

**IMPACT OF THE WESTERN BALSAM BARK BEETLE,
DRYOCOETES CONFUSUS,
AT THE SICAMOUS CREEK RESEARCH SITE, AND THE
POTENTIAL FOR SEMIOCHEMICAL-BASED MANAGEMENT
IN ALTERNATIVE SILVICULTURE SYSTEMS**

by

Leroy Harder

B.Sc. Biology, University of British Columbia, 1993

**A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF
THE REQUIREMENTS FOR THE DEGREE OF
MASTER OF PEST MANAGEMENT
in the Department
of
Biological Sciences**

**© Leroy Harder 1998
SIMON FRASER UNIVERSITY
December 1998**

All rights reserved. This work may not be reproduced in whole or in part, by photocopy or other means, without permission of the author.



National Library
of Canada

Acquisitions and
Bibliographic Services

395 Wellington Street
Ottawa ON K1A 0N4
Canada

Bibliothèque nationale
du Canada

Acquisitions et
services bibliographiques

395, rue Wellington
Ottawa ON K1A 0N4
Canada

Your file *Votre référence*

Our file *Notre référence*

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.

0-612-37542-0

Canada

Abstract

The western balsam bark beetle, *Dryocoetes confusus* Swaine, was the primary mortality agent for most of the standing dead subalpine fir, *Abies lasiocarpa* (Hook.) Nutt., at the Sicamous Creek Silvicultural Systems Project in the southern interior of British Columbia. Observation of felled, dead *A. lasiocarpa* showed that 100% of red trees, 97% of grey trees and 76% of snags had been infested by *D. confusus*. Frequency distributions based on the diameter of red, grey and snag trees, had disproportionately greater number of trees > 20 cm and fewer trees < 20 cm compared to unattacked trees. Also, *D. confusus* inhabited sections of standing boles > 22.5 cm in diameter, with successful brood development extending on average from 2–10 m above ground. Twenty-five to 31 % of standing *A. lasiocarpa* basal area consisted of dead trees in three areas surveyed. Aerial photographic interpretation indicated a 39% reduction of red trees in undisturbed areas from 1993 to 1995. Harvesting by single tree selection and small patch cuts (0.1 ha) intensified the reduction. Grid baiting of live subalpine firs with (±) – exo – brevicomin concentrated 83% and 79% of total mass attack within 10 m of bait centres in single- and paired-tree trials, respectively, indicating that baiting would be effective in concentrating beetle populations to be removed at harvest in silvicultural systems that offer alternatives to large-scale clearcutting. Foliage of baited mass attacked trees began turning red the summer following attack, while lightly attacked trees stayed green. Some lightly mass attacked trees may require two years before colour change is apparent. In late summer, about two months after attack, naturally attacked trees had more advanced brood development and harboured more associated insects than baited trees. Baited trees had a higher density of egg galleries, longer individual egg gallery lengths, and lower gallery system density than naturally attacked trees, but on average, less of the bole was utilized. Trees with advanced brood development had more of the bole occupied, and had a higher density of egg galleries than those with less advanced brood development. Areas of the bole with conspicuous resin flow had many failed gallery systems.

Acknowledgements

This research was supported financially by; the British Columbia Ministry of Forests, through the Science Council of B.C. and Forest Renewal B.C.; the Natural Sciences and Engineering Research Council; Ainsworth Lumber Co. Ltd.; B.C. Hydro and Power Authority; Bugbusters Pest Management Inc.; Canadian Forest Products Ltd.; Crestbrook Forest Industries Ltd.; Finlay Forest Industries Inc.; Gorman Bros. Ltd.; International Forest Products Ltd.; Lignum Ltd.; Manning Diversified Forest Products Ltd.; MB Research; Northwood Pulp and Timber Ltd; Pacific Forest Products Ltd.; Phero Tech Inc.; Riverside Forest Products Ltd.; Slocan Forest Products Ltd.; TimberWest Ltd.; Tolko Industries Ltd.; Weldwood of Canada Ltd.; West Fraser Mills Ltd.; Western Forest Products Ltd.; and Weyerhaeuser Canada Ltd.. I especially thank Dr. L.E. Maclauchlan who gave this research opportunity to me, provided advice and support during experimental design, data collection and analysis, and allowed me some freedom to satisfy my curiosity. I also thank: Kamloops Region Research Branch for their assistance, in particular the wildlife research group, who helped me at the SCSSP research area; Dr. J. Borden who gave invaluable advice throughout the project, in particular during thesis preparation; SFU Biological Sciences support staff for their many acts of kindness; and finally, my partner, Constance Cirkony, for her help and support throughout the entire process.

Table of Contents

	Page
Examining Committee Approval	ii
Abstract	iii
Acknowledgements	iv
Table of Contents	v
List of Tables	vi
List of Figures	vii
1.0 INTRODUCTION	1
1.1 Silvical Characteristics of Subalpine Fir	1
1.2 The Western Balsam Bark Beetle	3
1.3 Semiochemical-based Management	4
1.4 The Sicamous Creek Silvicultural Systems Project (SCSSP)	5
1.5 Objectives	6
2.0 MATERIALS AND METHODS	6
2.1 Past Infestation Characteristics and Impact	6
2.2 Pheromone Baiting Experiment	7
3.0 RESULTS	13
3.1 Past Infestation Characteristics and Impact	13
3.2 Pheromone Baiting Experiment	22
4.0 DISCUSSION	38
4.1 Past Infestation Characteristics and Impact	38
4.2 Pheromone Baiting Experiment	40
5.0 LITERATURE CITED	44

List of Tables

	Page
Table 1. Characteristics developed by Stock (1991) used to assign subalpine firs attacked by <i>D. confusus</i> to five attack classes.	10
Table 2. Foliage colour classes used to classify changes in subalpine fir trees 1 year after <i>D. confusus</i> mass attack.	12
Table 3. Numbers of red <i>A. lasiocarpa</i> in undisturbed and silviculturally-treated areas before and after treatment at the SCSSP site as seen in three consecutive years of aerial photographs.	14
Table 4. Evidence of past attack by <i>D. confusus</i> in red, grey and snag <i>A. lasiocarpa</i> .	19
Table 5. Comparison of numbers and ratios of grey, red and newly mass attacked <i>A. lasiocarpa</i> in pheromone baited and control areas.	23
Table 6. Occurrence of resin flow, <i>D. confusus</i> in various life stages and associated bark beetles in felled baited and unbaited mass attacked <i>A. lasiocarpa</i> .	31

List of Figures

	Page
Figure 1. Characteristic zones of occupation on <i>A. lasiocarpa</i> boles for resin flow, <i>D. confusus</i> galleries and exit holes as seen in felled red and grey trees. Average values for lower and upper limits are measured from the ground up.	8
Figure 2. Percentage of <i>A. lasiocarpa</i> basal area made up of unattacked, red, grey and snag trees in the combined area encompassed by the three pheromone bait treatments.	15
Figure 3. Frequency distributions of dbh (diameter at 1.3 m) of unattacked, red, grey and snag <i>A. lasiocarpa</i> in the three pheromone treatment areas. Chi square analyses all compare a given distribution with that of unattacked <i>A. lasiocarpa</i> .	17
Figure 4. Frequency distributions of the heights and diameters of lower and upper endpoints on the bole for <i>D. confusus</i> galleries, exit holes and <i>A. lasiocarpa</i> resin flow.	20
Figure 5. Percentage of attacked and mass attacked <i>A. lasiocarpa</i> baited singly or in pairs. The relative number of unattacked, attacked and mass attacked bait trees was significantly different (chi square=12.016, df=2, $P < 0.002$).	24
Figure 6. Distribution by percentage of <i>D. confusus</i> attacked and mass attacked trees around single-tree and two-tree bait centres (baited trees included). Solid bars indicate percentage of attack contained within a distance interval from the bait centre. Clear bars indicate cumulative attack as a function of distance from the bait centre. Distance labels on the X-axis are upper limits for the distance intervals (i.e. 2 refers to points \geq to 1 and $<$ 2 m).	26
Figure 7. Relationships between stage of brood development in <i>A. lasiocarpa</i> and egg gallery length, metres of bole occupation, egg gallery length/m ² , number of egg galleries/m ² and the number of gallery systems/m ² . Bars within a sub-graph with the same letter superscript are not significantly different, Bonferroni multiple comparison, $P < 0.05$. Bars marked by an asterisk are excluded from the multiple comparison because of low n.	28
Figure 8 The effect of baiting on <i>D. confusus</i> egg gallery length, metres of bole occupation, egg gallery length/m ² , number of egg galleries/m ² and the number of gallery systems/m ² in <i>A. lasiocarpa</i> .	32
Figure 9. The effect of resin flow in <i>A. lasiocarpa</i> on egg gallery length metres of bole occupation, egg gallery length/m ² , number of egg galleries/m ² and the number of gallery systems/m ² .	34
Figure 10. Percentage of single <i>A. lasiocarpa</i> trees baited in 1995 in different colour classes in June and August 1996.	36

1.0 INTRODUCTION

1.1 Silvical Characteristics of Subalpine fir

Subalpine fir, *Abies lasiocarpa* (Hook.) Nutt., is found in areas of heavy snowfall, high moisture, long winters and cold temperatures in western North America (Coupé et al. 1991). Typically, stands leading in *A. lasiocarpa* may experience frost any time of the year (Farnden 1994). At high elevations near the tree line, in areas of high moisture, it usually is the dominant species mixed with Engelmann spruce, *Picea engelmannii* Parry ex Engelm., white spruce, *Picea glauca* (Moench) Voss, or their hybrids (Coupé et al. 1991). In British Columbia (B.C.), it grows primarily in the Engelmann Spruce-Subalpine fir (ESSF) biogeoclimatic zone (Meidinger et al. 1991). As one moves north, the ESSF is found in progressively lower elevation sites with tree lines extending to 3650 m in Colorado, New Mexico and Arizona (Alexander 1987) but only to 950 m in northern B.C. (Yole et al. 1989). At the southern end of its range, subalpine fir is restricted to small patches high in the mountains, while in the northern part of its range, large contiguous blocks occur in which subalpine fir is the predominant species.

In B.C., subalpine fir comprises 12% of total timber volume (B.C. Ministry of Forests 1993), and has usually been harvested in conjunction with higher valued spruce. As low elevation stands are depleted in B.C., the amount of subalpine fir harvested in relation to other wood types is increasing. In the fiscal year 1995-1996, 14% of log volume production in the B.C. interior was made up of *A. lasiocarpa* compared to 8.39% in 1990-1991 (B.C. Ministry of Forests 1992, 1997). It is increasingly recognized that effective management strategies must be developed to maintain high elevation forest productivity.

Not much is known about *A. lasiocarpa* regeneration in harvested areas, but it is often unsuccessful (Butt 1990). Regeneration in the ESSF is narrowly constrained by moisture, snowpack, soil and air temperature regimes that restrict successful seed germination and cause heavy mortality of both planted and naturally grown seedlings (Farnden 1994). Risk of seedling mortality in logged areas may be influenced by the type of silviculture system used. Delays in regeneration of 30 to 50 years after fire have also been recorded (Jul 1983, Little et al. 1994), indicating that regeneration may depend on occasional stochastic events that allow seedling germination and growth past

vulnerable sizes. It is likely that a range of site-specific silvicultural prescriptions will be required to increase the probability of successful regeneration.

Other resource use concerns include the impact of clearcutting on water, visual quality and wildlife (Vyse 1997). Because of the sensitive nature of high elevation sites, a variety of alternative harvesting regimes have been suggested: in particular, patch and partial cutting in various scales. Increased commercial use of ESSF forest types has sparked increased interest in the abiotic and biotic disturbance factors that reduce living stand volume. Subalpine forests are shaped by the types of disturbances they experience. Fire is a stand replacing agent (Baker and Veblen 1990), that results in relatively even aged stands. Subalpine fir is fire intolerant, with trees dying from minor exposure (Fischer and Brindley 1987). However, due to high levels of moisture in the ESSF zone, fire return can be as long as 400 years (Baker and Veblen 1990), although in the Canadian Rockies, fire return can be as short as 60 years (Johnson et al. 1990). After fire, *A. lasiocarpa* will sometimes regenerate immediately. Other times it may replace seral species such as pine as the stand ages (Veblen et al. 1989, Kneeshaw and Burton' 1997). Generally, as a subalpine forest stand ages, small scale disturbance agents such as root disease, windthrow and bark beetles alter them into uneven-aged, multi-layered stands with dominant and suppressed components (Kneeshaw and Burton 1997). When dominant trees are removed, surrounding understorey trees are released (Veblen et al. 1991). A suppressed understorey tree may live for a long time before being released and becoming a dominant (Parrish 1997). Because of this, size is not a good indicator of age.

Root, butt and heart rots can kill *A. lasiocarpa*. Species of root rots that kill *A. lasiocarpa* include *Inonotus tomentosus* (Fr.:Fr.) S. Teng, *Armillaria ostoyae* (Romagnesi) Herink, *Fomitopsis pinicola* (Sw.:Fr.) D. Karst and unknown root diebacks (Pathocon Consulting 1987) but it is not clear to what degree they contribute to mortality. *Phellinus pini* (Thore:Fr.) Ames, is a common decay organism. Root rot organisms are ubiquitous in most stands of trees (Morrison et al. 1991). Rodents have been shown to strip large portions of the root collar on some trees (Merler 1997), but their overall impact is not known. While defoliation of subalpine fir by 2 year budworm, *Choristoneura biennis* Free., has been often reported (Wood and Van Sickle 1994), wide scale associated mortality has not. In the United States, mortality of subalpine fir has been caused by the balsam woolly adelgid (Gibson et al. 1997).

1.2 The Western Balsam Bark Beetle

The western balsam bark beetle, *Dryocoetes confusus* (Swaine), together with its pathogenic fungal associate, *Ceratocytis dryocoetidis*, Kendrick and Molnar, kills apparently healthy and root rot infected subalpine fir (Molnar 1965, Pathocon Consulting 1987). About a year following *D. confusus* colonization, a tree's foliage will turn a bright red-orange that is readily recognized from the air. These trees are called "reds" or "red tops" and are often counted in estimates of mortality due to *D. confusus* during aerial surveys (Unger 1992). Reds can retain their foliage for up to five years (Wood and Van Sickle 1989), after which the needles fade and fall off, leaving the fine branches. These trees are called "greys". Eventually the bark cracks and begins to slough off; the fine branches fall off and the tree becomes a "snag" (Stock 1991). The time frames for these degenerative processes are not well known, but the different tree classes have been used to estimate past mortality due to *D. confusus*.

Past estimates shows substantial mortality rates of *A. lasiocarpa* due to *D. confusus* in B.C.. For example, surveys in the Bulkley Timber Supply Area (TSA) in stands where *A. lasiocarpa* was a leading species, standing dead trees made up 38% of the total stand volume, of which 40% consisted of red and grey trees killed by *D. confusus* within an estimated time frame of six years (Stock 1991). Estimated average annual loss was 4.2 m³/ha per year in older stand age classes leading in *A. lasiocarpa*. Similar losses have been documented by Garbutt and Stewart (1991) and by Unger and Stewart (1986). Pathocon Consulting (1987) showed that *D. confusus* was associated with 55.8% of declining or recently dead *A. lasiocarpa* in the Bulkley and Morice TSAs. It is probable that *D. confusus* may act as the final causal agent of mortality in many dying trees. However, it is not known if the relationship between *D. confusus* and other mortality agents is suppressive, synergistic or additive.

High mortality in *A. lasiocarpa* is seen wherever losses are estimated over a large area. As the use of aerial surveys in B.C. increased, so did estimates of loss (Unger 1992, Wood and Van Sickle 1993). Although it is difficult to interpret survey numbers without detailed information about the methodology used and areas surveyed, it is apparent that many areas have a long sustained history of mortality due to *D. confusus* (Unger 1992). Understanding mortality patterns with time is necessary to make appropriate management decisions about *D. confusus* infestations.

Flight by *D. confusus* occurs in late spring and summer when temperatures are $\geq 15^{\circ}\text{C}$ (Stock 1981). Stock (1993) described two flight periods: a main flight that occurs

mid to late June and a smaller one in mid August. Gibson et al. (1997) found one or two flight periods, and one with moderate numbers of *D. confusus* flying all summer. Males make up most of the early flight, while females fly later, although Stock (1981) found a preponderance of females in early emergence from logs brought in from the field.

Males colonize suitable hosts first, making nuptial chambers in the phloem tissue. They mate with three to four females (Bright 1976) that burrow egg galleries radiating away from the nuptial chamber laying eggs in niches in the gallery walls as they go (Stock 1981). These adults may overwinter in the tree and produce a second brood in the same tree the following year. Mathers (1931) reported continued excavation in the same egg gallery over two years. Occasionally, after the second brood is produced, these adults leave their hosts to form a second minor late summer flight and attempt to establish a third brood (Stock 1981). Eggs hatch the same summer they are laid. Brood beetles spend their first winter as larvae and the second as callow adults that emerge in the following spring.

Living *A. lasiocarpa* colonized by *D. confusus* are killed by a beetle-vectored fungus complex that includes *C. dryocoetidis* and other *Ceratocystis spp.* that are introduced with burrowing activity (Kendrick and Molnar 1965, Molnar 1965). Subalpine fir may have two general defense reactions to *D. confusus* attack. In *Abies* species, the flow of constitutive resin into galleries is weak because resin blisters under the bark are rarely broken and resin canals are poorly developed (Raffa 1991). This constitutive mechanism is much weaker than that of other conifer genera that have large resin ducts throughout the bark and sapwood (Berryman 1972, Christiansen et al. 1987). One or two months after gallery systems are successfully initiated (J.H. Borden, pers. comm.), an induced reaction takes place with phloem parenchyma cells around a wound producing secondary resin, walling off bark beetle vectored pathogenic fungi from the surrounding tissues (Berryman 1969). Fungi contained in this way can break out even after a number of years (Christiansen et al. 1987). A hypersensitive response around a wound is characterized by dark staining of the phloem and sapwood. Despite the hypersensitive reactions, the bark beetle – vectored fungi can usually kill trees given enough inoculation points (Christiansen 1985).

1.3 Semiochemical-Based Management

Stock and Borden (1983) found evidence for the existence of a male produced aggregation pheromone in *D. confusus*. Subsequent work by Borden et al. (1987) and

Schurig et al. (1983), identified the major component as (+)-*exo*-brevicomin, while Camacho et al. (1993) found the complete pheromone to be a 9 to 1 blend of (+)-*exo*-brevicomin and (+)-*endo*-brevicomin. Stock et al. (1995) found the concentration of attack increased with the number of trees baited at a point source, and recommended a protocol in which two trees in a centre are baited with (\pm)-*exo*-brevicomin. Stock et al. (1994) found that grid baiting with 50 m between the baits using this protocol was sufficient to draw 90% of mass attack within 10 m of the baited trees.

In B.C., baiting trees with attractive semiochemicals is commonly used to induce attack by bark beetles so as to contain and concentrate populations in areas destined for logging (Borden 1990). Current operational pheromone baiting programs exist for a number of species (Borden 1995). In addition to restricting the area covered by bark beetle infestations, presumably the removal of bark beetles by harvesting baited stands either reduces populations below an outbreak threshold or prevents them from increasing to outbreak numbers.

1.4 The Sícamóus Creek Silvicultural Systems Project (SCSSP)

The SCSSP was set up by the B.C. Ministry of Forests to help address management concerns in the ESSF. The research site is located primarily in the wet cold subzone (ESSFwc2) that makes up the largest of seven ESSF subzones (Vyse 1997). The stand was classified as B(S) 841M6 with some SB841G6 (B.C. Min. For. Cover Map Legend). Five different cutting regimes were imposed on the site:

1. control - no removal;
2. single-tree selection, 33% of the volume removed over a 30 ha area on the first pass by cutting every fifth tree using faller's choice;
3. 0.1 ha, 33% of the volume removed over a 30 ha area by patch cuts approximately 33 by 33 m;
4. 1.0 ha, 33% of the volume removed over a 30 ha area by patch cuts approximately 100 by 100 m;
5. 10 ha, 33% of the volume removed over a 30 ha area by one 10 ha cut.

Imposed on these treatments are various site preparation treatments (Vyse 1997). Within this area, research projects have been set up to follow the short and long term effects of the different treatments on such diverse subjects as environmental

parameters, stand regeneration and populations of vertebrates, arthropods, ectomycorrhizal fungi and lichens.

1.5 Objectives

My objectives were:

1. to assess past infestation characteristics and impact of *D. confusus* at the SCSSP research site; and,
2. to test the efficacy of pheromone-based tree baiting for *D. confusus* as a pre-harvest tactic in variable retention silviculture systems.

2.0 MATERIALS AND METHODS

2.1 Past Infestation Characteristics and Impact

True colour aerial photographs at a scale of 1:5000 of the SCSSP research site for the years 1993, 1994 and 1995, were used to map the location of red trees over a 200 ha area that encompassed a large portion of the site not disturbed by silvicultural treatments. For each year, groups of red trees adjacent to each other (clusters) were identified on the photographs. The photographs were overlaid with transparencies and the locations of clusters of red trees were traced onto the transparencies with the aid of a stereoscope. The clusters were numbered and the number of red trees in each was counted. For each photograph, the locations of four to six permanent tie points such as unique trees and dead logs in swamps, were traced. The tie points were mapped on graph paper creating a network of known points thereby linking each photograph with the next. Using tie points, roads, harvested areas and swamps were drawn on the graph paper. Tie points and other features closest to a given cluster were used to align the transparencies on the graph paper to minimize photographic distortion. The coordinates of the geometric centre of each cluster of red trees were then recorded. Each clump was also coded in relation to silvicultural treatments that were subsequently done on the site as follows:

1. in undisturbed areas;
2. within 10 ha clearcuts;
3. within 1.0 ha patch cuts;
4. in leave areas between 1 ha patch cuts;

5. in 0.1 ha patch cut and leave areas combined; and
6. in area harvested by single tree selection.

A number of dead subalpine firs had been felled in accessible areas of the SCSSP. I examined 15 red trees, 31 grey trees, and 90 older snags. For red and grey trees, upper and lower zonal endpoints on the bole (Figure 1) were determined for *D. confusus* galleries, *D. confusus* exit holes and resinosis typical for *D. confusus* attack. The diameter and distance from the ground was measured for upper and lower zonal endpoints. The presence of live adults, pupae and larvae were also noted. Snags had usually undergone considerable degradation. In this case the presence or absence of *D. confusus* galleries, exit holes and resinosis was recorded. These data were gathered in early spring allowing observation of young adults before emergence.

2.2 Pheromone Baiting Experiment

In June 1995, Flexlure baits (Phero Tech Inc., Delta, B.C.) releasing the aggregation pheromone (\pm)-exo-brevicommin at 0.3 mg per 24 h (determined at 22°C by Phero Tech Inc., Delta, B.C.) were affixed to trees placed in a grid pattern in two of three areas. In a single-tree bait treatment, bait lines were 50 m apart, with baited trees at 25 m intervals. Baits were attached as high as possible on the north side of the nearest large *A. lasiocarpa*. In a two-tree bait treatment, bait lines were placed 33 m apart, with baits affixed every 66 m along the bait line, on each of two large *A. lasiocarpa*. Baits on adjacent lines offset each other by 33 m. In total, 86 single and 82 paired trees were baited. No baits were used in the control area.

In September 1995, a complete survey of the three areas was conducted, resulting in a stem map of baited, attacked, mass attacked, red and grey trees identified according to Stock's (1991) criteria (Table 1). The diameter at breast height (dbh = 1.3 m) of baited, attacked, mass attacked and red trees was taken and the number of snags tallied. In each treatment, 10 randomly placed 15 m radius circular plots were established where the dbh, species and tree class was recorded for each tree over 9 cm dbh.

The proportion of new mass attacked to red trees in the treatment areas were compared to the control area using a chi square test. A computer program was written to calculate the distance between attacked trees and bait centres for both single-tree and two-tree treatments, the bait centre in the latter case being the midpoint between

Figure 1. Characteristic zones of occupation on *A. lasiocarpa* boles for resin flow, *D. confusus* galleries and exit holes as seen in felled red and grey trees. Average values for lower and upper limits are measured from the ground up.

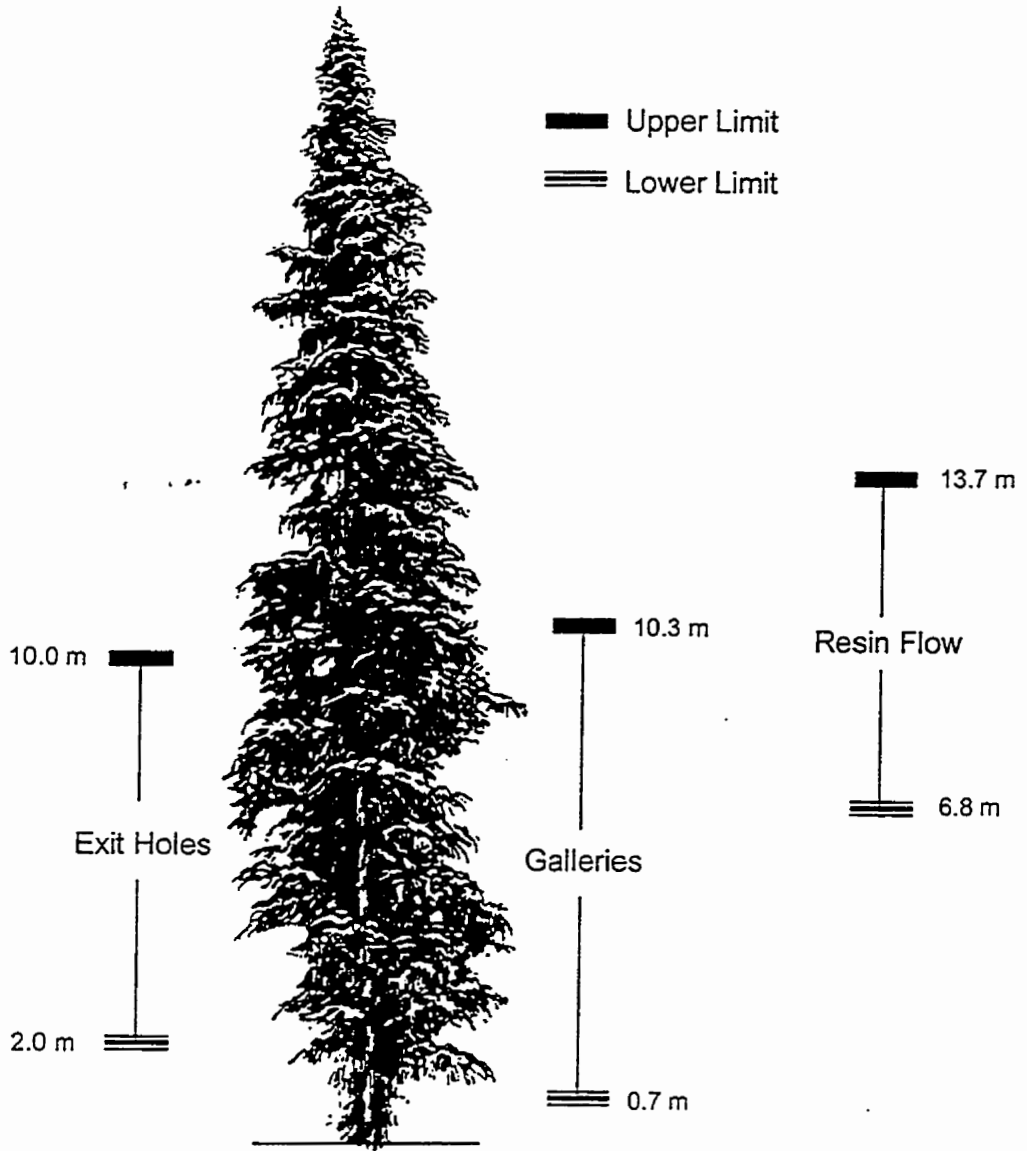


Table 1. Characteristics developed by Stock (1991) used to assign subalpine firs attacked by *D. confusus* to five attack classes.

Tree Class	Description
attacked trees	streams of resin on bole (presumably unsuccessfully attacked)
mass attacked	frass and possibly resin on bole (presumably successful intense colonization of tree)
red	red foliage present (represents old attack from which new mature beetles emerge)
grey	needles mostly gone but fine twigs present, bark generally intact (no beetles remaining in bark)
snag	a long dead tree minimum height and dbh 2 m and 12 cm, respectively, with bark loose or absent and fine twigs gone

the two baited trees. From this, incremental and cumulative percentage of attack, mass attack and combined attack totals around bait trees was calculated in 1.0 m intervals as a function of distance (up to 10 m for single-tree and 16 m for two-tree centres).

The survey data were also used to generate a dbh frequency distribution from the red trees in each area, and the fixed radius plots were used to generate dbh distributions for unattacked and grey trees. Tally data from the surveys, together with dbh data from the fixed radius plots were used to calculate the percentage of total *A. lasiocarpa* basal area for each tree class in each treatment area. Chi square tests ($\alpha=0.05$) were used to compare the red and grey and snag dbh frequency distributions to those of unattacked trees, and to compare the numbers of red and grey trees in each area.

Ten baited mass attacked trees in the single-tree bait treatment area and 13 green attack trees outside the baited area were felled in late August 1996, the same summer they were attacked. Starting from the stump, gallery systems were dissected within 10×30 cm bark sections every 1.5 m along the bole. For each sample, the number of gallery systems and the occurrence of associated species was recorded. Within each gallery system, the presence or absence of *D. confusus* life stages and resin was recorded, and the length of each egg gallery measured. The upper bole of the tree was examined for secondary scolytids. Zonal end points for conspicuous resin flow were also noted for each tree. These data were gathered from late August to mid September.

Twenty mass attacked baited and spillover trees from the two-tree pheromone bait area were felled in early July 1996, about a year after attack. The presence of any live adults, pupae, larvae and secondary scolytids was recorded, and foliage colour change was rated using a six point system (Table 2) for each tree. The number of trees containing various life stages was tabulated for trees that retained green foliage and those that obviously turned colour.

Baited trees from the single-tree treatment area were examined on 19 June and in 9 August 1996, about a year following attack. Frass production and foliage colour was rated using the six point rating system in Table 2.

Analysis: The numbers of failed gallery systems without egg galleries, in zones of the tree with or without exterior resin flow were compared using a chi square test. Means for length of bole occupied, the numbers of egg galleries per m², the numbers of gallery

Table 2. Foliage colour classes used to classify changes in subalpine fir trees 1 year after *D. confusus* mass attack.

Colour Classes	Description
0	No colour changes noticeable
1	Red flashing on some tree limbs, usually on the lower bole of the tree
2	Foliage on many tree limbs starting to turn red, usually on the lower bole of the tree
3	Half the foliage turned red
4	Most of the foliage turned red, some faded green left
5	Foliage completely red

systems per m², the length of egg galleries per m² and individual egg gallery length were compared by ANOVA using bait status, resin flow, and brood development as factors. Differences between the five levels of brood development were compared using a Bonferroni multiple comparison.

3.0 RESULTS

3.1 Past Infestation Characteristics and Impact

The overall number of red trees progressively decreased from 1993 to 1995 in both undisturbed and disturbed areas (Table 3). The number of red trees in the 10 ha clearcut was of course reduced to zero. Leave areas between the 1.0 ha patch cuts did not have reductions as large as in the combined 0.1 ha patch and leave area or the single-tree selection area indicating a relative lack of removal of dead trees from this area.

A large percentage of *A. lasiocarpa* basal area was composed of dead trees (Figure 2), totalling 31%, 28% and 25% for the single-tree bait treatment, two-tree bait treatment and the control area respectively. The dbh frequency distribution of red, grey and snag trees were significantly different from those of unattacked trees (Figure 3). Red and grey trees had dbh distributions that peaked between 19 and 49 cm range, while those of snags peaked between 9 and 39 cm approaching the distribution of unattacked trees.

All of 15 felled red trees and 30 of 31 grey trees showed evidence of past attack by *D. confusus* (Table 4). Twelve of 15 red trees had exit holes while only 4 of 15 had juvenile life stages and two had adults. In snags there was less evidence of attack possibly because of deterioration or loss of bark.

Figure 1 is a schematic representation of the average range of resinosis, as well as occupation of *D. confusus* galleries and exit holes on the boles of red and grey trees. From the ground up, *D. confusus* galleries occurred first followed by *D. confusus* exit holes (Figures 1,4) that faded out before gallery systems. The lower extent of resin flow started before the upper limit of exit holes ended, and continued past both exit holes and galleries. The zone of successful *D. confusus* development, as seen by exit holes, occurred along the lower part of the bole. In 32 trees that showed resinosis, resin flow usually overlapped the exit hole zone and in 28 trees, extended up past the exit holes a few metres. Separation between the end of *D. confusus* exit holes and the start of the resin zone was seen in 6 trees, while resin flow was contained within the zone of *D.*

Table 3. Numbers of red *A. lasiocarpa* in undisturbed and silviculturally-treated areas before and after treatment at the SCSSP site as seen in three consecutive years of aerial photographs.

Location of red trees	Size of sample area (ha)	Number of red trees in 1993 prior to treatment	Number of red trees after treatment	
			1994 roaded	1995 harvested
In undisturbed control area	108	801	665	485
Within 10 ha clearcut	10	53	79	0
Within 1.0 ha patch cuts	9	91	87	0
In leave area between 1.0 ha patch cuts	30	258	235	135
In 0.1 ha patch cut and leave areas combined	18	99	70	23
In single-tree selection harvest area	21	85	76	15

Figure 2. Percentage of *A. lasiocarpa* basal area made up of unattacked, red, grey and snag trees in the combined area encompassed by the three pheromone bait treatments.

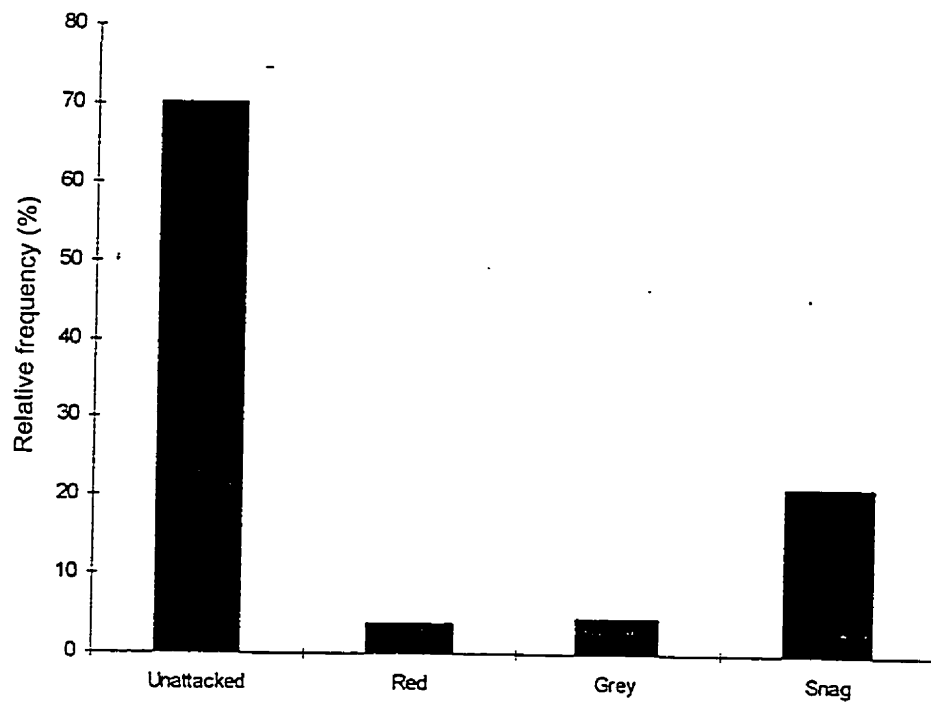


Figure 3. Frequency distributions of dbh (diameter at 1.3 m) of unattacked, red, grey and snag *A. lasiocarpa* in the three pheromone treatment areas. Chi square analyses all compare a given distribution with that of unattacked *A. lasiocarpa*.

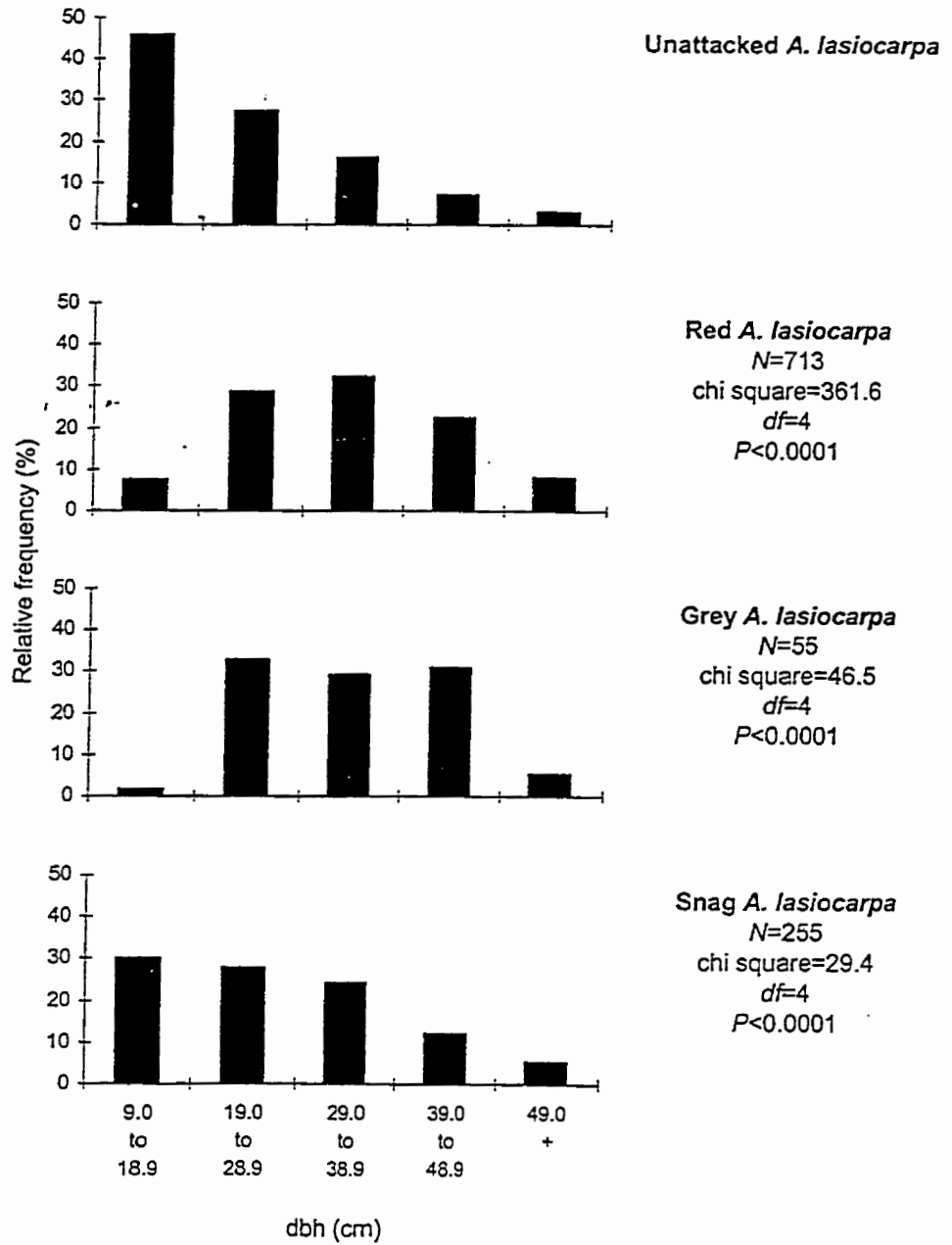
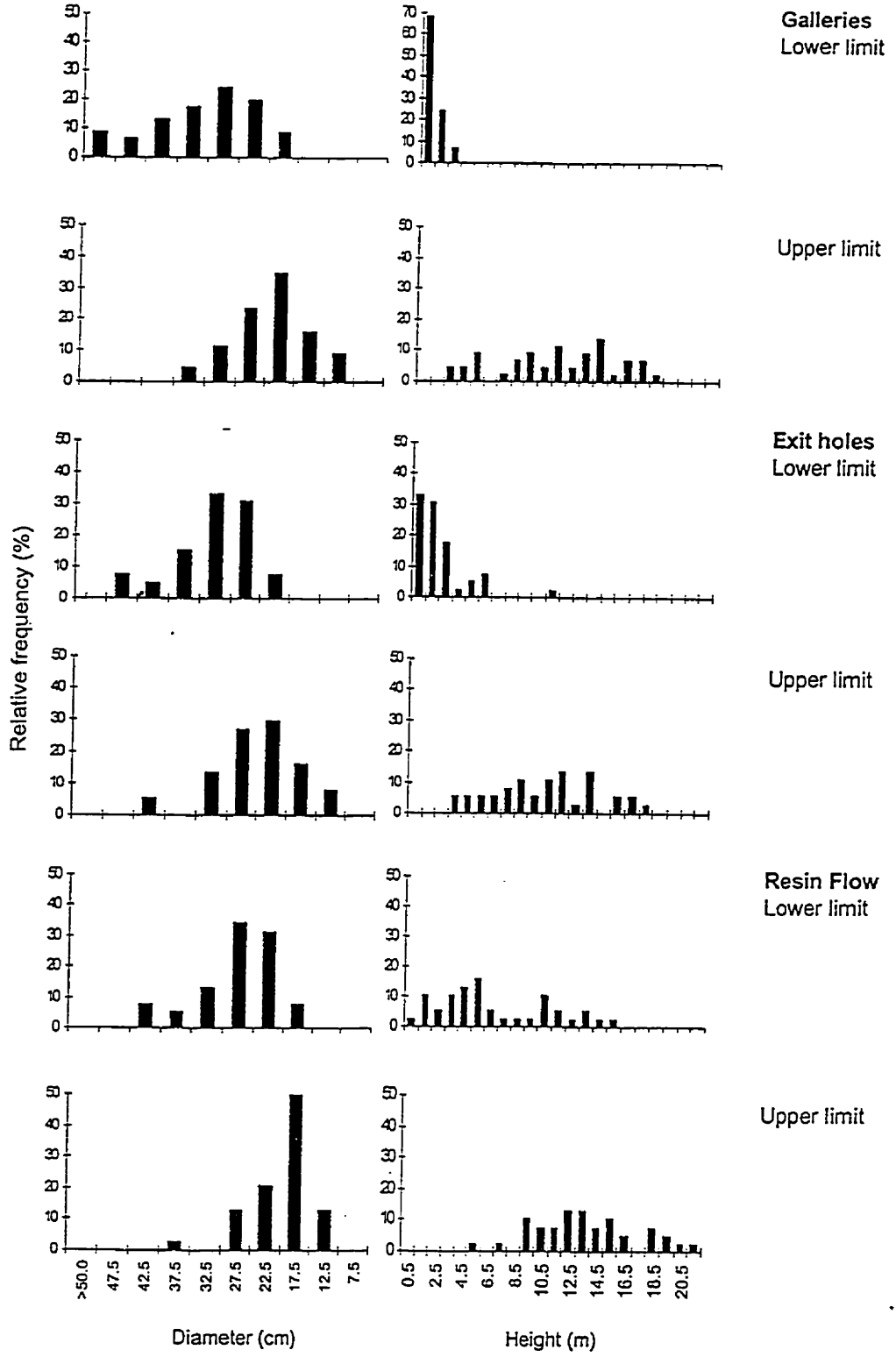


Table 4. Evidence of past attack by *D. confusus* in felled red, grey and snag *A. lasiocarpa*.

Category of tree	Number of trees	Characteristic assessed	Percentage of trees with characteristic
Red	15	<i>D. confusus</i> brood	27
		<i>D. confusus</i> adults	13
		galleries	100
		exit holes	80
		resin flow	93
		all characteristics combined	100
Grey	31	<i>D. confusus</i> brood	3
		<i>D. confusus</i> adults	3
		galleries	90
		exit holes	87
		resin flow	94
		all characteristics combined	97
Snag	90 ^a	galleries	70
	87	exit holes	63
	72	resin flow	56
	90	all characteristics combined	76

^a Fewer snags were assessed for exit holes and resin flow than in other categories because of deterioration and loss of bark.

Figure 4. Frequency distributions of the heights and diameters of lower and upper endpoints on the bole for *D. confusus* galleries, exit holes and *A. lasiocarpa* resin flow.



confusus exit holes in only 4 trees. Secondary scolytid exit holes were usually present before the resin flow zone began and extended up past the resin flow zone to the top of the tree. Secondary scolytid gallery systems in the lower bole were tentatively identified as those of *Pityokteines minutus* (Swaine) while those in the upper bole as those of a *Pityophthorus* spp.

Gallery systems close to the ground at or below the lower limit of exit holes had short egg galleries and few exit holes. The variation in the lower height limit of gallery systems and exit holes was small compared to the upper height limit. The opposite trend was found for variation in diameter (Figure 4).

3.2 Pheromone Baiting Experiment

Despite differences in the numbers of red trees per hectare among the three areas in the pheromone baiting experiment, the ratios of green to red attack in the single-tree and two-tree bait treatment areas were similar, and both were significantly higher than in the control area (Table 5). Trees baited in pairs were more frequently mass attacked and less frequently attacked than those baited singly (Figure 5).

With single-tree bait centres, the percentage of mass attacked trees was highest in the 0 to 1 m range because baited trees were consistently mass attacked (Figure 6). The percentage of mass attack was sporadic at greater distances. Cumulative mass attack steadily increased up to approximately 80%, 9 m away from the bait centre. The pattern was similar for attacked trees with cumulative attack levelling off at approximately 50% at the 7 to 8 m range. Approximately 70% of all attacked trees were concentrated within 9 m of the bait centre. Analysis was restricted to 10 m radii of bait centres because they were on average only 25 m apart.

For two-tree bait centres, mass attack peaked at 3 to 4 m, apparently corresponding to half the distance between two bait trees (Figure 6). The attack and mass attack distributions were dissimilar, probably because most baited trees were mass attacked in two-tree centres (Figure 5). Cumulative mass attack increased rapidly to 60% of total mass attack within 5 m of the bait centre, then increased steadily to about 75% at 10 m (Figure 6).

The range of utilisation of both baited and naturally mass attacked trees by *D. confusus* varied greatly with some trees having few gallery systems and adults and no brood, to those with advanced larval development, long galleries and large zones of occupation of the bole (Figure 7). Naturally mass attacked trees had more advanced

Table 5. Comparison of numbers and ratios of grey, red and newly mass attacked *A. lasiocarpa* in pheromone baited and control areas.

Area	Number of grey trees/ha	Number of red trees/ha	Number of mass attacked green trees/ha	Red:Grey	Green:Red
Control	15.5	18.5	4.5	1.19	0.24
Single-tree baited	23.6	8.7	4.9	0.37	0.56
Two-tree baited	19.6	27.3	14.1	1.40	0.52

^aThe proportion of green to red trees in both the single-tree and two-tree treatment areas are significantly higher than in the control area, chi-square=17.8, df=1, $P<0.001$, and chi-square=16.2, df=1 and $P<0.001$, respectively.

^bThe proportion of red to grey trees in all areas are significantly different, chi-square=147.8, df=2, $P<0.001$.

Figure 5. Percentage of attacked and mass attacked *A. lasiocarpa* baited singly or in pairs. The relative number of unattacked, attacked and mass attacked bait trees was significantly different (chi square=12.016, df=2, $P < 0.002$).

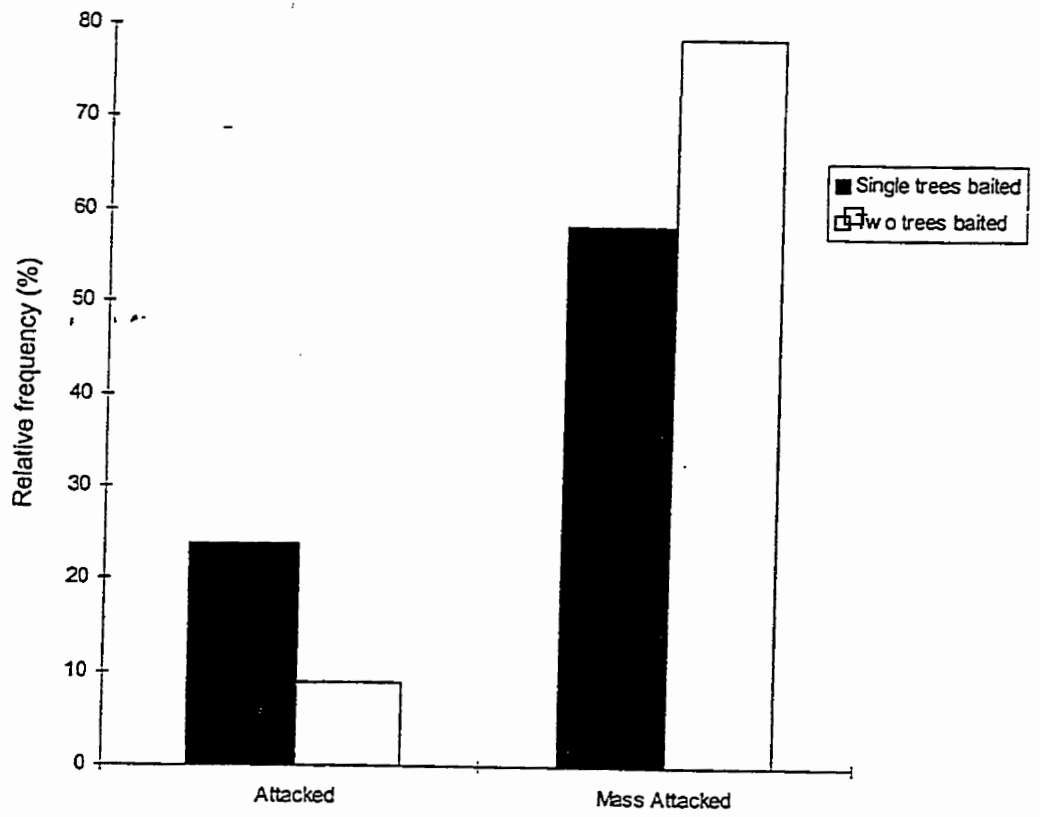


Figure 6. Distribution by percentage of attacked and mass attacked *A. lasiocarpa* by *D. confusus* around single-tree and two-tree bait centres (baited trees included). Solid bars indicate percentage of attack contained within a distance interval from the bait centre. Clear bars indicate cumulative attack as a function of distance from the bait centre. Distance labels on the X-axis are upper limits for the distance intervals (i.e. 2 refers to points ≥ 1 and < 2 m).

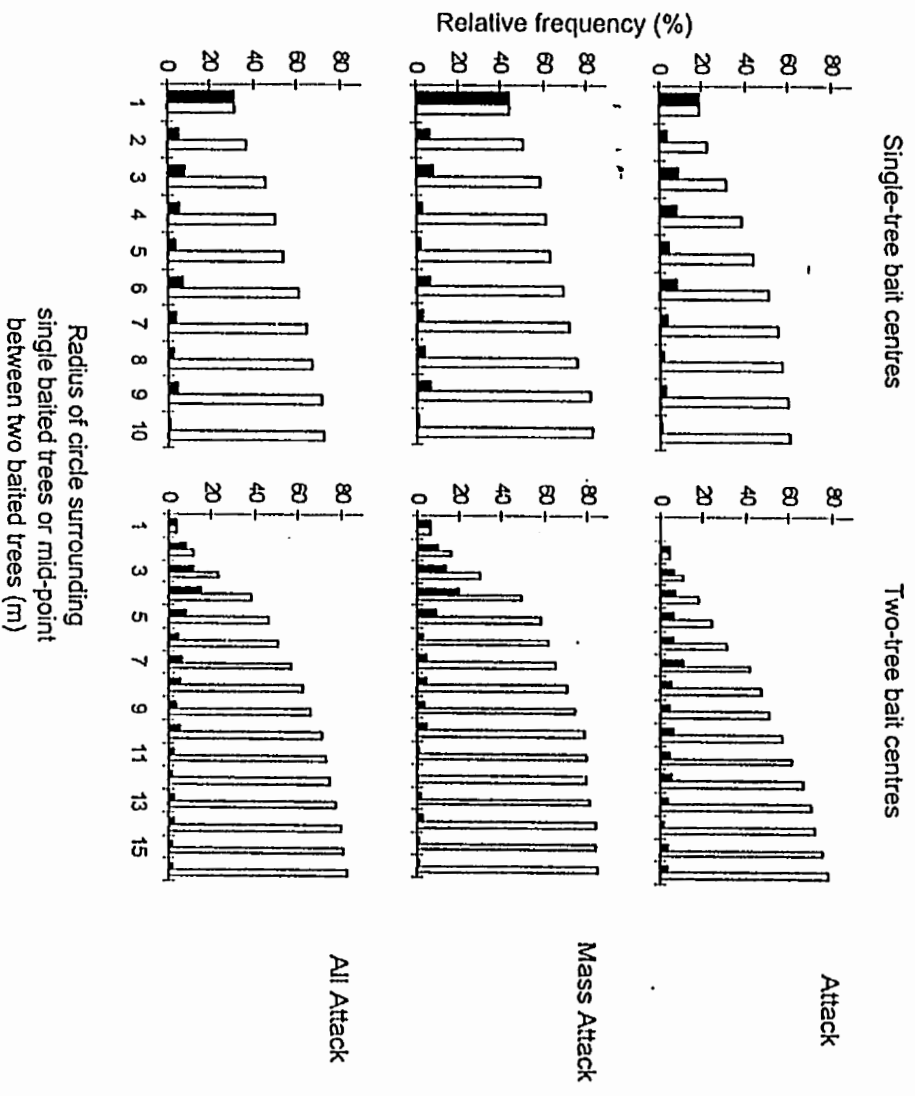
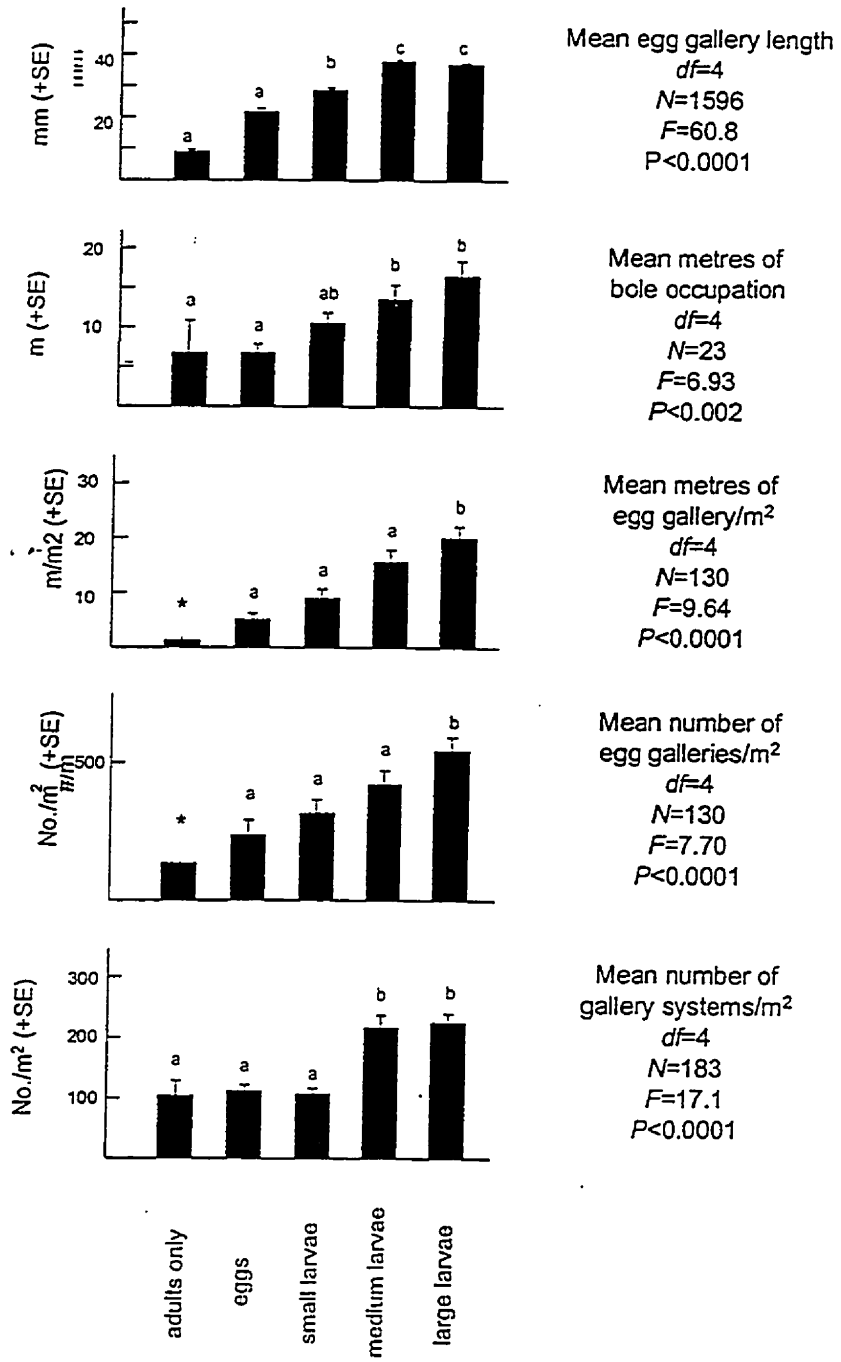


Figure 7. Relationships between stage of brood development in *A. lasiocarpa* and egg gallery length, metres of bole occupation, egg gallery length/m², number of egg galleries/m² and the number of gallery systems/m². Bars within a sub-graph with the same letter superscript are not significantly different, Bonferroni multiple comparison, $P < 0.05$. Bars marked by an asterisk are excluded from the multiple comparison because of low n.



brood development (Table 6) and more of the bole occupied. However, they had shorter egg galleries and a lower density of egg galleries and gallery systems, with an overall reduction of egg gallery length per m² (Figure 8). Some trees with low infestation levels had *D. confusus* gallery systems that contained >10 adults. These gallery systems were stained black. The egg galleries were so close together that the centre of the gallery system was completely excavated and the nuptial chamber and brood galleries were no longer distinguishable.

Of the 23 trees, only 13 had obvious signs of external resin flow originating in the year of attack. Nine of these had resin flow above and overlapping the zone of occupation by *D. confusus*. And two trees had resin zones contained by the zone of occupation. In resin flow zones, 96 % of failed gallery systems (no egg galleries) were pitched out, a significantly greater proportion than the 76% pitched out in areas without resin flow (chi-square=40.2, df=1, *P*, <0.001). Areas with resin flow had more gallery systems attempted but fewer and shorter egg galleries (Figure 9).

Trees attacked by *D. confusus* in the previous year could be divided into those turning red and those that remained green. All of the 14 trees that were turning red had larvae, evidence of successful attack, while four of the eight trees that remained green had parent adults and only one had larvae, evidence of delayed or partially successful attack.

Between June and August 1996, trees mass attacked in 1995 underwent a dramatic colour shift from a small percentage showing signs of colour change to a majority obviously turning red (Figure 10). Only one attacked tree and no unattacked trees showed definitive colour change by August 1996. These data indicate a high degree of success in classifying trees correctly in 1995.

Forty-six of the 49 baited trees that were classified as mass attacked in 1995 had some frass evident on the bole in 1996. Trees classified as mass attacked showing no colour change by August had frass evident in three of six cases. Some trees also showed new resin flow possibly from new attack in 1996. Ten of 19 attacked trees had frass present on the bole but seven of these still were green in August. Five of 15 green trees not attacked in 1995 also had new resin flow indicating new gallery initiation in 1996. No frass was produced on any unattacked baited trees indicating that these were correctly assessed and the slight colour change in June 1996 (Figure 10) was probably a seasonal artefact.

Table 6. Occurrence of resin flow, *D. confusus* in various life stages and associated bark beetles in felled baited and unbaited mass attacked *A. lasiocarpa*.

Insect or phenomenon observed ^a	Percentage of trees		Remarks
	Baited (n=10)	Unbaited (n=13)	
Resin flow	30	69	
<i>D. confusus</i>			
adults	100	100	
eggs	90	92	
small larvae	60	69	
medium-sized larvae	30	46	
large larvae	0	30	
Unidentified secondary bark beetle, probably <i>P. minutus</i>	10	23	Only a few adults in newly established galleries above zone of <i>D. confusus</i> colonization
<i>Crypturgus borealis</i>	40	69	In all trees with medium-sized or large larvae and half the other trees, galleries constructed off <i>D. confusus</i> galleries, often in large numbers
<i>Rhizophagus dimiatus</i>	40	76	Predaceous, found in association with <i>D. confusus</i>

^aSmall, medium-sized and large larvae may correspond to the first three of four larval instars (Stock 1991), but head capsule measurements were not made.

Figure 8. The effect of baiting on *D. confusus* egg gallery length, metres of bole occupation, egg gallery length/m², number of egg galleries/m² and the number of gallery systems/m² in *A. lasiocarpa*.

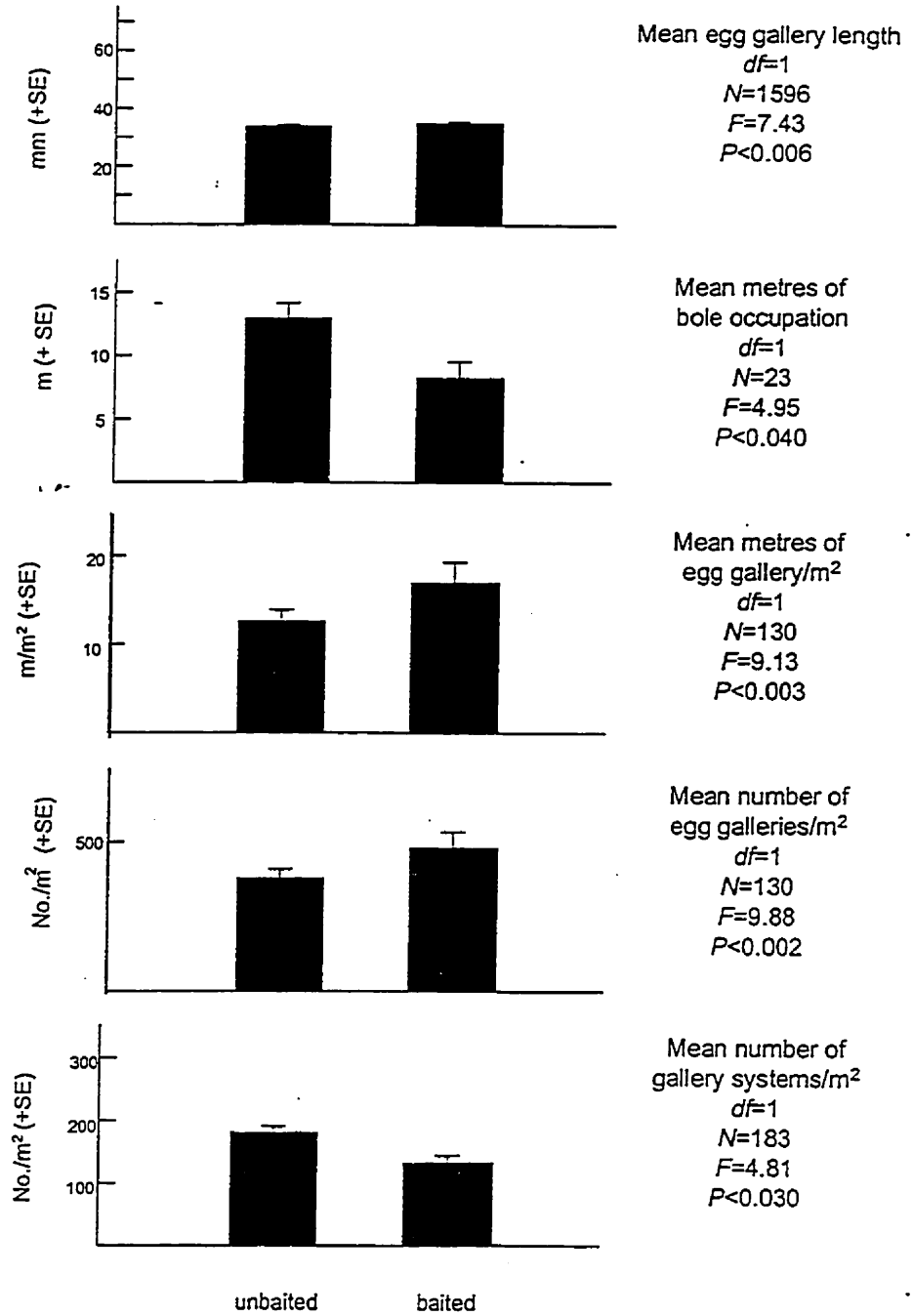


Figure 9. The effect of resin flow in *A. lasiocarpa* on egg gallery length metres of bole occupation, egg gallery length/m², number of egg galleries/m² and the number of gallery systems/m².

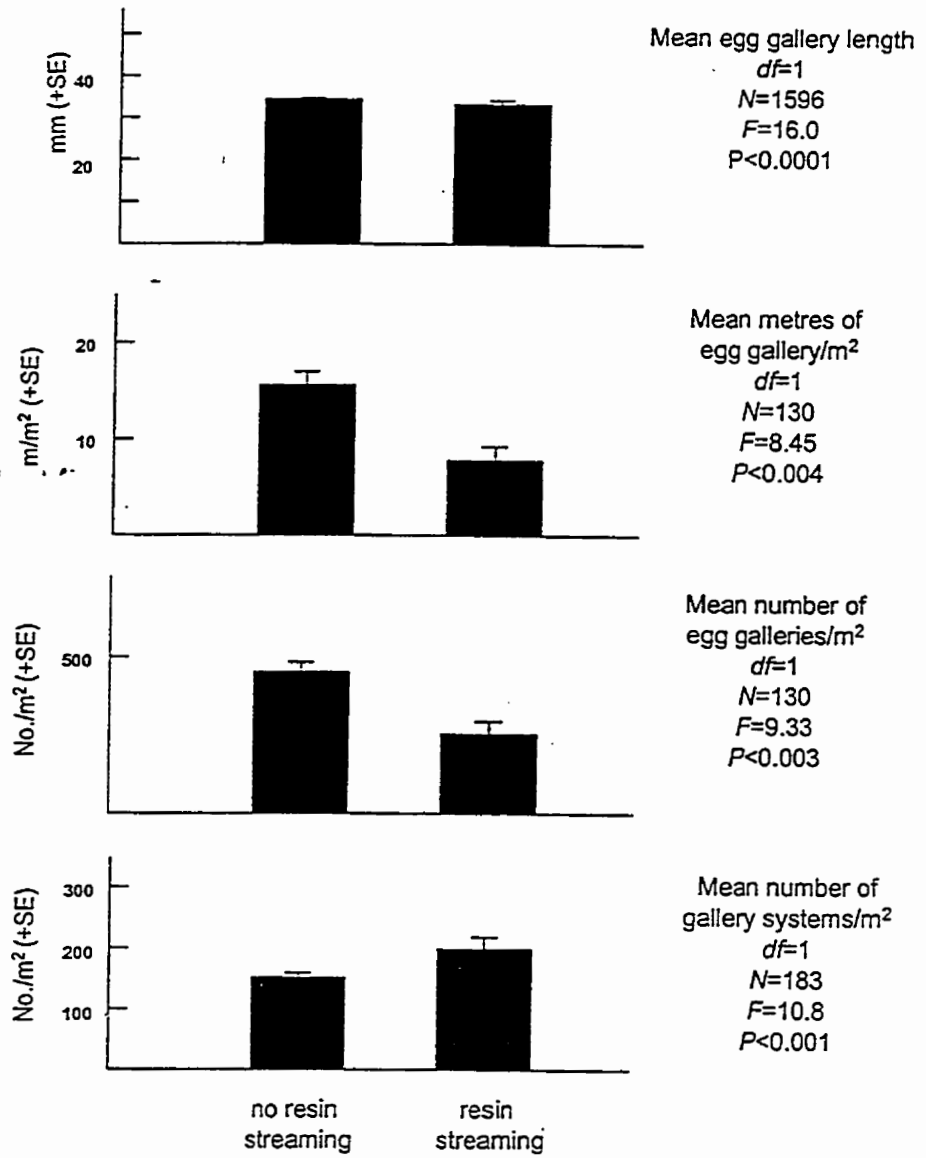
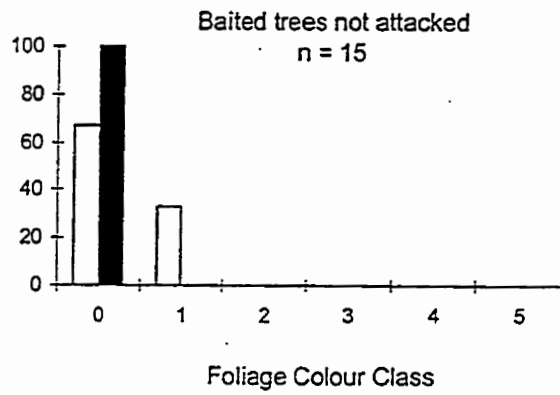
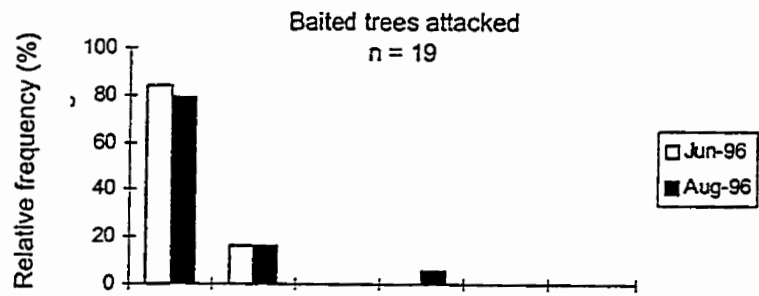
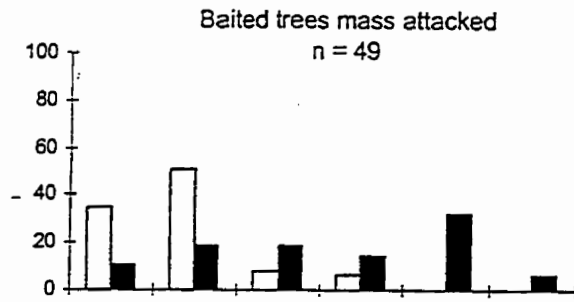


Figure 10. Percentage of single *A. lasiocarpa* trees baited in 1995 in different colour classes in June and August 1996.



In the year of attack, secondary scolytid colonization was limited to *Crypturgus borealis* and a few of what probably were *P. minutus* adults (Table 6). A year after mass attack, *P. minutus* was present in much larger numbers in about half of the baited trees examined.

4.0 DISCUSSION

My results show that *D. confusus* is a very significant disturbance agent in the old growth subalpine forest at the SCSSP, and that *D. confusus* may even have the status of a keystone species in old, large area stands leading in *A. lasiocarpa*. As such, *D. confusus* may interact with a great many vertebrate, invertebrate, plant, lichen and fungal (pathogenic and non-pathogenic) species, and may strongly affect stand characteristics, such as growth, standing biomass and spatial structure. Therefore, *D. confusus* should be considered not only with respect to silvicultural treatment, but also when conservation and other land use decisions are made. My results also elucidate infestation characteristics that should be useful in future determinations of impact and population change. Finally, they demonstrate that pheromone baiting of trees is a viable preharvest tactic to remove a large proportion of a *D. confusus* population in alternative silvicultural treatments, particularly single-tree selection and patch cutting.

4.1 Past Infestation Characteristics and Impact

The decline in red trees observed in aerial photographs (Table 3) should be interpreted carefully in light of widely differing rates of foliage colour change the year following attack (Figure 10) and the fact that red foliage can be retained for up to five years (Unger 1992). However, only 25% of red trees examined had *D. confusus* brood (Table 4), supporting a recent overall decline of *D. confusus* at the SCSSP site. In single-tree selection and 0.1 ha patch cut areas, the dramatic reduction in the number of red trees may be in part due to worker safety requirements that dictated the removal of dead trees in the cut area and in bordering leave areas. This would have left only green attacked trees in the stand, of which about 30% would have been taken out during harvest.

Two lines of evidence point to *D. confusus* being the major mortality agent for the standing dead trees in the SCSSP site. The dbh distribution of red and grey trees is weighted towards large trees mostly >20 cm dbh (Figure 3). This corresponds with the large diameter, lower part of the bole (≥ 22.5 cm diam.) in which successful development

occurs (Figure 4). A similar dbh distribution for naturally killed trees was found by Borden et al. (1987). Secondly, direct observation confirms *D. confusus* activity in all felled red trees, 30 of 31 grey trees and 76% of snags examined (Table 4). The reduced extent of *D. confusus* activity in snags may be due to weathering. Bark was often sloughed off or badly deteriorated, eliminating evidence of exit holes and resin flow and galleries not etched into the sapwood. The greater percentage of small diameter trees among snags than in red and grey trees (Figure 3), suggests that the small trees had been killed by *Armillaria ostoyae*. Merler (1997) found that *A. ostoyae* killed mostly subdominant *A. lasiocarpa* and spruce in the SCSSP site.

The 25-31 % of the total *A. lasiocarpa* basal areas represented by red and grey trees and snags collectively appears to indicate large losses similar to those documented by (Stock 1991), Garbutt and Stewart (1986), and Unger and Stewart (1993). However, Parrish (1997) found that class 1 and 2 snags (these classes only approximate Stock's (1991) red and grey snag classes) have been dead on average about 4 and 17 years, respectively. Older snags in classes 3 and 4 that were in good enough condition to be sampled, were dead for 30 and 45 years on average, indicating that losses took place over a long period of time. Stock (1991) regarded grey trees as a one year transition between the red and snag condition possibly biasing the calculation of loss as 4.2 m³/ha per year in his northern B.C. study sites.

The overall impact on stand biomass by *D. confusus* is unknown in the SCSSP site because replacement of biomass by surviving dominants and advanced regeneration has not been calculated nor have fallen snags been tallied. Parrish (1997) concluded that the stand presumably started after fire at least 337 years ago, the age of the oldest living tree sampled. A major disturbance event, probably caused by *D. confusus*, occurred in the 1860's as seen by a large increase in release rate in dendrochronological analysis. The current low-level release rate could reflect only moderate mortality due to *D. confusus*, or a density kept low enough that death of some trees did not release surviving trees from competition. Based on my data, I hypothesize that in a large old growth stand, *D. confusus* infestation rates would rise and fall with minor heterogeneously dispersed surges and declines, depending on environmental events, host availability and chance. The aerial photographic data suggest that the current infestation is in decline (Table 3) and the three-fold variation in red to grey ratios in the pheromone baiting plots (Table 5) indicates a heterogeneous pattern of tree mortality over time.

The examination of red trees showed that most emerging *D. confusus* adults had already left (Table 4), indicating that adults leave red trees before they become greys. Red trees are therefore not an accurate measure of infestation level, and calculated green to red ratios (Table 5) would tend to underestimate and overestimate the rate of infestation growth and decline, respectively.

The low variance in height of the lower limit of *D. confusus* galleries and exit holes, and the broad variance based on diameter (Figure 4) indicates that height is more important than diameter in limiting *D. confusus* occupation at the lower extreme of the bole. Poor gallery development from 1 to 2 m above the ground may be related to cold night time summer temperatures close to the ground typical for the ESSF (Farnden 1994). This region of the bark is also often very wet, possibly encouraging the growth of decay fungi that overgrow *D. confusus* galleries. In contrast, the upper limit was characterized by wide variation in height, indicating a weak influence (Figure 4). The upper limit for resin flow, however, is sharply compressed around the 17.5 cm peak (Figure 4), indicating a possible influence in limiting *D. confusus* attack. The 17.5 cm upper limit diameter peak for resin flow (Figure 4) is larger than the average 10 cm upper limit for attack on trees that were previously felled by Stock (1991), implying reduced utilization of living mass attacked trees compared to felled trees.

4.2 Pheromone Baiting Experiment

In the baiting trials, (+)-exo-brevicomin clearly concentrated a large part of new *D. confusus* attack on and around the bait centres (Figure 6). Because the number of red trees was much higher in the two-tree than in the single-tree treatment area (Table 5), interpretation of the results is uncertain. However, the green to red ratios in both single- and two-tree treatments were almost identical, suggesting an almost equal effect. It is not known whether the higher ratios in the baited *versus* the control areas were caused by retaining dispersing *D. confusus* within the baited areas or attracting beetles into them. No systematic research has been done on how far apart baits can be and still contain and concentrate scolytid populations. A limit of 25 m for spruce beetles, *Dendroctonus rufipennis* (Kirby), is suggested by Shore et al. (1990), and Gray and Borden (1989) found that the influence of pheromone baiting for the mountain pine beetle, *Dendroctonus ponderosae* Hopkins, extended up to 75 m from grid-baited stands. Stock et al. (1994) observed consistently higher green to red ratios within

300×300 m stands baited for *D. confusus* versus the 50 m wide buffer strips surrounding them, suggesting at least a 50 m range of influence of baited trees.

The changes in foliage colour and the continued production of frass in mass attacked baited trees one year after baiting is consistent with their original categorization (Figure 10). The colour change, frass production and even renewed resinosis in some trees originally classified as attacked implies that adults have managed to survive, allowing a year for associated fungi to overcome its defences. These trees may have become natural pheromone sources the year following baiting suggesting that in an operational setting, all attacked and mass attacked trees should be removed at harvest. Heavily attacked trees probably turn colour quickly, whereas lightly mass attacked trees may require more than one year to be girdled with little indication of colour change in the first year of attack. Hence, some trees that turn red may be initially mass attacked two summers before. The rapid change in foliage colour between June and August 1996 implies that aerial surveys should not be done until late summer or early fall.

In mass attacked baited trees, the density of gallery systems and the amount of bole occupied is less than that occurring in naturally mass attacked trees indicating a tree selection effect. Dispersing beetles have the option of avoiding vigorous, potentially resistant un-baited trees but may not be able to avoid similar baited trees because of the attractive pheromone. Once mass attack was induced, continued output of artificial pheromone may have delayed the effects of antiaggregation pheromones, resulting in a higher concentration of egg galleries (Figure 8). However, differences between baited and naturally mass attacked trees are small compared to those found between trees with different stages of brood development (Figure 7) suggesting other factors are more important.

In the summer of attack, there was little evidence of colonization by secondary scolytids except for *Crypturgus borealis*. *Pityokteines minutus* was present mostly in trees one year after attack. *Rhizophagus dimiatus* was also found mostly on trees with advanced *D. confusus* brood development. These probable predators (Langor 1991) may be attracted to *D. confusus* pheromones, as are predators of other scolytid species (Billings and Cameron 1984, Bowers and Borden 1992).

In one year old attack with green foliage, gallery systems from the previous year were mostly abandoned, with few surviving brood. New vigorous gallery excavation was being established away from zones of old gallery establishment. It is likely that the trees had responded to pathogenic infection by producing traumatic resin at the sites of

inoculation (Berryman and Ashraf 1970) and that new attack was initiated so as to avoid these toxic areas.

Attention given to the impact of *D. confusus* should be dependent on the tree mortality rate (Pederson 1996). If there is chronic small-scale mortality, then the time line for dealing with *D. confusus* infestation is pushed into the future as the forest manager deals with more urgent problems. However, if mortality is concentrated over a short period then a forest manager must make decisions quickly. The type of infestation dynamic may depend on the stage of stand development. Regeneration after fire comes in even aged pulses and resulting stands have a high density (Little et al. 1994). As a stand matures, it may become vulnerable to epidemic type *D. confusus* infestations (Unger and Stewart 1993) as might have happened in the 1860's at the SCSSP site. This initial disturbance would create more age and size variation in the stand. After this, chronic losses due to *D. confusus* may keep volumes down. High tree densities in early stand development may produce small, slow growing trees, while older more open stand types may produce fast growing, large trees (Parrish 1997). The relative productive capabilities and commercial values of these different stand types are not known. The strategy of a forest manager to either infestation dynamic may depend on typical fire return frequency and successional patterns for a given site, the overall mix of stand types currently available, the types of products produced and their associated values with a given stand type, the value of non-timber resources (e.g. water catchment) and the long term direction of the company. A capacity to control *D. confusus* infestation dynamics makes it possible to meet many different management objectives.

The potential use of pheromone baiting for managing *D. confusus* populations in single-tree selection and patch cut systems is promising. By varying the number and placement of bait trees, infestations of different magnitude could be controlled. The attractive drawing power of baits certainly seems to be sufficient to draw the majority of adult *D. confusus* from leave areas into very small areas designated for cutting. Operational tests need to be done over time to develop protocols for pheromone baiting that are consistent with a wide variety of possible harvesting regimes and infestation levels. These should be followed by long term monitoring to determine how *D. confusus* populations respond.

Harvesting methods may have a strong short term effect on the number of beetle infested trees. While eliminating all *D. confusus* infested standing trees in the cut itself, the 1.0 ha and 10 ha clearcuts left populations relatively untouched in the leave areas.

In harvesting the 0.1 ha and single-tree selection areas, most of the snags, grey and red trees were removed in spite of the fact that logging occurred under poor visibility conditions in winter. Even without pheromone baiting this would effectively remove most dispersing beetles from the area, leaving only about two thirds of the green attacked trees from the year before logging as sources of new infestation. Pre-harvest baiting of these stands would have allowed removal of most green attacked trees as well. However, baiting may not be necessary in the following situations: if the population of *D. confusus* in single tree selection and patch cut areas were reduced below a threshold level at which adults can successfully kill living trees; if the altered stand structure negatively affected *D. confusus* attack dynamics or brood survival; or if fragmentation of large stands makes them unsuitable for chronic infestation by *D. confusus*.

While the short term benefits in terms of reducing *D. confusus* populations in partial and patch cut systems are evident, there are reasons to be cautious in the long term because of the possible effects of windthrow in selection and patch cut areas (Novak et al. 1997). Stands harvested by single tree selection may be vulnerable to windthrow if they are too open (Coates 1997), while patch cut stands are fragmented and may be vulnerable to windthrow as they have large ratio of edges relative to patch size (Novak et al. 1997). Build up of *D. confusus* populations in windthrow would jeopardize the survival of the remaining standing trees and might result in populations too large for pheromone-based management. Moreover, mortality due to root and butt rot pathogens tends to increase to very high levels in stands that are partially cut (Morrison et al. 1991).

There are reasons to be cautious about removing *D. confusus* from *A. lasiocarpa* stands. Root rot induced mortality seems to be limited to suppressed *A. lasiocarpa* and spruce (Merler 1997) in spite of long term disturbance due to *D. confusus*. The relationship between *D. confusus* and root rots must be resolved. There are concerns about wildlife such as mountain caribou in these areas that may depend on old growth stand characteristics (Armeler and Waterhouse 1994). Birds, such as the three-toed woodpecker depend on snags for habitat and/or food (Klenner and Huggard 1997). Backhouse and Louiser (1991) list over 90 species of vertebrates that use snags. A large number of invertebrates, bryophytes and lichens are also likely to depend on large dead trees. The possible conservation importance of stands characterized by large *A. lasiocarpa* and the *D. confusus* dynamics contained within them may limit harvesting and managing options.

5.0 LITERATURE CITED

- Alexander, R.R. 1987. Ecology, silviculture, and management of the Engelmann spruce-subalpine fir type in the central and southern Rocky Mountains. USDA For. Serv. Agric. Handbook No. 659.
- Armeler, H. and M. Waterhouse. 1994. Wildlife diversity in managed high elevation stands. B.C. Min. For. Extension Note No. 14.
- Backhouse, F. and J.D. Louiser. 1991. Silviculture systems research: wildlife tree problem analysis. B.C. Ministry of Forests and B.C. Ministry of Environment, Lands and Parks, Wildlife Tree Committee, Victoria, B.C..
- Baker, W. L. and T.T. Veblen. 1990. Spruce beetles and fires in nineteenth century subalpine forests of western Colorado. *Arctic and Alpine Res.* 22: 65-80.
- Berryman, A.A. 1969. Responses of *Abies grandis* to attack by *Scolytus ventralis* (Coleoptera:Scolytidae). *Can. Entomol.* 101: 1033-1041.
- Berryman, A.A. 1972. Resistance of conifers to invasion by bark beetle-fungus associations. *BioScience* 22: 598-602.
- Berryman, A.A. and M. Ashraf. 1970. Effects of *Abies grandis* resin on the attack behavior and brood survival of *Scolytus ventralis* (Coleoptera:Scolytidae). *Can. Entomol.* 102: 1229-1236.
- Billings, R.F. and R.S. Cameron. 1984. Kairomonal responses of Coleoptera, *Monochamus titillator* (Cerambycidae), *Thanasimus dubius* (Cleridae), and *Terminochila virescens* (Trogositidae), to behavioral chemicals of southern pine bark beetles (Coleoptera:Scolytidae). *Environ. Entomol.* 13: 1542-1548.
- Borden, J.H. 1990. Use of semiochemicals to manage coniferous tree pests in western Canada. In: Behaviour modifying chemicals for insect management. R.L. Ridgway, R.M. Silverstein and M.N. Inscoe (Eds.). Marcel Dekker. New York. pp. 281-315.
- Borden, J.H. 1993. From identifying semiochemicals to developing a suppression tactic: a historical review. In: Application of semiochemicals for management of bark beetle infestations-proceedings of an informal conference. S.M. Salom, K.R. Hobson (Eds), USDA For. Ser. Gen. Tech. Rep. INT-GTR-318.
- Borden, J.H., A.M. Pierce, J.R. Pierce, L.J. Chong, A.J. Stock and A.C. Oehlschlager. 1987. Semiochemicals produced by western balsam bark beetle, *Dryocoetes confusus* Swaine (Coleoptera:Scolytidae). *J. Chem. Ecol.* 13: 823-836.
- Bowers, W.W. and J.H. Borden. 1992. Attraction of *Lasconotus intricatus* Kraus. (Coleoptera:Colydiidae) to the aggregation pheromone of the four-eyed spruce bark beetle, *Polygraphus rufipennis* (Kirby) (Coleoptera:Scolytidae). *Can. Entomol.* 124: 1-5.

- Bright, D.R. Jr. 1976. The insects and arachnids of Canada and Alaska. 2. The bark and ambrosia beetles of Canada and Alaska (Coleoptera: Scolytidae). Can. Dept. Agric. Publ. No. 1576.
- B.C. Ministry of Forests, 1992. Annual Report 1990-1991. Victoria, B.C..
- B.C. Ministry of Forests 1993. Annual report 1991-1992. Victoria, B.C..
- B.C. Ministry of Forests 1997. Annual report 1995-1996. Victoria, B.C..
- Butt, G. 1990. Forest regeneration in the ESSF subzone: a problem analysis. For. Can. and B.C. Min. For. FRDA Res. Memo No. 210.
- Camacho, A.D. 1993. Semiochemical-based communication in three species of bark beetles in subalpine forests of British Columbia. PhD thesis. Simon Fraser University, Burnaby, B.C..
- Camacho, A.D., H.D. Pierce, Jr., and J.H. Borden. 1993. Geometric and optical isomerism of pheromones in two sympatric *Dryocoetes* species (Coleoptera:Scolytidae), mediates species specificity and response level. J. Chem. Ecol. 19: 2169-2182.
- Christiansen, E. 1985. *Ips/Ceratocystis*-infection of Norway spruce: what is a deadly dosage? Z. angew. Entomol. 99: 6-11.
- Christiansen, E., R.H. Waring and A.A. Berryman. 1987. Resistance of conifers to bark beetle attack: searching for general relationships. For. Ecol. Manage. 22: 89-106.
- Coates, K.D. 1997. Windthrow damage 2 years after partial cutting at the Date Creek silvicultural systems study in the interior cedar-hemlock forests of northwestern British Columbia. Can. J. For. Res. 27: 1695-1701.
- Coupé, R., A.C. Steward and B.M. Wilkeem. 1991. Engelmann spruce-subalpine fir zone. In: Ecosystems of British Columbia. D. Meidinger and J. Pojar (Eds.). B.C. Min. For., Victoria, B.C. pp. 223-235.
- Farmden, C. 1994. Forest regeneration in the ESSF zone of north-central British Columbia. Pac. For. Cen., Can. For. Serv., Victoria, B.C. Inf. Rep. BC-X-351.
- Ferrell, G.T. 1983. Host resistance to the fir engraver, *Scolytus ventralis* (Coleoptera: Scolytidae): frequency of attacks contacting cortical resin blisters and canals of *Abies concolor*. Can. Entomol. 115: 1421-1428.
- Fischer, W.C. and A.F. Brindley. 1987. Fire ecology of western Montana forest habitat types. USDA For. Ser. Gen. Tech. Rep. INT-223.
- Garbutt, R. and A. Stewart. 1991. Forest insect and disease conditions. Prince Rupert Forest Region, 1990. Pac. For. Cen., For. Can. Serv., Victoria, B.C. FIDS Rep. No. 91-5.

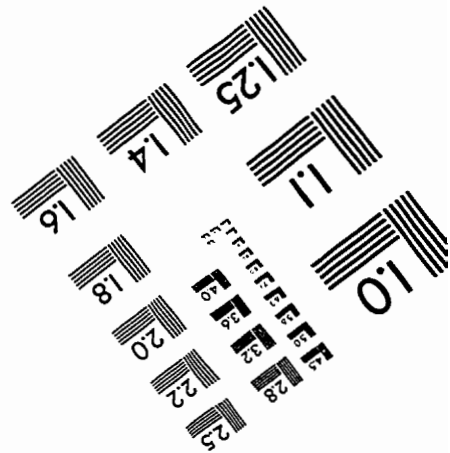
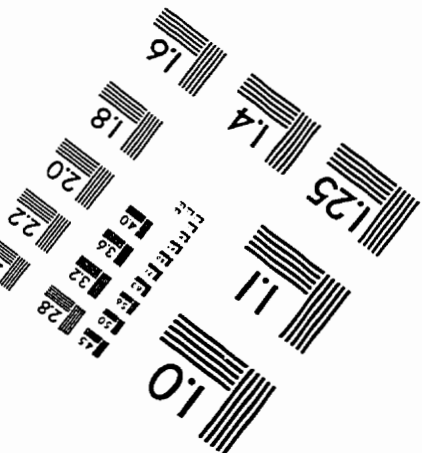
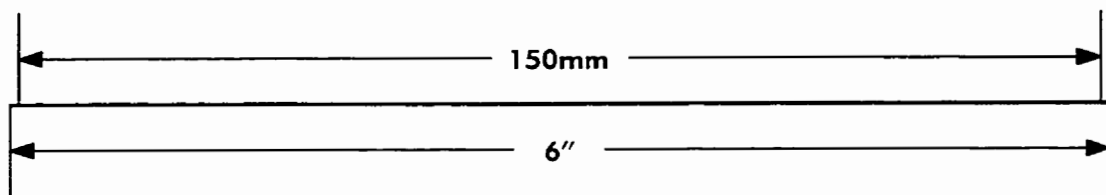
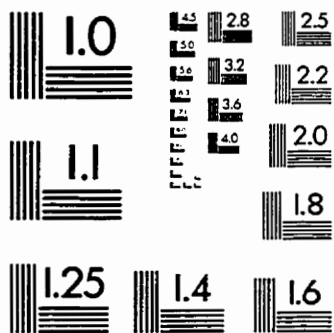
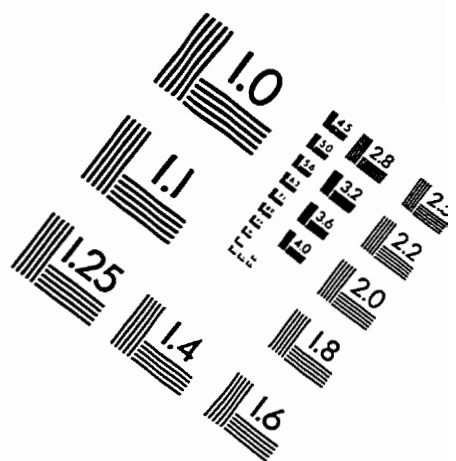
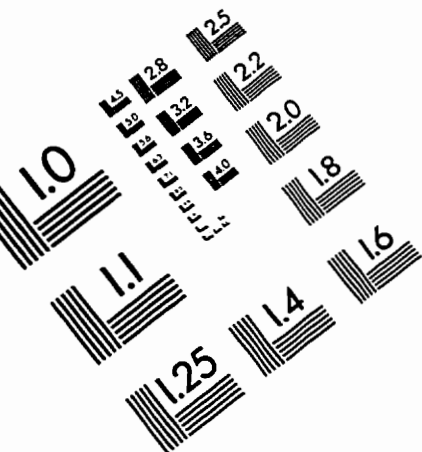
- Gibson, K., S. Kegley and B. Oakes. 1997. Western balsam bark beetle activity and flight periodicity in the northern region. USDA, For. Serv., Coop. For. and For. Health Protect. Rep. No. 97-3.
- Goldhammer, D.S., F.M. Stephen, T.D. Paine. 1990. The effect of the fungi *Ceratocystis minor* (Hedgecock) Hunt, *Ceratocystis minor* (Hedgecock) Hunt Var. *bassasii* Taylor and SJB 122 on reproduction of the southern pine beetle, *Dendroctonus frontalis* Zimmermann (Coleoptera:Scolytidae). Can. Entomol.122: 407-418.
- Gray, D.R. and Borden, J.H. 1989. Containment and concentration of mountain pine beetle (Coleoptera:Scolytidae) infestations with semiochemicals: validation by sampling of baited and surrounding zones. J. Econ. Entomol. 82: 1399-1405.
- Johnson, E.A., G.I. Fryer and M.J. Heathcott. 1990. The influence of man and climate on frequency of fire in the interior wet belt forest, British Columbia. J. Ecol. 78: 403-412.
- Jull, M.J. 1983. Long-term stand dynamics in high elevation Engelmann spruce-subalpine fir forests. MSc thesis. University of British Columbia, Vancouver, B.C..
- Kendrick, W.B. and A.C. Molnar. 1965. A new *Ceratocystis* and its *Verticicladiella* imperfect state associated with the bark beetle *Dryocoetes confusus* on *Abies lasiocarpa*. Can. Dep. Agric., Ottawa, Ont. Contribution No. 397 and For. Entomol. and Pathol. Br. Contribution No. 1114. pp. 39-43.
- Klenner, W. and D. Huggard. 1997. Three-toed woodpecker nesting and foraging at Sicamous Creek. In: Sicamous Creek Silvicultural Systems Project: Workshop Proceedings, April 24-25, 1996 Kamloops, British Columbia, Canada. C. Hollstedt and A. Vyse (Eds.). Res. Br., B.C. Min. For., Victoria, B.C. Work Pap. 24/1997. pp. 224-233.
- Kneeshaw, D.D. and P.J. Burton. 1997. Canopy and age structures of some old sub-boreal *Picea* stands in British Columbia. J. Veg. Sci. 8: 615-626.
- Langor, D.W. 1991. Arthropods and nematodes co-occurring with the eastern larch beetle, *Dendroctonus simplex* [Col.: Scolytidae], in Newfoundland. Entomophaga 36: 303-313.
- Little, R.L., D.L. Peterson, and L.L. Conquest. 1994. Regeneration of subalpine fir (*Abies lasiocarpa*) following fire: effects of climate and other factors. Can. J. For. Res. 24: 934-944.
- Mathers, W.G. 1931. The biology of Canadian bark beetles: the seasonal history of *Dryocoetes confusus* Sw. Can. Entomol. 68: 247-248.
- Meidinger, D., J. Pojar and W.L. Harper. 1991. Sub-boreal spruce zone. In: Ecosystems of British Columbia. D. Meidinger and J. Pojar (Eds.). B.C. Min. For., Victoria, B.C. Special Report Series No. 6. pp. 209-222.

- Merler, H. 1997. Forest Pathology at Sicamous Creek. In: Sicamous Creek Silvicultural Systems Project: Workshop Proceedings, April 24-25, 1996 Kamloops, British Columbia, Canada. C. Hollstedt and A. Vyse (Eds.). Res. Br., B.C. Min. For., Victoria, B.C. Work Pap. 24/1997. pp. 41-44
- Molnar, A.C. 1965. Pathogenic fungi associated with a bark beetle on alpine fir. Can. J. Bot. 43: 563-570.
- Morrison, D., H. Merler and D. Norris. 1991. Detection, recognition, and management of *armillaria* and *phellinus* root diseases in the southern interior of British Columbia. B.C. Min. For., Victoria, B.C. FRDA Rep. No. 179.
- Novak, M., A. Orchansky, R. Adams, W. Chen and R. Ketler. 1997. Wind and temperature regimes in the B-5 clearing at the Sicamous Creek Silviculture Systems Research Area: Preliminary results from 1995. In: Sicamous Creek Silvicultural Systems Project: Workshop Proceedings, April 24-25, 1996 Kamloops, British Columbia, Canada. C. Hollstedt and A. Vyse (Eds.). Res. Br., B.C. Min. For., Victoria, B.C. Work Pap. 24/1997. pp. 45-56.
- Parrish, R. 1997. Age and Size Structure of the forest at Sicamous Creek. In: Sicamous Creek Silvicultural Systems Project: Workshop Proceedings, April 24-25, 1996-Kamloops, British Columbia, Canada. C. Hollstedt and A. Vyse (Eds.). Res. Br., B.C. Min. For., Victoria, B.C. Work Pap. 24/1997. pp. 16-31.
- Pathocon Consulting. 1987. Causes of decline and mortality of subalpine fir in the Bulkley and Morice Timber Supply Areas of the Prince Rupert Forest Region. Forest Resource and Development Agreement Report to Canadian Forestry Service, Victoria, B.C.
- Pedersen, L. 1996. Kispiox Timber Supply Area: rationale for allowable annual cut (AAC) determination, effective December 30, 1996. B.C. Min. For., Victoria, B.C.
- Raffa, K.F. 1991. Induced defensive reactions in conifer-bark beetle systems. In: Phytochemical induction by herbivores. D.W. Tallamy and M.J. Raupp (Eds.). Wiley, New York. pp. 245-276.
- Shore, T.L., P.M. Hall and T.F. Maher. 1990. Grid baiting of spruce stands with frontalinal for pre-harvest containment of the spruce beetle, *Dendroctonus rufipennis* (Kirby) (Col.:Scolytidae). J. Appl. Entomol. 109: 315-319.
- Schurig, V., R. Weber, G.J. Nicholson, A.C. Oehlschlager, H.D. Pierce, Jr., A.M. Pierce, J.H. Borden, and L.C. Ryker. 1983. Enantiomer composition of natural *exo*- and *endo*-brevicommin by complexation gas chromatography/selected ion mass spectrometry. Naturwissenschaften 70: 92-93.
- Stock, A.J. 1981. The western balsam bark beetle, *Dryocoetes confusus* Swaine: secondary attraction and biological notes. MSc. Thesis. Simon Fraser University, Burnaby, B.C..

- Stock, A.J. 1991. The western balsam bark beetle, *Dryocoetes confusus* Swaine: impact and semiochemical-based management. PhD thesis. Simon Fraser University, Burnaby, B.C..
- Stock, A.J. and J.H. Borden. 1983. Secondary attraction in the western balsam bark beetle, *Dryocoetes confusus* (Coleoptera: Scolytidae). *Can. Entomol.* 115: 539-550.
- Stock, A.J., J.H. Borden and T.L. Pratt. 1994. Containment and concentration of infestations of *Dryocoetes confusus* (Coleoptera: Scolytidae), using the aggregation pheromone *exo-brevicommin*. *Can. J. For. Res.* 24: 483-492.
- Stock, A.J., J.H. Borden, T.L. Pratt, H.D. Pierce Jr. and B.D. Johnston. 1995. Enantiomeric composition and release rates of *exo-brevicommin* influence aggregation of the western balsam bark beetle, *Dryocoetes confusus* Swaine (Coleoptera: Scolytidae). *Can. Entomol.* 449-456.
- Unger, L. 1992. History of population fluctuations and infestations of important forest insects in the Nelson Forest Region, 1923-1991. *Can. For. Serv., Pac. For. Res. Cen., Victoria, B.C. FIDS Rep. No. 92-13.*
- Unger, L. and A. Stewart. 1986. Forest insect and disease conditions: Prince Rupert Forest Region-1986. *Can. For. Serv., Pac. For. Cen., Victoria, B.C. FIDS Rep. No. 86-5.*
- Unger, L. and A. Stewart. 1993. Forest insects and disease conditions: Nelson Forest Region-1992. *Can. For. Serv., Pac. For. Cen., Victoria, B.C. FIDS Rep. No. 93-3.*
- Veblen, T.T., K.S. Hadley, M.S. Reid and A.J. Rebertus. 1989. Blowdown and stand development in a Colorado (USA) subalpine forest. *Can. J. For. Res.* 19: 1218-1225.
- Veblen, T.T., K.S. Hadley, M.S. Reid and A.J. Rebertus. 1991. Methods of detecting past spruce beetle outbreaks in Rocky Mountain (USA) subalpine forests. *Can. J. For. Res.* 21: 242-254.
- Vyse, A. 1997. The Sicamous Creek silviculture systems project: How the project came to be and what it aims to accomplish. In: Sicamous Creek Silvicultural Systems Project: Workshop Proceedings, April 24-25, 1996 Kamloops, British Columbia, Canada. C. Hollstedt and A. Vyse (Eds.). *Res. Br., B.C. Min. For., Victoria, B.C. Work Pap. 24/1997.* pp. 4-14.
- Wood, C.S. and G.A. Van Sickle. 1989. Forest insect and disease conditions, British Columbia & Yukon-1988. *Can. For. Serv., Pac. For. Cen., Victoria, B.C. Inf. Rep. BC-X-306.*
- Wood, C.S. and G.A. Van Sickle. 1993. Forest insect and disease conditions, British Columbia & Yukon-1992. *Can. For. Serv., Victoria, B.C. Inf. Rep. BC-X-340.*

- Wood, C.S. and G. A. Van Sickle. 1994. Forest insect and disease conditions, British Columbia and Yukon-1994. Nat. Res. Can., Can. For. Serv., Pac. For. Cen., Victoria, B.C. Inf. Rep. BC-X-354.
- Yole, D., T. Lewis, A. Inselberg, J. Pojar and D. Holmes. 1989. A field guide for identification and interpretation of the Engelmann spruce-subalpine fir zone in the Prince Rupert Forest Region, B.C. Min. For., Victoria, B.C..
- Zar, J.H. 1984. Biostatistical analysis. Prentice-Hall, Inc., Englewood Cliffs, N.J..

IMAGE EVALUATION TEST TARGET (QA-3)



APPLIED IMAGE . Inc
1653 East Main Street
Rochester, NY 14609 USA
Phone: 716/482-0300
Fax: 716/288-5989

© 1993, Applied Image, Inc., All Rights Reserved