

# *Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae): Gallery Initiation on Lodgepole Pine During Aggregation<sup>1,2</sup>

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## ABSTRACT

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Gallery starts by the mountain pine beetle, *Dendroctonus ponderosae* Hopkins, were observed during aggregation on lodgepole pine, *Pinus contorta* Dougl. Two phases of gallery initiation were identified: acceleration and deceleration. The acceleration phase is characterized by an increasing rate of gallery initiation and was highly variable in the trees sampled. The deceleration phase is characterized by a decreasing rate of gallery initiation and was significantly and linearly correlated with cumulative gallery starts a day or more old ( $r = -0.24$ ). Transformation of the data to adjust for variation between trees increased the correlation between the deceleration rate and cumulative gallery starts a day or more old to  $-0.97$ . The resulting improvement in correlation suggests that variation in mountain pine beetle attack rates between trees can be attributed primarily to host factors. A linear model of gallery initiation during aggregation is presented.

The process of mountain pine beetle attack on lodgepole pine, *Pinus contorta* Dougl. var. *latifolia* Engl., can be divided into two phases, pre-aggregation and aggregation. The pre-aggregation phase is characterized by a period of random landing during which a few "pioneer" beetles initiate gallery starts (Hynum and Berryman 1980). Some of these pioneer beetles release pheromones to initiate the aggregation phase (Renwick and Vité 1970; Wood 1972; and Borden 1974). During this phase the rate of gallery initiation accelerates rapidly, then decelerates more gradually to the pre-aggregation rate. Deceleration of the gallery initiation rate is probably due to the production of anti-aggregants or "masking" pheromones (Rudinsky *et al.* 1974). Our objective was to describe the effect of beetle attack density and some host factors on the maximum rate of gallery initiation and the deceleration of this attack rate. We also present a simple mathematical model of the interaction.

## Methods

Eighty-seven lodgepole pines were observed in 1975 and 1976 in the Hellroaring Creek drainage across from the Squaw Creek Ranger Station, Gallatin County, Montana. Mensurational data were collected from each tree before beetle flight, including diameter at breast height (DBH), phloem thickness, and phloem terpenes ( $\alpha$ -pinene,  $\beta$ -pinene, and  $\beta$ -phellandrene). One meter sections of the bole were marked off on each tree with flagging at one m and 2 m. Within each section, gallery starts were counted and marked with a paper tag each morning for a period of two weeks during the major mountain pine beetle flight period: 15 July-1 August. Complete temporal records were obtained for 35 naturally infested trees. We first examined the relationship between the daily rate of gallery initiation,  $Y$ , and the cumulative num-

ber of previous attacks,  $X$ , using regression analysis. The variables are defined as:

$$X_n = \sum_{i=0}^{n-1} G_i,$$

$$Y_n = G_n,$$

where  $G_i$  is the number of gallery starts on day  $i$ , and  $n$  is the number of days from the first gallery start (e.g., if we had  $G_n$  attacks on day 4 then  $Y_4$  is set at this value and  $X_4$  is the sum of the gallery starts on days 0, 1, 2 and 3).

Data from each tree were first plotted to gain a visual appreciation of the variability between trees. Data for all trees were then pooled, plotted and analyzed by linear regression. Normalization involved dividing each  $X_n$  and  $Y_n$  value by their respective maxima estimated from the original regression (Fig. 1). Thus, the normalized variables were:

$$\hat{X}_n = X_n/X_{\max},$$

$$\hat{Y}_n = Y_n/Y_{\max},$$

and the normalized regression equation is:

$$\hat{Y}_n = \frac{Y_{\max}}{Y_{\max}} - \frac{Y_{\max}}{Y_{\max}} \cdot \hat{X}_n, \quad (1)$$

$$\text{or } \hat{Y}_n = 1 - \hat{X}_n$$

We then evaluated the effect of the measured host variables, DBH, phloem thickness, and phloem terpenes on the regression parameters  $Y_{\max}$  and  $X_{\max}$  using correlation analysis. Correlation coefficients for data from all trees combined prior to transformation and after transformation were computed using the Statistical Analysis System (SAS) (Barr *et al.* 1972).

## Results

The relationship between the daily current attack rate and previous attacks on individual trees showed 3 basic patterns (Fig. 2):

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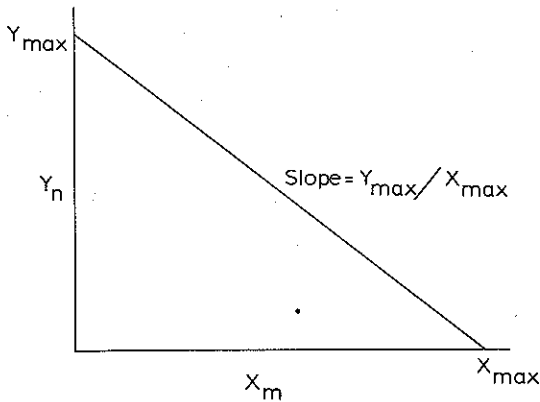


FIG. 1.—Hypothetical relationship between gallery starts per day ( $Y_n = G_n$  where  $n =$  the current day of the attack sequence) and cumulative gallery starts a day or more old ( $X_m = \sum_{m=0}^{n-1} G$  where  $m = 0$  to  $n-1$ ). Parameter  $Y_{max}$  represents the peak gallery initiation rate, parameter  $X_{max}$  is the final attack density, and  $-Y_{max}/X_{max}$  in the attack deceleration.

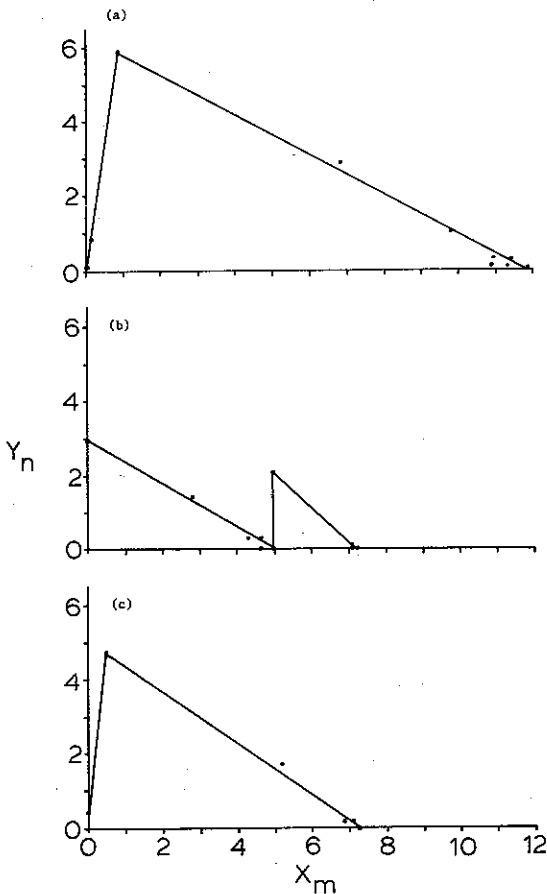


FIG. 2.—Relationship between gallery starts per day ( $Y_n$ ) and cumulative gallery starts a day or more old ( $X_m$ ) for (a) "slow starter", (b) resurgent and (c) typical trees. The slow starter and typical tree points near the origin represent the acceleration phase of gallery initiation.

1. Three trees showed what we call a "slow-start". The rate of attack accelerated for 2 to 3 days before declining linearly with cumulative previous attacks (Fig. 2a).
2. Four trees showed a second acceleration of attacks, or resurgence, after an initial period of deceleration (Fig. 2b).
3. On 28 trees the maximum rate of gallery initiation occurred on the day after the first (pioneer) attacks were observed. Thereafter, the rate of attack declined linearly with the cumulative number of previous attacks (Fig. 2c).

Because all the trees showed a typical pattern of attack deceleration as more and more attacks accumulated and only a few demonstrated the slow-start or resurgence phenomena, we decided to eliminate the latter from the analysis and concentrate attention on the dominant pattern of deceleration.

Analysis of the untransformed data produced the regression equation

$$Y = 1.85 - 1.37 X, r^2 = 0.06, \quad (2)$$

$$p = 0.02, N = 191,$$

indicating that only 6% of the variation could be accounted for by the postulated relationship between cumulative attack density and the rate of gallery starts. The variation in the data is illustrated graphically in Fig. 3. Values of  $Y_{max}$ , the maximum rate of attack, ranged from 1 - 10.3/900  $cm^2/day$  ( $900 cm^2 \approx 1 ft^2$ ) and  $X_{max}$ , the final attack density, ranged from 1.4 - 11.4 attacks/900  $cm^2$ . A significant correlation was also found between the maximum rate of attack,  $Y_{max}$ , and the final attack density,  $X_{max}$  ( $r^2 = 0.72, n = 32, p = 0.001$ ).

Analysis of the normalized data produced the regression equation.

$$\hat{Y} = 1 - \hat{X}, r^2 = 0.94, p = 0.001, N = 191. \quad (3)$$

indicating that 94% of the variation could be explained when between tree variation was suppressed through nor-

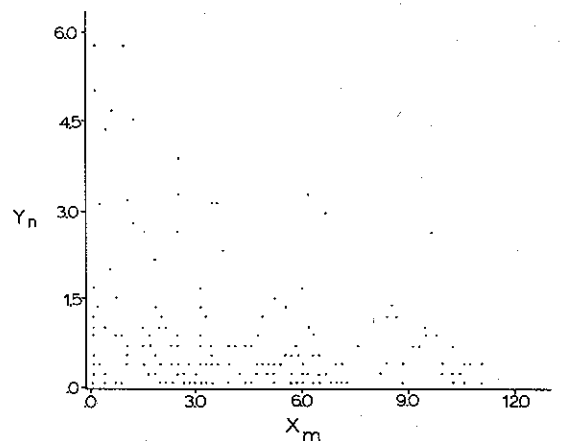


FIG. 3.—Scatter diagram showing relationship between gallery starts per day ( $Y_n$ ) and cumulative gallery starts a day or more old ( $X_m$ ) for all 35 trees.

malization. The variation in normalized data is illustrated graphically in Fig. 4. We concluded that, of the total variation, 6% can be explained by the postulated relationship between the gallery initiation rate and attack density, 88% (94-6) can be explained by the effect of individual variation between host trees, and 6% remains unexplained.

Of the host variables measured, only DBH showed a significant relationship to the regression parameters (Table 1). However the small variation explained by DBH suggests that other host variables must also be involved in the determination of these parameters. Interestingly, the linear equations of Table 1 show that the maximum rates of attack and the maximum attack densities are negative for trees less than about 4 in. DBH. The negative attack parameters for 4 in. DBH or smaller suggests that smaller trees cannot be attacked, a result which supports previous work (Cole and Amman 1969).

### Discussion

This study suggests that the aggregation of bark beetles on coniferous hosts involves two phases. First a period when the rate of gallery initiation accelerates with time. This phase appears to be linearly related to the number of previous gallery starts (Fig. 2 a,c). The phase of decelerating gallery initiation rate appears to be a linear negative function of cumulative previous gallery starts.

The acceleration phase always occurs at very low attack densities, fewer than 0.1 attacks per 900 cm<sup>2</sup>. On the first day of aggregation cycle, there are no day old gallery starts. Attacking beetles have only the chemical messages of the host and of beetles that have just begun galleries. There appears to be a time lag of between 0 and 24 hrs before attacking beetles are certain of the host condition and/or before beetles are physiologically activated for pheromone production (Pitman and Vite 1969). The variability in the number of gallery starts on the first day

may reflect this time-delay and whether pheromone release occurred during or after the period of maximum daily beetle flight activity.

Unfortunately, the sampling design was not particularly appropriate for measuring the acceleration phase because observations were only made once each day. In most trees this phase reached its maximum after only one day from the time initial attacks were observed. In addition, initial pioneer attacks may have occurred outside the sampling universe (one m of the tree's bole) which would cause us to miss much of the acceleration phase.

Where the acceleration phase was prolonged for more than 1 day (8% of trees with complete records), the rate of gallery initiation increased rapidly to a maximum with cumulative gallery starts and then declined characteristically during the deceleration phase (Fig. 2a).

In all trees the rate of gallery initiation declined linearly with cumulative gallery starts (Fig. 2). Even in those trees exhibiting the "resurgence" phenomena, the rate of attack was linearly related to attack density during the deceleration phase (Fig. 2b). The deceleration phase can be mathematically represented by:

$$G_n = G_{\max} - \left( G_{\max} \frac{\sum_{i=0}^{n-1} G_i}{\sum_{n=0}^N G_n} \right) \quad (4)$$

$$\text{or } G_n = G_{\max} \left( 1 - \frac{\sum_{i=0}^{n-1} G_i}{\sum_{n=0}^N G_n} \right)$$

where  $G_n$  is the daily rate of gallery initiation,  $G_{\max}$  is the maximum rate;  $N$  is the total number of days in the attack sequence and, therefore,  $\sum_{n=0}^N G_n$  is the final attack density on the tree. This relationship is moderated by two parameters, the maximum attack rate,  $G_{\max}$ , and the deceleration rate,  $d = 1/\sum_{n=0}^N G_n$ . Hence, we can rewrite (4) as:

$$G_n = G_{\max} \left( 1 - d \sum_{i=0}^{n-1} G_i \right) \quad (5)$$

Our results indicate that these two parameters vary due to differences in characteristics of the trees being attacked.

The maximum rate of gallery initiation,  $G_{\max}$ , is probably affected by the quantity and quality of pheromones being released by the attacking beetles, the quantity and quality of host produced synergists, and the density of beetles flying in the vicinity of the attacked tree which in turn is influenced by nearby trees coincidentally under attack. Differences in pheromone quantity and quality could be caused by host factors (terpenes are known precursors for bark beetle pheromones (Hughes 1973), or individual differences between beetles or their associated microflora (Brand *et al.* 1975, 1976, 1977). However, because pheromone release from a given tree comes from a relatively large population of beetles drawn from a very large and genetically mixed flying population, the latter hypothesis appears less tenable. It seems more likely that characteristics of the host determine the quantity and quality of the attractive source (pheromones plus syner-

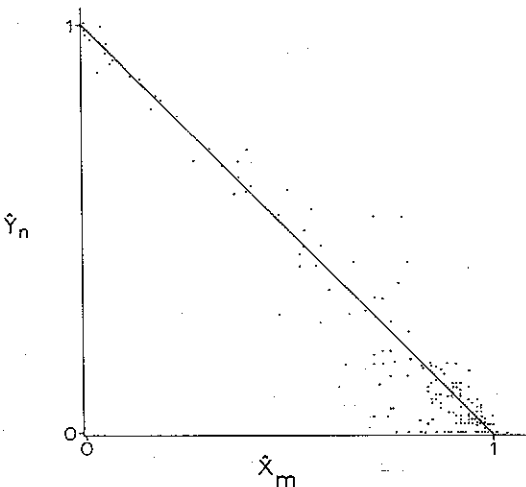


FIG. 4.—Scatter diagram showing relationship between gallery starts per day ( $Y_n$ ) and cumulative gallery starts a day or more old ( $X_m$ ) following data transformation for all 35 trees. Each  $Y$  value was divided by parameter  $Y_{\max}$  and each  $X$  value was divided by  $X_{\max}$  for a given tree.

Table 1.—Regression statistics for the relationship between the maximum rate of attack,  $Y_{max}$ , the maximum attack density,  $X_{max}$ , and host variables.

Dependent Variable	Independent Variable	a	b	r	P
$Y_{max}$	DBH	-3.84	0.891	0.51	0.0030
	Phloem thickness	3.00	0.359	0.23	0.2000
	$\alpha$ -Pinene	4.00	0.061	0.22	0.2300
	$\beta$ -Pinene	6.01	-0.058	-0.24	0.1780
	$\beta$ -Phellandrene	2.48	0.052	0.31	0.0830
$X_{max}$	DBH	-2.14	0.929	0.58	0.0004
	$\sqrt{DBH}$	-12.63	6.281	0.59	0.0001
	Phloem thickness	4.90	0.416	0.22	0.2340
	$\alpha$ -Pinene	5.64	0.097	0.28	0.1190
	$\beta$ -Pinene	8.73	-0.087	-0.29	0.1040
	$\beta$ -Phellandrene	4.87	0.049	0.23	0.2030

gists) either directly or through their effects on the beetle. However, none of the host variables measured in the present study were significantly related to  $G_{max}$  (Table 1).

Deceleration in the rate of gallery initiation begins at very low attack densities, usually less than 10% of the attacks needed to saturate a host at one to 2 m, suggesting that anti-aggregation behavior and masking pheromones (Rudinsky *et al.* 1974) are being released during the early stages of attack on many trees. Large differences in deceleration between trees again suggest that host factors are involved. Because the deceleration parameter, given a maximum rate of attack, governs the final density of attacks on the tree, and because the final density has been shown to be related to tree vigor or resistance to attack (Berryman 1976), we suspect that deceleration is largely determined by the resistant characteristics of the host (e.g., primary and secondary resin flow). This seems a reasonable working hypothesis because, as the resin flow and hypersensitive reactions (Berryman 1972) cease, fewer beetles are required to secure the tree for brood production. In addition, the only host variable which was significantly correlated with the deceleration parameter was DBH. This correlation between DBH and the deceleration parameter supports our interpretation because the larger trees should be more vigorous.

In the resurgence phenomena (Fig. 2b) we see evidence for delayed secondary hypersensitive resistant reactions. Resurgence was observed on numerous trees but only significantly (where the contribution to variance exceeded 5%) on 4 out of 34. In these cases, the gallery starts per day decreased characteristically with attack density but after a few days into the deceleration phase, a new burst of gallery initiation activity raised the attack rate up to a new deceleration line. It seems that resurgence of gallery initiation may be caused by a delayed, vigorous, secondary hypersensitive reaction to which beetles respond by calling for more help.

Because the parameters of the deceleration equation seem to be host specific, a study of their relationship to host factors, such as phloem chemicals, resin quantity or quality, and the speed of responses could lead to a mathematical definition of each parameter as a function of host factors. The most promising candidates appear to be secondary metabolic products (Price 1975) as indicated by the studies of Hughes (1973) and Hughes and Renwick (1977) with *D. ponderosae* and *D. brevicomis*.

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