DEGRADATION OF WOOD IN STANDING LODGEPOLE PINE KILLED BY MOUNTAIN PINE BEETLE

*Kathy Lewis**

Professor

Doug Thompson

Greenhouse Curator
University of Northern British Columbia
3333 University Way
Prince George, British Columbia
V2N 4Z9, Canada

Abstract.   Lodgepole pine is widely distributed throughout the Pacific Northwest and is an important commercial species. Although outbreaks of mountain pine beetle can kill extensive areas of pine stands, little attention was paid to postmortality rate of wood quality and quantity deterioration until the most recent outbreak, which because of its unprecedented size has resulted in extensive salvage harvesting. We used dendrochronology to determine the exact year of mortality and destructive sampling to quantify change in wood characteristics with time. We also estimated the fall-down rate of dead trees. Most trees did not start to fall until 8 yr postmortality. We found that change in wood moisture content was the main driver behind changes in wood properties. Dependent variables included checking (number and depth), blue-stain depth, saprot, and damage caused by wood borers and were explained by a small collection of biophysical variables. Biogeoclimatic unit and soil moisture regime were not important predictors of decay and degrade, except for development of saprot at the base of trees. Wood quality significantly changed within the first 1-2 yr postmortality and varied with position along the stem followed by a period of relative stability.

Keywords: Mountain pine beetle, decay, check, saprot, time-since-death, moisture content.

INTRODUCTION

Lodgepole pine (*Pinus contorta* Dougl. var. *latifolia* Englem.) is a common species in forests of western North America, extending from the Yukon Territories in Canada south to Colorado (Fowells 1965). Lodgepole pine is a seral species adapted for rapid colonization of disturbed sites and fast early growth, resulting in stands that tend to be even-aged and homogenous. It is an important commercial species in the Pacific Northwest, particularly in inland regions. In western Canada, lodgepole pine forests make up about 22% of the total forest cover (Koch 1996) and almost 15 million ha in British Columbia (BC) alone. In interior BC, lodgepole pine comprises more than 50% of the timber harvesting landbase, and overall across the province, pine is 25-30% of the provincial harvest (Government of British Columbia 2005).

Mountain pine beetle (*Dendroctonus ponderosae* Hopk. [Coleoptera: Scolytidae]) (MPB) is an indigenous bark beetle with a range similar to lodgepole pine. Periodic, landscape-level outbreaks of MPB are a natural part of pine ecosystems and lead to extensive mortality in stands of older, larger trees. This extensive mortality has important economic impacts, especially in forest-resource-dependent regions. It also has important ecological impacts on habitat types and distribution (Chan-McLeod et al 2009), carbon sequestration and storage (Brown et al 2008; Kurtz et al 2008), and hydrology (Bethlahmy 1974; Rex and Dubé 2009). MPB outbreaks have been recorded in BC since the early 1900s with the most recent (ongoing) by far the largest in area affected (Taylor et al

---

* Corresponding author: lewis@unbc.ca

2006). Despite this history of MPB outbreaks in western North America, the postmortality rate of wood quality and quantity deterioration and rate of change in stand structure caused by the fall of dead trees had not been well studied. A few studies examined deterioration of beetle-killed wood with time using samples from the current outbreak in BC (eg Trent et al 2006; Magnussen and Harrison 2009), and other studies have focused on changes in specific wood product recovery from beetle-killed wood (eg Byrne and Uzunovic 2005; Feng and Knudson 2005; Oliveira et al 2005; Orbay and Goudie 2006). Trent et al (2006) examined fine-scale wood quality variables, such as fiber length, and their relationship with time-since-death (TSD). They found a significant negative relationship between TSD and moisture content, however, no other variables tested were significant. TSD in Trent et al (2006) was determined from external indicators and local knowledge, which can be very inaccurate at the tree level (Newbery et al 2004). Recent work has shown that tests of wood deterioration with time at tree and stand level must use accurate measures of TSD, such as cross-dating (Stokes and Smiley 1968).

The magnitude of the current outbreak is such that significant decreases in wood supply are anticipated in the next few decades. These decreases can be limited by efficient use of beetle-killed wood for as long as possible, but to do this, relationships among TSD, fall rate, and wood quality and quantity variables must be known. This information is essential to plan timing and distribution of salvage harvests to recover the greatest value from wood and to maintain a future wood supply for forest-dependent communities in the beetle-affected area. Furthermore, rate of change in stand structure (eg fall-down rate) is essential to understand and plan for impacts on wildlife habitat and other nontimber values.

Objectives of this study were to determine 1) relationships among TSD, moisture content, and specific gravity in heartwood and sapwood, penetration depth of saprot, frequency and magnitude of checking, and frequency and magnitude of wood-borer infestation; 2) the effect of ecosystem characteristics, tree size, and location along the stem on the previously mentioned factors of wood quality and quantity; and 3) the rate of tree fall in beetle-affected stands.

Study scope was limited to biophysical variables that affect wood quality and quantity after mortality caused by MPB. A number of other factors significantly influence economic efficiency when dead wood is processed. These include delivered wood cost, technology used to process wood, actual product made, demand for product and selling price, and opportunity to harvest and process green wood with dead wood. These variables were not addressed in this study.

METHODS

Sampling Area

The study took place in the subboreal spruce biogeoclimatic zone (SBS) (Meidinger and Pojar 1991) and included two subzones: dry cool (SBSdk) and Kluskus moist cold (SBSmc3). Mean annual precipitation was 481 and 506 mm, with 1.88 and 1.97 m snowfall, in the two subzones, respectively. In SBSdk, mean annual temperature was 2.1°C with 70 frost-free days compared with 0.6°C and 18 frost-free days in SBSmc3 (Reynolds 1989). Three areas, the Fawnie Range, Nechako River, and Tetachuk Lake, were sampled across 2 yr. In the first sampling period (SP1), 31 stands, a minimum of 2 km apart, were selected in the Fawnie and Nechako areas based on infestation maps and field reconnaissance. These areas were dominated by trees that died up to 5 yr prior to sampling. The second sampling period (SP2) focused on the north slope of Tetachuck Lake (Fig 1). This area was affected by the earliest stages of the current outbreak (≈1995) and had trees that died between 6 and 10 yr prior to sampling. Candidate stands for sampling were identified using air photographs that showed areas with red trees from 1996 to 2000 that were not harvested at some later date. Based on this information, and limited accessibility by boat, five stands were selected at Tetachuk Lake.
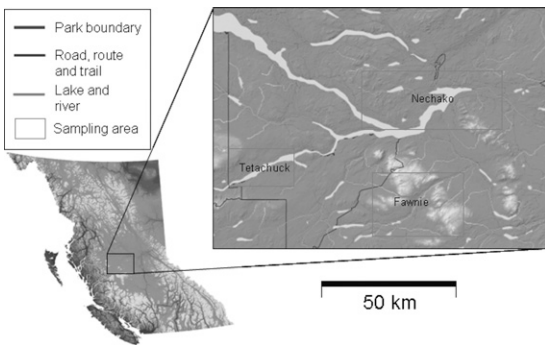
Figure 1.   Map of sample area, located approximately 150 km southwest of Vanderhoof, British Columbia. Sampling period 1 included the Fawnie and Nechako areas; sampling period 2 was along Tetachuck Lake.

Table 1.   Descriptions of external time-since-death categories for pine killed by mountain pine beetle.

Time-since-death category	Description
1	Green, yellowing, or freshly red needles, no needle loss
2	Freshly red to red needles, slight needle loss
3	Red needles, substantial needle loss
4	No needles and loss of fine branches

Field Sampling

During SP1, six plots were established systematically in each stand, and during SP2, three plots were established in each stand. Because of stand density, each plot varied in radius, ranging from 3.99 to 7.97 m. Within each plot, aspect, slope, elevation, moisture regime, species composition, stand density, diameter-class distribution, and number of standing and dead pine in one of four external time-since-death (ETSD) categories (Table 1) were recorded as predictor variables. Number and diameter of fallen trees were recorded as response variables.

Individual sample trees (killed by MPB, still standing) were selected during stand-level surveys. We selected 474 and 150 trees during SP1 and SP2, respectively, across the range of diameter at breast height (DBH) classes (measured 1.3 m from the ground: 125-225, 226-325, and 326+ mm), soil moisture regimes (SMR: dry = 1, mesic = 2, and wet = 3), and ETSD category. A maximum of one tree for each sample cell (DBH class $\times$ SMR $\times$ ETSD) from each plot was selected to decrease potential for spatial autocorrelation. Selected trees were free of defects along the merchantable stem (eg fire scars, double tops, crooks, or burls).

Each sample tree was felled, and merchantable stem length (from a 0.3-m-high stump to a 0.10-m-diameter top) was recorded. Twelve disks ($\approx$40 mm thick) were bucked from the stem of each tree. Disks 1 and 2 were removed from the stump and breast height. Disks 3-12 were cut at equal distances from breast height and height at which stem diameter equaled 0.10 m. From each disk, diameter, blue-stain depth, number of checks, average check depth, saprot depth, and wood-borer depth were recorded. Saprot depth was determined by splitting the cookie and then using a knife point to pick at wood on the radial surface. Sound wood snapped and had long slivers compared with decayed wood, which broke easily without making slivers and without a snapping noise.

Disk 1 (or another disk if bark was not present on disk 1) was brought to the laboratory to date mortality of each tree using visual and statistical cross-dating procedures. Disks were prepared following standard dendrochronology techniques (Stokes and Smiley 1968). Individual ring-width series were measured to the nearest 0.001 mm using the Velmex System (Velmex, Inc., Bloomfield, NY) in conjunction with MeasureJ2X (VoorTech Consulting, Holderness, NH). Ring-width series were visually cross-dated against master chronologies from the study area. Then the computer program COFECHA (Holmes 1983) was used to confirm or correct mortality dates. Only trees whose mortality dates could be confidently determined were used in further analyses.

Small samples of sapwood and heartwood from disks 1, 2, 4, and 8 were removed and fresh weights were measured in the field. Percentage moisture contents (oven-dry basis) and specific gravities were calculated for each disk based on the methods of Haygreen and Bowyer (1996).

Merchantable volumes per tree were calculated by summing section volumes, where volume of a section was determined using the formula for a cone frustum.

During SP2, the area within each stand was searched for fallen beetle-killed trees that had scarred a living tree at the time of fall, creating a tree-fall pair. Each tree-fall pair was sampled by cutting a disk from between stump height and DBH on the dead tree to determine year of mortality and by removing a disk of wood from the middle of the scar on the live tree to determine the year that the scar was created (year of fall of dead tree). Thirty pairs of trees were sampled.

Data Analysis

At plot level, a logistic regression on fallen/standing dead pine was run against DBH, and an analysis of variance (ANOVA) was used to determine if there were significant differences in percentage of fallen dead pine among SMR categories. These analyses were carried out for SP2 data only, because tree fall in SP1 was rare.

Preliminary analyses using General Linear Models (GLM) were conducted on data from SP1. Each GLM included mortality date and biogeoclimatic unit as fixed variables and SMR nested within biogeoclimatic unit as a random variable. Tukey multiple comparisons were conducted for significant terms in each GLM (SYSTAT 2004). These preliminary analyses demonstrated that there was no difference in response variables among the two subzones with the exception of measurements taken from the basal disk, which have been addressed in the analysis. Therefore, data from the two subzones and the two sampling periods were pooled. TSD in all analyses was the cross-dated year of mortality subtracted from year of sampling and was treated as a continuous variable, partly because of differences in sample size among different mortality years caused by spread dynamics of the beetle. Under the assumption that large trees would be attacked first in the outbreak and that large trees may be found on wetter sites, ANOVA was used to test for between-subjects effects. A strong relationship was found between DBH and TSD ($p < 0.001$) but not between DBH and SMR ($p = 0.522$). DBH was therefore treated as a covariate for some analyses.

Percentage moisture contents for both sapwood and heartwood were natural-log transformed to meet assumptions of normality for parametric analysis. To examine the importance of TSD and SMR as explanatory variables, a repeated-measures ANOVA was performed on the entire data set with sapwood to heartwood (wood type) and disk height as repeated measures. Following that, a multivariate GLM was developed with natural log of moisture content (sapwood and heartwood done separately) as the dependent variable and TSD and SMR as independent variables. Separate models were developed for four tree locations: disk 1 (0.3 m), disk 2 (1.3 m), disk 4 (one-third of merchantable height), and disk 8 (two-thirds of merchantable height). Also, interactions among independent variables (disk, TSD, SMR, and heartwood/sapwood) were examined with ANOVA. Mean moisture content was plotted against TSD separately by wood type, SMR, and disk. Specific gravity was analyzed with the same procedures as for moisture content.

To identify predictor variables (PVs) that may explain variation in response variables (RVs) that are influenced by sapwood proportion and/or tree size (ie blue-stain penetration depth, number of checks, depth of checks), we developed a Pearson correlation matrix for all RVs for each disk against PVs, including TSD; SMR; stand density; mean stand DBH; stand basal area; DBH; diameter growth during the last 10, 20, and 50 yr and change in diameter during the last 10, 20, and 50 yr relative to tree diameter at the start of the period; and specific gravity in sapwood and heartwood at each disk.

Percentage tree volume occupied by blue-stained wood was calculated for each tree using Eq 1, and mean values were plotted by TSD to examine blue-stain fungi colonization rate.

$$\text{Blue-stained wood volume} = \Sigma(\pi r_i^2 - \pi b_i^2) * L_i \tag{1}$$

where r = radius of section, b = depth of blue-stain in section, and L = length of section.

Blue-stain fungus is limited to sapwood, therefore, we expected growth measures to be important predictors of blue-stain depth. Results from Pearson correlations of blue-stain depth on growth measures were most significant for 20-yr growth. This led us to test the hypothesis that blue-stain depth was a function of absolute growth during the last 20 yr (ABS20) and/or DBH of the tree at the beginning of the last 20-yr growth period (PRE20). Both independent variables were natural-log transformed and tested for multicolinearity using SPSS version 16.0 (SPSS Inc 2008) and regressed on blue-stain depth.

Abundance and Prediction of Checking, Saprot, and Wood-Borer Damage

Percentage of trees with no measurable damage caused by checking at breast height (disk 2) and by saprot and wood borer (disk 1) was plotted against TSD. Number and depth of checks was plotted as a function of TSD and location on the tree. Number and depth of checks was modeled using disk 2, where effect of moisture absorption from ground content disappears. Check depth was also greatest in disks 2 and 3 (Fig 2),

therefore check depth was modeled using data from disk 2.

TSD; SMR; DBH; average stand density; diameter growth during the last 10, 20, and 50 yr; percentage change in DBH relative to estimated DBH 10, 20, and 50 yr ago; and specific gravity of sapwood and heartwood in basal and breast height disks were tested for significance in prediction of number and depth of checks at breast height and depth of saprot and wood-borer damage at stump height. Pearson correlation and scatterplot matrices were used to identify important PVs using $\alpha \leq 0.001$ because of large sample size. Multicolinearity was tested between PVs using SPSS, and if present, PVs easiest to measure in the field were retained for further analysis. Consecutive linear mixed-effects models with TSD, DBH, and average stand density as fixed effects and stand as a random effect were used to identify the best collection of PVs using Program R (R Development Core Team 2008). All RVs and TSD were natural-log transformed.

Akaike Information Criterion (AIC), using the "smallest is best" rule, compared each consecutive model. Based on the lowest AIC value, linear models were selected and equations were back-transformed.

Table 2 lists stand attributes grouped by biogeoclimatic unit and number of sample trees by biogeoclimatic unit and SMR. Figure 3 shows distribution of cross-dated sample trees by TSD. The range in actual mortality dates within the first three external TSD categories was up to 5 yr with trees in the fourth category showing even greater range in actual mortality dates (data not shown).

Results from cross-dating tree-fall pairs are seen in Fig 4, which shows distribution of mortality dates and distribution of years from mortality to fall for paired samples. Most sample trees died 9 yr prior to sampling, and most of these remained standing for more than 6 yr postmortality.
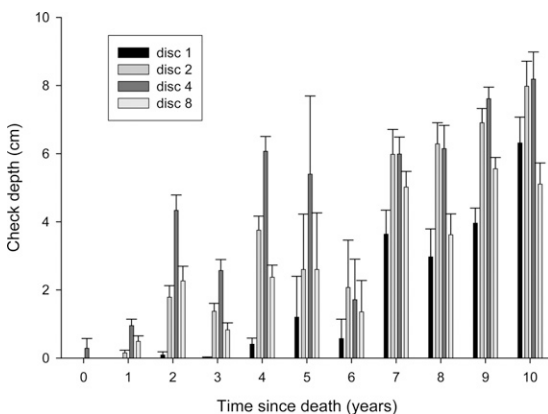

Figure 2. Number of checks by time-since-death and disk height. Disk 1 = 0.3 m, disk 2 = 1.3 m, disk 4 = one-third merchantable height, Disk 8 = two-thirds merchantable height.

Table 2. Number of plots and trees measured and cross-dated, stand structure, and cross-dating statistics grouped by biogeoclimatic subzone and soil moisture regime.

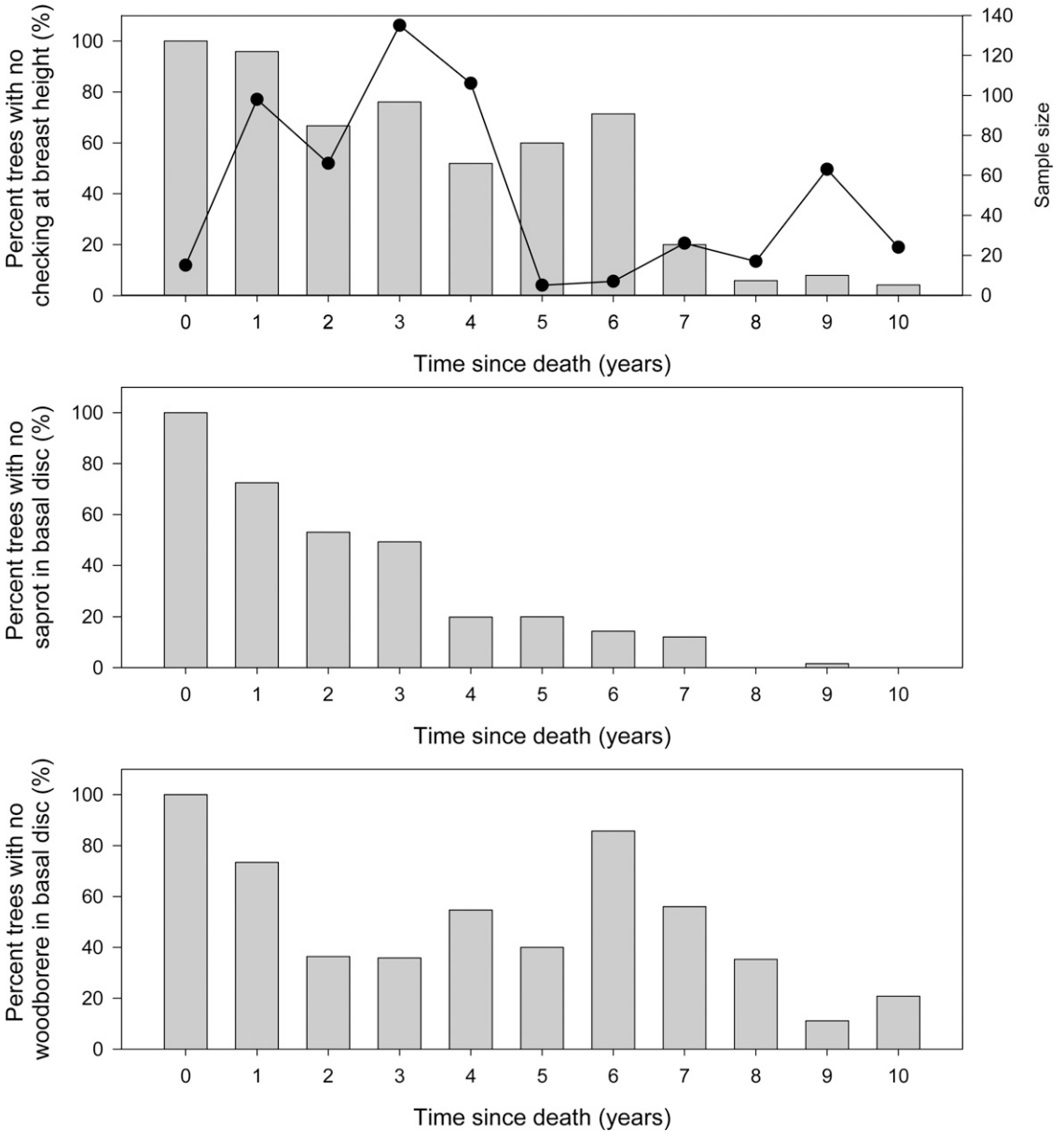| BEC unit | Sample period | Number of plots | Stems/ha | Percent pine | Percent down | No. of trees by soil moisture regime | | | Cross-date correlation |
						Dry	mesic	wet	
SBSdk	1	102	980-1225	68-90	<1	85	81	99	0.48-0.50
	2	15	500-1450	60-100	28 (range, 0-60)	37	63	26	0.40-0.43
SBS mc3	1	81	1000-1350	84-94	0	55	58	58	0.45-0.49

Figure 3. Bar graphs show percentage trees with no detectable checking, saprot, or wood-borer damage within each cross-dated level of time-since-death. The line plot shows sample size in each time-since-death year.
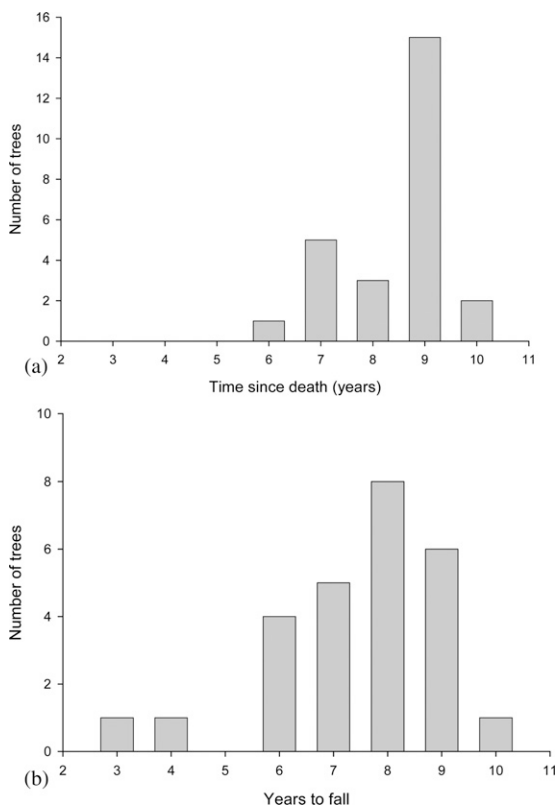
(a)

(b)

Figure 4. Frequency distributions of time-since-death of fallen sample trees killed by mountain pine beetle (A) and years from mortality to fall of same trees (B). Date of fall was determined by dating scars on live adjacent trees damaged when the beetle-killed tree fell over.

Trees sampled during the second period had been dead 6-10 yr and had a higher fall-down rate compared with trees dead 0-5 yr. Logistic regression of fallen/standing dead trees by diameter class was not significant ($p = 0.287$). A pattern with SMR was evident with 51.3, 25.3, and 18.7% of trees down in dry, mesic, and wet SMRs, respectively, although this was not statistically significant ($p = 0.083$).

Wood Moisture Content and Specific Gravity

Percentage moisture contents, grouped by disks 1, 2, 4, and 8, are shown separately for the two subzones in Figs 5 (sapwood) and 6 (heartwood). Moisture content of sapwood declined
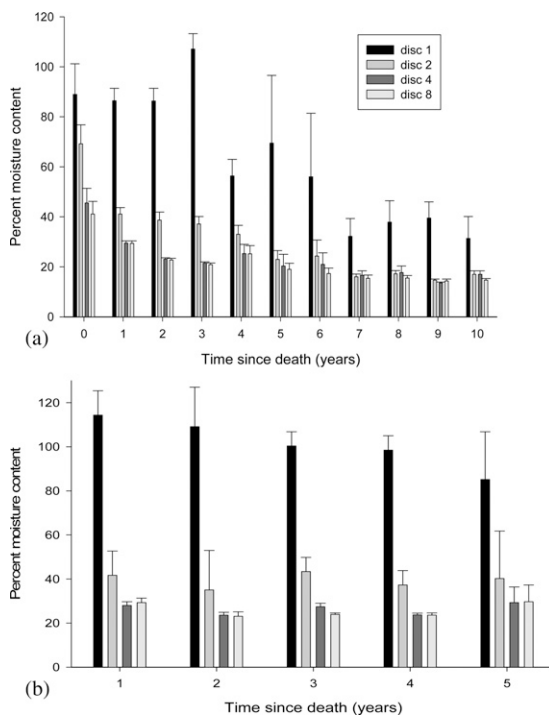

(a)

(b)

Figure 5. Percentage moisture content in sapwood vs time-since-death for SBSdk (A) and SBSmc3 (B) by disk. Bars equal standard error. Disk 1 = 0.3 m, disk 2 = 1.3 m, disk 4 = one-third merchantable height, disk 8 = two-thirds merchantable height.

sharply during the first 2 yr postmortality, becoming stable at approximately FSP (≈25%) by 2 yr postmortality. One exception is found at the base of the tree where moisture content remained above 80% for 5 yr or more. Figure 5 shows no difference in absolute sapwood moisture content or rate of drying among the two subzones. Moisture content in the heartwood showed a similar pattern of drying to a stable FSP by 2 yr postmortality, although heartwood started with lower moisture content than sapwood (Fig 6).

The repeated-measures ANOVA determined that both TSD and SMR were significant explanatory variables, but the amount of variation explained by SMR was very low (under 2%) (Table 3). Figures 5 and 6 show that moisture contents depended on wood type and disk height, therefore linear regressions were
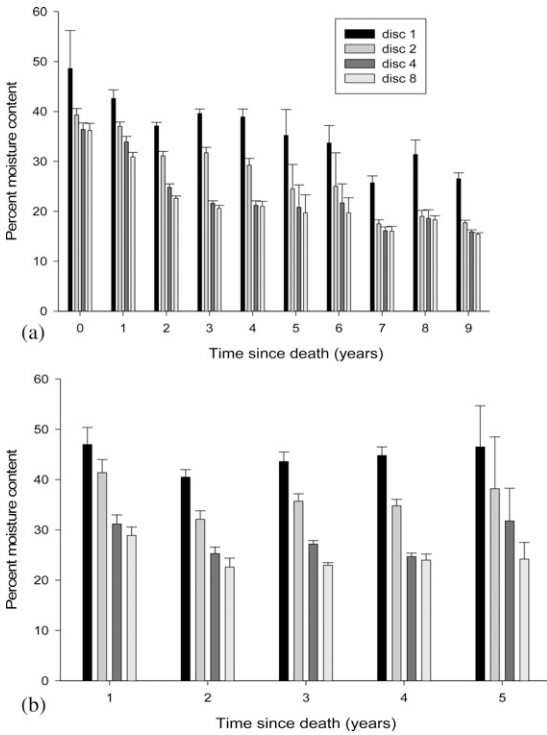
Figure 6. Percentage moisture content in heartwood vs time-since-death for SBSdk (A) and SBSmc3 (B) by disk. Bars equal standard error. Disk 1 = 0.3 m, disk 2 = 1.3 m, disk 4 = one-third merchantable height, disk 8 = two-thirds merchantable height.

Table 3. Analysis of variance of all data pooled with wood type (sapwood and heartwood) and disk height as repeated measures.

Source[a]	SS	df	MS	F	p	Partial eta^2
Intercept	5927.8	1	5927.8	15,190.6	<0.001	0.965
TSD	292.2	1	292.2	748.7	<0.001	0.577
SMR	3.0	1	3.0	7.7	0.006	0.014
Error	213.8	548	0.390			

[a] TSD, time-since-death; SMR, soil moisture regime.

developed to predict percentage moisture content separately in heartwood and sapwood by disk using the following model:

$$\text{Percentage MC} = e^{(\text{intercept} + \beta1 * \text{TSD} + \beta2 * \text{SMR})}$$

(2)

Table 4 provides regression parameters and descriptive statistics for the eight regression models developed (two wood types × four disk

locations). As seen by the slope parameters, moisture contents in disk 1 and 2 vary differently with TSD than moisture contents in upper disks (4 and 8). SMR makes a significant contribution to moisture contents at disks 1 and 2, although the importance of that contribution is much less than TSD.

The repeated-measures ANOVA using the total data set for specific gravity with disk and wood type as the repeated measures showed no significant effect of TSD and SMR on specific gravity ($p = 0.849$ and 0.345, respectively).

Blue-Stain Fungi

Within the first year of beetle attack, blue-stained wood volume reached near maximum levels and then declined with TSD as beetles attacked smaller trees at later stages of the epidemic. Tree growth rate, and therefore sapwood volume, was built into the following multilinear regression model:

$$\text{Blue-stain depth (cm)} = -1.26 + 0.917 \\ * \ln(\text{ABS20}) + 1.115 * \ln(\text{PRE20DBH})$$

(3)

The model was significant ($p < 0.001$) with an adjusted R^2 of 0.533.

Checking, Saprot, and Wood-Borer Damage

Percentage of trees with detectable signs of checking (at DBH), saprot, and wood-borer damage (at tree base) generally increased with advanced TSD, however, the trend was neither linear nor consistent with large year-to-year fluctuations, probably caused by sample size (Fig 3) and DBH.

The greatest number of checks occurred in the middle section of trees followed by the bottom. Negligible checking occurred near the top (Fig 7). Furthermore, within the bottom and middle sections, number of checks increased with TSD, suggesting that these sections are more likely to develop checking the longer they remain standing dead, but the pattern did not exist for the top (Fig 7).

Table 4. Regression parameters and model statistics for each of the eight regression models.[a]

DV	β-parameter[b]	β-value	p	Partial eta[2]
lnswmc1[c]	Intercept	4.423	<0.001	0.82
	TSD	−0.153	<0.001	0.299
	SMR	0.145	<0.001	0.029
lnhwmc1	Intercept	3.789	<0.001	0.952
	TSD	−0.062	<0.001	0.294
	SMR	0.026	0.074	0.006
lnswmc2	Intercept	3.696	<0.001	0.879
	TSD	−0.121	<0.001	0.379
	SMR	0.073	0.002	0.017
lnhwmc2	Intercept	3.638	<0.001	0.952
	TSD	−0.088	<0.001	0.474
	SMR	0.033	0.019	0.010
lnswmc4	Intercept	3.412	<0.001	0.935
	TSD	−0.081	<0.001	0.394
	SMR	0.001	0.971	0.000
lnhwmc4	Intercept	3.459	<0.001	0.956
	TSD	−0.075	<0.001	0.443
	SMR	−0.006	0.650	0.000
lnswmc8	Intercept	3.371	<0.001	0.936
	TSD	−0.082	<0.001	0.405
	SMR	0.004	0.774	0.000
lnhwmc8	Intercept	3.376	<0.001	0.957
	TSD	−0.068	<0.001	0.416
	SMR	−0.012	0.313	0.002

[a] Two wood types (sapwood, sw; heartwood, hw) and four disk heights (1 = 0.3 m, 2 = 1.3 m, 4 = one-third of merchantable height, 8 = two-thirds of merchantable height).
[b] TSD, time-since-death; SMR, soil moisture regime.
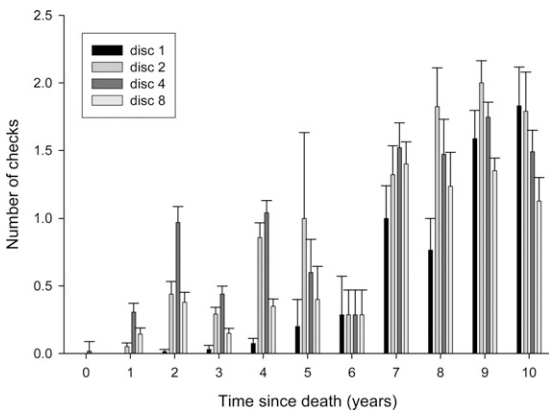[c] lnswmc1 = natural log of sapwood moisture content at disk 1.

Figure 7. Depth of checks (cm) by time-since-death and disk height. Disk 1 = 0.3 m, disk 2 = 1.3 m, disk 4 = one-third merchantable height, disk 8 = two-thirds merchantable height.

Checking occurs relatively quickly, and by Year 2, amount of trees that developed checks in the tree section most likely to check (middle) was above 70%. Check depth appeared to increase with TSD at most disk heights but was particularly notable at the basal disk (Fig 2).

Number and depth of checks and saprot and wood-borer damage were consistently predicted by TSD and DBH (Table 5). Average stand density was not retained in any final model. Eq 5-8 can be used to estimate each response variable. In general, number and depth of checks and saprot and wood-borer damage all increase with increasing TSD and DBH. Therefore, stands with less variation around mean TSD or DBH will have more consistent decay and degradation profiles.

Number of checks
$$= e^{(-0.429 + 0.317 * \ln[\text{TSD} + 1] + 0.014 * \text{DBH})} - 1 \quad (4)$$

Depth of checks
$$= e^{(-0.932 + 0.629 * \ln[\text{TSD} + 1] + 0.034 * \text{DBH})} - 1 \quad (5)$$

Depth of saprot
$$= e^{(-0.666 + 0.746 * \ln[\text{TSD} + 1] + 0.019 * \text{DBH})} - 1 \quad (6)$$

Depth of wood-borer damage
$$= e^{(0.536 * \ln[\text{TSD} + 1] + 0.011 * \text{DBH})} - 1 \quad (7)$$

DISCUSSION

This study examined biophysical variables that influenced change in properties of wood quality and quantity. The study design had some limitations because of MPB population dynamics and the need to collect data and develop models within a short time. To limit unexplained variation caused by geographic location of sample trees and preference by the beetle for larger trees as the host, the best sample design would be to select sample areas and sample trees from the same area across 10 yr or more to monitor change in wood properties with time from the same stand of trees and trees from the same size class. This was not possible given the timeframe. As a result, we had to select sample trees that were killed at different stages of

Table 5.   Linear mixed-effects model parameter estimates and statistics for each dependent variable (DV).

DV	IV[a]	β-parameter	SE	t[b]	p
Number of checks (NC)	Intercept	−0.429	0.097	−4.44	<0.001
	TSD	0.317	0.045	6.98	<0.001
	DBH	0.014	0.002	5.33	<0.001
Depth of checking (DC)	Intercept	−0.932	0.190	−4.91	<0.001
	TSD	0.629	0.090	7.03	<0.001
	DBH	0.034	0.005	6.44	<0.001
Depth of saprot (DS)	Intercept	−0.666	0.137	−4.88	<0.001
	TSD	0.746	0.062	12.0	<0.001
	DBH	0.019	0.004	4.69	<0.001
Depth of wood-borer damage (DW)	Intercept	−0.054	0.194	−0.276	0.782
	TSD	0.536	0.091	5.92	<0.001
	DBH	0.011	0.006	2.01	0.045

[a] TSD, time-since-death; DBH, diameter at breast height.
[b] n = 516 for all models.

the beetle outbreak across a large landscape. We controlled for autocorrelation between tree size and TSD by treating tree size (DBH) as a covariate when necessary. The problem of having a number of years since death that had few samples was handled by treating TSD as a continuous variable, and variation associated with differences in geographic area was addressed by treating the stand as a random effect when appropriate.

Subzone was not a significant factor in this study, possibly because the two subzones sampled were adjacent to each other and plant communities identified in SBSmc3 suggest that some areas we sampled may have been more transitional to SBSdk. There was a strong positive relationship between high sapwood moisture content at the tree base and wetter SMR. Saprot fungi require moisture to be effective decomposers (Manion 1981; Zak 2005), therefore the influence of subzone, as expressed in SMR, is probably important in this regard. As a result, we expected that very dry subzones would have significantly slower tree-fall rate than relatively wetter subzones. However, plot level measurements did not support this hypothesis. We found a higher fall-down rate on dry plots compared with wet plots. This could have been an artifact of little difference in actual soil moisture content between different regimes. Keen (1955) found that ponderosa pine trees killed by western pine beetle stood longer on

pumice soils (dry) than on loam soils (moist) but in that case, a difference in parent material could have resulted in large differences in soil moisture. Also, dry plots may be in rocky areas with shallow soils resulting in a fall-down rate that has little to do with saprot development at the base and more to do with local site conditions. Another possible explanation comes from our observation that carpenter ant activity (wood borers) was greater on drier sites, which is most likely a function of faster colony growth in dry (warm) habitats, because ants are thermophilic. Also, it may be that moisture requirements are only met at the tree base in dry environments, therefore ants confine their nests more to the base and into roots, whereas in cooler, wetter environments, they may preferentially extend the nest up the trunk because thermal properties would be suboptimal at the base. Thus, the base may be weakened faster in dry areas, affecting stability of trees more (Lindgren, 2010). Unlike Dahms (1949) and Keen (1955), who studied fall-down rates of ponderosa pine, we did not find diameter to have a significant effect on fall-down rate, although we did observe a similar trend. This could be caused by a shorter observation history in our study.

Our results indicated that wood moisture content had a major role in determining wood quality with time. Moisture content affected degree and depth of checking, particularly as wood dried to FSP. Trees with one or more checks at breast

height had sapwood moisture content less than 50%. Moisture is essential for saprot fungi to thrive, which explains the prevalence of saprot at the base of dead trees and the limited development of saprot at breast height and above. Moisture content was influenced primarily by TSD with some influence by SMR, but this was significant only for disks 1 and 2 (up to 1.3 m). Our results agree with other studies on lodgepole pine wood properties following mortality from MPB (Chow and Obermajer 2007; Magnussen and Harrison 2009), which showed a general marked decrease in sapwood moisture content in the first year following mortality to about FSP followed by a slower and linear decline to an asymptote that is reached several years later (Year 6 or 7 in our study). Dry trees are more susceptible to breakage during handling (Giles 1986), and therefore, we expect a significant increase in breakage between Years 2 and 6 postmortality that is sustained as trees age.

Blue-stain fungi are limited to sapwood (Solheim 1995), therefore depth of blue-stain penetration should vary with sapwood amount. Vigorous trees have a greater sapwood amount compared with declining trees (Munster-Swendsen 1987), therefore faster growing trees are expected to have greater sapwood proportion. We did find a significant relationship between indicators of tree growth (growth during the last 20 yr and tree DBH at the beginning of the 20-yr period) and penetration depth by blue-stain. Blue-stain enters and colonizes sapwood within the first year of successful attack but does not affect strength properties (Lum et al 2006). Therefore, products that are intolerant of stain aesthetically are devalued within the first year, but after Year 1, blue-stain has little influence on wood quality and potential use.

Independent variables that best explained number and depth of checks, saprot depth, and depth of wood-borer damage were TSD and DBH. Unlike Magnussen and Harrison (2009), we did not find a significant relationship with SMR, although the range of SMRs in our study area was substantially narrower than in their study. Similar to findings by Magnussen and Harrison

(2009), checks developed rapidly within the first 2 yr postmortality, mirroring decrease in moisture content during the same time. Dobie and Wright (1978) found that positive conversion rates for lumber could be achieved from lodgepole pine killed by MPB unless trees have developed severe checking. In our study, there is a 2-yr window for most trees in a stand, but there may be up to 6 yr or more window for small-diameter trees. Average stand density had a weak relationship with number of checks. This has been supported by observations from loggers who noted that trees growing in open forests had more checks than trees growing in dense forests. Presumably, open-grown trees tend to be more vigorous because of decreased competition and therefore have a greater sapwood proportion compared with trees from dense forests, and sapwood has higher moisture content than heartwood. Once dead, open-grown trees undergo a more dramatic change in sapwood moisture content during drying compared with densely grown trees, resulting in more checks in open-grown trees.

CONCLUSIONS

Most wood property changes occurred within the first 2 yr postmortality with slower decreases in wood quality thereafter (Fig 3). Therefore, a short window of opportunity existed to use recently dead trees that have wood characteristics similar to green trees with the exception of blue-stain, which became fully established within 6-8 mo. This window was about 1 yr, because number of checks increased substantially by the second year postmortality. Following Year 2, there was a period of stable wood properties with little change occurring, although existing checks deepened with time. Saprot continued to develop at the tree base because of higher wood moisture content, which supports decay fungi. Most trees remained standing until Year 8 (this would vary in different regions with different soil types), at which time the system became less stable and predictable as trees started to fall. This general relationship is diagrammed in Fig 8. As long as
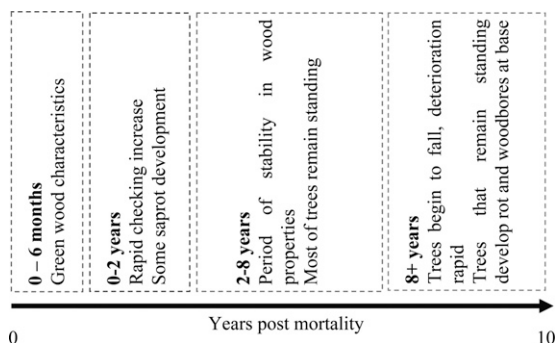
0 – 6 months
Green wood characteristics

0–2 years
Rapid checking increase
Some saprot development

2–8 years
Period of stability in wood properties
Most of trees remain standing

8+ years
Trees begin to fall, deterioration rapid
Trees that remain standing develop rot and woodbores at base

Years post mortality

0   10

Figure 8. Diagram of changes to wood properties as a function of time-since-death.

trees remained standing, there was little loss of actual wood fiber as evidenced by lack of relationship between TSD and specific gravity. Wood characteristics changed with time, but actual loss of cellulose and other constituents was limited to the tree base until the tree fell, at which point moisture absorption caused a rapid increase in decay processes. Tree-fall rate therefore is the single most important biological factor for supply of dead wood for bioenergy feedstocks and other uses of wood fiber.

REFERENCES

Bethlahmy N (1974) More streamflow after a bark beetle epidemic. J Hydrol (Amst) 23:185-189.

Brown M, Black T, Nesic Z, Fredeen A, Jackson P, Burton P, Trofymow T, Spittlehouse D, Grant N, Eggington V (2008) Impact of the mountain pine beetle on the carbon balance of lodgepole pine stands in western Canada. 28th Conference of Agricultural and Forest Meteorology of the American Meteorological Society, Orlando, FL, April 2008. Abstract.

Byrne T, Uzunovic A (2005) Addressing marketplace durability issues with post-mountain pine beetle lodgepole pine—A compilation of three reports. Mountain Pine Beetle Initiative Working Paper 2005-25. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, BC, Canada. 34 pp.

Chan-McLeod A, Zhu X, Klinkenberg B (2009) Factors affecting the ecological legacy of unsalvaged post-mountain pine beetle stands. Mountain Pine Beetle Working Paper 2008-19. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, BC, Canada. 20 pp.

Chow S, Obermajer A (2007) Moisture and blue stain distribution in mountain pine beetle infested lodgepole pine trees and industrial implications. Wood Sci Technol 41:3-16.

Dahms WG (1949) How long do ponderosa pine snags stand? Res Note PNW-57 USDA For Serv Pacific Northwest For Range Exp Stn, Portland, OR.

Dobie J, Wright DM (1978) Lumber values from beetle-killed lodgepole pine. Forest Prod J 28:44-47.

Feng MW, Knudson RM (2005) Improving value recovery of OSB from post-mountain pine beetle wood. Mountain Pine Beetle Initiative Working Paper 2005-13. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, BC, Canada. 84 pp.

Fowells H (1965). Silvics of forest trees of the United States. Agric Handb 271. US Department of Agriculture, Washington, DC. 762 pp.

Giles DR (1986) Harvesting and processing of beetle-killed pine. Pages 15–17 *in* R.W. Nielson, ed. Harvesting and processing beetle-killed timber: Proceedings of a seminar sponsored by Forintek Canada and COFI, Northern Interior Lumber Section, May 10, 1985, Prince George, BC. Forintek Canada Corp., Western Division, Special Publication No. SP-26, Vancouver, BC, Canada.

Government of British Columbia (2005) British Columbia's mountain pine beetle action plan 2005-2010. http://www.for.gov.bc.ca/hfp/mountain_pine_beetle/actionplan/2005/exec.htm (3 May 2010).

Haygreen JG, Bowyer JL (1996) Specific gravity and density. *In* Forest products and wood science: An introduction. 3rd ed. Iowa State University Press, Ames, IA. 484 pp.

Holmes R (1983) Computer-assisted quality control in tree-ring dating and measuring. Tree Ring Bulletin 43:69-78.

Keen FP (1955) The rate of natural falling of beetle-killed ponderosa pine snags. J Forestry 53:720-723.

Koch P (1996) Lodgepole pine in North America. Vol. 2, Chpt. 11, Gross characteristics of tree components. Forest Products Society, Madison, WI. 763 pp.

Kurtz W, Dymond C, Stinson W, Rampley G, Neilson E, Carroll A, Ebata T, Safranyik L (2008) Mountain pine

beetle and forest carbon feedback to climate change. Nature 452:987-990.

Lindgren, BS (2010) University of Northern British Columbia, Prince George, BC, Canada. Personal communication, January 10, 2010.

Lum C, Byrne T, Casilla R (2006) Mechanical properties of lodgepole pine containing beetle-transmitted blue stain. Forest Prod J 56:45-50.

Magnussen S, Harrison D (2009) Assessing the shelf life attributes of mountain pine beetle-killed trees. Mountain Pine Beetle Working Paper 2008-27. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, BC, Canada. 24 pp.

Manion PD (1981) Tree disease concepts. Prentice-Hall Inc., Englewood Cliffs, NJ. 399 pp.

Meidinger D, Pojar J (1991) Ecosystems of British Columbia. Special Report Series No. 6. Crown Publications Inc., Victoria, BC, Canada. 330 pp.

Munster-Swendsen M (1987) Index of vigour in Norway spruce (*Picea abies* Karst). J Appl Ecol 24:551-561.

Newbery JE, Lewis KJ, Walters MB (2004) Estimating time since death of *Picea glauca* × *P. engelmannii* and *Abies lasiocarpa* in wet cool sub-boreal spruce forest in east–central British Columbia. Can J For Res 34:931-938.

Oliveira LC, Wallace J, Cai L (2005) Optimizing drying of mountain pine beetle wood. Mountain Pine Beetle Initiative Working Paper 2005-12. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, BC, Canada. 37 pp.

Orbay L, Goudie D (2006) Quantifying lumber value recovery from beetle-killed trees. Mountain Pine Beetle Initiative Working Paper 2006-09. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, BC, Canada. 19 pp.

R Development Core Team (2008) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org. (accessed 20 March 2011)

Rex J, Dubé S (2009) Hydrologic effects of mountain pine beetle infestation and salvage-harvesting operations. Mountain Pine Beetle Working Paper 2009-05. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, BC, Canada. 44 pp.

Reynolds G (1989) Climate data summaries for the biogeoclimatic zones of British Columbia. BC Min. For. Research Branch, Victoria, BC, Canada. Unpublished report.

Solheim H (1995) Early stages of blue-stain fungus invasion of lodgepole pine sapwood following mountain pine beetle attack. Can J Bot 73:70-74.

SPSS Inc (2008) SPSS base 16.0 for Windows user's guide. SPSS Inc., Chicago, IL.

Stokes M, Smiley T (1968) An introduction to tree-ring dating. University of Chicago Press, Chicago, IL. 73 pp.

SYSTAT (2004) Cranes Software International. Vasanthnagar, Bangalore, Karnataka, India.

Taylor SW, Carroll AL, Alfaro RI, Safranyik L (2006) Forest, climate and mountain pine beetle outbreak dynamics in western Canada. Pages 67-94 *in* L Safranyik and B Wilson, eds. The mountain pine beetle a synthesis of biology, management, and impacts on lodgepole pine. Natural Resources Canada, Can For Serv, Pacific Forestry Centre, Victoria, BC, Canada.

Trent T, Lawrence V, Woo K (2006) A wood and fibre quality-deterioration model for mountain pine beetle-killed trees by biogeoclimatic subzone. Mountain Pine Beetle Initiative Working Paper 2006-10. Natural Resources Canada, Can For Serv, Pacific Forestry Centre, Victoria, BC, Canada. 23 pp.

Zak J (2005) Fungal communities of desert ecosystems: Links to climate change. Chapter 33 *in* J Dighton, J White, and P Oudemans, eds. The fungal community, its organization and role in the ecosystem. Taylor and Francis Group, Boca Raton, FL.