Attacks of Mountain Pine Beetle as Related to Tree Vigor of Ponderosa Pine

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ABSTRACT. The relationship between tree vigor, measured as stem growth per unit of leaf area, and susceptibility to mountain pine beetle attacks was examined in a stocking-level experiment of ponderosa pine (*Pinus ponderosa* Laws.) in central Oregon. Vigor decreased as both tree density (basal area) and leaf area index increased. Low vigor trees were more often attacked by beetles than high vigor trees. Attacks increased below a vigor threshold of about 100 g of wood produced per square meter of leaf area per year, corresponding in this study to a basal area of 21 m^2 ha^{-1} or a leaf area index of 2.9 m^2 m^{-2}. For management of ponderosa pine, maintaining vigor through thinning will reduce the risk of mountain pine beetle attacks. FOREST SCI. 29:395–402.

ADDITIONAL KEY WORDS. *Dendroctonus ponderosae*, *Pinus ponderosa*, tree mortality, thinning, stocking.

MOUNTAIN PINE BEETLE (*Dendroctonus ponderosae* Hopk.) is a tree-killing bark beetle that attacks several pine species in western North America (McCambridge and others 1979). Extensive outbreaks are now occurring in 80- to 120-year-old stands of lodgepole pine (*Pinus contorta* Douglas var. *latifolia* Engelmanni) (Safranyik and others 1975, Cole and Amman 1980). Although widespread outbreaks have also occurred in old-growth stands of ponderosa pine (*P. ponderosa* Laws.) (Blackman 1931, Parker and Stevens 1979), most recent outbreaks have been recorded in pole-sized second-growth stands (Sartwell and Stevens 1975).

The importance of host condition for successful attacks by mountain pine beetle has been repeatedly mentioned (e.g., Safranyik and others 1975, Berryman 1976, Cole and Amman 1980), although the mechanisms involved were not understood. Several studies have suggested that low vigor trees, although imprecisely defined, are the most susceptible (Sartwell and Stevens 1975, Berryman 1976, Schenk and others 1980). Raffa and Berryman (1981) suggested that the quantity of mono-terpenes produced in response to fungal inoculation was actually an index of vigor, and Mahoney (1978) illustrated some correlations between attack and periodic

stand growth. Theoretical discussions together with an abundance of peripheral data still have not provided persuasive evidence of variation in host susceptibility.

By exploiting the relationship between amount of wood produced per unit of leaf area in coniferous trees, however, Waring and others (1980) introduced a physiological index of growth efficiency, or vigor rating, easily and accurately applied to individual trees. Using this rating, Waring and Pitman (1980) found a good linear correlation between vigor of lodgepole pine and number of mountain pine beetles required to kill a tree. They concluded from staining the sapwood for starch that the trees attacked and killed had extremely low carbohydrate reserves and therefore probably lacked the ability to produce sufficient defensive chemical compounds such as oleoresins (R. H. Waring and G. B. Pitman, unpublished data).

In the present study, we examined the relationship between vigor and level of bark beetle attack, as developed by Waring and Pitman (1980), and assessed its applicability to ponderosa pine by examining the distribution of mountain pine beetle attacks over a range of tree vigors in a ponderosa pine stocking-level experiment in central Oregon. The experiment was part of a broad study on levels of growing stock in even-aged ponderosa pine (Myers 1967), the results of which will appear elsewhere (J. W. Barrett, manuscript in preparation).

METHODS

Study area.—The study site is located on Lookout Mountain in the U.S. Forest Service Pringle Falls Experimental Forest (43°N, 121°W, 1,500 m above sea level), about 60 km SW of Bend, Oregon. The *Pinus ponderosa/Ceanothus velutinus* plant community (Franklin and Dyrness 1973) is characteristic for the area. The experimental stand, almost pure ponderosa pine with an occasional grand fir [*Abies grandis* (Dougl.) Lindl.] in the understory, was 65 years old and averaged 2,800 trees ha^{-1}, basal area of 55 m^2 ha^{-1}, and tree diameter of 15.8 cm before treatment.

In the late summer and fall of 1965, six levels of growing stock, ranging from 7–34 m^2 ha^{-1}, were established (Table 1). These levels represented the basal area above which each stand was not allowed to grow. Although stocking level initially may have been below that prescribed, as trees grew and exceeded a minimum diameter (25.4 cm dbh in this experiment), the stand was thinned back to the assigned stocking level (Myers 1971, Barrett 1979). In this experiment, each of the six treatments was replicated 3 times and each replicate randomly assigned to one of 18 0.2-ha plots. Each plot was surrounded by a buffer area 10 m wide that had been thinned to the same stocking level as the inner plot, where trees were tagged and numbered. Tree growth was measured at 5-year intervals (1970, 1975, and 1980) and any mortality recorded. In 1981 we added nine 0.02-ha unthinned control plots, each located 30 m from a treated plot.

Measurements.—We counted the number of trees attacked when measuring tree growth in 1970, 1975, and 1980 by collecting data on cumulative beetle-caused mortality on trees for each of the previous 5-year periods. Then, in June–July 1981, before the beetle's flight period, all trees were searched for evidence of beetles, and those trees with more than five visible pitch tubes were considered attacked.

For rating vigor (i.e., amount of wood produced, in grams, per square meter of leaf area), six trees were randomly selected from each plot and three equally spaced increment cores taken from each at breast height during June–July 1981. Sapwood thickness (radius) and the previous year's growth ring were averaged for each tree from microscope measurements, and vigor was calculated (Waring and others 1980). Local volume equations (J. W. Barrett, unpublished data) based on tree diameter were used to determine the volume of stem wood produced. A constant

Growing-stock level (m^2 ha^{-1})	Stocking (trees ha^{-1})	Dbh[a] (cm)	Basal area (m^2 ha^{-1})	Leaf area index (m^2 leaf m^{-2} ground)
Control (54)[b]	1, 283 (177)	23.0 (1.5)	53.5 (4.0)	7.4 (0.55)
34	521 (93)	29.7 (2.1)	36.0 (1.2)	5.0 (0.17)
28	507 (78)	28.2 (2.0)	31.6 (0.7)	4.4 (0.10)
23	361 (29)	30.4 (1.2)	26.2 (0.2)	3.6 (0.03)
18	216 (9)	35.6 (0.7)	21.5 (0.03)	3.0 (0.004)
14	140 (17)	38.0 (1.8)	15.9 (0.6)	2.2 (0.08)
7	54 (5)	44.2 (1.0)	8.3 (0.1)	1.2 (0.01)

[a] Quadratic mean diameter.
[b] Data collected in 1981.

wood density of 400 kg m^{-3} was assumed for conversion to dry weight (Brown and others 1949). These equations agreed within 10 percent with the more general biomass equation of Gholz and others (1979).

Leaf area was estimated from sapwood area. One cm^2 of sapwood is equal to 0.25 m^2 of projected leaf area (Waring and others 1982). However, because this relationship was developed from measurements taken at the base of the live crown, we had to correct for our measurements, taken at breast height. To do so, we measured sapwood area and basal area both at breast height and at the base of the live crown from sample trees at three different stocking levels (7, 23, and 34 m^2 ha^{-1}) and found sapwood area at the base of the live crown to be 58 percent (SE = 1.8, n = 21) of that at breast height. No significant differences were found between the three levels of growing stock, so the same conversion factor was used for all treatments. Stand leaf area was estimated by converting basal area to sapwood area at breast height, then reducing that by 58 percent and multiplying by 0.25. Leaf area index, a ratio of square meter of foliage to square meter of ground surface, was obtained by dividing by 10,000, the number of square meters per hectare.

RESULTS

Average tree vigor decreased with denser tree spacing and larger leaf area index (Fig. 1, $P < 0.01$). In general, the number of trees attacked per plot decreased as average tree vigor increased. However, beetle attacks were not linearly related to vigor; instead, a threshold response was noted (Fig. 2). The average percentage of attacks was significantly higher ($P < 0.05$) on plots with a vigor less than 100 g m^{-2} yr^{-1}, as determined with an unpaired t-test. Current tree mortality was low on all plots, probably reflecting low beetle-population levels. The only mortality on plots with stocking control was at 34 m^2 ha^{-1}, which averaged 6.6 trees killed in 1981 (from 1980 attacks); of total trees attacked on thinned plots, as evidenced from visible pitch tubes, only 6 percent (n = 72) were killed.

However, variation in the percentage of trees attacked was considerable on plots with similar vigors, especially at low and intermediate values (Fig. 2). We found trees attacked in all of the nine control plots ranged from 6–20 percent of the those present. This variation could not be correlated with vigor, basal area, leaf area, or number of trees. Vigor among trees within all plots also varied considerably; the coefficient of variation averaged 26 percent in thinned plots, with no specific correlation to a given treatment, and 60 percent in the controls. On the
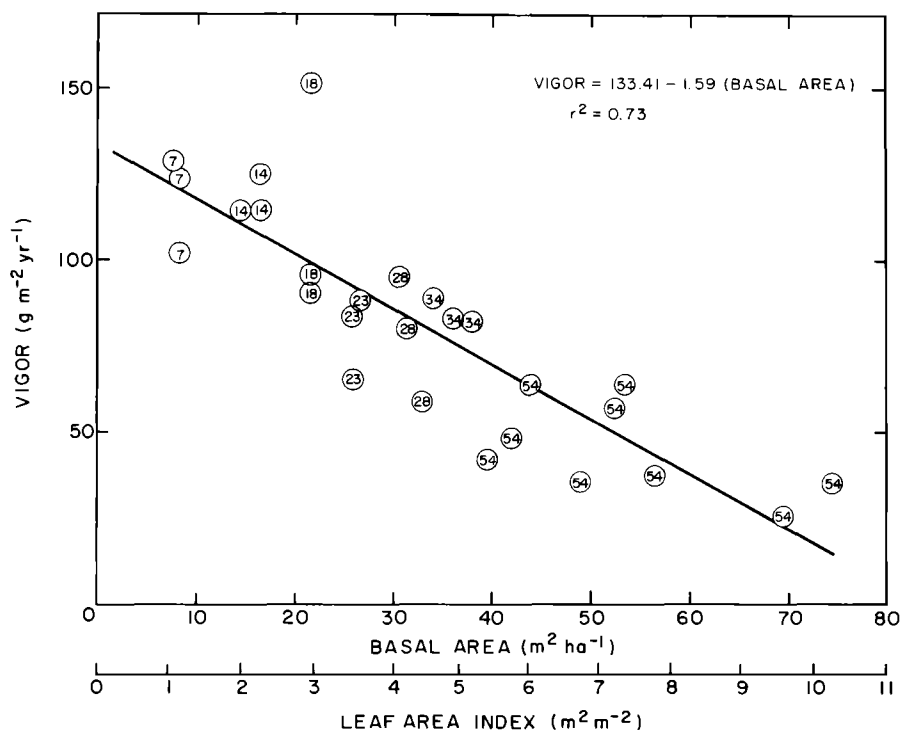
FIGURE 1. Mean tree vigor, measured as stem wood produced per unit of leaf area, in relation to stand basal area and the related leaf area index at different stocking levels. Values in circles represent the various levels (m² ha⁻¹) of growing stock.

two treated plots that had the most attacks, we estimated vigor on attacked and nonattacked trees; no significant differences were found when assessed with an unpaired t-test.

Surprisingly, cumulative mortality during 1976–80 was not significantly different among low and high vigor plots, as determined by a simple t-test. Almost all mortality, however, occurred in plots with a vigor less than 100 g m⁻² yr⁻¹, although several low vigor plots had no mortality. Only a single tree was killed on the plot with the highest vigor ranking (152 g m⁻² yr⁻¹), but that tree had a vigor of only 52 g m⁻² yr⁻¹.

To link previous mortality with vigor, we first correlated current vigor with current stocking (Fig. 1). If this correlation generally holds, density-related mortality during earlier periods (1966–70 and 1971–75) may well reflect changes in stand vigor. Cumulative mortality before thinning averaged 64 (SE 7.3) trees ha⁻¹, with considerable mortality noted on all plots (Fig. 3A). This pattern began to change during the period 1966–70, and in 1971–75 and 1976–80, the distribution of mortality was significantly altered, with by far the highest mortality at the upper levels of growing stock (Fig. 3B).

DISCUSSION

At low and intermediate vigors, we found variation in number of attacked trees and mortality among plots of similar vigors. Considerable variation in attacks also was found amoung control plots, seemingly without any correlation to stand characteristics. Generally, in this type of ponderosa pine stand, tree mortality at
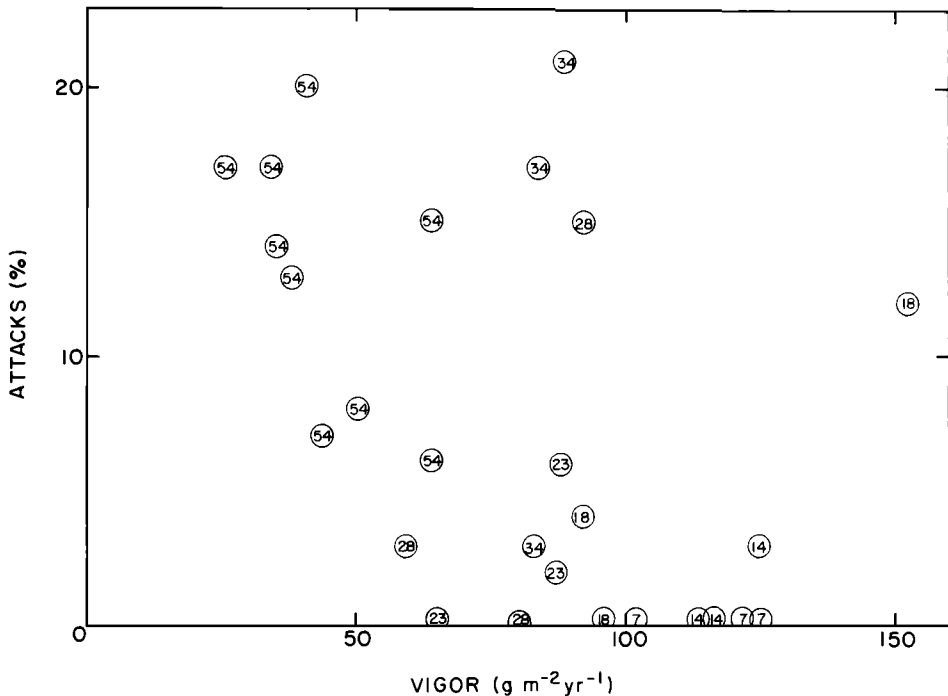
FIGURE 2. Percentage of trees per plot attacked in 1980 by mountain pine beetle in relation to tree vigor. Values in circles represent the various levels (m² ha⁻¹) of growing stock.

endemic populations affects <12 trees ha⁻¹ yr⁻¹ (Sartwell 1971). In this study, at a stocking level of 34 m⁻² ha⁻¹, mortality averaged 7 trees ha⁻¹ in 1980 and 6 trees ha⁻¹ yr⁻¹ for 1976–80 (Fig. 3B), which we interpret to reflect a rather low beetle population in the area. Unfortunately, we have no independent estimate of population size and can only reference the recorded tree mortality. At endemic population levels, mountain pine beetles are known to be distributed in patches throughout the forest (e.g., Berryman 1982). Consequently, we believe that the variation in attacks among plots of similar vigor resulted from a patchy distribution typical for endemic populations.

Low beetle population probably also accounted for the low percentage of killed trees (6 percent of all trees attacked on thinned plots). It is well known that a certain number of bark beetles are necessary to kill a tree (e.g., Berryman 1982), although only a few beetles are required to produce pheromones that attract others (Wood 1972). Because this did not occur on most of our trees, we again conclude that the beetle population was low. The few trees that were killed were found in low vigor plots, or in the case of the highest vigor plot, on a tree with about one-third the vigor of the other trees. This supports the hypothesis that comparatively few beetles are needed to kill low vigor trees (Waring and Pitman 1980, Berryman 1981). In the areas immediately surrounding the killed trees, a "switching over" probably occurred (Geiszler and Gara 1978); beetles were less discriminating with regard to tree vigor in selecting trees (cf. Raffa and Berryman 1981). This might explain why we could not find differences in vigor between attacked and nonattacked trees on some plots and why we noted some attacks on trees with very high vigor. In plots where no trees were killed, the switching phenomenon should have been less important; thus, the attacked trees should also represent those actively selected by the beetles.
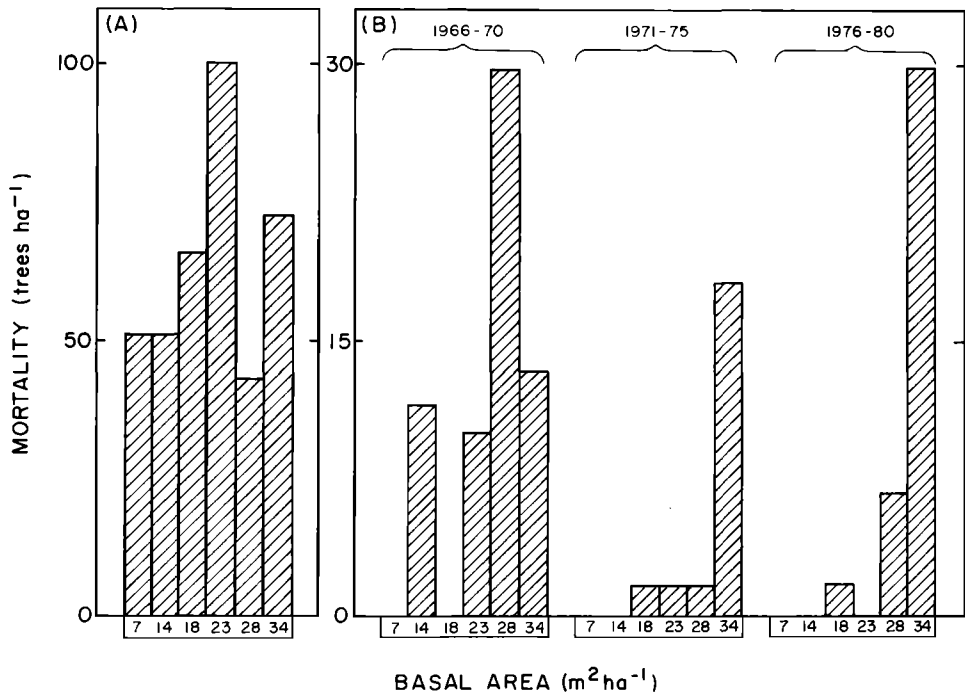
FIGURE 3. Cumulative tree mortality caused by mountain pine beetle at different levels of growing stock (A) just before treatment (1965) and (B) from different periods after stocking control was initiated.

We conclude, then, that the method of estimating beetle activity from visible pitch tubes for endemic population levels generally indicates which trees might have been killed had enough beetles been present. Superimposing the attack data on the mortality data, both recent and from earlier periods, we find strong evidence for a relationship between tree vigor and beetle attacks, in accordance with the findings of Waring and Pitman (1980).

The occurrence of a vigor threshold around 100 g m^{-2} yr^{-1}, above which attacks (and mortality) suddenly decrease, was similar to that reported for mountain pine beetle on lodgepole pine (Mitchell and others 1983). They found a change in tree mortality at a vigor of about 80 g m^{-2} yr^{-1}, corresponding to a leaf area index of 2 m^2 m^{-2}. Further, similar results have been reported from earlier studies in thinned stands of ponderosa pine, although in those studies no correlation was attempted with vigor or leaf area. Sartwell (1971) correlated the degree of mortality with tree density in eastern Oregon; he suggested thinnings to a basal area of 28–38 m^{-2} ha^{-1}, depending on site quality, to prevent mortality from mountain pine beetle. Sartwell and Stevens (1975) concluded from studies in both Oregon and the Black Hills of South Dakota and Wyoming that a stand basal area of 34 m^{-2} ha^{-1} should be a critical minimum, above which stands are liable to become severely infested. Our data on cumulative mortality during the periods 1971–75 and 1976–80 show a similar increase in mortality at or about a stocking level of 34 m^{-2} ha^{-1} (Fig. 3). In this study, we correlated basal area and vigor and found that a basal area of 34 m^{-2} ha^{-1} on our plots corresponds to a vigor of 80 g m^{-2} yr^{-1}—similar to the critical point predicted by our attack data from pitch tubes.

For management of ponderosa pine, we recommend careful attention to stocking control if the risk of mountain pine beetle is to be minimized. In this study, a

basal area below 34 m^{-2} ha^{-1} (equivalent to a leaf area index of <5) provided most trees with a vigor level at which they could withstand at least moderate attack. Maintaining stands at still lower stocking levels, as recommended for intensive management by Barrett (1979), can ensure a greater margin of safety. On better sites, including those supplemented by fertilizers and ameliorated by brush control, higher stocking levels may be feasible in maintaining vigor above the critical threshold. Compared with lodgepole pine, ponderosa pine can safely be grown at more than twice the leaf area and at 80 percent more basal area for stands of similar height (Mitchell and others 1983). This may reflect differences in growth rates related to site.

In summary, the susceptibility of ponderosa pine forests to damage from mountain pine beetle is closely related to tree vigor, which has been demonstrated to respond to stocking control. Although ponderosa pine can be grown at higher stocking levels and leaf areas than lodgepole pine, both have similar, critical vigor levels below which mountain pine beetle attacks are likely to be fatal.

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New IUFRO Working Party, S2.03-13, Breeding Southern Pines, Formed in January 1982—Joint Work Conference on "Provenance and Genetic Improvement Strategies in Tropical Forest Trees" to be held in Mutare, Zimbabwe, 9–14 April 1984

A new IUFRO working party, S2.03-13, Breeding southern pines, was formed effective January 1982. This notice is to solicit potential members and to announce the first meeting of the new working group.

A work conference on "Provenance and Genetic Improvement Strategies in Tropical Forest Trees" will be held jointly with IUFRO working parties S2.02-08, Tropical species provenances; S2.03-01, Breeding tropical species; and S2.03-13, Breeding southern pines, in Mutare, Zimbabwe, 9–14 April 1984. For further information regarding the conference please contact

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