Eastern White Pine Characteristics Related to Weevil Feeding[1]

By ROBERT C. STROH and HENRY D. GERHOLD[2]

(Received for publication December 27, 1964)

One of the major problems in the selection and breeding of eastern white pines (Pinus strobus L.) for resistance to the white pine weevil (Pissodes strobi PECK) has been that of defining a basis for selection. Direct selection of apparently weevil resistant white pines based on the absence of weevil injury in the main stems of the trees has been practiced by HEIMBURGER (1963) with encouraging early results. GERHOLD and STROH (1963) have suggested methods for improving upon the precision attained through direct selection, which is often low because of the random nature of weevil infestations. They proposed that correlated characters of the unweeviled trees, some of which may have escaped injury despite susceptibility, could be useful for future screening, for designing mating schemes, and for recognizing different types of resistance.

Two objectives were established as the purpose of this study: (1) to determine if significant correlations exist between various morphological traits of the leading shoots of eastern white pine and feeding by the white pine weevil under various environmental conditions and (2) to provide a biologically sound interpretation of such relationships with respect to the behavior of the weevil.

Review of Related *Literature*

Although no results of breeding for weevil resistance in eastern white pine can be found in the literature, several reports have been made concerning characteristics of the tree related to freedom from weevil attack.

One of the first such correlated characters to be reported was leader diameter (PLUMMER and PILLSBURY, 1929; MAC ALONEY, 1930; and HOLST, 1955). The general conclusion of these reports was that weevil injury increased as leader diameter increased. KRIEBEL (1954) demonstrated a similar relationship using diameter at breast height of trees in even aged, natural stands. It should be pointed out that KRIEREL did not have complete control of the age of the trees in his sample.

Closely associated with diameter is bark thickness. Again working at breast height and assuming that bark thickness at breast height was indicative of leader bark thickness, KRIEBEL (1954) found that the frequency of successful weevil attack increased as bark thickness increased. The problem of controlling the age and thus the years of exposure to the weevil of the sampled trees must be recalled when considering this result. A similar association of bark thickness and successful weevil attack was reported by SULLIVAN (1961) using measurements made directly on leaders. The possibility of a critical upper limit to bark thickness as well as a critical lower limit was discounted by SULLIVAN as probably being an artifact of the population that was sampled.

SULLIVAN (1961) also reported that the number of needle fascicles per unit area of the leader was not involved in the selection of a particular tree by the weevil.

One type of leader characteristic that has received almost no attention for its possible association with white pine weevil attack has been that of the number and distribution of cortical resin ducts. FOWLER (1958) made the observation that certain individuals of Pinus peuce GRISEB. demonstrated resistance to the weevil possibly due to the heavy resin flow of the species. Although the role of resin has not been thoroughly studied with respect to white pine weevil attack, the work being done with the pine reproduction weevil, Cylindrocopturus *eatonii* BUCH., has produced interesting results conoerning the association of resin with resistance to weevil attack. The backcross hybrid, ([Pinus jeffreyi GREV. & BALF. X P. *coulteri* D. DON] X P. jeffreyi), was reported by MILLER (1950) to display a degree of resistance when either the eggs or the larvae or both were engulfed in resin thus preventing serious damage. MILLER also noted that resin ducts often failed to form in the xylem of some susceptible trees subsequent to attack. In a study conducted by CALLAHAM (1960) it was found that the frequency of stem attack on Pinus *ponderosa* LAWS. was higher on surviving individuals as evidenced by the formation of resin droplets. Although the absence of a resin droplet does not nececcarily indicate the absence of stem attack, CALLAHAM concluded that the copious resin flow constituted a form of resistance to successful weevil attack by repeatedly repelling the insect from its feeding site and thus preventing serious damage. The toxicity of saturated resin vapors from various pine species and hybrids on adult *Dendroctonus* beetles was demonstrated by SMITH (1961a, 1961b, 1961c). SMITH hypothesized that the beetles were able to tolerate the saturated vapors of the host trees but could not tolerate those of the non-host trees.

The preceding literature citations demonstrate that the present knowledge of characteristics correlated with white pine weevil attack is limited. The reason for the association of leader diameter and leader bark thickness with weevil attack heretofore has not been explained and the role of the number and distribution of the cortical resin ducts in the selection of a host tree by the white pine weevil has not yet been studied.

Correlated Characters

Study Areas

Four plantations of eastern white pine were selected for the purpose of data collection. These areas were chosen on the basis of 'being of similar age, spacing, and height range plus being infested by the weevil; but, differing in exposure, slope, elevation, and geographic location. Areas 1 and 4 were located in Huntingdon County, Pennsylvania, and areas 2 and 3 were located in Clearfield County, Pennsylvania. All four areas were planted with seedlings purchased from state nurseries; however, no record of seed source was available.

---

[1] This paper is part of a dissertation submitted in 1964 to the Graduate School of The Pennsylvania State University in partial fulfillment of the requirements for the degree of Doctor of Philosophy. It was authorized for publication on July 15, 1964, as Paper No. 2919 in the Journal Series of the Pennsylvania Agric. Expt. Station. This study was part of a Northeast Regional Project NE-27, Forest Genetics and Site Productivity; a cooperative study involving Agric. Expt. Stations in the Northeast Region and supported in part by Regional Research funds.

[2] Graduate Assistant and Assistant Professor, respectively, School of Forestry, The Pennsylvania State University, University Park, Pennsylvania.

Measures of Weevil Attack

Four measures of weevil attack were considered as a basis for evaluating the leader characteristics of eastern white pine: (1) the numbers of weevil injuries recorded in the stems of the trees, (2) the numbers of feeding cavities on the upper three inches of the leaders of the trees, (3) the lengths of larval feeding measured downward on the leaders from the base of the terminal bud cluster, and (4) the numbers of adult weevils emerging from the trees following pupation.

Since the major objective of breeding weevil resistant trees is to minimize or eliminate weevil injury, the first of these measures of weevil attack may be considered the most useful. This viewpoint was held by HEIMBURGER (1963) in that he selected apparently weevil resistant white pine on the basis of the absence of weevil injury in the tree. Because under certain conditions this selection criterion is not an adequate measure of the resistance of individual trees, GERHOLD and STROH (1963) proposed that direct selection be employed to screen out those trees that exhibit some degree of susceptibility and subsequently practice indirect selection on the remaining trees. As a basis for developing the relationships in the present study, the numbers of past attacks observed ranged from zero to five per tree.

A second practical objective of breeding weevil resistant white pine is that of reducing the size of the weevil population through a disruption of weevil reproduction. The first indication that a tree is being attacked by the weevil is the excavation of feeding cavities on the upper portion of the leader. As feeding progresses, the female weevil deposits eggs in some of the feeding cavities. SULLIVAN (1961) reported that the number of eggs deposited is a linear function of the number of inches of adult feeding on the leader with a correlation coefficient of 0.956. Each egg may hatch into a single larva which begins feeding down the leader in the phloem and cortex. SULLIVAN (1961) has estimated that the mortality rate is about ninety percent during the larval stage and about sixty-eight percent during the prepupal stage. Each surviving larva eventually excavates a pupal chamber in the xylem of the stem where the immobile pupal stage occurs. When each pupa develops into an adult weevil, it chews an emergence hole through the thin layer of dry periderm covering the pupal chamber and emerges to join the fall population. From this brief description of weevil reproduction it may be seen that the number of feeding cavities is related to egg deposition; the length of larval feeding is a measure of larval development; and the number of adult weevils emerging is related to pupal development.

This biological description of the relationships among adult feeding, larval feeding, and adult emergence was evaluated statistically using the data collected according to the 1963 Sampling Procedure which is discussed in the next section. It was found that the linear correlation coefficient between the number of feeding cavities and the length of larval feeding was 0.771 in area 2A (d. f. = 17) and 0.560 in area 3A (d. f. = 29). The linear correlation coefficient between the length of larval feeding and the number of adults emerging was found to be 0.613 in area 2A (d. f. = 17) and 0.675 in area 3A (d. f. = 29). All four coefficients were significant at the ninety-nine percent level of confidence (*Figure 1*). SULLIVAN (1961) studied similar relationships using curvilinear techniques and also found significant associations.

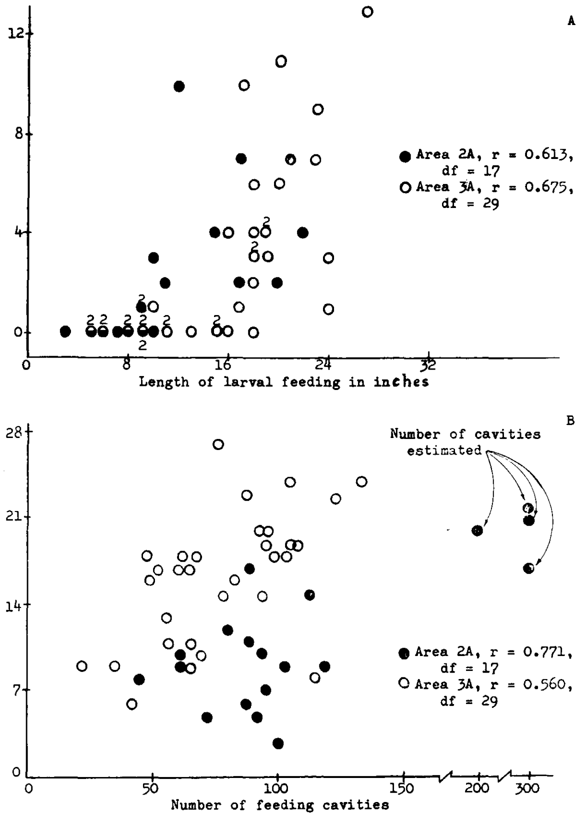


Figure 1. — Relationships between measures of weevil attack.

It is disappointing to note that the direct relationship between the number of feeding cavities and the number of adults emerging was not significant in either area 2A (r = 0.284, d. f. = 17) or area 3A (r = 0.265, d. f. = 29). Although SULLIVAN (1961) predicted adult emergence using estimates of egg deposition and mortality, no comparison was performed with field observations which could either support or refute the present findings. The reason for the lack of significant correlation is not yet known. It is possible, however, that the unexplained variation between adult feeding and larval feeding and between larval feeding and adult emergence was accumulated into the unexplained variation between adult feeding and adult emergence.

Recognizing that adult feeding and adult emergence were shown to be not significantly related, the number of feeding cavities on the upper three inches of the leader was chosen as the measure of weevil attack for the present study. The reasoning was that even though adult feeding and adult emergence were not directly related, trees that could resist weevil feeding would not have eggs deposited and thus would not sustain serious injury.

The goal of breeding white pine resistant to weevil feeding need not be immunity to feeding. The data plotted in *Figure 1 A*, indicated that no adult emergence was likely to occur with less than nine inches of larval feeding. Associated exclusively with nine inches or less larval feeding were from forty to forty-five feeding cavities or less (*Figure 1 B*). Thus if the leader morphology of eastern white pine could be altered through selection and breeding such that weevil feeding did not exceed forty-five cavities per leader, a considerable increase in resistance might result.

1962 Sampling Procedure

Because of improvements made in technique from 1962 to 1963, the two sampling procedures will be discussed separately.

A consideration of the correlated characters reported in the literature and an extension of some of the findings resulted in twelve morphological leader characteristics to be evaluated in this study:

1. Leader diameter three inches below the terminal bud cluster,
2. Number of needle fascicles on upper three inches of leader,
3. Bark thickness three inches below terminal bud cluster,
4. Number of inside cortical resin ducts three inches below terminal bud cluster,
5. Number of outside cortical resin ducts three inches below terminal bud cluster,
6. Radial depth of inside cortical resin ducts three inches below terminal bud cluster,
7. Radial depth of outside cortical resin ducts three inches below terminal bud cluster,
8. Tangential diameter of inside cortical resin ducts three inches below terminal bud cluster,
9. Tangential diameter of outside cortical resin ducts three inches below terminal bud cluster,
10. Sum of inside duct diameters three inches below terminal bud cluster,
11. Sum of outside duct diameters three inches below terminal bud cluster, and
12. Ratio of sum of all duct diameters over leader circumference three inches below terminal bud cluster.

The reference to inside and outside cortical resin ducts was made because of the more or less concentric arrangement of the resin ducts in the cortex as shown in *Figure 2.* Leader diameter was measured in the field with a vernier caliper to the nearest 0.1 millimeter. The number of needle fascicles and number of feeding cavities were also counted in the field. The upper three inches of the leaders were removed from the trees and placed in marked bottles of FAA, a standard fixative (Sass, 1958), which made it possible to make the internal measurements in the laboratory with a minimum of shrinkage or swelling. The internal measurements were made with the aid of a binocular dissecting microscope equipped with on ocular micrometer. This same sampling procedure was employed in sampling the most vigorous adjacent lateral branch of each tree. The data from the lateral branch were used in the development of an alternate sampling technique.

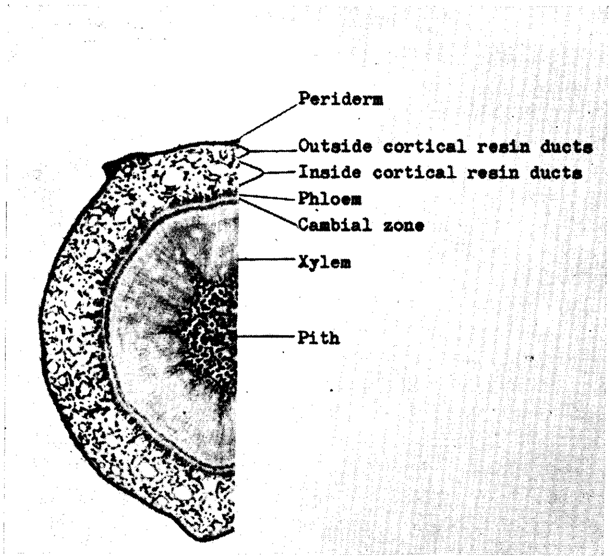


Figure 2. — Cross section of white pine leader.

Thirty trees were sampled in each of the four study areas during the period from May 26 to June 14, 1962. The trees selected for sampling were either dominant or codominant with respect to their neighboring trees to eliminate the influence of shading. An effort was made to sample trees with as wide a range as possible in the number of successful weevil attacks recorded in the stem.

The problems associated with the 1962 sampling procedure included: (1) sampling the leader characteristics over a period of twenty days after growth had started introduced a considerable amount of unexplained variation, (2) selecting dominant or codominant trees with a wide range in the number of past attacks required that the trees be scattered thus increasing the variability of the site and possibly the weevil population density, (3) sampling in areas in which weevil attack was not uniform and thus not exposing all trees equally to weevil attack may have led to erroneous conclusions, and (4) removing the top section of the leaders eliminated the possibility of sampling the same trees in two successive years as well as the possibility of measuring larval feeding and adult emergence.

1963 Sampling Procedure

Two areas were sampled in 1963 which were selected on the basis of containing an excess of unweeviled trees when compared to the expected number calculated from the sum of the binomial series of the percent annual attacks. These two areas, area 2A and area 3A, were ten tree by ten tree blocks of plantations 2 and 3, respectively, but did not contain trees sampled in 1962. Since Wright and Gabriel (1959) concluded that weevil attack occurred at random, the excess of unweeviled trees could be interpreted as weak evidence for the presence of resistant individuals.

A bark patch sampling technique was developed which permitted sampling of the internal characteristics without damaging the leaders of the trees. The patch included the bark from one-quarter or more of the circumference of the leader at a point three inches below the base of the terminal bud cluster. In all areas sampled, the bark patches were removed from the uphill side of the leaders of the trees. The variation in total leader morphology accounted for by sampling only one-quarter of the circumference of the leaders ranged from 52.0 to 92.4 percent.

Sixty dominant or codominant trees were sampled in both area 2A and 3A on April 16, 1963, prior to the start of the growing season. At this time the leader diameters were measured and the bark patches were removed. Each area was divided into two thirty-tree blocks which were further divided into three ten-tree plots. After the wounds left from removing the bark patches had been covered with hardened resin, each set of three ten-tree plots was randomly treated by releasing zero, two, and four weevils directly on the leaders. The weevils were released in area 3A on May 31 and in area 2A on June 1, 1963. The numbers of feeding cavities were recorded in both areas on June 25 when feeding and oviposition were nearly completed. The lengths of larval feeding were recorded on July 26 after emergence had begun although it was likely that not all larvae had entered pupation. The leaders with larval damage were removed from the trees on August 28 and stored at room temperature for ten days to promote further emergence. At the end of this storage period the numbers of emergence holes were counted.

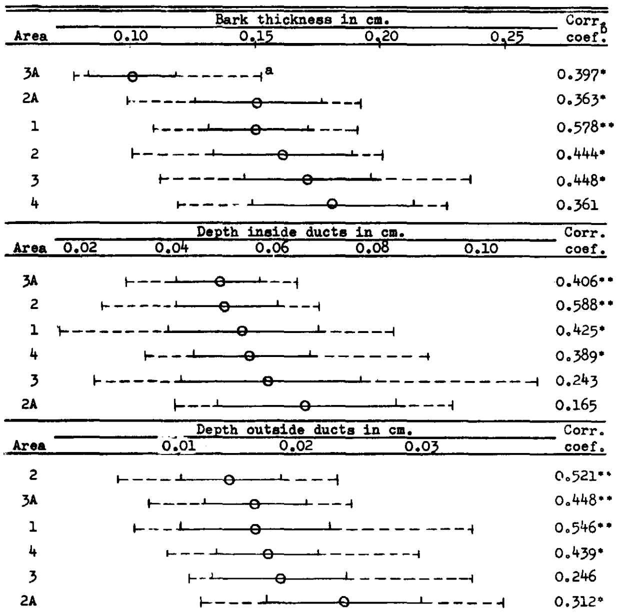
Analysis of Correlated Characters

The analytical procedures described in this section were designed to determine if a significant relationship existed between the observed leader characteristics and white pine weevil feeding. The techniques employed were analysis of variance to detect significant differences in leader traits between sampled areas and linear correlation to evaluate the association of leader characteristics with weevil feeding. The discrete traits, such as number of resin ducts, were transformed to $x = \sqrt{x + 1}$ as recommended by SNEDECOR (1957) to satisfy the assumptions underlying the statistical models. This technique, however, did not alter the results obtained when the original data were analyzed; thus the analytical procedures to be described were performed on the original data. The majority of the computations were performed on the IBM 7070/7074 data processing installation at The Pennsylvania State University.

Comparison of Study Areas

An analysis of variance for a completely randomized design was employed to compare the leader characteristics of the sampled areas. The results of these analyses are presented in *Table 1*. In both 1962 and 1963 the majority of the leader characteristics were found to differ significantly from area to area. It should be noted that the number of feeding cavities differed significantly among areas in 1962 but not in 1963. This result indicated that releasing weevils may have increased the uniformity of infestation. The fact that fewer cavities were observed in 1963 than in 1962 was possibly a result of adverse weather conditions experienced during the period of active spring feeding including a late spring frost and several days of rainfall.

An analysis of variance for a randomized block design was employed to determine if the three levels of weevil release had produced significantly different numbers of feeding cavities in 1963. The resulting F-ratio was not significant. The mean numbers of feeding cavities associated with the release of zero, two, and four weevils were 38.2, 50.0, and 46.4, respectively.



[a] Solid line represents 1.0 standard deviation, dashed line represents sampled range, and circle indicates average.
[b] Correlation coefficients in areas 2A and 3A have 38 degrees of freedom and others have 28 degrees of freedom.
*Significant at the 95% level of confidence.
**Significant at the 99% level of confidence.

Figure 3. — Leader characteristics related to weevil attack in eastern white pine.

Omitted from the 1963 sampling procedure were the number of needle fascicles, the sum of the inside duct diameters, the sum of the outside duct diameters, and the ratios of the sum of all duct diameters over leader circumference. The number of needle fascicles was found to be not significantly correlated with weevil feeding in 1962 which was in agreement with the finding reported by SULLIVAN (1961). The other three characteristics were omitted for not displaying significant correlation with weevil feeding in 1962; moreover, the multiple correlation of other characteristics which weevil feeding could be employed to measure essentially the same things.

Correlation Analyses

The linear correlation coefficients between the leader characteristics and the number of feeding cavities were calculated separately for each sampled area because the traits were found to differ significantly among areas. The statistic employed for testing the significance of the correlation coefficients was

$$t = r \sqrt{n - 2} / (1 - r^2)$$

Table 1. — Arithmetic averages and corresponding F-ratios for areas in 1962 and 1963.

Characteristics	1962 Sample					1963 Sample		
	Area 1	Area 2	Area 3	Areca 4	F-ratio ¹)	Area 2A	Area 3A	F-ratio ²)
No. feeding cavities	87.9	111.3	54.6	52.7	4.80**	43.9	45.9	0.03
Leader diam., cm.	0.89	1.01	0.99	1.07	10.11**	0.78	0.58	50.59**
No. needles	52.7	39.5	30.5	47.2	15.19**	³)		
Bark thickness, cm.	0.15	0.17	0.16	0.18	5.02**	0.15	0.10	83.00**
No. inside ducts	19.5	19.1	18.6	20.9	4.93**	18.7	18.5	0.03
No. outside ducts	22.2	21.1	19.5	21.5	1.04	42.8	30.1	19.06**
Inside duct diam., cm.	0.029	0.034	0.034	0.035	3.11*	0.032	0.029	4.38*
Outside duct diam., cm.	0.020	0.019	0.016	0.020	3.10*	0.014	0.012	17.07**
Inside duct depth, cm.	0.052	0.057	0.048	0.054	2.20	0.064	0.047	35.90**
Outside duct depth, cm.	0.016	0.018	0.014	0.017	4.33**	0.023	0.016	36.77**
Sum inside duct diam., cm.	0.56	0.65	0.64	0.73	4.67**	³)		
Sum outside duct diam., cm.	0.41	0.39	0.32	0.42	4.13**	³)		
Sum duct diam./leader circumfer.	0.35	0.33	0.31	0.34	2.02	³)		

¹) F-ratio with (3,116) degrees of freedom
²) F-ratio with (1,118) degrees of freedom
³) Not sampled in 1963

* Significant at the 95% level of confidence
** Significant at the 99% level of confidence

which is distributed as Student's-t with n-2 degrees of freedom. The means, standard deviation, ranges, and correlation coefficients of those characteristics found to be most consistently and significantly correlated with the number of feeding cavities are summarized in *Figure 3.* The correlation coefficients for areas 2A and 3A as shown in *Figure 3* were calculated from the data gathered from the forty sampled trees on which weevils had been released. The trees on which no weevils had been released were omitted from the correlation analyses in an effort to eliminate the variation these trees would have introduced. Although no significant difference was detected among the average number of feeding cavities resulting from the three levels of weevil release, the uniformity of attack was quite different. Of the trees on which two and four weevils had been released, 17.5 percent and 20.0 percent of the leaders, respectively, displayed no feeding cavities. Of the trees on which no weevils had been released, 47.5 percent of the leaders displayed no feeding cavities. The trees which had been attacked displayed very high numbers of feeding cavities thus accounting for the lack of significance among the three levels of weevil release. It was this high proportion of trees that had escaped attack that would have introduced the unexplained variation to the correlation analyses.

Fifty of the 120 trees sampled in 1963 displayed larval feeding. These trees were employed to determine if a significant correlation existed between leader morphology and either larval feeding or adult emergence or both. None of the characteristics studied, however, were significantly correlated with either of these measures of weevil attack.

A multiple regression analysis was conducted for each area to determine the accuracy with which the number of feeding cavities could be predicted from the leader characteristics. The regression model was

$$Y = B_0 + B_1X_1 + B_2X_2 + B_3X_3$$

where

Y = number of feeding cavities
X_1 = bark thickness in centimeters
X_2 = depth of inside resin ducts in centimeters
X_3 = depth of outside resin ducts in centimeters

A summary of the regression statistics is presented in *Table 2.* The amount of explained variation ranged from 19.1 percent to 49.1 percent.

Although the total model accounted for a significant amount of the variation in the sample space of each of the six sampled areas, this gave no indication of the relative importance of the variables individually. This information was obtained by partitioning the sums of squares due to the regression surface into the components due to each independent variable. The results of these analyses are presented in *Table 3.* The relative importance of the leader characteristics in the six regression models may be seen to vary considerably from area to area.

The variation in weevil feeding explained by the multiple regression analyses would have been greater had the three independent variables not been correlated. In both 1962 and 1963 bark thickness and the depths of the two sets of resin ducts were each significantly correlated with the other two characteristics. The correlation between bark thickness and the duct depths ranged from 0.45 to 0.83 and the correlation between the inside and outside resin duct depths ranged from 0.66 to 0.90.

Discussion of Correlated Characters

The only leader characteristics that were demonstrated to be at all consistently and significantly correlated with weevil feeding were bark thickness, depth of inside cortical resin ducts, and depth of outside cortical resin ducts.

The lack of a significant relationship between leader diameter and weevil feeding in 1962 was in direct opposition to the results of other reported studies. The reason for

Table 2. — Regression statistics for prediction of feeding using correlated characters in eastern white pine.

Independent variables	Partial regression coefficients					
	Area 1	Area 2	Area 3	Area 4	Area 2A	Area 3A
Intercept, B_0	−363.28	−37.46	−68.71	−69.99	−103.86	−44.63
Bark thickness, cm.	3142.81	337.83	869.40	−263.44	1215.60	331.09
Depth inside ducts, cm.	−2740.20	−1175.58	−408.63	3115.00	−1609.78	304.53
Depth outside ducts, cm.	6451.97	5502.40	210.96	2741.13	3421.17	2840.57
Multiple correlation coefficient	0.7005	0.4630	0.4514	0.6151	0.4368	0.4745
Percent explained variation	49.1%	21.4%	20.4%	37.8%	19.1%	22.5%

Table 3. — Analysis of error of estimate for prediction of number of feeding cavities.

Sources of variation 1)	1962 Analyses					1963 Analyses		
		F-ratios					F-ratios	
	D. F.	Area 1	Area 2	Area 3	Area 4	D. F.	Area 2A	Area 3A
Total	29					39		
Due to regression	3	20.27**	7.47**	7.13**	13.85**	3	9.31**	10.84**
Due to x_1 alone	1	3.49	10.29**	9.01**	8.82**	1	11.63**	10.80**
Due to x_2 and x_3	2	28.66**	6.06**	6.19**	16.36**	2	8.14**	10.86**
Due to x_2 alone	1	16.50**	17.55**	2.82	10.22**	1	1.74	11.29**
Due to x_1 and x_3	2	22.16**	2.44	9.28**	15.66**	2	13.09**	10.61**
Due to x_3 alone	1	19.84**	11.43**	2.85	12.98**	1	6.25*	13.72**
Due to x_1 and x_2	2	20.49**	5.49*	9.27**	14.29**	2	10.84**	9.39**
About regression	26					36		

1) Where x_1 = bark thickness
x_2 = depth of inside resin ducts
x_3 = depth of outside resin ducts

* Significant at the 95% level of confidence
** Significant at the 99% level of confidence

this lack of association was not definitely established. However, since leader diameter was significantly related to weevil feeding in 1963, it appeared that the variation introduced by the 1962 sampling procedure may have obscured the association. Probably the major contributing factor of the 1962 sampling procedure was that of gathering data over a period of twenty days during the active growing period of the trees.

The amount of variation accounted for by any one of the three correlated characters was very low, ranging from about nine percent to about thirty-six percent. Considering the three characteristics together in multiple correlation with weevil feeding, the amount of variation accounted for was somewhat greater, ranging from about nineteen percent to about forty-nine percent. These values were much too low to be of exclusive value as a quantitative basis for breeding weevil resistant trees.

Although the populations sampled produced relatively low correlation coefficients between the leader characteristics and weevil feeding, it was interesting to note in *Figure 3* that as the average resin duct depth decreased the strength of the correlations with weevil feeding increased. This suggested that the selection and breeding of trees with shallower ducts may produce an increase in the strength of the correlations with weevil feeding. This increase in correlation with weevil feeding was not realized when analyses were conducted using those portions of the samples with duct depths less than various upper limits. Such a relationship does not appear to be true for bark thickness when the results of both 1962 and 1963 are considered. However, within each year the strength of the correlation of bark thickness with weevil feeding is greater in the areas with leaders having thinner bark. This would suggest that in a natural population of trees weevils display a preference for leaders with thicker bark but are capable of feeding on leaders with thinner bark.

The relative amount of feeding accounted for by the leader characteristics varied considerably from area to area. In areas 1, 2, 4, and 3A the inside and outside duct depths accounted for more of the variation in weevil feeding than did bark thickness. In areas 3 and 2A this relationship was reversed. The reason behind this reversal appears to lie in a consideration of *Figure 3*. Areas 3 and 2A were observed to have greater average resin duct depths than the other four areas. Apparently the resin duct depths in these two areas were approaching the limit of absolute depth which could influence weevil feeding. Consequently the selection of a particular tree by the weevil was governed by a preference for leaders with thicker bark. The implication of this discussion is that outside resin ducts less than 0.018 centimeter deep and inside resin ducts less than 0.056 centimeter deep exert a quantitative influence on the feeding habits of weevils. Under conditions where these limits of duct depth are exceeded, the selection of a particular tree by the weevil becomes dependent upon a preference for leaders with thicker bark. It would therefore appear that the depth of the cortical resin ducts in the leaders of eastern white pine should be considered as a quantitative basis in breeding for weevil resistance. Bark thickness appears to be of less practical value since the bark thickness of a vigorous tree would not likely be below that thickness required for egg deposition at which bark thickness becomes critical (SULLIVAN, 1961).

Seed source data for the sampled trees were not available thus making it impossible to attribute the significant differences in leader characteristics among areas to either site differences or inherited differences. A tentative conclusion may be drawn concerning the effect of site differences on the leader characteristics by comparing area 2 with area 2A and area 3 with area 3A. These two pairs of study areas were different sections of the same two plantations. Assuming that plantations 2 and 3 were separate wild populations and noting the significant differences in average leader morphology between areas 2 and 2A and between areas 3 and 3A, it may concluded that environmental differences are of considerable importance in governing the expression of the genotype controlling leader morphology.

Biological Interpretation

The procedures discussed in this section were designed to determine how the depths of the cortical resin ducts of eastern white pine leaders influenced the feeding habits of white pine weevils. The relationships between bark thickness and weevil feeding will not be discussed. The observations and measurements of the sizes and shapes of feeding cavities gave no indication of a possible causal interpretation for the relationship. This statement is in no way meant to imply that such an interpretation does not exist. Future studies may consider the proposal made by SULLIVAN (1961) that differences in bark texture may account for weevil preference for thicker bark.

Sampling

Four eastern white pine leaders which displayed heavy weevil feeding were collected in May, 1963. The leaders were stored in FAA until measurements were completed. Approximately 215 feeding cavities were studied by cross sectioning the leaders at the points on the periderm where weevils had penetrated the bark. Only twenty of the 215 cavities were used in the analyses. These twenty cavities were selected on the basis of having contacted the epithelial cells of both inside and outside resin ducts. This restriction was placed on the population being sampled in an effort to observe the influence of both ducts on one cavity.

The data recorded for each of these twenty cavities included the depth and width of the cavity and the depth of the inside and outside ducts contacting the cavity. The presence or absence of an egg was also noted. No attempt was made to measure the vertical length of the cavities under the periderm of the bark.

Analysis of Biological Interpretation

Linear correlation analysis was employed as the analytical procedure. The hypothesis tested was that no significant linear relationship existed between resin duct depth and the dimensions of the feeding cavity. The implication of the hypothesis was that resistance to weevil feeding would be manifested in reduced feeding cavity dimensions.

It was calculated that the depth of the inside resin ducts was significantly correlated with both cavity depth *(Figure 4 A)* and cavity width *(Figure 4 B)*. The frequency distribution of egg deposition is also shown in *Figure 4*. No such quantitative relationship was detected between outside duct depth and feeding cavity dimensions.

While microscopically examining the feeding cavities, certain consistent observations were made. None of the 215 feeding cavities severed the epithelial cells of the resin ducts. Observation of the shapes of the cavities made it possible to theorize the sequence of events which occurred

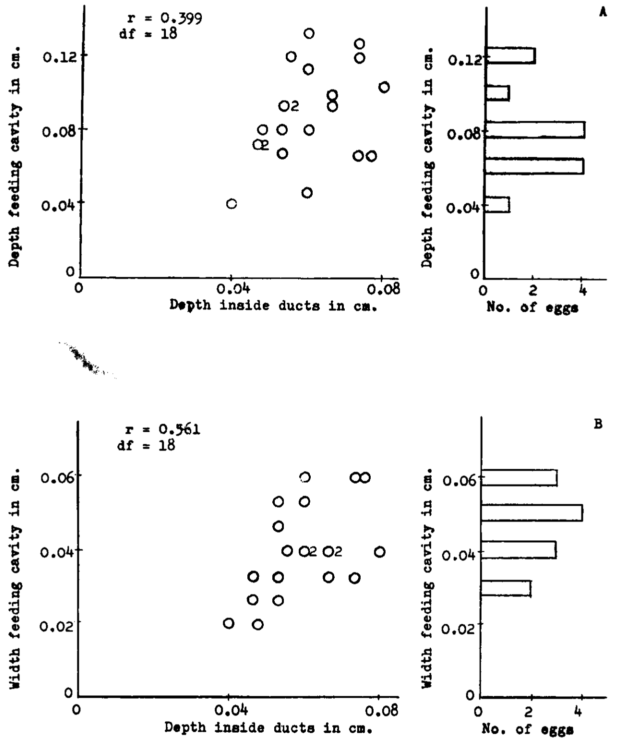


Figure 4. — Feeding cavity dimension related to depth inside resin ducts.

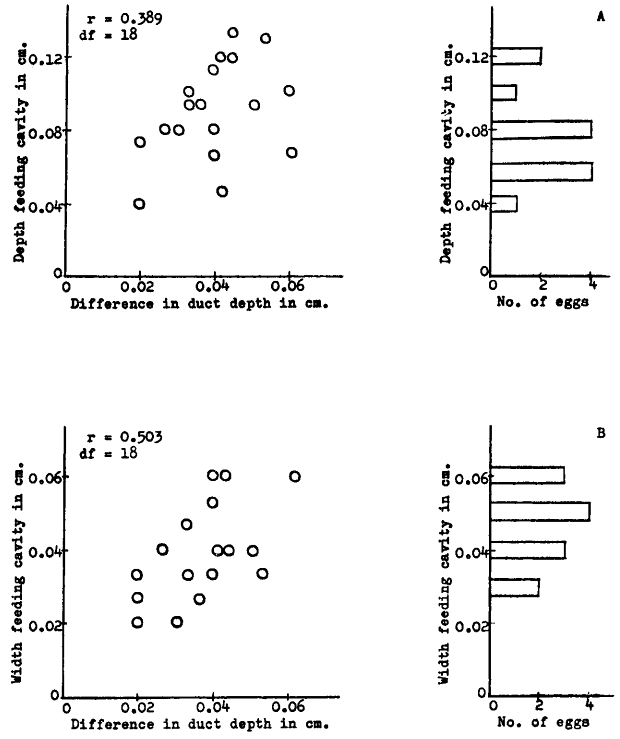


Figure 6. — Feeding cavity dimension related to difference in duct depths.

as the weevil fed. It appeared that when a weevil encountered the epithelial cells of a resin duct, the direction of feeding was reoriented and the excavation continued around the duct thus avoiding the epithelial cells. When the weevil encountered an outside resin duct immediately after penetrating the periderm of the bark, feeding at that point stopped as shown in *Figure 5.*

Considering these observations, the difference between the depths of the resin ducts was evaluated for its association with feeding cavity dimensions. The reason for this work was that, if the two sets of resin ducts were close together, feeding could not proceed around the inside ducts without contacting the epithelial cells of the outside ducts. It was found that the difference in duct depth was significantly correlated with both the depth of the feeding cavity *(Figure 6 A)* and the width of the feeding cavity *(Figure 6 B).* The similarity of the correlation coefficients in *Figures 4 and 6* was a result of the significant correlation between inside duct depth and the difference in duct depths (r = 0.451). Outside duct depth was not so correlated.

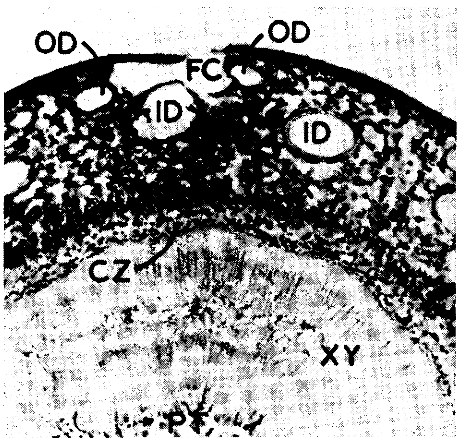


Figure 5. — Feeding terminated at resin ducts. — *OD* — Outside resin ducts. — *ID* — Inside resin ducts. — *FC* — Feeding cavity. — *CZ* — Cambial zone. — *CX* — Cortex. — *XY* — Xylem. — *PT* — Pith.

Discussion of Biological Interpretation

The population of feeding cavities which has been evaluated in this section consisted of the cavities which contacted both an inside and an outside resin duct. It was demonstrated that a significant linear association existed between inside duct depth and feeding cavity dimensions. A discrete relationship was observed between the outside ducts and weevil feeding. It was also found that the difference between the two duct depths was significantly related to the dimensions of the feeding cavity.

The interrelationships between these three leader characteristics with respect to the excavation of a feeding cavity may be best discussed by proposing the behavior of a weevil in the act of feeding as suggested by the preceding results and observations.

If a weevil initiates feeding directly over an outside resin duct, feeding will stop as soon as the epithelial cells of the duct are encountered. However, if the starting point of the excavation is offset to either side of the outside duct, the excavation will proceed by curving around the duct thus avoiding the epithelial cells. An inside duct may be encountered as feeding continues. Again the direction of the excavation is reoriented thus avoiding the duct. At this point the difference in duct depths would become critical. If the space between the two sets of ducts is such that the cavity cannot be advanced without contacting epithelial cells, feeding would apparently stop. If the space between the two sets of ducts is sufficiently wide, feeding proceeds around the inside duct to the phloem.

Considering the preceding description of weevil feeding, a hypothesis was formulated concerning the influence of resin duct depth on the number of feeding cavities present on the upper three inches of the leader: After a number of unsuccessful attempts at feeding due either to immediate contact of an outside resin duct or to encountering sufficient difficulty in feeding around an inside or an outside resin duct, or both, the weevil retreats and seeks a new site on the same or a different host tree to satisfy its instinctive efforts to feed, and in the case of females, to oviposit. This hypothesis suggests that a leader unsuited for weevil feeding due to the arrangement of the cortical resin ducts is likely to have fewer, but could, in fact, have a greater number of feeding cavities than other leaders more conducive to weevil feeding. The latter situation could arise when the weevil is repeatedly repelled from different feeding sites on the same leader. The likelihood of this situation occurring can only be determined by observing the action of weevils after encountering resin ducts while feeding.

It is interesting to note that only twenty or 9.3 percent of the 215 feeding cavities examined for this study were observed to contact the epithelial cells of both inside and outside resin ducts. This percentage is similar to the percent of the leader circumference occupied by outside resin ducts which ranged from ten percent to fifteen percent. Apparently the percent of the leader circumference occupied by the inside ducts had little influence on whether or not the feeding cavities contacted an inside duct. The microscopic observations indicated that, in fact, most feeding cavities do contact inside resin ducts. Apparently this was a result of the cavities being enlarged between the inside resin ducts and being limited either by the length of beak on the weevil or by encountering an inside duct *(Figure 7).*

Noticeably lacking in this discussion has been a statement concerning the number of resin ducts. It would seem intuitively reasonable that weevils feeding on leaders with large numbers of resin ducts would be likely to encounter the epithelial cells more frequently than on leaders with fewer resin ducts. The number of resin ducts, however, was not significantly correlated with weevil feeding. It was also noted that the number of resin ducts was not significantly correlated with resin duct depths in any of the areas studied in this investigation. This suggested that as duct depths decreased no more than random variation occurred in the number of resin ducts.

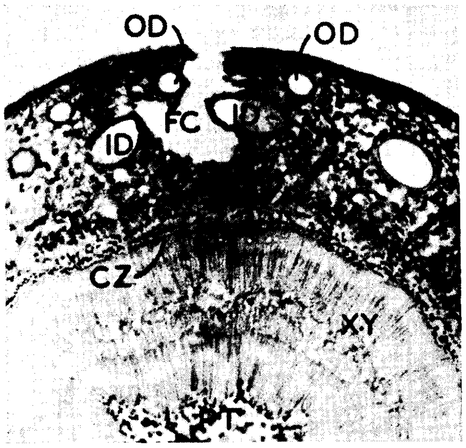


Figure 7. — Feeding cavity enlarged between inside resin ducts. — *OD* — Outside resin duct. — *ID* — Inside resin duct. — *FC* — Feeding cavity. — *CZ* Cambial zone. — *CX* — Cortex. — *XY* — Xylem. *PT* — Pith.

Summary and Conclusions

The linear relationships between twelve morphological leader characteristics of eastern white pine and weevil attack were evaluated in four locations in 1962 and in two locations in 1963. The eastern white pine plantations in which sampling was conducted were similar in age, height, and spacing but were otherwise quite different. The seed source of the trees could not be determined. The number of feeding cavities on the upper three inches of the leaders of the sampled trees was employed as the measure of weevil attack.

Bark thickness, depth of inside cortical resin ducts and depth of outside cortical resin ducts were found to be most consistently and significantly related to weevil feeding. None on the traits studied were so correlated with either length of larval feeding or number of adult weevils emerging following pupation.

The nature of the relationships between weevil feeding and bark thickness and resin duct depths was such that thinner bark and shallower ducts were associated with fewer feeding cavities. Individually the three correlated characters accounted for from nine percent to thirty-six percent of the variation in weevil feeding. Collectively, in multiple regression, the variation accounted for ranged from nineteen percent to forty-nine percent. The relative amount of variation accounted for by each of the three correlated characters in multiple regression was demonstrated to vary from location to location. The depths of the resin ducts were more important when outside duct depth was less than 0.018 centimeter and when inside duct depth was less than 0.056 centimeter. In areas in which these limits were exceeded, bark thickness accounted for a greater portion of the variation in weevil feeding. The role of bark thickness in the selection of a host tree by white pine weevils was concluded to be a matter of preference. That is, weevils demonstrated a preference for thicker bark but were capable of feeding on thinner bark.

The manner in which the depths of the cortical resin ducts influenced weevil feeding was investigated next. It was demonstrated that shallower inside resin ducts were associated with both shallower and narrower feeding cavities. Such a quantitative relationship was not detected for outside ducts. Microscopic observation indicated that no feeding cavity severed the epithelial cells of a resin duct. It was also observed that feeding cavities stopped upon contacting on outside duct immediately after penetrating the periderm if no room was available to circumvent the duct. The distance between the two sets of ducts was also investigated and found to be significantly correlated with feeding cavity dimensions. The relationships between these results and observations were summarized in the form of a hypothesis concerning their effect on weevil feeding: After a number of unsuccessful attempts at feeding due either to immediate contact of an outside resin duct or to encountering sufficient difficulty in circumventing the resin ducts, or both, the weevil retreats and seeks a new site on the same or a different host tree to satisfy its instinctive efforts to feed and, in the case of the females, to oviposit. Although the results of the present study indicated that the weevil retreats and seeks a new host tree, future work on this subject should recognize the possibility of different weevil responses. That is, under certain circumstances the weevil may respond to encountering cortical resin ducts by retreating and seeking a new feeding site on the same tree, resulting in an increase in the number of feeding cavities on the leader of a resistant tree.

The results of this study present an encouraging picture for selecting and breeding weevil resistant eastern white pines. The objective of such work should be to develop a variety with cortical resin ducts so arranged in the cortex of the leader bark that all weevil feeding activity will encounter the ducts. Although only eastern white pines of unknown seed origin have been considered in the present study, the racial variability of eastern white pine leader morphology will be discussed in a subsequent paper. The correlated characters should also be investigated in other white pine species and the possible interspecific hybrids. The correlated characters of these hybrids should be considered from three aspects: (1) improvement in F_1 hybrids, (2) increased variation of the correlated characters in the F_2 progeny, and (3) improvement in the progeny of the F_1 individuals backcrossed to the parents. Another useful aspect of the use of interspecific hybridization in the development of weevil resistant white pines is the possibility of incorporating as yet unrecognized forms of resistance into the progeny.

Résumé

Titre de l'article: *Relations entre les caractéristiques du pin Weymouth et la nutrition du charançon du pin.*

On a mis en évidence des relations linéaires entre 12 caractéristiques morphologiques de la flèche du pin Weymouth et des attaques de charançon du pin; l'expérience a été faite dans 4 stations en 1962 et 2 en 1963. Les plantations de pin Weymouth dans lesquelles les arbres faisant l'objet de cette étude ont été choisis, avaient le même âge, la même hauteur, le même espacement, mais étaient assez différentes pour d'autres traits. L'origine des graines utilisées n'a pu être établie. Le nombre de cavités nutritionnelles sur les 7 derniers centimètres de l'extrémité des flêches a été utilisé comme mesure de l'attaque du charançon.

Les caractères qui sont reliés à la nutrition de l'insecte de la manière la plus constante et la plus significative sont: l'épaisseur de l'écorce, la profondeur des canaux résinifères de la partie interne de l'écorce et la profondeur des canaux résinifères de la partie externe de l'écorce. Aucun des caractères étudiés n'est relié de façon aussi nette avec la longueur des cavités larvaires ou le nombre d'éclosions d'adultes.

Plus l'écorce est mince et plus les canaux résinifères sont superficiels, plus faible est le nombre de cavités nutritionnelles. Les trois caractères reliés rendent compte individuellement de 9 à 36% de la variation dans la nutrition du charançon. Pris ensemble, par régression multiple, on obtient 19 à 49% de la variation. La part de la variation attribuable à chacun des trois caractères liés dans l'analyse de régression multiple varie d'une station à l'autre. La profondeur des canaux résinifères est plus importante lorsque la profondeur des canaux de l'écorce externe est inférieure à 0,018 cm et lorsque la profondeur des canaux de l'écorce interne est inférieure à 0,056 cm. Dans les zones où ces limites sont dépassées, l'épaisseur de l'écorce rend compte d'une plus grande partie de la variation. Le rôle de l'épaisseur de l'écorce dans la sélection d'un arbre hôte par le charançon du pin, est une question de préférence: les charançons préfèrent les arbres à écorce épaisse mais sont capables de se nourrir sur des arbres à écorce mince.

On a étudié ensuite la façon dont la profondeur des canaux résinifères de l'écorce influence la nutrition du charançon. On a pu montrer que si les canaux de l'écorce interne sont assez superficiels, les cavités nutritionnelles sont à la fois plus superficielles et plus étroites. Une telle relation quantitative n'a pas été établie en ce qui concerne les canaux de l'écorce externe. Des observations microscopiques montrent que les cavités ne recoupent pas les cellules épithéliales d'un canal résinifère. On a également observé que les galeries sont arrêtées au contact d'un canal de l'écorce externe dès la pénétration du périderme s'il n'y a pas de place pour contourner le canal. La distance entre les deux séries de canaux est liée de façon significative avec les dimensions des cavités nutritionnelles. Ces résultats et observations ont permis d'établir une hypothèse concernant leur influence sur la nutrition du charançon: après un certain nombre de tentatives infructueuses pour se nourrir, dues soit au contact immédiat d'un canal externe ou à des difficultés recontrées dans le contournement des canaux, ou les deux, le charançon se retire et cherche un nouveau point d'attaque sur le même arbre ou sur un arbre différent, pour satisfaire ses efforts instinctifs pour se nourrir et dans le cas de femelles pour pondre. Bien que les résultats de la présente étude semblent indiquer que le charançon se retire et recherche un nouvel arbre, de nouveaux travaux sur ce sujet devraient envisager la possibilité de différentes réactions de l'insecte. En effet, dans certains cas, le charançon peut réagir à la rencontre de canaux résinifères externes en se retirant et en cherchant un nouveau point d'attaque sur le même arbre, ce qui aboutit à une augmentation du nombre de cavités nutritionnelles sur la flèche d'un arbre résistant.

Les résultats de cette étude laissent espérer que l'on pourra sélectionner et améliorer des pins Weymouth résistant au charançon. L'objectif d'un tel travail doit-être de produire une variété avec des canaux résinifères corticaux disposés dans l'écorce de la flèche, de telle sorte que toute activité nutritionnelle du charançon aboutira à la rencontre d'un canal. Bien que dans la présente étude on n'ait considéré que des pins Weymouth d'origine inconnue, la variabilité raciale de cette espèce, en ce qui concerne la morphologie de la flèche, sera étudiée dans un nouvel article. Les caractères liés devront également être étudiés dans d'autres espèces de pins à 5 feuilles et chez les hybrides interspécifiques existants. Les caractères liés de ces hybrides doivent être considéres de trois façons:

(1) Amélioration chez les hybrides F_1,

(2) Augmentation de la variabilité des caractères liés dans les descendances F_2 et

(3) Amélioration dans les descendances des hybrides F_1, croisés en retour avec les parents.

Un autre aspect intéressant de l'emploi de l'hybridation interspécifique pour développer la résistance au charançon du pin Weymouth est la possibilité d'inclure dans les descendances des formes de résistance encore inconnues jusqu'ici.

Literature Cited

Callaham, R. Z.: Observations on pine susceptibility to weevils. Pac. S. W. For. and Range Expt. Sta. Tech. Paper 51, 12 pp. (1960). — Fowler, D. P.: In discussion following: Heimburger, C.: Forest tree breeding work in Canada. Fifth N. E. For. Tree Improve. Conf. August, 1957, 26 pp. (1958). — Gerhold, H. D., and Stroh, R. C.: Integrated selection for white pine weevil resistance and its components. World Consult. For. Genetics Tree Improve., Stockholm (1963). — Heimburger, C.: The breeding of white pine for resistance to weevil. World Consult. For. Genetics Tree Improve., Stockholm (1963). — Holst, M. J.: Breeding for weevil resistance in Norway spruce. Z. Forstgenetik Forstpflanzenzüchtung 4: 33—37 (1955). — Kriebel, H. B.: Bark thickness as a factor in resistance to white pine weevil injury. Jour. For. 52: 842—845 (1954). — Mac

Aloney, H. J.: The white pine weevil (*Pissodes strobi* Peck). — Its biology and control. N. Y. State College For. Tech. Publ. 28, 87 pp. (1930). — Plummer, C. C., and Pillsbury, A. E.: The white pine weevil in New Hampshire. N. H. Agric. Expt. Sta. Bull. 247, 27 pp. (1929). — Sass, J. E.: Botanical Microtechnique. Iowa State College Press, Ames, 228 pp. (1958). — Smith, R. H.: Techniques for determining the toxicity of pine resin vapors to *Dendroctonus brevicomis* and *D. jeffreyi*. Jour. Econ. Ent. 54: 359—365 (1961 a). — Smith, R. H.: The fumigant toxicity of three pine resins to *Dendroctonus brevicomis* and *D. jeffreyi*. Jour. Econ. Ent. 54: 365—369 1961 b). — Smith, R. H.: Toxicity of pine resins to adult *Dendroctonus (Coleoptera: Scolytidae)*. Unpublished Ph. D. thesis. University of California, Berkeley, California (1961 c). — Snedecor, G. W.: Statistical Methods. Iowa State College Press, Ames, 5th Ed., 534 pp. (1957). — Sullivan, C. R.: The effect of weather and the physical attributes of white pine leaders on the behavior and survival of the white pine weevil, *Pissodes strobi* Peck, in mixed stands. Canad. Ent. 93: 721—741 (1961). — Wright, J. W., and Gabriel, W. J.: Possibilities of breeding weevil resistant white pine strains. N. E. For. Expt. Sta. Paper 115, 35 pp. (1959).

Newsletter - Berichte

An Expanding Tag for Seedlings

Workers in forest tree improvement often need to tag small seedlings to identify them after out-planting. If tags are applied before planting and possibly before lifting at the nursery, they must be durable and securely attached. The small size of many forest tree species makes the attaching of tags to limbs impractical. Tags attached with a wire or cord around the main stem too frequently girdle fast-growing seedlings.

In the spring of 1962 experimentally tagged Douglas fir seedlings were out-planted in progeny tests by the Industrial Forestry Association. Seedlings were identified with a tag conceived by John W. Duffield, then Technical Director, Industrial Forestry Association. This note reports on the success of his system after three growing seasons in the field.

Tags cut from soft aluminum, ½ inch by 3 inches, 0.006 inch gauge, were stamped in black ink with a number. A slight impression was made in the stamping process. Manufacturer of these particular tags was the Eastman Tag and Label Company of Richmond, California, but any manufacturer capable of cutting and stamping soft aluminum should be able to supply such tags. Cost, including the stamping, was approximately one cent per tag when purchased in lots of 5 to 10 thousand tags.

Tags were applied to the main stem in a spiral manner immediately after lifting in the nursery *(fig. 1, left)*. The tags unwound as the seedlings grew during the three subsequent growing seasons *(fig. 1, center and right)*. No girdling was observed on the many seedlings inspected in late 1964. Some trees did show a slight depression of the stem underneath the tag after one or two seasons. However, with continued growth there was no evidence of injury, and all observed tags were expanding with tree growth. With Douglas fir the tags should be removed after three to four growing seasons and either placed on limbs or replaced with more conventional tags.

Figure 1. — Stem sections from tagged Douglas fir seedlings: 2—0 nursery seedling *(left)*, after 2 growing seasons in the field *(center)*, after 3 growing seasons in the field *(right)*.

Joseph G. Wheat, Director,
Tree Improvement Laboratory,
Industrial Forestry Association
Nisqually, Washington

Proceedings of a Forest Genetics Workshop. Macon, Ga., October 25—27, 1962. Sponsored Publication No. 22 of the Southern Forest Tree Improvement Committee. Pp. 97.

Greene, J. T., and Porterfield, H. D.: Selection and progeny testing for early cone production in loblolly and slash pine *(p. 9)*: —

Für erfolgreiche Auslese auf frühes Blühen bei *Pinus taeda* und *P. elliottii* werden Beispiele gegeben. In der Nachkommenschaft relativ früh blühender Bäume traten Individuen auf, die im Alter von drei bis vier Jahren weiblich und männlich blühten. Teilweise war auch wiederholtes Blühen in aufeinanderfolgenden Jahren zu beobachten.

Callaham, R. Z., and Duffield, J. W.: Heights of selected *Pinus ponderosa* seedlings during 20 years *(p. 10)*: —

Die Durchführung dieses Frühtests ist verschieden von der Auslese einzelner überlegener Sämlinge im Baumschulbeet: Das Saatgut war auf gleiches Korngewicht sortiert und stammte aus einer einzigen bzw. aus 81 frei abgeblühten Nachkommenschaften. Unterschiede in der Herkunft und im Samengewicht konnten keinen Einfluß auf die Ergebnisse haben. Nach 12 bzw. 20 Jahren ließen sich keine Unterschiede zwischen den Bäumen mehr nachweisen, die nach 75 Tagen im Saatbeet auf große oder geringe Epikotyllänge ausgelesen waren. Die Kotyledonenzahl war nicht mit dem Höhenwachstum im Alter von 2, 5, 12 oder gar 20 Jahren korreliert. Zwischen der Kotyledonenlänge und dem Höhenwachstum im Alter 2 ergab sich eine Beziehung mit einer Bestimmtheit von etwa 0,2, späteres Höhenwachstum war nicht mehr mit der Kotyledonenlänge korreliert. Aufeinanderfolgende Höhenmessungen waren eng korreliert, die Höhen im Alter 12 und 20 jedoch nicht mehr mit der im Alter 2. Die Variation im Höhenwachstum der Einzelbäume im Alter 20 ließ sich etwa zur Hälfte aus der im Alter 5 und etwa zu drei Vierteln aus der im Alter 12 voraussagen. Bei mäßig starker Auslese (etwa 6%) nach 2 Jahren im Saatbeet ließen sich nach 15 Jahren noch Unterschiede zwischen drei gebildeten Klassen in Höhe, Durchmesser und Volumen des Schafts nachweisen. Es wird auf den Unterschied der Beziehungen zwischen den Messungen an Einzelbäumen und zwischen den Mitteln von Nachkommenschaften hingewiesen.

Reines, M.: Photosynthetic efficiency and vigor in pines: variation *(p. 14)*: —

Zwischen Nadelbündeln verschieden alter Kiefernzweige ließen sich Unterschiede in der CO_2-Absorption nachweisen; von der Spitze bis zum Grunde der Zweige nahm die Absorptionskapazität ab. Auch zwischen Himmelsrichtungen und zwischen verschiedenen Höhen in der Baumkrone gab es signifikante Unterschiede, erst recht zwischen Bäumen. Unter kontrollierten Bedingungen nahmen gedüngte Sämlinge mehr CO_2 auf. Unterschiede zwischen Familien und zwischen Sämlingen innerhalb Familien waren ebenfalls signifikant.

Derr, H. J.: Brown-spot resistance among F_1 progeny of a single, resistant longleaf parent *(p. 16)*: —