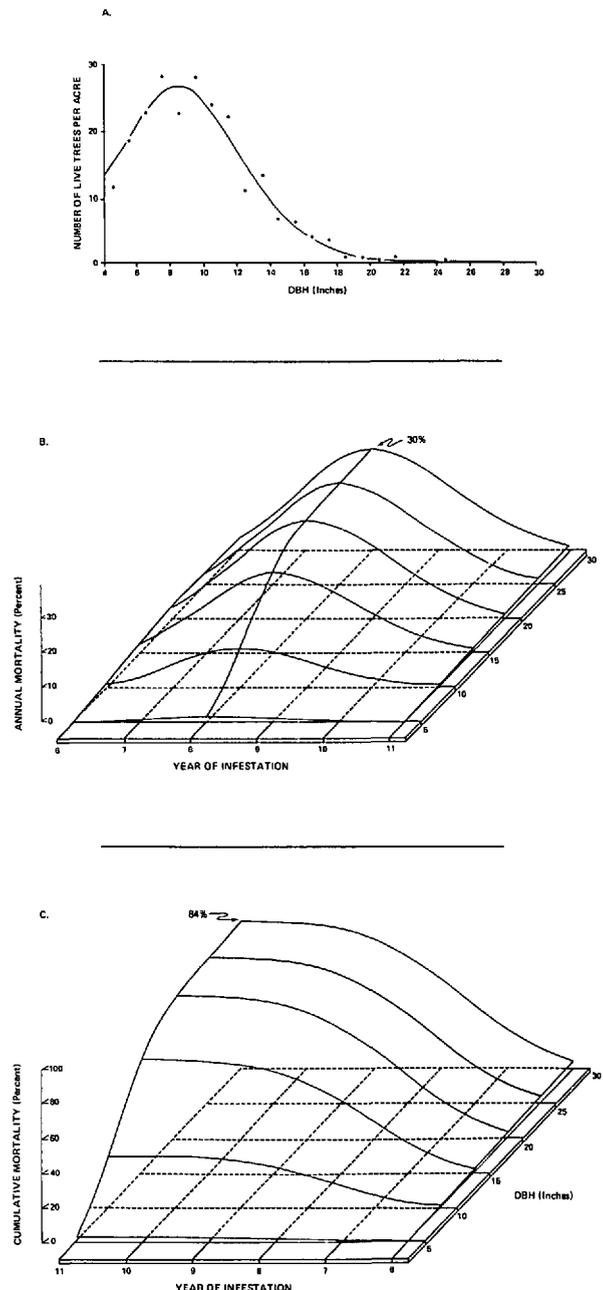


FIG. 1.—Green stand structure at the beginning of the mountain pine beetle infestation and losses of lodgepole pine by diam class and year during the infestation. A. Green stand model, $s_{y,x} = 1.9$, $r^2 = 0.97$; B. Annual mortality % of original stand, $s_{y,x} = 0.14$, $r^2 = 0.36$; C. Cumulative mortality %.

² Unweighted because sample size for the DBH-year groups were the same in most cases.

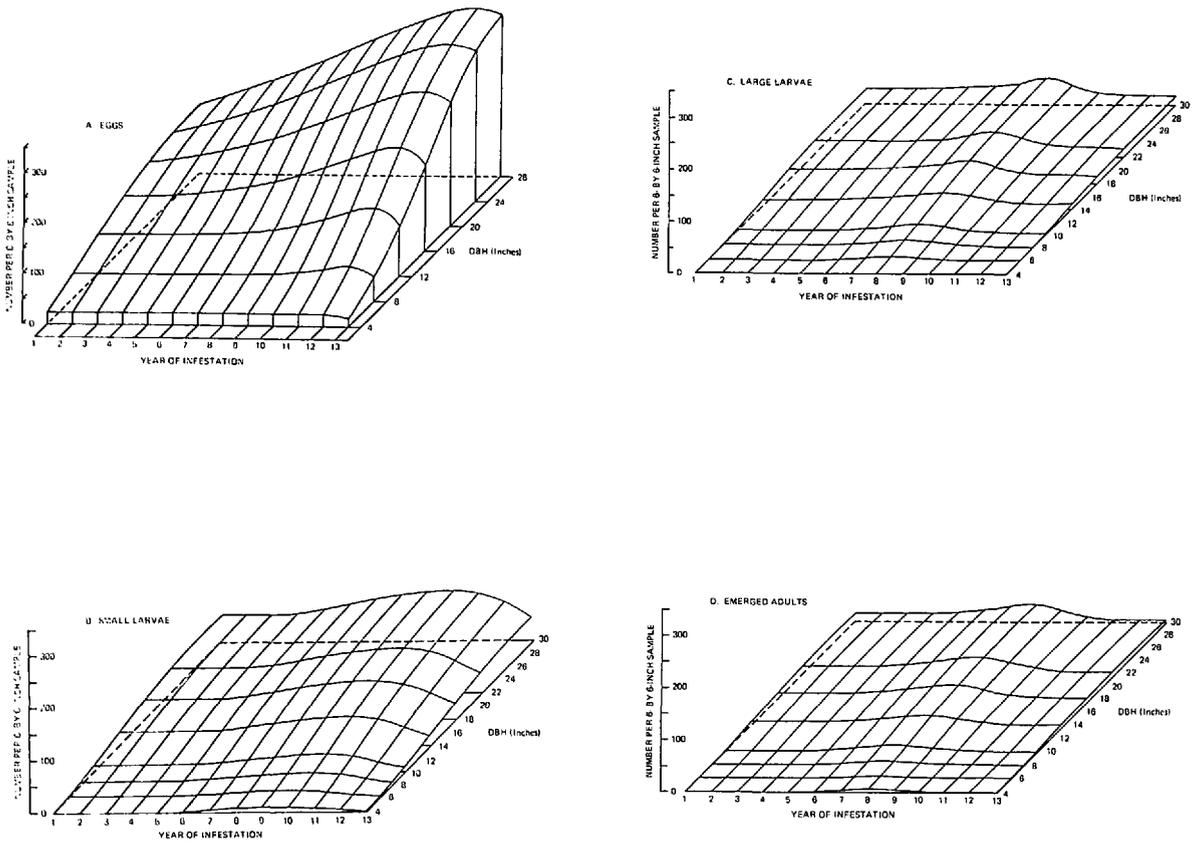


FIG. 2.—Densities of 4 life stages of the mountain pine beetle by tree diam for a 13-yr period. A. Eggs; B. Small larvae; C. Large larvae; and D. Emerged adults.

during a 6-yr period. Cumulative losses show that most large diam trees were killed during the infestation (Fig. 1C). Losses ranged from about 84% of the large trees to about 3% of the small trees. Losses shown in Fig. 1 are typical for stands of trees of similar size and distribution at similar elevations and latitudes (Amman and Baker 1972).

Densities for each of 4 life stages of the beetle are modeled in Fig. 2. Within any year of the infestation, egg density increases with diam, the combined result of increased gallery inches and eggs/in. of gallery in large trees which generally have thick phloem (Fig. 2A). The increase in egg density up to the 12th yr is primarily the result of increased gallery inches (Fig. 3). Of particular interest is the increase in egg density (Fig. 2A) beyond the peak year (yr 8) of emergence (Fig. 2D). Egg density declined slightly in yr 13 about 3 yr after emergence had returned to the endemic level.

Survival of small larvae through the winter (Fig. 2B) also increased with diam and peaked in the 10th yr, 2 yr before peak egg deposition. The decline in survival that starts with the 11th yr probably is related to intraspecific competition among larvae which continues to intensify as egg gallery starts and inches increase with years (Fig. 3).

Density of large larvae (Fig. 2C) peaked in yr 8,

2 yr before the peak for small larvae. Large larval density was relatively steady from year to year within all diam classes during the endemic period (yr 1-5). However, density increased substantially in yr 6-8. Low density of large larvae during the endemic years is related to low density of eggs laid/unit of bark as indicated by low density of egg gallery (Fig. 3B). Laboratory studies demonstrated that beetle emergence is directly related to inches of egg gallery when phloem is underutilized (Amman 1972a). As the infestation progressed and egg galleries increased, an apparent optimum was reached when maximum numbers of large larvae occurred (yr 8). After this year, increased competition among larvae and increased drying probably were responsible for decreased survival. Construction of egg galleries by adults promotes drying of the phloem, especially when gallery density is high. Drying also is enhanced by the feeding larvae as they exhaust the available phloem.

Adult density is similar to that of large larvae, but on a reduced level, with the peak occurring in yr 8 (Fig. 2D). Emergence within a diam class is fairly steady during the endemic period (yr 1-5) but is still greater in large diam classes. The transition of the infestation from endemic to epidemic appears to be dependent upon successful infestation of large trees.

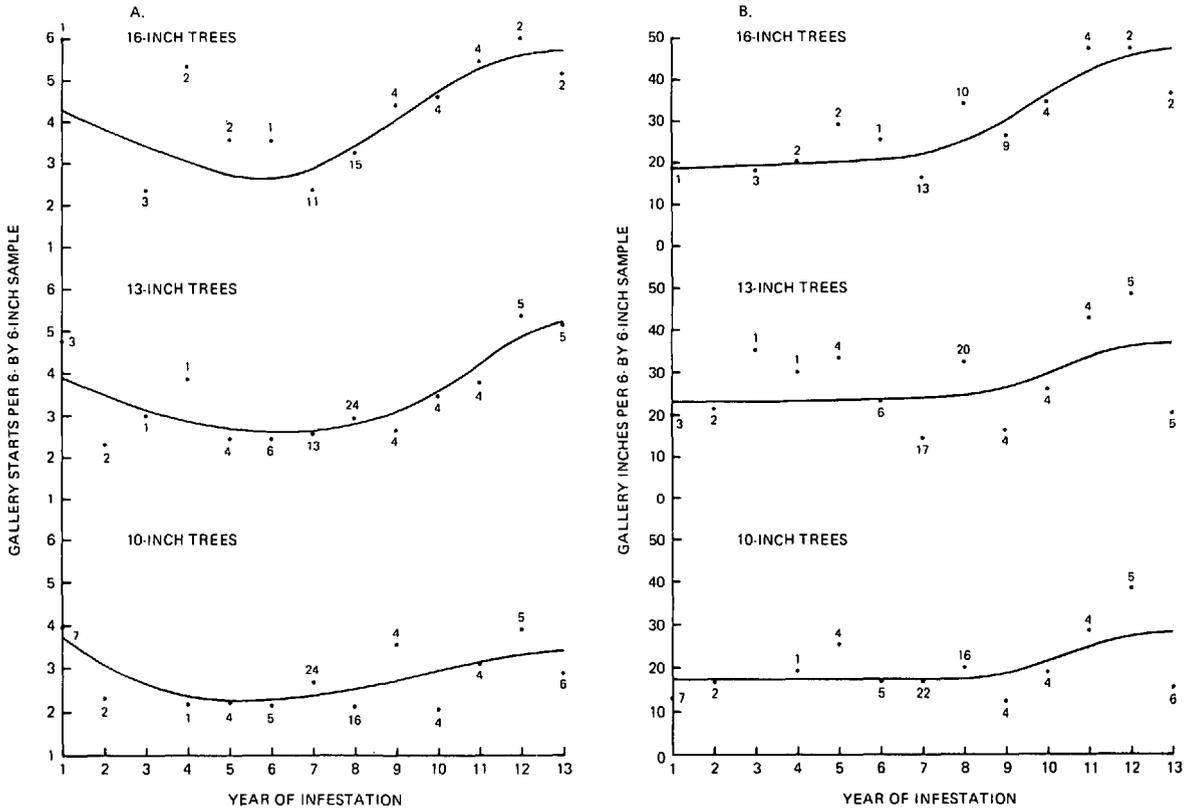


FIG. 3.—Mountain pine beetle egg gallery starts and egg gallery inches by diam for a 13-yr period. A. Egg gallery starts; B. Egg gallery inches. Number at each data point indicates number of trees sampled.

Toward the latter years of the epidemic (11–13), only large trees usually could be expected to produce enough brood to keep the infestation going. However, by this time most of these trees had been killed (Fig. 1C).

Stand models and beetle models were incorporated for selected years spanning the infestation to show interactions. Fig. 4A represents a year when the beetle population was endemic. Curves for beetle stages show expected survival in a tree of any specific diam if it becomes infested. The curve on the base shows structure of the stand in terms of numbers of live trees/acre in each diam class. Losses to the beetle are extremely small during the endemic period, constituting much less than a tree/acre during 1 yr.

During yr 8, both emergence and tree losses peaked (Fig. 4B, 1B). Compared to yr 1, both egg density and adult emergence approximately doubled. The fact that gallery inches (Fig. 3B) and egg densities (Fig. 2A) continue to rise in following years but emergence declines indicates that gallery density and subsequent larval populations reached an optimum in yr 8. Cumulative tree mortality is substantial, with about ½ of the trees killed by yr 8. Numerically, losses appear similar for the different diam classes; however, proportionately, losses are much greater for the large diam classes.

Year 10 (Fig. 4C) shows a large increase in eggs

but the number of small larvae surviving through the winter was about the same as in yr 8, and the number of surviving large larvae was much reduced. Emergence now approximates the level that occurred during the endemic period (Fig. 4A), but tree losses do not. Cumulative tree losses in yr 8 have almost doubled by yr 10 (Fig. 4C), primarily because of high emergence and correspondingly high tree losses during yr 9.

In yr 12 (Fig. 4D), the high egg densities resulted in high-larval mortality, probably from severe competition for food and drying of phloem. Subsequent emergence, in accordance with expectations, was even lower than in pre-epidemic years (1–5). Emergence should return to those levels when egg gallery densities return to their original endemic levels (yr 1). By yr 12, cumulative tree mortality had leveled off and annual tree mortality had returned to the endemic level. Cumulative losses in the stand do not appear overwhelming (Fig. 4D). However, most of the trees that were over 12 in. DBH had been killed. Mortality ranged from 49% of the 12-in. trees to over 80% for trees 19 in. and over (Fig. 1C).

In these models, the close association of beetle dynamics with numbers and sizes of trees that are infested can be seen at any point in the epidemic. For example, emergence diminishes rapidly as the large trees are killed. Beetles then tend to infest a higher

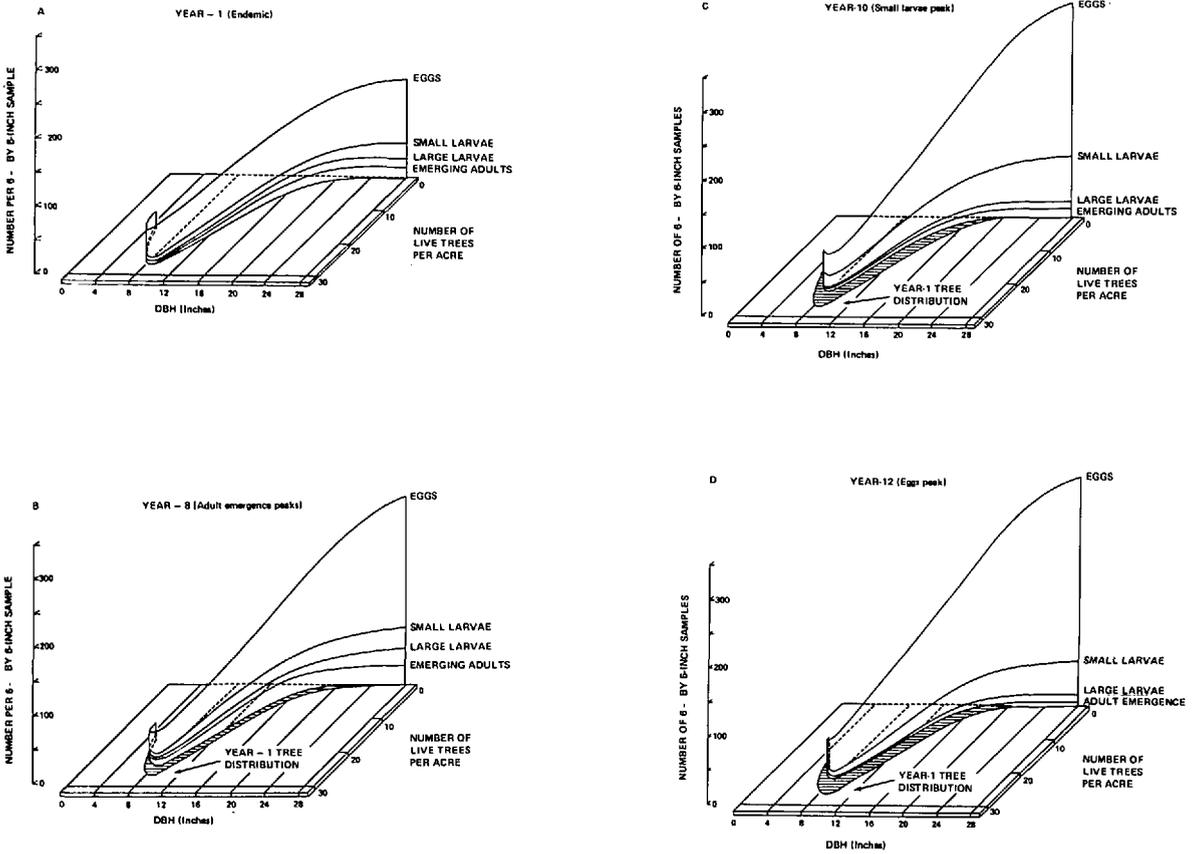


FIG. 4.—Interaction models of beetle survival and lodgepole pine losses. A. Year 1 (endemic beetle population level); B. Year 8 (peak adult emergence); C. Year 10 (peak small larval density); D. Year 12 (peak egg density). Shaded area shows cumulative tree mortality.

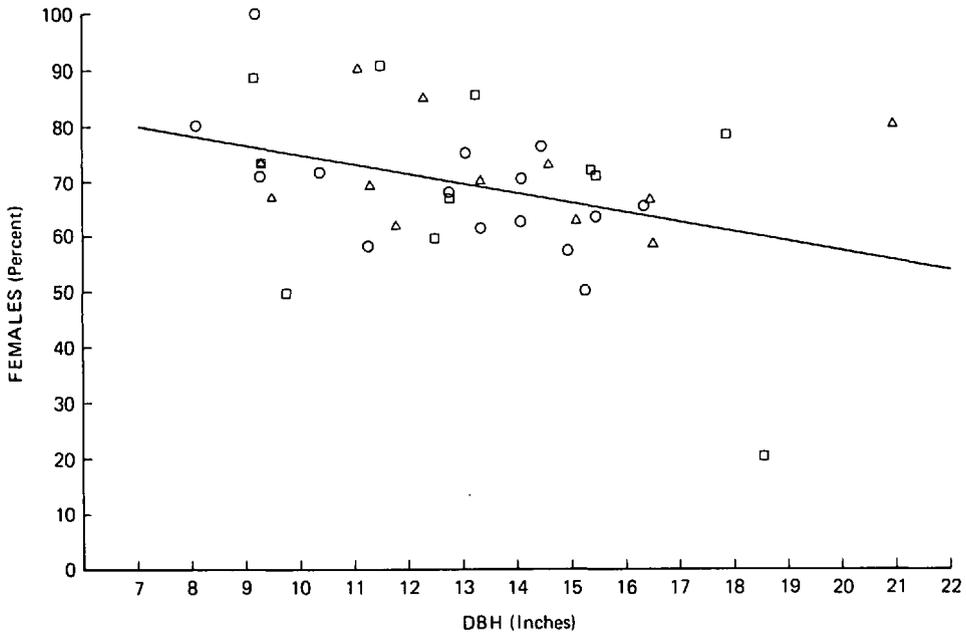


FIG. 5.—Proportion of ♀ tree in the emerging population from infested lodgepole pine on the Wasatch National Forest, 1972-74. $\hat{Y} = 91.8 - 1.68 x$; $s_{y,x} = 13.1$; $r^2 = 0.13$; $P < 0.025$.

proportion of smaller trees. Coincident with this are increased numbers of gallery starts, gallery inches, and subsequent egg densities. These continue to rise through yr 12, even though emergence has declined drastically. Brood in small trees having thin phloem generally tend to have higher proportions of ♀ than found in large trees having thick phloem (Fig. 5). Females survive better under stress than males. W. E. Cole (1973) demonstrated that ♀ survived in greater proportion than ♂ when crowding of larvae increased, and Amman and Rasmussen (1974) found that ♀ survival was greater than that of ♂ when drying of bark increased.

Starting about the time of peak emergence (yr 8), it appears that insufficient ♂ exist to mate most ♀ in a relatively short span of time. Hence, unmated ♀ continue to produce the aggregative pheromone, *trans-verbenol* (discovered by Pitman et al. 1968), which attracts additional females. Rudinsky et al. (1974) discussed the role of ♀ produced methylcyclohexenone (MCH) to mask the aggregative pheromone of Douglas-fir beetles. Pitman and Vité (1974) found that ♂ Douglas-fir beetles produced much more MCH than females. If ♂ mountain pine beetles also produce a powerful anti-aggregative pheromone (Rudinsky et al. 1974), our theory that increase in attack density over time is related to decrease in proportion of ♂ in the population is even more plausible.

We reason that after most large diam trees are killed, and the beetle infests primarily trees of small diam, the sex ratio shifts even further in favor of females. The attack density, and hence gallery inches then increase. Subsequent larval populations suffer heavy mortality from competition and drying, and emergence declines. The infestation then returns to the endemic level and does not become epidemic again until the stand of lodgepole has grown into diam and phloem distributions conducive to increased beetle survival, and more even sex ratios. We conclude that beetle dynamics are closely tied to those of lodgepole pine, and that epidemics are strongly dependent upon the presence of large diam trees having thick phloem.

Appendix

ENDEMIC GREEN STAND (GS)

$YR = 1$

$$GS = 26.96 * \text{EXP}(-(\text{ABS}(((\text{DBH}+18)/26.5-1)/.205)**1.8)) + .2$$

LIMIT

$$4 \leq \text{DBH} \leq 30$$

ANNUAL MORTALITY PERCENT (AM)

$6 \leq YR \leq 8$

$$TI = .235 * \text{EXP}(-(\text{ABS}(((30-\text{DBH})/25.5-1)/.225)**1.8)) + .365$$

$$EL = \text{EXP}(-(\text{ABS}(((YR-5.5)/2.5-1)/(1-TI))**1.8))$$

$$ER = \text{EXP}(-((1/(1-TI))**1.8))$$

$9 \leq YR \leq 11$

$$TI = .055 * \text{EXP}(-(\text{ABS}(((30-\text{DBH})/25.5-1)/.35)**3)) + .47$$

$$EL = \text{EXP}(-(\text{ABS}(((11.5-YR)/3.5-1)/(1-TI))**1.9))$$

$$ER = \text{EXP}(-((1/(1-TI))**1.9))$$

$6 \leq YR \leq 11$

$$YP = .3295 * \text{EXP}(-(\text{ABS}(((\text{DBH}-4)/26-1)/.8)**4.5)) - .0215$$

$$AM = 97.765 * YP * ((EL-ER)/(1-ER))$$

LIMITS

$$4 \leq \text{DBH} \leq 30, 1 \leq YR \leq 11, \text{integer values only}$$

LIMITS FOR ALL BROOD MODELS

$$4 \leq \text{DBH} \leq 30, 1 \leq YR \leq 13, \text{integer values only}$$

EGGS (EG)

FOR $1 \leq YR \leq 11.8$

$$BP = 177.918 * \text{EXP}(-(\text{ABS}((\text{DBH}/35-1)/.85)**3)) - 34.918$$

$$TI = .9533 * \text{EXP}(-(\text{ABS}(((35-\text{DBH})/35-1)/.63)**2.6)) - .0333$$

$$G = \text{ABS}(((YR-1)/10.8-1)/(1-TI))**1.6$$

$$P = 1.6$$

FOR $11.8 < YR \leq 13$

$$BP = 0$$

$$TI = .42 * \text{EXP}(-(\text{ABS}(((35-\text{DBH})/35-1)/.605)**5)) + .25$$

$$G = \text{ABS}(((17-YR)/5.2-1)/(1-TI))**3$$

$$P = 3$$

FOR $1 \leq YR \leq 13$

$$YP = 349.251 * \text{EXP}(-(\text{ABS}((\text{DBH}/35-1)/.68)**3.2)) - 11.251$$

$$ER = \text{EXP}(-1/(1-TI))**P$$

$$EG = ((\text{EXP}(-G)) - ER)/(1-ER) * (YP-BP) + BP**1.0144$$

SMALL LARVAE (SL)

FOR $1 \leq YR \leq 10$

$$BP = 50.186 * \text{EXP}(-(\text{ABS}((\text{DBH}/35-1)/.682)**4.5)) - .186$$

$$TI = .105 * \text{EXP}(-(\text{ABS}(((35-\text{DBH})/35-1)/.51)**5)) + .565$$

$$G = \text{ABS}((YR/10-1)/(1-TI))**2.6$$

$$P = 2.6$$

FOR $11 \leq YR \leq 13$

$$BP = 45 * \text{EXP}(-(\text{ABS}((\text{DBH}/35-1)/.593)**4)) + 1$$

$$A = .00025396 * (35-\text{DBH})**2.1 + .001$$

$$TI = .405 * \text{EXP}(-(\text{ABS}(((35-\text{DBH})/35-1)/.146)**2.6)) + A$$

$$G = \text{ABS}(((13-YR)/3-1)/(1-TI))**2.4$$

$$P = 2.4$$

FOR $1 \leq YR \leq 13$

$$YP = 98.53 * \text{EXP}(-(\text{ABS}((\text{DBH}/35-1)/.716)**3.6)) - 3.53$$

$$ER = \text{EXP}(-1/(1-TI))**P$$

$$SL = ((\text{EXP}(-G)) - ER)/(1-ER) * (YP-BP) + BP*.9565$$

LARGE LARVAE (LL)

FOR $1 \leq YR \leq 8$

$$BP = 31.093 * \text{EXP}(-(\text{ABS}((\text{DBH}/35-1)/.664)**4.3)) - .093$$

$$TI = .07598 * \text{EXP}(-(\text{ABS}(((\text{DBH}-4)/31-1)/.83)**5)) + .704$$

FOR $9 \leq YR \leq 13$

$$BP = 15 * \text{EXP}(-(\text{ABS}((\text{DBH}/35-1)/.625)**7))+1$$

$$TI = .1073 * \text{EXP}(-(\text{ABS}((\text{DBH}/35-1)/.674)**3.4))+.708$$

FOR $1 \leq YR \leq 13$

$$YP = 52.117 * \text{EXP}(-(\text{ABS}((\text{DBH}/35-1)/.695)**3.7))+.883$$

$$LL = (\text{EXP}(-(\text{ABS}((\text{YR}/8-1)/(1-TI))**1.5)) * (YP-BP)+BP) * .9865$$

EMERGENCE (EM)

FOR $1 \leq YR \leq 7$

$$BP = 17 * \text{EXP}(-(\text{ABS}((\text{DBH}/35-1)/.655)**6))$$

$$P = 2.3 * \text{EXP}(-(\text{ABS}(((35-\text{DBH})/29-1)/.13)**2.2))+2.2$$

$$G = \text{ABS}((\text{YR}/7.7-1)/.2)**P$$

FOR $8 \leq YR \leq 13$

$$BP = .13 * \text{DBH}$$

$$TI = .051 * \text{EXP}(-(\text{ABS}(((35-\text{DBH})/29-1)/.38)**7))+.69$$

$$G = \text{ABS}((\text{YR}/7.7-1)/(1-TI))**1.6$$

FOR $1 \leq YR \leq 13$

$$YP = 30.328 * \text{EXP}(-(\text{ABS}((\text{DBH}/35-1)/.715)**4.5))+2.672$$

$$EM = (\text{EXP}(-G)) * (YP-BP)+BP) * .995$$

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