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OPTIMUM EGG GALLERY DENSITIES FOR THE MOUNTAIN PINE BEETLE
IN RELATION TO LODGEPOLE PINE PHLOEM THICKNESS¹

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ABSTRACT

Laboratory studies were conducted to determine optimum densities of egg galleries constructed by the mountain pine beetle (*Dendroctonus ponderosae* Hopkins) in lodgepole pine (*Pinus contorta* var. *latifolia* Engelmann) phloem of different thickness. Beetle production per unit area of lodgepole pine bark occurred at egg gallery densities over 2.4 m per 30.4 cm² with greater production obtained from thick phloem. Beetle production began to flatten at about 2.1 m per 30.4 cm² in thin phloem and at 2.4 m in thick phloem. Production curves remained asymptotic to 3 m of egg gallery per 30.4 cm² the upper limit observed in this study. Beetle production per unit of egg gallery length was highest at the lowest gallery density in all phloem thicknesses. As expected, beetle production was greatest in thick phloem.

The largest brood adults emerged from thick phloem at all egg gallery densities. But, for thick and thin phloem alike, size declined after egg gallery densities exceeded about 1.5 m per 30.4 cm². Beetles were significantly smaller in thin phloem, even at the lowest gallery densities. Male survival was proportionately lower in thin phloem than in thick phloem. The smaller size of beetles and lower survival of males suggest a qualitative difference between thin and thick phloem that may be important in dynamics of mountain pine beetle populations.

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KEYWORDS: *Dendroctonus ponderosae*, *Pinus contorta*, phloem, bark beetle, beetle production, gallery density

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Several authors have conducted studies of mountain pine beetle (*Dendroctonus ponderosae* Hopkins) brood production and survival in lodgepole pine (*Pinus contorta* var. *latifolia* Engelmann) in relation to egg gallery or attack densities. Cole (1962) found that production per inch of gallery was greatly reduced at high attack densities in the laboratory. Reid (1963) reported that a similar relation existed in the field.

Both studies were made prior to the discovery of the importance of phloem thickness to brood production of the mountain pine beetle (Amman 1972a). Consequently, the purpose of this study was to determine optimum egg gallery densities for beetle production and beetle size in relation to phloem thickness. Data presented here should be useful in developing future models of mountain pine beetle production that incorporate food quantity coefficients such as those proposed by Berryman (1974).

MATERIAL AND METHODS

Four uninfested and four infested lodgepole pine trees were felled on the Wasatch National Forest south of Evanston, Wyoming, in November 1973. Billets 50 cm long were cut from each tree and the ends waxed to slow moisture loss. The billets then were taken to our laboratory in Ogden, Utah. Uninfested billets were stored at 2°C. Infested billets were kept at room temperatures of 19°-22°C so immature beetles could complete development and emerge.

In January 1974, 20 areas (15.2 cm wide by 30.4 cm high) were delineated on uninfested billets in each of four phloem thickness classes.

<i>Phloem class</i>	<i>Mean</i>	<i>SD</i>
	-----mm-----	
1	1.8	0.28
2	2.7	.23
3	3.8	.28
4	4.8	.23

A 2.5-cm strip of bark was removed around the perimeter of each of the 80 areas. Exposed sapwood and bark edges were waxed to slow moisture loss.

Vertical holes (5 mm in diameter and 2.5 cm deep) were drilled in the bark along the lower 15.2 cm edge of each area. One pair of beetles was introduced into each hole. Sex of beetles was determined by characteristics of the seventh abdominal tergum (Lyon 1958). The number of holes per area varied from one to five, depending upon desired attack density. Each attack density was replicated four times in each phloem thickness.

The newly infested billets were kept upright at room temperatures of 22°-26°C and humidity of 20-40 percent throughout the experiment. Plastic screen cages (32 by 32 mesh) were placed over each infested area and stapled to the sapwood. Plastic test tubes served to catch emerging beetles. Beetles were collected, counted, and sexed daily. Length was measured with an ocular micrometer in a dissecting microscope. After emergence was completed, bark was peeled from each of the 80 areas. Remaining beetles, meters of egg gallery, and successful attacks were counted.

Beetle production per unit area of bark.--Beetle production for similar gallery densities did not differ significantly ($P > 0.10$) between phloem thickness classes 1 and 2, nor between phloem thickness classes 3 and 4. Production between combined phloem classes 1 and 2 and that from combined 3 and 4 differed significantly, ($P < 0.005$). Consequently, the final model involved two regressions (fig. 1). Although the overall model is significant, the coefficient of determination is relatively low ($R^2 = 0.38$).

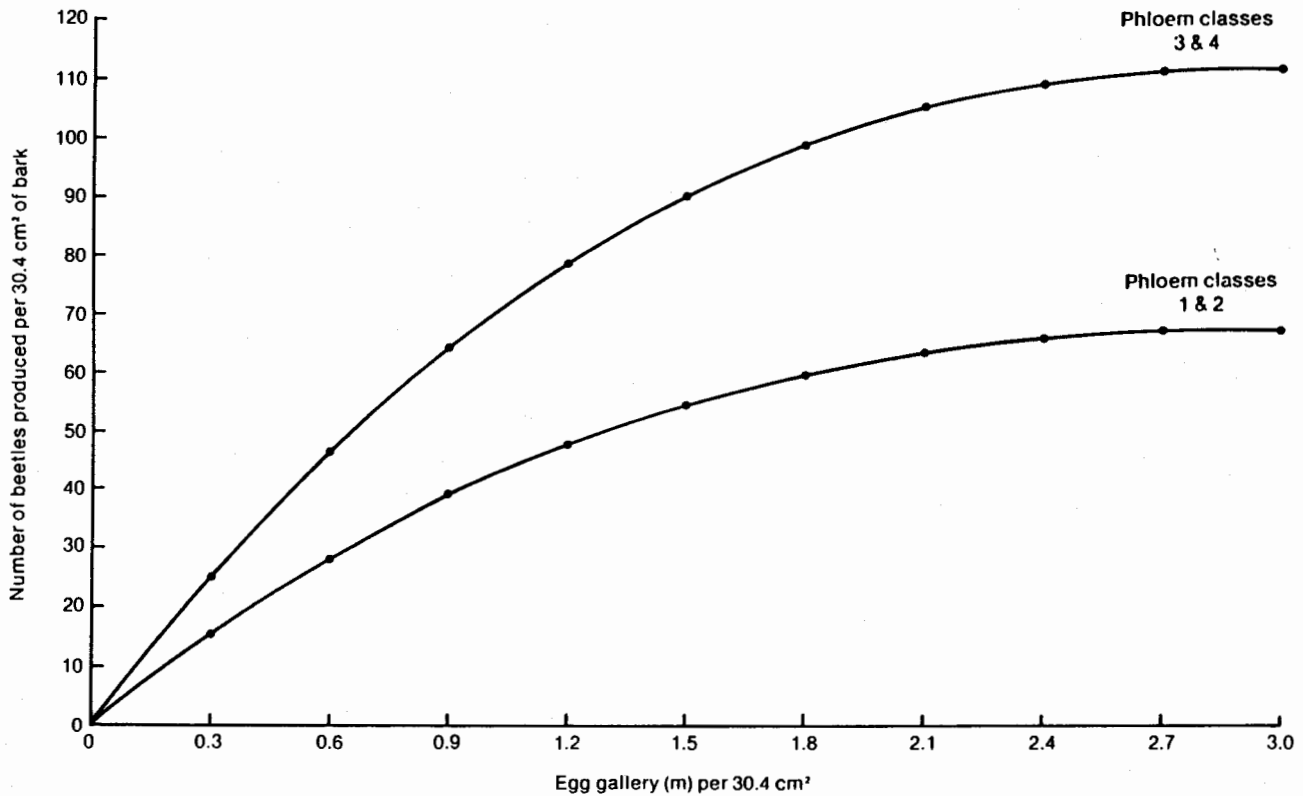


Figure 1.--Mountain pine beetle production per unit area of bark in relation to egg gallery density for two phloem thickness categories. Phloem classes 1 and 2 and phloem classes 3 and 4 were combined because they did not differ significantly.

$$\text{Phloem classes 1 and 2: } \hat{Y} = 67.262 - 4.816(3-X)^{2.4}$$

$$S_{y \cdot x} = 25.3$$

$$\text{Phloem classes 3 and 4: } \hat{Y} = 111.247 - 7.965(3-X)^{2.4}$$

$$S_{y \cdot x} = 34.5$$

$$\text{Limits: } 0 \leq x \leq 3$$

Production of beetles per unit area of bark followed previously reported expectations (Amman 1972a); the thickest phloem yielded the most beetles at all egg gallery densities. Beetle larvae have more food and space in thick phloem than in thin phloem. Consequently, neither starvation nor encounters between larvae that result in entomocide (one larva killing another) occur as frequently in thick phloem as in thin.

A decline in beetle production with increased gallery density was expected. However, the relation began to flatten at about 2.4 m of egg gallery per 30 cm² of bark. Gallery density was optimal between 2.3 and 2.7 m in Reid's (1963) field study. That the numbers of beetles per unit area of bark failed to decline at high egg gallery densities in the laboratory suggests (1) that the maximum number of beetles that can develop and emerge is reached at these levels and (2) that this number probably would remain constant at higher egg gallery densities than occurred in our study.

The shapes of curves for beetle production in relation to egg gallery density in this study differ from those of figure 2 in Amman (1972a). Amman (1972a) did not

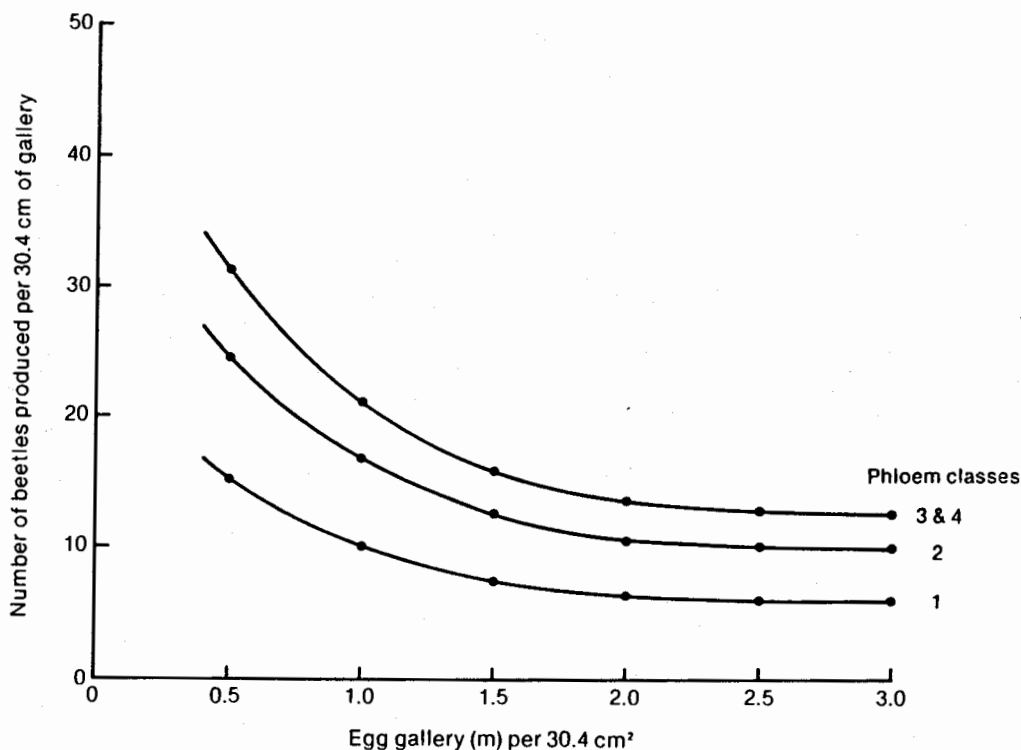


Figure 2.--Mountain pine beetle production per unit length of egg gallery for three phloem thickness categories:

$$\text{Phloem class 1: } \hat{Y} = 6.157 + 0.3597(3-X)^{3.5}$$

$$S_{y \cdot x} = 8.4$$

$$\text{Phloem class 2: } \hat{Y} = 10.0492 + 0.5870(3-X)^{3.5}$$

$$S_{y \cdot x} = 6.6$$

$$\text{Phloem classes 3 and 4: } \hat{Y} = 12.755 + 0.745(3-X)^{3.5}$$

$$S_{y \cdot x} = 8.6$$

$$\text{Limits: } 0.4 \leq x \leq 3$$

demonstrate an asymptotic relationship. Phloem in the 1972 study was thicker overall, ranging between 4.1 and 6.6 mm, and apparently was underutilized even at the highest gallery density (4.6 m per 30.4 cm²). This last is evident from the curve that continues to rise. An asymptotic relation would be expected at higher egg gallery densities.

The apparent asymptotic relation in the present study indicates that the upper limit to beetle numbers is governed by the absolute amount of food. Beetle production per cm³ of phloem was similar for all phloem thicknesses; the regression was not significantly different from zero ($P > 0.10$).

Although a constant beetle production occurred above about 2.4 m of egg gallery per 30.4 cm² in the laboratory, a decline in production occurred in the field when gallery densities exceeded about 2 m in small diameter trees, which usually have thin phloem, and about 3 m per 30.4 cm² in large diameter trees, which usually have thick phloem (Cole and others, 1976). Declines in the field indicate that beetle production at high gallery densities is reduced by some factor (s) other than competition. Drying is the most plausible factor.

Cole (1974, 1975) evaluated several mortality factors that were affecting a beetle population in the field. He concluded that no individual mortality factor that he studied--parasites, predators, temperature, crowding (competition), and all unknown factors--offered regulator influence on mountain pine beetle populations. However, he (Cole 1975) observed that cold winter temperatures accompanied by drying of the phloem significantly reduced beetle survival. He reported that beetles survived better in large trees, even when phloem in these trees was thin. This observation is another indication that drying may account for some of the difference in brood production between small- and large-diameter trees having similar phloem thickness.

Cole and others (1976) discussed the decline in field populations as gallery densities increased over time. They stressed that drying of phloem was an important mortality factor of developing brood at high egg gallery densities. The large amount of egg gallery that was constructed when attack densities were high promoted drying of the phloem. Drying also was intensified by large number of feeding larvae that depleted the available phloem. Consequently, drying becomes more important to beetle survival over time as attack and gallery densities increase.

Beetle production per unit length of egg gallery.--Beetle production per unit length of egg gallery was significantly different ($P < 0.05$) among phloem thickness classes (fig. 2). Phloem classes 3 and 4 were combined because they did not differ significantly ($P > 0.10$). The coefficient of determination for this model was relatively low ($R^2 = 0.31$); however, the model is significant ($P < 0.005$).

Survival per unit of egg gallery was highest at the lowest gallery density in all phloem thicknesses (fig. 2). This is not surprising since at this density physical encounters between developing larvae are low. With increased density, larvae from adjacent egg galleries are more likely to come in contact and losses to entomocide and to cannibalism can be expected to increase.

Our data suggest that, on the average, the minimum attack or egg gallery density in the field that will kill a tree or a large area of bark in a strip attack is also the density that will yield the greatest beetle survival from egg to emerged adult. An attack density below the minimum needed to kill the tree or a strip of bark results in galleries becoming impregnated with resin (resinosus) as observed in the field by Reid and others (1967) and failure of resin-enveloped eggs to hatch as demonstrated experimentally by Reid and Gates (1970).

Although the greatest production per unit length of egg gallery occurred at the lowest egg gallery density (fig. 2), the optimum density for maximum beetle production per unit area of bark occurred at high egg gallery densities (fig. 1). An aggressive bark beetle, such as the mountain pine beetle, infests scattered and temporary habitats (Atkins 1966), particularly during endemic periods when the best trees for brood production may be in short supply. Such trees usually are of large diameter and thick phloem. Mountain pine beetles have probably evolved behavior to make the most of a limited food supply furnished by any tree that is infested. Consequently, egg gallery density at which maximum beetle production per unit length of gallery occurs probably would never coincide with egg gallery densities at which maximum beetle production occurs in any phloem thickness. In addition, attacks and egg galleries must be sufficient to prevent complete loss of brood by resinosis.

Beetle size.--Length of female beetles did not differ significantly between phloem thickness classes 1 and 2 nor between phloem classes 3 and 4 ($P > 0.10$). However, the lengths of females from combined groups 1 and 2 differed significantly from combined 3 and 4 ($P < 0.005$) (fig. 3). The coefficient of determination was relatively low ($R^2 = 0.30$); however, the overall model was significant ($P < 0.005$).

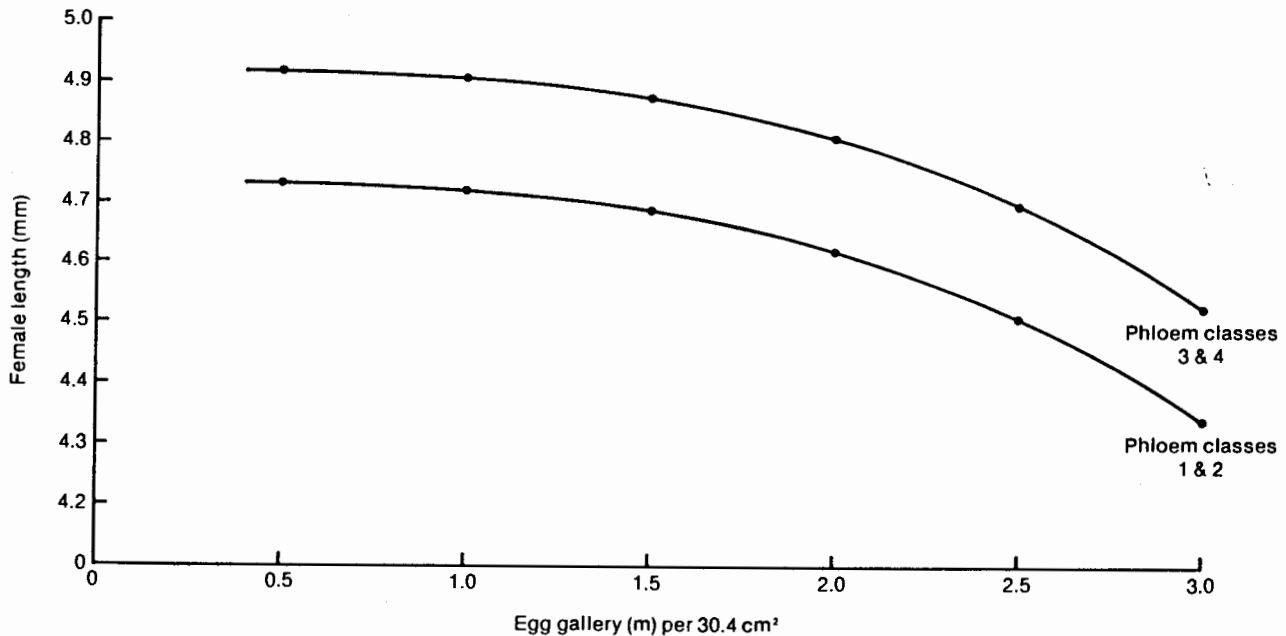


Figure 3.--Length of mountain pine beetle females in relation to egg gallery density for two phloem thickness categories. Phloem classes 1 and 2 and phloem classes 3 and 4 were combined because they did not differ significantly.

$$\text{Phloem classes 1 and 2: } \hat{Y} = 4.769 - 0.0146X^3$$

$$S_{y \cdot x} = 0.21$$

$$\text{Phloem classes 3 and 4: } \hat{Y} = 5.006 - 0.0146X^3$$

$$S_{y \cdot x} = 0.19$$

Limits: $0.4 \leq x \leq 3$

Optimum gallery density at which maximum beetle size occurred ranged between 0.4 and 1.2 m of gallery per 30.4 cm² (fig. 3). Emerging brood adults were smaller when gallery density exceeded about 1.2 m per 30.4 cm². The small adult size at increased gallery densities probably is related to each larva receiving less food. Much of the food was eaten during early larval development; consequently, less food was available than was needed for the surviving larvae to reach maximum size.

The beetles from combined phloem classes 1 and 2 are smaller than those from combined phloem classes 3 and 4, even at the lowest gallery densities where little crowding would be expected. This difference suggests a qualitative difference between thin and thick phloem as food for developing larvae.

Safranyik and Jahren (1970) found beetles in lodgepole pine of small diameter are smaller than those in trees of large diameter. The smaller beetles, that are produced when most large-diameter trees with thick phloem are killed and only small trees (usually with thin phloem) remain, could be important in the dynamics of beetle populations. Small beetles from field collections have been shown to lay fewer eggs than large beetles (Amman 1972b; McGhehey 1971; Reid 1962). In addition, Cole (1973) observed that crowding during the larval stage affected the oviposition rate for beetles of similar size; adults reared from the most crowded larvae produced fewest eggs.

Small size may also affect flight capacity. Atkins (1967) found that small Douglas-fir beetles, *Dendroctonus pseudotsugae* Hopkins, contained proportionately less fat than large beetles shortly after the adult stage was reached. He found that any size beetle with low-fat content failed to fly when placed on a flight mill and, therefore, probably would have low ability to disperse in the field situation. Mountain pine beetles of small size or having low fat content could be expected to react similarly. The capacity to disperse is low when the population is low in number during early stages of stand development or after a large beetle infestation has resulted in death of most large trees. Low dispersal capacity could serve to keep the population together so that a tree could be infested and killed. However, it might be a hindrance in finding the best tree for beetle production. In addition, the possible detrimental effect of inbreeding could be expected to increase where the population remains together.

Sex ratio.--A higher proportion of females emerged from the thinnest phloem (71.9 percent) than the other phloem levels (phloem class 2 = 61.1 percent; phloem class 3 = 62.2 percent; phloem class 4 = 65.8 percent). Different proportions of females in populations emerging from trees of different sizes were noted in field populations (Cole and others, 1976); on the average, small-diameter trees (thin phloem) yielded higher proportions of females than large-diameter trees (thick phloem).

Differences in sex ratios have been attributed to crowding (Cole 1973) and to length of cold storage (Safranyik 1976; Watson 1971) in laboratory studies and to drying in field studies (Amman and Rasmussen 1974; Cole and others 1976). Differences noted in this study could not be attributed to drying because most of the material used remained moist throughout the study. Nor could the differences be entirely related to crowding because differential survival of the sexes was also apparent at low gallery densities. The data suggest that at least some of the difference is related to phloem quality, especially between phloem class 1 and the other three levels. Probably, no single factor is responsible for differential survival of the sexes, but rather any factor or combination of factors that stresses the population will result in greater survival of females than males. The greater survival of females under adverse conditions provides a larger proportion of the population to search for suitable trees to infest. The reduced survival of males may not be detrimental to the population because each surviving male can mate with several females. However, the low number of males found on some trees under attack apparently resulted in low incidence of fertilization that led to failure of attacking beetles to kill the tree and subsequent loss of brood to resinosis (Amman 1975).

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