

A REEXAMINATION OF THE RELATIONSHIP BETWEEN BARK THICKNESS
AND SUSCEPTIBILITY OF EASTERN WHITE PINES
TO WHITE-PINE WEEVIL ATTACK

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ABSTRACT .--The relationship between bark thickness at breast height and susceptibility of eastern white pine (Pinus strobus L.) to repeated attacks by the white-pine weevil (Pissodes strobi Peck.) was reexamined. The least weeviled trees in a 25-year-old provenance test plantation had the thinnest bark, but overall the correlation between number of weevil attacks and bark thickness was low ($r = 0.24$). The least weeviled trees were also the smallest in diameter at breast height (dbh), and the correlation between dbh and bark thickness was high. Mean bark thickness adjusted for variation in dbh by covariance analysis was not significantly related to numbers of weevil attacks, and bark thickness varied widely within trees. Therefore, bark thickness at breast height does not seem to be a reliable criterion for distinguishing highly susceptible from more weevil-resistant white pines.

VARIATION IN SUSCEPTIBILITY of eastern white pines (Pinus strobus L.) to attack by the white-pine weevil (Pissodes strobi Peck.) is not purely random. Instead, this variation depends to some degree on relative growth rates of individual trees and on several morphological and biochemical characteristics of the host, although much of the variation in susceptibility remains unexplained. If sufficient numbers of host characteristics correlated with susceptibility can be identified, these characteristics could be useful for indirect or integrated selection for resistance (Gerhold 1962, 1966; Gerhold and Stroh 1963).

Bark thickness of the white pine terminal shoot is known to be involved in differential susceptibility among individual trees. Graham (1926) and MacAloney (1930) have both pointed out that an ample supply of phloem is of primary importance for attraction and normal development of weevils, but until recently this relationship had not been quantified. Bark thickness of white pine leaders has now been shown to be positively correlated with the extent of adult feeding on white pines in several plantations (Stroh and Gerhold 1965) and with susceptibility to repeated attacks over an 11-year period (Wilkinson In Press). In each case the amount of variation in either feeding or susceptibility attributable to variation in bark thickness was small. Nevertheless, bark thickness may yet prove to be a useful criterion for discriminating between highly susceptible and more resistant white

pinus, especially if other, complimentary characteristics could be identified that would explain additional variation in susceptibility.

If other correlated characteristics are found, then thickness of bark at breast height may be as reliable a measure of relative susceptibility as bark thickness of leaders. Kriebel (1954) reported that as much as one-third of the variation in attack susceptibility could be explained by a combination of bark thickness at breast height and tree diameter. Bark thickness at breast height is without question, much easier to measure than bark thickness of leaders. However, I question whether a host characteristic so far removed from the point of weevil attack could be as closely related to susceptibility as bark thickness of leaders, the site of adult weevil feeding, oviposition, and larval development.

In this study I have reexamined the relationship between bark thickness at breast height and susceptibility to repeated weevil attack in a 25-year-old plantation of white pines that had been heavily attacked by weevils for 11 years. The objective was to determine whether bark thickness at breast height is a reliable alternative to leader bark thickness as a criterion for indirect selection for weevil attack susceptibility.

MATERIALS AND METHODS

The trees used for this study were growing in a provenance test planted in 1960 on the Massabesic Experimental Forest, Alfred, Maine. The plantation consists of trees from 27 seed sources throughout most of the species' range. Each seed source was represented by 1-tree plots located in 24 randomized blocks, and the trees were planted in 15 rows of 44 trees each. The trees in the plantation were 12 years old from seed when they were first exposed to weevil attack in 1968.

Numbers of weevil attacks on each tree in the plantation were recorded annually for the first three years, 1968, 1969, and 1970, and then at 4-year intervals, in 1974 and 1978. Relative susceptibility was rated by total number of successful attacks--attacks killing the leader--during the entire 11-year period. In the spring of 1979, every other tree in each row was cut down to study the relationship between weevil attack susceptibility and leader morphology (Wilkinson In Press). In the fall of 1981, bark thickness of the remaining trees was measured to the nearest hundredth of an inch at breast height with a bark gauge. Four measurements, one in each of four quadrants, were made on each tree. At the same time, 25-year diameter at breast height (dbh) of each tree was measured to the nearest tenth of an inch. Bark thickness measurements on a few trees were made slightly above or below a point 4.5 feet from the ground to avoid uneven exterior bark at nodes. Measurements were made on a total of 259 trees.

Each of the trees was categorized by the number of years it had been successfully attacked. Differences in three measures of bark thickness--mean, minimum, and maximum from each tree--and in dbh between attack categories were tested for significance by one-way analysis of variance. A second analysis of variance, using four individual bark thickness measurements per tree, was done to partition variance between weevil attack categories, trees within attack categories, and within tree components. Correlations between numbers of weevil attacks, dbh, and bark thickness were calculated. Since bark thickness at breast height and dbh are closely related (Kriebel 1954), and dbh is in turn positively correlated with number of weevil attacks (Wilkinson In Press), covariance analysis was used to remove the effects of dbh on variation in bark thicknesses among weevil attack categories. A series of t-tests were used to test significance of differences in numbers of weevil attacks between thin-barked and thick-barked trees within classes of dbh.

RESULTS AND DISCUSSION

Annual white-pine weevil infestations in the test plantation were heavy during most of the 11-year period from 1968 through 1978. Weevils successfully attacked an average of 40 percent of the white pines in the plantation in each year, with a year-to-year range of 20 to 70 percent. There was considerable variation in weevil attack susceptibility among sample trees. Mean number of attacks per tree in the 259-tree sample was 3.9, and numbers of attacks per tree ranged from zero (3 trees) to 11 (1 tree).

Diameter of the white pines at breast height was the factor most closely related to differential susceptibility to repeated weevil attack. As expected, the least weeviled trees were the smallest in dbh (Table 1). The least weeviled trees also had the thinnest bark. Mean bark thickness and minimum bark thickness differed significantly between weevil attack categories. Maximum bark thicknesses measured on each tree were not significantly related to number of weevil attacks, mainly because trees with moderately thin bark often had thicker than average bark in one quadrant. Differences in maximum and minimum bark thickness measurements on individual trees averaged .09 inches and ranged from .01 inches to .29 inches. Overall, 34 percent of the total variation in bark thickness measurements was within trees. This extreme within-tree variation makes it difficult to determine how many bark thickness measurements are required to attain a representative average for each tree.

I found that the correlation between bark thickness at breast height and number of weevil attacks ($r = 0.24$) was not as high as the correlation between leader bark thickness and attack numbers ($r = 0.31$) in a comparable sample of trees from the same plantation (Wilkinson In Press). Since weevils attack white pine leaders, and some minimum leader bark thickness is necessary for the attack to be

successful (Kriebel 1954), it is not surprising that leader bark thickness is somewhat more closely related to numbers of successful attacks than bark thickness at breast height. It is somewhat surprising that the difference is so small. If comparative strengths of correlations with numbers of attacks were the only consideration, there would be little reason to choose one characteristic over the other for indirect selection.

A reliable characteristic for indirect selection must not only be correlated with variation in susceptibility; it must also be independent of variation in tree size and relative vigor. I found bark thickness at breast height to be more highly correlated ($r = 0.65$) with dbh than leader bark thickness ($r = 0.45$) (Wilkinson In Press). A strong interrelationship between dbh and bark thickness at breast height, and consequently, a strong interdependency in their relation to number of weevil attacks was more evident in the plantation I studied than it was in a similar study by Kriebel (1954). He found considerable variation in weeviling susceptibility correlated with bark thickness at breast height that was not detected by measurement of dbh alone in two of five stands of white pine. In contrast, I found that mean bark thickness adjusted for variation in dbh by covariance analysis did not differ significantly between weevil attack categories ($f = .62$ with 9 and 248 df).

Kriebel (1954) stressed the need to confine selection for thin bark to trees of the same age and of equal diameter to avoid negative selection for vigor. I found that fast-growing trees that were below the plantation mean of .35 inches in bark thickness were no less susceptible to repeated weevil attacks than trees of similar diameter with thicker bark (Table 2). Both fast-growing groups were attacked more often than all trees in the plantation combined, apparently because of their larger size. A greater difference in weevil attack susceptibility between thin-barked and thick-barked trees occurred among the less important group of trees that was below the mean of 8.4 inches in dbh, but this difference was not significant.

Kriebel (1954) pointed out that in more uniform stands bark thickness is a more critical factor in relative susceptibility to weevil attack than dbh. I measured bark thickness of white pines in a range-wide collection that was quite variable in dbh as well as in a number of other characteristics. This variability may be one reason why I could not verify Kriebel's research results. On the other hand, variation in both weevil attack susceptibility and bark thickness in a provenance test plantation should theoretically exceed that found in natural stands or plantations established with uniform nursery stock. I expected to find, therefore, a near-maximum expression of the quantitative relationship between bark thickness and susceptibility. Instead, I found a much lower correlation between bark thickness at breast height and number of weevil attacks than those reported by Kriebel (1954).

