SOME OBSERVATIONS ON WEEVIL RESISTANCE OF PINUS PEUCE

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Pinus peuce Griseb. is one of the more promising exotic white pines for introducing increased weevil resistance in a white pine breeding program in that it is hardy in central Ontario and also carries a considerable degree of resistance to blister rust. Grafts of this species have shown more weevil resistance than P. strobus at the Southern Research Station. A cooperative project with the Forest Insect Laboratory in Sault Ste. Marie was initiated in 1958, in order to study the reaction to weevil attack of selected P. strobus and P. peuce, field-grafted in 1957 on Scotch pine (P. sylvestris L.) in a small plantation near Thessalon, Ontario. The plantation in question was examined by Dr. C. R. Sullivan and assistants of the Forest Insect Laboratory annually (in the fall) from 1958 to 1963 and data were obtained on leader condition and reaction to weevil attack of all grafts at time of examination. The leader condition in any one year was used to determine the weevil suitability of the available leaders during the following year. The degree of weevil attack and of weeviling were thus determined on the basis of targets available to the weevil by leader growth in the previous year. The data have been presented by Dr. Sullivan in annual reports and have been assembled for joint publication by Dr. Sullivan and myself. The main results of these are presented in the following report.

Weevil resistance is subdivided into 3 classes: (a) unsuitability of leader to weevil attack depending largely on size (thickness, length); (b) unattractiveness, resulting in fewer than expected attacks on suitable leaders; (c) unsuccessful attacks causing various degrees of recovery of leaders after feeding and oviposition, and thereby interruption of the normal reproductive cycle of the weevil.

Leaders of white pine can resist weevil attack by being unsuitable, because of small size (slender leader types) (Belyea and Sullivan, 1956; Sullivan, 1959), or because of heavy resin flow interrupting an attack. Selection for slender leaders, if such are inherited, would possibly include selection for low nutrient uptake efficiency. If the leaders were unattractive to the weevil because of shortness, this would add the possibility of selection for slow growth. Selection for long slender leaders would include the possibility of selection for strong apical dominance, favoring satisfactory recovery from weeviling, and would not be directed

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against overall ecological efficiency and growth rate. The other kind of resistance to weevil attack is presumably based on heavy resin flow, making oviposition in feeding cavities unattractive and triggering an avoidance reaction (Gerhold, 1962; Stroh, 1964; Stroh and Gerhold, 1965).

Resistance to weeviling in white pine is based on heavy resin flow following a weevil attack, The resin flow would cause mortality of weevil larvae after hatching, favouring the recovery of attacked leaders. Heavy resin flow is, presumably, also influenced by environmental factors, such as hydration and adequate nutrient supply, and by morphological characteristics, such as size and distribution of resin canals in the cortex, and thickness of this cortex in leaders. Selection for heavy resin flow would not be directed against growth vigour and overall ecological efficiency nor against strong apical dominance. However, it would also not be directed against selection for leader thickness which in pines is strongly correlated with side-branch thickness, undesirable in the production of high lumber grades, The superior weevil resistance of P. peuce observed at the Southern Research Station is mostly based on better recovery after attacks than in P. strobus. It is thus a resistance to weeviling.

A third kind of resistance to weevil attack could, presumably, be based on chemical characteristics of oleoresins and/or other substances found on/in white pine leaders making these unattractive to the weevil and variously correlated with the morphological characteristics mentioned above (Plank and Gerhold, 1965), The syndrome of heavy weeviling thus consists of a heavy residual population of weevil attacking open-grown vigorous trees with strong (thick and long) leaders, having thick bark with few and small resin canals with poor resin flow, and with poor apical dominance. In addition to this, some genetic host-parasite interrelation ship between the coexisting white pine and weevil populations must be assumed.

The materials field-grafted in the spring of 1957 consisted of 20 scions of each of 5 clones of heavily weeviled and 5 clones of seemingly weevil resistant P. peuce from near Havelock, Ontario, and of 5 clones of P. strobus selected for good growth-form and freedom from weeviling in a plantation at Midhurst Provincial Forest Nursery and 5 clones of weeviled P. strobus at Thessalon, Ontario; a total of 400 scions, Every other tree in every other row was top-grafted with 2 white pine scions belonging to the same clone, resulting in 200 double grafts, Starting in the northeast corner of the plantation, 40 trees were grafted in each of 5 alternate rows with 80 scions belonging to 4 clones. The arrangement was one graft (2 scions) of P. peuce followed by a graft of P. strobus again followed by a graft of another P, peuce and of another P. strobus.This sequence was repeated 10 times in every grafted row, using the same 4 clones in the row. Each row thus contained 4 different white pine clones arranged systematically, with no replication of clones between the rows, Such an arrangement does not lend itself to an analysis of variance and only limited information could be obtained from a Chi-square evaluation of individual clones, This should, therefore, be interpreted as being of indicative value only. However, it was possible to make valid Chi-square tests of groups of clones distributed over the entire test plantation in respect to several important attributes related to weevil attack.

GRAFTING COMPATIBILITY

The results of graft survival tallies made in the fall of 1958 are as follows:

	Living		Dead		Total	
strobus	99	49.5%	101	50.5%	200	Chi-square 177.12
peuce	168	84%	32	16%	200	P<0.01 for 1 d.f.

P. strobus grafts on P. sylvestris have a significantly lower survival than P. peuce grafts. This is in accord with the results of preliminary field grafting at Maple, Ontario.

Resistant P. strobus compared with susceptible P. strobus:

	Living	Dead	Total	
Resistant	35	65	100	Chi-square 15.67
Susceptible	64	36	100	P<0.01 for 1 d.f.

Resistant P. strobus grafts have a significantly lower survival than susceptible P. strobus. The scions of resistant P. strobus were collected one week prior to grafting while scions of susceptible P. strobus were collected immediately before grafting. Thus an adverse effect of scion storage may have influenced grafting success. The scions of resistant P. strobus were of the slender leader type while the scions of susceptible P. strobus were of average thickness. The lower grafting success of the resistant P. strobus may thus, in part, be attributed to smaller scion

Resistant P. peuce compared with susceptible P. peuce:

	Living	Dead	Total	
Resistant	97	3	100	Chi-square 32.83
Susceptible	71	29	100	P<0.01 for 1 d.f.

Resistant P. peuce have a significantly higher graft survival than susceptible P. peuce. All P. peuce scions were collected at the same time in the same locality and belong to the same general population.

TRADER SUITABILITY

During the annual examinations of the grafts for weevil damage, the living leaders were classified as being of good, moderate or poor vigor. Only living grafts with leaders of good and moderate vigor in any one year have been considered suitable for weevil attack during the following year.

P. strobus compared with P. peuce:

	Leaders suitable		Leaders not suitable		Leaders available	
strobus	196	69.3%	87	30.7%	283	Chi-square 11.11
peuce	452	77.5%	131	22.5%	585	P<0.01 for 1 d.f.

The leaders of P. strobus grafts are significantly less suitable for weevil attack than P. peuce. There is a possibility that the poorer graft survival of P. strobus as compared with P. peuce is, in part, based on lower graft compatibility decreasing the leader vigor of surviving grafts.

Resistant P. strobus compared with susceptible P. strobus:

	Leaders suitable		Leaders not suitable		Leaders available	
Resistant	300	85.2%	52	14.8%	352	Chi-square 59.06
Susceptible	152	65.8%	79	31.2%	231	P<0.01 for 1 d.f.

The leaders of resistant P. peuce grafts are significantly more suitable for weevil attack than susceptible P. peuce. Since resistant P. peuce have a higher graft survival than susceptible P. peuce, it is probable that this also has an influence on leader vigor, thus influencing suitability for weevil attack.

LEADER ATTRACTIVENESS

When a leader suitable for weevil attack is visited and attacked by the weevil, it is considered being attractive to the weevil. An attack may range from the infliction of a single feeding cavity to the successful oviposition and hatching of larvae from several such cavities. Leader attractiveness is strongly influenced by the number and distribution of suitable leaders in relation to the present weevil population available for attack, and on various environmental conditions favoring an attack, These influences are probably stronger than in the case of grafting compatibility and leader suitability, The relative strength of such influences can be determined by an analysis of variance to which this experiment is not suited because of its layout. Genetic and other factors influencing the relative aggressiveness of a given weevil population will also, in part, be expressed by the number of leaders attacked in relation to those suitable for attack. Leader attractiveness is thus an expression of frequency of weevil attack.

P. strobus compared with P. peuce:

	Leaders attacked		Leaders missed		Leaders suitable	
strobus	18	9.2%	178	90.8%	196	Chi-square 37.31
peuce	131	28.9%	321	71.7%	452	P<0.01 for 1 d.f.

Leaders of P, strobus grafts are significantly less attractive to the weevil than P. peace.

Resistant P. strobus compared with susceptible P. strobus:

	Leaders attacked		Leaders missed		Leaders suitable	
Resistant	4	6.3%	59	93.7%	63	Chi-square
Susceptible	14	10.5%	119	89.5%	133	1.14 n.s.

Leaders of resistant P, strobus are not significantly less attractive to weevil attack than susceptible P, strobus. The number of leaders attacked is too small in this experiment to reach significance.

Resistant P. peuce compared with susceptible P. peuce:

	Leaders attacked		Leaders missed		Leaders suitable	
Resistant	73	24.3%	227	75.7%	300	Chi-square 24.32
Susceptible	58	38.2%	94	61.8%	152	P<0.01 for 1 d.f.

Resistant P. peuce grafts are significantly less attractive to weevil attack than susceptible P. peuce. Thus, in spite of showing greater survival and suitability for weevil attack than susceptible P. peuce, the resistant P. peuce have been found more resistant to weevil attack by being somewhat less attractive to the weevil.

RESISTANCE TO WEEVILING

Successful weeviling will result in the death or loss of apical dominance of attacked leaders. For the purposes of this study, only killed, attacked leaders are classified as having been weeviled.

P. strobus compared with P. peuce:

	Leaders killed		Leaders not killed		Leaders attacked	
strobus	11	61.1%	7	38.9%	18	Chi-square 7.92
peuce	40	30.5%	91	69.5%	131	P<0.01 for 1 d.f.

Leaders of P. strobus grafts are significantly more weeviled if compared with P. peuce. The difference in this respect does not reach a level of significance in comparison with all grafts. This may be caused by the low numbers of attacked P. strobus leaders in comparison with those of P. peuce.

Resistant P. strobus compared with susceptible P. strobus:

	Leaders killed		Leaders not killed		Leaders attacked	
Resistant	1	25%	3	75%	4	Chi-square 4.52x
Susceptible	10	71.4%	4	28.6%	14	

The low significance is probably caused by the low numbers of leaders attacked.

Resistant P. peuce compared with susceptible P. peuce:

	Leaders killed		Leaders not killed		Leaders attacked	
Resistant	20	27.4%	53	72.6%	73	Chi-square
Susceptible	20	34.5%	38	65.5%	58	1.64 n.s.

Resistant P. peuce are not significantly more resistant to weeviling than susceptible P. peuce. The greater weevil resistance of the P. peuce initially selected for freedom from weeviling under conditions of heavy attack, must thus be attributed to resistance to attack caused by the leaders being less attractive to the weevil. This is confirmed in the next comparison:

	Leaders killed		Leaders not killed		Leaders suitable	
Resistant	20	6.7%	280	93.3%	300	Chi-square 11.08
Susceptible	20	13.2%	132	86.8%	152	P<0.01 for 1 d.f.

Leaders of all suitable P. peuce grafts are significantly less weeviled than leaders of susceptible P. peuce.

Equal numbers of grafts were made of P. strobus and P. peuce on planted Scotch pine from ortets selected respectively for freedom from weeviling and heavy weeviling under conditions of heavy weevil attack. The grafts of P. peuce showed better survival than those of P. strobus. They produced a higher proportion of leaders suitable to weevil attack than grafts of P. strobus during 1958-1963. During the same period they also produced a higher proportion of leaders that were attacked by the weevil. However, a smaller proportion of such leaders were weeviled than in P. strobus. P. pence has shown to be more weevil resistant than P. strobus because of its higher resistance to weeviling.

Grafts of P. peuce, initially selected for freedom from weeviling, were also found to produce a higher proportion of leaders suitable to weevil attack, but to be less attractive to the weevil, than grafts from trees selected for heavy weeviling. Because of low survival after grafting, the P. strobus materials could not be evaluated to the same extent as P. peuce, in respect to these attributes.

It is probable that the resistance of P. peuce is based mainly on a heavier resin flow after weevil attack than in P. strobus. In addition, some as yet unknown factors influence the attractiveness of leaders of P. peuce selected for resistance to weeviling by making them more resistant to weevil attack.

The initial selection of the P. peuce ortets for resistance to weeviling under conditions of heavy attack has thus been successful in demonstrating the greater resistance of their grafts to weevil attack. This again indicates a fairly high gross heritability of the characteristics in question and offers a profitable field for selection and breeding.

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DISCUSSION

CARLAW - I have a question directed to Dr. Gerhold. I note that two of your soft pine species are exotics in your part of the country. Would you speculate that the establishment or lack of establishment due to a foreign climate might have something to do with the susceptibility and, as a corollary to this, would you suspect that a natural white pine seedling or well established planting stock would be less susceptible to weevil attack?

GERHOLD - I really don't have any solid information for comparing the susceptibility of exotic species with native ones. I wouldn't be very concerned about the exotic species being out of their natural habitat so long as they seem to be growing normally and vigorously. In comparing the susceptibility of natural seedlings with planted ones, I have no reason to expect any difference between the two categories.

HEIMBURGER - It depends on the origin of the planted stock. There is a very interesting plantation on Lake of Two Rivers, Algonquin Park, about 20 to 30 years old now. It is very heavily weeviled, and yet in 1947-48 we found some unweeviled trees, all natural seedlings, between the rows of planted trees. The planted trees came from Angus and probably an origin of low elevation, probably more juicy, succulent, attractive to the weevil than the native stock.

GERHOLD - But you're attributing this difference to an inherent difference between the two sources rather than to the method of regeneration.

HEIMBURGER - Yes.

CONNOLA - I might inject a little story here. In New York we have an area of white pine in Warren County, one of the sources of the trees I reported on, where weeviling is a very minor problem. I have seen plantations in Warren County that are surrounded with natural regenerated white pine with little or no weeviling, and yet the plantations are all weeviled. These are trees that came from the Saratoga Nursery from seed of unknown source. Now, presumably, much of the white pine seed that is collected by natives around the State come from big wolf trees or trees that were left over from logging operations, presumably heavily weeviled trees. These are easy picking, and I have a strong suspicion that that is where most of the seed comes from.

GERHOLD - I've been told that there are portions of the range of Pinus strobus where no weevil is present. I understand this is true in parts of Ohio and Tennessee, and perhaps the area you mentioned.

CONNOLA - And you do have a resistant strain there, The reason I say that is because of the Warrensburg area in New York where it's really no problem, and yet we're right in the center of white pine growing area and there's weevil all around us.

HEIMBURGER - The planted white pine there are probably of Lake States origin and southern in relation to the white pine around them. It therefore would be reasonable to expect that they would not be having as early lignification of leaders in the fall, nor as rapid growth in the spring.

MEAGHER - I understand that in North Carolina the weevil is a very minor problem if it's a problem at all. Yet there the trees grow very well, with very long needles, very long leaders and I suppose thick, succulent shoots. Is this the case, and if so, is the reduced incidence of weevil damage a matter of very heavy resin flow or a very small weevil population? Is there any indication from the white pine provenance study which is established in North Carolina and the rest of the species ran ge that there is variability in weevil attractiveness or susceptibility to damage?

GERHOLD - As I understand it, Dr, Schreiner, most of these plantations are being protected against weeviling, except the one near New Haven.

SCHREINER - Yes, that's right, we're interested in a population study on growth rate and growth habit, and if we let these plantations become weeviled, it's neither fish nor fowl. The entomologists at New Haven have all of these progenies and they presumably are testing these against weeviling, It is a fact that without spraying we have little weeviling in West Virginia and in southern Maryland, which is out of the white pine range, In New Jersey, at Washington Crossing, there was very heavy weeviling in an old stand, We have had white pines there now for a number of years; the weevil hasn't come back. So we do have the possibility of the weevil disappearing from an area for a while, But we are protecting our provenance tests against weeviling because we wish to evaluate growth rate, tree form, etc.

KIST - We have one of Dr, Heimburger's old provenance experiments at the Petawawa Experiment Station where a number of lots from the Northeast were tested, The Northeastern trees, which were originally selected for blister rust resistance, were coarse and faster growing than local stock, and were also much more weeviled in the early days. I made a count of it when I came there in 1950.

DORN - Has there been any work done to determine how far these weevils will travel or what influence climatic factors might have on the distance of their travel. I don't mean from one tree to another but from one stand to another.

SULLIVAN - There has been very little work done on the long-range dispersal of the insect. I have records of adult weevils travelling at least a quarter of a mile over open land. Once airborne, they proved to be strong fliers, With a tail wind of 5 to 15 m.p.h. I cannot think of any reason why the weevil could not easily cover distances of 4 to 15 miles. Most of my work deal t with short-range flights within stands by adults labelled with the isotope CO°. The spring population of adults proved to be much more active fliers than the autumn population and flight was mainly associated with mating and oviposition. Flight was commonly observed on warm, calm days.

CONNOLA - The New Haven Station did some studies with irradiated weevils, and I think they found that in one flight in the plantation where they were doing their studies, they measured the flight to be 600 feet. Barnes, who did his doctorate on white pine weevil in 1927 at Cornell and was working for the New York State Conservation Department, made several observations of weevils flying around in the plantations that he was studying. He also noted a number that flew out of sight, whatever that means I don't know. But the consensus is that they are short flyers; in other words they don't fly very far in one hop, but if they do get a tail wind they could go quite a distance, I would guess, and once they get into a plantation I think it's generally agreed that they stay in the plantation and build up, There are some migrants but most of the population are those that were bred right there,

GERHOLD - Barnes did state that they are strong fliers, they have strong muscles, and they're capable of rather long flights,

SULLIVAN - I do not think anyone has ever determined the potential flight range of the weevil on a flight mill in still air. Since it is particularly difficult to follow adults over long distances in the field, I think laboratory experiments on flight potential are a natural prerequisite to making inferences on this kind of vitality within weevil populations.

FOWLER - Dr. Connola, did you notice any difference in the percentage of attack in cages containing a single white pine strain in comparison to attack in cages containing a mixture of strains?

CONNOLA - There was much more feeding where there was a choice on the Oneonta trees; in other words the Oneonta trees showed more susceptibility. We had 2 trees that were weeviled; they were the only 2 that were weeviled and they were Oneonta trees. In the Warrensburg cage none of the trees became weeviled. Now we did make some counts of weevil feeding. We found much heavier feeding on the Oneonta trees in the cage that had the Oneonta plus Warrensburg trees.

FOWLER - If you have a preferred strain, say a non-susceptible strain, in mixture with something else, is it going to do better than in a pure stand or pure planting?

CONNOLA - Our daily weevil counts on the pure Warrensburg trees, where we had no mixture, showed fewer weevils on the trees each day than we had in the other cage. The weevils were in there, our cages were weevil proof; we know that. We found them on the ground and we found them on the screen, but they were not on the trees.

GERHOLD - This is really an extraordinary result, isn't it?

CONNOLA - Yes, I think so.

GERHOLD - How many weevils per tree were there?

CONNOLA - We put 260 weevils in each cage, on 32 trees.

GERHOLD - This is a large number of weevils per tree. Had the dates when the weevils were put into the cages anything to do with this? Were they sick?

CONNOLA - Well, the dates were a little different this year than in 1964. I don't know if your spring was the same as ours, but we had a cold spring and actually it didn't warm up until rather late, so the actual putting of the weevils into the cages came at a later date than it did in 1964. How this affected oviposition I don't know, but we tried to collect the weevils at the same stage of bud elongation of the white pine in the field. In other words there was about the same bud elongation both years.

GERHOLD - What was the date this year?

CONNOLA - It was in May, on the 22 or 23, whereas in '64 it was about 2 weeks earlier. I'm not absolutely sure of those dates, but I think there was about a 2-week difference in the 2 years.

GERHOLD - If the weevils were fully vigorous in the cages it suggests the trees might be quite resistant.

SULLIVAN - What about the micro-climate around the trees themselves? Did you take any measurements inside the cages?

CONNOLA - We took daily temperature readings and one of our cages had a hygrothermograph so we have all those measurements that we're going to compare with 1964. We haven't got to that yet, but we have the maximum-minimum temperatures for each cage, plus the hygrothermograph weekly readings.

GABRIEL - I have a question for you, Mr. Connola. Has the thought ever occurred to you that perhaps the caged weevils showed a higher preference for the Oneonta origin rather than the Oneonta origin being less resistant? Have you considered weevil variability? Would it have been possible if you had had collections of weevils from a half dozen origins in your cages that the Warrensburg trees may have been attacked more heavily, and that the preference for the Oneonta trees wouldn't have been so obvious?

CONNOLA - Last year we went out and collected weevils in the Oneonta area and we collected them in the Warrensburg area and we ran two cages, in other words weevils from the same source as the trees. Unfortunately we ran into some DDT trouble and we lost the whole experiment, but in running the test this year we thought we had better go back to our 1964 source for our weevils, which was geographically midway between the two sources, so that at least we were not drawing from the same source as the tree.

HOLST - One last question. From your data it appeared that the Warrensburg trees were not slower growing than the other ones. Is Warrensburg much colder than the Oneonta area?

CONNOLA - There is 150 miles difference between them and one is colder. Warrensburg is considered northern New York and the other is considered southern New York.

HOLST - Shorter growing season? 1,000 degree days?

CONNOLA - This is something we'll have to study.