PAST INFESTATIONS OF THE WHITE PINE WEEVIL, *PISSODES STROBI* PECK,
(COLEOPTERA: CURCULIONIDAE) WITHIN NATURALLY REGENERATED
STANDS OF THE MCGREGOR MODEL FOREST, PRINCE GEORGE, BRITISH
COLUMBIA

by

Troy Teruo Mori Kimoto

B.Sc. (Biology) Simon Fraser University, 1993

THESIS SUBMITTED IN PARTIAL FULFILLMENT OF
THE REQUIREMENTS FOR THE DEGREE OF
MASTER OF PEST MANAGEMENT

in the Department

of

Biological Sciences

© Troy Kimoto 1997

SIMON FRASER UNIVERSITY

April 1997

All rights reserved. This work may not be
reproduced in whole or in part, by photocopy
or other means, without permission of the author
The author has granted a non-exclusive licence allowing the National Library of Canada to reproduce, loan, distribute or sell copies of this thesis in microform, paper or electronic formats.

The author retains ownership of the copyright in this thesis. Neither the thesis nor substantial extracts from it may be printed or otherwise reproduced without the author's permission.

L'auteur a accordé une licence non exclusive permettant à la Bibliothèque nationale du Canada de reproduire, prêter, distribuer ou vendre des copies de cette thèse sous la forme de microfiche/film, de reproduction sur papier ou sur format électronique.

L'auteur conserve la propriété du droit d'auteur qui protège cette thèse. Ni la thèse ni des extraits substantiels de celle-ci ne doivent être imprimés ou autrement reproduits sans son autorisation.
APPROVAL

Name: TROY TERUO KIMOTO

Degree: Master of Pest Management

Title of Thesis: 

PAST INFESTATIONS OF THE WHITE PINE WEEVIL, PISSODES STROBI PECK (COLEOPTERA:CURCULIONIDAE), IN NATURALLY REGENERATED STANDS OF THE MCGREGOR MODEL FOREST, PRINCE GEORGE, BRITISH COLUMBIA.

Examining Committee:

Chair: Dr. J. Rahe, Professor

Dr. J. Borden, Professor, Senior Supervisor
Department of Biological Sciences, SFU

Dr. R. Alfaro, Research Scientist
Pacific Forestry Centre

Dr. R. Brooke, Associate Professor
Department of Biological Sciences, SFU

Dr. A. Harestad, Associate Professor
Department of Biological Sciences, SFU
Public Examiner.

Date Approved: 11 April 1987
ABSTRACT

Past infestations of the white pine weevil, *Pissodes strobi* Peck, were reconstructed by examining standing and felled trees in naturally regenerated interior spruce, *Picea engelmannii* (Parry) Engelm. x *P. glauca* (Moench) Voss, stands within two Sub-Boreal Spruce (SBS) biogeoclimatic subzones of the McGregor Model Forest. Naturally occurring infestations were frequent in both the SBS wet cool (SBS wk) and SBS very wet cool (SBS vk) subzones, demonstrating that weevil attacks are not primarily a consequence of present day forest management practices. All 16 felled trees in each subzone had stem defects (scars, crooks, or forks), approximately one-third of which were verified to be caused by the weevil. In the SBS wk and SBS vk subzones, respectively, 56.3 % and 81.3 % of felled trees contained defects caused by the weevil, with approximately two such defects per tree. Trees in the SBS vk subzone had significantly more weevil attacks high on the bole than spruce trees in the SBS wk subzone. The height of first weevil attack was also significantly higher on the bole in the SBS vk than in the SBS wk subzone. Three hypotheses suggested for this observation are: 1) a lack of overstory shade in the SBS vk allowing successful attacks high on the stem; 2) longer spruce leaders in the SBS wk producing larger adult weevils that are capable of dispersal as stand becomes unsuitable for weevils; and 3) shorter fire return interval in the SBS wk than SBS vk, which could provide more susceptible hosts in the SBS wk subzone. I hypothesize that large-scale disturbances in interior forest ecosystems may have lead to a close coevolutionary relationship between weevil and it’s tree host, leading in turn to greater selection pressure for the development of resistance to the weevil in the interior of British Columbia than in the coastal fog belt where large-scale disturbances are infrequent.
The results suggest that mature trees could be surveyed to determine potential weevil problems for future stands and thus aid in incorporating weevil management plans into silvicultural prescriptions.
Dedication

To: my parents, Ron and Eiko, for enduring the costs and enjoying the benefits of investing time, energy, and love in parental care; my wife Carmen for $\infty$ reasons; my son Dylan John Mori Kimoto; the memory of my grandpa Isamu Kariya, wise owl and funny bone.
Acknowledgments

I am deeply indebted to Dr. John Borden, my senior supervisor for his enthusiasm throughout this degree. I also thank him for not embarrassing me when I got the MPM van stuck in the mud. I extend my deepest gratitude to Dr. Rene Alfaro of the Canadian Forest Service and the McGregor Model Forest Association for providing me the opportunity to work on the McGregor Model Forest research team and to Dr. Robert Brooke for advice on my thesis. I gratefully acknowledge: Emil Wegwitz and Cheryl Horvath for making data collecting a pleasurable experience; Bob Doratty, Northwood Pulp and Timber Ltd., for assistance in locating sample sites within the Model Forest; Ross Benton for contributing retrospective climate data; Dr. Brad Hawkes for assistance in site selection and contributing fire history data; all the staff and personnel at the McGregor Model Forest Association and Canadian Forest Service in Prince George for their assistance and warm hospitality; Brian Sieben for contributing hazard rating data; Roy and Gineen Warnock for filling my belly and sharing their household; Jeff Lemieux for the warm hospitality and introduction to rock climbing; Dr. Alton Harestad for many enjoyable teaching assistantships and sagely advice; Gordon Downie, Theo Fleury and Charles Bukowski for creative inspiration; the Borden Lab for their assistance; MPM colleagues especially Dave Holden, Dave Onyabe, Marnie Duthie and Sherah VanLaerhoven, Caroline Bedard for making this degree a very unreserved and enjoyable experience; Five High Fiving White Guys for allowing me to pretend I was Guy Lafleur once a week; secretarial staff in the biology department for their hard work; Department of Biological Sciences for financial assistance in the form of teaching assistantships; and finally my family for continual support.
Table of Contents

Approval ii
Abstract iii
Dedication v
Acknowledgments vi
Table of Contents vii
List of Tables ix
List of Figures x
Introduction 1

Biology of the white pine weevil 4
McGregor Model Forest 7
Objectives 10

Methods and Materials 11

Results

Stand characteristics 19

Reconstruction of past weevil attacks 23

Discussion

Reconstruction of past weevil attacks 30

Differences in distributions of weevil attacks by height on the bole of interior spruce, possible hypotheses:

a) Lack of overstory shade in SBS vk subzone 34

b) Larger spruce leaders in the SBS wk subzone 35
c) Longer fire return interval in the SBS vk subzone

Hypothetical differences in *Pissodes strobi* ecology within Sitka spruce and interior spruce stands

Literature Cited
List of Tables

Table 1. Characteristics of sampled stands within the SBS biogeoclimatic subzones in the McGregor Model Forest. 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. 20

Table 2. Distribution of interior spruce and subalpine fir within crown class in stands sampled in the McGregor Model Forest. 21

Table 3. Frequency of attack by the white pine weevil on naturally regenerated spruce in two biogeoclimatic subzones of the McGregor Model Forest. 22
List of Figures

Figure 1. Biogeoclimatic subzones of the McGregor Model Forest (Tree Farm License 30), Prince George, British Columbia. Alpine-Tundra, Engelmann Spruce-Subalpine Fir (ESSF) Wet Cool (wk), Interior Cedar-Hemlock (ICH) Very Wet Cool (vk), Sub-Boreal Spruce (SBS) Moist Cold (mc), SBS Very Wet Cool (vk), SBS Wet Cool (wk) (Meidinger and Pojar 1991). Site locations are marked with an “X”. Two sites were located approximately 40 km southwest of the model forest, both within the SBS wk subzone.

Figure 2. Stem defects in the bole of interior spruce associated with past weevil attacks. Defects were recorded as: scars (injury almost healed); minor crooks (bole deviation above site of assumed weevil attack ≤ 50 % off vertical axis of stem below attack); major crooks (> 50 % deviation); or forks (two stems occurring above assumed site of weevil attack) (Alfaro 1989).

Figure 3. Confirmed evidence of weevil damage on spruce stem. The old terminal leader is associated with pupal chambers.

Figure 4. Confirmed evidence of weevil damage on spruce stem. The old terminal leader is associated with oviposition punctures.
Figure 5. Relationship between numbers of verified weevil attacks observed on undissected felled interior spruces, and total number of all defects per felled tree. Data pooled for SBS vk and SBS wk biogeoclimatic subzones, and transformed by $\log_{10} (X+1)$ prior to analysis. $r^2=0.43$, $P=0.001$. 

$Y=-1.40 + 0.53X$.  

Figure 6. Relationship between numbers of verified weevil attacks observed on undissected felled interior spruces, and total number of all defects per tree detected visually before felling. Data pooled for SBS vk and SBS wk biogeoclimatic subzones, and transformed by $\log_{10} (X+1)$ prior to analysis. $r^2=0.36$, $P=0.001$. 

$Y=0.46 + 0.76X$.  

Figure 7. Distributions of weevil attacks by height on the bole of interior spruce in the SBS vk and SBS wk biogeoclimatic subzones. Distributions significantly different, $\chi^2=14.16$, $P=0.028$.  

Figure 8. Frequency distributions of type of defect caused by white pine weevil attack in the SBS vk and SBS wk biogeoclimatic subzones. Differences between distributions approaches significance, $\chi^2=6.53$, $P=0.088$.  

INTRODUCTION

Natural and Human-caused Disturbances in Forest Landscapes

Forest landscape structure is shaped by two general disturbance processes: 1) natural disturbance regimes including wildfire (stand-replacing or stand-maintaining fires), landslides, windthrow, and insect and disease outbreaks; and 2) harvesting practices including clearcutting, partial cutting, selective logging and silvicultural treatments such as juvenile spacing and suppression of weed species. Within British Columbia, the impact of disturbance agents on forest landscape structure has changed dramatically over the last 40 years. Stand-replacing fires continue to be the most dominant disturbance agent affecting some sub-boreal forest landscapes. However, in parts of the Prince George Forest Region clearcutting has surpassed stand-replacing fires as the most dominant disturbance agent affecting sub-boreal forests. The forested area affected by wildfires has probably decreased because of increases in fire suppression (Delong and Tanner 1996).

The effects of wildfire and harvesting on forest stand and landscape structure differ considerably. The effects of each type of disturbance can be either detrimental or beneficial to pest and non-pest organisms. In sub-boreal forests in the Prince George Forest Region, wildfire tends to create either small (< 50 ha) or large (> 500 ha) stands, while clearcutting creates stands of intermediate area. A three-pass harvesting system in old-growth forests has also been implemented such that clearcuts, currently limited to 80 ha, are regularly distributed throughout the landscape, allowing for two future harvests (Delong and Tanner 1996). This practice causes a homogeneously fragmented landscape with limited areas of forest interior, much different from the landscape mosaic of naturally disturbed sites (Hansen et al. 1991). Homogeneous forest fragmentation in eastern North
American forests appears to have adverse affects on forest-dwelling migratory songbirds (Terebough 1992) and caribou (Racey et al. 1991). Clearcuts also have much shorter boundaries than do complex polygons caused by wildfires (Delong and Tanner 1996). The geometric shapes may channel wind into cutblock corners, increasing the prevalence of wind thrown trees and exacerbating problems with pests such as the spruce beetle, *Dendroctonus rufipennis* Kirby, which often reaches outbreak populations by breeding in blowdown or excess logging debris (Schmid and Frye 1977; Veblen et al. 1991a).

Clearcutting also reduces the structural complexity of forest stands more so than wildfires, by removing approximately 90% of the live stem volume and reducing the amount of coarse woody debris incorporated into the subsequent stand (Spies et al. 1988; Hansen et al. 1991). Coarse woody debris provides a habitat for many floral and faunal species, as well as influencing nutrient cycling, and stream ecology (Spies et al. 1988). It also provides habitat for ants and shrews which prey upon larvae of the spruce budworm, *Choristoneura occidentalis* Freeman, a major forest pest (Moeck and Safranyik 1984; Youngs and Campbell 1984; Torgerson and Bull 1995). Woodpeckers that use standing snags as nesting sites prey on pests such as bark beetles (Schmid and Frye 1977; Moeck and Safranyik 1984). Removal of coarse woody debris by clearcut harvesting could thus increase pest populations in subsequent stands by affecting predator populations.

Clearcutting and natural disturbances have a positive effect on organisms by creating disturbed sites in which many pioneer plant and animal species thrive. Clearcutting is currently the most feasible method for managing forests that are heavily infected with dwarf mistletoe because it removes both the inoculum and the host (Unger 1992; Anonymous 1995a).
The intensity of forest management in British Columbia has increased (Enns 1994) due to the desire to meet the conflicting objectives of increasing the harvested volume, while at the same time using forests for non-commercial values. Silvicultural practices such as site preparation, planting, brushing and weeding, and thinning are used to increase forest productivity. Site preparation employs prescribed burning or mechanical site alteration to create planting sites and enhance microsite conditions. In doing so it may also remove coarse woody debris and degrade the soil (Breadon 1987). It is hypothesized that intensive site preparation could negatively affect some wildlife species, especially those that employ subterranean burrows (Enns 1994). Preliminary studies suggest that browse for elk, moose, and deer is less abundant in scarified than unscarified areas (Stelfox and Cormack 1962), which may cause fewer ungulates to use scarified cutblocks (Stelfox et al. 1976). Conversely, site preparation may positively influence populations of carabid beetles, collembola, and arachnids (Perry and Rodgers 1986). Insectivorous organisms may benefit in turn from an increase in prey population.

Brushing and weeding with chainsaws and chemical herbicides is employed when coniferous crop trees are being out-competed for water, nutrients, or light by herbaceous or non-commercial woody plants. The creation of fine woody debris and the removal of browse, shade and thermal cover affects animals that use these resources. Glyphosate-treatments in clearcuts altered cover, forage and microclimate for herbivorous and insectivorous small mammals for up to three years post-treatment (Santillo et al. 1989). These treatments caused a decrease in forage and food that lead to a decrease in these small mammal populations.
Wildfires, harvesting and silvicultural treatments have different impacts on the complexity of forest and landscape structure. 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 historical 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. 1995; Delong and Tanner 1996).

Only for some insects is it possible to reconstruct their history 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 neighboring tree ring widths can also be used to determine past spruce beetle outbreaks (Veblen et al. 1991a). 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).

**The white pine weevil**

The white pine weevil is a serious pest of young white spruce, *Picea glauca* (Moench) Voss, and Engelmann spruce, *Picea engelmannii* (Parry) Engelm., throughout interior British Columbia. The common name “interior” spruce, *P. engelmannii* × *P.*
*glauca,* is used in British Columbia and in this thesis to denote spruce growing in the zone of hybridization (Meidinger and Pojar 1991; Coates *et al.* 1994) between Engelmann and white spruce. Sitka spruce, *Picea sitchensis* (Bong.) Carr, is host to the weevil along the Pacific coast but the weevil is absent from the Queen Charlotte Islands (McMullen 1976a; Humble *et al.* 1994).

The white pine weevil is univoltine (Wallace and Sullivan 1985; Alfaro *et al.* 1995). In late April, hibernating adult weevils emerge from the duff and migrate to the host’s leader where feeding and copulation occur. Between May and June, females begin ovipositing underneath the bark of terminal shoots unless feeding or oviposition is deterred by chemicals or by a barrier of constitutive resin ducts in the outer bark (Tomlin and Borden 1994, 1996; Tomlin *et al.* 1996). Within two weeks, the eggs hatch and the larvae burrow downwards side by side in a feeding ring within the phloem tissue. At this point, if a tree is unable to defend itself, through induced resinosis (Alfaro 1995), the larvae eventually kill the terminal leader. There are four to five larval instars which require approximately five to six weeks to complete larval development. In late July, pupae form chip cocoons within the pith of the leader. Adult weevils eclose in mid-to late summer, emerge from the leader, feed on the bark of lateral branches, and then migrate down the stem to seek overwintering sites in the duff. Following a successful attack, lateral branches compete for apical dominance, forming crooks, scars, and forks on the stem. A decrease in wood quality, sawlog volume and a two year reduction in height growth occurs after such attacks (Brace 1971; McMullen 1976a; Alfaro 1989). In many sites along coastal British Columbia, planting of Sitka spruce is not recommended because young spruces are unable to grow into lumber-yielding trees because of repeated weevil
attacks (Alfaro 1982; Hall 1994; Alfaro et al. 1995). Planting of Sitka spruce seedlings has been restricted to areas of low weevil hazard (Ying 1991).

As for all poikilotherms, weevil activity and development are temperature dependent (Wallace and Sullivan 1985). Adult behavior such as flight, feeding, copulation and oviposition occur at bark temperatures between 15 to 30 °C. Temperatures below and above this range result in cessation of these behaviors (Wallace and Sullivan 1985). Development from egg to emergence of adults from the leader requires a minimum temperature of 7.2° C and 785 or 888 degree days in the interior and coast of British Columbia, respectively (McMullen 1976b). Reducing ambient temperatures by providing shade from deciduous overstory trees has been effective in reducing weevil attacks on interior spruce (Taylor and Cozens 1994), Sitka spruce (McLean 1989), and eastern white pine, *Pinus strobus* L. (Stiel and Barry 1985). Degree-day summations have also been used to hazard rate areas in British Columbia for susceptibility to weevil attacks (McMullen 1976a; Spittlehouse et al. 1994).

The white pine weevil 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 > 30 years old, attack intensities rapidly decline and eventually reach zero 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 or by changes in microclimate around the terminal leaders (Alfaro 1994).
McGregor Model Forest

Within the last few years, several Model Forests have been established worldwide (B. MacArthur, pers. comm., McGregor Model Forest Association, Prince George, British Columbia). 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 (Northwood Pulp and Timber Ltd. Tree Farm License 30) (Fig. 1), is an approximately 165,000 ha management unit, located 100 km northeast of Prince George, British Columbia. It is comprised of four biogeoclimatic zones, Interior Cedar-Hemlock (ICH), Engelmann Spruce-Subalpine Fir (ESSF), Alpine-Tundra (AT), and the Sub-Boreal Spruce (SBS) (R. Doratty, pers. comm., Northwood Pulp and Timber Ltd., Prince George, British Columbia). It includes 33,000 ha of immature forests, primarily in the SBS zone, which are at risk to weevil attack (B. MacArthur, pers. comm.).

The SBS zone has a continental climate characterized by long cold winters and relatively warm moist and short summers (Meidinger and Pojar 1991; Coates et al. 1994). Mean annual temperatures range from 1.7-5.0 °C with mean temperatures < 0 °C for four to five months and > 10 °C for two to five months. Mean annual precipitation is 440-900 mm of which 25-50 % falls as snow. Throughout the SBS, interior spruce is the dominant climax tree. In cool wet subzones, subalpine-fir, *Abies lasiocarpa* (Hook.) Nutt., is also a dominant climax species; it gradually out-competes spruce as the stand ages.
Fig. 1. Biogeoclimatic subzones of the McGregor Model Forest (Tree Farm License 30), Prince George, British Columbia. Alpine-Tundra, Engelmann Spruce-Subalpine Fir (ESSF) Wet Cool (wk), Interior Cedar-Hemlock (ICH) Very Wet Cool (vk), Sub-Boreal Spruce (SBS) Moist Cold (mc), SBS Very Wet Cool (vk), SBS Wet Cool (wk) (Meidinger and Pojar 1991). Site locations are marked with an "X". Two sites were located approximately 40 km southwest of the model forest, both within the SBS wk subzone.
Trembling aspen, *Populus tremuloides* Michx., and lodgepole pine, *Pinus contorta* var. *latifolia* Engelm., are seral species in the SBS zone and are abundant in the drier subzones. Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco, is a long lived seral species commonly found in dry, warm subzones, although it occurs sporadically in wet areas.

**OBJECTIVES**

Prior to forest management, stand-replacing fires were the dominant disturbance agent within the SBS zone (Delong and Tanner 1996). These fires eliminate most of the overstory vegetation, exposing the mineral soil which favors interior spruce germination (Coates *et al.* 1994). Patches of young interior spruce then become established and, depending upon the hazard for that stand, can be susceptible to white pine weevil attacks. Twenty percent of the McGregor Model Forest and a large area of British Columbia’s forests are at risk to white pine weevil attacks. Presently, the differences in weevil epidemiology between naturally regenerated and harvested forests is unknown.

My objective was to reconstruct weevil attack history in naturally regenerated stands that occurred after natural wildfires within 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. They will then be able to adjust management objectives to mimic or "improve" on natural processes so that sustainability is assured.
METHODS AND MATERIALS

For each of the wet cool and very wet cool subzones of the SBS zone (SBS vk and SBS wk, respectively) (Meidinger and Pojar 1991), four sites containing spruce as the numerically dominant species were selected (Fig. 1). Two sites, both within the SBS wk subzone, were approximately 40 km southwest of the Model Forest. Trees within each site were even-aged. Fire history was indicated by the presence of charcoal and scarcity of veteran trees. Two fixed-radius circular plots per stand were established ≥ 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 larger plot radius was implemented when tree density was relatively low. Diameter at breast height (dbh-1.3 m) and the crown class (dominant, codominant, intermediate, or suppressed) (Anonymous 1980) were recorded for all conifers ≥ 7.5 cm in dbh. Elevation and aspect of each plot were determined using alimeter 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. Defects were classified as: scar; minor crooks; major crooks; and forks (Fig. 2). 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. Total tree height and height to base of
Fig. 2. Stem defects in the bole of interior spruce associated with past weevil attacks.

Defects were recorded as: scars (injury almost healed); minor crooks (deviation above site of assumed weevil attack ≤ 50 % off vertical axis of stem below attack); major crooks (> 50 % deviation); or forks (two stems occurring above assumed site of weevil attack) (Alfaro 1989).
scar

minor crook

major crook

fork
living crown were recorded. The type and height of all defects were noted, as were those defects associated with old terminal leaders containing pupal chambers or oviposition holes. These defects provide positive evidence of damage caused by weevil attacks (Fig. 3, 4).

Statistical analyses

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 were done to determine differences between the means for some data. For each subzone, the numbers of confirmed weevil attacks occurring at 2 m intervals along the bole were recorded. The frequency distributions 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 the independent and dependent variable respectively. The relationship between numbers of weevil attacks per felled tree and numbers of all defects as determined by ocular assessment before felling was compared by linear regression, pooling all felled trees in both subzones. Similarly, linear regression was also used to examine the relationship between numbers of weevil defects per felled tree and total numbers of all defects per felled tree. As heteroscedasticity occurred among
Fig. 3. Confirmed evidence of weevil damage on spruce stem. The old terminal leader is associated with pupal chambers.
Fig. 4. Confirmed evidence of weevil damage on spruce stem. The old terminal leader is associated with oviposition holes.
the residuals, variables were transformed to $\log_{10}(X+1)$ (Zar 1996).

**RESULTS**

**Stand characteristics**

Stand elevations ranged from 620-760 m in the SBS vk subzone and 470-780 m in the SBS wk (Table 1). Stand densities in the two subzones were comparable (means of 1272 and 1231 stems per ha in the SBS vk and SBS wk, respectively) and the predominant trees were interior spruce (70.1 and 79.4% in the SBS vk and SBS wk, respectively) (Tables 1,2). 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 (Table 2). Twenty six percent of all spruces were dominant and 13 % were suppressed; for subalpine fir the respective percentages were 10 and 34 %. Stands in the SBS vk were 32.5 % shorter than in the SBS wk. However, only a portion of this difference was due to differences in stand age (means of 41.3 and 48.8 years in the SBS vk and SBS wk, respectively), because trees in the SBS vk grew 20 % less rapidly than in the SBS wk (means of 0.32 and 0.40 m of vertical growth per year in the SBS vk and SBS wk, respectively) (Table 3).
Table 1. Characteristics of sampled stands within the SBS biogeoclimatic zone in the McGregor Model Forest. 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.

<table>
<thead>
<tr>
<th>Biogeoclimatic subzone a</th>
<th>Stand no.</th>
<th>Elevation (m)</th>
<th>Aspect</th>
<th>Stand height (m) (X ± SE)</th>
<th>Stand age (yrs)</th>
<th>Number of trees per ha all conifers</th>
<th>Number of trees per ha spruce</th>
</tr>
</thead>
<tbody>
<tr>
<td>SBS vk</td>
<td>1</td>
<td>715</td>
<td>north</td>
<td>12.8 ± 2.8</td>
<td>34</td>
<td>988</td>
<td>688</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>760</td>
<td>south</td>
<td>18.1 ± 3.8</td>
<td>50</td>
<td>1614</td>
<td>1063</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>730</td>
<td>none</td>
<td>13.9 ± 3.4</td>
<td>46</td>
<td>1276</td>
<td>1063</td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>620</td>
<td>none</td>
<td>9.1 ± 2.2</td>
<td>35</td>
<td>1271</td>
<td>791</td>
</tr>
<tr>
<td>SBS wk</td>
<td>5</td>
<td>780</td>
<td>west</td>
<td>22.4 ± 3.9</td>
<td>58</td>
<td>1777</td>
<td>1439</td>
</tr>
<tr>
<td></td>
<td>6</td>
<td>470</td>
<td>none</td>
<td>24.5 ± 2.6</td>
<td>57</td>
<td>971</td>
<td>891</td>
</tr>
<tr>
<td></td>
<td>7</td>
<td>620</td>
<td>west</td>
<td>8.6 ± 1.9</td>
<td>21</td>
<td>811</td>
<td>520</td>
</tr>
<tr>
<td></td>
<td>8</td>
<td>680</td>
<td>north</td>
<td>24.6 ± 4.2</td>
<td>59</td>
<td>1364</td>
<td>1063</td>
</tr>
</tbody>
</table>

aSub-boreal spruce (SBS) very wet cool subzone (vk) and SBS wet cool subzone (wk)
Table 2. Distribution of interior spruce and subalpine fir within crown class in stands sampled within the McGregor Model Forest

<table>
<thead>
<tr>
<th>Biogeoclimatic subzone</th>
<th>Stand no.</th>
<th>Number of interior spruce&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Number of subalpine fir&lt;sup&gt;a&lt;/sup&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>D</td>
<td>CD</td>
</tr>
<tr>
<td>SBS vk</td>
<td>1</td>
<td>9</td>
<td>16</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>21</td>
<td>26</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>28</td>
<td>19</td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>18</td>
<td>15</td>
</tr>
<tr>
<td>SBS wk</td>
<td>1</td>
<td>32</td>
<td>34</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>33</td>
<td>26</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>9</td>
<td>13</td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>21</td>
<td>26</td>
</tr>
</tbody>
</table>

<sup>a</sup> D=dominant; CD=codominant; I=intermediate; S=suppressed
Table 3. Frequency of attack by the white pine weevil on naturally regenerated spruce in two biogeoclimatic subzoens of the McGregor Model Forest.

<table>
<thead>
<tr>
<th>Category of tree</th>
<th>Number of trees examined</th>
<th>Criterion assessed</th>
<th>SBS wk</th>
<th>SBS wk</th>
<th>Statistical evaluation</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>SBS wk</td>
<td>SBS wk</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>standing</td>
<td>306</td>
<td>344</td>
<td>Percent of spruce with defects detected by visual assessment</td>
<td>39.80%</td>
<td>44.40%</td>
</tr>
<tr>
<td></td>
<td>306</td>
<td>344</td>
<td>Numbers of defects detected by visual assessment per spruce tree</td>
<td>$0.56 \pm 0.86$</td>
<td>$0.70 \pm 0.96$</td>
</tr>
<tr>
<td></td>
<td>59</td>
<td>62</td>
<td>Annual spruce height growth (m/yr) (tree height/tree age)</td>
<td>$0.42 \pm 0.05$</td>
<td>$0.33 \pm 0.08$</td>
</tr>
<tr>
<td>felled</td>
<td>16</td>
<td>16</td>
<td>Percent of trees with defects</td>
<td>100.00%</td>
<td>100.00%</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Percent of spruce with defects verified as weevil-caused</td>
<td>56.30%</td>
<td>81.30%</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Percent of all defects verified to be weevil-caused</td>
<td>31.20%</td>
<td>31.80%</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Mean number of defects per spruce tree</td>
<td>$6.0 \pm 1.7$</td>
<td>$6.7 \pm 2.7$</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Mean number of defects per spruce tree verified as weevil-caused</td>
<td>$1.9 \pm 2.0$</td>
<td>$2.1 \pm 1.7$</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Mean height on spruce bole of first weevil attack</td>
<td>$3.30 \pm 1.13$</td>
<td>$5.67 \pm 2.47$</td>
</tr>
</tbody>
</table>
Reconstruction of past weevil attacks

A very important discovery is that large proportions of the naturally-regenerated spruce trees in both subzones contained defects that arose from weevil attacks (Table 3), indicating that a high incidence of weevil infestation is a natural occurrence in the SBS biogeoclimatic subzone.

There was a significant positive linear relationship between numbers of weevil attacks per felled tree and total number of all defects per felled tree (Fig. 5), indicating that almost half of all defects could be attributed to being weevil-caused, even without further verification by tree dissection. There was also a significant positive linear relationship between numbers of weevil-caused defects per felled tree and number of all defects assessed visually before felling (Fig. 6).

Distributions of height of weevil attack on the bole differed significantly between subzones (Fig. 7). 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 SBS vk, the wetter and cooler subzone. No attacks occurred at a height > 16 m. The height of first weevil attack was also significantly lower in the SBS wk subzone than in the SBS vk (Table 3). Both the total number of all defects per felled tree and the number of weevil caused defects per felled tree did not differ significantly between the two subzones (Table 3). The percentage of all defects per felled tree caused by weevils was also similar (approximately one third) for both subzones. However, only 56.3 % of spruce trees
Fig. 5. Relationship between numbers of verified weevil attacks observed on undissected felled interior spruces, and total number of all defects per felled tree. Data pooled for SBS vk and SBS wk biogeoclimatic subzones, and transformed by $\log_{10} (X+1)$ prior to analysis. $r^2=0.43$, $P=0.001$.

$Y=-1.40 + 0.53X$. $n=32$. 
Number of Verified Weevil Attacks per Felled Tree (values transformed by $\log_{10}(x+1)$)

Number of Defects per Felled Tree (values transformed by $\log_{10}(x+1)$)

95% confidence intervals ---
Fig. 6. Relationship between numbers of verified weevil attacks observed on undissected felled interior spruces, and total number of all defects per tree detected visually before felling. Data pooled for SBS vk and SBS wk biogeoclimatic subzones, and transformed by $\log_{10} (X+1)$ prior to analysis.

$r^2=0.36, P=0.001$. $Y=0.46 + 0.76X$. $n=32$. 
95% confidence intervals

Number of all Defects per Tree Detected before Felling (values transformed by $\log_{10}(x+1)$)

Number of Weevil Attacks per Felled Tree Detected after Felling (values transformed by $\log_{10}(x+1)$)
Fig. 7. Distributions of weevil attacks by height on the bole of interior spruce in the SBS vk and SBS wk biogeoclimatic subzones. Distributions significantly different, $\chi^2=14.16$, $P=0.028$. 
Height of Weevil Attacks (m)

Number of Weevil Attacks

- SBS vk
- SBS wk

0-2 2-4 4-6 6-8 8-10 10-12 12-14 14-16
in the SBS wk had verified weevil-caused defects compared to 81.3 % on spruce trees in the SBS vk (Table 3).

There was a marginally significant difference in the frequency of each type of weevil-caused defect between subzones (Fig. 8). Minor crooks were the predominant defect in both subzones. Trees in the SBS vk had almost equal numbers of scars, major crooks, and forks, while those in SBS wk had very few scars or forks.

DISCUSSION

Reconstruction of past weevil attacks

In mature undisturbed Sitka spruce forests along coastal British Columbia, the white pine weevil seems to be a rare species (Alfaro 1994). However, in young naturally regenerated spruce forests in the SBS vk and SBS wk biogeoclimatic subzones of the interior British Columbia weevil damage was extensive on many trees (Table 3). Over 50 % of felled spruce trees in both subzones contained defects caused by the white pine weevil. The positive relationship between verified weevil attacks and all defects (Fig. 5) suggest that dissection of felled trees might have revealed an even higher incidence of attacked trees. Thus these data may be very conservative. Therefore, it appears that the white pine weevil has been a prevalent natural component of these sub-boreal forest ecosystems that predated human intervention. *Pissodes strobi* is probably the most significant biotic factor affecting terminal leader mortality of spruce in the McGregor Model Forest.
Fig. 8. Frequency distributions of type of defect caused by white pine weevil attack in the SBS vk and SBS wk biogeoclimatic subzones. Differences between distributions approaches significance, $\chi^2=6.53$, $P=0.088$. 
Climatic data were used to determine hazard ratings for all the sampled stands. Unshaded leaders and, in some years, shaded leaders in all sampled stands accumulated > 785 degree days (B. Sieben, pers. comm., Faculty of Forestry, University of British Columbia, Vancouver). This is enough heat accumulation to allow for weevil development.

It is apparent that weevils can affect a large proportion of potential timber in a natural forest, but the impact of attack can vary with ecological factors. The number of defects per felled tree and the number of verified weevil-caused defects per felled tree were similar in both subzones even though fewer spruces in the SBS wk contained verified weevil-derived defects than in the SBS vk (Table 3).

Approximately one half of all defects on felled trees were caused by the white pine weevil. This research suggests that systematic pre-harvest surveys for weevil-caused defects in mature trees could be used to hazard rate stands as a basis for weevil management plans that could be incorporated into silvicultural prescriptions. Forests that have a high incidence of weevil-attacked trees may warrant a silvicultural prescription consisting of an integration of the following: use of a hazard rating system; planting of weevil resistant trees; high density planting; and a mixing of spruce with a deciduous overstory (Alfaro et al. 1995).

Currently, other researchers are collecting data regarding the impact of *P. strobi* in reforested plantations. This will allow comparison of weevil attack parameters between managed and unmanaged stands, and will help determine the impact, if any, of forestry practices on the white pine weevil.
The lower height of first weevil attack on spruce boles in the SBS wk than in the SBS vk suggests weevils may initiate attacks on younger or smaller spruce trees in the SBS wk than in the SBS vk. Because wood volume is greatest near the base, the quantity of defect-free timber obtained from stands in the SBS wk may thus be less than from SBS vk. However, this reduction in timber volume and quality may be offset by the apparently greater number of forks per felled tree on spruces growing in the SBS vk (Fig. 8).

As expected (Alfaro and Omule 1990) weevil attacks in relation to height on the bole were normally distributed in both subzones with lower and upper limits beyond which there was no attack (Fig. 7). However, the frequency distributions for attacks in relation to height differed significantly between subzones, with attacks extending higher up the bole in the SBS vk subzone than in the SBS wk subzone. I propose three hypotheses that could explain this difference.

Lack of Overstory Shade in SBS vk Subzone Hypothesis

Insect behavior and development are temperature dependent. Therefore, one would expect attacks to decrease with height as temperatures, especially at night, also decrease with distance from the ground. Because the SBS wk subzone is drier and presumably warmer than the vk (B. Sieben, pers. comm.), one would expect the trend in Fig. 7 to be reversed. One hypothesis for this difference could be attributed to overstory shade. Weevil attacks on interior spruce (Taylor and Cozens 1994; Taylor et al. 1996), Sitka spruce (McLean 1989), and white pine (Stiel and Berry 1985) decreased significantly with overstory and side shading provided by deciduous trees. Shading may decrease weevil attacks by: 1) reducing spruce leader temperatures and prolonging larval development,
thus increasing exposure of larvae to predators, parasitoids and abiotic factors (Wallace and Sullivan 1985); 2) negatively affecting weevil orientation to spruce leader silhouettes (VanderSar and Borden 1977); and 3) reducing spruce leader length and diameter, thereby reducing weevil feeding and oviposition (Alfaro 1994; Taylor and Cozens 1994; Taylor et al. 1996). Paper birch, *Betula papyrifera* Marsh, black cottonwood, *Populus balsamifera trichocarpa*, and trembling aspen were present in three of the four SBS wk sites, but were absent in all SBS vk sites. These trees were either dominant or codominant and their canopies covered some spruce trees, possibly shading them enough to affect adult weevil behavior and larval development. In the early stages of stand development, deciduous canopies would probably not be as extensive, contributing to higher numbers of weevil attacks low on the stem in the warm climate of the SBS wk. The absence of shade-producing hardwoods in the four SBS vk stands, may allow the terminal leader temperatures in the SBS vk to exceed those in the SBS wk and, may explain the large number of weevil attacks high the bole. Moreover, in the SBS vk, the wetter of the two ecosystems, growth rates of some large-growing shrubs (e.g. thimbleberry, *Rubus parivflorus* Nutt.) and herbaceous plants (e.g. lady fern, *Athyrium filix-femina* L. Roth) may be greater than in the SBS wk (Meidinger and Pojar 1991; Coates et al. 1994). Large heights attained by these plants may create sufficient shade to reduce weevil attacks to heights less \( \leq 2 \) m.

**Larger Spruce Leaders in the SBS wk Subzone Hypothesis**

Spruce trees grew significantly faster in the drier SBS wk subzone than in the SBS vk. A faster growth rate implies that the leaders on trees in the SBS wk were also longer
than those in the SBS vk. Reduced leader growth may have negatively affected larval growth, and thus adult size and fat reserves. Small adult weevils may not have the metabolic capacity to disperse to new habitats when the current habitat is degenerating. Slansky and Haack (1986) demonstrated that poor larval food (thin phloem) negatively affected larval growth, and body size and mass of adult *Ips calligraphus* (Germar).

Within in each sex, lipid content, mean flight duration, and mean lifetime flight duration were less in *I. calligraphus* reared on thin than thick phloem logs. In *I. paraconfusus* (Lanier.) (Hagen and Atkins 1975), *Dendroctonus pseudostugae* (Hopk.) (Atkins 1975), and *I. sexdentatus* (Boern.) (Jactel 1993), adults with a high lipid content have a greater flight capacity than those with low lipid content. Female white pine weevils reared on 5 % ground white pine bark diet were heavier than weevils reared on 1 % bark diet (Trudel *et al.* 1994). Bark beetles with a greater lipid content flew for longer periods before they ceased flight and engaged in host selection behaviour (G. Gries, pers. comm., Simon Fraser University, Burnaby, British Columbia). Hypothetically, as stand quality degenerates, adult weevils emerging from large, nutritious leaders in the SBS wk subzone may have sufficient lipid reserves to stimulate dispersal to younger spruce stands, while adults reared on the smaller leaders within the SBS vk subzone may not be capable of dispersal.

Longer Fire Return Interval Within the SBS vk Subzone Hypothesis

Most wildfires in the SBS are stand-replacing fires (Delong and Tanner 1996) which create patches of young even aged stands. If the fire return interval, the average number of years between two successive fire events within a given area, is relatively long as in the SBS vk (B. Hawkes, pers. comm., Pacific Forestry Centre, Victoria, British Columbia)
only a small proportion of the landscape would burn each year and the number of suitable weevil habitats would be low. In the McGregor Model Forest the fire return interval within the SBS vk is estimated to be 500-700 years, considerably longer than previously thought (B. Hawkes, pers. comm.). Approximately 0.14% of this subzone would burn every year as a result of lightning-induced fires. The fire return interval in the SBS wk is unknown, but presumably shorter than in the SBS vk (B. Hawkes, pers. comm.). Therefore many patches of young stands would be created per unit time and would be available as weevil habitats. In areas with longer fire return intervals, the choice that dispersing female weevils have with respect to oviposition site is low and they may accept and remain in aging stands because of the lack of young, more suitable stands to which they could disperse. In support of such an hypothesis, Singer (1983) determined that female *Euphydryas editha* Bdv. would oviposit on previously unacceptable host if females did not encounter or were prevented from laying eggs on preferred hosts.

Fire is not the sole disturbance regime within sub-boreal forests. Spruce beetle, western balsam bark beetle, *Dryocetes confusus* Swaine, and wind throw can remove large overstory trees creating openings of various sizes. For either beetle during sub-outbreak situations, only a few trees die thus releasing the more shade tolerant subalpine-fir trees (Coates *et al.* 1994). Beetle outbreaks kill a greater number of trees and may provide a suitable seedbed for spruce germination or the release of spruce saplings. Interior spruce prefer to germinate upon mineral soil (Coates *et al.* 1994) which may be exposed by windthrown beetle killed trees. Interior spruce can also germinate on coarse woody debris (Coates *et al.* 1994) and seedlings could be released upon beetle outbreaks. Forty years after a spruce beetle outbreak in Colorado, Engelmann spruce and subalpine-fir seedlings
and saplings dominated outbreak areas with respect to stem number and volume (Veblen et al. 1991b). Small spruce seedlings, < 140 cm, and spruce saplings, > 140 cm but < 20 cm in diameter, were abundant in outbreak areas but less common than subalpine-fir (Veblen et al. 1991b). Age of spruce seedlings ranged from 18 to 44 years, while saplings were 72 years old. These spruce trees could be potential weevil hosts, and spruce beetle outbreaks may influence weevil population dynamics, especially where fire return interval is long. It has not yet been determined if white pine weevils will attack spruce trees (i.e. old saplings) that have been suppressed and released. It is also uncertain, but highly likely if these outbreak areas are weevil habitats, that size of a spruce beetle outbreak will affect suitability of host trees to weevils.

Development and implementation of weevil-resistant trees is considered to be a critical component of integrated pest management for P. strobi (Alfaro et al. 1995). For Sitka spruce, the most prevalent resistance is found in areas of high hazard for the weevil, presumably because the weevil is a driving force in the evolution of resistance (Ying 1991). In the northern interior, parents from the SBS produce the most resistant progeny and parents from the ESSF the least resistant (Alfaro et al. 1996). Within the SBS, subzones that have short fire cycles may be the best locations to find weevil resistant genotypes.

Hypothetical differences in ecology of P. strobi between Sitka spruce and interior spruce stands

Within British Columbia, Engelmann and white spruce inhabit different ecosystems than Sitka spruce. Speciation of these trees is thought to have occurred after the genus
was established in North America (Harris 1978). I hypothesize that the weevil-host interaction along the Pacific coast may have followed a different coevolutionary pathway than in the interior of British Columbia.

I believe one reason for this difference is due to the frequency and magnitude of natural disturbances that have occurred in each area. Fire plays a minor role in shaping ecosystems within the Coastal Western Hemlock biogeoclimatic zone. Small disturbances created by fallen trees (gaps) dominate the landscape whereas large stand-replacing disturbances are rare (Lertzman and Krebs 1991; Anonymous 1995b; Lertzman et al. 1995). Most gaps in Sitka spruce-western hemlock forests are usually < 1000 m² (Taylor 1990) creating a matrix of regenerating and mature trees. The amount of sunlight reaching the lower canopy would be reduced within these gaps and shading could reduce leader size, temperature, and silhouette. Therefore, many gaps would be unsuitable weevil habitats. Within these gaps, regenerating spruce would be competing for the limited amount of light and may allocate more energy reserves towards vertical growth.

Resin is the main defensive mechanism against weevils (Alfaro 1995; Tomlin and Borden 1994; Tomlin et al. 1996) and it may be metabolically costly to manufacture (Gershenzon 1994). Employing costly weevil defenses within gaps may limit vertical growth of spruce and these trees may be outcompeted by it's neighbors. Therefore, selection pressure for Sitka spruce to evolve costly weevil defense mechanisms may be quite low because many spruce are growing in areas unsuitable for weevils.

In contrast with coastal British Columbia, larger stand-replacing disturbances are more common in the interior and much larger, with some up to 34,000 ha (B. Hawkes, pers. comm.; Delong and Tanner 1995). These naturally regenerating stands would be
favorable weevil habitats because they would be young and even-aged with most spruce leaders exposed to sunlight. In these open stands, light may not be as limiting as within the gaps of Sitka spruce forests and the regenerating spruce could afford to allocate more energy reserves towards weevil defense. Within interior ecosystems, natural selection may favour spruce trees that evolve defense mechanisms to combat continual weevil attacks.

This hypothesis could be a factor in explaining why some coastal plantations of Sitka spruce have been devastated by weevil attacks, while interior spruce plantations have not (Alfaro 1982; Taylor et al. 1991; Hall 1994; Alfaro et al. 1995). It may also provide an explanation why hybrid white-Sitka spruce tended have fewer weevil attacks (Ying 1991) and have more outer resin ducts than Sitka spruce (Tomlin and Borden 1994) within Sitka spruce provenance trials.
LITERATURE CITED


Ministry of Forests, Victoria, B.C.


