# CHARACTERISTICS OF TREES INFESTED BY DOUGLAS-FIR BEETLES IN KOOTENAY LAKE FOREST DISTRICT

by

Tamaki Kano

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Abstract

Some characteristics of Douglas-fir trees and their immediate surroundings were assessed for their association with Douglas-fir beetle infestation in Kootenay Lake Forest District. Examination of trees in plots paired within 50 m revealed that a small crown and clumping of Douglas-fir trees were related to infestation for trees larger than 40 cm diameter at breast height (1.3 m). Relative probability of infestation between trees in plots within 50 meters can be calculated using live crown ratio and basal area occupied by Douglas-fir trees in a 0.01-ha range. Live crown ratio and average diameter of trees within a 0.01-ha plot around the tree were important. Carbon isotope ratio of wood samples from a 5-year period prior to infestation was significantly related to infestation status, possibly indicating moisture stress in infested trees previous to infestation.

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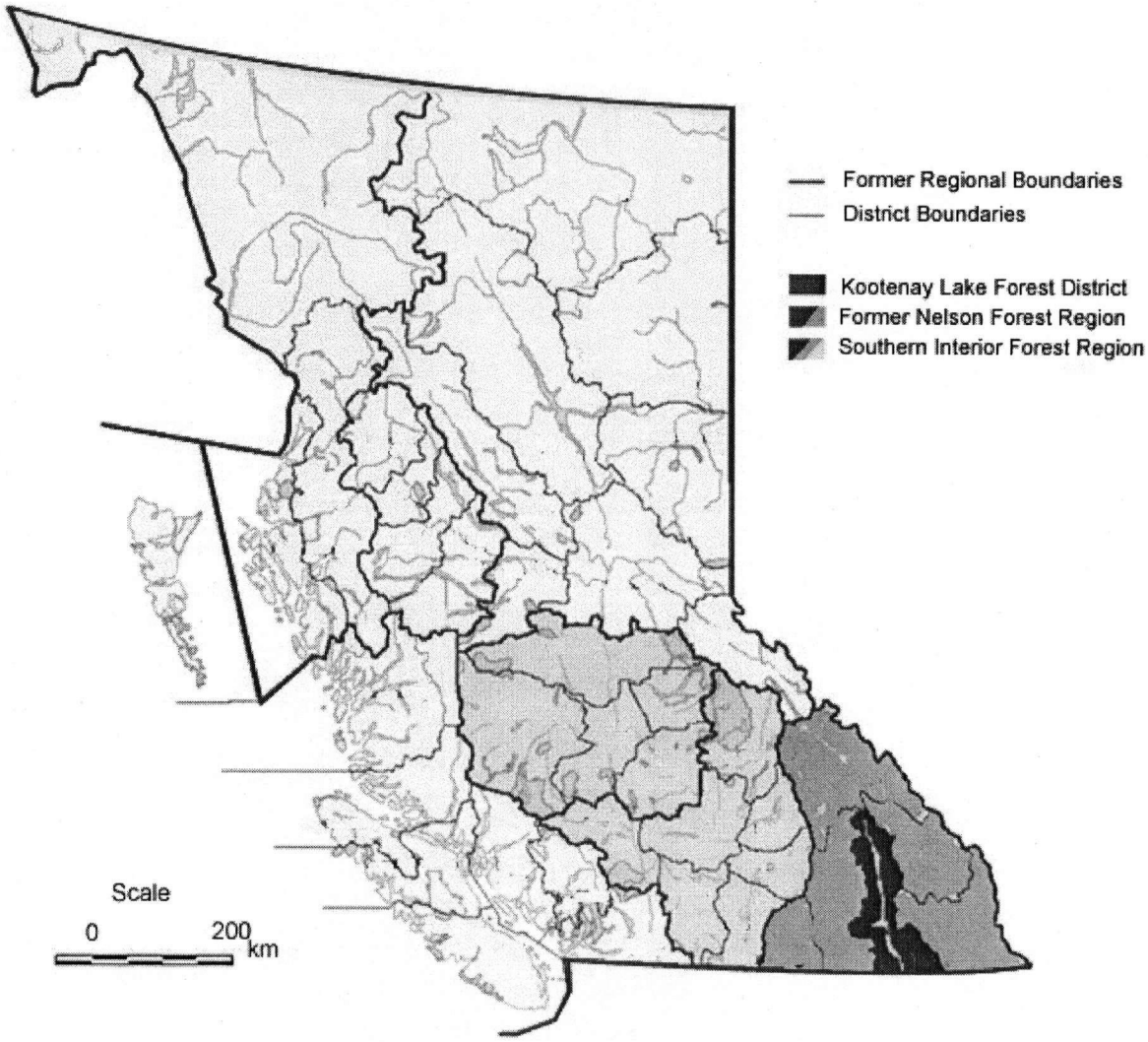
# 1. Introduction

## 1.1. Douglas-fir beetle in the Kootenay Lake Forest District

Although the current outbreak of the mountain pine beetle (*Dendroctonus ponderosae* Hopk.) is monopolizing the attention of public, media, and professionals, other bark beetle (Coleoptera: Scolytidae) species also threaten British Columbia's forests and forestry. An outbreak of spruce beetle (*Dendroctonus rufipennis* (Kirby)) affected 60,000 hectares of forests in the Prince George Region in the late 1970's, and re-planting of the area was not completed until 1999 (Cozens 2004). In 2003, Douglas-fir beetle (*Dendroctonus pseudotsugae* Hopk.) infested about 23,000 hectares in B.C. (Ministry of Forests, 2004).

In 1994, local forest-health professionals in the Kootenay Lake Forest District (KLFD) were alarmed when numerous patches of mature Douglas-fir trees on the highly visible north shore of the west arm of Kootenay Lake turned red (Hawe 1996, J. Castonguay, personal communication). Douglas-fir beetle (DFB) had previously killed trees in small groups (i.e. a few trees, commonly called "spot" infestations) in the area, but many of these larger groups (called "patch" infestations) consisted of more than 40 trees.

Figure 1. Location of Kootenay Lake Forest District in British Columbia (Map adopted from http://www.for.gov.bc.ca/mof/maps/regdis/nKLFD.htm)




DFB is one of four bark beetle species listed as most damaging to B.C.'s forests in the Bark Beetle Management Guidebook for British Columbia (Province of British Columbia 1995). In the Nelson Region in 2000, DFB was fourth in the ranking of disturbance agents by area affected after mountain pine beetle, western balsam bark beetle (*Dryocoetes confusus* Swaine), and pine

needle cast (*Lophodermella concolor* (Dearn.) Darker). In the Nelson region DFB infested more than 20 times the area forest fire burnt in 2000 (Ministry of Forests 2005).

Large, old interior Douglas-fir trees (*Pseudotsuga menziesii* var. *glauca* Mirb. Franco) are common at lower elevations in KLFD, occurring in the dominant or co-dominant class, mixed with western redcedar (*Thuja plicata* Donn ex D. Don) and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) of various ages and sizes. Douglas-fir occurring in the Interior Cedar-Hemlock (ICH) zone (Meidinger and Pojar 1991) are aesthetically sensitive, being close to the lake, campgrounds, and highways (see Maps 1 and 2 in Appendix A). The local public are emotionally attached to the large, old Douglas-fir trees in the forests. In areas that are not as visibly sensitive, Douglas-fir are desirable timber for their size, popularity of their wood grains, and ease of access. The value of salvaged beetle-kill timber is immediately diminished because of blue stain, excessive drying, and cracking of sapwood caused by symbiotic fungi, e.g. *Ophiostoma pseudotsugae* (Rumbold) von Arx (Solheim and Krokene 1998). Later advanced decay is caused by veiled polypore (*Cryptoporus volvatus* (Pk.) Shear), better known as pouch mushroom or pouch fungus, that DFB spreads (Parry *et al.* 1996). Despite aggressive efforts by district officers to reduce the damage by removing the pest population through trapping of beetles and logging the infested timber while it still contained beetle brood (e.g. Hawe 1996), DFB infestations were conspicuous throughout KLFD within the next few years (J. Castonguay, personal communication).

### 1.2. How the DFB outbreak started and persisted in KLFD: DFB ecology and population dynamics

Local forestry professionals believe that the DFB epidemic in the Kootenay Lake area was triggered by major windthrow events (J. Castonguay, personal communications 2000). The first increase in infestation was observed in 1993 following a 1991 windthrow event; again in 1996, as

the beetle population was starting to decline, there was a second major windthrow event and DFB population spread along the main lake in subsequent years.

Trees killed or severely damaged in disturbances are preferred breeding and feeding sites for secondary bark beetles (McMullen and Atkins 1962, Schroeder 2001). In B.C., mountain pine beetle is the only species that must infest live trees, and others preferentially infest freshly dead trees or severely weakened trees (Furniss and Carolin 1977). Female DFB bore through the bark, construct egg galleries along the direction of the grain in the phloem-cambium region, and lay eggs in niches made in the side of the gallery. Eggs hatch, and larvae feed on the phloem and cambium across the grain, excavating larval galleries. When they mature, they construct a small circular pupal chamber. They then hatch as teneral adults and continue feeding inside the bark. DFB usually overwinter as later-instar larvae but may overwinter in any of these juvenile stages inside the bark. They emerge out of the bark in early summer to fly, search, and infest a new host.

Disturbances such as blowdowns (Powers *et al.* 1999, Schroeder 2001) and fire (Hood *et al.* 2003) frequently precede outbreaks of secondary bark beetle species, presumably because they provide an ample supply of preferred host material, thus alleviating one of the major population regulators for bark beetles (Zhang *et al.* 1992, Wallin and Raffa 2003). Once the population size of secondary bark beetles erupts, their rate of successful attack of live trees increases (Wallin and Raffa 2004). Live trees defend against invasions from bark beetles and associated fungal symbionts by secreting resin (Lieutier *et al.* 1993, Raffa and Smalley 1995, Kyto *et al.* 1996, Philips and Croteau 1999), producing induced or constitutive phenolics (Brignolas *et al.* 1998), or through physical properties like lignin content (Wainhouse *et al.* 1990). Many secondary bark beetle species are capable of overwhelming tree defence systems by their sheer numbers ("mass attack"). The symbiotic blue-stain fungi, such as *O. pseudotsugae* associated with DFB, also

hamper tree defences by growing into the sapwood and cutting off water uptake (Christiansen and Solheim 1990, Ross and Solheim 1997, Croisé *et al.* 2001).

Amplification of DFB population is often associated with abundance of the host, favourable weather patterns for the pest, and/or undesirable weather patterns for the host. Much of KLFD burned in a major forest fire in the beginning of the 20th century, and those Douglas-fir trees that regenerated after the fire are now about 100 years old, often over a meter in diameter and thus attractive to DFB. The trees may also suffer from overcrowding stress, which further encourages DFB, as their densities are believed to be higher than the ecosystems in the area would naturally carry at the same seral stage, as a result of fire suppression. There were 151 forest fires reported to the Southeast fire centre in 2005 (Ministry of Forests 2005), all of which were attended to by the Protection Branch of the B.C. Ministry of Forests. If fires burned naturally in the ICH zones, they would create patches of old stands amid regenerating stands, rather than an entire landscape of mature forests containing Douglas-fir (Arsenault 1998). Cutblocks can also break the continuity, but most of the ICH in KLFD is considered visually sensitive (see Map 1 and Map 2 in Appendix A), so logging is restricted to areas not visible from the highway, hiking trails, or the lake (J. Castonguay, personal communication). This history created not only abundance but also an unnaturally large expanse of mature forests containing Douglas-fir. Before the aesthetics of forests became a concern, trees were logged on the hillsides, but high-grading ("cut the best, leave the rest") was common until the 1990's. By removing the largest trees without defects, high-grading may have removed the trees that were the most resistant to bark beetle infestation.

Continuity of mature forests benefits beetle intensification in two other ways: undisrupted chemical communication and reduced beetle mortality during flight and host search. Bark beetles have to emerge, fly, and search for new host material after they mature inside the bark. Bark

beetles use semiochemicals to detect a candidate host material and avoid non-host material (Pureswaran and Borden 2004) and to communicate with members of their own species (Knopf and Pitman 1972, Pureswaran and Borden 2005). Wind speed is lower within stands than in the open (Kimmins 1997), so in a continuous forest, semiochemical plumes are not disturbed or diluted by wind. In other bark beetle species, mortality during flight (i.e. host search) is high and increases considerably with increasing flight time during which beetles are exposed to dangers such as adverse weather, predators, and energy exhaustion (Byer *et al.* 1998). Furthermore, bark beetles suffer a higher mortality rate in openings, such as those created by previous fires, than in forested areas in the same amount of time (Byers and Löfqvist 1989). Because all of these factors need to be suitable, major landscape-level DFB outbreaks are usually decades apart.

Favourable weather patterns for bark beetles are hot, dry summers and mild winters. High temperatures at the time of gallery construction in summer increase fecundity of beetle (Wermelinger and Seifert 1999), and dry summers decrease mortality by allowing flight without disruption by rain. Mild winters decrease overwinter mortality rates as demonstrated with mountain pine beetle (Amman 1973, Safranyik 1998), a closely-related species (Furniss and Carolin 1977). Weather patterns that are favourable for beetles are also taxing for the Douglas-fir trees in the area. Dry springs and hot summers can reduce growth rates in Douglas-fir (Zhang *et al.* 1999). Weather patterns that reduce growth rates have been associated with successive bark beetle infestation (Zhang 1999). While defence mechanisms of trees increase when they are under slight stress, resin responses to invading agents diminish when stress increases (Raffa and Berryman 1983, Lorio *et al.* 1986, Lorio *et al.* 1995, Reeve *et al.* 1995, Croisé *et al.* 2001).

### 1.3. Moisture stress and host resistance

When beetles burrow into the bark of a live tree, the host tree exudes constitutive and induced

resin to wash out beetles and beetle-vectored fungi ("pitching out") (Lorio *et al.* 1995). Resin consists primarily of carbon compounds (Kramer *et al.* 1979), and its production depends on carbon assimilation from carbon dioxide ($CO_2$) in photosynthesis. One of the elements that limits the rate of photosynthesis is $CO_2$ inflow through stomata. When plants close stomata to reduce moisture loss under drought stress, it also cuts off $CO_2$ inflow. This affects the ratio of the two isotopic forms of carbon ($^{12}C$ and $^{13}C$) (Taiz and Zeiger 1998).

Plant tissues usually contain higher ratios of $^{12}C$ to $^{13}C$ than air for two reasons: 1) $^{12}CO_2$ diffuses faster because it is lighter and smaller, and 2) Rubisco, an enzyme responsible for carbon fixation in photosynthesis, "prefers" $^{12}C$ (Cregg and Zhang 2000). When stomata are closed, there is reduced incoming $CO_2$ from the bulk atmosphere ($C_a$), and the $CO_2$ concentration inside the leaf ($C_i$) goes down. Discrimination rates then decrease, and $^{13}C$ -to-$^{12}C$ ratios in plant tissues increase (Le Roux *et al.* 1996, White *et al.* 1996, Zhang *et al.* 1997, Johnsen *et al.* 1999, Zacharisen *et al.* 1999, Guy and Holowachuk 2001). Therefore, higher ratios of $^{13}C$ to $^{12}C$ can indicate moisture stress. A ratio of $^{13}C$ to $^{12}C$ is commonly expressed using $\delta^{13}C$ in per mill against a standard (std) called Vienna Pee Dee belemnite ($\delta^{13}C$ = 0 ‰) as shown in equation 1 (Taiz and Zeiger 1998).

$$\delta^{13}C = 1000\left[\left\{\left(\frac{^{13}C}{^{12}C}\right)_{sample} \Big/ \left(\frac{^{13}C}{^{12}C}\right)_{std}\right\} - 1\right] \qquad [1]$$

Increased $\delta^{13}C$ values indicate a reduction in $C_i/C_a$, the ratio of intercellular to ambient $CO_2$ concentrations, and consequently elevated water-use efficiency (WUE), i.e. amount of carbon fixed for unit water loss (Guy and Holowachuk 2001).

## 1.4. Current beetle control tactics

Indigenous bark beetle species are a part of the natural ecosystem and rely on the propagation of their host species for survival. Current large-scale outbreaks of many bark beetle species, therefore, may indicate that the beetle-host equilibrium has been disturbed by human-caused stand alterations such as fire suppression. It is, thus, imperative to reduce the extent and intensity of bark beetle infestations not only for the economics of the forestry industry but also for sustainability of forest ecosystems.

Efforts to control bark beetle infestations are currently put into three categories of tactics: removal of beetles, reduction of available host materials, and modification of stand structures. These tactics are implemented when an eruptive beetle population threatens adjacent high-susceptibility stands and/or high-value areas (e.g. parks and residential areas) and/or when other forest values (e.g. wildlife, land stability, and aesthetics) may be damaged by large-scale tree mortality.

Beetles are removed from stands by pheromone trapping, baiting, and sanitation logging. Trapping uses a combination of Lindgren funnel traps (Lindgren 1983) with a vertical silhouette that imitates a standing tree and lures that contain combinations of semiochemicals to attract beetles. Operational trapping is usually done to detect or monitor the population size and time of flight (i.e. population dispersal and expansion) as it requires a great number of traps to capture enough beetles to impede the spread of infestation ("mass trapping"). Tree baiting, on the other hand, is used to reduce or redirect an active population. Commercially synthesized semiochemical baits are placed on live or downed trees and scheduled to be removed, burned, or debarked (Shore *et al.* 2005) before the new brood emerge. Effective use of baiting was demonstrated in 1998 when the KLFD forest-health officer set out beetle baits in stands adjacent to the Kokanee Creek Provincial Park and protected the park from the spreading DFB infestation

(J. Castonguay, personal communication). Sanitation logging is the removal of freshly-attacked standing trees before the new brood of beetles emerge. For sanitation logging, however, access and resources for logging have to be quickly arranged as the location of infestation can rarely be predicted and time is limited. The mechanisms of population migration are not well understood (Byers 1999); currently, the only way to speculate on the chances of infestation, i.e. the "risk," is the distance from an active population. This is not a consistent method as it is frequently observed that the beetle populations "skip" adjacent stands even when they have susceptible characteristics. This phenomenon may be because bark beetles require flight exercise before they are antennally active and able to smell and detect the host trees (Bennett and Borden 1971). Modification of stand structure to boost host resistance to beetle infestation is commonly called "beetle-proofing." Where the characteristics of stand structure that make stands susceptible to beetle infestation are identified, stands may be modified to reduce susceptible features. For instance, downed trees, snags, and/or susceptible standing trees can be removed to increase competition for breeding and feeding sites for beetles and increases host-searching time, resulting in higher mortality of beetles. The characteristics of a forest stand that make it more attractive to beetles than other stands and/or more likely to suffer mortality once the population arrives in the stands are collectively called the "hazard" of a stand. The bark beetle management guidebook of British Columbia (Province of British Columbia 1995) presents a formula for rating hazard of Douglas-fir stands for the Douglas-fir beetle.

### 1.5. Kootenay Lake Forest District

The hazard rating system for Douglas-fir beetle described in the Bark Beetle Management Guidebook was empirically constructed based on previous research and field experience and was uniformly applied to many ecosystems across the province. This system had not been widely tested; therefore, the local forest health professionals were eager to investigate factors that could be affecting susceptibility of Douglas-fir trees specifically in the KLFD.

This study focuses on the ICHdw (dry-warm) subzone because the majority of the lower-elevation stands in KLFD are in that subzone (Map 2 in Appendix A). Many of the ICH forests in KLFD naturally have a very high $\alpha$-diversity of tree species. The pioneer species are ponderosa pine (*Pinus ponderosa*), lodgepole pine (*Pinus contorta* var. *latifolia*), western larch (*Larix occidentalis*), Douglas-fir, and many deciduous species such as maple (*Acer spp.*), alder (*Alnus spp.*), and birch (*Betula spp.*). In mid-seral stages, western white pine (*Pinus monticola*), western hemlock (*Tsuga heterophylla*), western redcedar (*Thuja plicata*), western yew (*Taxus brevifolia*), and grand fir (*Abies grandis*) emerge. This mix is nicknamed the "Kootenay Mix." Most of these species can also be found in the late seral stages, which are usually dominated by western redcedar and western hemlock.

## 1.6. Study objectives

The objective of this research was to determine the characteristics of Douglas-fir trees which increase their susceptibility to Douglas-fir beetle infestation in the ICHdw subzone in the Kootenay Lake Forest District. To achieve this objective, I investigated the association between infestation status and characteristics of the trees such as height, diameter, live crown ratio, density and growth rate, as well as site factors such as slope and aspect. I also studied the link between DFB infestation and moisture stress by comparing carbon isotope discrimination ratios in infested and uninfested Douglas-fir trees.

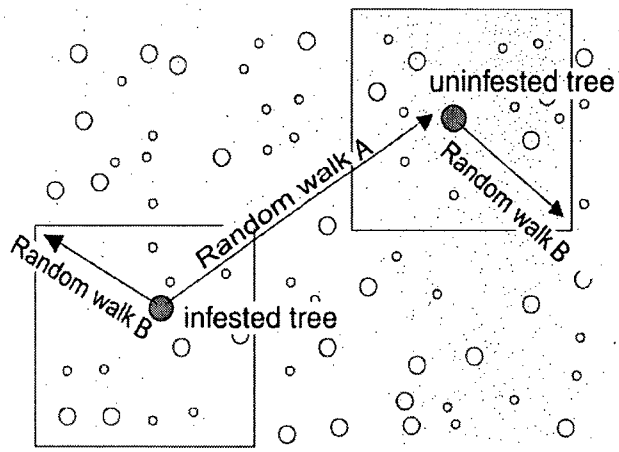
## 2. Methods

### 2.1. Relative susceptibility assessment in close proximity

Characteristics of infested and uninfested trees were first compared in a paired-tree study. Pairing in close proximity should ensure that the trees are similar in most stand and site characteristics, such as stand density, elevation, and age as well as beetle pressure (i.e. size and density of beetle population at the particular location). Thirty infested trees larger than 40 cm in diameter at breast height (dbh) were randomly selected from the KLFD inventory. Seven of these 30 trees were later excluded because they could not be accessed at the time of sampling because of seasonably high water flow in the streams. The minimum size limit was used to lessen the effects of diameter, which is well-documented and often a dominating characteristic of beetle susceptibility. Selected trees were located using the ground-survey maps provided by KLFD, and infestation was confirmed by examination for symptoms of DFB such as red crown, boring dust on the boles, and entrance/emergence holes.

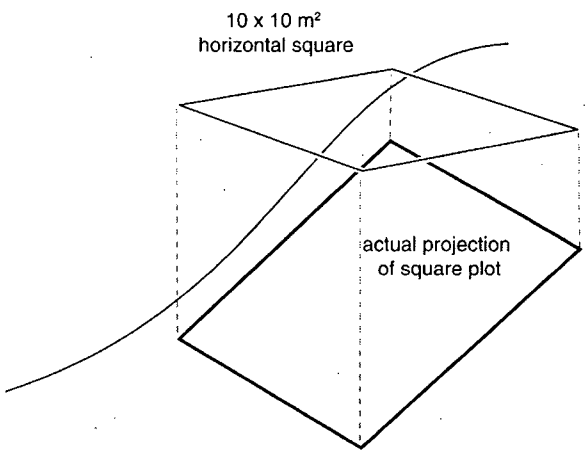
For each infested tree, a nearby uninfested tree was selected by walking at a random bearing for a random distance between 10 and 50 m ("random walk A"), and then selecting an uninfested tree within 3 m of the end of the random walk (Figure 2). A 10x10-m plot was set up around each tree, the first corner of which was determined by taking a random walk (random walk B) between 1 and 10 m and establishing sides according to the four compass directions.

Figure 2. Procedure for selecting infested – uninfested tree pairs. Circles represent trees; squares represent 10x10-m plots).




The small plot size (0.01 hectare) ensured that the measurements reflected the environment immediately around the selected trees. The steep slopes were corrected for by projecting the 10x10-m square plot onto the slope (Figure 3).

Figure 3. Procedure for correcting plot size for steep slopes in study area

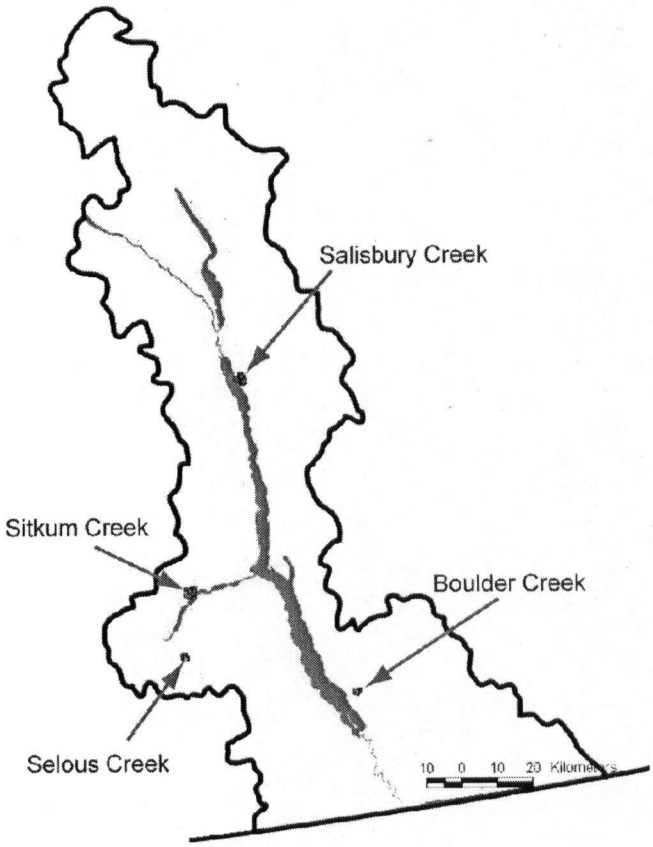


In each plot, slope, aspect, and longitude/latitude were recorded. DBH, species, and any deforming damages were measured for each stem. Height and live-crown ratio (LCR) were measured on the two tallest Douglas-fir trees without visible evidence of prior defects in each plot. Increment cores were collected at 1.3 metres from the ground from the south side of the same two trees, and were preserved in a freezer at the end of each day. In the winter of the same year, the radial growth rate, age, bark thickness, and phloem thickness of the cores were measured using Windendro®. Basal area (BA), i.e. the horizontal area occupied by the stem at breast height, of each stem, each species, total for the plot, and Douglas-fir purity (proportion of total BA occupied by Douglas-fir) were calculated. Based on growth rate data, BA increase for the last five and ten years was calculated. The variables were analyzed using Wilcoxin's signed-rank test ($\alpha = 0.05$). All variables were also entered into stepwise logistic regression to create a model that assesses susceptibility of trees within a 50-meter radius.

## 2.2. Generally applicable model

To further assess the susceptibility of Douglas-fir trees to Douglas-fir beetle infestation, another set of randomly selected plots was used to build a susceptibility model. Within the same forest district, four watersheds were selected because of existing ground access and abundant Douglas-fir beetle infestation: Selous Creek, Sitkum Creek, Salisbury Creek, and Boulder Creek (Figure 4). The four watersheds were located at the north and south ends of the main lake and north shore and at the west end of the west arm (Map 4 in Appendix). The ICHdw area in the south-east side of the district was not included because of lack of ground access. The resulting model is not to be extracted to this area.

Figure 4. Location of study plots in KLFD for generally applicable model study.




One hundred plots were selected for this study. To ensure that rare types of stands would not be missed or under-represented, a three-dimensional target matrix was created (Table 1) using standing volume, crown closure, and Douglas-fir purity data from the Forest Inventory Planning database. By sampling even numbers of plots from each category ("cell"), the extremes of the regression model will be over-represented but enforced.

Values that equally divide total area into two groups for crown closure and Douglas-fir purity and three groups for volume were selected to define the cells. Three of these cells did not exist in the four study areas. It was originally intended that equal sampling effort be allocated to infested

points and uninfested points (described below), but the number of plots sampled per cell varied due to small sizes of some of the cells. The data from each cell for each of the four areas were weighted to ensure that each unit area had the same importance to the regression using the ratio of the proportion of dots sampled in a cell to the total number of dots counted in the cell. This is analogous to area sampled over total area.

Table 1. Target matrix with area in hectares for each cell

| | | | | **Standing volume of all species ($m^3$)** | | |
|---|---|---|---|---|---|---|
| | | | | Low (<210) | Med (≥210, <300) | High (≥300) |
| Crown Closure | Low (<58%) | Fd Purity | low (<48.5%) | 5855.7 | 1906.7 | 814.1 |
| | | | high (≥48.5%) | 4463.9 | 3698.4 | 1169.5 |
| | High (≥58%) | Fd Purity | low (<48.5%) | 5226.1 | 5631.0 | 4921.7 |
| | | | high (≥48.5%) | 2019.3 | 7062.5 | 12174.8 |

Each plot was selected as a dot in a numbered-dot grid over a map. The grid was laid over the infestation inventory map, and the dots were categorised as infested (within infested parts of the map) and uninfested (within the uninfested parts of the map). The target matrix was applied to each category separately, making the infestation status the fourth dimension. The modified dot grid measures 100 actual metres between the dots. One hundred dots, or locations, were selected; 27 were later rejected due to lack of ground access, and 73 plots were entered into the dataset for model construction.

Plots of 0.01-hectare were used to measure clumping conditions. The diameter limit of 40 cm was not used this time so that it would be more widely applicable. Coordinates for selected stands were determined using Mapview and entered into a hand-held GPS unit to assist in finding them on the ground. A Douglas-fir tree closest to the coordinate was selected as the "centre tree" and a 0.01-hectare plot was set up with it in the center and the sides facing the four compass directions. If no Douglas-fir trees were found within 100 metres of the coordinate, it was

rejected.

The following variables were recorded or collected for every stem within each plot (unless otherwise noted).

- Dbh of every stem greater than 7.5 cm in dbh.
- Tree species
- Crown class, loosely using the terms from even-aged stands for the multi-age stands
- Infestation status of Douglas-fir trees as healthy, green (current attack), red (previous-year attack), grey (two years or more previous), and dead (either old beetle-kill or undetermined causes).
- Height and length of live crown of every Douglas-fir tree in the canopy class.
- Site factors: slope, aspect, and presence of irregularities in topography and soils.
- Two tree cores on south side at 1.3 m above ground of every Douglas-fir tree for growth measurements and $\delta^{13}C$ measurements.

From the cores collected, the following were measured and/or calculated:

- Radial growth increment of a 5-year period prior to infestation (1999)
- Basal area growth increment of a 5-year period prior to infestation (1999)
- Sapwood area
- Proportion of sapwood to basal area
- Bark thickness

From the variables measured, the following were calculated:

- LCR: proportion of length of live crown to height
- Douglas-fir purity: proportion of BA occupied by Douglas-fir to total BA

Phloem thickness was not measured as the infested trees had been dead for more than a year, during which time phloem desiccated.

Logistic regression was used to create a model that determines useful variables for assessing DFB infestation susceptibility of Douglas-fir trees.

## 2.3. Carbon isotope discrimination as an indicator of susceptibility

Cores from 19 infested and 18 uninfested trees were randomly selected from the samples collected for the general model study for $\delta^{13}C$ analysis. The annual rings corresponding to a 5-year period immediately prior to the 1999 infestation (between 1994 and 1998) were extracted and hand-filed to powder with a well-washed steel file. The sample was analysed for $\delta^{13}C$ with an isotope ratio mass spectrometer (IRMS) at the Stable Carbon Isotope Laboratory at the Earth and Ocean Science department of the University of British Columbia, Vancouver. Student's t-test was used to compare the means of two groups of trees. The accepted level of probability for all tests was $\alpha = 0.05$.

## 3. Results

### 3.1. Relative susceptibility assessment in close proximity

Aspect, LCR, BA of all species, and BA of Douglas-fir were all significantly different in infested and uninfested trees (Table 2). Correlation among the variables are presented (Table 3). Infested trees had lower LCR, larger azimuths for aspect, higher BA of all species, and higher BA of Douglas-fir alone (Figures 5 to 8).

Table 2. Results from Wilcoxon's signed-rank test and the significance of difference at $\alpha$ = 0.05. (Bold letters indicate significant differences) Average is indicated for reference as this is not a test of means.

| Variables | average values | | P-value |
|---|---|---|---|
| | infested | uninfested | |
| Slope (per cent) | 53.55 | 53.23 | 0.298 |
| **Aspect (degrees)** | **181.05** | **181.95** | **0.038** |
| DBH* of centre tree (cm) | 58.01 | 58.07 | 0.476 |
| BA** of centre tree ($cm^2$) | 4.96 | 4.46 | 0.444 |
| Height (m) | 38.42 | 37.78 | 0.468 |
| **LCR*** ** | **0.41** | **0.51** | **0.034** |
| bark thickness (mm) | 3.55 | 3.78 | 0.281 |
| phloem thickness (mm) | 0.89 | 1.11 | 0.108 |
| BA growth over 5 years ($mm^2$) | 76.05 | 91.87 | 0.179 |
| BA growth over10 years ($mm^2$) | 154.39 | 196.61 | 0.108 |
| radial growth increment over 10 years (mm) | 8.21 | 11.98 | 0.215 |
| density of all species (stems per plot) | 8.41 | 7.68 | 0.236 |
| density of Douglas-fir trees (stems per plot) | 4.45 | 4.55 | 0.433 |
| **BA of all species ($cm^2$)** | **9297** | **7985** | **0.049** |
| **BA of Douglas-fir ($cm^2$)** | **7685** | **5840** | **0.009** |
| Plot Douglas-fir purity (proportion) | 0.84 | 0.78 | 0.138 |
| average dbh all stems (cm) | 35.55 | 36.86 | 0.278 |
| average dbh of Douglas-fir (cm) | 44.57 | 40.64 | 0.309 |
| average dbh of Douglas-fir of dbh ≥ 25 cm | 52.19 | 49.96 | 0.236 |

* DBH = diameter at breast height (1.3 meters)
** BA = basal area calculated as the horizontal area of tree stems at breast height.
*** LCR = Live crown ratio

Table 3. Pearson correlation coefficient table of the variable measured in close proximity study,

| | variable | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | Aspect (degrees) | 1.000 | | | | | | | | | | |
| 2 | BA Pi5 ($cm^2$) | 0.082 | 1.000 | | | | | | | | | |
| 3 | BA Pi10 ($cm^2$) | 0.124 | 0.963 | 1.000 | | | | | | | | |
| 4 | BA centre tree ($cm^2$) | 0.264 | 0.173 | 0.285 | 1.000 | | | | | | | |
| 5 | Bark thickness (mm) | -0.166 | 0.264 | 0.246 | 0.073 | 1.000 | | | | | | |
| 6 | DBHTYG (cm/mm) | -0.009 | -0.739 | -0.712 | -0.202 | -0.206 | 1.000 | | | | | |
| 7 | LCR | 0.060 | 0.198 | 0.212 | 0.092 | 0.263 | -0.416 | 1.000 | | | | |
| 8 | Phloem (mm) | 0.107 | 0.437 | 0.515 | 0.077 | -0.113 | -0.460 | -0.038 | 1.000 | | | |
| 9 | radial Pi10 (mm) | 0.035 | 0.914 | 0.898 | -0.108 | 0.153 | -0.630 | 0.198 | 0.488 | 1.000 | | |
| 10 | Purity (%) | 0.342 | 0.117 | 0.135 | 0.158 | -0.034 | -0.042 | -0.267 | 0.373 | 0.100 | 1.000 | |
| 11 | avg dbh of Fd>25cm | 0.178 | 0.221 | 0.346 | 0.758 | 0.188 | -0.257 | 0.271 | 0.006 | -0.004 | -0.025 | 1.000 |
| 12 | avg dbh Fd (cm) | -0.010 | 0.184 | 0.282 | 0.513 | 0.049 | -0.118 | 0.121 | -0.091 | 0.003 | -0.131 | 0.816 |
| 13 | avg dbh all species (cm) | 0.139 | 0.229 | 0.299 | 0.498 | 0.078 | -0.350 | 0.173 | 0.308 | 0.092 | 0.404 | 0.447 |
| 14 | dbh Centre tree (cm) | 0.268 | 0.185 | 0.288 | 0.979 | 0.135 | -0.252 | 0.159 | 0.100 | -0.108 | 0.212 | 0.771 |
| 15 | density Fd (per plot) | 0.242 | -0.023 | -0.052 | 0.117 | -0.038 | 0.087 | -0.162 | 0.204 | -0.052 | 0.483 | -0.367 |
| 16 | density all spp (per plot) | -0.138 | -0.215 | -0.233 | -0.022 | 0.052 | 0.196 | -0.128 | -0.299 | -0.246 | -0.574 | -0.038 |
| 17 | Height of centre treet (m) | 0.089 | 0.163 | 0.239 | 0.601 | -0.129 | -0.166 | 0.014 | 0.313 | -0.012 | 0.091 | 0.572 |
| 18 | plot BA Fd ($cm^2$) | 0.305 | 0.264 | 0.322 | 0.671 | 0.068 | -0.138 | -0.081 | 0.160 | 0.035 | 0.394 | 0.521 |
| 19 | plot BA all ($cm^2$) | 0.110 | 0.195 | 0.238 | 0.558 | 0.029 | -0.143 | 0.108 | -0.025 | -0.033 | -0.236 | 0.484 |
| 20 | Slope (%) | 0.032 | -0.047 | -0.026 | -0.011 | -0.024 | -0.065 | 0.311 | -0.075 | 0.036 | -0.221 | 0.016 |
| 21 | Infestation status | 0.012 | -0.070 | -0.125 | 0.078 | -0.077 | 0.108 | -0.399 | -0.098 | -0.205 | 0.101 | 0.056 |

| | Variable | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 12 | avg dbh Fd (cm) | 1.000 | | | | | | | | | |
| 13 | avg dbh all species (cm) | 0.296 | 1.000 | | | | | | | | |
| 14 | dbh Centre tree (cm) | 0.503 | 0.549 | 1.000 | | | | | | | |
| 15 | density Fd (per plot) | -0.505 | 0.107 | 0.148 | 1.000 | | | | | | |
| 16 | density all spp (per plot) | -0.026 | -0.601 | -0.104 | -0.047 | 1.000 | | | | | |
| 17 | Height of centre tree (m) | 0.438 | 0.532 | 0.590 | -0.053 | -0.138 | 1.000 | | | | |
| 18 | plot BA Fd ($cm^2$) | 0.488 | 0.528 | 0.665 | 0.360 | -0.055 | 0.549 | 1.000 | | | |
| 19 | plot BA all ($cm^2$) | 0.549 | 0.377 | 0.544 | 0.136 | 0.209 | 0.538 | 0.747 | 1.000 | | |
| 20 | Slope (%) | -0.001 | -0.098 | -0.091 | -0.167 | 0.172 | -0.103 | 0.069 | 0.089 | 1.000 | |
| 21 | Infestation status | 0.118 | -0.070 | 0.034 | 0.070 | 0.191 | 0.094 | 0.301 | 0.185 | -0.070 | 1.000 |

Figure 5. Pair-wise comparison of azimuths of aspect (degrees): each x indicates a tree pair; values below the line indicate that the value for the infested tree was greater than the uninfested tree.

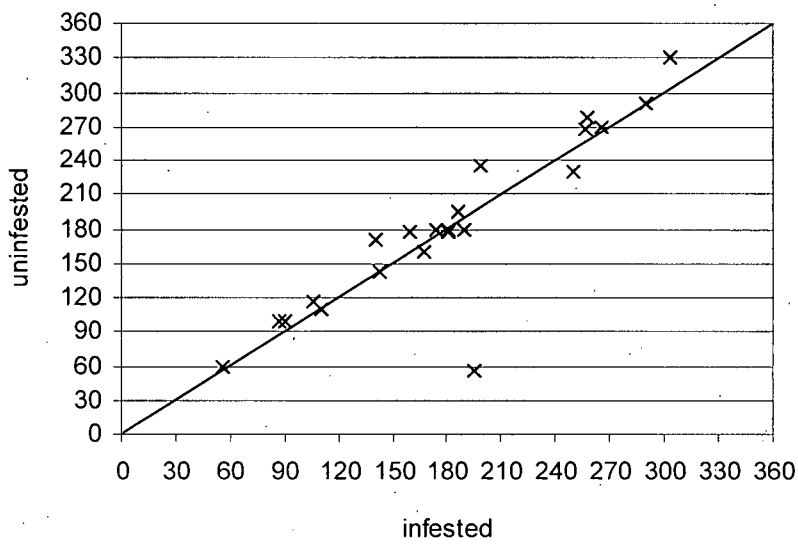



Figure 6. Pair-wise comparison of Live Crown Ratio (proportion of total height): each x indicates a tree pair; values below the line indicate that the value for the infested tree was greater than the uninfested tree.

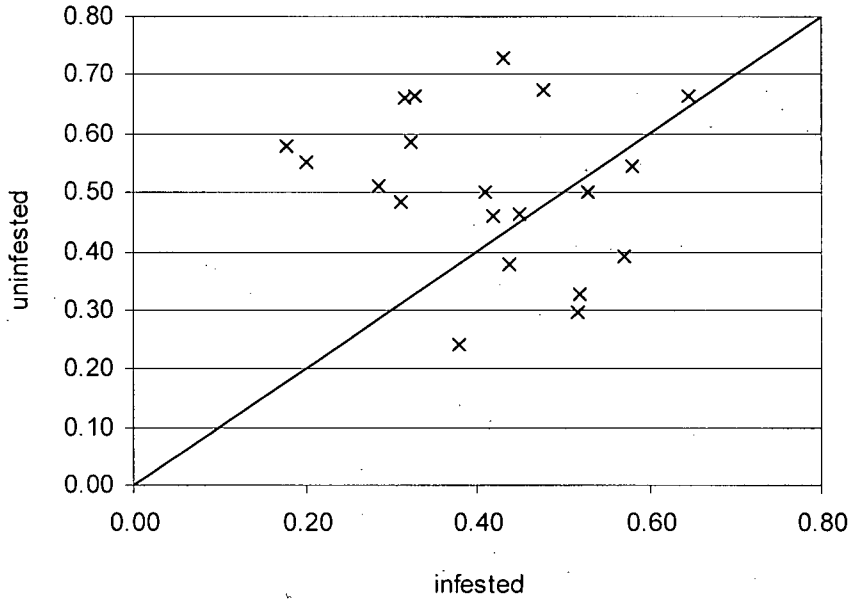


Figure 7. Pair-wise comparison of total BA for Douglas-fir ($m^2$/0.01ha): each x indicates a tree pair; values below the line indicate that the value for the infested tree was greater than the uninfested tree.

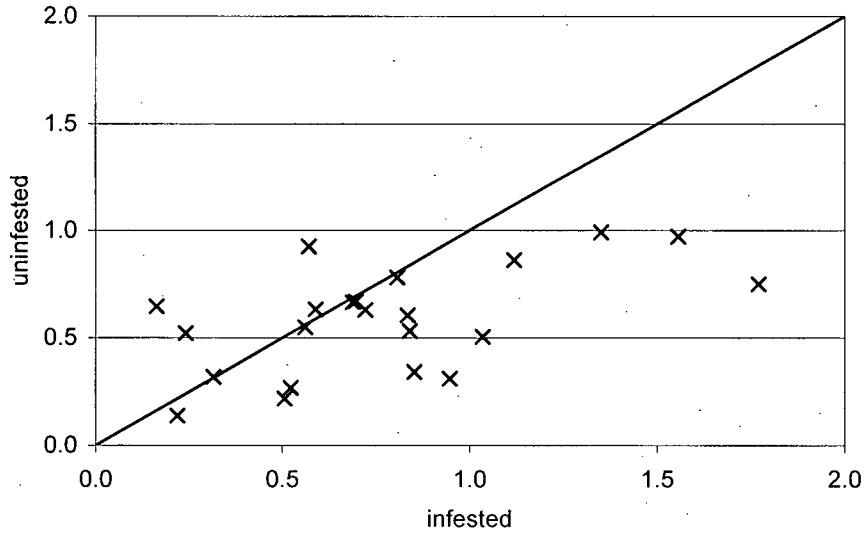
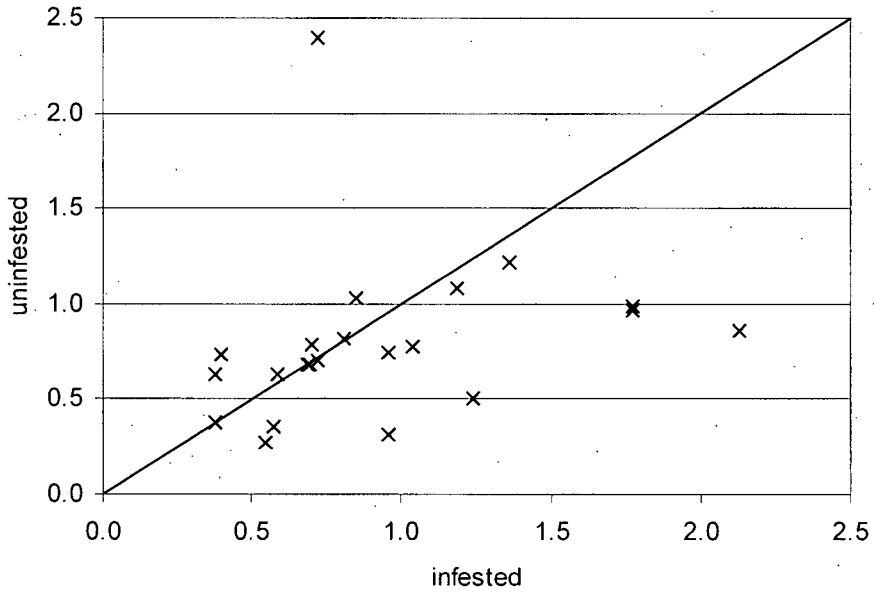



Figure 8. Pair-wise comparison of total BA for all species ($m^2$/0.01 ha): each x indicates a tree pair; values below the line indicate that the value for the infested tree was greater than the uninfested tree.



Stepwise logistic regression (entry significance level at $\alpha$ = 0.15 and removal significance level at $\alpha$ = 0.20) produced the likelihood of a given tree infested ($P_i$) to be:

$$P_i = e^{(1.6827-6.8206\,LCR+2.1552\,BAofFd)} \Big/ \left(1 + e^{(1.6827-6.8206\,LCR+2.1552\,BAofFd)}\right) \qquad [2]$$

This model is significant (likelihood ratio test P = 0.01). The application of this equation is limited to the sampled population: i.e. Douglas-fir trees greater than 40 cm in dbh in ICHdw of KLFD.

3.2. Generally Applicable Models

BA, dbh, and BA periodic increment variables were square-root transformed to meet the normality assumption. Data were weighted for the appropriate weighting factor for the Target matrix. Logistic regression with stepwise selection ($\alpha$ = 0.15 for entry and $\alpha$ = 0.20 for removal of variables) indicated that LCR and average dbh (avgDBH) of plots were significant in assessing the probability of a given tree being infested:

$$P_i = e^{(-0.0254-7.5823\,LCR+0.0602\,avgDBH)} \Big/ \left(1 + e^{(-0.0254-7.5823\,LCR+0.0602\,avgDBH)}\right) \qquad [3]$$

This model is significant (P=0.013) using the likelihood ratio test.

A large LCR, i.e. a longer crown, and a smaller average diameter were associated with lower probability of infestation. This model applies to the study areas in ICHdw of KLFD. Further testing and verification are required before the model is extrapolated into adjacent areas.

3.3. Carbon Isotope discrimination as an indicator of DFB susceptibility

The mean $\delta^{13}C$ value for infested trees (-24.19) was significantly higher than that for uninfested trees (-24.64), indicating that infested trees were more water-use efficient than uninfested trees. Both values are quite high, suggesting that both infestation classes expressed high water-use efficiency. A model to predict probability of infestation was found to be:

Equation 3.

$$P_i = e^{(18.0209+0.7405\delta^{13}C)} \Big/ 1 + e^{(18.0209+0.7405\delta^{13}C)}$$

This model was significant (likelihood ratio test, $p < 0.05$).

## 4. Discussion

The comparisons of infested and uninfested Douglas-fir trees in this study indicated that the tree, stand and site characteristics most closely associated with DFB infestation are: live crown ratio, basal area and aspect. Stepwise logistic regression indicated that LCR and BA of Douglas-fir in the plot were the factors most closely associated with infestation. Uninfested trees tended to have lower BA of Douglas-fir and/or larger LCR.

A large LCR is indicative of a tree having grown in a relatively open stand where light reaches the lower branches. Open stands allow higher wind speed (Spittlehouse *et al.* 2004), which is adversary to beetles' flight and olfactory detection of suitable host. A larger LCR may also indicate that uninfested trees have greater photosynthetic ability, which would boost growth and defence; however, LCR does not always directly translate to leaf area. A longer crown may simply act as a physical obstacle to DFB which attack mid to higher bole. This finding suggests that silvilcultural practices which increase LCR by reducing crown cover around a tree early in its development, such as pre-commercial thinning, thinning, or species mix, may reduce the

likelihood of the tree being attacked by DFB.

Clumping of trees, measured as BA in a plot, may improve conditions for beetles by reducing wind speed, allowing for better semiochemical communication and easier flight. Also, the resulting competition for resources may weaken tree defense systems, making them more susceptible to mortality from DFB. The greater basal area of host species in plots with infested trees is consistent with reports that clusters of bait trees are more effective in capturing bark beetles than individual bait trees (J. Castonguay, personal communication). The basal area of Douglas-fir was even more closely related to DFB infestation, possibly because intraspecific competition among trees is stronger for resources such as moisture and light than interspecific (Smith and Grant 1986). Douglas-fir purity was not found to be important in this study. This is not consistent with previous models (Province of British Columbia 1995, Shore and Safranyik unpub). Combined with the significant result from BA of Douglas-fir, it suggests that amount of other species, which affects the calculation of purity, is not important.

These findings both indicate that reducing the basal area of trees, particularly reducing the clumping of Douglas-firs in these forests, may reduce their susceptibility to DFB.

It is generally believed that south-facing slopes are more susceptible to DFB (Province of British Columbia 1995, Shore *et al.* 1999), but there was little evidence of this in this study. In the general model, there was no significant relationship between aspect and DFB infestation. In the paired-tree study, the aspect influence was significant, but there was no apparent trend that was easily interpreted. Specifically, there was little evidence of trees on south-facing slopes to be susceptible, which would appear on a 1-to-1 graph as data points below the 1-to-1 line below 180 degrees (i.e., south) and above the line elsewhere.

Some findings were consistent with previous reports, but a few were contradictory. Growth rates

(Province of British Columbia 1995, Shore *et al.* 1999, Shore and Safranyik, unpub) and phloem thickness (Shore *et al.* 1999) have been reported as important parameters in assessing hazard. In this study, 5- year and 10-year radial growth rates and their variations (e.g. basal area growth) were not correlated with infestation status (r = 0.1) or phloem thickness (r = 0.1). However, I found phloem thickness difficult to measure from cores as it desiccates after trees are killed and crumbles upon coring. The influence of age was not studied, although it was previously reported as important for assessment of susceptibility (Province of British Columbia 1995, Shore *et al.* 1999, Shore and Safranyik unpub.), because the majority of trees had stem rot and did not allow for measurement of age. The radial size of the rot and the size of the remaining woody tissue were not different between infested and uninfested groups. The apparent discrepancy of results of this study and previous models may be ascribed to the scale of study. I focused on tree-scale factors while others examined stand-scale factors.

### 4.1. Carbon isotope discrimination as an indicator of susceptibility

Infestation status of trees had a significant relationship with $\delta^{13}C$ values from wood samples representing a five-year period previous to infestation. Isotopic composition did not correlate highly with any of the other measured variables (e.g. dbh, height, LCR, sapwood area, and aspect); therefore, $\delta^{13}C$ assessment may provide an independent tool for assessing tree susceptibility to DFB. Higher $\delta^{13}C$ values for infested trees support the hypothesis that moisture stress increases bark beetle susceptibility, but further studies are needed as $\delta^{13}C$ values could also be affected by other factors such as nutrient availability and light (Sparks and Ehleringer 1997, Smith *et al.* 1976). Note also that genetic differences in water-use efficiency and isotopic discrimination between individuals are well-documented in trees (e.g. Zhang 1997). This result suggests that physiological attributes influence susceptibility, possibly related to genetics and/or phenotypic expression.

In this research, whole wood samples (including fugal hyphae) were powdered and analyzed. Including fungal tissues in samples is beneficial if fungi fractionate carbon isotopes when growing in tree tissues, leaving behind carbon isotopes in a different ratio than before fungal infection. Bias could result, however, if fungi transport carbon across the annual growth rings, bringing in or extracting carbons of different isotope ratio into or out of the sampled area. Examination of extracted cellulose may eliminate the latter concern.

### 4.2. Management implications: Reduction of DFB hazard

Douglas-fir trees in ICHdw of KLFD should be planted in areas or spots that offer greater moisture availability. Ones in moister spots, such as depressions should be left during pre-commercial thinning. To promote larger live-crown ratios, young Douglas-fir trees should be given wide spacing. The age at which spacing is required and the distance of spacing required needs be determined by further studies combined with critical LCR limit calculated using Equation 2. Forest managers should avoid growing mature Douglas-fir trees in clumps to minimize susceptibility to DBF infestation. Susceptibility of mature Douglas-fir trees in ICHdw in KLFD can be determined by BA of 0.01-ha plots around trees combined with LCR using Equation 2.

## 5. Conclusions

- Large live crown is associated with lower susceptibility of Douglas-fir trees to Douglas-fir beetle infestation.

- Crowding of Douglas-fir trees is associated with higher susceptibility.

- A Douglas-fir tree surrounded by large-diameter trees is more susceptible than those surrounded by smaller stems.

- Infested trees had higher proportions of $^{13}C$ than uninfested trees, linking susceptibility with moisture stress.

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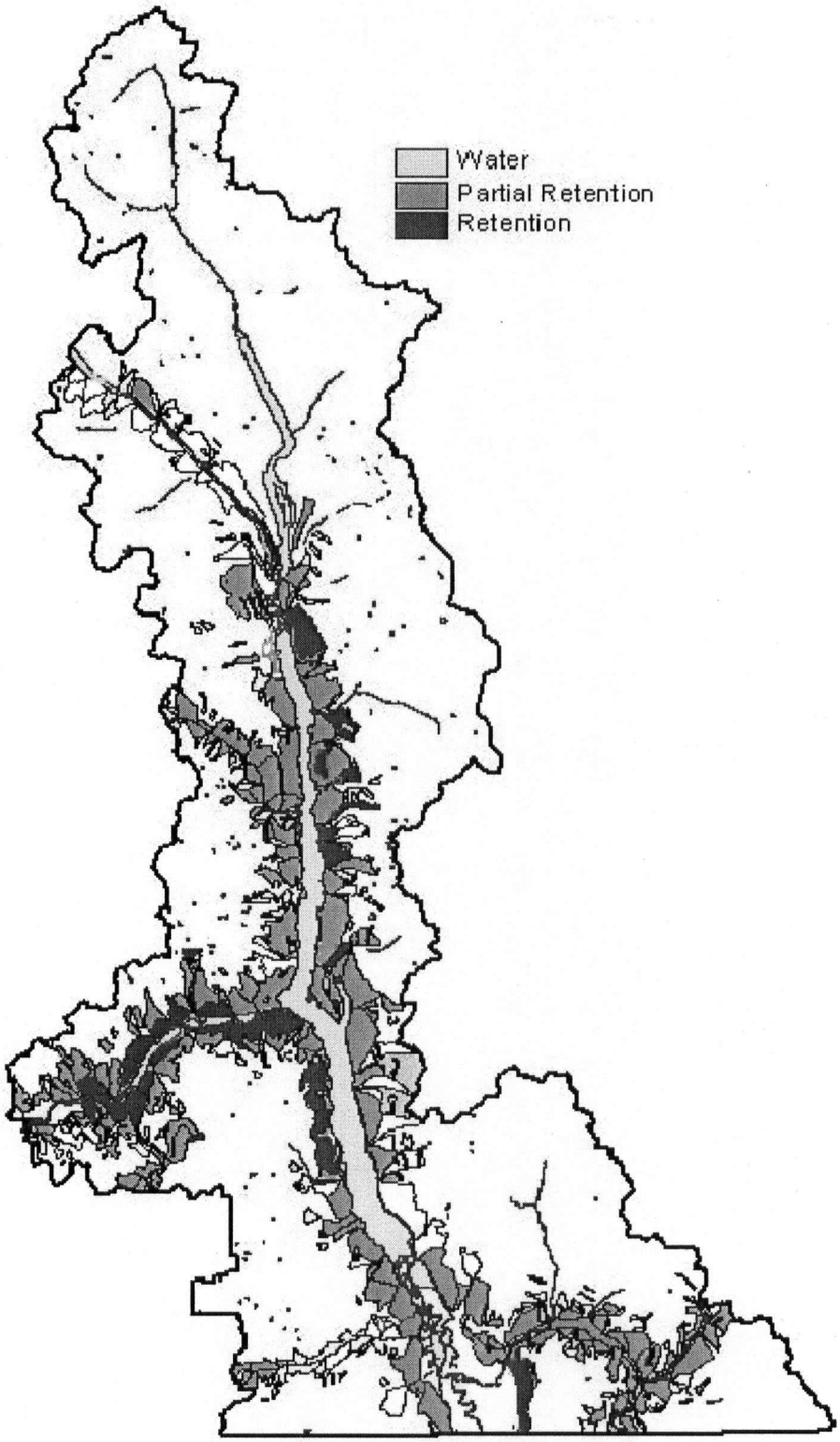
## Appendix A: Maps

Map 1. Visibly sensitive areas in KLFD. (http://www.for.gov.bc.ca/KLFD/planning/visual.htm)



Map 2. Interior Cedar-Hemlock dry-warm subzone (ICHdw) in KLFD. (Map adapted from http://www.for.gov.bc.ca/KLFD/planning/bio.htm)

Map 3. Operability distribution in KLFD.
(http://www.for.gov.bc.ca/KLFD/planning/oprabil.htm)