Effects of fertilization on resin canal defences and incidence of *Pissodes strobi* attack in interior spruce

Lara vanAkker, René I. Alfaro, and Robert Brockley

Abstract: The effects of six fertilization treatments on tree height and incidence of attack by the white pine weevil, *Pissodes strobi* (Peck), on interior spruce (a hybrid, *Picea glauca* (Moench) Voss × *Picea engelmannii* Parry ex Engelm.) were explored in a field study. In a corresponding laboratory study, changes in constitutive and traumatic resin canal defences in response to fertilization were measured. Incidence of weevil attack increased with fertilization intensity. This trend was explained by increased resources available for weevil feeding (adults and larvae) as a result of increased leader size and bark thickness, as well as by an observed weakening in the tree's constitutive resin canal defences. The ability of interior spruce to produce a traumatic resin response was not influenced by fertilization. Although incidence of weevil attack was greatest in trees from the most intense fertilization treatments, height losses due to weevil attack were not as great as height gains due to fertilization treatment. Therefore, we concluded that fertilization is a feasible option for increasing productivity of interior spruce plantations, particularly if other weevil control alternatives are implemented.

Résumé : Les effets de six traitements de fertilisation sur la hauteur des tiges d'épinette de l'intérieur (une espèce hybride entre *Picea glauca* (Moench) Voss × *Picea engelmannii* Parry ex Engelm.) et sur l'incidence de l'attaque du charançon du pin blanc, *Pissodes strobi* (Peck), ont été étudiés sur le terrain. Les changements causés par la fertilisation dans la réaction de défense impliquant les canaux résinifères d'origine constitutive ou traumatique ont été mesurés au cours de travaux correspondants faits en laboratoire. L'incidence de l'attaque du charançon a augmenté avec l'intensité de la fertilisation. Cette tendance s'expliquait par l'augmentation des ressources alimentaires disponibles pour le charançon (adulte et larve) en raison de l'accroissement de la dimension de la pousse terminale et de l'épaisseur de l'écorce, de même que par l'affaiblissement observé de la réaction de défense impliquant les canaux résinifères constitutifs. La capacité de produire de la résine en réponse à un traumatisme dont fait preuve l'épinette de l'intérieur n'était pas influencée par la fertilisation. Malgré que l'incidence de l'attaque du charançon ait été plus élevée chez les arbres qui avaient reçu les traitements de fertilisation les plus intenses, les pertes de croissance en hauteur causées par l'attaque du charançon n'étaient pas aussi importantes que les gains dus à la fertilisation. En conséquence, nous concluons que la fertilisation constitue une option viable lorsqu'il s'agit d'augmenter la productivité de l'épinette de l'intérieur, particulièrement si d'autres méthodes de contrôle du charançon sont également mises en oeuvre.

Introduction

Interior spruce (white spruce, *Picea glauca* (Moench) Voss; Engelmann spruce, *Picea engelmannii* Parry ex Engelm.; and their hybrids) are important commercial tree species in the interior of British Columbia. In 2001, the harvested volume of interior spruce, 11.6×10^6 m^3, accounted for 24% of the total harvest from interior forests (BCMOF 2002). From 1984 to 1997, approximately 1.3×10^9 spruce seedlings were planted in the interior of the province; these seedlings represented 45% of the provincial planting pro-

gram during that period (BCMOF 2000). This vast, second-growth spruce resource has created ideal conditions for the development of white pine weevil (*Pissodes strobi* (Peck)) populations. As a result, extensive areas of these single-species spruce plantations are now at, or will soon reach, a size that makes them susceptible to damage from this serious pest. In recent years, more and more of the spruce seedlings planted in the interior of British Columbia have been grown from genetically improved seed. In 2001, almost three quarters of spruce seedling requests were for class A seed (BCMOF 2002). Damage from the white pine weevil poses a serious threat to this valuable investment.

Native to North America, this weevil is distributed from coast to coast throughout the continent, attacking spruce and pine (*Pinus*) species (Humble et al. 1994). The main hosts of the white pine weevil include white pine (*Pinus strobus* L.) and Norway spruce (*Picea abies* (L.) Karst.) in eastern Canada and the United States and Sitka spruce (*Picea sitchensis* (Bong.) Carrière), Engelmann spruce (*P. engelmannii*), white spruce (*P. glauca*), and interior spruce hybrids (*P. engelmanni × P. glauca*) in the west. Damage by *P. strobi* results from repeated destruction of the terminal leader, which

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causes severe growth losses and stem defects. Severe infestations can reduce lumber quality and stand yield by as much as 40% (Alfaro et al. 1997b). Growth losses due to weevil damage significantly increase the time required to reach free-to-grow status (Alfaro 1989), and heavily attacked plantations often require rehabilitation (Hall 1994).

Overwintered adult weevils emerge and crawl or fly to host trees in the spring to feed on phloem and cortical tissues. Mating occurs from May to early July, and eggs are deposited in feeding punctures near the top of terminal leaders, which are then covered with a fecal plug. Larvae consume the phloem beneath the bark, feeding in a downward direction. As they grow, the larvae aggregate and feed in synchrony, forming a feeding ring that girdles and kills the leader. Damage becomes evident as the needles change color and the current year's leader droops in a distinctive "shepherd's crook". In August, after five larval instars, pupation occurs in chip cocoons in the xylem or pith. The pupal stage lasts about 2 weeks, and adults emerge in the early fall, chewing their way out through the bark. Adults overwinter in the duff beneath host trees or on tree boles under moss or bark scales close to the ground (Silver 1968).

Genetic variation in tree resistance to weevil has been detected in both Sitka spruce and interior spruce hybrids (Alfaro and Ying 1990; Kiss and Yanchuk 1991), and a number of putative resistance mechanisms have been identified (reviewed by Alfaro et al. 2002). Briefly, weevil resistance has been correlated with tree size and leader morphology (Silver 1968; King et al. 1997); bark thickness (Stroh and Gerhold 1965); chemical composition (Alfaro et al. 1980; Nault and Alfaro 2001); antibiotic attributes (Sahota et al. 1994); tree phenology (Hulme 1995); characteristics of constitutive (preformed) defences, such as the distribution of cortical resin canals (Stroh and Gerhold 1965; Tomlin and Borden 1997); and the ability of trees to produce a wound-induced (traumatic) response (Alfaro 1995).

In British Columbia, forest fertilization is widely viewed by forest practitioners and planners as a potentially feasible strategy for sustaining the flow of harvested wood from interior forests (BCMOF 1999). Because interior spruce plantations will undoubtedly play a critical role in British Columbia's future wood supply, documenting how fertilization affects their health and growth is important. Preliminary research indicates that interior spruce plantations are potentially responsive to added nutrients (Brockley 1992), but large-scale fertilizer operations are currently discouraged because of an observed increase in the incidence of white pine weevil damage in coastal Sitka spruce plantations (Xydias and Leaf 1964; BCMOF 1995). However, there have been no formal studies of the relationship between fertilization and susceptibility to attack.

Effective use of genetic resistance in weevil management programs requires knowledge of the effects of fertilization on plant resistance and defence traits. Past studies have indicated that fast-growing trees with long, thick leaders are more susceptible to attack than those with smaller leaders (Alfaro et al. 1993). This trend may be explained by a natural reduction in cortical resin canal defences as the trees grow (Jou 1971; Brescia 2000). However, several studies of fertilizer effects on number, size, and density of resin canals in the xylem of Corsican pine (Smith et al. 1977) and in the

needles of several conifer species (Björkman et al. 1998; Wainhouse et al. 1998) have indicated increases in these constitutive defences after fertilization. Tree vigour is also thought to play a role in regulating the ability of trees to respond to trauma. Traumatic defence responses, such as the production of traumatic resin or resin canals in response to injury, place immediate, heavy demands on plant resources (Berryman 1988; Nagy et al. 2000), which can result in decreased growth (Tomlin et al. 1998). Therefore, trees that are at an energetic disadvantage as a result of limited resources may be less capable of producing an effective traumatic response.

The goals of this study were to (i) determine the effects of fertilization treatments on incidence of *P. strobi* attack, as well as on the constitutive and traumatic resin canal defences of interior spruce; and (ii) determine the combined effect of fertilization and weevil attack on tree height (for the purpose of guiding management decisions). We hypothesized that fertilization will cause (i) an increase in incidence of weevil attack in response to increased leader size; (ii) a reduction in density of constitutive resin canals in the cortex of the tree leader; and (iii) an increase in traumatic-response intensity, defined as the density of traumatic resin canals produced in the xylem in response to simulated weevil attack.

Methods

Location and site description

The study site is located approximately 40 km southeast of Hixon, British Columbia (53°22′N, 122°06′W), on tree-farm licence 53 (Dunkley Lumber Ltd.), within the Willow Wet Cool variant of the Sub-Boreal Spruce biogeoclimatic zone (DeLong 1996). On the basis of slope position, soil characteristics, and the dominant shrub and herb species, the site most clearly matches the mesic 01 site series for this variant. The site has an east aspect, with slopes ranging from 5% to 25% and a mean elevation of approximately 1030 m above sea level. Soils are derived from morainal parent material (largely metasediments and minor mica schist) and are well to moderately well drained. The soil is classified as an Eluviated Dystric Brunisol (Soil Classification Working Group 1998) and is fairly stone free, with sandy loam texture.

The previous mature forest was clear-cut harvested in 1985 and subsequently broadcast burned. In 1987, the site was planted with interior spruce seedlings (2+1 bare root) of unknown weevil resistance status, at a density of approximately 1100 stems/ha.

Treatment and experimental design

In 1995, a "maximum productivity" fertilization research installation was established within the 12-year-old plantation. The objectives of the trial were to study the effects of intensive, repeated fertilization on the growth and yield of interior spruce and to document the effects of repeated nutrient additions on various ecosystem processes (Brockley 1999). Each of six treatments was replicated three times for a total of eighteen, 0.164-ha treatment plots, arranged in a randomized complete-block design. To monitor the growth and development of 64 permanently tagged white spruce

Table 1. Fertilization treatments employed at the British Columbia Ministry of Forests maximum productivity research trial at Lodi Lake, British Columbia.

Treatment code	Treatment
ON$_2$	Fertilized yearly to maintain foliar N levels at 1.6%, other nutrient levels maintained at optimal levels
ON$_1$	Fertilized yearly to maintain foliar N levels at 1.3%, other nutrient levels maintained at optimal levels
Complete	Fertilized every 6 years with 200N, 100P, 100K, 50S, 25Mg, 1.5B
NSB	Fertilized every 6 years with 200N, 50S, 1.5B
NB	Fertilized every 6 years with 200N, 1.5B
Control	Not fertilized

Note: For each treatment, numbers preceding each nutrient symbol represent nutrient application rate (kg/ha). B, boron; K, potassium; Mg, magnesium; N, nitrogen, P, phosphorus; S, sulphur.

trees, an inner assessment plot of 24.16 m × 24.16 m (0.058 ha) was established within each treatment plot. The assessment plot was offset at one end of the treatment plot to reserve an area for possible future destructive sampling.

Treatment descriptions and fertilization summaries are shown in Tables 1 and 2. The NB, NSB, and complete treatments were initially fertilized in the spring of 1996, then refertilized in the spring of 2002. The ON$_1$ and ON$_2$ plots typically received 50–100 and 100–200 kg N/ha, respectively, each spring. Other nutrients were supplied in amounts and frequencies required to maintain balanced foliar nutrition, determined on the basis of the results from foliar sampling the previous fall. From 1996 to 2001, the ON$_1$ and ON$_2$ plots received a total of 450 and 800 kg N/ha, respectively. Urea (46:0:0, N–P–K) was the major source of N, with some N also added as monoammonium phosphate (11:52:0) and ammonium nitrate (34:0:0). Other nutrient sources were muriate of potash (0:0:60), sulphate of potash magnesia (0:0:21:21:11, N–P–K–S–Mg), ammonium sulphate (21:0:0:24, N–P–K–S), ProMag36 (36% Mg, 6% S), and granular borate (15% B). Total quantities of nutrients added for each of the treatments are shown in Table 2.

Field sampling

Weevil attacks were first noted at this site in the early 1990s. Since then a severe weevil infestation has developed. In May 2001, all 64 trees in each plot were surveyed from the ground for new and old weevil damage. New damage was recognized by the presence of a shepherd's crook formed by the current year's growth, whereas old damage was evidenced by the presence of crooks and forks in the bole, accompanied by an old, dead leader or leader stub if the dead leader had broken off. The total number of attacks on each tree was recorded.

The height of all trees in each plot was measured with a laser hypsometer in the fall of 1995, before the first fertilization treatment and before the site became heavily weevil infested, and again in the fall of 2001. The heights of trees with top kill due to weevil attack were measured to the tallest live growth and were included in the means.

Laboratory measurements

In late May 2001, leader samples were collected for analysis of constitutive resin canal defences. Samples were collected from 10 trees randomly chosen from the treated buffer of each plot. Trees that had sustained weevil attacks within

Table 2. Fertilization summary by year and treatment employed at the British Columbia Ministry of Forests maximum productivity research trial at Lodi Lake, British Columbia.

Treatment code	1996	1997	1998	1999	2000	2001
ON$_2$						
N	200	100	100	100	150	150
P	100	50	50			
K	100	50	50		50	
S	50	50	49		63	8
Mg	25	100	50		32	50
B	1.5		1.5			
ON$_1$						
N	100	50	50	50	100	100
P	100	50	50			
K	100	50	50		50	
S	50	50	49		63	
Mg	25	100	50		32	
B	1.5		1.5			
Complete						
N	200					
P	100					
K	100					
S	50					
Mg	25					
B	1.5					
NSB						
N	200					
S	50					
B	1.5					
NB						
N	200					
B	1.5					

Note: Nutrient symbols are as follows: N, nitrogen; P, phosphorus; K, potassium; S, sulphur; Mg, magnesium; B, boron. Values are nutrient application rates (kg/ha). See Table 1 for explanation of treatments.

the past 3 years were rejected. Four-centimetre sections of terminal growth were collected, starting approximately 2 cm below the apical bud, in the area where weevil oviposition would usually occur.

Samples were fixed in formalin – acetic acid – alcohol (FAA) for 48 h and then transferred to 70% EtOH for storage until sectioning. Terminal cross sections approximately 60 μm thick were made with a sliding microtome. Sections were stained with 0.1% aqueous safranin and mounted in glycerin between a glass slide and coverslip. Microscopic images were video-captured and measured with the SigmaScan® image analysis software (SPSS Inc., Chicago, Ill.).

To measure the strength of the traumatic response, we used the artificial wounding techniques described by Tomlin et al. (1998). In late May 2001, ten trees from each of the fertilized buffer areas of plots 1–12 were randomly selected for artificial wounding. A dremel drill equipped with a 1-mm drill bit was used to wound the leader of each tree. Eighteen punctures were made through the bark of the leader in three vertical rows of six punctures in the region where weevil egg laying would normally take place (about 4 cm below the apical bud). The wounding was performed on 25 May, which is within the normal period of weevil feeding and mating at this location. In September 2001, 4-cm sections of stem were sampled from the area of wounding. To assess the strength of the traumatic resin response, we prepared and scanned slides of stem cross sections, using the same methods as for constitutive resin canal analysis.

To describe the distribution of constitutive resin canals in the leader cortex, we measured or derived the following variables: average number and size of inner and outer resin canals (NIN, NOUT, SZIN, and SZOUT) (see Table 3 for explanation of acronyms), average distance between inner resin canals (GAP), resin canal density as expressed by the proportion of bark area occupied by inner and outer resin canals (AOCC), and the total number of resin canals per square millimetre of bark (NMMS). Resin canal density and size have been positively correlated with weevil resistance in past studies (Tomlin and Borden 1994; Alfaro et al. 1997a). Leader diameter and bark thickness were also measured.

Traumatic response intensity was rated on a scale from 0 (no resin canal formations or preformations) to 6 (two complete rings of resin canals in the xylem), as per Brescia (2000).

Statistical analyses

Block and fertilizer effects on tree size, constitutive resin canal variables, and weevil attack rates were detected by performing analysis of variance (ANOVA), using plot means as experimental units. Type III sums of squares were calculated using general linear model (GLM) procedures (STATISTICA, StarSoft, Tulsa, Okla.). Fertilization was treated as a fixed effect. Duncan's multiple-range test was performed to detect differences between groups, and effects were considered significant at $p < 0.05$. A square-root transformation was applied to SZIN to reduce the correlation between plot means and variances. Fertilizer effects on the traumatic wound response (TRAU) were detected using Kruskal–Wallis ANOVA.

A linear regression model using GLM procedures was developed to predict tree height (HEIGHT) based on fertiliza-

Table 3. Summary of ANOVA for analysis of the effects of fertilization (FERT, $F_{[5,10]}$) and block (BLOCK, $F_{[2,10]}$) on tree size and constitutive resin canal variables of interior spruce maintained under six fertilizer regimes.

Variable	F	p >F
Height		
FERT	10.927	0.00085
BLOCK	6.824	0.01352
Leader diameter		
FERT	4.110	0.02764
BLOCK	0.120	0.88596
Bark thickness		
FERT	6.725	0.00541
BLOCK	0.817	0.46932
Number of inner resin canals (NIN)		
FERT	4.239	0.02495
BLOCK	6.903	0.01308
Number of outer resin canals (NOUT)		
FERT	0.927	0.50268
BLOCK	0.955	0.41738
Size of inner resin canals (SZIN)		
FERT	5.480	0.01100
BLOCK	0.604	0.56561
Size of outer resin canals (SZOUT)		
FERT	3.222	0.05442
BLOCK	0.528	0.60522
Bark area occupied by resin canals (AOCC)		
FERT	1.177	0.38484
BLOCK	0.634	0.55028
Resin canal density (NMMS)		
FERT	4.958	0.01528
BLOCK	0.315	0.73691
Average distance between resin canals (GAP)		
FERT	0.458	0.79901
BLOCK	1.693	0.23261

tion treatment (T_k), number of weevil attacks per tree (ATTK), and height before fertilization (HT95). Data were collapsed at the block level so that data points were averages of observations from three trees. Fertilizer treatments were represented by a set of dummy variables (T_k): T_1 was coded 1 for control trees and 0 otherwise; T_2 was coded 1 for NB trees and 0 otherwise; T_3 was coded 1 for NSB trees and 0 otherwise; T_4 was coded 1 for complete trees and 0 otherwise; and T_5 was coded 1 for ON_1 trees and 0 otherwise. A logarithmic transformation was performed on the average number of weevil attacks per tree, to meet the assumption of normality. The elimination method was used to select variables for inclusion in the model, which may be expressed as follows:

$$\text{HEIGHT} = \beta_0 + \beta_1 \text{HT95} + \beta_2 \text{ATTK} + \gamma_1 T_1 + \gamma_2 T_2 + \gamma_3 T_3 + \gamma_4 T_4 + \gamma_5 T_5 + \mu$$

Results

Fertilizer effects on tree size and weevil attack rates

Fertilizer treatment significantly influenced weevil attack rates ($F_{[5,12]} = 3.678$, $p < 0.04$). More than twice as many

trees in the ON_2 treatment had sustained weevil attacks after the fertilizer treatments commenced (54% attacked) than in the control treatment (24% attacked) (Fig. 1). However, regardless of increased weevil attacks, trees from the more-intense fertilizer treatments were on average taller and had thicker leaders with thicker bark than trees from the control and less-intense treatments (Tables 3 and 4). Height was also significantly influenced by block effects (Table 3).

The effects of fertilizer treatment, initial tree height, and number of weevil attacks per tree, as expressed in the regression model (Table 5), significantly influenced tree height in 2001 ($p < 0.001$). Collectively, these variables had an adjusted R^2 of 0.85, and the signs of the coefficients are interpretable. The model indicates that height increases with increasing fertilization treatment and initial height and decreases with increasing number of weevil attacks. Initial height alone explained 68% of the variance.

A plot of the curves generated by the regression equation for each fertilization treatment clearly indicates that although incidence of weevil attack increases with fertilization intensity, the height loss due to weevil attack is not as great as the height gained due to fertilization (Fig. 2).

Fertilizer effects on resin canal defences

There was a significant effect of fertilization on several of the constitutive resin canal variables (Table 3). Only one variable, number of inner resin canals (NIN), was significantly influenced by block effects. Both the number and the size of inner resin canals (NIN and SZIN) increased with increased fertilization (Table 6). The number and the size of outer resin canals (NOUT and SZOUT) were not significantly affected. Increasing fertilization did not affect resin canal density when expressed as AOCC; however, there was a tendency toward lower NMMS with increasing fertilization (Table 6). There was no statistically significant effect of fertilization on GAP; however a general trend of increasing GAP with increasing fertilization was apparent (Table 6).

Mechanical wounding induced traumatic responses, which ranged in intensity from 0 (no response) to 4 (complete ring of traumatic resin canals). However, Kruskal–Wallis ANOVA indicated no significant effects of fertilization on the traumatic response rating ($H_{[5,N=120]} = 9.056$, $p > 0.1$). Response intensity has been shown to vary with wound intensity and tree phenology and genotype (Tomlin et al. 1998; Brescia 2000). Although wound intensity was held as constant as possible, any of these factors may have influenced the results of this study. The lack of a significant difference between the traumatic response rating of control trees and that of fertilized trees may indicate that none of the trees in this study were sufficiently nutrient stressed to influence the ability of the tree to produce a traumatic response.

Discussion

Fertilization improved the growth of interior spruce, but it also increased the incidence of weevil attack. This is likely due to superior brood survival in vigorous leaders with thick bark, because larger leaders can support more oviposition punctures and larger larval populations than small, thin-barked leaders. Our findings are also in accordance with

Fig. 1. Percentage of 16-year-old interior spruce trees that have sustained weevil attacks within 5 years after the initiation of six fertilizer treatments. Treatments with the same letter are not significantly different (Duncan's multiple-range test, $p > 0.05$). See Table 1 for explanation of treatments.
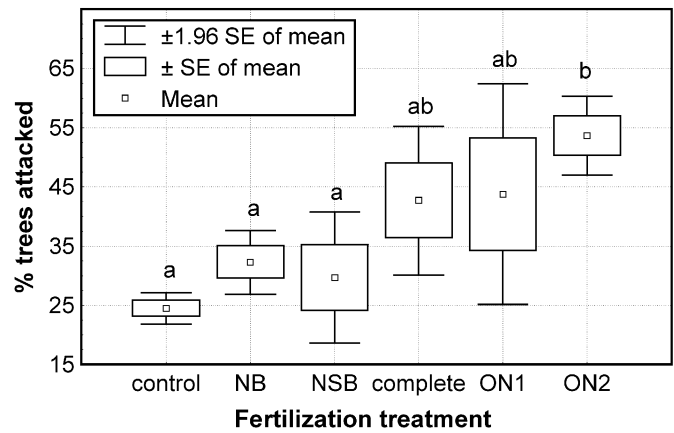

Table 4. Average tree-size variables for 16-year-old interior spruce treated with six fertilizer regimes for 6 years.

Fertilization treatment	Height (m)	Leader diameter (cm)	Leader bark thickness (mm)
Control	3.92a	8.22ab	1.66ab
NB	4.60b	7.55a	1.53a
NSB	4.80bc	8.38abc	1.75bc
Complete	4.69bc	8.62abc	1.77bc
ON_1	5.10cd	9.07bc	1.93c
ON_2	5.29d	9.43c	1.93c

Note: Values with the same letter are not significantly different within columns (Duncan's multiple-range test, $p > 0.05$). See Table 1 for explanation of treatments.

studies by Alfaro et al. (1993) and King et al. (1997), which show a preference of *P. strobi* for vigorous hosts.

The observed increase in incidence of weevil attack may be the result of fertilizer effects, not only on tree size variables, but also on constitutive resin canal defences. In fact, fertilization caused a statistically significant dilution of the tree's constitutive resin canal system by causing an increase in the distance between inner resin canals (albeit not statistically significant) and a decrease in the number of resin canals per unit area of bark.

Although there was an overall dilution (reduction in density) in the constitutive resin canal system, fertilization caused an increase in the number and size of cortical resin canals. This observation has been reported by others and has been attributed to fertilizer effects on tree growth (Smith et al. 1977; Wainhouse et al. 1998). The observed stability in the proportion of bark area occupied by resin canals was likely the result of increasing resin canal size as the bark thickened with fertilization. However, the observed increase in the number and size of resin canals was apparently not substantial enough to maintain the high resin canal densities observed in the lower fertilization treatments, and regardless of its stability, it provided inadequate protection against the weevil. A combination of thin bark and high density resin

Table 5. Parameter estimates and associated statistics for predicting height of interior spruce trees treated with six fertilizer regimes and attacked by *Pissodes strobi*.

Independent variable	Unstandardized coefficient	SE	t	p
INIT	1.28	0.044	28.924	>0.0000
T_1	–94.90	5.055	–18.773	>0.0000
T_2	–47.75	4.693	–10.174	>0.0000
T_3	–39.60	4.632	–8.548	>0.0000
T_4	–38.75	4.581	–8.458	>0.0000
T_5	–18.81	4.469	–4.209	>0.0001
ATTK (transformed)	–49.19	4.197	–11.719	>0.0000
Intercept	246.62	11.427	21.581	>0.0000

Note: INIT, height before fertilization treatment, recorded in 1995; T_1–T_5, a set of dummy variables representing the fertilization treatments in Table 1; ATTK, number of *P. strobi* attacks.

Table 6. Average constitutive resin canal characteristics observed in quarter cross sections of leaders from 16-year-old interior spruce grown under six fertilizer regimes for 6 years.

Fertilization treatment	NIN	NOUT	SZIN (mm^2)	SZOUT (mm^2)	AOCC (%)	NMMS	GAP (mm)
Control	7.5a	7.5a	0.02448a	0.01400a	3.595a	1.979ab	0.388a
NB	7.0a	7.3a	0.02458a	0.01097a	3.869a	2.302a	0.380a
NSB	7.5a	8.2a	0.02358a	0.01483a	3.526a	1.994ab	0.396a
Complete	7.5a	7.3a	0.02743a	0.01735a	3.752a	1.793b	0.401a
ON$_1$	7.5a	8.0a	0.03512b	0.01758a	4.028a	1.664b	0.419a
ON$_2$	8.4b	8.7a	0.03448b	0.02173a	4.232a	1.716b	0.416a

Note: Values with the same letter are not significantly different within columns (Duncan's multiple range test, $p > 0.05$). AOCC, bark area occupied by resin canals; GAP, average distance between inner resin canals; NIN, number of inner resin canals; NMMS, resin canal density; NOUT, number of outer resin canals; SZIN, size of inner resin canals; SZOUT, size of outer resin canals. See Table 1 for explanation of treatments.

Fig. 2. Predicted height of interior spruce, based on height before fertilization, fertilization treatment, and the number of *Pissodes strobi* attacks per tree. The observed average number of attacks per tree is indicated by ●. See Table 1 for explanation of treatments.
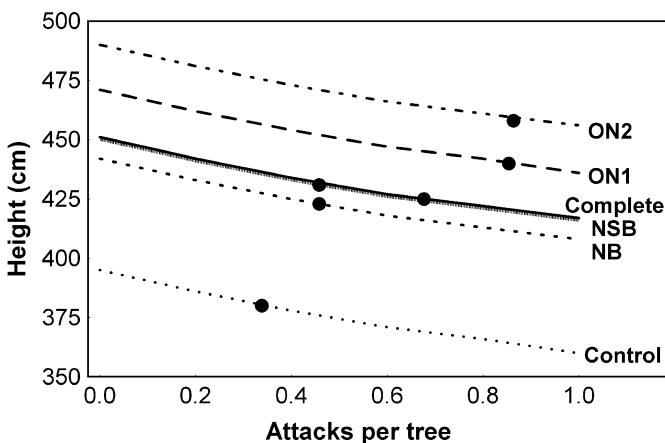
canals, as seen in the trees in the lower intensity fertilization treatments, contributes to resistance against *P. strobi* (Tomlin and Borden 1997).

Fertilization also affected the spatial distribution of inner resin canals within the cortex. The observed increase with fertilization in the average distance between inner resin canals (GAP) may affect the rate of oviposition, feeding behaviour, and survival of adults and larvae by influencing the ability of the weevil to successfully avoid inner resin canals (Stroh and Gerhold 1965) or to ultimately deactivate them by severing their connection to the vascular bundles (the canal's food source) (Alfaro et al. 1999). Because average diameter of the weevil snout is 0.4 ± 0.02 mm (Manville et al. 2002), the average GAP values from low-intensity fertilizer treatments would likely limit adult feeding to the area of the bark outside the inner resin canal ring. Adults feeding on trees from more intense fertilizer treatments would be more likely to feed between inner resin canals than adults feeding on trees from less intense fertilizer treatments. The average width of the head capsule of a first instar weevil larva is in the range of 0.237–0.451 mm (Silver 1968). These values indicate that large first-instar larvae might be limited to feeding on the bark outside the inner resin canal ring of trees from the less intense fertilization treatments.

Conclusions

The use of fertilizers to improve growth in young interior spruce caused an increase in the incidence of weevil attack of up to 30%. Enhanced leader length, diameter, and bark thickness due to fertilization increased the resources avail-

able for weevil feeding and oviposition and led to a dilution of the tree's cortical resin canal defences. Although the incidence of weevil attack was greater in trees from high-intensity fertilization treatments, the height losses due to weevil attack were not as great as the height gains due to fertilization.

Results from this study indicate that the beneficial effects of fertilization on the height growth of young interior spruce trees likely outweigh the negative effects associated with increased incidence and severity of leader damage from the white pine weevil. This analysis, however, does not take into account weevil-induced losses in lumber quality. When combined with genetically improved stock, development of weevil-resistant genotypes, and improved pest management strategies, intensive fertilization may offer great potential for improving the productivity of second-growth spruce plantations in the interior of British Columbia.

Acknowledgements

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