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Screening of sitka spruce (*Picea sitchensis*) seedlings for resistance to the white pine weevil (*Pissodes strobi*) in a caging experiment

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Abstract

Four weevil pressure treatments (4, 8, 16 and 24 weevils per cage, equivalent to 1/2, 1, 2 or 3 weevils per seedling) were tested in a caging experiment on 2-year-old potted Sitka spruce seedlings (emblings : seedlings derived via somatic embryogenesis) or seedlings from weevil-susceptible (control) and -resistant sources. An increase in weevil pressure resulted in an increase in the numbers of both feeding punctures and adult weevils present on the seedlings, at least on susceptible ones. Over a five-week period, at the highest weevil pressure, an average of 0.95 weevils per seedling was observed on weevil-resistant seedlings versus 3.45 weevils per seedling on susceptible ones. Neither the number of feeding nor oviposition punctures was useful in detecting seedling resistance. However, differences did occur in the number of adults emerging from weevil-resistant and weevil-susceptible seedlings. A total of 37 weevil adults emerged : 31 from weevil-susceptible seedlings and 6 from a single weevil-resistant seedling. Larval feeding was the main cause of seedling mortality, and adult overfeeding was a secondary factor. Fourteen seedlings were killed, 12 of which were susceptible and two resistant. This experiment indicated that the main mechanisms of resistance in the seedlings were blockage of the host selection process and toxicity to larvae and eggs. We concluded that caging experiments, where weevils have a choice between resistant and susceptible seedlings, provide a useful tool for mass screening of resistant clonal material.

Keywords : caging experiments, commercial application, screening for plant resistance, feeding and oviposition, adult emergence.

Introduction

The white pine weevil (WPW), *Pissodes strobi* (Peck) (Fig. 1), is a major pest of young spruce, *Picea* spp., and pine, *Pinus* spp., species throughout British Columbia (B.C.) and other regions of North America (HUMBLE *et al.*, 1994). In coastal regions of B.C., Sitka spruce, *Picea sitchensis* (Bong.) Carr., is so severely damaged that pure planting of this species is not currently recommended in most of these areas (ALFARO *et al.*, 1995). Adult white pine weevils emerge in late March and April from overwintering sites in the forest duff, and locate and climb suitable hosts where they feed on the bark and phloem of lateral branches and the main stem. Later they move to the 1-year-old terminal shoots (leaders), where they continue to feed, and then mate and lay eggs (SILVER, 1968; ALFARO, 1994; ALFARO *et al.*, 1995). Adults feed on bark, leaving round holes known as feeding punctures. Under natural conditions, one to four eggs are laid near the tip of the leader, inside oviposition punctures that are plugged with fecal material (ALFARO, 1996a). After hatching, the larvae synchronously mine downwards, eating phloem, and later producing a characteristic feeding ring as galleries merge, causing girdling and destroying the leader (SILVER, 1968). Pupation takes place in chambers (chip cocoons) excavated in the xylem and covered with wood fibre. Adults emerge from August to early October. They feed, disperse and later hibernate in the duff near the host tree (SILVER, 1968). Repeated weevil attacks cause height-growth loss, leader destruction, and stem deformities.

Fig. 1. Habitus of *Pissodes strobi* (Peck).

Currently, most authors regard the colonization process of a plant by a herbivorous insect as an interaction at various levels. PANDA & KHUSH (1995), for example, describe plant defenses as a set of hurdles the insect must overcome to successfully settle, feed and reproduce on the plant. Some of these hurdles can be nutritional (inadequate nutrients to support insect development), constitutive (usually structures such as resin canals, trichomes, etc.) and inducible defenses. The latter include a number of host defense reactions in response to injury, such as the local synthesis of resin in pines attacked by Scolytidae bark beetles (RAFFA & BERRYMAN, 1983).

Several defense mechanisms to prevent successful weevil colonization have been postulated in spruce. These include variable phenology, repellent odours, dense bark resin canals, traumatic resin canals, fluid resin to inundate galleries, insufficient nutrition (thin bark) (ALFARO, 1996a, b; TOMLIN & BORDEN, 1994, 1996, 1997), and chemical inhibition of the female reproduction system and changing weevil behaviour (SAHOTA *et al.*, 1994; SAHOTA *et al.*, 1998; NAULT *et al.*, 1999). Induced or traumatic resinosis also seems to play a major role in deterring weevil attacks (ALFARO, 1995; ALFARO, 1996b; TOMLIN *et al.*, 1998). Weevil strategies to overcome tree defenses are more or less successful depending on individual trees. The natural selection of trees by weevils leads to elimination of less resistant trees and survival of resistant ones in natural stands. Resistant Sitka spruce genotypes were first observed in B.C. in the 1930's (ALFARO & WEGWITZ, 1994), and recently, host resistance was demonstrated in replicated trials (ALFARO, 1982; ALFARO & YING, 1990; ALFARO, 1995, 1996a, b; KING *et al.*, 2000; YING, 1991).

A program for mass-selection of weevil-resistant genotypes of Sitka and interior spruce is being conducted by the BC Ministry of Forests (KING *et al.*, 2000). This has led to the development of a somatic embryogenesis program for the clonal selection and propagation of resistant genotypes from open-pollinated families (CYR *et al.*, 1995, 1997). Given the long-term nature of selection in field trials, the intent of this research was to initiate the development of a simple early screening tool for selection of weevil-resistant clonal lines from somatic embryogenesis.

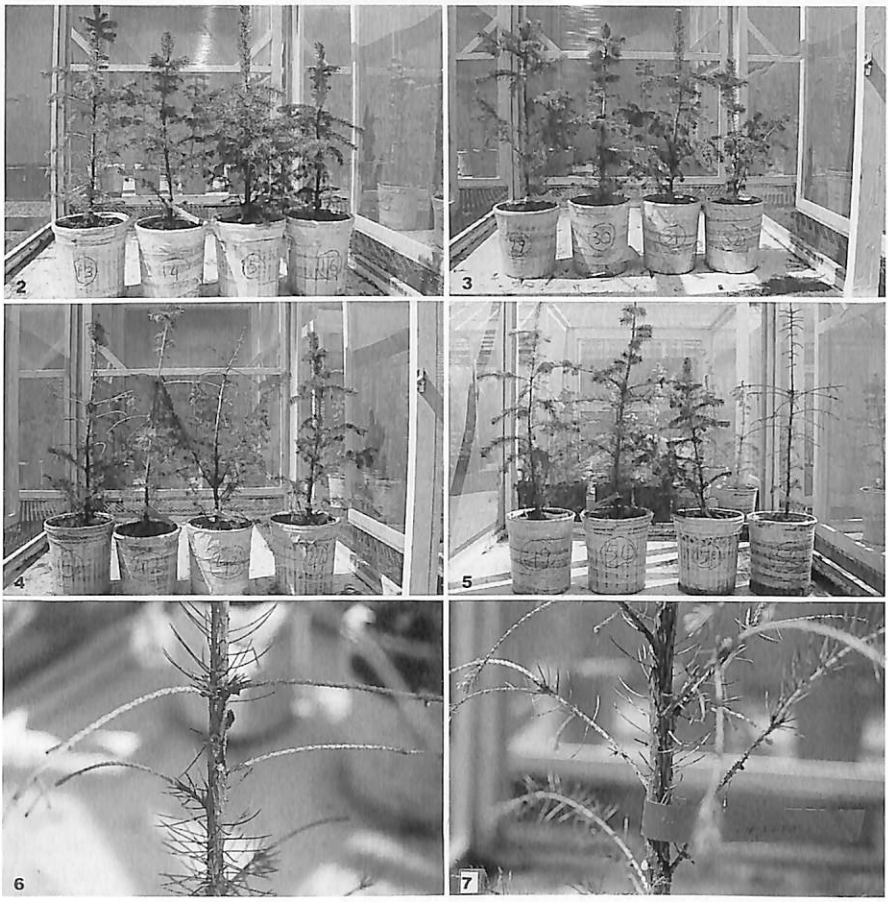
Materials and Methods

Weevils (Fig. 1).

Adult weevils used in this experiment were reared from infested leaders collected in northeastern Vancouver Island at Benson Lake and Eve River, in the fall of 1997. They overwintered in a shade house, in 5-gallon pails containing cut spruce branches, and were used the following spring (1998).

Seedlings (Figs 2-7)

Sixty-four Sitka spruce seedlings were transplanted into 1-gallon pots during September and October 1997 (3 : 1 peat : vermiculite with slow-release



Figs 2-7. 2-3 : Examples of seedlings that had survived weevil attacks at the end of the experiment (13, control; 14, Q1-624; 15, PM1-18; 16, PM1-7; 29, QB-1001; 30, control; 31, PM1-18; and 32, Q1-624). 4-5 : Examples of seedlings that survived the experiment and of seedlings killed by weevil larvae by the end of the experiment (41, control; 42, control; 43, QB-1001; 44, PM1-7; 49, QB-1001; 50, control; 51, PM1-7; and 52, control). 6-7 : Examples of emergence holes of adult weevils in susceptible seedlings in August 1998.

fertilizer). Seedlings were kept well-watered prior to and during the experiment.

Seedlings used as controls (susceptible) were 2-year-old Sitka spruce derived from Prince I upert Stock, 54°14'-129°35', elevation 30 m; average height 54 cm (standa d deviation (SD) : 5 cm), average diameter at ground level 9.1 mm (SD : 1.(mm).

Three-year-old som itic seedlings (emblings) used in the experiment (four BC Research clonal l nes) were derived from three putatively resistant Sitka spruce families : Qualicum bulk, (line QB-1001); Qualicum 1, (line Q1-624);

Pitt Meadows 1, (lines PM1-7 and PM1-18). The candidate clonal lines and seedlings were randomly selected.

Seedlings had an average height of 40 cm (SD : 6 cm), and an average diameter at ground level of 8.7 mm (SD : 1.9 mm). Seedlings from wild trees originating from the Qualicum and Pitt Meadows trees have shown consistent resistance to weevil attack in various field trials (ALFARO & YING, 1990; YING, 1991; YING & EBATA, 1994; ALFARO *et al.*, 1999). However, it is important to bear in mind that the emblings were derived from seeds of open-pollinated parents and, therefore, not all the lines from these seed-lots are equally resistant.

Natural stands of Sitka spruce begin to be attacked by the white pine weevil when trees are approximately 5 years old. The age of the attacked plants is probably conditioned by the thickness of bark available for larval development (KRIEBEL, 1954; SULLIVAN, 1961). Therefore, a screening program based on field infestations is slow. In the present experiment, we used 2-3-year-old plants with the intent of developing an early testing system for spruce trees attacked by the white pine weevil. SOLES & GERHOLD (1968) previously demonstrated the feasibility of screening small eastern white pine seedlings in cages for weevil resistance.

Experimental design

The experiment was conducted in the spring and summer of 1998 at the Pacific Forestry Centre, Victoria, British Columbia. In a manner similar to SOLES & GERHOLD (1968), four weevil pressure treatments were tested on Sitka spruce seedlings in a caging experiment : 2, 4, 8 or 12 male-female pairs were placed in each cage of eight seedlings, resulting in 1/2, 1, 2 or 3 weevils per tree. The experiment was conducted in eight screened cages (dimensions : 100 cm × 96.5 cm × 105.5 cm) elevated about 30 cm above the ground (Figs 2-5), and laid out in two complete blocks of four cages with one weevil pressure treatment per cage within each block. Each cage contained eight randomized seedlings, four susceptible seedlings and four resistant ones (one of each : QB-1001, Q1-624, PM1-7, PM1-18). Weevils were released on 21 April 1998 in the middle of each cage, on the cage floor, and were free to choose the plants for feeding and oviposition. Adults, and feeding and oviposition punctures, were counted on all internodes on each seedling 12 and 24 h after release, and 1, 2, 3, and 5 weeks after release. Emergence holes were counted on 6 August 1998, at the end of the experiment. Seedlings were numbered, and the outside surface of each pot was covered with masking tape to facilitate weevil access to plants (Figs 2-5). Feeding and oviposition punctures were counted on a cumulative basis.

Counts were analyzed with generalized linear mixed models and the GLIMMIX macro of SAS® (LITTELL *et al.*, 1996). Conditionally, on the fixed and random part of each model, counts were assumed to follow a Poisson distribution with mean equal to the exponential of the linear combination of fixed and

random effects. The link function for the generalized part of the model was thus logarithmic. This is approximately equivalent to, but somewhat better than, fitting an ordinary mixed linear model to the log transform of each count. Dependencies between cumulative counts are accounted for in this analysis.

There were too many plants with zero feeding punctures at 12 and 24 h to include these counts in the analysis. The model for the number of feeding punctures present on each seedling at the end of the first, second, third and fifth weeks after weevil release included fixed effects for weevil pressure (4, 8, 16, and 24 adults per cage), plant susceptibility (two categories : control, (= susceptible), and resistant), their interaction, time (1, 2, 3, and 5 weeks after release), and the interactions between time and the previous effects. The effects of weevil pressure and time were separated into their linear, quadratic and cubic components with orthogonal polynomials, the cubic component being considered as a measure of lack-of-fit to the quadratic regression curve. The random part of the model included effects for blocks, cages, and trees within cages and resistance categories. The structure of the variance-covariance matrix for the four repeated measures on each tree was initially assumed symmetric. The random part of the model, starting with the variance-covariance structure, was reduced according to the procedures described by MILLIKEN & JOHNSON (1984) for random effects, and LITTELL *et al.* (1996) for the variance-covariance matrix of the repeated measurements, before final inference and estimation of fixed effects.

Oviposition punctures per tree, per counting time were too few to be analyzed in the same manner as the number of feeding punctures. Therefore, only the last cumulative count, 5 weeks after weevil release, was analyzed after summing over the four trees within each resistance category, within each cage. The model for this total included fixed effects for weevil pressure treatment, resistance and their interaction, and random effects for blocks and cages. The number of emergence holes (Table 1) was not analyzed statistically because no adults emerged from 53 of the 64 trees in the experiment.

Table 1. Number of *P. strobi* emergence holes (emer.) and oviposition punctures (ovip.) as counted at the end of the experiment, on 6 August 1998, per weevil pressure treatment on resistant and susceptible seedlings.

Number of adult weevils released per cage	Resistant plants		Susceptible plants		Total	
	Emer.	Ovip.	Emer.	Ovip.	Emer.	Ovip.
4	0	2	8	17	8	19
8	0	15	2	3	2	18
16	6[1]	10	8	11	14	21
24	0	5	13	49	13	54
Total	6	32	31	80	37	112

[1] These six emergence holes all occurred on the same QB-1001 seedling.

At each counting time, adults that could actually be found on each tree were also scarce, and the number of adults was summed over the four trees within each resistance category in each cage before analysis. The model for the number of adults was thus similar to that for the number of feeding punctures, except that the random tree effects were replaced by a random effect for the group of four trees within a resistance category in each cage. Observations at 12 and 24 h were excluded from the analysis.

Results

On 6 August, 37 larvae had developed and emerged as adults : 31 from 10 susceptible seedlings and 6 from one resistant (QB-1001) seedling (Table 1). The experiment thus demonstrated that under caged conditions, the weevils are able to develop into adults on small spruce plants, in agreement with the results of SOLES & GERHOLD (1968).

On average over the four counting times and over resistant and susceptible seedlings, the number of feeding punctures counted on all internodes increased 1.1-fold for every additional adult weevil released ($p \leq 0.0001$ for the linear component of the effect of weevil pressure on the logarithm of the number of feeding punctures, $p > 0.4$ for the quadratic and lack-of-fit components, Table 2). The addition of four adults multiplied the number of feeding punctures by a factor of 1.4. The addition of eight adults doubled the number of feeding punctures. There was no evidence that resistance had any effect on the number of feeding punctures per seedling ($p = 0.20$) or that the effect of weevil pressure on feeding differed between resistant and susceptible plants ($p = 0.16$). The effect of time on the number of feeding punctures was highly significant ($p \leq 0.0001$), but more complex than that of weevil pressure. This could reflect a variation in nutritional needs of *P. strobi* over the season. In the first 3 weeks after release, the number of feeding punctures roughly doubled each week; the increase was not so large during the fourth and fifth weeks (Table 3). These facts were reflected in the analysis by significant linear and quadratic components of the effect of time on the logarithm of the number of feeding punctures ($p \leq 0.0001$ for both components). The effect of time was constant across weevil pressure treatments and resistance categories ($p > 0.9$ for the three interactions involving time).

Over 5 weeks, 112 oviposition punctures appeared on the 64 seedlings : 80 on control trees, 32 on resistant trees. The 2.5-fold increase in susceptible plants relative to resistant ones was not statistically significant, however ($P = 0.16$), because the degrees of freedom in the denominator of the test were fewer than 5 which yields very low power. There was no clear evidence for a significant effect of weevil pressure on oviposition ($P = 0.66$).

Oviposition activity peaked in the third week following release of the adults : 84 oviposition punctures (75%) appeared in that week; 11 (10%) appeared in the second week, and 13 (12%), in the first.

Table 2. Average number of *P. strobi* feeding punctures and its confidence interval per weevil pressure treatment (means of 64 observations : 16 trees per weevil pressure treatment with 4 counts per tree over time).

Number of adult weevils released per cage	Feeding punctures	95% confidence limits	
		Lower	Upper
4	4.0	1.5	10.5
8	8.6	4.6	16.1
16	16.1	10.3	25.2
24	27.9	19.4	40.1

Table 3. Average number of *P. strobi* feeding punctures per weevil pressure treatment (means over 64 trees) per counting time.

Time (weeks)	Feeding punctures	95% confidence limits	
		Lower	Upper
1	3.8	2.3	6.1
2	8.5	5.9	12.3
3	18.8	14.0	25.2
5	25.6	19.9	33.0

Table 4. Average number of adult *P. strobi* weevils per group of four seedlings, by weevil pressure treatment and resistance category (means of 8 values : 4 observation times and 2 cages)[1].

Number of adult weevils released per cage	Resistant	Susceptible	Difference	Standard error of the difference
4	1.3	1.3		
	0.27	*0.27*	*-0.00*	*0.38*
8	4.1	1.2		
	1.42	*0.20*	*-1.22*	*0.34*
16	4.1	6.3		
	1.40	*1.84*	*0.44*	*0.22*
24	3.8	13.8		
	1.33	*2.63*	*1.30*	*0.22*
Mean	3.0	3.4		
	1.11	*1.24*	*0.13*	*0.15*

[1] Numbers in italics below each mean and in the "difference" and "standard error of the difference" columns are on the logarithmic scale.

The number of weevils present on each tree, on each sampling date, was summed over the four trees of any resistance category within each cage. The interaction between weevil pressure and resistance had a significant effect on the number of adults present on groups of four trees ($p \leq 0.0001$, Table 4). On susceptible seedlings, the number of adult weevils per four seedlings was multiplied by 1.14 for every additional released weevil; this rate was approximate-

ly constant over the range of weevil pressures tested ($p \leq 0.0001$ for the linear component, $p > 0.07$ for the quadratic and lack-of-fit components). The total number of adults per group of four susceptible seedlings increased from 1.3 on average in cages where four adults had been released, to 13.8 when 24 adults had been released. On resistant seedlings, the number of adult weevils per group of four seedlings also increased with the number of released adults, but the increase was much smaller, from 1.3 to 3.8, and did not follow a simple trend ($p = 0.006$, $p = 0.005$, $p = 0.02$ for the linear, quadratic and lack-of-fit components, respectively). This indicated that weevils had a tendency to stay away from resistant trees.

Over time, the number of adult weevils present on groups of four seedlings increased during the first 3 weeks after release, and decreased over the fourth and fifth weeks ($p = 0.44$ for the linear component of the effect of time, $p = 0.009$ for its quadratic component, $p = 0.99$ for lack-of-fit, Table 5). This effect held at all levels of weevil pressure and resistance ($p > 0.24$ for the three interactions involving time).

Table 5. Average number of adult *P. strobi* weevils per group of four seedlings 1, 2, 3 and 5 weeks after release (means of 16 values including both resistant and susceptible plants : 4 weevil pressures, 2 resistance categories, 2 cages).

Time (weeks)	Number of adults on four trees	95% confidence limits	
		Lower	Upper
1	2.9	2.4	3.5
2	3.7	2.9	4.7
3	3.9	3.2	4.7
5	2.6	1.7	4.0

Discussion

Plants have evolved an array of defensive strategies against herbivores (MATTSON *et al.*, 1988). These interfere with the chain of behaviours or processes that lead to the successful utilization of a plant as a food source (PANDA & KHUSH, 1995). In *Pissodes strobi*, this chain consists of location of host, settling and accepting the host as suitable for feeding and oviposition, egg laying in sufficient numbers to overcome induced and constitutive resinosis, larval survival (to resins, other toxic host components and pathogenic agents) and pupation.

Earlier work (VANDERSAR & BORDEN, 1977a, b; ALFARO & BORDEN, 1982; ALFARO, 1996a, b; TOMLIN & BORDEN, 1994, 1996, 1997) has indicated that weevils choose suitable plants using early detection mechanisms such as visual cues, phagostimulants and phagodeterrents. This form of resistance has been considered to operate as preference or non-preference of host plant and is expressed by weevil behaviour in response to host signals such as host silhouette, odour, taste, and texture. Other resistance mechanisms such as pro-

duction of traumatic resin (ALFARO, 1995), operate through toxic effects on eggs and larvae. An additional resistance mechanism has been postulated by SAHOTA *et al.* (1998), who proposed that inhibition of reproductive weevil physiology, influenced by feeding on resistant Sitka spruce trees, is an important resistance factor. However, to be effective, this mechanism requires that weevils feed on the host to sustain physiological inhibition.

In the present experiment, there was no statistical evidence that, on average, the number of feeding or oviposition punctures differed between resistant and susceptible plants. Most emergence holes, however, were found on susceptible plants where the number of adults increased steadily with weevil pressure. On resistant plants, the number of weevils did not change much when weevil pressure increased beyond eight adults per cage. Yet the number of feeding punctures was approximately the same on resistant and susceptible plants, even if weevils were more numerous on susceptible plants at high weevil pressures. This suggests that weevils on resistant plants increased their feeding activity, compared with those on susceptible seedlings, to fulfill their nutritional needs. Although this difference was not statistically significant, oviposition punctures were more than twice as numerous (80) on susceptible trees than on resistant ones (32). This is in agreement with the lower number of weevils visiting on resistant plants. Clearly, the larvae could not develop adequately on resistant seedlings, except for one seedling, as shown by the emergence rate from oviposition punctures on resistant and susceptible seedlings (Table 1). This suggests that a toxic effect on larvae was an important weevil resistance mechanism.

In this caging trial, released weevils dispersed and were more often observed walking on pots and screens during the first two counts (12 and 24 h after release) than at later dates. However, after a week, most released adults had settled on plants. At high weevil pressures, significantly more weevils could be found on susceptible than on resistant plants (Table 4). ALFARO (1996a) found a non-preference for different genotypes of resistant Sitka spruce. Weevils that were present on a seedling one week after release often remained there until the fifth week.

Larval development did not occur in the seedling leaders (i.e., grown in 1997) but instead mainly in the 1996 (34 seedlings), and 1995 (3 seedlings) internodes. This is likely a consequence of the insufficient amount of bark in the leaders due to young seedling age, or to increased density of resin canals per unit bark area in the leader. Similar results were obtained by ALFARO (1996a). Resin canals are denser in the leader than in the lower internodes (ALFARO, 1996a). Emerged adults were notably smaller than those originally released in the experiment, probably due to the insufficient amount of bark in tested seedlings (2-3 years old). Seedling mortality was caused mainly by larval feeding and rarely by adult overfeeding on individual plants.

There are several interaction levels between weevils and their host plants, which form a complex web of interdependencies. Some of these are listed in

Table 6, with an indication of their potential significance as weevil resistance screening criteria. They include : early adult detection of resistant and susceptible plants, adult feeding and oviposition activity on resistant and susceptible plants, and larval mortality on resistant and susceptible plants. Successful weevils are those which are capable of detecting susceptible plants as early as possible, feeding on them and depositing eggs on the substrate (bark) that gives them the highest probability of developing into larvae and emerging as adults of the next generation.

Table 6. Evidence for behavioural or developmental blockage in *P. strobi* from this experiment.

Behaviour or process blocked	Possible mechanism	Evidence from this experiment	Rationale
Host selection - Locating and settling on plant	- Repellency	Yes	Significantly more adults present on susceptible than on resistant plants at high weevil pressure
Adults feeding on plant	- Repellency	No	Similar average number of feeding punctures on resistant vs. susceptible plants
Oviposition on plant	- Repellency - Inhibition of egg development	Not clear	The 2.5-fold increase in oviposition punctures in susceptible relative to resistant plants was not statistically significant
Egg and larval development	- Toxicity of resin and other chemicals	Presumably yes	Higher mortality on resistant than on susceptible plants

Based on this experiment, the main mechanisms of resistance in these seedlings were blockage of the host selection process (repellency or non-preference) and toxicity to larvae and eggs (Table 6). Similar results were shown in an earlier caging experiment by ALFARO, 1996a. Also, ALFARO *et al.* (2000) and HULME (1995) found that, under field conditions, weevils tended to have lower visitation and departed earlier from resistant plants than from susceptible plants. Toxicity to eggs and larvae was supported by the significantly lower emergence to oviposition puncture ratio found on resistant than on susceptible plants (Table 1).

Conclusions

Results from the present experiment are intended for application in preliminary screening for resistance of somatic seedlings to the white pine weevil. Complete larval development and adult emergence should be considered as the most useful selection criteria for plant resistance.

In future screening experiments, we recommend that the following factors be considered : 1. All plants should be of the same age (preferably at least 3 years old). 2. Weevil pressure should be similar to the highest used in our experiment : two males and two females per plant. 3. More cages per treatment are recommended to increase the power of the test. 4. Resistant and susceptible candidate seedlings should each constitute half of the total number of plants used within any cage.

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