

DEVELOPMENT OF SITKA SPRUCE PHENOTYPES
RESISTANT TO THE SPRUCE WEEVIL:
A SUMMARY OF RECENT AND PLANNED RESEARCH
PROJECTS IN B.C.

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SUMMARY

The development of spruce weevil-resistant Sitka spruce phenotypes has absorbed, directly or indirectly, considerable research effort in B.C. in recent years. This report reviews the progress of this research and examines the status of plans for continued work in this regard.

Only one current project in B.C. may lead directly to the isolation of a few resistant genotypes; several putatively resistant individual Sitka spruce trees, mostly from a B.C. Forest Service provenance trial at Sayward, B.C., have been cloned, rootgrafted, and planted in a high hazard weevil area on the west coast of Vancouver Island to test them for weevil resistance.

Most of the topic research in B.C. has been concerned with the elucidation of the mechanisms of the weevil's host selection behavior, which eventually may lead to methods for selecting or breeding resistant trees. Results to date indicate that the weevil's host selection behavior is mediated by a complex mixture of physical and chemical cues emanating from the host. The weevil can feed upon, and oviposit in, a number of conifer species, but appears to have a genetically controlled preference for its primary host species.

These observations suggest that "resistance" in spruce is relative, whereby the weevil will successfully utilize, in order of preference: susceptible Sitka spruce, resistant Sitka spruce, and finally other sympatric conifers, depending on the availability of the more preferred material. The development of resistant phenotypes of Sitka spruce is, therefore, unlikely to be a panacean solution for the control of coastal weevil infestations. Rather, an integrated approach using resistant phenotypes together with other selected weevil control techniques, appears to be the most promising direction for future research.

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A. INTRODUCTION

The spruce weevil(1) (Pissodes strobi) has effectively destroyed attempts to grow Sitka spruce (Picea sitchensis) regeneration in much of coastal B.C. It has been reported to be the most damaging insect pest of regenerating Sitka spruce in the Pacific Northwest (McMullen 1976; Alfaro 1982). In 1982 and 1983 an extensive survey of Sitka spruce plantations in the Vancouver Forest Region confirmed that serious levels of damage were being caused by this pest (Heppner and Wood 1984), prompting the Forest Service in 1985 to impose a ban on Sitka spruce planting over most of the Region(2). In addition, many Sitka spruce plantations established prior to the 1985 ban have been rehabilitated and converted to alternative conifer species (D. Harris, pers. comm.).

Although a number of control techniques have been proposed and attempted, as summarized by Cozens (1983), none to date has proven to be sufficiently effective nor practical to implement. Among the proposed control methods, perhaps the greatest research efforts have been directly or indirectly concerned with the development of resistant Sitka spruce phenotypes. This report presents a summary of recent and planned research efforts in this regard in B.C.

B. RECENT RESEARCH PROJECTS

Recent topic research projects in B.C. can be discussed in three separate categories:

In the first category are those projects involved with the selection, field testing and clonal propagation of putatively resistant individuals. These individuals have been observed to be weevil-free in conditions where neighboring spruce trees were being

(1) Also known as "white pine weevil", but commonly referred to as "spruce weevil" in B.C. for its habit of infesting Sitka spruce, Engelmann spruce, white spruce, and hybrids among these species.

(2) Vancouver Circular VR 85-471 Re: Sitka spruce weevil management. May 23, 1985.

attacked. The intention is to develop a genepool of weevil-resistant Sitka spruce. If successful, these genotypes can be cultivated in a seed orchard and the open pollinated seed can be used for coastal reforestation.

In the second category are those projects that are concerned with the mechanisms by which *P. strobi* selects individual host trees for feeding and oviposition. Elucidation of these mechanisms eventually may provide a basis for screening candidate resistant trees for propagation.

In the third category are projects designed to uncover the mechanisms of resistance in Sitka spruce. Elucidation of these host mechanisms also may provide a basis for the selection of resistant phenotypes. They are not necessarily related to the weevil preferences being examined in the second category.

1. Field Testing of Putatively Resistant Genotypes

a) Sayward provenance trial

The Ministry's Research Branch is conducting a field test in an attempt to isolate several weevil resistant genotypes, as described below.

Under the direction of Dr. Cheng Ying, the Ministry has 15 on-going Sitka spruce provenance trials. Some of these trials are on Vancouver Island, some are on the Queen Charlotte Islands, and some are near Terrace. During periodic assessments of these trials, observations of weevil damage are noted (C. Ying, pers. comm).

In one of these trials, near Sayward on Vancouver Island (E.P. 702), a full assessment of weevil damage was conducted in 1981, seven years after planting and eleven years from seed germination (Ying, 1982). This provenance trial consists of 433 wind pollinated families (i.e. seeds from 433 individual trees, presumably "plus" trees), from 38 seed sources (provenances). The seed sources are from locations on the east and west coasts of Vancouver Island, the lower

mainland, the Queen Charlotte Islands, the Skeena River area, and from the southern portion of the Alaska Panhandle.

In the 1981 assessment, 40.7% of the 6 936 living trees were observed to be weevil attacked. Weevil attack among the provenances varied from 16 to 62% with provenances along the Skeena River being the least attacked. It is suspected (Ying, 1982) that provenances from the mid and upper Skeena River areas may be hybrids of Sitka spruce and white spruce. Thirty-eight of the 433 families were free from weevil attack in 1981.

As it was uncertain whether weevil-free trees at Sayward were unattacked by chance, or due to site conditions, or due to inherent properties that inhibit weevils, an experiment to further test the putatively resistant trees was initiated in 1982. Scions from four individuals from each of nine families (i.e. 36 genotypes), were root grafted on potted rootstock at the Cowichan Lake Research Station, tended for two years, and in 1984 were outplanted in a high weevil hazard area near Zeballos (Fair Harbour) in the Campbell River Forest District (White, 1986). Most of the Sayward trees selected were weevil-free or demonstrated excellent recovery from weevil damage. A few of the trees were heavily weevil infested. These were used as "controls" (C. Ying and R. White, pers. comm.).

An assessment of weevil damage in this outplanting was scheduled for autumn 1986. Due to staff and funding shortages, however, Research Branch was unable to conduct this assessment (C. Ying, pers. comm.). It is possible that funding in 1987 or 1988 may allow for an assessment.

b) Green Timbers clones

Adjacent to the Green Timbers Nursery in Surrey, a Sitka spruce plantation established in the 1930's was subjected to intense weevil attack for many years.

Five individual trees, however, demonstrated resistance to weevil attack (Alfaro, 1982), while the remaining trees were stunted, deformed, and overtopped by other species. Most of these suppressed trees eventually died. It is believed that this plantation was originally established as a provenance trial using seed that was from the Queen Charlotte Islands.

Clones of the five resistant trees have been propagated.

In 1972 clones of three of these resistant trees were established (E.P. 704) at the Forest Service Research Laboratory in Victoria (White, 1986). In 1982, scions from these clones were included in the Sayward outplanting experiment (see above).

In 1983, after learning of the imminent destruction of the original five resistant trees at Green Timbers, pest management staff at the Vancouver Forest Region collected scions from all five trees and sent them to the Cowichan Lake Research Station where they have been successfully grafted in a clone bank (C. Ying, pers. comm.). These ramets have not been scheduled for further grafting and field testing for weevil resistance.

c) Other selection projects

To the best of the author's knowledge, no other outplantings have been conducted in B.C. to specifically field test Sitka spruce for weevil resistance.

There are, however, plantations at the Green Timbers Nursery that were established in 1955 to test for possible resistance in P. glauca, P. abies, and hybrids of P. sitchensis x glauca (Silver and Ruth 1966; Harris and Brown 1970). The seed sources for these trees were from various locations in eastern Canada and Europe. At the time of the last recorded measurements of weevil attack in these plantations (approximately 1975), some of the Sitka-white hybrids were displaying good growth characteristics and apparent weevil resistance (L. McMullen, pers. comm.).

Scions from most of these trees have been rootgrafted and tended in a clone bank at Cobble Hill (a Canadian Forestry Service experimental plantation) (M. Hulme, pers. comm.).

The Forest Service has a good candidate group of putatively resistant trees in a Sitka spruce provenance trial along the Nass River Road near Terrace (C. Ying, J. Borden and J. Brooks, pers. comm.). Despite heavy weevil infestations in the trial, a number of individuals are expressing apparent resistance. Two provenances, the Kitwanga and Big Qualicum provenances, appear to be particularly resistant (Brooks, et al. 1986). This trial also has a better layout and has been better tended than the Sayward trial. The Sayward trial has considerable microsite variation and has been partially overgrown with alder and cottonwood (C. Ying, pers. comm.). Under these conditions, there is a greater chance that putatively resistant trees are weevil-free due to site conditions unfavorable to the weevil, rather than to inherent properties of resistance. If funding can be secured, Research Branch would like to conduct further field tests on these apparently resistant trees in the Nass River trial (C. Ying, pers. comm.).

There have also been attempts to grow Engelmann spruce at low elevations (less than 600 m) near Hope, Pemberton, Gold River and Zeballos (H. Hahn, pers. comm.). These test sites are primarily being monitored for growth responses but weevil damage is also being noted. Although feeding bioassay studies (see next section) have demonstrated that weevils from Sitka spruce equally prefer Engelmann spruce, it is possible that these sites may reveal some resistance. The four test sites at Gold River and Zeballos are still young for weevil attack (4 or 5 years since establishment), but so far have demonstrated very poor growth response (B. McCutcheon, pers. comm.).

2. Elucidation of the Mechanisms of Pissodes strobi Host Selection Behavior.

For more than a decade, researchers in B.C., mostly working at Simon Fraser University, have been making remarkable progress toward the elucidation of the mechanisms by which Pissodes strobi selects host trees for feeding and oviposition. Most of this work has been specifically concerned with coastal populations of B.C. weevils and their primary host, Sitka spruce.

As explained by Miller and Strickler (1984), insects follow a specific behavioral sequence for finding and accepting host material:

- "(a) finding: initiated by random movement not influenced by plant cues, progressing to oriented movement towards the plant in response to non-contact cues (visual, olfactory) and concluding in arrestment on plant (cessation of movement).
 - (b) examination of the plant by scanning with its sensory organs, including gustatory sensors (nibbling).
 - (c) consuming: sustained feeding or acceptance for oviposition".
- (from Alfaro and Borden, 1985)

This behavioral sequence presupposes that, under operable conditions, the insects are guided by innate (inherited) behavioral patterns whereby they appropriately respond to physical or chemical cues emanating from the host.

For P. strobi, these stages have been explored in a series of studies conducted in B.C. Results to date indicate that physical cues from the host help the weevils to find host leaders and, when contact is made, to search for suitable feeding and oviposition sites. On contact, the weevil uses chemical cues from the host to locate optimal feeding and oviposition sites, to sustain feeding, and presumably to induce successful oviposition. Chemical cues have not yet been demonstrated to play a role in the weevils' pre-contact search for suitable host leaders. For the purposes of this discussion, physical and chemical factors are discussed separately below, although a complex combination of these factors is undoubtedly involved.

a) Physical factors

In their search for suitable host material, adult weevils must distinguish between the host and a number of sympatric conifer and non-conifer species. VanderSar and Borden (1977a) demonstrated that at close range this process appears to be mediated by visual stimuli. In laboratory experiments, overwintered (i.e. spring feeding) weevils oriented toward black cardboard silhouettes that mimicked spruce leaders. The weevils were significantly more attracted to vertical (or near vertical, within 15 degrees) silhouettes, especially those near 3 cm in width, and preferred the taller of silhouettes that were near 3 cm wide.

This paper also reports field measurements that confirm that, in the spring, weevils prefer the taller leaders in the stand and the larger diameter leaders, which averaged near 3 cm in silhouette diameter.

These results indicate that visual stimuli are involved in guiding the weevils to leaders as opposed to lateral branches in their spring search for suitable host material, and that visual stimuli may also be involved in the weevils' selection of the taller and wider (i.e. more vigorous) leaders that are available.

VanderSar and Borden (1977b) also demonstrated that once in contact with a leader, weevils are stimulated by positive phototaxis and negative geotaxis to both feed and oviposit in the uppermost portion of vertical leaders.

In a separate experiment, VanderSar and Borden (1977) observed that pre-wintered (i.e. autumn feeding) adults preferred to feed on larger diameter lateral branches rather than smaller diameter branches. As the chemical differences between larger and smaller branch sections were unlikely to be significant, the authors surmised that visual stimuli were probably involved.

Harris, *et al.* (unpublished) noted that in choice feeding bioassays, weevils preferred spruce bark agar with needles stuck in it over spruce bark agar alone.

Equal preference was given to genuine spruce needles or surrogate needles (toothpicks), indicating that the weevils express a positive touch response (thigmotaxis). It is possible, therefore, that spring feeding weevils may prefer leaders with denser needle spacing.

b) Chemical factors

In a series of bioassay studies, some of the chemical stimulants and deterrents to which P. strobil responds for feeding and oviposition have been at least roughly characterized.

VanderSar and Borden (1977) found that in no-choice feeding bioassays, weevils fed equally well on twigs cut from Sitka spruce, Douglas-fir and western hemlock, but did not feed on western red cedar. In choice feeding experiments, both sexes preferred Sitka spruce to either western hemlock or western red cedar. When given a choice between Sitka spruce and Douglas-fir, females preferred Sitka spruce, but males did not discriminate between the two species. In further tests, the weevils fed on extracts of Sitka spruce bark, suggesting to the authors that Sitka spruce bark contains chemical feeding stimulants.

VanderSar (1978) conducted similar tests on overwintered P. strobil from Engelmann spruce in the Kootenays. In these tests, weevils accepted both Engelmann spruce and western white pine leaders for feeding, although a preference was expressed for Engelmann spruce. Female weevils, however, would oviposit only in Engelmann spruce. From these results VanderSar postulated that the chemical stimulants for feeding either do not induce oviposition, or are present in insufficient concentrations. This hypothesis may be equally valid for coastal populations of weevils in Sitka spruce.

Subsequent feeding experiments by Alfaro et al. (1980), using Vancouver Island weevils reared in Sitka spruce, and a feeding bioassay methodology

developed by Alfaro (1979), demonstrated in more detail that the feeding stimulants and deterrents consist of a complex mixture of volatile and non-volatile compounds.

The non-volatile fraction of Sitka spruce bark, needles and phloem appears to be the primary determinant of feeding behaviour. In particular, non-volatile constituents in the cuticle of leaders and needles are highly stimulatory. However, the needles also appear to contain a volatile deterrent, thereby restricting feeding to the leader bark alone.

Volatile fractions to spruce bark (monoterpenes in particular) did not induce the weevils to feed when used alone. However, low concentrations of the monoterpenes alpha-pinene, beta-pinene and beta-myrcene acted as synergists to enhance the stimulatory effects of the non-volatiles. (+)-Camphor and limonene were also synergistically stimulating at low concentrations, but inhibiting at higher concentrations. It is interesting to note that the concentration of limonene has been observed to increase in vigorous leaders at the time when spring feeding adults are seeking host trees (Carlson 1971), leading to the supposition that limonene may induce host acceptance by the weevils. However, as Alfaro, *et al.* (1980) note, beyond a certain concentration, limonene is inhibitory and therefore may be a resistance mechanism in the Sitka spruce. Another monoterpene, piperitone, was observed in the Alfaro, *et al.* (1980) study to have a strong feeding deterrent effect, but was mostly confined to needles. Piperitone also increases through the growing season (Hrutfjord, *et al.* 1974) and therefore could also be a defense mechanism in the spruce.

Alfaro, *et al.* (1981) studied the weevils' responses to the components of western red cedar foliage and branchlets in order to characterize the feeding deterrent effect of this tree species. They discovered that water soluble extracts had no deterrent effect, and ethanol fractions were stimulatory. Only the volatile

fractions (i.e. "cedar leaf oil") were inhibitory. The authors felt that the commercial use of cedar leaf oil as a topically applied repellent is impractical, as relatively high concentrations are required to inhibit feeding.

In a similar feeding bioassay study, pine oil (a by-product of the pulping industry composed of a complex mixture of monoterpenes and other assorted compounds) was demonstrated to be an effective feeding deterrent (Alfaro, et al. 1984).

McLean and Carlson (1983) used pine oil as a deterrent for oviposition in field trials on the west coast of Vancouver Island. Weevils were successfully repelled from leaders that directly had received an application of pine oil. However, the volatile pine oil vapours in the immediate environment of treated leaders, failed to protect adjacent untreated leaders. Some phytotoxicity was also observed on treated leaders.

In order to determine if the feeding stimulants in Sitka spruce were also present in other plants, Alfaro and Borden (1982) conducted feeding bioassays on 33 conifers (native and exotic), five angiosperm species sympatric with Sitka spruce, and sword fern. Vancouver Island weevils reared from Sitka spruce were used. In forced (i.e. no-choice) feeding bioassays, the weevils fed on all conifer species, but there was almost no feeding on non-conifers. The feeding response on spruce and pine species was similar to (or higher than) Sitka spruce. This confirmed earlier studies (VanderSar et al. 1977) where weevils reared from naturally infested Sitka spruce did not discriminate between Engelmann spruce, Sitka spruce and eastern white pine. However, Alfaro and Borden (1982) also observed that Douglas-fir, western hemlock, red and yellow cedars, and a few other conifers all elicited significantly lower responses than did Sitka spruce. Although these latter observations appear to differ from the results obtained by VanderSar and Borden (1977) in which the weevils fed equally on Douglas-fir,

western hemlock and Sitka spruce, the experiment demonstrated that feeding stimulants are found in a wide variety of conifers, but are probably confined only to conifers.

In choice feeding bioassays, Alfaro and Borden (1982) observed that Engelmann spruce, white spruce, and a few pine species induced similar feeding responses as Sitka spruce, whereas most of the spruce and pine species tested, as well as the other conifers, all produced lower responses.

Of particular relevance in B.C. is that the weevils, when given a choice, actively discriminated against those species that are sympatric with its B.C. hosts, in favor of Sitka spruce. This indicates that Sitka spruce and Engelmann spruce have optimal concentrations of feeding stimulants. In the absence of these hosts, however, the weevil can feed on several other sympatric species.

Alfaro and Borden (1982) also conducted choice feeding bioassays using Sitka spruce bark mixed together with the bark of other species. In this test they found that Douglas-fir, subalpine fir, western hemlock and western red cedar contain feeding deterrents. Lodgepole pine and wetern white pine, on the other hand, did not deter feeding when added to Sitka spruce bark, indicating that the weevils' lack of feeding preference for these species is due to sub-optimal qualities or quantities of stimulants, rather than to the presence of deterrents.

Alfaro (1987) demonstrated that weevils reared in Sitka spruce and weevils reared in Engelmann spruce both could be forced to oviposit in lodgepole pine leaders. Of greater significance, however, was the observation that the resulting adults reared from lodgepole pine preferred to feed on the original host of their parents, Sitka spruce or Engelmann spruce. The author therefore concludes that the weevils' preference for spruce is genetically pre-determined, and not easily influenced by exposure to another tree species.

3. Mechanisms of Resistance in Host Trees

In B.C. relatively little work has been done to determine directly the possible mechanisms by which the host expresses resistance to weevil attack.

Brooks *et al.* (1986) examined the monoterpene spectra of putatively resistant and susceptible Sitka spruce. This study was an attempt to identify a diagnostic spectrum (i.e. chemotype) for resistant spruce, thereby enabling the systematic screening of candidate trees for the propagation of resistant phenotypes. While no cause and effect relationship was necessarily implied between the monoterpenes and resistance, the use of monoterpene profiles was chosen as a potentially reliable and stable indicator, as these compounds have been reported to be under strong genetic control and not easily affected by environmental influences (Wilkinson *et al.* 1971; Squillance 1976; Squillance *et al.* 1980). Susceptible and apparently resistant trees from Nootka Island, the Sayward and Nass River provenance trials, and from some of the original resistant Sitka spruce trees at the Green Timbers Nursery were examined.

Overall, none of the monoterpenes alone, nor profiles of several monoterpenes, was consistently indicative of resistance in all the populations of trees tested. As there are large variations in monoterpene composition within and between individual trees, differences between resistant and susceptible trees would have to be large to be significant. This study did demonstrate some significant differences in some of the provenances tested, but these differences were not consistent among all the provenances. Similar results were obtained in earlier work by Harris *et al.* (1983) in which a significantly different profile was observed between the five resistant Green Timbers trees and neighboring susceptible trees.

Most notable in the study by Brooks *et al.* (1986) were two compounds (unique to Sitka spruce; J. Brooks, pers. comm.), isoamyl isovalerate and isopentenyl isovalerate, which were the most consistently different between

resistant and susceptible trees. However, the degree of overlapping concentrations of these compounds, 0.3 - 9.1% in resistant trees and 0.5 - 11.2% in susceptible trees, was considered to be too great to accurately define a resistant chemotype if used alone. An additional characteristic that correlates to resistance would help to strengthen the positive identification of resistant trees (J. Borden, pers. comm.). In terms of a cause and effect relationship, the authors postulated that "resistant trees may in part lack a characteristic spruce odor that is imparted by these compounds."

Brooks *et al.* (1987) monitored the monoterpene profile of developing buds and new shoots over a nine month period between April and October from Sitka spruce trees in the Sayward provenance trial and from the U.B.C. Research Forest in Maple Ridge. In general their results are consistent with observations by Hrutfiord *et al.* (1974) in Sitka spruce in Washington state. Of most significance in the Brooks *et al.* (1987) study was that there were "no significant differences at any date in monoterpene composition between buds from resistant and susceptible trees." The authors concluded that qualitative differences in bud monoterpenes are probably not host resistance mechanisms, although it is possible that total quantities could be influential.

These studies represent the host resistance work that has been conducted in B.C. However, it is important to note that relevant work in this regard has been reported elsewhere, particularly with *P. strobi* on eastern white pine. Possible host resistance to the weevil has been postulated in terms of bark thickness (Kriebel 1954; Wilkinson 1983b); the size, depth and frequency of resin canals (Stroh and Gerhold 1965; Su-Mei Jou 1971); and other mechanisms.

The quality of recovery from attack can also be considered a resistance mechanism and is especially important from a pragmatic viewpoint. In B.C., White (1986) selected attacked trees that demonstrated good recovery, for further field testing at Zeballos (see section B, 1a). These trees originated from provenances at

Fair Harbor and Kitwanga. Similarly, J. Brooks (pers. comm.) has observed provenances in the Nass River provenance trial that demonstrated excellent recovery with little net damage to stem form despite previous weeviling.

An interesting and important observation on the clonal propagation of resistant trees has been observed by J. Borden and J. Brooks (pers. comm.). While examining the monoterpene spectra of the three Green Timbers resistant clones at the Forest Service Research Laboratory in Victoria, it was noted that these rootgrafted ramets appear to be expressing the monoterpene spectra of the rootstocks rather than the grafted clones. This has important implications for the field testing of rootgrafted putatively resistant clones.

C. PLANNED RESEARCH PROJECTS

At this time very few projects are planned in B.C. for the development of weevil-resistant Sitka spruce phenotypes.

The Ministry's Research Branch intends to survey the Zeballos field trial plantation for weevil damage in 1987 or 1988 if funding is available. The Branch would also like to survey the Nass River provenance trial for weevil incidence and clone some of the more resistant trees for future outplanting to test for weevil resistance, although funding and plans have not been arranged (C. Ying, pers. comm.). The Branch continues to note weevil damage during periodic assessments of the Ministry's Sitka spruce provenance trials.

At Simon Fraser University, John Borden (pers. comm.) would like to investigate host resistance mechanisms, but no firm plans have yet been established.

To the best of the author's knowledge, no other relevant research projects have been planned in B.C.

D. DISCUSSION AND CONCLUSIONS

In this summary, it can be seen that considerable research has been conducted in B.C. that may lead to the development of Sitka spruce phenotypes resistant to the spruce weevil. It can also be seen that more research is required before resistant phenotypes are available for production use in reforestation and that a number of obstacles must be overcome in the process. Some of the research to date also suggests that if resistant spruce are successfully developed, they may not be a panacean solution to weevil damage; the use of resistant spruce will likely have to be augmented with additional weevil management techniques in an integrated approach. These issues are discussed below.

1. Zeballos Field Trial for Weevil Resistance

The field trial at Zeballos, using Green Timbers clones and selected trees from the Sayward provenance trial, is the only trial in the province to date that may lead directly to the isolation of some resistant genotypes. However, there are a few concerns with this trial:

Firstly, by itself, there are not enough trees (genotypes) at Zeballos from which to develop a production seed orchard of resistant Sitka spruce. According to one estimate, a minimum of about 30 successfully proven resistant genotypes would be required to make a production seed orchard (C. Ying, pers. comm.). More trees need to be tested in order to meet this minimum requirement. The Nass River provenance trial may be a good source of candidate trees for testing.

Secondly, without replicates, the Zeballos trial cannot distinguish between inherent resistance and resistance that is environmentally influenced. Some resistance mechanisms such as bark thickness, the density of resin canals, or perhaps some chemical stimulants or deterrents may be at least partially influenced by environmental conditions

(D. Lester, pers. comm.). Replicates of the Zeballos experiment in different areas are required to help make these distinctions.

Thirdly, the method of propagation used at Zeballos is now suspect. Although resin monoterpenes have been reported to be under strong genetic control and not easily influenced by environmental factors, preliminary observations by Borden and Brooks (pers. comm.) suggest that the monoterpenes expressed in grafted clones unfortunately may be under the genetic control of the rootstalk. Admittedly, monoterpenes do not appear to be the primary determinants of feeding behavior in the weevil, but the observation lends suspicion to the reliable expression of other inheritable traits, particularly chemical stimulants and deterrents, in rootgrafted clones. A possible alternative methodology is to use rooted cuttings.

2. The Selection and Propagation of Resistant Phenotypes

The studies that have been conducted on the weevils' feeding and oviposition preferences, and on host resistance mechanisms may eventually lead to "shortcuts" in the selection process.

The current empirical selection method, where individual trees that appear to be resistant are chosen from the natural population, has a few disadvantages. Whether these trees are cloned or their seed is sown (half-sib progeny), they must be replicated and outplanted for field testing for weevil resistance (as in the Zeballos experiment). This process takes several years. It is also difficult to find putatively resistant trees. The Nass River and Sayward provenance trials, being subjected to heavy weeviling, have offered good selection opportunities. Other candidates may be found in plantations, but it is difficult to distinguish between trees that are likely to be resistant from those that have escaped attack by chance (J. Brooks, pers. comm.).

In the B.C. studies to date, three general possibilities for developing a "shortcut" selection method have emerged.

Firstly, the search for resistant chemotypes, in the work by Harris *et al.* 1983; Brooks *et al.* 1986; and Brooks *et al.* 1987, offers the possibility of "fingerprint" identification of resistant trees, although a cause and effect relationship is not necessarily implied. In these studies, the significant differences in monoterpene profiles appear to apply locally rather than province-wide. Nevertheless, if combined with an additional resistance characteristic (yet to be discovered), this approach may be operationally feasible. Further field testing of trees selected by this method would undoubtedly be required to give the method validity.

Secondly, the identification of key chemical deterrents may provide the opportunity to select genotypes that express high concentrations of these deterrents (or to manufacture repellents for direct topical application).

The third possibility, the identification of key chemical stimulants, appears to offer less opportunity. Research to date suggests that the weevil responds to a multi-component chemical message (J. Borden, pers. comm.) and that the effort required to identify all the compounds that are involved would take many years of chemical analysis and bioassay testing (R. Alfaro and J. Borden, pers. comm.). If the key stimulatory compounds and their optimal profiles were identified, it likely would be difficult to find trees that are significantly lacking these compounds. Incidentally, the use of stimulatory chemicals to develop lures (ie. semiochemical baits) also appears unlikely from the current knowledge of this insect's behavior. Once in contact with the host, the weevil appears to be stimulated by the non-volatile components of spruce (Alfaro *et al.* 1980). Prior to contact, chemical cues have not yet been demonstrated to play a role in the weevils' search for susceptible host material.

To date, the research in B.C. has used natural populations of Sitka spruce (including possible hybrids with white or Engelmann spruce) as the source for potentially resistant trees. Breeding offers an alternative approach.

Obviously, fully controlled pollination between genotypes that are either empirically selected, or selected on the basis of chemical or physical resistance features, offers the possibility of enhanced resistance in the full-sib progeny. On a more operational basis, however, the Forest Service's coastal seed orchards offer excellent opportunities for partially controlled pollination. Their locations away from natural Sitka spruce populations allow for the in-breeding of the open pollinated trees in the orchard (J. Konishi, pers. comm.). Most of the postulated host resistance mechanisms, such as bark thickness, frequency of resin canals, or the relative concentrations of chemical stimulants and deterrents, are probably expressions of additive variance (D. Lester, pers. comm.), and therefore the general level of resistance likely would increase in the seed from these orchards.

Alfaro and Borden (1985) suggest interbreeding Sitka spruce with Serbian spruce, Picea omorika (Pancic) Purkyne, presumably based on their earlier work (Alfaro and Borden 1982) in which this species appeared to be the least preferred of the spruce species tested in choice feeding bioassays.

There are also suggestions (Harris and Brown 1970; Ying 1982) that hybrids of P. sitchensis x glauca may express greater resistance to the weevil than most Sitka spruce.

Vegetative propagation has also been suggested as a method for the clonal reproduction of proven resistant genotypes. In theory, it ensures the identical genetic features of the originally selected trees, as opposed to the half-sib progeny produced in a seed orchard. In practice, however, state-of-the-art vegetative propagation is still short of operational feasibility for forest nurseries. Cloned conifer seedlings grown from apical meristem cells in artificial media have not yet produced adequate roots and have never been tested in natural outdoor environments (L. Chong, pers. comm.). It is also suspected that vegetatively propagated trees would reach physiological maturity sooner than naturally produced trees (ie. from seed), resulting in less volume production per hectare (C. Ying, pers. comm.).

The Sitka spruce in the Nass River and Sayward provenance trials that have been observed to be expressing good recovery from weevil attack require special note. Propagation of these trees has obvious advantages. They offer the possibility of good form preservation despite weevil attacks. Other than a loss of height growth, they may be able to produce acceptable crop trees that have sustained little net damage in terms of volume loss, reduced lumber recovery or lumber degrade. As with other susceptible trees, however, repeated attacks may effectively prevent these trees from developing. As two years of leader growth are usually killed with each successful attack, repeatedly weeviled trees may quickly become suppressed.

3. Degrees of "Resistance"

Several of the studies summarized earlier in this report demonstrated that spruce weevil is a highly adaptive insect. The weevils' preference for Sitka spruce appears to be genetically pre-determined, but when sufficient host material is lacking, the weevil can lower its thresholds of preference and feed, oviposit, and rear its brood in non-host, sympatric species. This has serious implications for the development of "resistant" Sitka spruce. It implies that, for *P. strobi*, the term "resistance" is relative; it may attack "resistant" Sitka spruce if more attractive Sitka spruce are not available, and other species if no Sitka spruce are available. For spruce weevil control, therefore, the development of resistant phenotypes of Sitka spruce is unlikely to be a panacea.

4. Integrated Pest Management

Although the development of resistant phenotypes of Sitka spruce may not solve the weevil problem alone, when augmented with other weevil management techniques it may.

If resistant spruce are developed, it would appear that planting pure stands of resistant spruce would be to place the weevil in a no-choice situation where it would be

forced to attack the resistant trees (R. Alfaro and J. Borden, pers. comm.). Planting susceptible, non-crop spruce alongside the resistant trees, as decoys, would also be required. In turn, the weevil population pressure would likely build in the susceptible trees and threaten the resistant trees. To prevent this situation, control of the weevil in the susceptible trees would also be required, using techniques such as leader clipping and/or parasite enhancement (biological control), for example.

When practised in an intergrated manner, the use of resistant trees in combination with a few other techiques, could likely produce fully stocked, high quality stands of Sitka spruce that have evaded weevil attack.

E. RECOMMENDATIONS

1. The Vancouver Forest Region should continue to encourage and support research into the development of resistant phenotypes of Sitka spruce. Support should be given, however, with the understanding that the successful isolation of "resistant" phenotypes is unlikely to provide, by itself, a final solution for the control of coastal spruce weevil infestations.
2. Equal support should be given to the development of alternative methods of weevil control, such that in an integrated manner, resistant spruce, together with alternative methods will allow for the cost effective production of Sitka spruce crops.
3. Specifically, the Region should consider support for the replication of the Zeballos field trial and the development of similar field trials using additional ^{normally -}putatively resistant genotypes (from the Nass River provenance trial, for example). These projects are the most likely to produce resistant phenotypes in the short term.
4. Additional support should be considered for research that leads to methods that will allow for the systematic screening of candidate resistant trees.

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