Past infestations of the white pine weevil in naturally regenerated spruce stands

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Past infestations of the white pine weevil, *Pissodes strobi* (Peck), were reconstructed by examining standing and felled trees in naturally regenerated interior spruce stands in the McGregor Model Forest in northern B.C. Infestations were common in both the Sub-Boreal Spruce (SBS), wet cool (SBSwk) and very wet cool (SBSvk) biogeoclimatic subzones, demonstrating that frequent weeviling is a natural event that predates human intervention. Approximately one-third of all stem defects in 32 felled trees were verified as caused by the weevil. In the SBSwk and SBSvk 56.3% and 81.3% of felled trees contained weevil-caused defects, with 1.9 and 2.1 defects per tree, respectively. Trees in the SBSvk had significantly more weevil attacks high on the bole than trees in the SBSwk.

Key words: white pine weevil, *Pissodes strobi*, white spruce, Engelmann spruce, *Picea engelmannii* × *P. glauca*

Les épidémies antérieures du charançon du pin blanc, *Pissodes strobi* (Peck), ont été reconstituées par l'examen des arbres debout et abattus dans les peuplements de l'intérieur régénérés naturellement d'épinettes dans la Forêt modèle de McGregor. Les épidémies ont été retrouvées tant dans les sous-zones biogéoclimatiques de l'épinette sub-boréale (SBS), que pour les sous-zones fraîches et humides (SBSwk) et fraîches et très humides (SBSvk), illustrant que les épidémies fréquentes de charançon constituent un événement naturel qui date d'avant l'intervention humaine. Près du tiers de toutes les tiges défectueuses des 32 arbres abattus ont été identifiées comme ayant été attaquées par le charançon. Dans les sous-zones SBSwk et SBSvk, 56,3 % et 81,3 % des arbres abattus contenaient des défauts provoqués par le charançon, atteignant pour chaque sous-zone, 1,9 et 2,1 défauts par arbre. Les arbres de la sous-zone SBSvk ont connu significativement plus d'attaques du charançon haut sur la tige que dans le cas des arbres de la sous-zone SBSwk.

Mots-clés: charançon du pin blanc, *Pissodes strobi*, épinette blanche, épinette d'Engelmann, *Picea engelmannii* × *P. glauca*

Introduction

Forest landscape structure is shaped by two general processes: natural disturbance regimes, including stand-replacing or stand-maintaining wildfires and forest management activities including silvicultural treatments and harvesting. Within much of the British Columbia (B.C.) interior, clearcutting has surpassed stand-replacing fires as the most dominant disturbance agent (Delong and Tanner 1996).

Understanding the effects of forest management practices on insect pests is important if stand productivity is to be maintained or increased. However, such an understanding requires background knowledge of pest history in naturally regenerated forests. This is particularly important if forest management activities are to emulate natural disturbances as currently recommended by some ecologists. It is assumed that indigenous flora and fauna are better adapted to natural than to human-caused disturbance regimes and that the adverse impacts of forest practices may be minimized if they mimic natural disturbances (Hansen *et al.* 1991, Swanson *et al.* 1994, Delong and Tanner 1996).

For some insects it is possible to reconstruct the history of infestations in naturally regenerated stands. For example, outbreaks of defoliating lepidoptera can be tracked by episodic reductions in the width of tree rings caused by reduced photosynthetic capacity during periods of intense defoliation (Alfaro *et al.* 1982). Changes in neighbouring tree ring widths can be

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used to determine the occurrence of past outbreaks of bark beetles (Heath and Alfaro 1990, Veblen *et al.* 1991). It is also possible to reconstruct the retrospective stand epidemiology of the white pine weevil, *Pissodes strobi* (Peck), because most attacks leave a killed leader and a characteristic deformation in the bole of the tree (Alfaro 1989), both of which long remain visible on trees, sometimes into maturity.

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In the interior of B.C., the white pine weevil is a serious pest of young white spruce, *Picea glauca* (Moench) Voss, Engelmann spruce, *Picea engelmannii* (Parry) Engelm., and "interior" spruce, *P. engelmannii* × *P. glauca*, growing in the zone of hybridization (Meidinger and Pojar 1991, Coates *et al.* 1994) between Engelmann and white spruce. The weevil

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begins to attack susceptible spruce plantations as young as four to five years old; maximal attack intensities (numbers of trees attacked per year) occur in 10–30 year old stands. In plantations more than 30 years old, attack intensities gradually decline as the stand matures (Alfaro and Omule 1990). This decline may be caused by intraspecific competition between trees that reduces terminal leader size and thus food supply, by changes in leader microclimate, or by a decrease in susceptibility to the weevil (Alfaro 1994).

Model Forests have recently been established across Canada⁴. In these forests, research on socio-economic factors, ecological processes and forest practices is intended to facilitate the development and adoption of forest management strategies and decision support systems that will aid in sustainable resource management. The McGregor Model Forest, which encompasses Canadian Forest Products Ltd. Tree Farm License 30, is an approximately 165 000 ha management unit, located 100 km northeast of Prince George, B.C. It is comprised of four biogeoclimatic zones (Meidinger and Pojar 1991): Interior Cedar-Hemlock, Engelmann Spruce-Subalpine Fir, Alpine-Tundra, and Sub-Boreal Spruce (SBS). The Model Forest includes 33 000 ha of immature forests, primarily in the SBS zone, which are at risk to weevil attack.

The SBS zone has a continental climate characterized by long cold winters and relatively warm moist and short summers (Meidinger *et al.* 1991, Coates *et al.* 1994). Mean annual temperatures range from 1.7–5.0°C with mean temperatures less than 0°C for four to five months and more than 10°C for two to five months. Mean annual precipitation is 440–900 mm of which 25–50% falls as snow. Interior spruce is the dominant climax tree. Two of the 10 subzones, the wet cool and the very wet cool subzones (SBSwk and SBSvk, respectively, hereafter referred to without the terms “zone” or “subzone”) occur in the McGregor Model Forest (Meidinger *et al.* 1991).

Stand-replacing fires are the dominant natural disturbance agents within the SBS (Delong and Tanner 1996). These fires eliminate most of the overstory vegetation, exposing the mineral soil, which favours interior spruce germination (Coates *et al.* 1994). Patches of young interior spruce then become established and, depending upon the weevil hazard for that stand (Spittlehouse *et al.* 1994), can be susceptible to white pine weevil attacks. However, the differences in weevil epidemiology between naturally regenerated forests after a fire and plantations after harvest is unknown.

Our objective was to reconstruct weevil attack history in naturally regenerated stands that occurred after natural wildfires in the SBSwk and SBSvk within and near the McGregor Model Forest. Reconstruction of past weevil attacks will allow forest managers to determine whether present day weevil infestations are brought about, intensified, or lessened by current forest management practices. A companion study in post-harvest plantations in the McGregor Model Forest is nearing completion (J.A. McLean, Faculty of Forestry, University of B.C., Vancouver, personal communication).

Methods

For each of the SBSvk and SBSwk, four sites containing naturally regenerated spruce as the numerically dominant species were selected (Table 1). Stand age ranged from 21 to 59 years; trees within each site were even-aged. Fire history was obtained from existing records and confirmed by the presence of charcoal in the soil and fire scars on the few remaining veteran trees. Two fixed-radius circular plot centres per stand were selected at least 20 m into the stand and at least 50 m apart. Plot radii were 11.28 or 12.61 m, yielding plot areas of 399.7 and 499.6 m², respectively (Watts 1983). The large plots were used when tree density was relatively low. Diameter at breast height (dbh=1.3 m) and crown class (dominant, codominant, intermediate, or suppressed) (Anonymous 1980) were recorded for all conifers at least 7.5 cm dbh. Elevation and aspect of each plot were determined using altimeter and compass.

The bole of each spruce tree within each plot was visually assessed from the ground for the type and approximate height of defects, classified as: scar, minor crooks, major crooks, and forks (Alfaro 1989). Ten dominant and codominant trees per plot were aged using increment borers and their height assessed using clinometers (Watts 1983).

To confirm whether defects were caused by weevil damage or some other factor, two dominant or codominant spruce trees per plot, each bearing abundant external evidence of defects, were selected to be felled. The height of each tree was recorded, and the type and height of all defects were noted, as were those defects associated with old terminal leaders containing pupal chambers or oviposition holes. Although other defects may be weevil-caused, only these latter defects provide proof of weevil attacks, unless the tree is dissected.

Data were analyzed using SAS® (release 6.10) and Minitab® (release 10.1) statistical software packages. In all cases $\alpha = 0.05$. Student's t-Tests and Chi-square tests were used to determine respective differences in means or proportions between subzones. The frequency distributions of confirmed weevil attacks occurring at 2 m intervals along the bole were compared between subzones by a Chi-square test, with subzone as the independent variable and height of weevil attack as the dependent variable. The distributions of each type of weevil attack were also compared between subzones by a Chi-square test, with subzone and defect type as independent and dependent variables, respectively. The relationship between numbers of confirmed weevil attacks per felled tree and numbers of all defects as determined visually was analyzed by linear regression, pooling all felled trees in both subzones.

Results

Stand elevations ranged from 620–760 m in the SBSvk and 470–780 m in the SBSwk (Table 1). Stand densities were comparable (means of 1287 and 1231 stems per ha in the SBSvk and SBSwk, respectively) and the predominant trees were interior spruce (70.1 and 79.4% in the SBSvk and SBSwk, respectively) (Table 1). The frequency distributions of interior spruce and subalpine fir within each crown class did not differ significantly within a species and subzone, but for pooled data, the distributions did differ significantly between species ($\chi^2 = 54.5$ $P = 0.001$). This was due primarily to differences in occupancy of dominant and suppressed classes. Twenty-six percent of all spruces were dominant and 13% were suppressed;

⁴Evaluation of the Canadian Model Forest Program, PE223/1996, May 1996. Report prepared by Gardner Pinfold Consulting Economists Ltd., Halifax for National Advisory Committee for the Model Forest Program Evaluation, Natural Resources Canada, Ottawa.

Table 1. Characteristics of sampled stands within the Sub-Boreal Spruce biogeoclimatic zone in the McGregor Model Forest north of Prince George, B.C. Age calculated from 20 trees within two fixed radius plots per stand, and densities calculated from all dominant, codominant, intermediate and suppressed trees within the plots.

Biogeoclimatic subzone ^a	Stand no. ^b	Coordinates	Elevation (m)	Aspect	Stand height (m) ($\bar{x} \pm \text{SE}$)	Stand age (yr)	Number of trees per ha	
							all conifers	spruce
SBSvk	1	54°22'N, 122°18'W	715	north	12.8 $\pm$ 2.8	34	988	688
	2	54°24'N, 122°15'W	760	south	18.1 $\pm$ 3.8	50	1614	1063
	3	54°24'N, 122°14'W	730	flat	13.9 $\pm$ 3.4	46	1276	1063
	4	54°21'N, 122°15'W	620	flat	9.1 $\pm$ 2.2	35	1271	791
SBSwk	5	54°16'N, 122°23'W	780	west	22.4 $\pm$ 3.9	58	1777	1439
	6	53°54'N, 122°20'W	470	flat	24.5 $\pm$ 2.6	57	971	891
	7	53°54'N, 122°20'W	620	west	8.6 $\pm$ 1.9	21	811	520
	8	54°01'N, 122°27'W	680	north	24.6 $\pm$ 4.2	59	1364	1063

^aSub-boreal spruce (SBS) very wet cool subzone (vk) and SBS wet cool subzone (wk).

^bStand nos. 7 and 8 were ca. 40 km south of the McGregor Model Forest.

Table 2. Frequency of attack by the white pine weevil on naturally regenerated spruce in two biogeoclimatic subzones of the McGregor Model Forest.

Category of tree	Number of trees examined		Criterion assessed	SBSwk	SBSvk	Statistical evaluation between subzones	
	SBSvk	SBSwk					
Standing	306	344	Percent of spruce with defects detected by visual assessment	39.8%	44.4%	$\chi^2=1.79$	$P=0.181$
	306	344	Mean ($\pm$ SE) number of defects per spruce tree detected by visual assessment	0.56 $\pm$ 0.86	0.70 $\pm$ 0.96	$t=1.93$	$P=0.054$
	59	62	Mean ($\pm$ SE) annual spruce height growth (m/yr) (tree height/tree age)	0.42 $\pm$ 0.05	0.33 $\pm$ 0.08	$t=-7.18$	$P=0.000$
felled	16	16	Percent of trees with defects	100.00%	100.00%		
	16	16	Percent of spruce with defects verified as weevil-caused	56.3%	81.3%	$\chi^2=2.33$	$P=0.127$
	16	16	Percent of all defects verified to be weevil-caused	31.2%	31.8%	$\chi^2=0.01$	$P=0.936$
	16	16	Mean ($\pm$ SE) number of defects per spruce tree	6.0 $\pm$ 1.7	6.7 $\pm$ 2.7	$t=0.88$	$P=0.387$
	16	16	Mean ($\pm$ SE) number of defects per spruce tree verified as weevil-caused	1.9 $\pm$ 2.0	2.1 $\pm$ 1.7	$t=0.38$	$P=0.709$
	16	16	Mean ($\pm$ SE) height (m) on spruce bole of first weevil attack	3.30 $\pm$ 1.13	5.67 $\pm$ 2.47	$t=3.02$	$P=0.007$

for subalpine fir the respective percentages were 10 and 34%. Stands in the SBSvk were 32.5% shorter than in the SBSwk. However, only a portion of this difference was due to differences in stand age (means of 41.3 and 48.8 years in the SBSvk and SBSwk, respectively), because trees in the colder SBSvk grew 20% less rapidly than in the SBSwk (means of 0.33 and 0.42 m of vertical growth per year in the SBSvk and SBSwk, respectively) (Table 2).

Large proportions of the naturally regenerated felled spruce trees in both subzones contained defects that arose from weevil attacks (Table 2). On average, a naturally regenerated interior spruce could be expected to sustain two weevil attacks in its lifetime. These results indicate that in the absence of human intervention, a high incidence of weevil infestation is a natural occurrence in the SBS.

There was a significant, but very weak relationship between the numbers of defects detected before felling and the number of confirmed weevil attacks per tree ($y = 0.8x + 0.4$, $r^2 = 0.006$, $P < 0.006$), indicating that mature trees must be felled to obtain accurate estimates of past weevil attack.

Distributions of height of weevil attack on the bole differed significantly between subzones (Fig. 1). In both subzones most attacks were between 2 and 16 m high, but there were fewer weevil attacks low and more attacks high on the bole for trees growing in the SBSvk, the wetter and cooler subzone. The height of first weevil attack was also significantly lower in the

SBSwk than in the SBSvk (Table 2). On felled trees, neither the total number of defects nor the number of weevil-caused defects differed significantly between the two subzones (Table 2). Weevils caused approximately one third of all defects per felled tree in both subzones. However, only 56.3% of spruce trees with defects in the SBSwk had verified weevil-caused defects compared to 81.3% on spruce trees in the SBSvk (Table 2).

Distances to the four closest openings ranged from 100–3000 m from the sampled stands (Table 3). In almost every case the openings occurred from logging more than 30 years after the sample stand was established, well beyond the 30-year window of susceptibility of the sample stands, ruling out the possibility of invasion of weevils from man-made disturbances. However, for stand number 7 the 30-year susceptibility window overlapped that of the disturbed areas by 14 to 24 years. The 24-year overlap occurred for an opening 2000 m distant, and it would probably have taken 5 to 10 years for a sufficient number of migrating weevils to have emerged from that site and found the sample stand.

Differences in the frequency distributions of each type of weevil-caused defect between subzones approached significance (Fig. 2). Minor crooks were the predominant defect in both subzones. Trees in the SBSvk had almost equal numbers of scars, major crooks, and forks, while those in SBSwk had very few scars or forks.

Fig. 1. Distributions of weevil attacks by height on the bole of interior spruce in the SBSvk and SBSwk biogeoclimatic subzones.

Fig. 2. Frequency distributions of type of defect caused by white pine weevil attack in the SBSvk and SBSwk biogeoclimatic subzones.

Discussion

In mature undisturbed Sitka spruce forests along the B.C. coast, attacks by the white pine weevil are rare (Alfaro 1994). In the coastal fog belt accumulated degree days during the summer are too low to sustain weevil development (McMullen 1976). However, in naturally regenerated spruce forests in the SBSvk and SBSwk weevil attacks were frequent and the damage substantial. Because some evidence for past weevil attacks may have been buried in the sapwood of mature trees, dissection of felled trees might have revealed an even higher incidence of attack. Thus, selection of trees with obvious defects for felling may have been offset by a conservative measure of the number of attacks. However, even on external examination, the record held by trees many years after attack provides irrefutable evidence that the white pine weevil has been a prevalent natural component of these sub-boreal forest ecosystems that predated human intervention. This conclusion is consistent with the findings of Alfaro (1996) in fire-regenerated stands near Williams Lake, more than 200 km south of our study sites, and is supported by the evidence in Table 3 that it is impossible or (in one case) extremely unlikely that weevils in the sampled stands could have originated in sites disturbed by mankind. It also conforms with calculations based on recorded climatic data

Table 3. Relationship of sampled stands (Table 1) to four nearest openings from which migrating weevils could have originated.

Stand no.	Distance to four nearest openings disturbed by logging or burning (m)	Date of disturbance	Duration to first possible weevil attack in disturbed area after sample stand established (years) ^a
1	350	1990	29
	1350	1993	32
	2400	1989	28
	2770	1994	33
2	930	1994	49
	1130	1989	44
	1350	1989	44
	1500	1994	49
3	300	1989	40
	400	1994	45
	1050	1994	45
	2150	1989	40
4	1000	1996	36
	1140	1995	35
	1350	1994	34
	1650	1995	35
5	250	1980	43
	750	1979	42
	900	1998	61
	950	1981	44
6	100	1956	18
	300	1959	21
	800	1977	39
	1600	1981	43
7	550	1991	16
	650	1990	15
	1500	1991	16
	2000	1980	6
8	100	1994	58
	1200	1994	58
	1600	1995	59
	3000	1971	35

^aCalculated as date of disturbance minus date sample stand established, based on age of trees in sample plot.

that unshaded leaders and, in some years shaded leaders, in all sampled stands accumulated more than 785 degree days (B.G. Sieben, Faculty of Forestry, University of British Columbia, Vancouver, personal communication), enough heat accumulation to allow for successful weevil development.

The lower height of the first weevil attack on spruce boles in the SBSwk than in the SBSvk suggests that weevils may initiate attacks on younger or smaller spruce trees in the SBSwk than in the SBSvk. Because wood volume is greatest near the base, the quantity of defect-free timber obtained from stands in the SBSwk may thus be less than from SBSvk. However, this reduction in timber volume and quality may be offset by the large number of forks per felled tree on spruces growing in the SBSvk. Severe defects (major crooks and forks) accounted for 38% and 41% of all defects in the SBSwk and SBSvk, respectively. In eastern white pine, *Pinus strobus* L., Brace (1972) calculated that such defects reduced the value of lumber recovered from attacked trees by 25%. If similar losses are sustained in naturally-regenerated interior spruce, as appears

likely, effective weevil management in managed plantations could greatly increase the value of the trees at harvest.

As expected (Alfaro and Omule 1990), weevil attacks in relation to height on the bole were more or less normally distributed in both subzones. The higher extent of attacks on the bole in the SBSvk than in the SBSwk could be explained by three hypotheses, among others. Firstly there may be less overstorey shade in the SBSvk than in the SBSwk. Although not counted or measured, paper birch, *Betula papyrifera* Marsh., black cottonwood, *Populus trichocarpa* Torr. and Gray, and trembling aspen, *Populus tremuloides* Michx., were present as dominants or co-dominants in three of the four SBSwk sites, but were absent in all SBSvk sites. These trees might have provided sufficient shade during the early life of a stand in the SBSwk to limit most attacks to a height of 8m or less (Taylor and Cozens 1994, Taylor *et al.* 1996). Secondly, small leaders in the SBSvk may have negatively affected larval growth, and produced small adults with limited fat reserves. Like bark beetles (Atkins 1975, Hagen and Atkins 1975, Jactel 1993) adult weevils with low lipid content might not have had the metabolic capacity to disperse to new habitats, extending the duration and raising the height of attacks in the SBSvk. Thirdly, in the McGregor Model Forest the natural return interval for stand-replacing fires (DeLong and Tanner 1996) within the SBSvk is estimated to be 500 to 700 years (B.C. Hawkes, Canadian Forest Service, Pacific Forestry Centre, Victoria, B.C., personal communication), which would result in only 0.14% of this subzone burning every year. The fire return interval in the SBSwk is unknown, but presumably shorter than in the SBSvk (B.C. Hawkes, personal communication). Therefore, weevils in the SBSvk may accept and remain in ageing stands and attack very high leaders, while in the SBSwk many patches of young stands would be created per unit time and would be available as new habitats for dispersing weevils that departed from ageing stands.

We suggest that surveys for weevil-caused defects in fire-regenerated mature trees could be used to supplement hazard rating based on climate and elevation (Spittlehouse *et al.* 1994, Taylor 1997) as a basis for weevil management plans that could be incorporated into silvicultural prescriptions. Forests that have a high hazard rating may warrant a silvicultural prescription that includes planting of weevil-resistant trees (Kiss *et al.* 1994, Alfaro *et al.* 1996), high density planting, and a mixing of spruce with a deciduous overstorey (Taylor and Cozens 1994, Alfaro *et al.* 1995, Taylor *et al.* 1996).

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