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Variation in attack by Sitka spruce weevil, *Pissodes strobi* (Peck), within a resistant provenance of Sitka spruce

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ABSTRACT

Variation in tree height and numbers of attacks by the Sitka spruce weevil (= white pine weevil), *Pissodes strobi* (Peck), were studied among families of a resistant provenance of *Picea sitchensis* (Bong.) Carr. at two Vancouver Island sites. At Sayward, after 14 years, the number of trees attacked varied by family from 0 to 80%. A significant association was found between the percentage of trees attacked in a family and the mean height of the family. Tall families were generally attacked more. At Fair Harbour (a clonal test), only 12% of the trees from the resistant provenance have been attacked after seven years, with all but one of the attacks concentrated on one of the two families tested. A multigenic or multicomponent basis for resistance is proposed and discussed.

INTRODUCTION

The Sitka spruce weevil (=white pine weevil), *Pissodes strobi* (Peck), is a major cause of failure in reforestation programs with Sitka spruce, *Picea sitchensis* (Bong.) Carr., in coastal British Columbia (B.C.), Washington, and Oregon (Furniss and Carolin 1977). The adults emerge from overwintering in early spring, and move to the 1-year old terminal shoot (leader) where the females lay eggs under the bark near the tip. If the weevil larvae become established, they move downwards, mining and consuming the phloem and eventually killing the leader (Silver 1968). In the literature, the successful colonization and destruction of the tree leader by *P. strobi* is generally called a weevil attack; this terminology is also used here. Repeated leader destruction causes height-growth loss and stem deformities which reduce the tree's value (Alfaro 1989a, 1992). Although the tree survives the attack, stunted trees are often suppressed by competing vegetation (Alfaro 1982). Other important tree species damaged by this insect are eastern white pine, *Pinus strobus* L., in eastern North America (MacAloney 1930), Engelmann spruce, *Picea engelmannii* Parry, and white spruce, *Picea glauca* (Moench) Voss., in central British Columbia and the prairie provinces (Stevenson 1967).

Analysis of several trials in British Columbia provided strong evidence of genetic variation

in the susceptibility of Sitka spruce to weevil damage (Ying 1991, Alfaro and Ying 1990). Genetic resistance to weevil attack was also demonstrated for interior spruce by Kiss and Yanchuk (1991). These analyses indicate that some provenances and families show resistance in the form of reduced numbers of weevil attacks. This was the case in Sitka spruce trees from the Haney provenance in trials at Sayward and Fair Harbour, which grew well and were the least damaged (Ying 1991, Alfaro and Ying 1990). Mechanisms of resistance are currently under investigation; one based on supernumerary resin canals has been proposed (E. Tomlin and J.H. Borden, personal communication, Simon Fraser University).

Ying (1991) noted that resistant provenances of Sitka spruce originate from areas of high weevil hazard, such as Haney or Squamish on the B.C. mainland. He hypothesized that herbivore selection may have favored a resistant gene pool in these areas so that survivors have high levels of resistance. Alfaro and Ying (1990) identified the Skeena River area of B.C. as another area where higher frequency of resistant individuals could be found. In this area, extensive hybridization of Sitka with white spruce occurs. Variation in susceptibility among different *Picea* species and their hybrids has been reported (Mitchell *et al.* 1990).

Alfaro and Ying (1990) also demonstrated variation in the ability of trees to recover from weevil damage, since the type of defect formed after attack varied by provenance and family. Some provenances had above-average numbers of attacks per tree but still were able to develop into merchantable trees. An example of tolerance to weevil damage was the Big Qualicum provenance, which was among the tallest at the Sayward trial even though it sustained repeated attacks.

The objectives of this paper were to examine the rates of repeated attacks among families, trees and clones of the most resistant provenance found to date in B.C. (the Haney provenance), and to describe some of the factors that determined attacks on individuals of this provenance. In particular, we tested whether the demonstrated preference of the weevil for the tallest and fastest growing trees in a plantation (Mitchell *et al.* 1990, Alfaro 1989b, Gara *et al.* 1971, Silver 1968) also holds true within the Haney provenance. For this study, we used data collected at Sayward and Fair Harbour in 1988, 1991 and 1992.

MATERIALS AND METHODS

The Sayward provenance test was established in the spring of 1974 in the Salmon Valley, near Sayward, B.C., with the purpose of comparing growth and survival of a collection of open-pollination families from several B.C. provenances. The plantation was first attacked by *P. strobi* when the trees were 5 years old. The site was assessed in the fall of 1988; for every tree we recorded: total height, diameter at breast height (DBH), and the number of times the trees had sustained weevil attack. Weevil attacks were recognized because, in most cases, remains of the destroyed leader were present and pupal chambers were evident. The plantation originally consisted of two blocks, A and B, but only Block B was assessed because Block A had suffered flood damage. Block B consisted of 141 rows occupying 2.8 ha, and contained 4389 living trees from 34 provenances. Each provenance consisted of a variable number of wind-pollinated families. The resistant Haney provenance, which was the object of this study, was represented by 81 trees from 8 families. Further details on this plantation and on the geographic location of provenance sources can be found in Alfaro and Ying (1990).

The 1988 records for the Sayward plantation (Block B) were assessed to determine the number of past attacks and the height of trees in the Haney provenance. Because of limitations of the experimental design of this test no attempt was made to analyze the components of the variance or to calculate other genetic parameters. Instead, we relied on non-parametric tests of variance and association. The Kruskal-Wallis test (Sokal and Rohlf 1969) was used to test for family variation in mean number of attacks per tree. The Spearman rank correlation coefficient (Sokal and Rohlf 1969) was used to test for a significant association between percentage of trees attacked in a family and mean family height. The same procedure was used to test for association between the mean number of attacks per tree in a family and mean family height.

The Fair Harbour plantation is a clonal trial (grafting) established in 1984 to test the repeatability of provenance resistance to weevil attack observed in provenance tests (Ying 1991). The

donor parents (ortets) originated from trees in eight provenances tested at the Sayward site, plus two trees from the Green Timbers plantation which showed high resistance to weevil attack (Alfaro 1982). Eight trees from the resistant Haney provenance (four trees each from family 0 and 1) were included in the test. The layout of the test consisted of 16 blocks in which a total of 640 grafts were tested; each ortet was represented by 16 grafts (ramets), one ramet in each block.

The attacks on the ramets at Fair Harbour were counted in October 1991 and on the ortets at Sayward in October 1992.

To determine if attacks on trees occurred independently of each other or if the presence of one attack enhanced the probability of a subsequent attack on the same tree, the distribution of the attacks per tree at both sites was compared to that expected from a Poisson distribution. Data collected in 1988 were used for the analysis of the Sayward site and 1991 data for the Fair Harbour site. However, because of the low attack rates at Fair Harbour, a Chi-square-test of goodness-of-fit (Sokal and Rohlf 1969) was done only for the Sayward data.

Table 1

Mean tree height, number of Sitka spruce weevil attacks per tree and percent of trees attacked among trees of the resistant Sitka spruce Haney provenance (standard deviation in brackets). Data collected in 1988 at Sayward and in 1991 at Fair Harbour.

Location and family No.	Number of trees	Mean Ht (m)	Mean No. attacks per tree		% trees attacked
Sayward					
0	6	6.6 (1.6)	0.3	(0.5)	33
1*	5	—	—		—
3	30	6.0 (1.2)	1.1	(1.1)	60
4	22	5.3 (1.9)	0.5	(0.7)	32
5	4	4.0 (1.0)	0.0	(0.0)	0
8	7	4.2 (0.6)	0.9	(1.6)	29
12	7	5.1 (0.6)	0.4	(0.8)	29
13	5	6.0 (1.0)	1.8	(1.1)	80
Fair Harbour					
0	62	4.6 (0.9)	0.03	(0.25)	2
1	63	4.7 (0.9)	0.25	(0.54)	22

* This family was present only at Sayward Block A, which was not assessed in 1988. An assessment in 1992 indicated that 60% of the trees in this family had been attacked at least once.

Table 2

Frequency distribution of Sitka spruce weevil attacks per tree among trees from the resistant Sitka spruce Haney provenance. The expected frequencies from a Poisson distribution are given in brackets. Data collected in 1988 at Sayward and in 1991 at Fair Harbour.

Attacks per tree	Sayward No. trees[1]	Fair Harbour No. trees[1]
0	46 (36)	111 (109)
1	14 (29)	10 (15)
2	15 (12)	4 (1)
3	5 (3)	—
4	1 (1)	—

1. For the Sayward site, a Chi-square-test detected a significant departure of the number of attacks per tree from predicted Poisson frequencies (P<0.01). Because of the small number of attacks, and low cell frequencies, no statistical tests were done on the Fair Harbour data.

RESULTS

Sayward Test

The 1988 attack records indicated that only 43% of trees from the Haney provenance were attacked one or more times, whereas 76% of the trees in the entire Sayward Block B had been attacked. The percentage of trees attacked among families within the Haney provenance varied significantly (Chi-square test, P<0.05) by family from 0% (Family 5) to 80% (Family 13) (Table 1). The mean number of attacks per tree for the Haney provenance was 0.8 (ranging from 0 to 4) which was about half of the mean number of attacks per tree recorded for the entire Block at 1.5 (range 0 to 7, Alfaro and Ying 1990). The mean number of attacks per tree varied significantly among the Haney families from 0 (Family 5) to 1.8 (Family 13) (Table 1) (Kruskal-Wallis Test, P<0.05).

The distribution of the number of attacks per tree departed significantly (Chi-square test, P<0.01) from the values expected from the Poisson distribution, indicating a clumped distribution. There were higher numbers of trees that remained undamaged and higher numbers having repeated attacks than expected if the attacks occurred at random (Table 2). This allowed us to conclude that the presence of one attack on a tree enhanced the chances of a tree being attacked again. Alfaro and Ying (1990) arrived at the same conclusion when they examined the attack distribution for the entire Sayward Block B plantation.

In 1988, the Haney provenance trees averaged 5.5 m in height, almost 2 m taller than the average height for the entire site (3.6 m). However, there was considerable variation in height by family (range 4.0 to 6.6 m). The Spearman rank correlation test detected a significant association between the percentage of trees attacked in a family and the mean height of the family ($rs = 0.88$, P= 0.01) (Fig. 1). Because of the negative effect of weevil damage on height growth, this correlation is only a measure of association, rather than a cause-effect relationship. No significant correlation was found between the number of times an individual tree was attacked and tree height.

Fair Harbour Test

Overall, 12% of the trees from the Haney provenance at the Fair Harbour site were attacked (14 trees up to 1991). This is much lower than the 69% found for the entire site. As at the Sayward site, more trees had repeated attacks than predicted by the Poisson distribution (Table 2). There were four trees attacked twice; if attacks occurred at random, only one tree would have been so attacked (Table 2). However, because at this site weevil damage is still light and this resulted in low cell frequencies, a Chi-square test was not done. All but one of the attacks occurred among trees of Family 1, resulting in attack rates of 2% for Family 0 and 21% for Family 1 (Table 3). Mean height of the Haney ramets varied from 4.0 to 5.2 m. No correlation was found between the percentage of trees attacked in a clone and mean clonal height (Spearman rank correlation test not significant).

A comparison of the attack rates on the Fair Harbour ramets with attack rates on the respective ortets at Sayward indicated a very good correspondence (Table 3). There was a very low attack rate on both ortets and ramets from Family 0, with only one tree being attacked at each site. Both ortets and ramets from Family 1 had sustained higher attack rates than Family 0, with three of the four ortets at Sayward and 13 of 63 ramets at Fair Harbour being attacked (Table 3). In both families there was one ortet attacked at Sayward but no attack among the respective Fair Harbour ramets. There were also attacks among ramets from ortets which remained free from attack at Sayward, e.g. tree No. 6 from Family 1.

DISCUSSION

The low attack rate of the Haney provenance at the Sayward and Fair Harbour sites confirms the existence of resistance to weevil attack in this provenance (Ying 1991, Alfaro and Ying 1990). This study also suggests that individual trees and families from the same Haney provenance differ in degree of resistance.

The large number of trees of the Haney provenance that remained free from weevil attack at both sites is probably not due solely to genetic resistance. One factor influencing the probabil-

Table 3

Attacks by the Sitka spruce weevil on two Sitka spruce families planted at the Sayward site and cloned at the Fair Harbour site. Data collected in 1992 at Sayward and in 1991 at Fair Harbour.

| | | Plantation | | | | |
| | | Sayward Ortets | | Fair Harbour Ramets | | |
Family No.	Tree No.	Trees	Attacks per tree	Grafts alive	Grafts attacked	Attacks* per graft
0	2	1	0	16	0	0
	5	1	0	14	0	0
	6	1	0	16	1	2
	7	1	1	15	0	0
1	1	1	1	15	0	0
	2	1	2	16	3	1
	3	1	2	14	8	1.4
	6	1	0	15	2	1

* Mean number of attacks on attacked grafts.

ity of attack on a tree is its rate of growth. Several reports indicate that the Sitka spruce weevil prefers the fastest-growing trees in a stand (Mitchell *et al.* 1990, Alfaro 1989b, Gara *et al.* 1971, Silver 1968). Alfaro and Ying (1990) found that, at the Sayward site, trees growing in patches of severe attack were significantly taller (3.8 m) than trees growing in areas of low attack (3.5 m). This preference was also evident in this study among the trees of the resistant provenance (Fig. 1). The only Haney family at Sayward which was free from weevil attack was Family 5, which was also the shortest.

The preference of *P. strobi* for the fastest-growing families (even among the resistant provenance) is different from the findings of Kiss and Yanchuk (1991) who found the opposite among families of white spruce attacked by the same insect. A possible explanation for this apparent contradiction is that *P. strobi* may seek to maximize the amount of larval food during host selection. *P. strobi* larvae consume the leader phloem, therefore, leaders with thicker phloem are probably more attractive than leaders with thin phloem. In Sitka spruce, thick phloem is correlated with long leaders (Alfaro, unpublished data). It is possible that, because of the different growth characteristics of white spruce (much slower growth than Sitka spruce) thick phloem may be negatively correlated with leader length in this species. Therefore, a negative correlation between attack rate and rate of growth would result. However, further research is required to prove or disprove this hypothesis.

The spatial distribution of weevil attacks in a plantation is highly clumped (Alfaro and Ying 1990, Graham 1951). This study demonstrated that, at both test sites, attacks on trees from the resistant provenance were also aggregated and that, once trees were attacked, their chances of further attack increased. This distribution probably results from the low dispersal ability of the weevil and from the tendency of the weevils to overwinter near the attacked tree. Moreover, the formation of multiple leaders on attacked trees increases the probability of further attack. This aggregation in the weevil population must be considered when selecting for resistance. A susceptible tree may appear resistant and be undamaged if it happened to occur in an area of low weevil density. Therefore, selection for resistant trees should be done in areas of the plantation of high weevil density.

The low overall attack rates among the Haney trees at the Fair Harbour site as compared with the Sayward site (Table 2) could result from several factors which are different between the two plantations. The Fair Harbour test was initiated 10 yr after the Sayward test, therefore trees have had a shorter exposure to the weevil. The Fair Harbour trees were clones produced by grafting, and thus could differ from the wind-pollination trees at Sayward due to an influence of
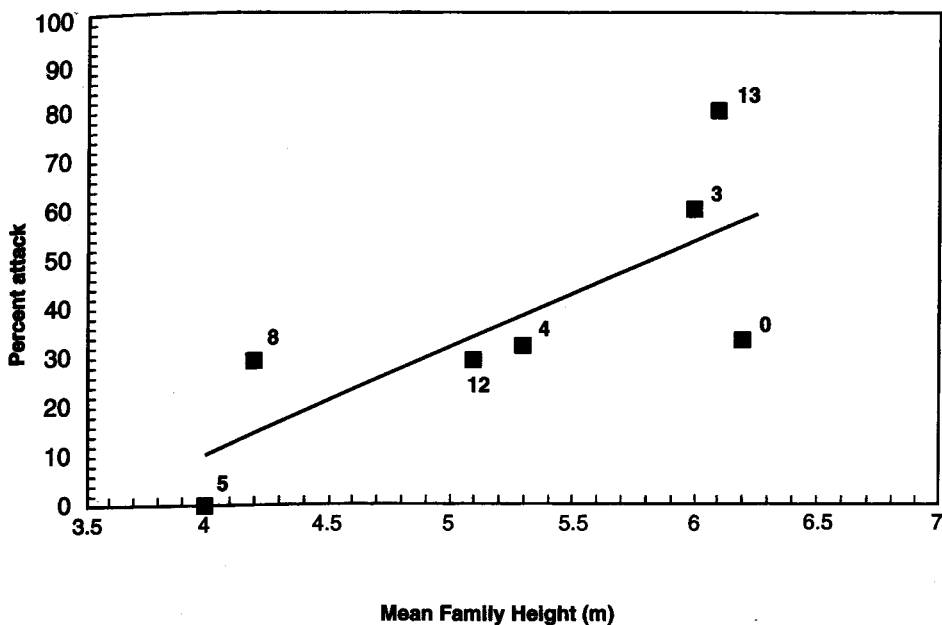
Figure 1. Relationship between the percentage of Sitka spruce trees in a family attacked by the Sitka spruce weevil at Sayward and mean family height. All families (indicated by numbers) are from the resistant Haney provenance. Data collected in 1988.

the root stock on the physiology of the tree. However, the ranking of resistance among the two families was the same at both sites: Family 0 was more resistant than Family 1 (Table 3). This indicated that selection for resistance at an early age (9 years at Sayward) may be reliable.

The large variation in the percentage of trees attacked among the wind-pollination families of the Haney provenance, as well as the existence of a gradation in resistance with several provenances showing intermediate resistance, e.g. Squamish (Alfaro and Ying 1990), suggest a resistance mechanism that has a multi-allelic or multigenic basis or to the existence of several resistance mechanisms which accumulate and perhaps synergize in different trees. Future research should concentrate on the elucidation of the resistance mechanisms and on understanding their genetic basis. Ying (1991) noted the desirability of developing varieties which combine different resistance mechanisms and thus run a lower risk of inducing the evolution of weevil populations which can overcome tree resistance. However confirmation of this hypothesis requires the establishment and evaluation of progeny tests.

Ultimately, it is likely that the degree of attack by *P. strobi* on a Sitka spruce tree, family, or provenance is due to a combination of factors: resistance factors and growth characteristics of the trees which are subject to both genetic and environmental influences, plus an element of chance. Some of these factors could be manipulated, along with silvicultural treatments such as shading (McLean 1989) or spacing (Alfaro and Omule 1990), in an integrated pest management program for control of this destructive insect.

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Life history and pheromone response in *Pissodes schwarzi* Hopk. (Coleoptera: Curculionidae)

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ABSTRACT

Pitfall traps baited with live *Pissodes schwarzi* Hopk. males plus pine sections captured 46 female *P. schwarzi* from 1 June to 1 September, 1989, indicating the presence of a male-produced sex pheromone. No weevils were captured in unbaited traps, or those baited with females on pine or pine sections alone. Seasonal response of *P. schwarzi* females to the male-baited pifall traps indicated peak periods of activity in early June, representing overwintered adults, and mid- to late July, corresponding to the emergence of new adults. Development time of *P. schwarzi* varied depending on oviposition location on the tree. Overwintered brood adults began to oviposit in May and continued through August.

INTRODUCTION

The Yosemite bark weevil, *Pissodes schwarzi* Hopk., attacks and breeds in the bole, root collar and large roots of stressed or dying trees (Wood 1964; Stevens 1966). Hopkins (1911) and