Preliminary evaluation of genetic variation of weevil resistance in interior spruce in British Columbia

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White pine weevil (*Pissodes strobi* (Peck)) damage in three interior spruce open-pollinated progeny tests in north central British Columbia was evaluated to examine the patterns of attack among families. While the overall incidence of damage was different across sites (i.e., Quesnel 9%, Red Rock 37%, and Aleza Lake 63%), correlations on a family-mean basis (percentage attacked per family) at Red Rock and Quesnel as well as Red Rock and Aleza Lake were significant (r = 0.63 and 0.71, respectively). Estimates of family heritability across sites for damage was high ($h_f = 0.77 \pm 0.11$), but individual heritability was only moderate ($h_i = 0.18 \pm 0.03$). More vigorous families, as determined by 10-year family mean height superiority prior to weevil attack, were damaged less frequently than those with average and poorer performance. Negative correlations of mean family height at 10 years of age with incidence of damage (on a family-mean basis) and mean family diameter with incidence of damage were significant ($r = -0.51$ and -0.44, respectively). These data suggest that there is a moderate genetic basis for resistance to weevil attack in interior spruce and that selection for height and diameter growth may improve resistance to weevil attack.

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Les dégâts causés par le charançon du pin blanc (*Pissodes strobi* (Peck)), sur des épinettes de l'intérieur du continent furent évalués sur trois tests de progéniture à pollinisation libre dans le centre nord de la Colombie-Britannique de façon à examiner les modes d'attaques de l'insecte entre les familles. Tandis que l'incidence totale des dégâts variait selon les sites (c.à.d., Quesnel 9%, Red Rock 37% et lac Aleza 63%), les corrélations sur la base des moyennes par famille (pourcentage d'attaque par famille) étaient significatives autant pour Red Rock et Quesnel que pour Red Rock et lac Aleza (r = 0,63 et 0,71 respectivement). Les estimés de l'héritabilité familiale pour les dégâts à travers les sites étaient élevés (h_f = 0,77 ± 0,11) bien qu'au niveau des arbres pris individuellement les estimés étaient seulement modérés (h_i = 0,18 ± 0,03). Les familles les plus vigoureuses, tel que déterminé par la moyenne décennale de croissance en hauteur de la famille avant les attaques du charançon, furent moins fréquemment attaquées que celles avec des performances moyennes ou plus faibles. Des corrélations négatives significatives ont pu être établies entre la hauteur moyenne de la famille à 10 ans et l'incidence des dégâts (sur la base des moyennes par famille) de même qu'entre le diamètre moyen des arbres de la famille et l'incidence des dégâts (r = −0,51 et −0,44 respectivement). Ces données suggèrent qu'il existe une base génétique modérée de résistance des épinettes de l'intérieur du continent face aux attaques du charançon et qu'une sélection basée sur les performances de croissance en hauteur et en diamètre pourrait améliorer la résistance aux attaques du charançon.

[Traduit par la Rédaction]

Introduction

Interior spruce (the complex of white spruce (*Picea glauca* (Moench) Voss), Engelmann spruce (*P. engelmannii* Parry), and their hybrid swarms) is of vital importance to the forest economy of British Columbia. In 1987–1988 nearly 19×10^6 m^3 of interior spruce was harvested and over 95×10^6 spruce seedlings were planted (British Columbia Ministry of Forests 1988). In 1989, over 98×10^6 interior spruce seedlings were raised for planting. Given the importance of interior spruce to the British Columbia economy, any pest that might interfere with the health and growth of young plantations should be thoroughly investigated.

The white pine weevil, *Pissodes strobi* (Peck), can cause serious damage in young spruce plantations (Stevenson 1967; Silver 1968; McMullen 1976; Wood and McMullen 1983; Alfaro and Omule 1990). Many of the interior spruce plantations established in the 1960s are now reaching a height where they may be susceptible to damage by the white pine weevil, and their growth and value could be seriously decreased by repeated attacks.

The white pine weevil deposits its eggs from mid-May to mid-July into leaders produced the previous year. The larvae feed on the cambium of 1- and 2-year-old stems. A major weevil attack may destroy 3 years of growth, as the destruction of the previous years' stem will kill the current year's growth as well (Cozens 1983).

While the impact of white pine weevil damage on interior spruce stand growth and yield is unknown, the effects of weevil damage on yield and product value in other conifers have been investigated. Brace (1971), studying two stands of white pine (*Pinus strobus* L.) of age 60 and 90, found that repeated weevil attacks can reduce white pine tree height by as much as 3 m and reduce volume yield by 3 to 20%. Product value loss averaged 25%. In British Columbia,

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white pine weevil also attacks Sitka spruce (*Picea sitchensis* (Bong.) Carr.) and substantially reduces survival, volume production, and quality. Sitka spruce is no longer being planted in areas where it is highly susceptible to the white pine weevil (Alfaro 1982). It is likely that similar losses could be expected for interior spruce.

A number of techniques have been investigated for controlling the white pine weevil, including chemical control agents, repellents, insect growth regulators, silvicultural manipulations (e.g., stand densities), and biological agents. In addition, Cozens (1983) suggested that genetic selection might be an effective tool to reduce the impact of weevil damage.

The British Columbia Forest Service initiated a comprehensive tree improvement program of interior spruce in 1968. Part of this program involved the selection of large numbers of parent trees tested in open-pollinated progeny trials (Kiss 1976). Following 10-year height measurements, but prior to recording the 15-year height and diameter measurements, light to moderate attacks by the white pine weevil were observed in two of the three progeny plantations. Another plantation of these progenies, established as a pilot project 1 year prior to establishing the major trials, exhibited a heavier infestation by the weevil. Cursory field examination indicated a pattern of differential attack among families. A study was therefore undertaken to evaluate the plantations and quantify the levels of attack.

The objectives of this study were to (*i*) determine the level of genetic variation in resistance to white pine weevil attack in the three plantations of the interior spruce tree improvement program, (*ii*) examine the magnitude of interactions among families and plantations for resistance, and (*iii*) determine if there is a relationship between resistance to weevil attack and growth attributes.

Materials and methods

A total of 173 trees were selected in the Prince George Selection Unit and tested on three progeny test sites (Red Rock, Quesnel, and Barbie Lake) in 1973 (Kiss and Yeh 1988). A fourth test site containing the same progenies was established 1 year earlier as a pilot project near Aleza Lake. All four of these test sites are in the north central interior of British Columbia. Three sites were included in this study because the Barbie Lake progeny plantation was not suitable for weevil damage assessment. Here repeated and severe frost damage obfuscated the accurate assessment of weevil damage.

The following plantations were used in this study:

Aleza Lake — Longitude 54.1°N, latitude 122°W, elevation 600 m. Site preparation included deep discing. The experimental design was a randomized complete block design (five replications), with 15 seedling rows representing each parent in each replication. Height measurements were carried out at the time of establishment and at plantation ages 3 (1974), 6 (1977), and 10 (1981) years. Because of the moderate weevil damage before the 10-year height measurements (and heavier weevil damage after 10 years), and difficulty of access to the site, 15-year growth measurements were not taken. Plantation survival at age 10 was 95%.

Red Rock — Longitude 53.8°N, latitude 122.7°W, elevation 650 m. Site preparation was extensive and included deep discing. The experimental design was a randomized complete block design (10 replications), with 10 seedling rows representing each parent in each replication. This site included the same parents that were represented at Aleza Lake. Plantation maintenance consisted of periodic brushing and weeding as needed. Data collection included height measurements at establishment and at plantation ages 3 (1975), 6 (1978), 10 (1982), and 15 (1987) years. Diameter measurements at breast height (dbh) were also taken in 1987. Survival of this plantation was 97% at age 15.

Quesnel — Longitude 53°N, latitude 122.2°W, elevation 1000 m. The only site preparation was prescribed burning. The design and data collection of the plantation were identical with those of the Red Rock plantation. Maintenance was less rigorous and survival was lower at age 15 (82.4%). Losses were mainly due to competition and some recent vandalism.

TABLE 1. Comparison of the mean percent damage of the top 44 families and the plantation

Site	Mean damage (%)	
	Plantation	Top 44 families
Quesnel	9.0	5.6
Red Rock	37.3	24.9
Aleza Lake	62.9	52.4

NOTE: The top 44 families (the 25% highest ranking trees) were selected based on the overall family heights at 10 years of age at Red Rock, Quesnel, and Barbie Lake.

Weevil damage assessment was carried out during the fall and winter of 1988–1989. At this time the Aleza Lake plantation was 17 years old and the other two plantations were 16 years old. Each live tree was evaluated for the presence or absence of weevil damage. Damage prior to 1988–1989 was recorded, as well as damage during the year of assessment. The majority of damage had occurred in the 3 years prior to assessment. Percent damage was calculated for each family in each replication (plot) based on the number of live trees (weevil damage was not responsible for any mortality). Slight imbalance existed in the data set in that 448 plots were missing across the three test sites.

Analysis of variance (PROC VARCOMP (SAS Institute Inc. 1988)) was used to derive variance component estimates, with all sources of variation considered as random effects. Adjustments to the basic data, for the analysis of variance, were made when the percentage of trees damaged per plot was either 0 or 100% (Bartlett 1947). Adjustments were as follows: $P = 1 - (1/4m)$, when all trees were attacked per plot, and $P = 1/4m$, when no trees were attacked per plot; where m is the total number of trees per plot and P is the percentage of trees attacked per plot. The percentages were then transformed into arc sine square roots (in degrees) to approximate a normal distribution. Calculations of heritability from the transformed data were based on the methods used by Becker and Marsden (1972). Approximations of standard errors of heritability estimates were derived as shown by Becker (1984).

The relationships between incidence of damage and initial, 3-, 6-, and 10-year family height means at the respective sites were examined using correlations on family means. Also,

TABLE 2. Analysis of variance of adjusted and transformed weevil attack data of interior spruce on three sites in central British Columbia

Source	df	MS	EMS[a]	Variance[b]
Site	2	348 912[c]	$\sigma_e^2 + (1/h)\sigma_b^2 - (1/h)\sigma_d^2 + k_7\sigma_{sf}^2 + k_8\sigma_f^2 + k_9\sigma_r^2 + k_{10}\sigma_s^2$	310.5 (63%)
Rep.(site)	22	1 535*	$\sigma_e^2 + (1/h)\sigma_b^2 - (1/h)\sigma_d^2 + k_4\sigma_{sf}^2 + k_5\sigma_f^2 + k_6\sigma_r^2$	10.1 (2%)
Fam.	159	1 196*	$\sigma_e^2 + (1/h)\sigma_b^2 - (1/h)\sigma_d^2 + k_2\sigma_{sf}^2 + k_3\sigma_f^2$	41.8 (8%)
Site × fam.	283	296*	$\sigma_e^2 + (1/h)\sigma_b^2 - (1/h)\sigma_d^2 + k_1\sigma_{sf}^2$	19.3 (4%)
Rep.(site) × fam.	3050	114	$\sigma_e^2 + (1/h)\sigma_b^2 - (1/h)\sigma_d^2$	114.4 (23%)

where

$$h_i^2 = \frac{4(41.81)}{821 + 24.48^d + 19.26 + 41.81} = 0.18 \pm 0.03$$

and

$$h_f^2 = \frac{41.81}{\dfrac{114.37 + 19.26k_2}{k_3} + 41.81} = 0.77 \pm 0.11$$

NOTE: Rep., replication; fam., family; MS, mean square; EMS, error mean square.

[a]$\sigma_b^2 = 821$; h (harmonic mean of trees/plot) = 9.1333; $\sigma_e^2 - (1/h)\sigma_d^2$ is variance due to plot effect; σ_{sf}^2 is variance due to site × family interaction; σ_f^2 is variance due to families; σ_r^2 is variance due to replication; σ_s^2 is variance due to sites; $k_1 = 7.58$; $k_2 = 8.47$; $k_3 = 21.96$; $k_4 = 0.02$; $k_5 = 0.02$; $k_6 = 140.67$; $k_7 = 7.78$; $k_8 = 0.33$; $k_9 = 140.42$; $k_{10} = 1118.2$.

[b]Percentage of total is given in parentheses.

[c]No appropriate error term is available in EMS presented, i.e., k_4 and k_5 are close to 0.

[d]$MS_{r(s)\times f} - (1/h)\sigma_b^2 = 24.48$.

*Significant at the $P < 0.01$.

the relationships between the average incidence of weevil damage and 15-year family heights and family mean diameters (age 15) were studied at Quesnel and Red Rock. Family means for weevil damage used in the correlation analysis with growth traits were derived from untransformed plot means of percentage of trees attacked.

To examine the magnitude of observed differences in weevil attack after a level of family selection based on growth, families were ranked (using 10-year overall family mean heights of the three progeny plantations (Red Rock, Quesnel, and Barbie Lake)), and the tallest 44 (approximately 25%) families were selected. The Barbie Lake plantation data were included in this selection for growth as they are part of the data set used in the operational tree improvement program for the Prince George Selection Unit. Average percent damage of each of the 44 families was calculated at Red Rock, Quesnel, and Aleza Lake and compared with the mean incidence of damage of all families at the respective sites. Similarly, based on average incidence of damage at the three sites (Red Rock, Quesnel, and Aleza Lake), the least frequently damaged 44 families were selected and mean heights of these 44 families were compared with plantation means at various ages (differences were expressed as the percentage of the respective plantation's mean). These same differences were also calculated for dbh, and where available, relative volume percent differences were also obtained using the following formula:

$$V_g = \frac{d_i^2\mathrm{ht}_i - d_m^2\mathrm{ht}_m}{d_m^2\mathrm{ht}_m} \times 100$$

where

V_g is percent volume difference
d_i is the mean dbh of the top 44 families
ht_i is the mean height of the top 44 families
d_m is the mean dbh of the plantation
ht_m is the mean height of the plantation

Results and discussion

As expected, the intensity of damage varied across sites: 9% of the trees were damaged at Quesnel, 37% at Red Rock, and 63% at Aleza Lake (Table 1).

Analysis of variance indicated that family effects were highly significant and accounted for 8% of the total variance (Table 2). Because of this relatively large component for family variance, the estimated heritability on a family mean basis, was high ($h_f^2 = 0.77 \pm 0.11$); however, the heritability on an individual tree basis was only moderate ($h_i^2 = 0.18 \pm 0.03$, Table 2).

Family-mean correlations between incidence of damage at Red Rock and Quesnel, and Red Rock and Aleza Lake, were strong ($r = 0.63$ and 0.71, respectively) and therefore suggest that susceptibility to weevil damage across plantations is quite similar. This was especially evident between the two sites where the percentage of trees attacked on a plantation basis was higher (i.e., Red Rock and Aleza Lake). Also, the site by family interaction was approximately one-half of the family variance (Table 2), again indicating the relative stability of families across sites even with large average differences in percent damage.

Earlier reports suggested that in Sitka spruce, white pine weevils preferentially attack the longest and thickest leaders of the tallest trees (VanderSar and Borden 1977; Kline and Mitchell 1979; Wood and McMullen 1983). Should this be the case in interior spruce as well, the chosen breeding strategy of selection and breeding of trees or families, based on height and diameter superiority, is questionable. Alfaro (1989) reported that leader length and population levels generally are important in predicting weevil damage, but other factors will determine whether a tree is or is not attacked.

The present study suggests that the genetic composition of individual trees may be more important than leader dimensions. The relationship between average family heights, combined for the Red Rock and Quesnel test sites

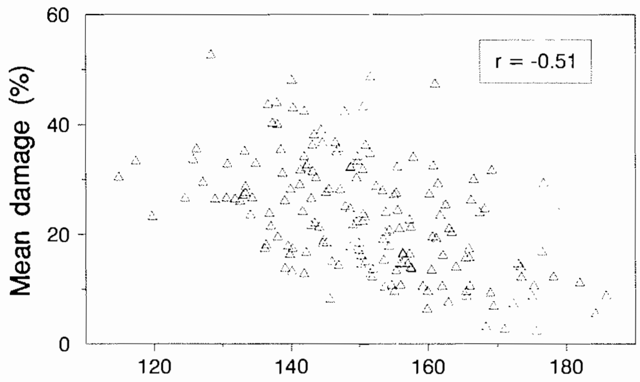

FIG. 1. Relationship between percent damage by spruce weevil and 10-year height at Red Rock and Quesnel combined, on a family-means basis.

TABLE 3. Mean 10-year heights of the top 44 families and the plantation and the percent difference between the mean 15-year volume of the top 44 families and the plantation

	10-year mean height (cm)		
Site	Plantation	Top 44 families	15-year vol. diff.
Red Rock	164.3	176.8	30.3
Quesnel	137.4	145.8	21.4
Barbie Lake	141.7	147.9	28.0
Aleza Lake	157.8	174.1	na

NOTE: The top 44 families (the 25% highest ranking trees) were selected based on the least overall mean damage at Quesnel, Red Rock, and Aleza Lake combined.

at 10 years of age, and the average percent weevil damage at 16 years of age at the two sites showed a significant inverse correlation ($r = -0.51$, Fig. 1). This indicates that faster growing families are less frequently damaged than the slower growing ones. It is important to note that at this age the height growth data are not confounded with weevil damage, because there was no weevil damage apparent in these two plantations at age 10. Also, we found a significant inverse correlation ($r = -0.44$) between dbh at age 15 and incidence of weevil damage at the two sites. This indicates that families with larger average dbh are damaged less frequently than those with smaller dbh. Both correlations suggest that selection of families for greater yield will not necessarily increase spruce susceptiblity to weevil damage. On the contrary, the opposite may be true. When 15-year height data are substituted for 10-year heights, the inverse correlation is even stronger ($r = -0.66$). However, the growth reduction due to weevil attack seriously affects these results. To further corroborate this relationship, we looked at data of the same trees at younger ages and found that there were moderate negative correlations between 6-year height and incidence of damage ($r = -0.44$) and even between 3-year height and incidence of damage ($r = -0.35$).

When comparing the overall damage proportion with the proportion of families that were selected for superior growth, the selected families always fared better. Incidence of damage among the top 25% of families (based on height growth performance at 10 years of age for the Red Rock,

TABLE 4. Differences at various ages and various sites between the mean height of the top 44 families and the mean height of the plantation

	Difference from site mean (%)			
Plantation age (years)	Red Rock	Quesnel	Barbie Lake	Aleza Lake
0	5.0	4.1	6.3	1.8
3	6.1	5.1	5.8	3.0
6	5.8	5.4	6.0	3.6
10	7.6	6.1	4.4	10.3
15	11.1	8.6	8.4	na
dbh	8.2	5.6	6.9	na
Vol.	30.0	21.0	27.9	na

NOTE: The top 44 families (the 25% highest ranking trees) were selected based on the least overall mean damage at Quesnel, Red Rock, and Aleza Lake combined. Differences for dbh and volume are also included where applicable.

Quesnel, and Barbie Lake plantations combined) compared with the plantation average indicates that the incidence of damage in the selected group of families would be lower at every site (Table 1).

When the lowest combined incidence of damage at Quesnel, Red Rock, and Aleza Lake are used as the selection criteria, the best 44 families were superior in height growth at every site at 10 years of age and the volume differential at 15 years of age is substantially higher (Table 3). This growth superiority is not unique to 10- and 15-year performance: the group of 44 families performed better at every site and every age compared with the respective plantation mean (Table 4).

Calculation of expected genetic gain, or correlated response among growth and weevil resistance, is difficult because later height measurements may already reflect the differences due to the weevil damage. Also, the values would be quite arbitrary, as the white pine weevil infestations in the three plantations are a one-point sample in time of three seemingly unrelated weevil populations at different levels of buildup. However, considering the reduced frequency of damage noted in progenies of selected families, and the high family heritability, genetic gains are likely to be moderate to high, depending upon the level of selection employed.

In terms of genetic improvement for white pine weevil resistance, it is likely that if attack levels approach 100%, resistance will have to be measured as number of attacks per tree rather than attacked versus not attacked, as in this present study. This type of information may be more valuable as weevil-resistant material is likely to be planted in areas of high weevil hazard and different levels of family variation may occur. Nevertheless, it is clear that at these low to moderate levels of attack, substantial genetic variation exists in preferences of the weevil to various open-pollinated families of interior spruce in Brisith Columbia.

Before an active program of weevil-resistance breeding is initiated, additional information would be helpful, particularly the determination of the resistance mechanism(s). It is possible that the incidence of adult attacks is similar but in some families an active defence mechanism, such as resin flow, stops the ovipositing adult and (or) larvae before they can damage the tree. Santamour and Zinkel (1976*a*, 1976*b*) suggested that strobic acid in the oleoresin of white pine may affect resistance to weevil attacks. They suggested that oleoresins with high concentrations of strobic acid will crystallize upon contact with the weevil larvae, whereas resins without strobic acid will remain in a liquid state thereby killing the larvae.

This theory was questioned by Bridgen *et al.* (1979) and Wilkinson (1980), who associated apparent resistance or susceptibility with threshold concentrations of monoterpene combinations (α-pinene and limonene). Should this conclusion be correct, the mechanism would probably be repellency. Wilkinson (1983) also studied the effects of leader and growth characteristics in white pine on weevil susceptibility and concluded that only a small amount of variation was explained by those traits.

In addition to these questions, it would be important to know what may occur if a plantation is established from genetically improved seedlings. White pine weevils have been shown to have great flexibility in what they will eat in force feeding experiments (Alfaro and Borden 1982). Will the weevil be able to attack successfully material that previously appeared resistant, or will their potential population explosion be suppressed by the more weevil-resistant seedlings? These and other questions will be best addressed through cooperative studies with experts in the fields of biochemistry and entomology.

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