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Assessing the shelf life attributes of mountain pine beetle-killed trees

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Mountain Pine Beetle Working Paper 2008–27

MPBP Project #7.46

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2009

Library and Archives Canada Cataloguing in Publication

Magnussen, S
Assessing the shelf life attributes of mountain pine beetle-killed trees
/ by Steen Magnussen and Dave Harrison.

(Mountain pine beetle working paper ; 2008-27)
Includes abstract in French.
Includes bibliographical references.
ISBN 978-1-100-11920-5
Cat. no.: Fo143-3/2008-27E

1. Lodgepole pine--Diseases and pests--British Columbia--Vanderhoof Region. 2. Dead trees--British Columbia--Vanderhoof Region. 3. Wood--Quality --British Columbia--Vanderhoof Region. 4. Mountain pine beetle--British Columbia --Vanderhoof Region. I. Harrison, David S II. Pacific Forestry Centre III. Title. IV. Series: Mountain Pine Beetle Initiative working paper 2008-27

SB945 M78 M33 2009 634.9'7516768 C2009-980055-1

ABSTRACT

In 2006, a total of 360 lodgepole pine trees were destructively sampled from 45 sites that had been killed by mountain pine beetle. The trees were sampled from the Sub Boreal Spruce (SBS) Biogeoclimatic zone within north central British Columbia. The trees were distributed evenly across the geographic areas as well as across a sample matrix that included three classes of time since death, three classes of diameter at breast height, and three classes of soil moisture regime.

A previous report described the procedures used to the collect the data and summarized the data collected for each of the sample trees. The current study analyzes the data and presents a detailed assessment of the changes in the wood quality attributes of mountain pine beetle-killed trees that occur within 5 years since death.

Keywords: wood checks, moisture content, blue-stain, wood quality, spiral grain, bark beetle

RÉSUMÉ

En 2006, un total de 360 pins ponderosa (PP) tués par le dendroctone du pin ponderosa répartis sur 45 sites ont fait l'objet d'échantillonnages par essai destructif. Les arbres échantillonnés se trouvaient dans la zone biogéoclimatique subboréale d'épinette (SBS) du centre-nord de la Colombie-Britannique. Les arbres étaient répartis uniformément dans la zone géographique et ont été échantillonnés selon un modèle comprenant trois catégories de temps écoulé depuis la mort, trois catégories de diamètre à hauteur de poitrine et trois catégories de régime hydrique du sol.

Les procédures suivies pour recueillir et résumer les données relatives à chacun des arbres échantillonnés sont décrites dans un rapport antérieur. L'objectif de la présente étude consiste à analyser les données et à présenter une évaluation détaillée des changements qui se produisent dans les propriétés du bois des arbres tués par le dendroctone du pin ponderosa durant les cinq années suivant leur mort.

Mots-clés : gerçure du bois, taux d'humidité, bleuissement, qualité du bois, fil tors, scolyte

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INTRODUCTION

British Columbia is experiencing the most severe epidemic outbreak of the mountain pine beetle (*Dendroctonus ponderosae* Hopkins) in recorded history. Lodgepole pine (*Pinus contorta*, *var*. *Latifolia* Dougl. ex Loud) is the primary host. It is estimated that since the late 1990s the beetle has killed more than 300 million m^3 of lodgepole pine timber (www.for.gov.bc.ca/hfp/mountain_pine_beetle Accessed Feb. 12, 2009). In 2006 newly infested areas covered 9 million ha. It is anticipated that the current epidemic will decline to endemic levels by 2010; at that time the mature lodgepole pine stands will have been severely decimated.

In response to the severity and spatial extent of the infestation, there has been a sharp increase in the harvest of dead standing beetle-killed trees. Several wood attributes of standing beetle-killed trees change with time since death and are often sufficiently different from live trees to warrant the concern of those who handle and process these trees (Woo et al. 2005a, Byrne et al. 2005a, Woo et al. 2005b, Byrne et al. 2005b, Orbay and Goudie 2006, Trent et al. 2006, Chow and Obermajer 2007). The sapwood of infested trees shows discoloration by blue-stain fungi introduced by the beetle a few weeks after the initial attack, and the moisture content of sapwood and heartwood is known to decrease below fibre saturation with time since death (Woo et al. 2005b). Checks created by the release of drying stress are also much more frequent in standing dead beetle-killed trees than in live trees. Finally, as time since death increases, the risk of a secondary attack by either wood-boring beetles, infections by rot- or decay-causing fungi, or damage by insect-seeking birds and mammals increases sharply (Kim et al. 2005, Lewis and Hartley 2005, Byrne et al. 2005a, Trent et al. 2006).

The sheer magnitude of beetle-killed dead standing wood volumes expected to be harvested over the next few years makes it important to understand how time since death and site factors impact wood quality. Woo et al. (2005b) found that sapwood and heartwood from beetle-attacked trees had a substantially lower moisture content and specific gravity than sound wood (see also Harrison 2006, Byrne et al. 2005b). Infested sapwood had significantly lower concentrations of extractives, lignin, and hemicellulose, and was more permeable to solvents. These changes are known to influence the quality of both wood and fibre products. Chow and Obermajer (2007) confirmed a rapid decline in moisture content with time since death which calls for specific handling and drying procedures for beetle-killed wood.

Blue-staining of the sapwood following a beetle attack is caused by *Ophiostoma* spp. fungi for which the beetle is a vector (Kim et al. 2005, Byrne et al. 2005a, Zhu and Myers 2006). Mechanical properties and rot resistance of blue-stained lodgepole pine wood is at par with properties of non-stained wood (Byrne and Uzunovic 2005, Lum et al. 2006), and Kraft pulp production yield and costs are not adversely affected (Zhu and Myers 2006). Blue-stained wood has been mistakenly considered as being in the first stages of decay (Byrne et al. 2005a), and mechanical pulp prepared from blue-stained wood may need additional bleaching before it is considered acceptable. The extent and type of decay in standing blue-stained beetle-killed trees is generally not much different from that of non-attacked trees, at least during the first years following the attack (Kim et al. 2005, Byrne and Uzunovic 2005).

Unquestionably, the most serious loss of volume recovery and value from beetle-killed lodgepole pine arises from checking (Byrne et al. 2005a, Orbay and Goudie 2006). Checks as deep as several centimeters and up to several decimeters in length, develop within a year after the tree dies (Lewis and Hartley 2005, Harrison 2006). Checks continue to expand in both numbers and size with time since death. Studies indicate that volume losses of approximately 5% two years following attack can be expected. Orbay and Goudie (2006) found the volume recovery value was a simple linear function of check severity index (no. of checks × relative check depth × relative check length). Veneer recovery rates are also adversely affected (Wang and Dai 2005, Byrne et al. 2005a). Site conditions (wet, mesic, dry), weather conditions, handling and mill operations attenuates the effect of checks on yield and value produced (Byrne et al. 2005a, Eng et al. 2007).

The objective of this study was to assess the effects of site conditions and time since death on *i*) checking, *ii*) blue-stain, *iii*) rot and decay, and *iv*) moisture content of standing beetle-killed lodgepole pine. A large number of sample trees (360) taken from three areas, each represented by 15 sites with contrasting soil moisture regimes (dry, mesic, wet) located in the epicenter of the current epidemic allow us to quantify practically relevant effects.

MATERIAL AND METHODS

During the summer of 2006, 360 beetle-killed lodgepole pine trees from 45 sites were felled in north-central British Columbia and bucked into 2.5 m lengths with stem analysis discs taken for detailed measurements of moisture content, checking, blue-stain, and rot and decay. Stem discs were taken at stump height (0.3 m), breast height (1.3 m), and at 2.5 m intervals from stump. A final disc was taken at a location where the under-bark diameter was approximately 10 cm. The year of beetle attack (*YA*) and death of the trees was estimated using local knowledge and dendrochronology techniques. Estimates ranged from 1 to 8 years.

Sites were located in UTM grid 10 in the sub-boreal spruce (SBS) Biogeoclimatic zone in the Quesnel (16), Vanderhoof (14), and Burns Lake (15) areas (Figure 1). The 16 sites in the Quesnel area were located between Northings 5846895 and 5899403 and Eastings 499264 and 579804. For the Vanderhoof area the 14 sites were between Northings 5963819 and 6016804 and Eastings 374893 and 389510. Corresponding numbers for the 15 sites in the Burns Lake area were 5957415-6027704, and 318004-694616. Between 5 and 14 trees - with an average of 8 - were sampled per site. Sites and trees were selected to conform to a uniform distribution with respect to the following three classes: time since attack *YA* ={1-2, 3-4, ≥ 5}, three diameter at breast height classes (12.5 cm – 22.5 cm, 22.5 cm – 32.5 cm, and ≥ 32.6 cm), and three classes of soil moisture regime (dry, mesic, and wet). A total of 121 trees were in the first *YA* class, 119 in the second, and 120 in the third. Tree heights varied from 15.6 m to 34.2 m (mean: 23.9 m, standard deviation 3.2 m). On each site, sample trees were selected from within an approximately 100 × 100 m (1.0 ha) area located at least two tree-lengths from any stand edge or openings.

Area, site, tree, and disc attributes measured in the field and laboratory are listed in Tables 1 and 2. All disc measurements were carried out in the field within two to three hours of felling. Discs were protected from sun and rain until they could be processed. Increment cores for determining *YA* were collected from 22 live trees in the Quesnel area, and 21 in the Vanderhoof area. No suitable live tree was located in the Burns Lake Area.

Statistical analysis and data processing

The main focus of the statistical analyses was to quantify the effect of *YA* (time since attack/death), soil moisture regime (*SMR*) and site and tree attributes on: 1) the number, depth and width of checks; 2) the moisture content of sapwood and heartwood; 3) the incidence of rot and extent of decay; and 4) the extent of blue-stain. Most analyses were done on a per tree basis (total or average) or for observations pertaining to the first 2.5 m of the stem. When the attribute of interest depends on the stem location, the analyses were done on a per disc basis. The effects (β) considered for both *YA* and *SMR* include interactions with observed area, site, tree, and disc attributes. All available area, site, and tree attributes were considered for inclusion as predictors of the attribute of interest in a given model. However, predictors that were non-significant at the 0.05 level of statistical significance were dropped from a model (backwards stepwise elimination procedure based on *F*-tests (Draper and Smith 1981)). We employed generalized linear and non-linear mixed models with site considered as a random effect and trees within a site as equal-correlated random variables (McCulloch and Searle 2001). When disc data were used as the dependent variable, the model was extended to include the disc as a random variable with a first-order autoregressive within-stem covariance structure (Christensen 2001). For proportions (or percent data) and binary data we used a logit link function between the data (*y*) and the expected value (μ). For count data a Poisson model (Lawless 1987), a zero-inflated Poisson model (Ridout et al. 2001), and a negative binomial model (White and Bennetts 1996) were considered. We allowed for over-dispersion in attributes expressed as counts, and proportions (percent) by including a gamma–distributed random variable acting as (constant) variance multiplier (McCulloch 1997). Throughout Akaike's corrected information criterion, AIC_c, (Akaike 1977, Vaida and Blanchard 2005) was used as a guide for choosing the final model.

Given the inexact nature of *YA* and the fact that we have no prior expectation of a specific trend in the dependent variable across values of YA, we treated *YA* as a categorical variable with five nominal levels $\left(YA = \{"1","2","3","4","5+"\}\right)$, i.e. a constant off-set (β) from the general mean was estimated for each distinct *YA* value. The sum of the estimated *YA* effects sums to zero. We formed various linear contrasts of *YA* effects and tested them with a Wald's test for significant deviations from zero (Rencher 1995). A similar procedure was followed for tests of significant *SMR* effects. To summarize a trend that appeared linear, we estimated, by generalized least squares, the estimated slope of the trend.

<u>Checks</u>. It was assumed that each check registered on a disc was independent of all other checks recorded for the same tree. We also assumed that there were only a few minor (missed) checks between extracted discs. In short, the total number of checks observed on the discs is assumed to be close to but less than the actual number of checks. Large trees had more checks on extracted discs than smaller ones (correlation 0.52 for trees with checks). Therefore, our analyses used an estimate of the surface exposed to bark-beetle attack as a covariate to adjust for tree size effect. The exposed surface area was computed from the disc measurements assuming that the shape of each stem section was that of a cone-frustum (Avery and Burkhart 1983). Volume-weighted tree averages of check size (depth and width) and their variation were calculated by standard methods.

To estimate the potential loss of sawn timber wood volume, we computed for each tree a relative check depth as a volume-weighted average of the ratio of the depth of a check to the under-bark diameter of the disc. On each disc, the wood from the cambium to 1.1 times the maximum check depth was considered potentially lost for sawn timber. The area of this loss was computed for each disc and a volume-weighted relative basal area loss was computed for each tree. A relative index of a potential log-volume loss was also obtained for each tree. If, for a given stem segment, the under-bark diameter of a disc was ≥ 12.5 cm but the diameter of a check free core was less than 12.5 cm, the segment was considered unsuited as a saw-log. Again, 1.1 times the maximum check depth on a disc was used to delineate a check-free core. The proportion of log-volume potentially lost due to checks was then computed as a volume-weighted average for each tree.

<u>Moisture content (*MC*)</u>. Nine *MC* measurements were taken on each disc with a Delmhorst J-2000 meter: at the pith and in the middle of the sapwood and heartwood at each cardinal direction (Table 2). The point of measurement was moved, if needed, to avoid knots. A large number of readings were cross-checked with a second meter. Moisture content values obtained with the two meters were consistently within 1.0% of each other. Calibration measurements on 14 oven-dried discs revealed a systematic bias of the two meters of -2.1% and -2.4%, respectively. This bias persists in the results reported here. Since the meter readings were truncated to the interval from 6% to 40%, it was necessary to address the impact of this censoring process. About 8% of the readings were recorded as 40% while only one was recorded as 6%. Inspection of histograms of moisture readings suggested that a reading of 40% should be transformed to a uniform distribution between 40% and 50% for sapwood and 40% and 45% for heartwood *MC*. This transformation was achieved by adding a random term drawn from a uniform distribution on the interval [0%, 10%] in the case of sapwood, and from [0%, 5%] in the case of a heartwood. No attempt was made to address the lower bound censoring. Sapwood and heartwood moisture readings were averaged per disc before analysis.

Moisture readings from the four cardinal directions were highly correlated (sapwood > 0.89, heartwood > 0.94) and there was no important difference in heartwood *MC* between the four directions. Northwardly exposed sapwood, however, had a slightly higher (0.5%-1.2%) *MC* than sapwood exposed to other directions. Moisture content showed, as expected (for example, Chow and Obermajer 2007), an almost linear decrease with height above ground. A disc-level analysis was, therefore, pursued.

Decay and rot. The type, location (heartwood, sapwood) and extent (area) of rot and decay was classified and measured on each disc according to a protocol established by the BC Ministry of Forests and Range. Table 2 lists the recognized types of either decay or rot. The data does not allow for analyses by type; instead all decay (rot) types are pooled.

Blue-stain. The width of blue-stain was measured on each of four disc quadrants and the blue-stained area estimated in percent (Table 2). A volume-weighted tree average of the ratio of blue-stain width to stem radius under-bark was computed. A volume-weighted estimate of the blue-stained percent of the stem cross-sectional area was also obtained for each tree.

RESULTS

Checks

The observed number of checks per tree from a given area and year of attack (*YA*) followed a distribution that resembled a negative binomial more than a Poisson or a zero-inflated Poisson distribution. Histograms detailing the distributions are in Figure (2). As YA increase, the proportion of check-free trees decreases sharply and the distribution of checks per tree becomes increasingly right-skewed. In $YA=1$ the upper 95% limit was 7 checks per tree and for earlier attacks ($YA \geq 2$) this limit fluctuated between 17 and 25. One tree had 52 checks.

Sites influenced the frequency of checks but the variation was not significantly related to *SMR* ($P > 0.45$) or any other recorded site attribute. The number of checks per tree was proportional to the exposed stem surface of the tree (*SURF*), and significantly higher for trees with spiral grain (*SG*). Recently ($YA = 1$) attacked trees had fewer checks than trees that were attacked earlier ($YA > 1$ year). After adjusting for *YA*, stem surface, and spiral grain, the influence of area became non-significant. Based on AIC_c, we chose the model in (1) for the expected number of checks per tree. The among-tree distribution of the number of checks per tree on a given site was assumed to follow that of a negative binomial distribution with expectation (non-significant terms have been dropped):

$$[1] \qquad E\left(\#_{checks} \mid site = j\right) = Exp\left[\mu + \nu_j + \beta_{sg}\delta_{sg} + \beta_{surf}x_{surf} + \sum_{YA=1}^{5+}\beta_{YA}\delta_{YA}\right]$$

where μ is the overall specific mean, ν_j is a random effect of the *j*th site, β_{var} is a regression coefficient (effect) for variable '*var*', δ_{sg} is an indicator variable for spiral grain (no = 0, yes = 1), x_{surf} is the stem surface area of a tree in m^2, $\delta_i \; i = 1,\ldots,5+$ is an indicator variable taking the value 1 if *YA* = i and otherwise 0. We assume that $1/\left(1+\nu_j\right)$ is distributed as a Beta(*r,s*) random variable. Accordingly, the number of checks per tree follows a negative binomial distribution.

Conditional (*COND*) and marginal (MARG) maximum log-likelihood estimates (McCullagh and Nelder 1989) of the model coefficients are in Table 3 with estimated standard errors. Conditional coefficients apply to a typical site (mode) for which we have $\nu = 0$. Marginal coefficients are obtained after integrating out the random effects from the likelihood. Thus, MARG coefficients apply to a regional inference (across a large number of stands/sites).

The estimated difference between COND *YA* = 1 and YA = 2 effects are about 50% smaller than the corresponding MARG difference. It is a result that follows from the increase over *YA* in the among-site variation of the number of checks per tree. A model fitted to the check count on the first 2.5 m of the stem indicates a much larger increase in the number of checks between *YA* = 1 and YA = 2 than for the entire tree, and a much more pronounced effect of spiral grain. The among-tree variation within a site was substantial as witnessed by a very large variance to mean ratio close to 3 (Table 3).

Presence of spiral grain was the single most important factor (Table 3). Close to 27% of all trees showed signs of spiral grain. In Quesnel, 56 (47%) of the trees had this attribute; in contrast, just 14% and 19% of the trees did in Vanderhoof and Burns Lake, respectively. Trees with spiral grain had about 1.7 (MARG) or 1.8 (COND) times as many checks as trees without spiral grain. For the first 2.5 m of the stem, this ratio was between 13 (COND) and 8 (MARG). There was no important interaction between *YA* and presence or absence of spiral grain. Overall, the number of checks per tree would increase by about 2% (COND and MARG) for every 1 m^2 increase in stem surface area. However, this trend could not be confirmed for the first 2.5 m of the stem.

Year since death had a significant effect on the number of checks per tree (Table 3). Trees recently attacked (*YA* = 1) had an average of 2.5 (± 3.1) checks compared to 8.1 (±8.1) for trees attacked earlier (*YA* > 2, *P* <0.001). While the difference between *YA = 1* and *YA* = 2 was not significant in COND (*P* = 0.07), the number of checks in *YA = 2* trees was significantly lower (about 33%) than in trees with *YA* > 2. In MARG the number of checks in *YA* = 2 was significantly higher than for *YA = 1*. However, none of the *YA* > 1 effects were significantly different from each other (or zero). For the first 2.5 m of the stem no COND effect of *YA* reached the 0.05 level of significance, but in the MARG model the *YA = 1* effect was significantly lower than the average effect for *YA* > 1, yet *YA = 2* effects were, surprisingly, also significantly higher than for *YA* > 2.

The proportion of trees with no checks declined at an average rate of 25% (±7%) with an increase of one in *YA*. While 42% (± 5%) of the trees were check-free if *YA* ≤ 2 no more than 10% (± 2%), were free of checks when *YA* > 2 (*P* < 0.001). Again, presence of spiral grain made the odds of no checks as low as 0.05 (±0.05). Larger trees were also less likely to be free of checks. Sites explained about 45% of the variation, but areas or SMR were not significant ($P > 0.19$). Absence of checks on the lower 2.5 m of the stem did not seem to be governed by any other factor other than spiral grain.

Trees with checks were more prone to secondary damage by insect-feeding and cavity-nesting birds. The number of checks per tree was a good indicator of the extent of secondary damage by these birds. Figure 3 summarizes the trend in the multinomial probabilities of bird damage class (0 = none, 1 = low, 2 = medium, 3 = high) given the number of checks. Area, SMR, *YA* status, and spiral grain status were non-significant predictors ($P > 0.26$) and consequently dropped from further analysis. In the 'no' damage class (0), the average number of checks was 3.8 (± 4.1) compared to 16.3 (±8.8) in the 'high' (3) class.

Check size (depth and width) was dependent on soil-moisture regime, *YA* status, and presence/absence of spiral grain, but otherwise not significantly influenced by any other recorded factor once the effects of these three factors were accounted for (model: generalized linear mixed model). The within-tree variation was not in any obvious way related to either position or exposition. Significant conditional effects in volume-weighted per tree average size of checks are listed in Table 4. Marginal effects were within 2% of these values and are not listed. Trees on drier sites had significantly wider and deeper checks ($P < 0.01$) than trees on either mesic or wet sites. Differences between the two wetter categories were non-significant ($P > 0.59$), so the effects of these two *SMR* have been pooled in Table 4. Mean width of cracks on the drier sites was 3.6 mm (±1.6), but only 2.8 mm on the wetter sites (±1.1 mm). Depth of checks averaged 5.3 cm (± 1.7 cm) on the drier sites compared to 4.7 cm (±1.4 cm) on the wetter sites. A very strong effect of site moisture regime was noted in the length of checks in the first 2.5 m of the stem ($P < 0.01$). With an average length of 38 cm (±60 cm), the checks on this *SMR* was almost four times longer than on the other two SMR categories (mean: 10.2 cm ± 26 cm).

Check depth in trees with $YA > 2$ was, on average, about 5.1 cm (± 1.6 cm) or almost 1 cm deeper than in trees with $YA \leq 2$ ($P < 0.001$). No other *YA* contrast emerged as significant. Average width of checks for $YA > 2$ was 0.3 cm (± 0.1) or about 50% above the average width of 0.2 cm (±0.1) for $YA \leq 2$ ($P < 0.001$). No other *YA* contrast was significant. The within-tree variation in check size increased with *YA*. For the standard deviation of depth the increase was about 0.17 cm (± 0.03) per year and for width, 0.016 cm (± 0.002) per year. Table 4 gives further details. In consequence, the average (volume-weighted) maximum check depth also increased steadily with *YA*, from just under 3 cm (± 3 cm) in recently attacked trees ($YA = 1$) to 7 cm (± 3 cm) for trees attacked 5 or more years earlier. For check width the corresponding numbers were 0.2 cm (± 0.2 cm) and 0.6 cm (± 0.3 cm), respectively. As checks become deeper they also widen (correlation coefficient of 0.76).

Temporal trends in three measures (relative depth, relative basal area, and relative (log) volume) of a potential volume loss are illustrated in Figure 4. Results for trees with spiral grain were, for every *YA*, significantly ($P < 0.001$) different from those without spiral grain. Model-based estimates of COND and MARG effects of *YA* and spiral grain were very similar (differences were less than 1.5%). We state only the MARG results. The average relative depth of checks increased from about 5% (±6%) in *YA* = 1 to about 17% (±10%) at $YA \geq 5$. The ratio for $YA \leq 2$ was significantly lower than for $YA \geq 3$ ($P <$ 0.001) irrespective of presence or absence of spiral grain, but differences between *YA* = 1 and *YA = 2* were not significant ($P > 0.60$). For trees with spiral grain the ratio was, in most *YA,* about twice as high as the ratio in trees with no spiral grain and the ratio for *YA* =2 was significantly lower than the average ratio for $YA \geq 2$.

Temporal changes in the proportion of under-bark *BA* affected by checking were similar to those reported for relative check depth, except that the ratios were about three times higher. Potential log-sized volume losses were, in general, similar to those seen in *BA* except for an unusually high proportion of 74% (±19%) for *YA = 2* in trees with spiral grain. Statistical inference for relative *BA* and *VOL* losses confirmed the pattern already established for the relative depth.

Visual inspections of checks (number and length) on the first 2.5 m of a stem did not seem to produce reliable predictors of the number and size of checks on a per tree basis (correlations were below 0.42 and no interpretable trend emerged).

Moisture content (MC)

Within a tree, the moisture content declined from 1.3 m above ground to the top of a tree nearly linearly with relative tree height (*RHT, RHT* at base ≡ 1/ tree height, *RHT* at top of tree ≡ 1). The final model for moisture content (*MC*) for the *k*th disc $\left(k = 2,3...,15\right)$ in the *j*th tree on the *i*th site was (model selection criterion: AIC_c)

$$MC_{ijk} = \mu + \sum_{SMR} \beta_{SMR} \times \delta_{SMR} + \sum_{YA=0}^{4_+} \beta_{YA} \times \delta_{YA} + \beta_{sg} \times \delta_{sg} + \left(\beta_{RHT} + \beta_i\right) \times RHT_{ijk} + \varepsilon_i + \varepsilon_{ij} + \varepsilon_{ijk} \qquad [2]$$

where notation is as per equation (1), β_i and ε_i are random site specific intercept and slope modifiers in the regression of *MC* on *RHT*, ε_{ij} is a random tree (within site) effect, and ε_{ijk} is a residual error. Restricted maximum likelihood estimates of the model parameters are listed separately in Table 5 for heartwood and sapwood, and a basal area weighted average of both is also listed. Models with random tree-level slope and intercept effects had a higher AIC_c than the model in (2). Both sites and trees accounted for a significant amount of the variation in *MC*. Wood in trees with spiral grain were, on average, 1% drier ($P < 0.001$) than wood in trees with no spiral grain. Also, *MC* of sapwood dropped by an average of 0.1% (±0.02%) for every counted check, about twice the rate estimated for heartwood (Table 5).

Moisture content of wood in dead standing trees declined, as expected, with time since beetle attack. In *YA = 1* the moisture content was, on average, close to 25% (± 6%) which is below the fibre saturation point (Chow and Obermajer 2007). Wood moisture declined by approximately 1.5% per year (± 0.1%) between *YA =1* and *YA = 4*, but the decline was much steeper between *YA = 2* and *YA =3* than between *YA =2* and *YA = 1*

(Table 5) and overall slightly faster in the sapwood (2.1% ± 0.1 %) than in the heartwood (2.0% ± 0.1%). Moisture content differences between *YA =1* and *YA = 2* were in the order of 0.5% for sapwood but close to zero for heartwood (non-significant, *P* > 0.53). Differences between *YA = 2* and *YA = 3* $(\approx 1\%)$ and between *YA = 3* and *YA =4* $(\approx 2\%)$ were significant (*P* < 0.01). Year of beetle attack effects for *YA = 4* and *YA ≥ 5* were statistically not significantly different from zero (*P* ≥ 0.92).

Moisture content of sapwood on the dry sites was, on average, 2.4% (±1.1%) lower (*P* = 0.03) than on wetter sites, but no *SMR* effect was significant for heartwood or when the two wood types were combined (*P* > 0.21).

Tree discs taken at stump height (*RHT* = 0) had a *MC* that was significantly higher (*P* < 0.001) than at any other position within the tree. For sapwood the moisture differential between the stump and the remaining tree was 9% (sapwood) and 8% (heartwood). Sapwood at stump height appeared to dry at a somewhat faster rate than higher up in the stem (rate difference: 3% *P* = 0.66).

Moisture content measurements under-bark at breast height can be used to obtain a reasonable prediction of the average within-tree *MC* (correlation = 0.67). Figure 5 illustrates the case for wood moisture content. Predictions of sapwood moisture content would be slightly better (correlation = 0.75).

Rot and decay

A total of 101 trees (28%) had some form of rot or decay in one or more stem section. The rot and decay was concentrated in just 6% of the examined discs. Sap rot was the dominant type of rot/decay with 127 cases, followed by insipient rot (79) and *Phellinus pini* (78). About 90% of the incidence of rot/decay was found in the first 2.5 m of the stem. A mixed-effects logistic model with sites as random effects and area, *YA, SMR*, and spiral grain as fixed effects was entertained for the estimation of conditional and marginal odds ratio of rot/decay incidence. The significance of the difference between two fixed effects was assessed with a likelihood ratio test.

Rot and decay incidence increased with *YA* but most rapidly between *YA* = 2 and *YA* = 3 and between *YA* = 3 and *YA = 4* (Table 7) where the changes were highly significantly different from zero (*P* < 0.001). With *YA* = 1 taken as the baseline of rot/decay odds, the COND odds of a rot/decay incidence was 1.1 (±0.8, *P* = 0.87) in *YA* = 2, 3.5 (± 2.4, *P* = 0.06) in *YA* = 3, 8.0 (± 6.3, *P* < 0.01) in *YA* = 4, and 13.7 (± 9.7, *P* < 0.001) in *YA* ≥ 5. Corresponding MARG odds were 1.07 (± 0.7, *P* = 0.9), 3.1 (± 1.8, *P* = 0.06), 4.9 (± 3.1, *P* = 0.01), and 7.4 (± 4.3, *P* < 0.001). Site variation accounted for 40% of the total variation in rot/decay incident rates.

The rot/decay incidence rate in trees with spiral grain was 0.48 (±0.50) as opposed to only 0.20 (±0.40) in trees with no spiral grain (Table 6). Site variation accounted for 40% of the total variation in rot/decay incident rates. The COND odds that a tree with spiral grain has some rot/decay was 3.4 (± 1.3, $P < 0.001$) times higher than for trees with no spiral grain. In comparison, MARG odds were 2.9 (± 0.8, $P < 0.001$).

The incidence rate of trees with some rot/decay was significantly higher in Burns Lake than in Quesnel and Vanderhoof (Table 6). In the Burns Lake area 38% of the trees had some rot or decay as opposed to just 23% and 22% in Quesnel and Vanderhoof respectively. If Quesnel is taken as the baseline (odds = 1), then the COND odds of some rot/decay in Burns Lake were 4.7 (± 3.3, $P = 0.03$) and 1.5 (± 1.1, $P = 0.54$) in Vanderhoof. Corresponding MARG odds were (2.9 ± 1.5, $P = 0.03$) and 1.1 (± 0.6, $P = 0.81$).

Dry sites had a significantly higher incidence rate of rot/decay than mesic and wet sites (Table 6). Differences between the mesic and wet sites were not significant ($P > 0.08$). With wet sites as the baseline (odds = 1), the COND odds of some rot/decay were 6.0 (± 4.1, $P = 0.007$) on dry sites and 1.2 (± 0.8, $P = 0.74$) on mesic sites. Corresponding MARG odds were 3.8 (±1.8, $P = 0.005$), and 1.2 (± 0.6, $P = 0.61$).

Extent of rot and decay when averaged over all trees was 1.7% (±5.7%) of the volume-weighted average basal area and the average (volume-weighted) of the maximum disc specific extent was 8.0% ±18.4%. Means and standard deviations for the fixed effects (*YA*, spiral grain, area and *SMR*) are in Table 6. A generalized mixed effects model with a logit link was used to estimate COND and MARG fixed effects. Time since death had a significant impact on the extent of rot/decay, but only the COND/MARG contrast between $YA \leq 2$ and $YA \geq 3$ was significant ($P < 0.01$). In the latter group the (COND) extent was 3.6 ±1.2 ($P < 0.01$) times larger than in the former group of *YA*. Trees with spiral grain had slightly more rot/decay than trees with no spiral grain (Table 6). The difference of 0.2% in volume-weighted extent of basal area was not statistically significantly different from 0% ($P = 0.77$, *t*-test). The COND extent of rot/decay on a dry site was 5.6 ±3.5 ($P = 0.006$) times higher than on a (typical) wet site. For MARG the corresponding estimate was 2.7 (±3.4, $P = 0.44$).

Blue-stain

All trees had some blue-stain (minimum 4% of volume-weighted tree basal area). There was a weak but general trend for the relative extent of blue-stain to first increase and then decrease along the vertical stem axis. A second-order polynomial with a maximum at about 2/3 of the tree length best describes the trend but the overall coefficient of determination was only 0.07 and no single regression coefficient was significant at the 5% level. Therefore, the trend was ignored and all results are given on a per tree basis (volume-weighted averages of stem disc results). Blue-stain tends to fade with age of attack and an ocular detection and delineation of older blue-stain may have been difficult and associated with measurement errors. Consequently the highest average of the relative width and extent of blue-stain was found in $YA = 1$ trees (Table 7) and the lowest in trees with $YA \geq 5$. The drop was about 1% on average per year. The number of checks per tree had a small but positive ($P < 0.01$) effect by increasing the relative measure(s) of blue-stain by about 0.2% per check in both COND and MARG analyses. Otherwise only

$YA = 1$ was significant in the MARG effect estimates $\left(\hat{\beta}_1 = 4.6\% \pm 2.2\%\right)$ and differences between COND and MARG estimates were unimportant (< 10%). Sites accounted for approximately 40% of the total variance in extent of blue-stain.

In terms of relative width of blue-stain, the only identified significant effect was for the number of checks (an increase of 0.1% per 1 added check, $P = 0.03$) in the MARG analysis. Sites explained almost 70% of the total variation in the relative width of blue-stain.

A solid stain pattern (as opposed to a patchy pattern) was the dominant stain type (82%). No consistent trend with YA could be established for trees with this stain type ($P \approx 0.8$ in both COND and MARG analyses). The relative frequency of trees with a patchy stain type, however, appeared to increase with YA from 6.2% at $YA = 1$ to 23% at $YA \geq 5$, probably due to the aforementioned fading of the blue-stain over age.

DISCUSSION

Findings of this study confirmed general expectations of a fairly rapid decline in important wood quality attributes of dead standing beetle-killed trees (Woo et al. 2005a, Byrne et al. 2005a, Trent et al. 2006, Chow and Obermajer 2007).

Checking in standing beetle-killed lodgepole pines is considered the most important factor determining the volume recovery and value of sawn lumber (Orbay and Goudie 2006, Lewis et al. 2006). Three to five years after being killed by the beetle virtually all standing dead lodgepole pines will have numerous and large (> 2 cm) checks in every 2.5 m stem section (Harrison 2006). Our study reiterated this general finding. In a review of the literature, Lewis and Hartley (2005) cite studies in which the volume recovery from older dead logs was around 2/3 of the volume recovered from live logs. Chippable volume, of course, showed the inverse relationship. Veneer recovery resembled that of volume recovery. Other studies have indicated volume losses of dead standing trees of 4% after about one year, 8%, after three to six years and 14% for older dead standing trees. Product grade mix is also negatively affected by checks. It is, however, difficult to compare our field results to actual milling studies (Orbay and Goudie 2006, Brdicko 2007) as the volume recovery and grade mix depends on the raw material (size and dimensions, and defects not related to time since death), milling technology, and market conditions (Lewis et al. 2006). This study clearly identified the proportion of trees with spiral grain as an important determinant of the severity of checking. With a large variation in stand-level proportions of trees with spiral grain it is difficult to predict the severity of checking from YA alone. As illustrated by our results, the checking will be most severe on drier sites due to faster drying rates of the wood on dry sites (Lewis et al. 2006, Trent et al. 2006). The large increase in the number and size of checks in dead standing trees killed two years earlier, reported here, suggests a fairly narrow operational window for avoiding a substantial increase in loss of lumber volume and value. A loss that, according to our results, will be considerably higher on drier sites, and on sites with a high prevalence of trees with spiral grain. It is interesting to note that a report by the BC Ministry of Forests and Range (Eng et al. 2007) suggested that wetter sites would show more severe checking. Our results could not support this expectation.

During the first year after a beetle-kill the moisture content of both sapwood and heartwood of dead trees drops to about fibre saturation point (Woo et al. 2005b, Trent et al. 2006, Lewis et al. 2006, Chow and Obermajer 2007). After reaching that point the moisture loss continues at rates of 1%-5% depending on the climate and site condition (Lewis and Hartley 2005, Byrne et al. 2005a, Harrison 2006, Trent et al. 2006, Lewis et al. 2006). Our results generally confirmed these observations and also determined that trees with more checks will dry faster than trees with fewer checks. Since dry wood is more prone to breakage during handling than green wood and is also more difficult to process (Orbay and Goudie 2006), the profitability of processing dead wood is likely to be negatively influenced by a declining moisture content. With this study and those before it, the sawmill operators and handlers of bark beetle-killed lodgepole pine ought to have sufficient information to predict -- with reasonable accuracy -- the water content of standing dead trees, at least for a period covering the first 4-5 years post beetle-attack.

It is generally expected that rot and decay in standing beetle-killed trees would be more abundant on wetter sites (Lewis and Hartley 2005, Lewis et al. 2006, Eng et al. 2007) and that the incidence rates and extent of rot and decay would remain fairly constant during the first four to five years following death (Lewis and Hartley 2005, Byrne et al. 2005a). The marked increase in rot incidence (approximately fourfold over 5+ years) found in this study points towards an aggressive invasion of rot-causing fungi possibly peaking two years after death. Invasions that are facilitated by checks, blue-stain, and drying processes (Kim et al. 2005, Byrne et al. 2005a, Byrne et al. 2005b, Kim et al. 2005, Lewis et al. 2006). We surmise that increased (moisture) stress on the drier site has favoured establishment of rot-causing fungi. Our results regarding the extent of rot/decay were more in line with the aforementioned general expectations.

Blue-stain in wood from beetle-killed lodgepole pines may exclude it from use where appearance is of overriding importance (Byrne and Uzunovic 2005). Otherwise, the blue-stained wood ought to qualify for virtually the same product mix as non-stained wood (Zaturecky and Chiu 2005, Byrne et al. 2005a, Byrne et al. 2005b, Lum et al. 2006, Trent et al. 2006). Profitability may be reduced if additional sorting and bleaching is required for some products. Our results confirmed that all beetle-killed trees have some blue-stain (Byrne et al. 2005a). One year after the beetle has killed a tree one should expect 100% of the sapwood to show blue-stain. The apparent trend of a drop in the extent of blue-stain as YA increases found in this study is merely a consequence of the stain fading due to oxidation in wood with a moisture content below fibre saturation (Kim et al. 2005, Byrne et al. 2005a, Byrne et al. 2005b). In a laboratory study Chow and Obermajer (2007) found an increase in blue-stain (by volume) during the first three years after death, suggesting that blue-staining fungi continues to invade the wood (Kim et al. 2005).

The sheer magnitude of beetle-attacked wood volume available for harvest in British Columbia makes immediate harvesting of the bulk of all beetle-killed trees with subsequent storage under sprinklers (Feng and Knudson 2005) until processed at a mill an unlikely scenario. As pointed out by Rogers (2001), the economics of storing large volumes of wood in water are not compelling in today's marketplace. For the time-being beetle-killed trees can economically be stored only as standing dead. The results from this study will help provincial and industrial planners quantify opportunity costs in their scheduling harvest operations of standing dead beetle-killed lodgepole pines in British Columbia. The extensive and balanced sampling of a broad spectrum of stand conditions makes this study valuable as it quantified a considerable among-stand variation in all important examined wood quality traits. That variation points to the need of stand-level information to further this planning.

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Table 1. Site and field data, and measured tree attributes.

Attribute	Description
Area	Quesnel, Vanderhoof, or Burns Lake
Site	1-45
Tree	1-360
Date	Date the site was sampled
BEC	Biogeoclimatic unit (BEC zone, subzone and variant)
SS	BEC Site Series
SMR	BEC Soil Moisture Regime
SNR	BEC Soil Nutrient Regime
Zone	UTM Zone at the Integrated Plot Center
Northing	UTM Northing at the Integrated Plot Center
Easting	UTM Easting at the Integrated Plot Center
Elevation	Elevation (m) at the Integrated Plot Center
Weather	General description of the weather at the time of sampling
MPB	General extent and history of mountain pine beetle attack in stand
Feature	Area features affecting site conditions
Crown Class	Crown class: (D) dominant; (C) codominant; (I) intermediate
Slope	Slope of the ground at the tree (%)
Aspect	Aspect of the area at the tree in degrees; 0 = no aspect
SlopePos	Slope position of the area at the tree
SoilMoist	Broad soil moisture estimate of the ground at the tree (W) wet; (M) mesic; (D) dry
FoliageRem	Visual estimate of the foliage remaining (%)
FoliageCond	Visual estimate of the foliage condition: (E) early red; (L) late red; (G) grey
LooseBark	Loose bark at breast height measured by pressing the bark: (Y) yes; (N) no
BarkIntact	Percent of bark intact at breast height measured with a steel diameter tape (%)
BITree	Visual estimate in the field of the percent of bark intact for the entire tree (%)
CheckDepth	Maximum depth (cm) of checking in first 2.5 m log from stump height measured on the standing tree
CheckLen	Average length (m) of checking in first 2.5 m log from stump height measured on the standing tree
CheckNum	Number of checks in first 2.5 m log from stump height measured on the standing tree
Spiral	Maximum spiral grain (%) in first 2.5 m log from stump height measured on the standing tree
BirdDamage	Visual estimate in the field of the severity of bird damage for the entire tree: (N)one; (L) low; (M) moderate; (H) high
Notes	General notes regarding the sample tree
TreeLen	Measured tree length (m) on the ground using a fiberglass tape

Table 2. Stem disc attributes. Moisture content (%) was measured with the Delmhorst J2000 meter with a functional range from 7% to 40%. Values outside this range were set to 6%, and 41%, respectively.

Attribute	Description
Tree	1-360
Disc	Numbered up the tree from stump height (0.0m) = 1
Pos	Actual position of disc which may differ from the 2.5m target log length (m)
DOB	Diameter outside bark measured with a steel diameter tape (cm)
BT	Average bark thickness for disc (cm)
Prop	Proportion of the bark intact as a percent of circumference and measured with a steel diameter tape (%)
	Numbered clockwise from north
Check	
Depth	Check depth (cm) from cambium
Width	Check width (cm) at cambium
Brng	Bearing from pith (degrees);
Pattern	Pattern: (S) straight; (C) curved; (D) doglegged; (P) splintered
Blue-stain	
Quad	Quadrant delineated on the disc face, clockwise from north: 1 (NE); 2(SE); 3(SW) or 4(NW)
Width	Average width (cm) of stain measured from cambium towards pith in each quadrant
Degree	Visual estimate of blue-stain intensity in each quadrant: 1=Light; 2=Moderate; 3=Dark
Pcnt	Visual estimate of blue-stain percent in each quadrant (%)
Pattern	Visual determination of blue-stain pattern in each quadrant: (S) solid; (P) patchy
Rot and decay	
Location	Decay location in the disc: (S) sapwood; (H) heartwood; (B) both
Type	Decay type: (IS) Insipient Stain; (BC) Brown Cubical; (BR) Buttrot; (PP) *Phellinus pini*; (PR) Punky Rot; (SR) Saprot; (TD) Termite Damage;
Extent	Decay extent measured as an area on the disc face (cm2)
Moisture content	Moisture content in percent of fresh weight. Measured with the Delmhorst J2000 meter. Observations are censored to a minimum of 6% and a maximum of 41%.
SN	North axis sapwood moisture %
SE	East axis sapwood moisture %
SS	South axis sapwood moisture %
SW	West axis sapwood moisture %
HN	North axis heartwood moisture %
HE	East axis heartwood moisture %
HS	South axis heartwood moisture %
HW	West axis heartwood moisture %
Pith	Pith moisture measured %

Table 3. Conditional (COND) and marginal (MARG) estimates of the coefficients in the negative binomial model for the expected number of checks per tree (eq 1). Standard errors (s.e.) of the coefficients are computed with sites as random effects and trees within a site as correlated random effects. Non-significant ($P \geq 0.05$) model terms have been dropped for brevity.

	whole tree				first 2.5 m of stem			
Coefficient	COND	s.e.	MARG	s.e.	COND	s.e.	MARG	s.e.
$\hat{\mu}$	-0.42	0.21	-0.42	0.26	-2.20	0.39	-1.00	0.32
$\hat{\beta}_{surf} \times 10$	0.21	0.02	0.24	0.03	-0.00	0.00	-0.00	0.00
$\hat{\beta}_{sg}$	0.59	0.10	0.54	0.13	2.56	0.22	2.12	0.18
$\hat{\beta}_1$	-0.81	0.22	-0.66	0.26	-0.80	0.45	-0.73	0.42
$\hat{\beta}_2$	-0.41	0.20	-0.04	0.23	0.52	0.32	1.10	0.31
$\hat{\beta}_3$	-0.08	0.16	0.04	0.21	0.03	0.34	0.26	0.32
$\hat{\beta}_4$	0.13	0.17	0.02	0.22	0.18	0.32	0.56	0.32
$\hat{\beta}_{5+}$	-0.03	0.15	-0.08	0.21	-0.13	0.30	0.53	0.29
$\frac{\hat{\sigma}^2(tree \mid site)}{\widehat{mean}}$	2.86	0.07	n.a.		3.57	0.15	n.a.	

Table 4. Conditional estimates of model coefficients for volume-weighted per tree average and standard deviation (*s*) of check size. *CD* = check depth, *CW* = check width. Standard errors of coefficients are in parentheses. Analysis is based on trees with at least one check.

	CD (cm)	s(*CD*)[a] (cm)	*CW* (cm)	s(*CW*)[a] (cm)
$\hat{\mu}$	5.2	1.9	0.32	0.16
	(0.3)	(0.2)	(0.03)	(0.02)
$\hat{\beta}_{spiral\ grain}$	0.7	0.4	0.09	0.04
	(0.3)	(0.1)	(0.02)	(0.01)
$\hat{\beta}_{mesic,wet}$	-0.6	-0.2	-0.08	-0.03
	(0.3)	(0.2)	(0.03)	(0.02)
$\hat{\beta}_1$	-1.3	-0.8	-0.10	-0.06
	(0.5)	(0.2)	(0.03)	(0.02)
$\hat{\beta}_2$	-1.2	-0.6	-0.09	-0.04
	(0.4)	(0.2)	(0.03)	(0.03)
$\hat{\beta}_3$	-0.3	-0.4	-0.05	-0.05
	(0.4)	(0.2)	(0.03)	(0.02)
$\hat{\beta}_4$	-0.3	-0.5	-0.02	-0.03
	(0.4)	(0.2)	(0.04)	(0.02)
$\hat{\beta}_{5+}$	-0.6	-0.2	-0.03	0.00
	(0.4)	(0.2)	(0.03)	(0.02)

[a] average within-tree standard deviation

Table 5. Restricted maximum likelihood estimates of parameters in mixed linear model ([2]) of moisture content (*MC*%) in sapwood (*sap*), heartwood (*heartw*) and combined (*wood*). *sd* = standard deviation (of random effects). Numbers in parentheses are the estimated standard error of an estimate. Sites are treated as random effects and trees within sites as correlated random variables.

	MC_{sap}	$MC_{heartw.}$	MC_{wood}
$\hat{\mu}$	27.3 (0.8)	26.3 (0.9)	27.0 (0.8)
$\hat{\beta}_{sg}$	-1.0 (0.4)	-0.8 (0.4)	-0.9 (0.4)
$\hat{\beta}_{check}$	-0.1 (0.0)	-0.0 (0.0)	-0.0 (0.0)
$\hat{\beta}_{Dry}$	-2.4 (1.1)	-0.6 (1.3)	-1.4 (1.1)
$\hat{\beta}_1$	3.9 (0.7)	3.3 (0.7)	3.1 (0.6)
$\hat{\beta}_2$	3.4 (0.6)	3.7 (0.6)	3.3 (0.6)
$\hat{\beta}_3$	1.9 (0.5)	2.1 (0.5)	1.9 (0.5)
$\hat{\beta}_4$	0.0 (0.6)	0.0 (0.6)	0.0 (0.5)
$\hat{\beta}_{5+}$	0.0 (0.6)	0.0 (0.5)	0.0 (0.5)
$\hat{\beta}_{RHT}$	-17.7 (0.7)	-14.9 (0.8)	-16.8 (0.6)
$\widehat{sd}(\beta_{site})$	4.0 (0.6)	4.8 (0.6)	3.5 (0.5)
$\widehat{sd}(\varepsilon_{site})$	2.6 (0.4)	3.1 (0.4)	2.6 (0.3)
$\widehat{sd}(\varepsilon_{tree})$	1.9 (0.2)	2.4 (0.1)	2.2 (1.2)
$\widehat{sd}(\varepsilon_{resid})$	6.1 (0.1)	3.2 (0.0)	4.7 (0.1)

Table 6. Incidence and extent (% of volume-weighted average basal area) of tree-level rot/decay by area, soil moisture regime, and years since attack (*YA*). Numbers in parentheses are among tree standard deviations.

	P(rot/decay)	Rot/Decay%
Years since attack		
1	0.10	0.6
	(0.31)	(1.9)
2	0.14	1.2
	(0.35)	(5.6)
3	0.28	2.6
	(0.45)	(7.7)
4	0.30	1.9
	(0.46)	(6.4)
≥ 5	0.43	2.0
	(0.50)	(5.0)
Spiral grain		
0 (no)	0.20	1.7
	(0.40)	(0.1)
1 (yes)	0.48	1.9
	(0.50)	(0.1)
Area		
Burns Lake	0.38	1.3
	(0.49)	(4.6)
Quesnel	0.23	1.2
	(0.42)	(3.7)
Vanderhoof	0.22	2.2
	(0.41)	(4.1)
Soil moisture regime		
Dry	0.46	3.0
	(0.50)	(7.0)
Mesic	0.22	1.3
	(0.41)	(5.2)
Wet	0.18	1.1
	(0.38)	(4.5)

Table 7. Per tree average of blue-stain relative width and relative basal area. Numbers are in percent of volume-weighted stem average of diameter under-bark and under-bark basal area, respectively. Volume weights (wt) are per total volume (*TVOL*) or log volume (*LVOL*) with a minimum diameter of 12.5 cm. Numbers in parentheses are the among-tree standard deviation across all sites.

YA	Width% (*wt = TVOL*)	Width% (*wt = LVOL*)	*BA%* (*wt = TVOL)*	*BA%* (*wt = LVOL)*
1	30	30	39	39
	(11)	(11)	(12)	(12)
2	29	29	37	38
	(10)	(11)	(11)	(12)
3	26	25	32	32
	(7)	(7)	(8)	(8)
4	26	26	33	33
	(7)	(7)	(8)	(9)
5+	26	27	31	31
	(9)	(9)	(10)	(10)

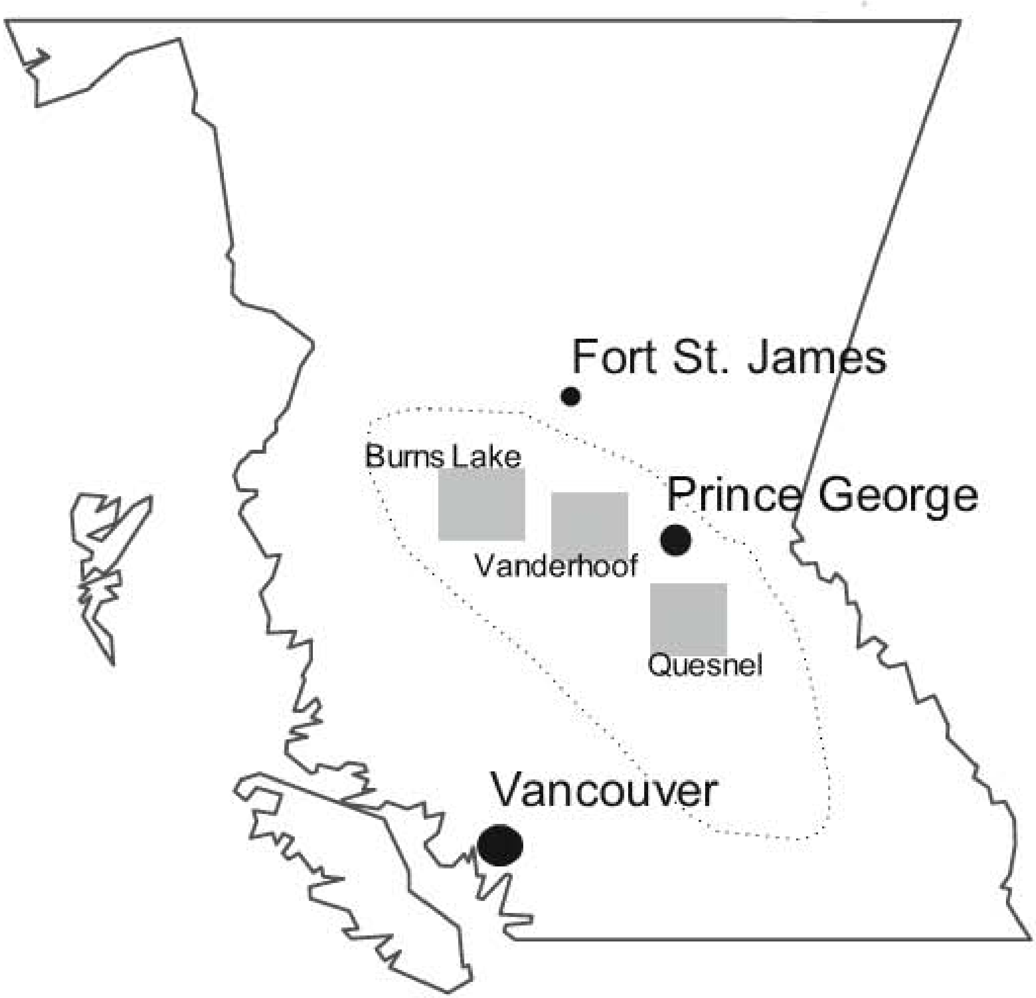


Figure 1. Overview map of the approximate location of the three study areas (Burns Lake, Vanderhoof, and Quesnel) in British Columbia. The core area of the current mountain pine beetle infestation is indicated by the dotted line.

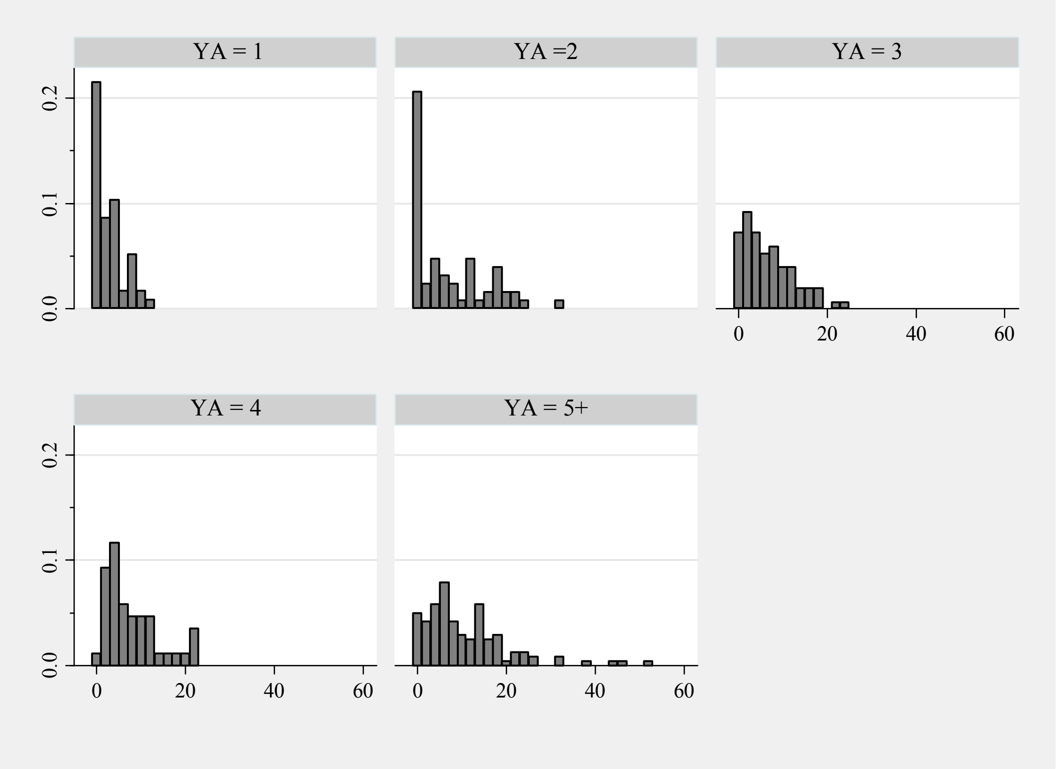


Figure 2. Proportions (*y*-axis) of trees with 0, 1-2, 3-4, ... , 51-52 checks per trees (*x*-axis).

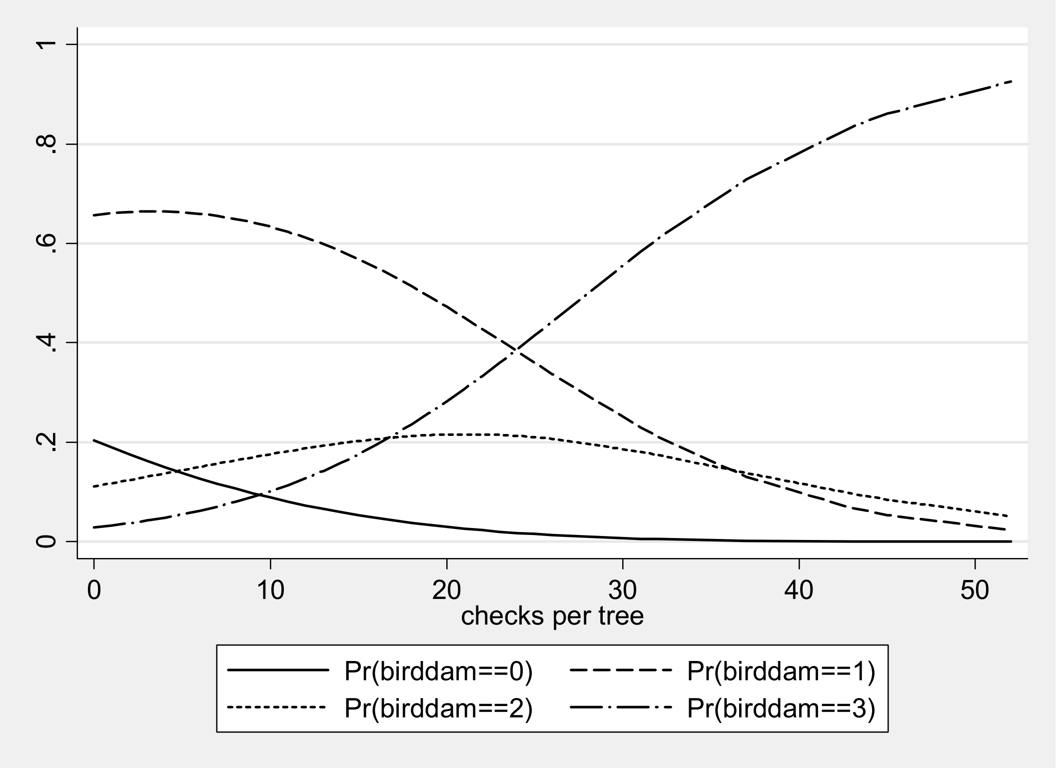
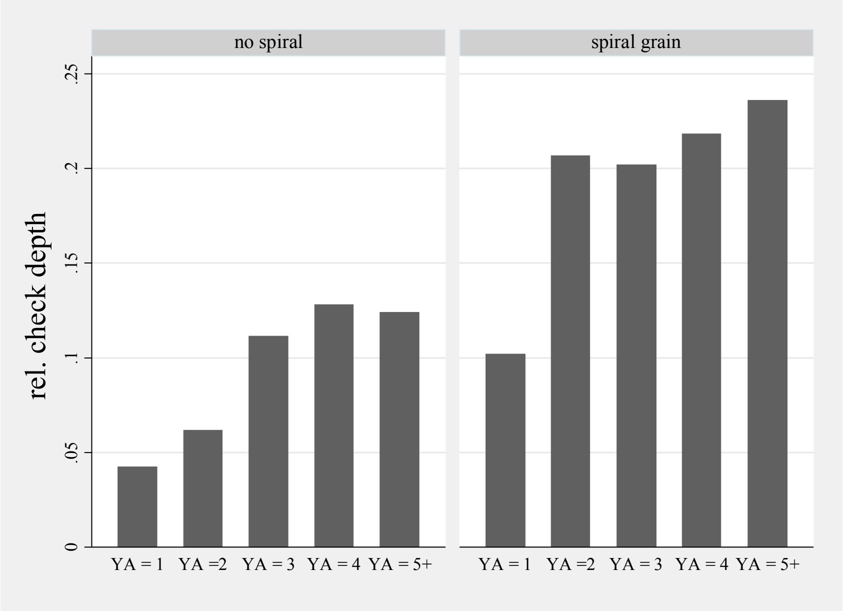


Figure 3. Estimated trends in multinomial probabilities of bird damage class as a function of the number of checks per tree.



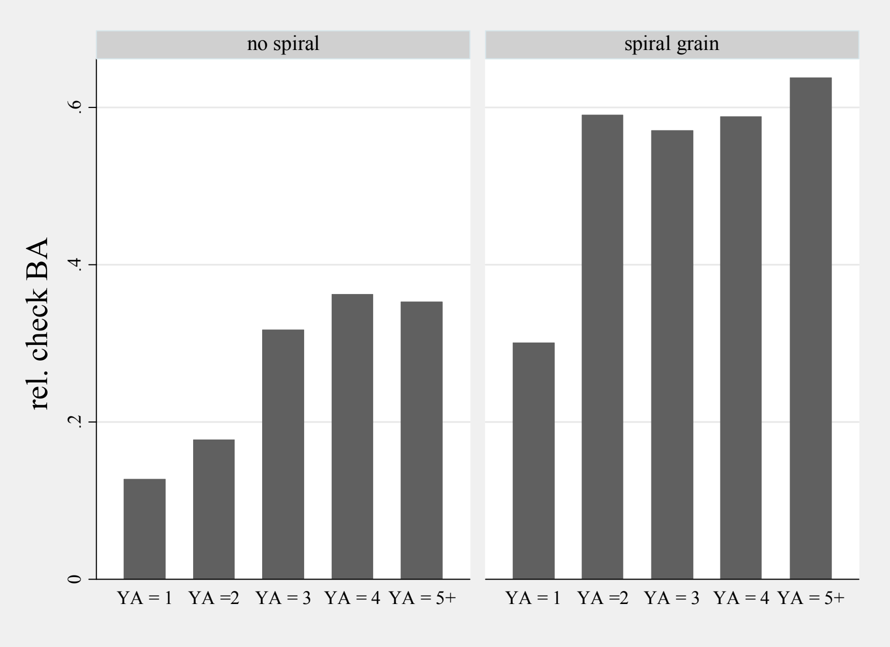


Figure 4. Average proportions of under-bark stem diameter (top), basal area (*BA*, bottom) and log size volume (VOL, next page) affected by checks. Proportions are volume-weighted averages of stem disc recordings (continued on next page).

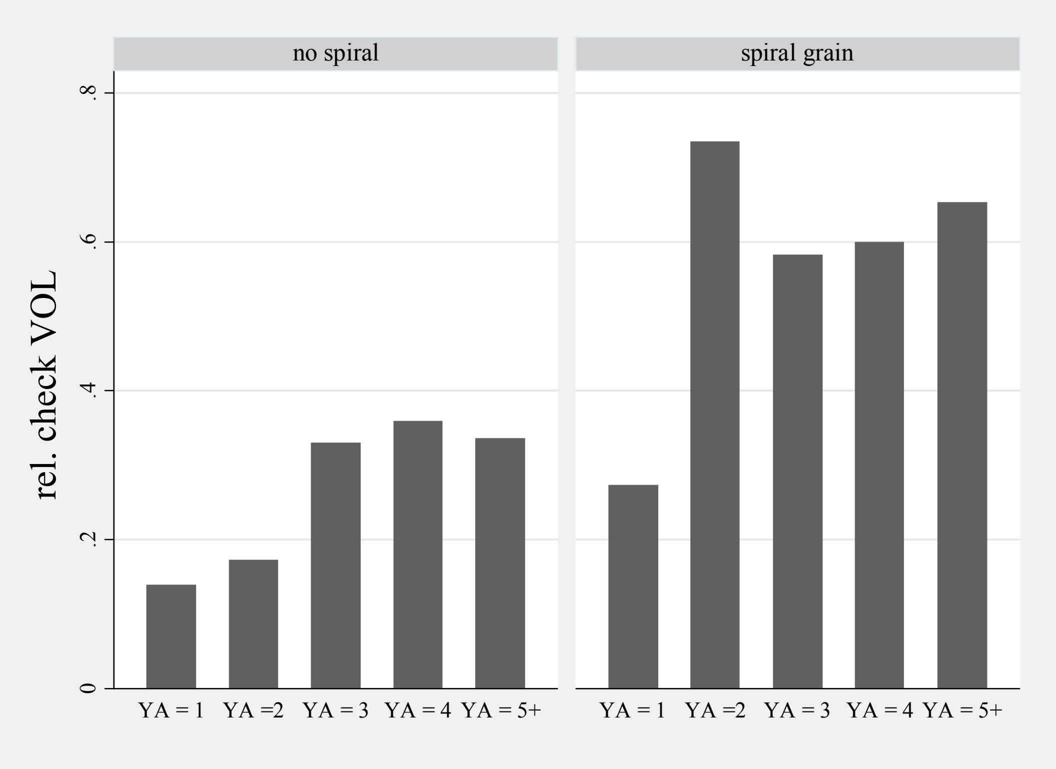


Figure 4 continued from previous page: Average proportions of under-bark stem diameter (top of previous page), basal area (*BA*, bottom of previous page) and log size volume (VOL, above) affected by checks. Proportions are volume-weighted averages of stem disc recordings.

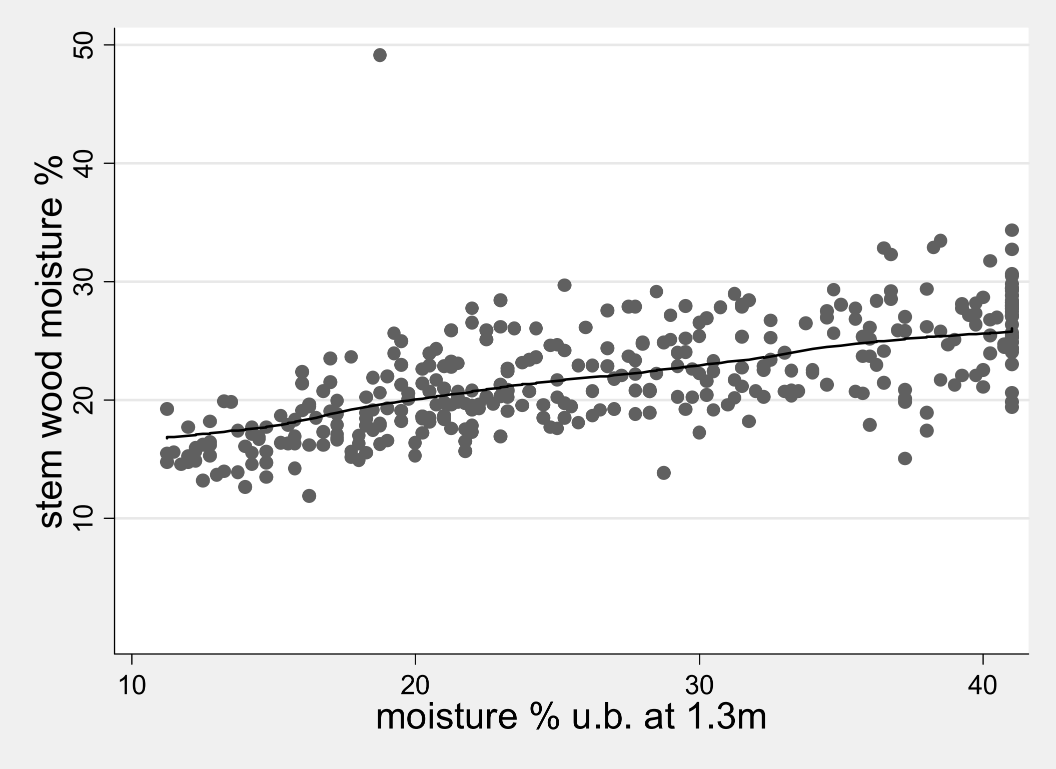


Figure 5. Relationship between whole tree wood moisture (%) and moisture content (%) under-bark (u.b.) at 1.3 m above ground. Solid line is the running mean trend (band width = 0.6).