TESTING WHITE PINES FOR WEEVIL RESISTANCE

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The desirability of having a white pine strain resistant to the white pine weevil is not likely to be questioned by a single forester in the Northeast. The possibilities of producing such a strain were investigated by Wright and Gabriel (1959), who reported the existence of "enough proven resistance to form the basis of weevil- resistant strains with desirable growth characters", and stated that "the production of a white pine that is genetically resistant to the white-pine weevil is a worth-while undertaking - - -. " Although these authors regarded many of their conclusions as tentative, they are promising enough to encourage the selection and testing of white pines for weevil resistance. This paper seeks to relate what is known about the biological interrelationships of *Pinus strobus* L. and *Pissodes strobi* Peck to some of the problems involved in the selection process. The discussion will center on the testing of weevil resistance after original parental selections have been made.

Let us begin by considering what should be accomplished in the selection process. Regardless of the methods employed, it is desired (1) to measure precisely the degree of weevil resistance, and (2) to classify accurately the types of weevil resistance inherent in white pine progeny groups. Testing procedures should discriminate between genetic and environmental components, and permit reproducible comparisons among the progeny groups either under a variety of natural conditions with high exposure to weevil damage, or under artificial conditions in which results are closely correlated with those of natural conditions.

Complete immunity of a white pine strain to weevil damage represents an ideal solution, but probably an unrealistic goal. According to Painter (1951), who is an authority on insect resistance in plants, "there are few, if any, varieties which are immune to the attack of any specific insect known to attack varieties of the same plant species." Of the various white pine species examined by Wright and Gabriel (1959), *Pinus monticola*, considered by them to be the most promising known source of weevil resistance, incurred 8 to 21 percent as much weevil damage as did comparable P. *strobus*; none of the species was reported to be immune to weevil damage.

Perhaps the most useful measure of the degree of weevil resistance is based on the number of trees tallied according to the number of weevilings per tree. It is applicable to all three types of resistance, which will be discussed subsequently. Comparisons between trees of different ages, or growing on different sites, are possible through the use in all tests of a standard susceptible white pine strain, or by recording supplementary information on the number of years of exposure to weevil attack and the weevil population density in each year. Refinements in this rather simple technique of measuring resistance will probably be desirable after the early screening process has yielded a limited number of outstanding trees chosen for further breeding.

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The three types of resistance recognized by Painter (1951) are (a) non-preference, (b) antibiosis, and (c) tolerance. Thus weevil resistance can result from (a) the weevil not being attracted to, or being repelled from, feeding and ovipositing on a tree, or (b) after feeding on a tree, the weevil being killed, injured, or prevented from completing its normal life cycle, or (c) recovery of a tree from weevil attack by a population approximately equal to that damaging a susceptible host. Evidence of the three types of resistance, briefly, would consist of (a) few if any signs of feeding and oviposition, (b) signs of feeding by adults, and possibly also larvae, followed by a smaller than average number of adults emerging, and (c) the absence of forking and crooks in the main stem, all of these in the presence of large weevil populations. It will become evident later that all three types of resistance may be present in white pines, and these could be exemplified by a wide variety of different resistance mechanisms. The three types of resistance also appear to be present in the resistance of western yellow pines to the pine reproduction weevil (Smith, 1960) and in many other plant-insect relationships (Painter, 1951). Separate genes would be expected for each type of resistance, the recognition of which would greatly enhance the effectiveness of a breeding program.

The trees to be tested might come from several sources. Wright and Gabriel (1959) suggest that these could include exotic white pines such as P. monticola, P. griffithii, P. peuce, and P. ayacahuite, hybrid combinations of P. strobus and exotic white pines, and possibly ecotypes of P. strobus. To this list I would add P. strobus mutants, which can be produced artifically by irradiating seeds with gamma rays dosages below 4, 000 roentgens (A. D.. Rhodes, personal communications; McMahon and Gerhold, 1961). In view of the genetic diversity of such a collection, which it is hoped would contain considerably more weevil resistance than P. strobus, one might well ask under what conditions weevil resistance could best be measured and classified.

Ultimately, the value of weevil resistant white pine strains must be judged under the natural conditions in which they will be grown. But natural attacks of the weevil have several characteristics that would be disadvantageous during the intensive testing period of an improvement program. When a white pine stand first becomes susceptible, at an age of perhaps four to six years, the damaged trees are often localized in a small portion of the stand, and the percentage of weeviled trees is often quite small for a few years. This is due to the limited dispersion and gregarious feeding habits of adults (Barnes, 1928; Sullivan, 1953, 1957). Thus the trees are not equally exposed to attack. Thereafter, the percentage of weeviled trees may increase rapidly if there is a heavy weevil population in the immediate vicinity, or it may increase gradually and at a fluctuating rate (MacAloney, 1930; Graham, 1926).

A high incidence of weeviling can be encouraged in several ways. Test plantings should be located on unshaded sites where conditions are favorable for rapid and vigorous leader growth, for such conditions favor heavy weeviling (Graham, 1926; MacAloney, 1930; Sullivan, 1957, 1960). Although the maximum rate of weeviling in an illustration by Graham (1926) occurred with less than 200 trees per acre, a reasonable compromise might be on the order of 400 to 700 trees per acre.

In most plantations in which weeviling has occurred for several years, the incidence of weeviling follows the binomial or the Poisson distribution (Wright and Gabriel, 1959). MacAloney reported the annual rate of weeviling in heavily weeviled stands to be over 50 percent, and in the most heavily weeviled stand reported by Wright and Gabriel (1959), the average number of weevilings per tree was 4.00 at age 19. Under such conditions, a stand of white pine would theoretically have to be exposed continuously for 10 to 15 years before the expected percentage of weeviled trees would approach 100, according to the Poisson distribution. Such a high level of weeviling is not necessary for adequate comparisons of the mean resistance of progeny families, but it would be desirable for selecting a reasonably small number of trees for breeding purposes.

To summarize the disadvantages of natural attack, initially it may be non-random; it will require at least 10 to 15 years of exposure, and in some cases the desired intensity of weeviling may never be attained; and the ways in which the data may be treated statistically are limited, even if the cumbersome arc-sine transformation of the Poisson distribution is employed. Therefore, it would seem desirable to investigate alternatives to selection after natural attack.

Caged attack is a variation of natural attack which has been used to increase the intensity and uniformity of infestation, though not always successfully (Painter, 1951). If complete white pine trees were to be caged for several years of exposure, the cages would need to be very large and therefore expensive. We experimented this year by enclosing 12 inch portions of single white pine leaders with screen cages 1.5 inches in diameter, and then introduced either 4, 8, or 16 weevils into each. One of the objectives was to find how many weevils could be employed successfully in this manner. so that the variability in a weevil population could be adequately sampled. Fairly large variability has been demonstrated in the responses of individual weevils to naturally occurring repellents in white pine and several spruces (Anderson and Fisher, 1956, 1960) which appears to be an important basis of host specificity. The results of our trials were somewhat discouraging, for even the leaders exposed to only four weevils were fed upon heavily, so that the larvae starved to death in many cases. There was also considerable mortality of adults, possibly due to low temperatures, so that the intensity of attack was not uniform. These difficulties could be overcome by enlarging the cages so that they could enclose large portions of trees, and by placing only fertilized females into the cages. But determining the sex of weevils is a time consuming process, and not completely accurate. A suitable technique of caging could no doubt be developed. But it would probably be expensive, and if weevils were not given a choice of several trees certain types of possible resistance classified under non-preference would not be detected.

Another variation of natural attack might be termed reinforced natural attack, which differs only in that insect populations would be maintained more uniformly and in greater numbers than would occur naturally. Two ways can be suggested for accomplishing this with the white pine weevil.

Adults can be collected in other areas and introduced in a uniform pattern into the test area. They can be collected either early in the oviposition period (at a rate of 60 per man hour), or infested leaders can be collected and disseminated just prior to emergence of the adults (probably at a faster rate, but some of these would not survive the winter, about 30 percent according to Barnes, 1928). In this manner the initial attack will be evenly distributed, at a controlled intensity, and caused by whatever biotype of the weevil has been chosen. A similar procedure has been used in studying the resistance of wheat to the hessian fly (Painter, 1951).

After a heavy weevil population has been established, an adequate supply of susceptible trees will be required for its maintenance. The facts that *Pissodes strobi* is rarely found beyond the range of *Pinus strobus* (Sullivan, 1957) and that weeviling is less prevalent when less susceptible species are planted in mixture with white pine (MacAloney, 1930), suggest that test plantings of resistant white pine strains should contain a sizable proportion of highly susceptible white pines, for example in alternate rows. These can serve the dual purpose of providing for the feeding and reproduction of the weevils, and providing a standard measure for comparison of weevil resistance. If the *a priori* assumption holds, that any two adjacent trees are equally exposed to weevil attack, then the infestation calculated from the standard susceptible strain can be applied in evaluating the resistance of other strains. The placement of a test plot in a larger area of susceptible plants, or the interplanting of rows of known susceptible varieties among those being tested has been used in studying the resistance of cotton to leafhoppers, and the resulting heavy infestation has been called a "bombardment effect" (Parnell *et al*, 1949).

"The most useful insect population (density) is one which gives the maximum difference between resistant and susceptible types" (Painter, 1951). In the case of the white pine weevil, this would probably approach the maximum population which can be maintained over a period of several years, because even in heavy natural infestations the incidence of weeviling is low (a characteristic of Poisson distributions), and because the risk of moderately resistant trees being killed due to weeviling is practically nil, except for very small trees. The maximum population which can be maintained must be determined experimentally. Its theoretical upper limit can be approximated from the data of Sullivan (1957) as being about 8 weevils per susceptible tree at the time of emergence. After the winter, perhaps an average of 56 of these would survive (Barnes, 1928), of which half, or 2.8, would be females (Sullivan, 1957; Sutherland and Gerhold, 1961). These 2. 8 females could deposit an average of perhaps 130 eggs each (Barnes, 1928: 150; Graham, 1926: 115; MacAloney, 1930: 50 to 150, mean 125; Plummer and Pillsbury, 1929: 25 to 201, mean 129), or a total of 360 which would develop into 8 adults, the number previously mentioned. Even with a greater number of eggs per leader, the average number of adults emerging appears to be limited to about 8. With a population of such high density, however, it is quite possible that the actual mortality due to various causes would be higher than the theoretical, so that it might be impossible to maintain the population at this level without annual additions. Barnes (1928) found that population levels of 23 to 24 weevils per 100 susceptible trees were associated with annual weeviling rates of 24 to 27 percent. A higher rate is desired, and therefore trials can be conducted in the range of perhaps 50 to 600 weevils per 100 susceptible trees at oviposition time to determine the optimal population. A considerable increase in the incidence of weeviling might result in the data being almost normally distributed, which would be of considerable statistical advantage.

It seems quite likely that a suitable technique can be developed for reinforced natural attack, so that several disadvantages of natural attack would be overcome, and its desirable features would be retained. The initial attack would be intense and

Sullivan (1957) has reported data bearing on the tolerance of white pine to weevil attack. If the extent of larval damage was less than 10 inches in length some trees survived the attack, though with reduced height growth. On those trees with more than 10 inches of larval damage, all leaders were killed. The recovery of a tree with 10 inches or more larval damage would therefore constitute evidence of resistance through tolerance. Ten inches of larval damage was found to be equivalent to about five inches of adult attack, corresponding to 88 eggs per leader. An average of 2.3 weevils would emerge from 88 eggs, and if this would be the maximum rate of emergence in a plantation, little increase in weeviling would be expected without continuing immigration. Another form of tolerance which I have observed occurs in trees with partial forking. When one fork is weeviled, the other becomes the leader with almost no crook. When such a tree is not weeviled, one fork is dominated by the other so that only one central stem develops. It is possible that the forking is caused by physiological maladjustment to the environment, in which case this might represent pseudoresistance, which has only limited usefulness.

In order to be assured of success via the causative mechanism approach to selection, three types of evidence should be presented, as suggested by Painter (1951):

> (1) experimental evidence of an intimate relation between supposed cause and the insect physiology, plant physiology, or insect behavior; (2) evidence of complete association between an assigned cause and a given genetic factor wherever this factor occurs, but particularly in segregation following crosses between resistant and susceptible plants; and (3) statistical evidence in field tests in the form of high correlation between the assigned cause and resistance. "

Such evidence is not now available for weevil resistance. A long period might be required to obtain it. But this approach should not be neglected, for it could eventually lead to more rapid and far reaching progress than might otherwise have been possible.

This discussion would not be complete without some mention of the permanence of weevil resistance. Some recent developments in Wisconsin and Michigan gave cause for concern (Graham and Satterlund, 1956; Trefts, 1958). Prior to 1950, the white pine weevil attacked red pines occasionally, but the larvae succumbed before reaching the adult stage. By 1954, weevils had completed development in red pine, with adults emerging in large numbers. During 1955 emergence rates were comparable with those from favored hosts such as white pine, Scotch pine, and Norway spruce, and at certain locations the infestation rates were increasing steadily. If the weevil can adapt itself to red pine in a five year period, could it not also overcome the resistance in newly developed white pine strains ? It is true that a certain risk is involved, for the same genetic principles that apply to white pine also applies to the weevil, and it has the advantage of much shorter generations. But this eventualitycan be guarded against successfully if improved strains are adequately tested by exposure to various biotypes of the weevil, and if different strains of white pine each containing a different type of resistance are mixed in plantations, or if the several types of resistance are incorporated into a single strain.

This look into the future helps to put into perspective the relative usefulness of selection via natural attack or its refinements, and via the causative mechanism approach. Both have a place in a program for producing weevil resistant white pines.

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DISCUSSION

BUCKINGHAM - Mr. Hocker, how many pounds of fertilizer did you use per tree? I didn't quite get that.

HOCKER - The average was 21 pounds per tree for both stands. We apportioned it on an area basis, 1/10 of a pound per square foot of projected crown area. So that small trees got less fertilizer than big trees which may account partly for that diameter fertilizer interaction. This is what we want to try to isolate and test if we can.

NIETZOLD - I'd like to ask Mr. Hocker a question on the spacing of trees in the various age groups. Have you any figures on the 50-year age group, on the number per acre, or on spacing?

HOCKER - I coudn't tell you in so far as what the stand basal area might have been. We were more interested in individual trees than in groups, and it wasn't an entirely uniform stand that we dealt with in either case.

HEIMBURGER - I have questions for all three speakers. I think that the paper by Hocker is very interesting but of course it is related to site. Under his particular conditions we get certain response to fertilizer treatment. With white pine everything is fine, but there is a lot of danger to generalize in that I think moisture relationships also enter into the question. We have at one time at Maple tried to girdle some white pine on a rather moist site, a rich site in a ravine, and did not get any response. Apparently deficiency water relationships also have a role, and of course, also the nutrients in the soil themselves have some relation to the fertilizer applied. If there is a difference in certain nutrients, naturally the response to these particular nutrients will be stronger than to others and will probably be shown in cone production.

In the second paper, we in tree breeding are concerned with male flowers much more than female flowers because grafts taken from the top of a tree produce female flowers first. Seedlings of white pine also produce female flowers first and young plantations produce empty cones because of lack of pollen. We will be very interested in stimulating male flower production. Therefore, it is interesting to know that male strobili are found in the fall. That means that anything we do to white pines can be investigated in the fall in buds and we can then find out whether our results are successful or not.

Now the third paper is open to considerable argument and I hope that we can start something interesting here. I believe that in any breeding for resistance to insects we may often spoil our work by too drastic measures. Supposing there is no adequate resistance in any white pine and that we have some resistance in *P. strobus*, *peuce*, *monticola*, and *griffithii*. We subject our materials to a reinforced natural attack and may spoil the whole works. I would suggest a more moderate procedure to begin with. Supposing we first find that we have resistance to moderate attack, that we have some pines that can stand two or three ovipositions by the weevil, and recover beautifully. Then, eventually, we can probably intensify the attacks as we get materials that can stand moderate attacks. After all, we did not produce Jersey cows from buffalo heifers in a few generations. It took many generations to produce these. Until we know more about it, we must assume that resistance is inherited in a polygenic manner. We thus may need more than a few generations of selection to obtain the resistance levels we desire, and a very heavy attack during the initial stages of our work, especially a reinforced natural attack, may obscure the picture. It may kill off the leaders of individuals that are resistant to moderate attack, and yet these are the most promising ones to build on, if we cannot find anything that is resistant to heavy attack. Therefore, I would suggest that we subject our test materials to moderate attack and find out something there, If we actually find something that is promising, then we have something to build on and can gradually reinforce the attacks. We are then at least limiting our tests to materials that can stand moderate attacks and among these we can select further for resistance to more intensive attacks. This reasoning applies also to breeding for resistance to blister rust.

GERHOLD - I would agree in part, but suggest that even under heavy natural attack there is considerable risk of individual trees not being weeviled even though they might be susceptible, and therefore in order to reduce the selected trees to a reasonable number for further breeding, I think a heavy attack would be desirable. The trees would not be lost under heavy attack, but the relative resistance could be measured. Under natural conditions, I would guess that the damage to comparable trees would be quite a bit lighter than under reinforced natural attack.

FOWELLS - I would like to address a comment to Dr. Gerhold. Some of you may have seen N. T. Mirov's recent technical bulletin on the terpenes of the pines. Although he characterizes various pines with rather definite amounts of terpene constituents, he doesn't infer that these are exact. I wonder whether some of the olfactory attractions that Dr. Gerhold reports may be due to some very subtle differences in white pine terpene constituents. Some of the terpenes that Mirov finds are quite odorous. This could be done very easily now with gas chromatography. I think it would be well worth while following up.

GERHOLD - It is quite interesting to me that someone else independently arrived at an opinion similar to mine. We have in fact been trying to get some financial support in order to carry on some of this work. It would require equipment that would cost about $8, 000, but I think there are some good possibilities.

LARSSON - I was interested in Mr. Hocker's talk on fertilizer. What kind of fertilizer did you use ?

HOCKER - Eastern States Farmers Exchange 10-10-10. We debated as to what we should use and on the basis of Wenger's results with loblolly, I felt that if we got somewhere around 20 pounds of fertilizer to the trees with a fair amount of nitrogen we might expect to jolt the trees out of their lethargy. It was a "flier" that we took in the hope that it would pan out. I think we did get some leads, but I don't think, to answer Dr. Heimburger's comment, that our results are anywhere near conclusive for all sites. The treatments worked on the stands that we had and with the trees that we had. I think these results provide us with some things that we should be following up.

LARSSON - What was the width of your girdle ? I understand from talking to nurserymen that they recommend a girdle of approximately 1/8 inch in conjunction with pruning to stimulate fruit production. We are also interested in this technique to stimulate the production of seed on silver maple and for this reason I am curious of its affects on pine.

HOCKER - We used a standard bark scribe with about a half-inch blade. Treatment was a single girdle with a half-inch bark scribe. We had only one casualty that could possibly be traced to girdling. One of the younger trees appeared to have been weakened; it was snapped off at the girdle. Aside from that most other girdled trees appear to have survived the treatment fairly well and overgrew the girdle in a relatively short period of time (one year).