THE EFFECTS OF MOUNTAIN PINE BEETLE ATTACK ON LODGEPOLE PINE WOOD MORPHOLOGY AND CHEMISTRY: IMPLICATIONS FOR WOOD AND FIBER QUALITY

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ABSTRACT

The mountain pine beetle, *Dendroctonus ponderosae* Hopkins, is currently devastating the lodgepole pine resource in western Canada, and in an attempt to circumvent the problem significant volumes of infested or dead wood are being harvested. In order to fully utilize the killed resource, it is crucial to understand how the pine beetle impacts wood quality. A thorough analysis of beetle-killed and sound lodgepole pine trees indicated that the infested sapwood and heartwood had substantial moisture loss, and that the moisture content decreased with increasing tree height when compared to sound wood. The infested wood was also shown to have a lower specific gravity than sound wood, and tended to decrease with increasing tree height. Chemical analysis indicated that the infested sapwood contained significantly lower concentrations of extractives when compared to sound sapwood, and that extractives content increased towards the crown. Additionally, the infested sapwood also had lower lignin and hemicellulose contents when compared to the sound sapwood. Wood permeability showed that infested sapwood was more permeable than sound sapwood, while the opposite was true for the heartwood, with the sound heartwood being more permeable than the infested heartwood. Permeability in both sapwood and heartwood varied with tree height and correlated with extractives content. These chemical and morphological changes significantly influence the quality of wood and fiber obtained from this substantial resource.

Keywords: Mountain pine beetle, lodgepole pine, sapwood, heartwood, moisture content, specific gravity, extractive content, lignin content, carbohydrate content, permeability.

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INTRODUCTION

The mountain pine beetle, *Dendroctonus ponderosae* Hopkins, is native to North America, and is one of the most damaging bark beetles attacking lodgepole pine. Geographically, it is known to inhabit an area spanning northern Mexico (latitude 31° N) to northwestern British Columbia (latitude 56° N), and from the Pacific Coast east to the Black Hills of South Dakota. In Canada, the range of the mountain pine beetle is continuing to extend east of the Cypress Hills in Alberta, covering an area 1100 km long and 450 km wide (Safranyik et al. 1999). The beetle has been known to infest all native pines and several exotic species in its range. However, in western Canada, lodgepole pine is the beetle's preferred host (Safranyik 1978; Safranyik et al. 1999).

The attacking behavior of the mountain pine beetle is very intricate, and is mediated by pheromones (insect produced) and kairomones (host produced) (Klein et al. 1978). The female beetle releases an aggregating pheromone, transverbenol, after penetrating into the bark of the tree, and this pheromone is combined with small amounts of exo-brevicomin, which is produced by the male beetle. This combination, along with terpenes produced from the host, directs other beetles to the tree, and consequently becomes a signal for mass attack. Terpenes in lodgepole pine are largely comprised of β-phellandrene, with small amounts of α-pinene and myrcene (the two most influential terpenes), as well as β-pinene, 3-carene, and camphene (Shrimpton 1973; Koch 1996).

The mountain pine beetle generally breeds in the moist phloem of large-diameter trees (Moeck and Simmons 1991; Koch 1996), and is known to fly and disperse at mid-bole region of lodgepole pine tree in both thinned and unthinned stands. Typically, the average height of initial attack ranges between 2.0 and 5.0 m, and infestation then spreads up, down and around the bole (Amman and Walter 1983).

During mass attack, the mountain pine beetles inoculate the tree with blue-staining fungi, primarily the *Ceratocystis* species and several species of *Europhium.* The presence of these fungi ultimately results in tree mortality. The fungus is introduced into the sapwood of trees under beetle attack from pouch-like structures (mycangium) in the head of the beetle (Harvey 1979; Koch 1996). However, the associated blue-staining fungi do not appear to be essential to mountain pine beetle nutrition (Whitney 1971; Shrimpton and Thomson 1982; Koch 1996). As the beetles tunnel into the inner bark region, they inoculate a "fungal complex" into the host, and propagules of the complex develop and grow in the beetle feces within the beetle galleries. Eventually, hyphae grow into the radial parenchyma tissue of the sapwood to where they are initially confined (Whitney 1971; Ballard et al. 1983). The fungal hyphae then penetrate the primary cell walls or ray parenchyma and very quickly propagate. Subsequently, the hyphae penetrate the tracheids and maneuver from tracheid to tracheid via pit pairs (Ballard et al. 1983). Ballard et al. (1983) suggest that the proliferation of the blue stain fungi impede transpiration by increasing the frequency of aspirated pits, and disrupting the flow of resin. Although the mechanism of staining in host colonization is not entirely clear, earlier investigations demonstrated that stained portions of the sapwood were generally drier than unstained portions, and that water conduction was impaired in the stained portions (Nelson 1934; Bramble and Holst 1940).

Following infestation, standing trees begin to rapidly deteriorate before tree death through the incursion of blue stain. Blue stain is a major problem as it significantly impacts lumber value (Fahey et al. 1986; Koch 1996), and irreversibly impacts wood quality (Reid 1961). For example, it has been shown that killed trees are routinely prone to stem splitting, which affects value-added product recovery in sawmills, chip quality and pulping (Fahey et al. 1986). The substantial reduction in moisture content of the sapwood is believed to be associated with the presence of blue stain in the sapwood, and with the successful development of the beetle broods. However, it has not been established which or whether any of these conditions are causal and which are merely effect (Reid 1961; Nebeker et al. 1993).

In British Columbia, lodgepole pine stands constitute a major commercial resource, such that they comprise 50% of the province's interior an-

nual harvest. Recent figures suggest that the volume of dead lodgepole pine attributed to the mountain pine beetle epidemic in BC alone, encompasses more than 108 million cubic meters, which has been estimated to be worth roughly $9 billion USD to the forest industry (Penner 2002). In an attempt to circumvent this crisis, abundant volumes are currently being harvested and entering the market. This measure is only a response to the problem, not a preventive remedy. This paper describes an exploratory study that attempts to characterize the chemical and morphological changes in lodgepole pine wood resulting from the infestations by the mountain pine beetle.

MATERIALS AND METHODS

Sample procurement

A dead (infested with mountain pine beetle) and sound standing lodgepole pine tree were harvested from the same site in the dry, warm subzone of the sub-boreal spruce zone, at the University of British Columbia Alex Fraser Research Forest located in Williams Lake, BC. The trees were harvested after ecological assessment of the plot was completed to give an estimate of site quality. Trees sampled for this study were roughly 12 m in length, 440 mm in diameter at breast height and approximately the same age (85–95 years). The infested tree had been attacked by mountain pine beetle approximately 8 months prior to harvest.

Both the sound and infested lodgepole pine trees were bucked and debarked. A biscuit was cut from the boles at breast height (1.5 m) and following in four-meter increments (5.5 m and 9.5 m). Each biscuit was analyzed for sapwood and heartwood using a sapwood-heartwood indicator (equal volumes of *o*-anisidine hydrochloride and 10% sodium nitrite) for pines. The biscuits were cut in half; one quarter of the biscuit was used for moisture content determination, while the other quarter was used for wood specific gravity and permeability determination. The other half of the biscuit was used to investigate wood chemistry; including total extractives (gravimetric), total lignin (acid soluble and acid insoluble), and carbohydrate content, as well as for microscopic analyses.

Chemical characterization

Wood chemical analyses were determined according to the standard TAPPI methods in quintuplet. In short, all samples were first ground in a Wiley mill to pass through a 0.4-mm (40-mesh) screen. The ground wood was then soxhlet-extracted with 100 mL acetone for 8 h to remove extractable components, and to minimize the formation of "pseudolignin" during Klason analysis. The total weight of extractable components was determined gravimetrically by rotary-evaporation, and expressed as a percentage of the original weight of wood sample. The extracted lignocellulosic material was air-dried to remove solvent and then analyzed in quintuplet for sugar and lignin composition as follows.

A 0.2-g sample of extracted wood was transferred to a 15 mL reaction vial in an ice bath. A 3 mL aliquot of 72% (w/w) H_2SO_4 was added to the sample and thoroughly mixed for 1 min. The test tube was immediately transferred to a water bath maintained at 20°C, and was subsequently mixed for 1 min every 10 min. After 2-h hydrolysis, the contents of each test tube were transferred to a 125 mL serum bottle, using 112 mL nanopure H_2O to rinse all residue and acid from the reaction vial. The serum bottles (containing 115 mL 4% (w/w) H_2SO_4 plus wood) were sealed with septa and autoclaved at 121°C for 60 min. Samples were allowed to cool, and the hydrolyzates were vacuum-filtered through preweighed medium coarseness sintered-glass crucibles, and then washed with 200 mL warm (~50 °C) nanopure H_2O to remove residual acid and sugars, and dried overnight at 105°C. The dry crucibles were re-weighed to determine Klason (acid-insoluble lignin) lignin gravimetrically. The filtrate was then analyzed for acid-soluble lignin by absorbance at 205 nm according to TAPPI Useful Method UM250.

The concentration of sugars in the filtrate was determined using High Performance Anion Exchange Liquid Chromatography (HPAELC). The HPLC system (Dionex DX-500, Dionex, CA, USA) was equipped with an ion-exchange PA1 (Dionex) column, a pulsed amperometric detector with a gold electrode, and a Spectra AS3500

autoinjector (Spectra-Physics, CA, USA). Prior to injection, samples were filtered through 0.45 μm HV filters (Millipore, MA, USA) and a 20 μL volume of sample was loaded, containing fucose as an internal standard. The column was equilibrated with 250mM NaOH and eluted with de-ionized water at a flow rate of 1.0 mL/min.

The extractives were analyzed for composition by gas chromatography. Gas chromatography (GC) analysis was performed on a Hewlett-Packard 5890 Series II Gas Chromatograph equipped with a Hewlett Packard 6890 Series injector and a 10 m DB-XLB column (J&W Scientific) using a modification of the method of Fernandez et al. (2001).

Wood moisture content and specific gravity

The moisture content was determined using the standard TAPPI Test Method T 263 cm-97 for basic density and moisture content of pulp wood. Wood specific gravity evaluation was performed on triplicate wood core samples for the sound and infested trees, for heartwood and sapwood, as well as at different positions along the height of the trees for a total of 36 samples, in accordance to the ASTM Standard Test Method B (D 2395–93 re-approved 1997)—Volume by Water Immersion, Mode IV.

Wood permeability

Longitudinal specific permeability was determined using the falling water volume displacement method (Siau 1984, 1995). Permeability analysis was performed on triplicate wood samples (18-mm × 50-mm cylinders), taken randomly from heartwood and sapwood areas from the sound and infested trees; as well as along different positions of the trees, starting at breast height and followed by 4-m increments. In order to eliminate the influence of moisture content on permeability, the wood samples were conditioned in a conditioning chamber (4.5 cubic ft Climate-Lab) at 23°C for two weeks so to equilibrate the moisture content to 12%. Using a razor blade, surface cuts were made on each end of the wood sample prior to inserting the specimen into the apparatus. Longitudinal specific permeability was then determined by using the following equation:

$$k_g = \frac{V_d CL\left(P_{atm} - 0.074\ \bar{z}\right)}{tA(0.074\bar{z})\left(P_{atm} - 0.037\ \bar{z}\right)} \times \frac{0.760 m\ Hg}{1.013 \times 10^6\ Pa} \quad (1)$$

$$C = 1 + \frac{V_r(0.074\ \Delta z)}{V_d\left(P_{atm} - 0.074\right)\bar{z}} \quad (2)$$

where:

k_g = longitudinal superficial permeability ($\mu m^3/\mu m$)
V_d = $\pi r^2 \Delta z$ (r = radius of measuring tube (m)) (m^3)
C = correction factor for gas expansion as a result of change in static head and viscosity of water
L = length of wood specimen (m)
P_{atm} = atmospheric pressure (mHg)
$\bar{z}$ = average height of water over surface of reservoir during measurement (m)
t = time (s)
A = cross-sectional area of wood specimen (m^2)
Δz = change in height of water during time t (m)
V_r = total volume of apparatus above point 1 (including volume of hoses) (m^3)

Microscopy

Duplicate wood samples were randomly selected from the heartwood and sapwood in both the infested and sound trees at three different tree heights. The samples were cut into rectangular-shaped blocks measuring 10 mm × 10 mm × 20 mm. Tangential, radial, and transverse splits were made with single-edged razor blades for each sample. The wood specimens were then placed into scintillation vials and submerged in acetone for 24 h. After 24 h, the wood samples were removed from the vials, dried on bibulous paper, and then mounted on Scanning Electron Microscope (SEM) aluminum stubs and sputter-coated

with 60:40 gold palladium alloy using a Hummer VI Sputtering System. The sample mounts were then observed in a JEOL JSM-840A scanning electron microscope (Japan Electron Optics Laboratory) using 10 kV accelerating voltage.

Statistical analysis

Statistical analysis was conducted using a SPSS-X Version 10 software program. Two-way analysis of variance (ANOVA) was performed on the wood chemistry and permeability data to evaluate differences between samples at the 95% confidence level.

RESULTS AND DISCUSSION

Moisture content

As expected, the moisture content of the sound sapwood was higher than that of heartwood (Fig. 1). This can be explained by the fact that heartwood does not contain living cells and does not function in conducting water from roots to foliage. Sapwood, however, contains a significant proportion of living cells, which are involved in the active metabolism of the tree, and it is through the sapwood that water and nutrients are transported from roots to foliage (Koch 1996). The infested sapwood and heartwood both had substantially lower moisture contents when compared to the sound sapwood and heartwood. The sound sapwood had an average moisture content of 110%, while the infested sapwood had an average of 25%, which constitutes an 85% reduction in moisture content.

In contrast, the average moisture content of the sound and infested heartwood was 34% and 27%, respectively. These results concur with previous studies, which demonstrated that the moisture content of logs from beetle-killed lodgepole pine were frequently below 30% (fiber saturation point) of oven-dry weight (Reid 1961; Giles 1986). The moisture content of sound sapwood did not appear to vary with tree height; however, the sound heartwood and infested sapwood and heartwood moisture content appeared to decrease slightly with increasing tree height. It has been previously suggested (Nebeker et al. 1993) that water stress may likely be due to the blockage of xylem tracheids by toxic fungal metabolites produced by the fungal hyphae, or by aspiration of tracheids when propagating hyphae penetrate the cell walls. Either phenomenon may occur after fungal inoculation, but neither has been proven responsible for the loss in moisture content and subsequent tree death (Nebeker et al. 1993).

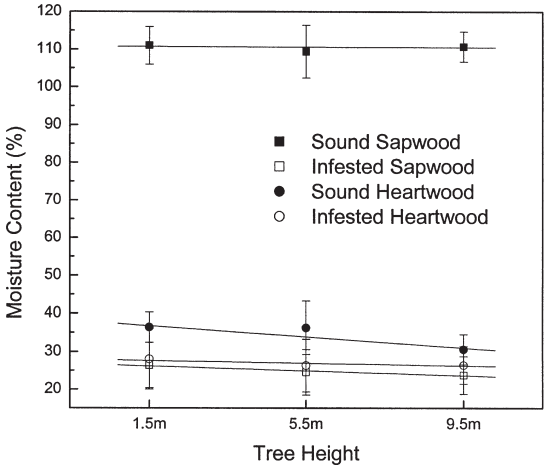

FIG. 1. Moisture content of sound and infested lodgepole pine sapwood and heartwood at different tree heights. Errors bars indicate range.

Specific gravity

Specific gravity analysis (Fig. 2) indicated that the infested sapwood (390–425) and heartwood (395–435) were statistically less dense than the sound sapwood (445–480) and heartwood (470–480). It has previously been suggested that the decline in specific gravity (density) in infested (dead) trees is a function of time since death (Koch 1996). The decrease in specific gravity in infested wood implies that the chemistry of the infested wood may be altered compared to that of the sound wood. Koch (1996) reported that sapwood density ranged from 401–476 kg/m^3 and between 405–502 kg/m^3 for heartwood in live lodgepole pine trees. Additionally, both Koch (1996) and Lieu et al. (1979) found that heartwood had significantly

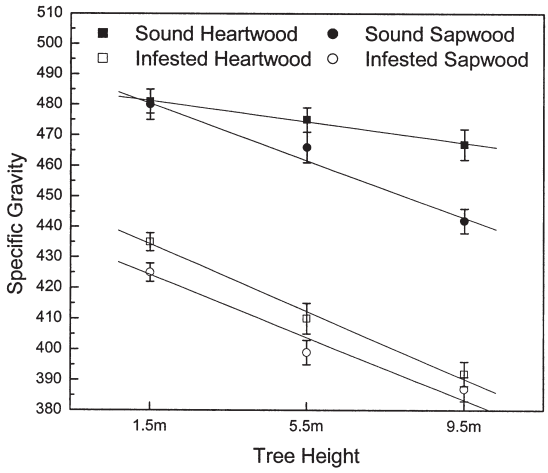

FIG. 2. Specific gravity of sound and infested lodgepole pine sapwood and heartwood at different tree heights. Error bars indicate range.

higher density values than sapwood, which concurs with our current findings. Lieu et al. (1979) hypothesized that the higher density of heartwood is likely due to the greater extractive content present.

In addition, for both sound and infested heartwood and sapwood, significant differences in specific gravity distribution at different tree heights were observed, as specific gravity tended to decrease with increased tree height. This is attributed to the fact that with increased tree height, more juvenile wood is present and therefore is of lower specific gravity. Juvenile wood tends to have shorter cells compared to mature wood cells and have different cellular structures. Juvenile wood has relatively few latewood cells and has a high proportion of thin-wall layered cells. The end result is lower density and con-

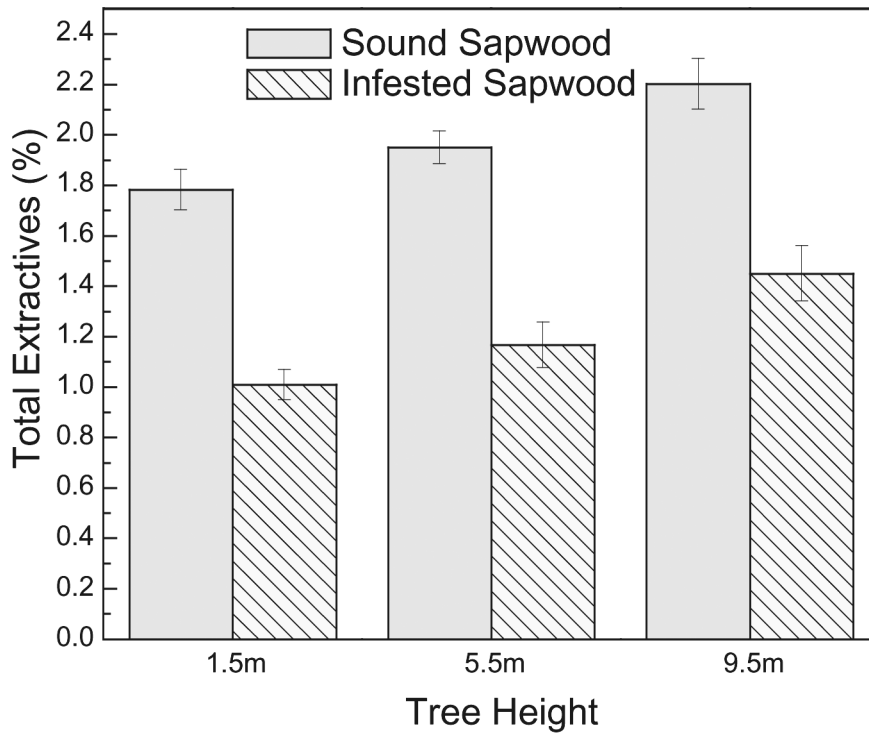

FIG. 3. Total extractive content in sound and infested lodgepole pine sapwood at different tree heights. Error bars indicate 95% confidence interval.

comitant lower strength (Jozsa and Middleton 1994).

Wood chemistry

Extractives.—Although extractives make up only a small percentage of the total chemical composition of wood, it has significant impacts on the pulp and paper processing. Extractives are important from an industrial perspective because they can impact the pulping process by causing pulp color reversion, and give rise to pitch deposits. Economic losses related to pitch problems in Kraft mills have been estimated to account for as much as 1–2 % of sales (Back and Allen 2000). Extractive content also affects the time required for chip seasoning, which is the outdoor storage of chips that allows for hydrolysis and oxidation of extractives to prevent pitch (wood resin deposits) and paper machine friction problems (Back and Allen 2000).

The percentage of extractives in sound lodgepole pine varied from 1–2% in sapwood and 2–4% in the heartwood (Fig. 3), corresponding to previous findings (Kim 1988; Shrimpton 1973; Lieu et al. 1979), who observed that green lodgepole pine contained moderate amounts of extractives, ranging from 1 to 4%. The heartwood extractive content was not significantly different between sound and infested wood. However, it decreased as tree height increased in both sound and infested wood. In contrast, there was a statistically significant difference in sapwood extractives content with changes in tree height, and between infested and sound wood (Fig. 3). Extractives content in the sapwood increased particularly towards the crown wood, and extractives content in the heartwood was higher compared to sapwood, as expected. However, it was apparent that infested sapwood had lower levels of extractives than the corresponding sound sapwood. Shrimpton (1973) previously hypothesized that the reduced level of extractives in infested sapwood could be attributed to the attacking beetle and invading fungi that utilize the cellular components.

A comprehensive analysis of the individual classes of extractives indicated that the relative proportion of extractives in the infested sapwood had also changed due to the beetle (fungal) infestation (Fig. 4). The infested sapwood generally exhibited lower total extractives content than sound sapwood, and a higher proportion of fatty and resin acid, but a lower proportion of sterols, steryl esters, and triglycerides when compared to sound sapwood. It is fair to conclude that a decrease in these classes of extractives is a result of fungal invasion, as fungi readily degrade triglycerides, steryl esters, and sterols (Shrimpton 1973; Lieu et al. 1979). Higuchi (1985) has also suggested that wood triglycerides are the most readily degraded extractives component, which results in the liberation and accumulation of fatty acids. Back and Allen (2000) suggested that an increase in concentration of resin and fatty acids in the sapwood may be due to early death of parenchyma cells. In addition, the relative proportion of extractives in both sound and infested sapwood tended to increase with tree height, which concurs with the trend demonstrated in total extractives content. The relative proportion of extractives in sound and infested heartwood were similar; however, the extractive content tended to decrease with increased tree height.

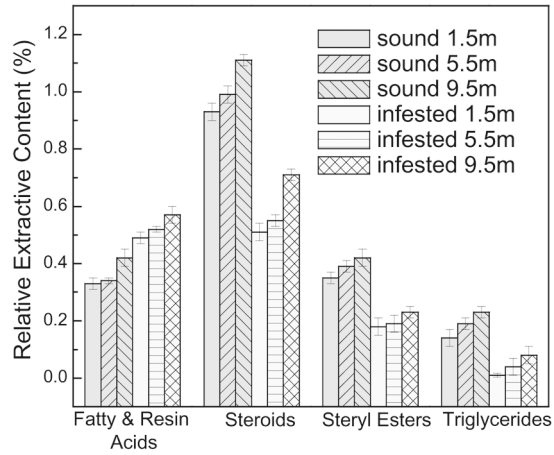

FIG. 4. Relative proportion of extractives in sound and infested lodgepole pine sapwood at different tree heights. Error bars indicate standard deviation.

Lignin content.—In general, lodgepole pine sapwood exhibits lower lignin content than

TABLE 1. *Total lignin content in sound and infested lodgepole pine sapwood at different tree heights.*

Tree height (sound)	Acid-soluble lignin (%)	Acid-insoluble lignin (%)	Total (%)
1.5 m	1.25 (0.2)	27.79 (0.5)	29.04 (0.4)
5.5 m	1.31 (0.2)	27.05 (0.3)	28.36 (0.5)
9.5 m	1.29 (0.1)	27.28 (0.2)	28.57 (0.4)
Tree height (infested)	Acid-soluble lignin (%)	Acid-insoluble lignin (%)	Total (%)
1.5 m	2.25 (0.2)	25.60 (0.4)	27.85 (0.3)
5.5 m	2.33 (0.4)	25.31 (0.2)	27.64 (0.3)
9.5 m	2.30 (0.2)	25.22 (0.2)	27.52 (0.5)

* Standard deviation shown in parentheses (n=5).

heartwood (Lieu et al. 1979). There was no significant difference in the percentage of total lignin content between sound and infested heartwood. The heartwood is not normally attacked as it contains defensive compounds (lignans, extractives, etc. . . .), and requires more than a year for the beetles to reach the heartwood—by which time the larvae will have already developed into adults and have left the tree (Reid 1962; Amman and Walter 1983). In contrast, infested sapwood lignin content was significantly different in comparison to sound sapwood (Table 1). These results correlated well with the results of Lieu et al. (1979) who showed a decrease in lignin content in the sapwood following beetle infestation. As blue-staining fungi are the primary colonizers in mountain pine beetle-killed wood, and are known not to degrade lignin, Scott et al. (1996) and Koch (1996) suggest that other decay fungi are likely present and associated with the incipient decay that often is invisible and difficult to detect. Therefore, the decrease in lignin content may be attributed to the presence of accompanying decay fungi, such as white-rot basidiomycetes which are known to preferentially degrade wood lignin.

In addition, sapwood and heartwood lignin content do not appear to vary with tree height. Infested sapwood and heartwood had significantly more acid-soluble and less acid-insoluble lignin than sound sapwood (Table 1). The difference in acid-soluble and acid-insoluble lignin in the infested wood is likely a result of the presence of fungi associated with beetle attack (insoluble lignin may be slightly modified to increase the total amount of soluble lignin present), but requires further examination before a firm conclusion can be drawn.

Carbohydrate Content.—Total carbohydrate content in the sound sapwood increased with tree height, as there is a statistically significant difference when comparing carbohydrate content at diameter at breast height (1.5 m) to mid-bole height (5.5 m) and crown wood (9.5 m). This result is attributed to the fact that photosynthesis occurs higher up the tree, in the crown, and thereby produces more sugars (Koch 1996). Carbohydrate analysis indicated that sound sapwood had higher average total carbohydrate content (66.6%) than infested (62.5%) sapwood (Fig. 5).

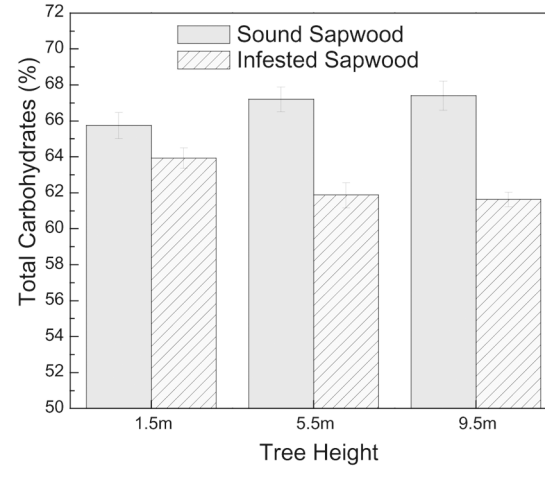

FIG. 5. Total carbohydrate content in sound and infested lodgepole pine sapwood at different tree heights. Error bars indicate 95% confidence interval.

Earlier studies (McGovern 1951; Lieu et al. 1979) also demonstrated that holocellulose (cellulose and hemicellulose) content in sapwood of green lodgepole pine wood had slightly higher carbohydrate content than infested wood. Furthermore, the difference in carbohydrate content between sound and infested sapwood suggests that it is due to the removal (consumption) of low molecular, soluble carbohydrates by microorganisms in the infested wood. It has been shown that fungi typically penetrate, invade, digest, and absorb soluble constituents when invading wood (Zabel and Morrell 1992).

The carbohydrate content of the infested sapwood decreased with increasing tree height. This latter phenomenon is likely due to the fact that the tree is more prone to beetle attack near the mid-bole of the tree (Amman and Walter 1983). As the mountain pine beetles and associated fungi invade the host, they decompose and consume elements critical to plant photosynthesis (Zabel and Morrell 1992). There was not a significant difference in heartwood carbohydrate content between sound and infested wood, or among tree height levels.

A thorough evaluation of the specific carbohydrates indicated that the infested sapwood had a significant decrease in hemicellulose-derived sugars for all tree heights. This result is due to the fact that hemicellulose sugars are soluble, and the first material consumed by fungi during incipient growth on lignocellulosic materials (Higuchi 1985; Zabel and Morrell 1992). Table 2 shows that aside from glucose, mannose is the dominant constituent of hemicellulose, followed by xylose, galactose, and arabinose. The infested sapwood had lower contents of all hemicellulose sugars (with the exception of glucose); however, mannose, xylose, and arabinose appeared to be the most readily degraded sugars. In both infested heartwood and sapwood, there is significantly more glucose content (by weight) compared to sound wood, which is likely related to the removal of other cell-wall constituents during fungal infestation. No significant difference with regards to glucose and hemicellulose content with tree height was apparent.

Longitudinal specific permeability and microscopy

The sapwood was significantly more permeable than heartwood. Furthermore, it was shown that infested sapwood was significantly more permeable than sound sapwood, while sound heartwood was more permeable than infested heartwood (Figs. 6 and 7). A microscopic analysis clearly showed the presence of fungal hyphae in infested sapwood (Fig. 8). In addition, substantially more fungal hyphae were observed higher up the tree in the mid-bole and crown wood. Thus, it is fair to conclude that the infested sapwood may be more permeable as a result of fungal infestation, as the fungi penetrate and proliferate within the pit membranes and primary cell walls of ray parenchyma cells. The majority of decay fungi generally maneuver through the wood by direct pit penetration, and

TABLE 2. *Carbohydrate composition of sound and infested lodgepole pine sapwood at different tree heights for a total of 30 samples.*

Tree height (sound)	Arabinose (%)	Galactose (%)	Xylose (%)	Mannose (%)	Glucose (%)
1.5 m	2.04 (0.1)	2.14 (0.2)	5.62 (0.4)	11.51 (0.2)	42.51 (0.5)
5.5 m	2.13 (0.2)	2.23 (0.2)	5.98 (0.4)	11.44 (0.5)	42.72 (0.4)
9.5 m	2.11 (0.1)	2.34 (0.3)	6.13 (0.3)	11.32 (0.3)	42.76 (0.4)
Tree height (infested)	Arabinose (%)	Galactose (%)	Xylose (%)	Mannose (%)	Glucose (%)
1.5 m	1.46 (0.5)	2.01 (0.3)	5.27 (0.3)	10.94 (0.4)	44.22 (0.3)
5.5 m	1.45 (0.5)	2.00 (0.6)	5.30 (0.2)	10.35 (0.1)	44.53 (0.4)
9.5 m	1.45 (0.4)	2.07 (0.4)	5.34 (0.2)	10.21 (0.2)	44.70 (0.3)

* Standard deviation shown in parentheses (n=5).

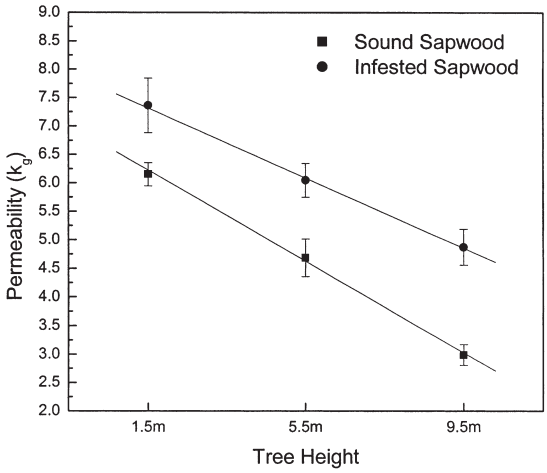

FIG. 6. Longitudinal specific permeability of sound and infested lodgepole pine sapwood at different tree heights. Error bars indicate 95% confidence interval.

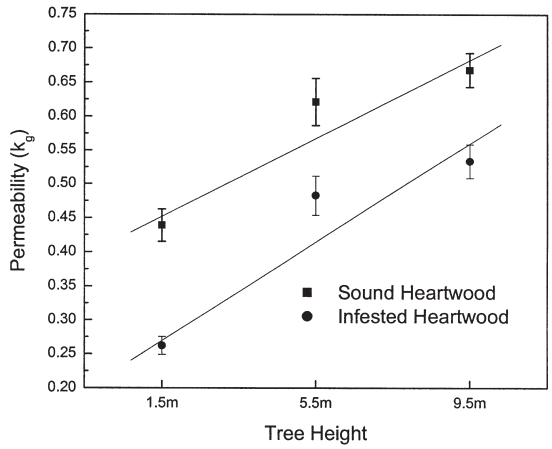

FIG. 7. Longitudinal specific permeability of sound and infested lodgepole pine heartwood at different tree heights. Error bars indicate 95% confidence interval.

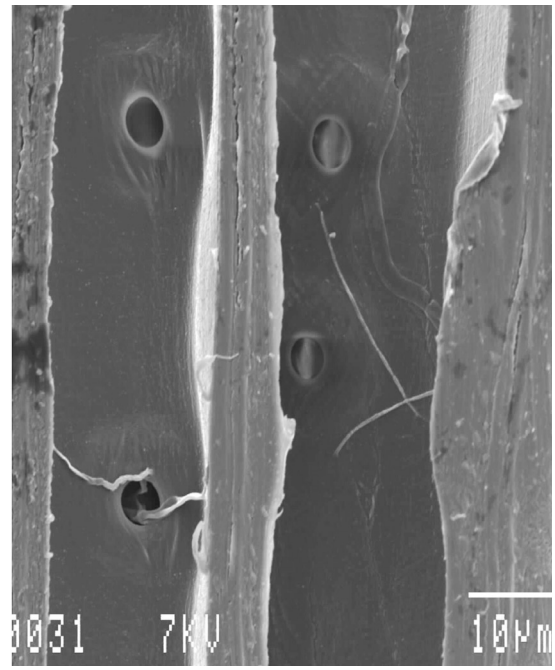

FIG. 8. Scanning electron micrograph of fungal hyphae in infested lodgepole pine sapwood at mid-bole height (1800× magnification).

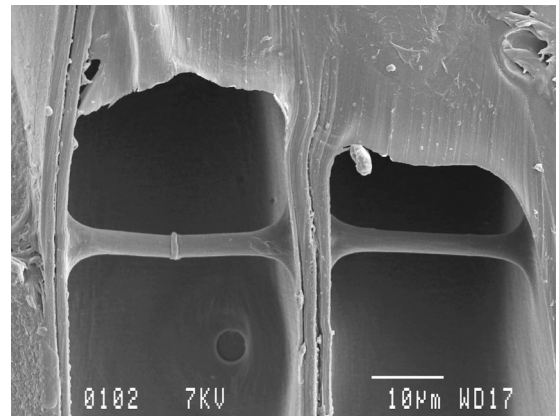

FIG. 9. Scanning electron micrograph of trabeculae in infested lodgepole pine sapwood at mid-bole height (2400× magnification).

with the removal of the pit membrane (through enzymatic digestion), the wood becomes more receptive to the movement of fluids. Consequently, the changes induced by fungal pit degradation result in the infested wood's increased capacity to absorb and desorb liquids more readily than sound wood (Zabel and Morrell 1992). In addition, trabeculae were also observed in the tracheids (Fig. 9) of the infested sapwood; these structures are rod-like extensions of cell wall material that occasionally transverses the lumens of wood cells from one tangential wall to another. Trabeculae have been thought to form as a result of tree wounding and

cambial exposure to fungal attack (Butterfield and Meylan 1979).

It was also shown that the heartwood contained an abundant number of aspirated pits, and thus supported the observed lower permeability (Fig. 10). However, for the infested heartwood, unaspirated pits were undetectable, which has been attributed to rapid removal of water from the onset of infestation. Unlike the trend in sapwood, the permeability of sound heartwood was significantly higher than infested heartwood, possibly because fungal penetration was absent.

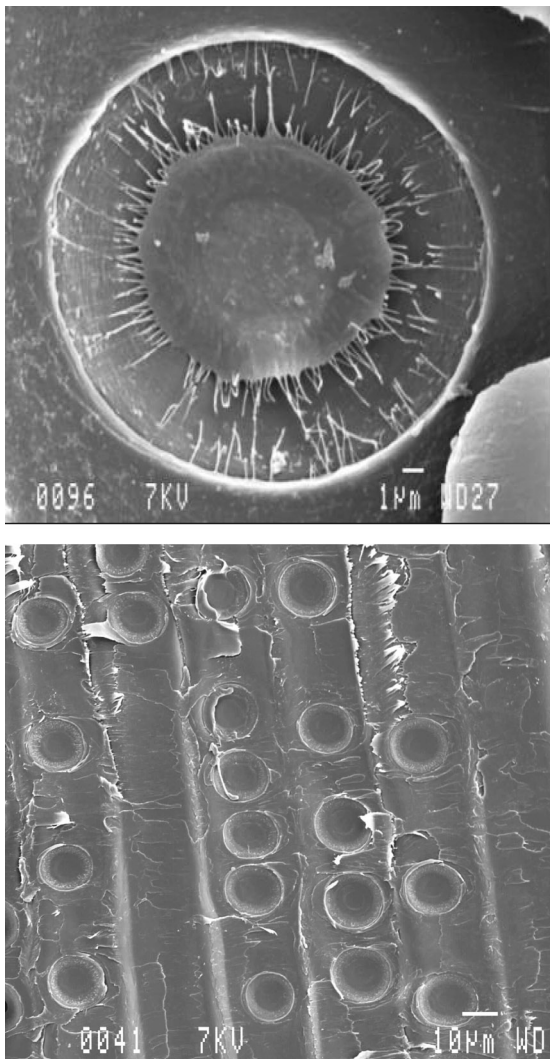

FIG. 10. Scanning electron micrographs of (A) an unaspirated pit in sound lodgepole pine (4500× magnification) and (B) aspirated pits in infested lodgepole pine heartwood at mid-bole height (2200× magnification).

The effect of tree height on permeability showed that for both the sound and infested heartwood, permeability tended to increase with tree height. This increase in permeability with tree height is likely due to the decreased concentration of extractives towards the crown. Conclusions by Koch (1996), Flynn (1995), and Rice and D'Onofrio (1996) all support these findings, as they independently indicated that differences in permeability are generally due to differences in aspiration and the total amount of extractives. Resin deposition can vary substantially within the tree, and extractives in wood are known to impede flow through the cells and decrease permeability (Flynn 1995; Rice and D'Onofrio 1996). In addition, Koch (1996) suggested that the tree height at which heartwood no longer occurs varies from 7 m to 14 m, and is comprised of mostly juvenile wood and earlywood cells. The concentration of juvenile wood increases with tree height, and is distinguished by thinner cell walls and lower latewood content, which is known to possess fewer and smaller bordered pits compared to earlywood (Jozsa and Middleton 1994). Since permeability is largely related to the number of pit membrane openings and is limited by the amount of latewood (Koch 1996; Bao et al. 1999), the increase in permeability in heartwood towards the upper bole can also be explained by the increased presence of earlywood and juvenile wood, and the decrease in latewood content. Conversely, the sapwood permeability results indicated that permeability tended to decrease towards the upper bole, which is likely related to the increased concentration of extractives towards the crown. Extractives content and permeability were also found to be closely correlated for both sound and infested sapwood and heartwood (Figs. 11 and 12). Vologdin et al. (1979) also noticed that permeability increased progressively with the removal of extractives (phenolics). Furthermore, Rice and D'Onofrio (1996) reported that there are variations in permeability with tree height; however, they concluded that there is no consistent trend in terms of tree height and permeability.

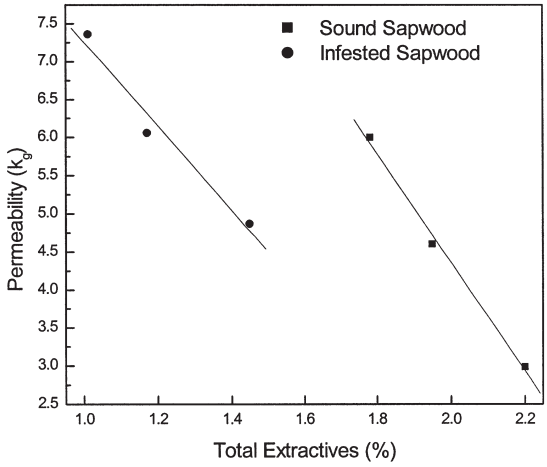

FIG. 11. Longitudinal specific permeability versus total extractives content for sound and infested lodgepole pine sapwood.

CONCLUSIONS AND IMPLICATIONS

Currently, the loss of lodgepole pine timber due to mountain pine beetle infestation is substantial. In an attempt to reduce the losses, the industry has increased the harvest of infested lodgepole pine. However, one of the deterrents to using killed trees is the lack of information on how mountain pine beetle-killed wood fiber quality is affected, and therefore the cost to industry in using this material. Based on the results of this exploratory study, it is apparent that following beetle attack, wood morphology and chemistry undergo significant changes. The greatest changes that occur are the incursion of blue stain fungi and the resultant severe water stresses in the sapwood that follow beetle invasion, which are believed to be the primary causes of tree death. The results indicate that infested sapwood and heartwood exhibit substantial moisture loss, and that the moisture content decreases with increased tree height. A severe loss in moisture content affects wood chip quality, as dry wood is known to generate more fines and pins during log chipping.

Additionally, the specific gravity (density) analysis demonstrated that infested wood is less dense than sound wood, and this is likely related to the fungal degradation of cell-wall constituents, such as lignin and carbohydrates. Specific gravity was also shown to decrease with increased tree height for both sound and infested wood. This result may be attributed to more juvenile wood being present with increased stem height. Moreover, the chemical analysis indicated that infested sapwood contains lower levels of extractives when compared to sound sapwood. No significant difference was found between infested and sound heartwood. The lower extractive content in infested sapwood is likely due to the fact that fungi utilize soluble cellular components to sustain life. Generally, increased extractives content towards the crown was shown in sound and infested sapwood, and a decrease in extractives content towards the upper bole was shown in heartwood. Although extractives make up only a small percentage of the total chemical composition of wood, it has significant impacts on pulp and paper processing, causing pulp color reversion and the formation of pitch deposits. The results of the current study imply that chips from heartwood and the top-wood section in the sapwood will require more seasoning, as more extractives are present. However, seasoning for the infested wood will not be a priority, as immediate use of this resource will be required to prevent further wood loss from decay. A comprehensive analysis of the individual classes of extractives indicated that infested wood consisted of higher fatty and resin acid proportions and lower sterol, steryl ester, and triglyceride proportions. The increased concentration of resin acids could have significant effects on aquatic ecosystems, as these components have been shown to be highly toxic to marine life.

The klason lignin analysis demonstrated that the lignin content was lower in infested sapwood compared to sound, and that no trend was found for heartwood. The reduced total lignin content in infested sapwood can be attributed to fungal infestation, as evidenced by the increased acid soluble lignin content in the infested sapwood. No apparent trend was found in the influence of tree height on lignin content. Lignin content affects pulp quality in terms of kappa number (residual lignin content), pulp yield, and chemical con-

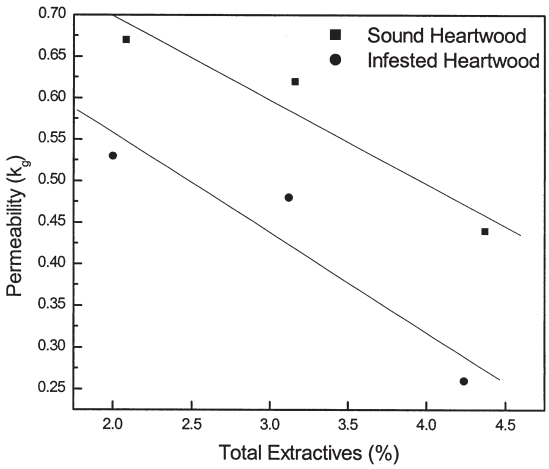

FIG. 12. Longitudinal specific permeability versus total extractives content for sound and infested lodgepole pine heartwood.

sumption in the pulping process because chemical pulping processes separate wood fibers by dissolving away this cellular component. The results imply that the infested sapwood and heartwood might be more readily pulped, as there is a lower total lignin content and more acid-soluble lignin. However, as mentioned earlier, care must be taken not to allow this material to be excessively seasoned, as it has already been subject to a beetle-fungal season before harvesting.

The carbohydrate analysis showed a reduction in carbohydrate content for infested wood as fungi consume the soluble carbohydrates more vigorously. Carbohydrate content generally increased with tree height in sound sapwood. However, carbohydrate content decreased with increased tree height in the infested sapwood, as the tree is more prone to beetle attack, particularly towards the lower bole. No trend was found for heartwood. An evaluation of carbohydrate content indicated that infested wood contained less hemicellulose-derived sugars as this material is typically the first to be consumed by fungi.

The analysis of wood permeability demonstrated that infested sapwood is more permeable than sound sapwood; while sound heartwood is more permeable than infested heartwood. From the microscopic analysis, it was found that fungal hyphae are present in infested sapwood, which is likely the primary reason for increased permeability in infested sapwood (degraded pit membranes). In contrast, the presence of aspirated pits may contribute to the heartwood being less permeable than the sapwood. Variation in permeability with tree height was shown in both sapwood and heartwood, and is likely related to the differences in concentration of extractives towards the upper bole. In wood utilization, permeability plays an important role since it directly affects lumber processing characteristics such as drying and treatment with preservatives, as well as the penetration of cooking chemicals during the Kraft pulp process.

Clearly, mountain pine beetle attack and associated blue stain fungi affect the morphology and chemistry of the wood. As the mountain pine beetle epidemic spreads, recovery of green-stage trees will be difficult, and therefore the forestry sector may be forced to utilize red and grey stage trees. The present investigation provides some insight into the effect of the mountain pine beetle and the associated blue stain fungi on wood quality. However, much more research is necessary to expand our understanding. In order to effectively use the ever-growing quantities of mountain pine beetle-killed lodgepole pine, a more comprehensive understanding of the interrelationships between time of tree death, beetle activity, wood quality, and pulp quality is required.

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