

A DISPERSAL-AGGREGATION MODEL FOR MOUNTAIN PINE BEETLE IN LODGEPOLE PINE STANDS¹

D. G. BURNELL

Department of Entomology, Washington State University, Pullman,
Washington 99163, U. S. A.

INTRODUCTION

Mountain pine beetles, *Dendroctonus ponderosae* HOPKINS, attack and kill lodgepole pines, *Pinus contorta* var. *latifolia* ENGELMANN, by boring egg galleries beneath the bark. Mountain pine beetle epidemics frequently occur in mature lodgepole forests often causing intensive mortality over extensive forest areas. Since 1971 an effort has been made to develop mathematical models for the mountain pine beetle-lodgepole pine system under the auspices of the International Biological Program and, later, the Integrated Pest Management Program.

Development of a model for the mountain pine beetle-lodgepole pine system was predicated upon the use of a stand growth model constructed by STAGE (1973). Progress to date has yielded a beetle production model (BERRYMAN *et al.*, unpublished) which, for an attacked tree of given characteristics and attack density, provides the density of emerging beetles. Other remaining efforts have been directed toward the development of insect dispersion and attack models to interface the stand growth and productivity models.

Mountain pine beetle populations attack lodgepole pines in relationship to diameter (HOPPING and BEALL, 1948; COLE and AMMAN, 1973; SAFRANYIK *et al.*, 1974). This led to the conclusion by some authors that the beetles actively select larger diameter trees (COLE, 1973). SAFRANYIK *et al.* (1974), however, showed that trees are killed within a diameter class according to the contribution of that class to the total basal area of the stand, suggesting that the trees are attacked in proportion to the "barrier" presented to the flying beetles.

In this paper a dispersal-attack theory is developed from a set of simple assumptions, and the resulting theoretical model is fit to data from four epidemic studies. Implications of the theory are discussed in relation to the dynamics of lodgepole pine-mountain pine beetle interactions.

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THE DISPERSAL-AGGREGATION THEORY

The theory is based on three assumptions:

1. Pioneer, or first attacking, beetles attack with random distribution over the available bark surface area.
2. Any tree has a threshold of aggregation which is a measure of the numbers and distribution of pioneer beetles required to induce aggregation.
3. Any tree which becomes an aggregator, in the sense of assumption 2, will be mass attacked and killed by the beetles.

The first assumption is reasonable if we assume no primary attraction and can be explained as a relative perception mechanism. Investigators observed the earlier or first emerging bark beetles attack at random and subsequent mass attacks depend upon the reaction of the host to initial attacks (MOECK, unpublished; BERRYMAN and ASHRAF, 1970; HYNUM, personal communication). HYNUM also noticed that pioneer mountain pine beetles failed to differentiate between non-aggregating live lodgepole, dead lodgepole and non-host trees. That is, there was little difference between insect numbers collected in traps attached to any of the trees, viable host or otherwise, as long as the trees did not become aggregators. SHEPHERD (1966) noted mountain pine beetles move towards dark objects on a light background and that larger objects are more attractive. However, he did not state whether the attraction was proportional to size which is implicit from assumption 1. The notion 'threshold of aggregation' is not a quantification of the number of insects required to kill a tree but is a measure of the numbers and distribution of attacking insects required to set up the synergistic chemical and behavioral mechanisms which induce pheromone production and hence, aggregation. Assumptions 1 and 2 will be used to set up the dispersal-aggregation theory and, while not strictly true, assumption 3 simplifies the resulting mortality prediction model.

Assume the tree surface areas are measured in equivalent units, for example, square feet. If x is the pioneer beetle attack density per that unit, then, by assumption 1 and using the Poisson distribution function (Parzen, 1960), the probability of having one or more pioneer beetles attack a given unit area is

$$P(x) = 1 - \exp(-x).$$

Let τ be the threshold of aggregation for a given tree with available surface area A . That is, τ is the number of square units of the tree which must be attacked by one or more pioneer beetles to induce aggregation. Then the probability of the tree becoming an aggregator is

$$I_{P(x)}(\tau, A - \tau + 1)$$

where I is the incomplete beta function ratio (ABRAMOWITZ and STEGUN, 1944). The incomplete beta function ratio predicts the likelihood of τ or more squares being attacked by one or more beetles given that average density of pioneer beetles per square unit is x and the number of available square units is A . For the remainder

of the discussion let

$$J_x(\tau, A) = I_{P(x)}(\tau, A - \tau + 1).$$

Then $J_x(\tau, A)$ is the probability of a tree becoming an aggregator given a threshold of aggregation τ , available surface area A and pioneer beetle attack density x .

MORTALITY PREDICTION MODEL

In the case of an epidemic we will assume τ is uniform across both diameter and years of the epidemic. Let $(T_{m,n})$ be the number of surviving trees per acre in diameter class n for year m and let $A(d)$ be a function which estimates the area available for attack on a tree of diameter at breast height, d . Then the surface area killed in the m th year is

$$S_m = \sum_{n=1}^N (T_{m-1,n} - T_{m,n}) \cdot A(d_n) \quad \text{for } m=1, \dots, M$$

where N is the number of diameter classes.

For a given stand with a fixed τ , define the predicted residual stand distribution, $(T'_{m,n})$, by:

$$T'_{0,n} = T_{0,n}$$

for $n = 1, 2, \dots, N$ and

$$T'_{m+1,n} = T'_{m,n} (1 - J_{x_{m+1}}(\tau, A(d_n)))$$

for $n=1, 2, \dots, N$ and $m=0, 1, \dots, M-1$ subject to the constraints that: a. $x_{m+1} > 0$

and b. $S'_m = S_m$ where $S'_m = \sum_{n=1}^N (T'_{m-1,n} - T'_{m,n}) \cdot A(d_n)$ for $m=1, \dots, M$.

That is, for each year the predicted surface area mortality is forced to be the same as the observed by 'adjusting' the pioneer beetle attack density, x_{m+1} . The proper x_{m+1} could be determined in such a way the constraint b above holds by using a simple algorithm—for example, a binary search.

FITTING THE MODEL

In order to fit the model to actual data let

$$R(\tau) = \sqrt{\frac{\sum_{n=1}^N \sum_{m=1}^M (T'_{m,n} - T_{m,n})^2}{NM-1}}$$

Then $R(\tau)$ is a measure of the difference between the actual and predicted residual stands. The total surface killed per year is forced to be the same in both actual and predicted residual stands. We define the threshold of aggregation for the stand to be the τ which minimizes $R(\tau)$. Since R has only one minimum for $\tau > 0$ the determination of the threshold of aggregation, τ , was accomplished using a quadratic fit to find the next 'best' until the change in τ was judged to be reasonable.

Briefly, the surface area of the killed trees in the predicted and residual stands are forced to be the same by adjusting x_m , the pioneer beetle attack density for year m . The predicted residual stand is derived from the year by year deletion of the

trees which become aggregators. For a given stand the threshold of aggregation is determined by finding the τ which minimizes the difference between predicted and residual stands.

The model was fit to four sets of data. PARKER (1973) provided a residual stand analysis of a square mile plot in Yellowstone National Park for the years 1966 through 1972. Another set of experimental data was taken from STIPES' (1974) study of an epidemic in the Spring Creek area of the Bridger-Teton National Forest from 1967-1973. The remaining two sets of data are from plots set out in Hell Roaring Creek and Logger Creek drainages of the Gallatin River by the author and his colleagues and are summarized in Table 1.

Table 1. Residual stand data for Logger and Hell Roaring Creeks.
Items are in live stems/acre.

1 A. Logger Creek Plot						
Year	DBH Class (inches)					
	6	8	10	12	14	16
0	78.8	104.3	91.4	30.5	2.0	0.8
1	78.8	104.3	87.4	30.5	2.0	0.8
2	78.8	101.0	73.1	19.4	1.0	0.0
3	72.7	71.7	44.7	5.5	0.0	0.0

1 B. Roaring Creek Plot						
Year	DBH Class (inches)					
	6	8	10	12	14	16
0	192.6	112.0	48.7	11.6	3.7	1.6
1	192.6	112.0	46.6	10.1	3.7	1.6
2	192.6	112.0	46.6	10.1	3.7	0.8
3	192.6	105.3	40.2	5.8	1.6	0.8
4	192.6	103.6	29.6	3.6	0.5	0.0

Fits were made using the initial stand composition and the year by year surface mortality in each stand. In all cases the function

$$A(d) = 8.835d - 40.82$$

was used to determine the surface area of a tree with diameter at breast height d . The function, A , was obtained from a linear regression fit ($r^2 = 0.94$) of average surface area attacked to diameter at breast height using data provided by KLEIN (personal communication).

The incomplete beta function ratio values were computed using GAUTSCHI's algorithm (1964).

Once the model has been used to obtain τ (τ such that R is minimized) then two estimates of over-epidemic mortality can be obtained:

1. Observed mortality for a given dbh class, n , can be computed from the raw data:

$$M_p(n) = (T_{0,n} - T_{M,n}) / T_{0,n}$$

where M is the number of years in the epidemic period.

2. If x_m is the pioneer beetle attack density in year m and τ is the threshold of aggregation for the stand then let the expected mortality of a tree of diameter at breast height d be defined by:

$$M_f(d) = P(d, M)$$

where $P(d, m)$ is defined recursively from: $P(d, 1) = Jx_1(\tau, A(d))$ and $P(d, m+1) = Jx_{m+1}(\tau, A(d)) \cdot (1 - P(d, m)) + P(d, m)$ for $m=1, \dots, M-1$.

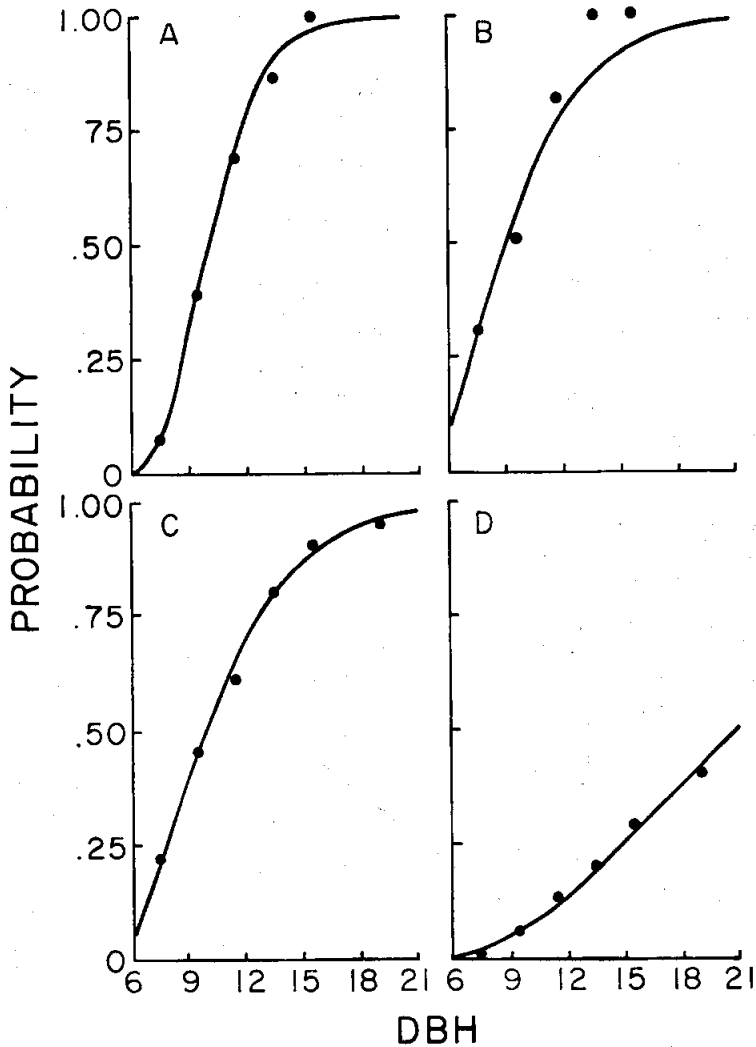


Fig. 1. Tree Mortality expectation by diameter (inches). A. Roaring Creek Plot — $\tau = 4.28$, B. Logger Creek Plot — $\tau = 2.06$, C. Yellowstone Plot — $\tau = 2.02$ and C. Bridger-Teton Plot — $\tau = 2.15$.

The model was fit to the data from all four plots and the over-epidemic estimates (1 and 2) above were computed. The results are shown graphically in Figs. 1a through 1d. The observed data are summarized by points representing $M_p(n)$ and the curvilinear graph summarizes the fit as given by $M_f(d)$.

DISCUSSION

The thresholds of aggregation for the four plots were approximately 2.0 with the exception of Hell Roaring Creek which was 4.28. In Hell Roaring Creek attack densities and host resinosis, as defined by REID *et al.* (1967), were generally higher indicating this stand was more resistant to attack. The threshold of aggregation concept, therefore, takes on some biological significance, and can be thought of as a measure of stand resistance.

From my definition of pioneer attack density it is reasonable to expect a relationship between it and total numbers of beetles flying. This generally seems to hold as pioneer attack density was considerably lower on the Bridger-Teton plot which was 2000 feet higher than the others (Table 2; AMMAN *et al.* (1973) showed emergence of beetles from infested trees is inversely related to elevation). In addition, data from KLEIN (personal communication) allowed estimation of total emerging beetle population

Table 2. Predicted pioneer beetle attack density by year of epidemic.

Plot	Year						
	1	2	3	4	5	6	7
Hell Roaring Cr.	.0283	.0222	.0556	.0031	—	—	—
Logger Cr.	.0053	.0189	.0377	—	—	—	—
Bridger-Teton	.0050	.0032	.0048	.0062	.0042	.0024	.0013
Yellowstone	.0047	.0075	.0141	.0227	.0107	.0060	.0026

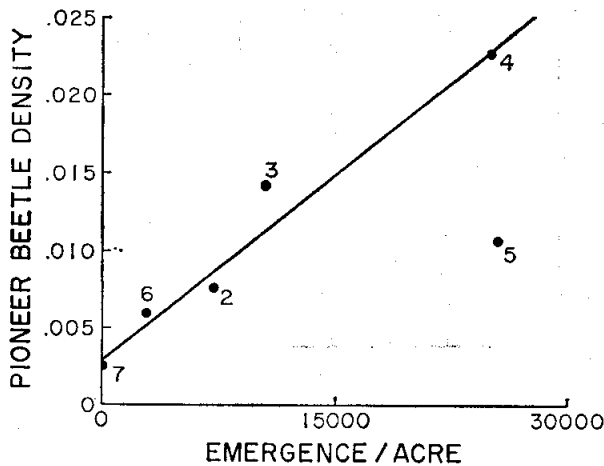


Fig. 2. Predicted beetle emergence/acre vs. predicted pioneer beetle attack density per square foot.

by year and there seems to be a good relationship to pioneer attack density, with the exception of year 5 (see Fig. 2). The fifth year marked the beginning of the population decline and large numbers of emerging beetles probably emigrated from the study plot because of the drastic reduction in the food supply (PARKER 1973).

The model, though based on rather simple assumptions, reasonably accounts for mortality distribution by diameter. The 'large diameter' effect discussed by COLE *et al.* (1976) is explained without requiring notions of 'selection of larger trees' beyond that required by a random model. In the early part of the epidemic the pioneer density is low and the comparative probabilities of large tree mortality vs. small tree mortality is large. As the epidemic progresses pioneer density rises and smaller trees are attacked because of this and the depletion of larger trees. Towards the end of the epidemic pioneer beetle density decreases because emergence from infested trees declines, and as a result the epidemic collapses.

Further modeling efforts will include the coupling of dispersion-aggregation, beetle production and stand growth models. To do this the following functions are required:

1. Determination of the threshold of aggregation for a stand and/or trees within a stand from mensurational data generated by a stand growth model. This may be achieved by interpretation of τ as a function of stand vigor measured by crown competition, age, etc.
2. Determination of pioneer beetle attack density from given emergence estimates, generated by the beetle production model, and other variables such as residual stand characteristics.

SUMMARY

In this paper a dispersal-attack theory for bark beetle attacking trees is developed from a set of simple assumptions, and the resulting theoretical model is fit to data from four epidemic studies. Implications of the theory are discussed in relation to the dynamics of lodgepole pine-mountain pine beetle interactions.

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Lodgepole 松の林におけるキクイムシの 分散と集合を記述する 1 モデル

D. G. BURNELL

Lodgepole 松を害するキクイムシ *Dendroctonus ponderosae* の分散と攻撃のパターンを記述する 1 つのモデルを単純な仮定のもとに導き、野外研究からのデータへのあてはめを試みた。またその意味を松とキクイムシの相互作用の動態の見地から考察した。