

Delivering Sitka spruce with resistance against white pine weevil in British Columbia, Canada¹

by René I. Alfaro², John N. King³ and Lara vanAkke⁴

ABSTRACT

The Sitka spruce (*Picea sitchensis* [Bong.] Carr) breeding program for resistance against the white pine weevil *Pissodes strobi* Peck (Coleoptera: Curculionidae) is arguably one of the most successful pest resistance breeding programs for plantation forest species in North America, with a substantial proportion of the planting stock in BC and Washington State currently coming from this breeding program. Using conventional selection and breeding, and by screening Sitka spruce populations using artificial weevil infestations, we identified sources of heritable and stable weevil resistance. We also used this program to investigate potential causes behind this resistance and identified several heritable resistance mechanisms, including anatomical characteristics, such as constitutive resin canals and sclereid cells in the bark, terpene defenses and variation in tree phenology. We concluded that resistance is conferred by a suite of traits whose composition varies among resistant sources. In addition, we evaluated the efficiency of screening for resistance using weevil population enhancement as a screening method. Our results culminated in the establishment of seed orchards, and the availability of resistant seed that is contributing to the return of Sitka spruce as a species of choice in coastal British Columbia.

Keywords: *Picea sitchensis*, *Pissodes strobi*, forest pest management, genetic resistance

Dedication: This paper is dedicated to Dr. John Borden of Simon Fraser University (retired) who championed this topic and whose vision inspired so many entomologists in North America – René Alfaro.

RÉSUMÉ

Le programme de sélection de l'épinette de Sitka (*Picea sitchensis* [Bong.] Carr) visant à accroître la résistance au charançon du pin blanc *Pissodes strobi* Peck (Coleoptera: Curculionidae) est sans aucun doute l'un des programmes de sélection pour la résistance aux ravageurs qui a connu le plus de succès chez les espèces forestières utilisées en plantation en Amérique du Nord et il produit une partie importante des stocks plantés actuellement en C.-B. et dans l'État de Washington. En utilisant des méthodes de sélection et de culture classiques, et en soumettant les populations d'épinette de Sitka à des infestations artificielles de charançon, nous avons identifié des sources de résistance au charançon qui sont transmissibles et stables. Nous avons également utilisé ce programme pour étudier les causes potentielles de cette résistance et avons identifié quelques mécanismes de résistance transmissibles, notamment des caractéristiques anatomiques, comme les canaux résinifères transversaux et les cellules sclérites de l'écorce, les terpènes de défense et les variations dans la phénologie de l'arbre. Nous en concluons que la résistance vient d'un ensemble de traits dont la composition varie entre les sources résistantes. De plus, nous avons évalué l'efficacité du dépistage pour la résistance en intensifiant des populations de charançon pour effectuer criblage. Nos résultats ont mené à la création de vergers à graines et à la production de semences résistantes qui ont permis le retour de l'épinette de Sitka parmi les espèces de choix pour la côte de la Colombie-Britannique.

Mots clés : *Picea sitchensis*, *Pissodes strobi*, contrôle des ravageurs forestiers, résistance génétique

Dédicace : Cet article est dédié au Dr John Borden de l'Université Simon Fraser (retraité) qui s'est consacré à ce sujet et dont la vision a inspiré de nombreux entomologistes en Amérique du Nord – René Alfaro.

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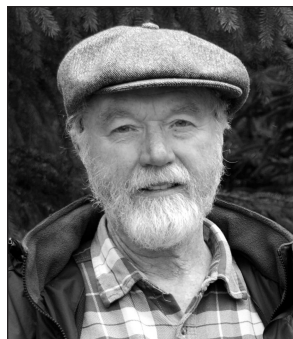
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Introduction

Sitka spruce (*Picea sitchensis* [Bong.] Carr.) is an integral component of the coastal rainforest of western North America, ranging from southern Alaska to northern California. The species is highly valued for its vigorous growth and excellent wood properties. However, over the last three decades, reforestation with Sitka spruce has been limited in many sites where it naturally occurs because young trees are highly susceptible to terminal leader damage by the white pine weevil, *Pissodes strobi* Peck (Coleoptera: Curculionidae). This weevil occurs naturally across Canada and the northern United States, feeding mainly on spruce species in the west, and pine and spruce species in the east of its range (Wallace and Sullivan 1985, Kiss and Yanchuk 1991).

In the spring, around the time of bud flushing, adult weevils emerge from overwintering sites in the duff and crawl to the uppermost terminal leaders to feed, mate and lay eggs. Eggs are laid in feeding punctures in the bark, below the apical bud of the tree leader (Fig. 1). In early summer the eggs hatch and, mining downwards, the larvae consume the phloem, girdling and killing the previous year's leader and depriving the current leader of nutrients and water. In late summer, larvae carve pupal chambers in the xylem and form chip cocoons. Adults emerge in the early fall (Silver 1968).

The symptoms of weevil attack include fading of the terminal shoot and droop of the current growth in a distinctive crook (Fig. 1). The death of the host's terminal leader causes one or more lateral branches to turn upwards resulting in crooks and forks in the main stem (Alfaro 1989). Repeated leader death can cause severe deformation of the main stem, rendering the tree non-merchantable. Although the weevil does not directly cause tree mortality, by stunting tree growth, susceptible trees—usually the most vigorous trees in the stand—may be eliminated from the site by competing vegetation (Alfaro 1982). Using a stand simulator, (Alfaro *et al.* 1996) estimated 37% losses to net volume in Sitka spruce stands by age 80 when severe weevil attack rates were assumed throughout the juvenile stage of the plantation. Studying Norway spruce, Daoust and Mottet (2006) reported a 23.7% decrease in lumber monetary value in stems deformed by weevil attack.

Until recently, available control options, such as leader clipping to remove the brood, have been ineffective and impractical at the operational level (Hall 1994) and this has led to very limited planting of Sitka spruce in British Columbia, with planting limited mainly to Haida Gwaii where the

weevil does not occur, or to low weevil hazard areas (Krakowski 2010) on the mainland and Vancouver Island. Sitka spruce planting has also declined in Oregon and Washington due to weevil damage (King and Alfaro 2009).

In natural stands, where spruce normally regenerates under shade or in small gaps created by fallen trees, white pine weevil populations exist in low numbers. Similar negative

effects of shading on weevil populations have been reported for white spruce (Taylor *et al.* 1996). However, widespread adoption of clearcutting in the 1960s and '70s, and the planting of single-species stands created optimal conditions for weevil population increase. Planted in open stands, spruce regeneration is vigorous, resulting in a large food supply for *P. strobi*, which feeds preferentially on large leaders (King *et al.* 1997). Increased host availability combined with sufficient heat accumulation for weevil development, results in conditions leading to weevil population outbreaks that can last for several years. In areas with insufficient heat accumulation, *P. strobi* populations cannot build to levels that cause significant damage (McMullen 1976).

To guide forest managers in planting Sitka spruce, weevil hazard zones have been delineated based on summer heat sums and potential vapour pressure deficit regimes (McMullen 1976, Spittlehouse *et al.* 1994, MFLNRO 2009). These systems are based on the fact that *P. strobi* requires 888 degree days above a threshold temperature of 7.2°C to complete development on the BC coast (McMullen 1976). Stand Establishment Decision Aids developed by the BC Ministry of Forests for the coastal forest region have typically recommended limited planting of Sitka spruce in high hazard areas to only 10% of the stocking (Heppner and Turner 2006) for the purpose of maintaining biodiversity.

The discovery of genetic resistance to the weevil offers the best chance of restoring Sitka spruce within the coastal forest management system. Sitka spruce trees resistant to the white pine weevil were first noted in British Columbia in the early 1940s at the Green Timbers site in Surrey, BC (Alfaro 1982). A severe weevil infestation left only two trees unattacked among hundreds established in pure Sitka spruce plantations (Silver 1968, Alfaro 1982). Differential resistance to weevil was also reported among spruce species and their hybrids during a study of spruce crosses in Oregon and Washington states (Mitchell *et al.* 1974) and it was concluded that resistance was heritable and could be exploited in tree improvement programs (Mitchell *et al.* 1990). Early provenance trials established by the B.C. Forest Service (BCFS), under the auspices of IUFRO (International Union of Forest Research Organizations), also showed indications of provenance-level weevil resistance (Alfaro and Ying 1990, Ying 1991).

Improvement of agricultural crops by selection of plants with desirable characteristics has been practised by humans for thousands of years, since the early domestication of cereal crops (Fuller *et al.* 2009). The discovery of pest-resistant crop

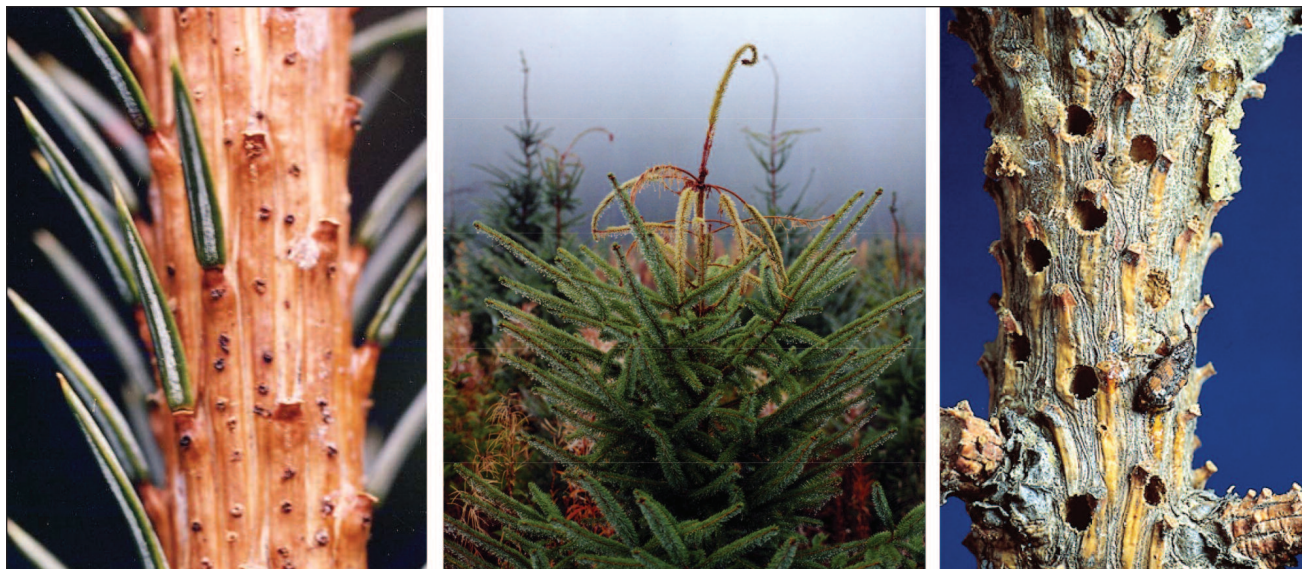


Fig. 1. Stages of damage by *Pissodes strobi* on Sitka spruce. Left: egg punctures on leader (spring). Center: dead leader (late summer). Right: emergence holes (late summer) (photo credit: British Columbia Ministry of Forests, Lands and Natural Resource Operations).



Fig. 2. Resistant genotype 898 standing tall and unattacked amidst weevil susceptible genotypes in a 20-year-old plantation with high levels of weevil damage.

varieties dates back to the late 1700s with the report of a wheat cultivar resistant to the Hessian fly (Panda and Khush 1995) and breeding programs to address losses in wheat crops to black stem rust were being developed in the late 1800s (Walker 1966). The overuse of persistent pesticides in the first half of the twentieth century and the widespread development of resistance of pests to these insecticides encouraged

research to explore alternative pest control strategies, and the use of breeding for genetic resistance to control insects and disease in agricultural crops has become widespread.

While examples of successful breeding for resistance in agriculture are common (Pathirana *et al.* 2000, Bockus *et al.* 2001, Khush and Brar 2003, Broekgaarden *et al.* 2011, Fetch *et al.* 2011), the long lifespan of forest trees causes research

involving tree breeding to lag behind agriculture. Consequently, examples of successful development and deployment of resistant forest trees are rare and usually address pathogens. Impressive gains have been reported in *Pinus taeda* L. and *Pinus elliottii* Engelm. resistant to fusiform rust in the southern United States (Brawner *et al.* 1999).

In their review of the topic of pest resistance in forest trees, Yanchuk and Allard (2009) found only two traditional breeding programs addressing resistance to insect pests that had reached the operational deployment stage, one for spruce aphid (*Elatobium abietinum* [Walker]) resistance in Europe (Harding *et al.* 2003) and another for white pine weevil resistance in North America, which is summarized in this paper.

An understanding of how plants express resistance, and identification of traits conferring resistance, allows for the selection of plants with specific traits for inclusion in breeding programs. Resistant plants were defined by Painter (1958) as those "...that are inherently less damaged or less infested than others under comparable environmental conditions in the field...". Plants generally express resistance in three ways: plants may 1) avoid or escape the attack, 2) can be tolerant of the attack, or 3) employ various defence mechanisms, such as constitutive or induced defences (Berryman 1988). Constitutive defenses are those defence systems that are already pres-

ent in the plant prior to herbivory, and generally cause toxicity and repellence or hindrance to the herbivore. Plants have evolved chemical compounds and mechanical structures (such as terpenes and resin canals) that directly influence host selection and the ability of insects to feed and lay eggs. Induced defenses, or traumatic responses, are those produced only in response to damage or stress caused by herbivores or pathogens and can include synthesis of chemical compounds and the formation of specialized tissues and structures. Synchrony of pest/host development rates or phenology can also influence host resistance. Chemical compounds and tissue structures change seasonally and can influence host selection and affect quality and quantity of food available. This causes some host individuals that have different phenology relative to the pest population, to escape attack or sustain minimal damage. Sitka spruce employs constitutive, induced and phenological defences against *P. strobi* (Alfaro *et al.* 2000, King *et al.* 2011, Moreira *et al.* 2012).

Here we summarize over twenty years of research, utilizing traditional breeding, which culminated in the operational field deployment of Sitka spruce with resistance to *Pissodes strobi*. We hope that this review will help in the design and execution of resistance breeding programs for other pests of young stands.

Table 1. BC Ministry of Forests Sitka spruce trials monitored by the Canadian Forest Service for the purpose of screening for weevil resistance

Site	Material	Year planted	# Families or clones	# Trees	# Years assessed
Big Tree Creek, Sayward	provenance	1974	321	4389	5
Jordan River	half sib	1991	75	1722	9
North Arm, Cowichan Lake	half sib	1992	75	1477	5
Hamlet, OR	half sib	1994	24	2104	1
Nehalem (South Coal), OR	half sib	1994	24	2116	1
Browns Main, Port Renfrew	half sib	1994	72	813	6
Snowden Forest, Campbell R.	half sib	1994	72	1336	6
Kaouk River, Fair Harbour	clonal	1984	38	629	3
Espinosa Creek, Zeballos	clonal	1991	151	2331	9
Armishaw + Glenroy, Sayward	clonal	1992	168	2581	10
Sandcut, Jordan River	clonal	1997	33	251	5
Menzies Bay, Campbell River	clonal	1997	52	570	6
Gold River, Hisnit	clonal and susceptible	1995	3	384	8
Coombs Pub	half sib	1999	126	3024	6
Errington	half sib	1999	92	1104	3
Harrison Mills	half sib	1999	126	3024	6
Upper Harrison	half sib	1999	88	1056	3
Michelson Point	half sib	1999	82	984	1
Klanawa River	half sib	1999	92	1104	3
Adam River	half sib	1999	93	1116	2
Camp 4, Campbell River	half sib	1995	84	2124	7
Grafton, French Creek F1	full sib	2000	4	552	2
Mainline, Jordan River F1	full sib	2004	110	3300	3

Materials and Methods

Sources tested for resistance

The first quantitative observations of population-level weevil resistance were made in provenance trials established by IUFRO on northern Vancouver Island, BC, and which were designed to select Sitka spruce for desirable growth characteristics (Alfaro and Ying 1990, Ying 1991). The tested provenances covered the entire coastal range of the species, as well as the inland Sitka–white spruce hybridization zone around the Nass and Skeena Rivers of north-coastal BC. Measurement of natural weevil attack in these trials indicated differential susceptibility by provenance, with some particular individuals from the Haney area of the BC mainland showing remarkably high incidence of resistance (Alfaro and Ying 1990, Ying 1991). Based on these results, well-replicated clonal trials were established by Dr. Cheng Ying (BC Ministry of Forests, retired) to further test the individuals showing resistance. Results of these clonal tests confirmed the high levels of resistance, particularly of the Haney 898 clone (Alfaro *et al.* 2002), which is easily identified in the field by its excellent stem form and height growth (Fig. 2). King *et al.* (2012) present evidence suggesting major-gene or “total resistance” in this clone.

Based on these promising results, the BC ministry of Forests enlarged the Sitka spruce weevil resistance program by hiring a dedicated geneticist (Dr. John King) and engaging additional scientists from the Canadian Forest Service in Victoria, BC (Dr. John Harris, Dr. Mike Hulme, Dr. Tara Sahota, Dr. I. Leal). With funding from provincial and federal sources, family trials were established and monitored for resistance as part of the provincial Sitka spruce weevil resistance tree improvement program. New seed collections were conducted to systematically test various sources and delineate the boundaries of the resistant tree populations (King and Alfaro 2009). Twenty trial sites were established, ranging in location from northern Vancouver Island to Northern California and represented material from the entire range of Sitka spruce (Table 1, Fig. 3). Material from each seed series was represented at a minimum of two trial sites to test for stability of resistance over sites. Plantations included replication at block and family levels to allow for robust statistical comparisons and heritability calculations.

Screening for resistance

Early observation of weevil resistance was conducted in provenance trials designed to test spruce genotypes for growth characteristics rather than to specifically test for weevil resistance. Selection for resistance in these trials was conducted by measuring damage rates resulting from infestations that developed naturally. Results based on natural infestations of trial sites re-confirmed the area of Haney, BC as a source of resistant genotypes, and identified two new geographic sources of Sitka spruce resistance: the Big Qualicum River area on eastern Vancouver Island and the Skeena River area of BC’s mainland, which falls in the introgression zone where Sitka and white spruce hybridize (Alfaro and Ying 1990, Ying 1991, King 1994, Ying and Ebata 1994, Ying 1997, King *et al.* 2004) (Fig. 3). Sources from Haida Gwaii proved to be particularly susceptible to weevil damage.

These early tests demonstrated that basing a large screening program on natural infestation of test trials had shortcomings. The build-up of natural weevil populations is slow

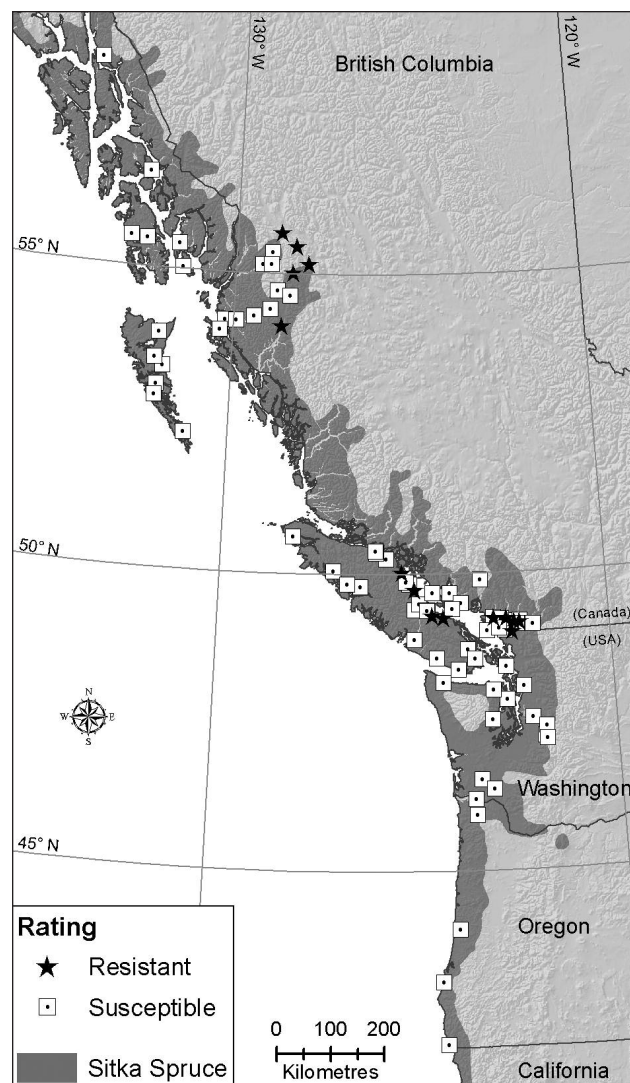


Fig. 3. Range of Sitka spruce in western North America (dark grey). White dots indicate sources tested for genetic resistance to weevil damage. Stars indicate sources found to consistently produce progeny with resistance.

and aggregated, and thus makes screening a long and unpredictable process, to the point that some trials had to be abandoned due to insufficient weevil attack pressure for meaningful screening (Fig. 4). Susceptible trees may appear resistant if they have simply escaped attack due to uneven weevil population density. Variation in weevil population levels also prevented comparisons of results across sites. Consequently, we designed a selection program aimed at rapid and reliable screening of spruce genotypes for resistance based on augmentation of the natural weevil populations present in a test site, by releasing a fixed number of field collected and laboratory-reared weevils (usually three or four weevils per tree) onto every test tree in a site. This allowed us to standardize our screening procedures by creating an even weevil pressure across large plantations. Screening of over 29 000 trees at 10 trials, comprised of half-, full-sibling, or clonal material, was conducted on test plantations that were at least three to four

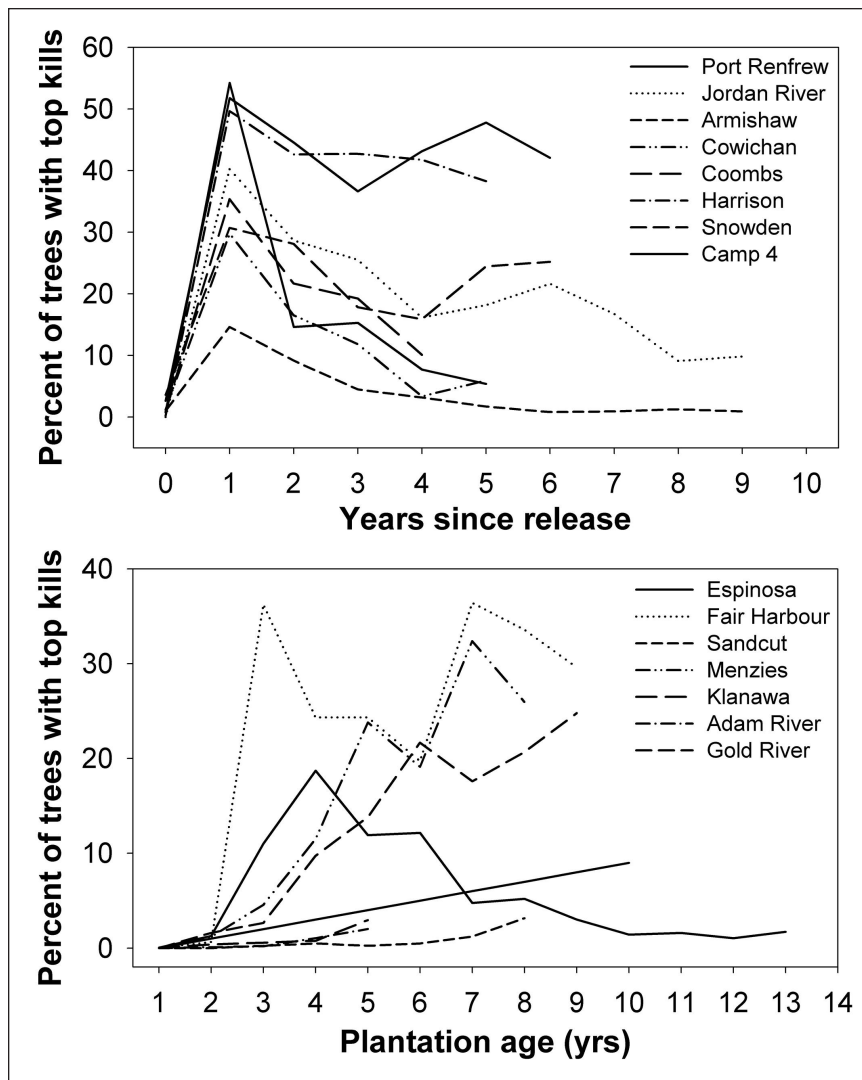


Fig. 4. Percentage of trees with weevil-caused top-kills. Top: Annual attack in Sitka spruce genetic resistance trials in which weevil populations were artificially augmented for screening purposes. Bottom: Annual attack in Sitka spruce genetic resistance trials naturally infested with weevils.

years old (Table 1). The screening process, under different weevil population pressures, was reviewed by Alfaro *et al.* (2008).

Observations in these artificially infested tests were made annually for several years to determine the stability of resistance over time. Each tree was classified as: 1) healthy, 2) successfully attacked (oviposition had occurred and larval feeding had caused the death of the leader), or 3) unsuccessfully attacked (oviposition had occurred but larvae failed to cause the death of the leader and no new adults were produced). Families or clonal lines were ranked based on observations of attack rates, defined as the percentage of individuals within families sustaining at least one successful attack over the observation period, and attack intensity, defined as the mean number of attacks sustained by individuals within families.

These trials also provided the opportunity to study the mechanisms contributing to weevil resistance in order to

identify specific traits that conferred resistance, with the purpose of incorporating them into the Sitka spruce breeding program (King *et al.* 2011).

Highly resistant and susceptible Sitka spruce parents were selected for the production of a progeny generation resulting from controlled crosses (F1). The establishment of this F1 progeny trial provided the opportunity to investigate the inheritance of weevil resistance in Sitka spruce, the resistance rankings of the controlled-cross F1 progeny generation and the heritability of anatomic traits that may be used as indicators of defensive mechanisms against the weevil.

Results

Sustained efforts over two decades, aided by continuous funding, resulted in the successful screening and identification of genotypes with heritable levels of resistance to white pine weevil. As of 2013, genotypes with different levels of resistance are now in seed orchards and producing seeds for reforestation (Table 2).

Screening for resistance to weevil

Screening by augmentation of natural weevil populations proved to be an efficient and reliable way to identify sources of weevil resistance. Family performance has been shown to be stable under variable weevil population levels and at different sites (Alfaro *et al.* 2008). Results confirmed that resistance is heritable (King *et al.* 2004, Moreira *et al.* 2012). If a mean

Table 2. Number of Sitka spruce seedlings planted in British Columbia, including Haida Gwaii^a (HG) (formerly called the Queen Charlotte Islands) and the proportion of seedlings planted in the non-HG portion of the province that were weevil-resistant (WR)

Year	Total planted	Total WR planted	Total planted in HG	Proportion WR planted in areas susceptible to weevil
2005	795 890	2850	428 676	0.01
2006	718 680	105 775	394 261	0.33
2007	871 061	169 850	471 090	0.42
2008	758 233	1846	527 182	0.01
2009	464 640	32 621	231 250	0.14
2010	375 332	47 420	269 285	0.45
2011	242 613	77 568	152 675	0.86

^a*Pissodes strobi* does not occur in Haida Gwaii.

cumulative attack rate of 50% is achieved through weevil population augmentation (50% of trees within trial have sustained at least one weevil attack over the study period), selections that are consistent among replicates and stable over time can be made in as little as four years following population augmentation (Alfaro *et al.* 2008). This is a relatively short turnaround time for a study in tree resistance to insect pests in temperate forests.

Mass screening indicated significant provenance variation in weevil resistance, with some open pollinated parents consistently producing offspring with statistically demonstrable resistance to *Pissodes strobi* in F1 trials (Fig. 5 and Fig. 6) (Alfaro *et al.* 2008, Moreira *et al.* 2012). Weevil attack rates in resistant stock were less than half of that of regular planting stock (Fig. 5). The initial three geographic sources of resistance identified in earlier studies were confirmed and further defined (King and Alfaro 2009). Resistant families have average height growth, indicating that resistance does not come at the expense of tree growth (Alfaro *et al.* 2008). In fact, King *et al.* (1997) report that while weevils prefer longer leaders, inherently faster-growing interior spruce families tend to have higher levels of genetic resistance.

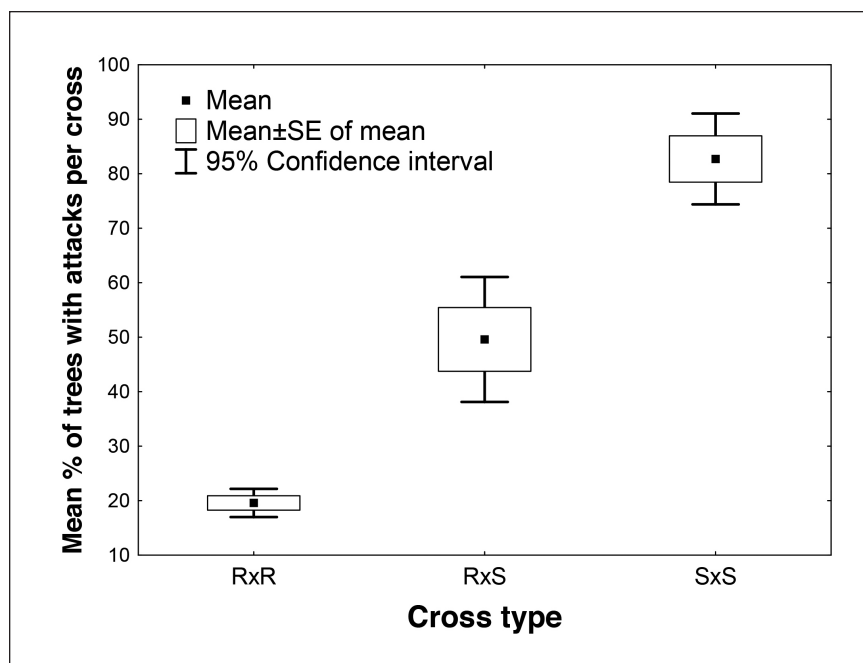


Fig. 5. Mean attack rate in a F1 Sitka spruce generation produced by crossing parents Resistant (R) or Susceptible (S) to white pine weevil, at Jordan River Mainline trial.

Screening by natural infestation versus weevil population augmentation

Sitka spruce trees become susceptible to weevil attack as early as two years following planting. The natural rate of weevil population increase and eventual decline depend mainly on

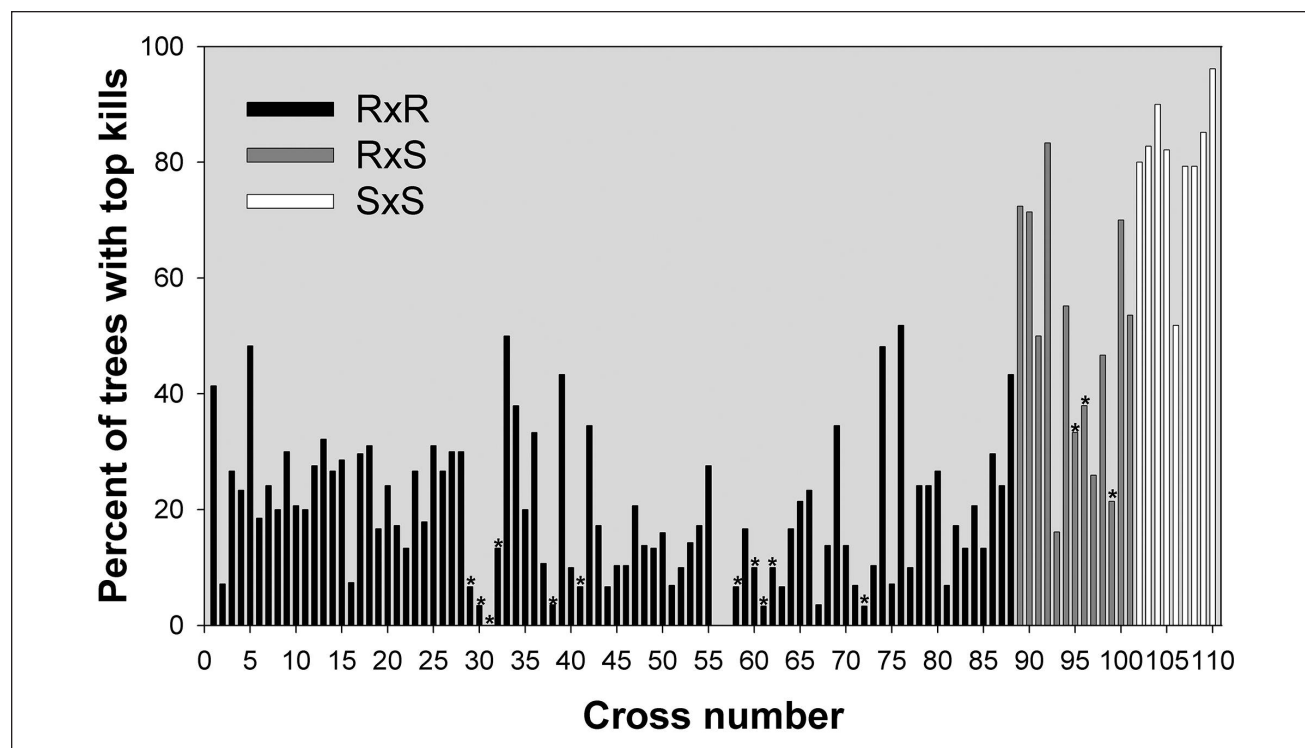


Fig. 6. Performance of the F1 Sitka spruce generation produced by crossing parents Resistant (R) or Susceptible (S) to white pine weevil, at Jordan River Mainline trial. Crosses that had genotype #898 as one of the parents are indicated by *.

four factors: host availability, quality of leaders (vigorous leaders produce more weevils), heat accumulation and the abundance of natural enemy populations. In favorable habitat conditions (heat sums above 888 degree days above 7.2°C) natural weevil populations can increase rapidly, infesting up to 50% of the trees annually when plantations are between 10 and 15 years old (Alfaro 1994). Annual attack rates generally reach an upper limit, since it usually takes two years for attacked trees to recover apical dominance and produce a leader of sufficient diameter to be attractive to weevils (Alfaro 1994). Also, trees that sustain repeated attacks may never regain apical dominance and retain a bushy form with multiple thin leaders, which are not preferred by female weevils for their brood. Population levels then tend to remain relatively stable for a few years before declining to annual infestation levels below 10% (Alfaro and Omule 1990, Mitchell *et al.* 1990). A combination of decreased host availability (resulting from trees reaching heights of around 18 m), increased natural predator populations and cooler within-stand conditions causes the populations to decline and remain at low levels as trees grow and plantation conditions change when trees reach canopy closure. Augmentation of weevil populations in the test trials resulted in a decrease in the length of time to reach maximum infestation levels (plantation age 4.6 years at augmented sites vs. 6.4 years in natural populations, Fig. 4). At all sites where populations were artificially augmented, maximum attack rates were achieved in the year following weevil release. Population augmentation also increased the average maximum infestation level (38.3% of trees with top kills annually in augmented sites vs. 12.5% in naturally infested sites, Fig. 4).

Weevil populations at trial sites located in areas designated as high weevil hazard (defined by Krakowski [2010]) tended to remain high (more than 20% of trees attacked annually) for longer periods of time (a minimum of nine years) whereas in lower hazard areas populations declined to less than 10% annual attack after an average of seven years, regardless of whether the population had built up naturally or had been augmented. The difference in infestation severity and duration between high hazard and low hazard areas reflect the differences in environmental suitability for the weevil.

Clone 898

Over the study period several individual trees and families were identified that exhibited exceptional resistance to *P. strobi*. One genotype in particular, clone 898 from the Haney provenance, has been studied intensely in various trials. This clone was represented at four sites by over 100 individuals and remained almost completely free of weevil damage, even under the extremely high weevil pressure present at some sites. In addition to field observations, a number of experiments were conducted in a greenhouse setting in order to observe weevil behaviour on this clone. We found that given a choice, weevils move away from 898 and prefer to feed on other trees. However, in no-choice trials, weevils will feed on and occasionally lay eggs in this 898 clone but larvae will not survive to kill the leader (Alfaro and vanAkker, unpublished data). In addition to being highly weevil-resistant, this clone also has excellent height growth and form (Fig. 2).

Resistance mechanisms

Tree characteristics underlying Sitka spruce resistance to white pine weevil have been studied by several researchers (Hulme 1995, Leal *et al.* 1997, Tomlin and Borden 1997, Alfaro *et al.* 2000, King *et al.* 2011, Moreira *et al.* 2012). Impediments to weevil feeding and egg laying were explored by quantifying bark characteristics that contribute to defenses in conifers, such as resin canals (King *et al.* 2011), stone or sclereid cells (King *et al.* 2011) and constituent terpenes (Byun-McKay *et al.* 2006). Differences in phenological development rates among families were examined to determine whether some families may escape attack because their development is not synchronized with weevil development (Hulme 1995, Alfaro *et al.* 2000). Induced responses including production of traumatic resin canals in the xylem and terpene synthase gene expression have also been explored (Byun-McKay *et al.* 2006). However, none of these characteristics alone is a strong predictor of resistance. We found that resistant populations employ a suite of resistant mechanisms that vary depending on the tree provenance, with the relative importance of various traits changing depending on genotype, the environment and the interaction between these two factors (Alfaro *et al.* 2002). For example, in the Fraser Valley population, resistance is correlated with high sclereid cell density, while the Big Qualicum population expresses resistance primarily through high densities of resin canals in the cortex (King *et al.* 2011).

Heritability of resistance: Results of F1 tests

Augmenting weevil populations also allowed us to quickly proceed with the development of an F1 population to determine the heritability of resistance and to increase our understanding of the mechanisms that underlie it (Moreira *et al.* 2012). The F1 spruce progeny demonstrated that progeny from resistant parents (R × R progeny) sustained significantly fewer weevil attacks than progeny from susceptible parents (S × S progeny) or progeny with one resistant and one susceptible parent (R × S progeny) (Fig. 5 and Fig. 6). Individual and family heritability estimates of weevil resistance were 0.5 and 0.9, respectively (Moreira *et al.* 2012). We also related the level of resistance in the F1 crosses to two constitutive mechanisms of resistance, the density of cortical resin canals and the amount of sclereid cells in the leader cortex, and calculated their heritability value (Moreira *et al.* 2012). Constitutive defenses were significantly higher in R × R progeny than in R × S or S × S progeny. We also observed a negative correlation between the percentage of trees attacked in each cross and the average density of the resin canals or sclereid cells for each cross.

Utilization of the resistant seed

The use of wild seed collected from provenances identified as weevil-resistant (Class B+ seed), such as Big Qualicum, has been recommended as a low-cost deployment option for low-hazard sites or mixture plantings on medium-hazard sites since the early 1990s (King and Alfaro 2009). Since then, seedlings from these sources have effectively halved the attack rate of those from more susceptible sources (King *et al.* 2004).

Our selections of weevil-resistant parents are now in seed orchards, producing regeneration material for operational planting (Class A seed and seedlings). As of 2012, there are two orchards in British Columbia producing weevil-resistant Sitka spruce seed on southern Vancouver Island; the objectives of these programs are co-ordinated through the Forest Genetics Council of British Columbia (King and Alfaro 2009). Both orchards produced their first marketable weevil-resistant seed crop in 2004 and the first seedlings were planted in an operational setting in 2005. To date, more than 400 000 orchard-produced weevil-resistant seedlings have been planted in the Pacific Northwest, in areas where the weevil poses a threat to Sitka spruce regeneration. Over 80% of the seedlings planted are weevil-resistant stock (Susan Zedel, BC Ministry of Forests, Lands and Natural Resource Operations, Tree Improvement Branch, Victoria, personal communication) (Table 2).

Successful deployment of weevil-resistant stock resulted in the updating of silviculture guidelines for the province of BC. Where coastal reforestation guidelines for high weevil hazard areas once recommended exclusion or limited planting of spruce, current guidelines prescribe up to one-half Sitka spruce in moderate- or high-hazard areas if A+ seed is used (most resistant seed) and about a third if B+ seed is used (seed with mid-resistance rankings) (Heppner and Turner 2006). The deployment and seed transfer guidelines will be further updated to allow more flexibility, reflecting further recognition of the stability of weevil resistance, which will lead to the recovery of Sitka spruce as a species of choice in coastal rain-forests.

Discussion

Tree improvement is measured by genetic gain, an estimate of the percentage increase in performance of an improved seedlot over that expected from wild-stand material (Hadley *et al.* 2001). Gains are referenced to specific traits such as stem volume, wood density, or pest resistance. Genetic gain due to weevil resistance is expressed as Genetic Worth Resistance (GWR) and ranges from 0 (most susceptible), for sources from Haida Gwaii to 100 (most resistant). Early genetic gains in weevil resistance were achieved within 10 years following the first observations of weevil resistance, by the use of class B+ seed. On average a minimum of 50% reduction in weevil damage was achieved. It took approximately 23 years to reach the operational deployment phase of genetic class A seedlings from seedlots with GWR averaging about +87, the deployment of which is expected to result in a reduction of over 80% in weevil attack levels (King and Alfaro 2009).

There has been an overall worldwide reduction in tree breeding programs and research is now focused on a limited number of species and traits (FAO n.d.). However, as pest risk is likely to increase in the future as a result of increased introduction of exotics and pest range expansion due to climate change (Murdock *et al.* 2013), resistance breeding programs are likely to continue to contribute to the management of insect and diseases. Also, resistance to pests may be useful in tree planting programs aimed at climate change mitigation and to facilitate tree adaptation to new ranges through assisted migration. For this, it will be necessary to develop

tools and methodology to speed up the process. Yanchuk and Allard (2009) concluded that future programmes to tackle increased pest and disease incidence caused by rapid climate change will not be successful if they rely on conventional breeding approaches. Recent advances in biotechnology and the use of molecular markers has allowed the development of more rapid breeding/selection systems, including the techniques of “breeding without breeding” (El-Kassaby *et al.* 2011), which will significantly shorten the breeding process.

The success of genetic resistance programs for other pathosystems will depend on demonstrating significant damage by the pest to warrant the required funding. Once the economic justification is in place, success will require steady funding and close cooperation between entomologists and geneticists.

Foresters selecting regeneration species are now utilizing Sitka spruce more frequently, especially on Vancouver Island where this species is also valued for its inherent resistance to elk and deer browse (A. vanNeijenhuis, Western Forest Products Inc., Campbell River, BC, personal communication). In Washington and Oregon foresters are currently replacing off-site Douglas-fir plantations with weevil-resistant spruce from British Columbia (D. Pigott, Yellow Point Propagation Ltd., Ladysmith, BC, personal communication). As more weevil-resistant seed becomes available and the gains from early operational deployments recognized, we expect that Sitka spruce will become once again a species of choice for regeneration in coastal forests.

Improving forest tree species is a lengthy process, with many stages. Our results indicate that the screening stage of breeding for weevil resistance can be accomplished in as few as four years by augmenting weevil populations. This is a fairly quick turnaround time for studying resistance of forest trees from temperate regions. This promising result will encourage resistance programs for other regeneration pests.

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