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Wood decay and degradation in standing lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.) killed by mountain pine beetle (*Dendroctonus ponderosa* Hopkins: Coleoptera)

Kathy Lewis, Doug Thompson, Ian Hartley and Sorin Pasca

Mountain Pine Beetle Initiative
Working Paper 2006-11

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Abstract

Despite the number of past outbreaks of mountain pine beetle (*Dendroctonus ponderosa* (Hopkins)), little is known about the rate of change in stand structure, and the rate of deterioration of wood properties with time since death. In this study, we examined the rate of tree fall in beetle-affected stands, and determined the biophysical factors that affect wood quantity and quality in individual trees following mortality. We surveyed 30 stands, and destructively sampled 450 trees. External indicators used to estimate year of mortality were not accurate, particularly for trees that had been killed in the earlier stages of the epidemic. Sample trees were cross dated against live trees to determine their year of mortality. Drying, blue stain and checking were the major causes of decline in wood quality and quantity in recently killed trees (1 to 2 years after death). Saprot and ambrosia beetles became established during the first 2 years after mortality, but then held steady and did not increase depth of penetration, except within the basal section of the tree, where moisture content remained well above fibre-saturation point, thereby allowing continued colonization by decay fungi. Location along the stem and tree size are major contributors to variation detected in the factors of wood quality and quantity.

Keywords: Lodgepole pine, mountain pine beetle, shelf life, wood quality, wood quantity, moisture content, specific gravity, blue stain, saprot, checking, wood bores, dendrochronology

Résumé

Même si on a connu de nombreuses infestations de dendroctones du pin ponderosa (*Dendroctonus ponderosa* [Hopkins]), on sait très peu de choses sur la rapidité avec laquelle la structure des peuplements change et sur le taux de détérioration des propriétés du bois à partir du temps écoulé depuis la mort des arbres. Dans cette étude, on examine le taux de chute des arbres dans les peuplements touchés par le dendroctone du pin ponderosa et on détermine les facteurs biophysiques qui ont une incidence sur la quantité et la qualité du bois issu d'arbres individuels après leur mort. On a étudié 30 peuplements et effectué des essais destructifs sur 450 arbres. Les indicateurs externes utilisés pour estimer l'année de la mort des arbres n'étaient pas précis, en particulier pour les arbres qui ont été tués dans les premiers stades de l'épidémie. On a établi la date de la mort des arbres échantillonnés en les comparant à des arbres vivants. Les principales causes de la diminution de la qualité et de la quantité du bois issu d'arbres tués récemment (de un à deux ans) sont le dessèchement, le bleuissement et les gerces. La pourriture de l'aubier et les infestations de scolytes se sont manifestées durant les deux premières années qui ont suivi la mort de l'arbre, mais sont demeurées stables et n'ont pas pénétré davantage en profondeur, à l'exception de la section basale L'emplacement le long de la tige et la grosseur de l'arbre contribuent de façon importante à la variation notée parmi les facteurs qui ont une incidence sur la qualité et la quantité du bois.

Mots-clés : Pin tordu, dendroctone du pin ponderosa, durée de conservation, qualité et quantité du bois, teneur en eau, densité, bleuissement, pourriture de l'aubier, gerce, perce-bois, dendrochronologie

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Introduction

The present mountain pine beetle (*Dendroctonus ponderosa* [Hopkins]) outbreak within the central interior of British Columbia is considered the largest outbreak ever in North America, affecting an area in excess of 8.5 million ha (BCMoF 2006). The initial stages of this outbreak can be traced back to the early 1990s, observed concurrently within four provincial jurisdictions: the Entiako Protected Area, Tweedsmuir Provincial Park, and the Lakes and Vanderhoof forest districts (Figure 1). During the mid-1980s, an outbreak of comparable magnitude and intensity occurred upon the Caribou Plateau, immediately south of the present outbreak. Despite the most recent outbreaks, there are a limited number of studies that focus on the rate of deterioration, degrade and fall of lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.) killed by mountain pine beetle, particularly within British Columbia (Lewis and Hartley 2006).

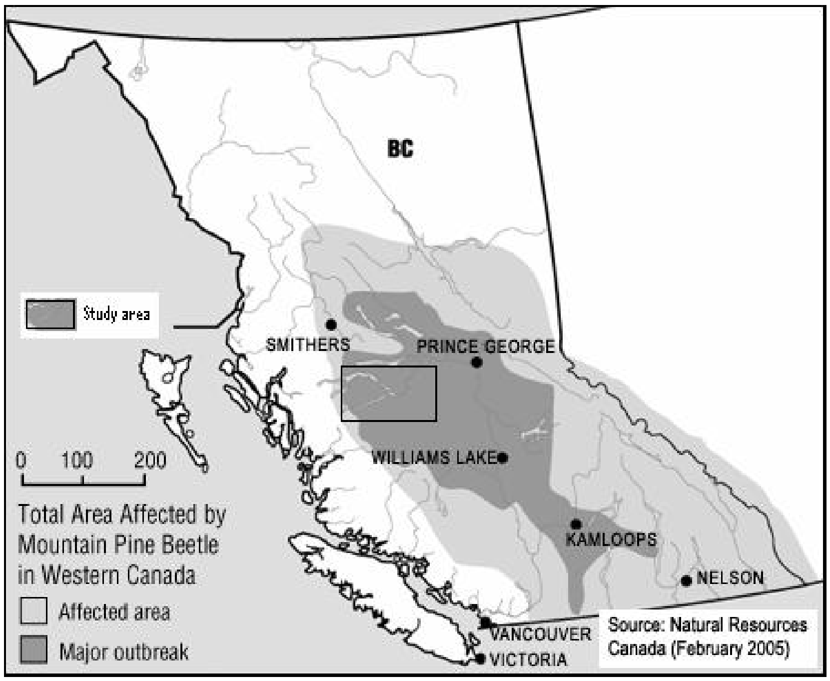

Figure 1. Study area and areas affected by mountain pine beetle within British Columbia.

To reduce the impacts of the current and future mountain pine beetle outbreaks, it is necessary to know the relationships between time since death and factors of wood quality and quantity. Factors determining wood quality and quantity include moisture content, specific gravity, wood volume, blue stain, saprot, checking and wood-borer damage. The wood products that can be manufactured from beetle-killed wood depend on these factors and on the technology used for production. Such information is essential in order to plan the timing and distribution of salvage harvests to recover the greatest value from the wood over time, and to maintain a future wood supply for forest-dependent communities in areas affected by the beetle. Also, understanding the rate of change in stand structure (e.g., rate of tree fall) is essential for strategic planning of wildlife habitat areas and other non-timber values. Therefore, our research is focused on factors of wood quality and quantity.

We examined the rate of tree fall in beetle-affected stands to determine the frequency of tree fall resulting from the mortality of trees killed by mountain pine beetle. We also examined the biophysical factors that affect wood quantity and quality in individual trees (i.e., tree-level study) following mortality.

Material and Methods

Study area and stand-level study

Stands were selected using three criteria:

1. Stands were in areas affected during the initial stages of the mountain pine beetle outbreak and areas currently infested (Figure 1). In total, 17 stands were located within the Dry Cool Sub-Boreal Spruce (SBSdk) biogeoclimatic subzone and 14 stands within the Kluskus Moist Cold Sub-Boreal Spruce (SBSmc3) biogeoclimatic variant;
2. Stands represented a range in soil moisture regimes, relative to each biogeoclimatic unit and;
3. Stands were accessible by road.

Within each stand, six plots were established systematically. Plot radii ranged from 3.99 m to 7.97 m, depending on stand density. Species composition, stem density, diameter at breast height (measured 1.3 m above the ground), and the number of standing dead and fallen pine within one of four external time-since-death categories were recorded (Table 1). Time-since-death categories historically have been used to approximate the year of death based on external characteristics. The time-since-death approach was adapted within our study to identify stands across a broad range of mortality dates.

Table 1. Description of the time-since-death categories for pine killed by mountain pine beetle.

Time since Death	Description
1	green, yellowing or freshly red needles; no needles loss
2	freshly red to red needles; slight needle loss
3	red needles; substantial needle loss
4	no needles; loss of fine branches

Tree-level study

A sampling matrix was used to define sample cells using three diameter at breast height classes (12.5 to 22.5; 22.6 to 32.5, and ≥32.6 cm), three relative soil moisture regimes (dry, mesic, and wet), and the four time-since-death categories. Within the study area, the time-since-death categories within the SBSdk and SBSmc3 units ranged from 1 to 3, and from 3 to 4, respectively. The target sample size per cell was 10 trees (n = 450). From each plot, one tree per cell was used to limit spatial-autocorrelation. Trees had to be free of defects along the merchantable stem (e.g., fire scars, double tops, crooks or burls).

Stem dissections

Each tree was felled, and merchantable stem lengths (from a 0.3-m-high stump to a 10-cm-diameter top) were recorded. From each tree, 12 discs (≈ 4 cm thick) were bucked from the stem. Discs 1 and 2 were removed from stump and breast height. Discs 3 to 12 were cut at equal distances between breast height and the height at which the stem diameter equalled 10 cm. From each disc, the diameter (cm), blue-stain depth (cm), number of checks, average check depth (cm), saprot depth (cm), and wood-borer depth (cm) was recorded.

Dendrochronological materials and analyses

From each tree, discs 1 and 8 were brought to the lab. Discs 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. 1992) and MeasureJ2X (VoorTech Consulting 2004). Series were cross-dated by matching ring-width patterns against ring-width series of live lodgepole pine within the study area. We used the computer program, COFECHA (Holmes 1983), and inspected each sample to detect measurement and cross-dating errors. Disc 8 was included for three reasons: (1) to confirm the cross-dating of disc 1; (2) trees with suppressed and intermediate positions within the canopy tend to put on greater radial growth higher on the stem relatively to the base of the stem (Smith et al. 1997), assuming this would reduce missing, partial or locally absent rings; and (3) we assumed there would be less saprot in discs taken at higher position within trees of older mortality dates, resulting in fewer missed rings. After each tree was dated, we assumed that the outer ring was the last ring formed prior to mortality if the bark was intact, or if the sapwood was present and firm. If both discs showed signs of terminating radial growth, the sample was removed from further analyses.

Moisture content and specific gravity

From discs 1, 2, 4 and 8 from each tree, sapwood and heartwood samples were removed, and fresh weights were measured in the field. Percent moisture contents (oven-dry basis) and specific gravities were measured for each disc, based on the methods of Haygreen and Bowyer (1996). Sapwood and heartwood percent moisture content and specific gravity measures were examined separately, via a repeated-measures analysis of variance, with discs 1, 2, 4 and 8 as repeated-measure factors, using the approach suggested by Moser et al. (1990). The general linear model procedure of SYSTAT (SYSTAT 2004) was used to perform each analysis, and all general linear models included mortality date and biogeoclimatic unit as fixed factors, and soil moisture regime nested within biogeoclimatic unit as a random factor. The mean square of the nested term was used as the mean-square error to detect differences among biogeoclimatic units following the approach suggested by Bennington and Thayne (1994).

Merchantable stem volumes

Merchantable volumes per tree were calculated by summing section volumes between each disc, where the volume of a section was determined using the formula of a cone frustum. The general linear model procedure was used to examine how merchantable volumes varied by mortality date, biogeoclimatic unit and soil moisture regime nested within biogeoclimatic unit; Tukey multiple comparisons were conducted for significant terms (SYSTAT 2004).

Blue-stain fungi

The depth of blue-stain penetration measured at breast height was correlated with diameter at breast height (SYSTAT 2004). The depths of blue-stain penetration in discs 1, 2, 4 and 8 were examined via repeated-measures analysis of variance, with discs 1, 2, 4 and 8 as repeated-measure factors. The general linear model included mortality date and biogeoclimatic unit as fixed factors, and soil moisture regime nested within biogeoclimatic unit as a random factor.

Checking

Each tree was divided into bottom-, middle- and top-stem sections (i.e., discs 1 and 2, 6 and 7 and 11 and 12, respectively), and the following analyses were replicated within each section. First, sections with ≥ 1 check were tallied and percentages were calculated by mortality date. Second, the samples were split into sections with and without checking; for those with, Kruskal-Wallis tests were used to analyze variation in the number of checks and depth of checking (cm) by mortality date and then by diameter at breast height class (SYSTAT 2004). Third, for samples with checking, the number of checks and checking depth means and standard errors were plotted by mortality date and diameter-at-breast-height class.

Saprot

Trees with saprot were tallied and percentages were calculated by mortality date. The depths of saprot penetration in discs 1, 2, 4 and 8 were examined via repeated-measures analysis of variance, with discs 1, 2, 4 and 8 as repeated-measure factors. The general linear model included diameter at breast height as a covariate, mortality date and biogeoclimatic unit as fixed factors, and soil moisture regime nested within biogeoclimatic unit as a random factor.

Wood borer

The percentage of sample trees with wood borers was calculated by mortality date. The sample population was split into trees with and without wood borers. For the samples with wood borer detected, average wood-borer depth was correlated against average blue-stain depth (SYSTAT 2004). The average wood-borer depth was calculated based on the discs with wood borer; the average blue-stain depth was calculated based on blue-stain depths of all 12 discs.

Results

Stand-level study

Table 2 lists the stand attributes grouped by biogeoclimatic unit and soil moisture regime. In total, five of 1997 (≈ 0.25 %) lodgepole pine had fallen, with mountain pine beetle as the cause of mortality.

Table 2. Total number of plots measured, average stand densities, species compositions, downed pine killed by mountain pine beetle, grouped by biogeoclimatic (BEC) unit and soil moisture regime

BEC unit	Soil moisture regime	Number of plots	Average stems/ha	Average species comp. (%)[a]	Downed pine killed by mountain pine beetle (%)
SBSdk	Dry	27	1225	$Pl_{89}Sx_{8}Sb_{2}At_{1}$	0.6
	Mesic	39	1007	$Pl_{79}Sx_{18}Sb_{1}Ba_{3}$	0.7
	Wet	36	979	$Pl_{68}Sx_{27}Sb_{3}At_{2}$	0
SBSmc3	Dry	21	999	$Pl_{94}Sx_{6}$	0
	Mesic	23	1197	$Pl_{84}Sx_{15}Sb_{1}$	0
	Wet	37	1344	$Pl_{88}Sx_{11}Ba_{1}$	0

[a] Species composition: Pl, pine; Sx, hybrid spruce; Sb, black spruce; Ba, subalpine fir; At, trembling aspen. Numeric subscripts indicate the percentage of the average stems/ha.

Tree-level study

Table 3 outlines the frequency of sample trees by biogeoclimatic unit and soil moisture regime. In total, 474 trees were identified for the tree-level study, and 444 were felled and measured. A total of 436 trees were successfully cross-dated; correlation values ranged from 0.22 to 0.71, with a mean of 0.49 (Table 3). The range in mortality dates within each time-since-death category ranged up to 5 years, suggesting that external time-since-death categories are not good predictors of mortality date (Table 4). The frequencies of cross-dated sample trees with mortality dates prior to 2001 were infrequent, so all further analyses were limited to sample trees with mortality dates from 2001 to 2005.

Table 3. Frequency of sample trees and cross-dating statistics, grouped by biogeoclimatic (BEC) unit and soil moisture regime

BEC unit	Soil moisture regime	Trees identified	Trees Felled	Trees successfully cross-dated	Correlation of cross-dating		
					Min.	Max.	Mean (S.E.)
SBSdk	Dry	86	85	85	0.22	0.69	0.48 (0.01)
	Mesic	98	81	81	0.25	0.68	0.50 (0.01)
	Wet	104	102	99	0.28	0.71	0.50 (0.01)
SBSmc3	Dry	62	57	55	0.34	0.68	0.49 (0.01)
	Mesic	61	60	58	0.28	0.71	0.49 (0.01)
	Wet	63	59	58	0.26	0.68	0.45 (0.01)

Table 4. Frequency of sample trees grouped by time-since-death category and mortality date.

Time since Death	Mortality date 2005	2004	2003	2002	2001	≤2000
1	15	47	16	3	2	0
2	0	37	23	22	10	0
3	0	12	24	56	55	7
4	0	2	3	54	39	9

Moisture content and specific gravity

Percent moisture content measures, grouped by sapwood and heartwood, and by discs 1, 2, 4 and 8, were positively skewed. The data were square-root transformed to meet assumptions of normality and homogeneity of variance. Significant differences were found in sapwood moisture content due to mortality date and disc height; however, there was also significant mortality date–disc height interaction (Table 5). The sapwood moisture contents within disc 1 remained somewhat constant through time and, with increasing heights along the stem, there was a decline in moisture content; however, this rate of decline through time was not constant with greater heights within the stem (Figure 2). Heartwood moisture content showed similar relationships with mortality date, disc height and their interaction term (Table 6, Figure 2).

Table 5. Analysis of sapwood moisture content within disc 1, 2, 4 and 8 by mortality date, biogeoclimatic unit and soil moisture regime nested within biogeoclimatic unit.

Source	df	Wilks' λ [1]	MS	F	p
Mortality Date	4		44.313	7.236	<0.001
Biogeoclimatic Unit	1		24.939	2.215	0.211
Soil Moisture Regime (Biogeoclimatic Unit)	4		11.260	1.839	0.121
Error	410		6.124		
Disc Height	3	0.473 (408)		151.705	<0.001
Disc Height × Mortality Date	12	0.944 (1079)		1.997	0.022
Disc Height × Biogeoclimatic Unit	3	0.991 (408)		1.302	0.273
Disc Height × Soil Moisture Regime (Biogeoclimatic Unit)	12	0.951 (1079)		1.732	0.055

[1] Wilks' λ is a multivariate test (with error df given in parentheses) applied to the repeated-measures factor disc height and its interaction with between-subject terms.

Table 6. Analysis of heartwood moisture content within disc 1, 2, 4 and 8 by mortality date, biogeoclimatic unit and soil moisture regime nested within biogeoclimatic unit.

Source	df	Wilks' λ [1]	MS	F	P
Mortality Date	4		40.272	16.160	<0.001
Biogeoclimatic Unit	1		12.668	7.352	0.053
Soil Moisture Regime (Biogeoclimatic Unit)	4		1.723	0.691	0.598
Error	410		2.492		
Disc Height	3	0.521 (408)		125.047	<0.001
Disc Height × Mortality Date	12	0.885 (1079)		4.249	<0.001
Disc Height × Biogeoclimatic Unit	3	0.998 (408)		0.231	0.875
Disc Height × Soil Moisture Regime (Biogeoclimatic Unit)	12	0.980 (1079)		0.692	0.761

[1] Wilks' λ is a multivariate test (with error df given in parentheses) applied to the repeated-measures factor disc height and its interaction with between-subject terms.

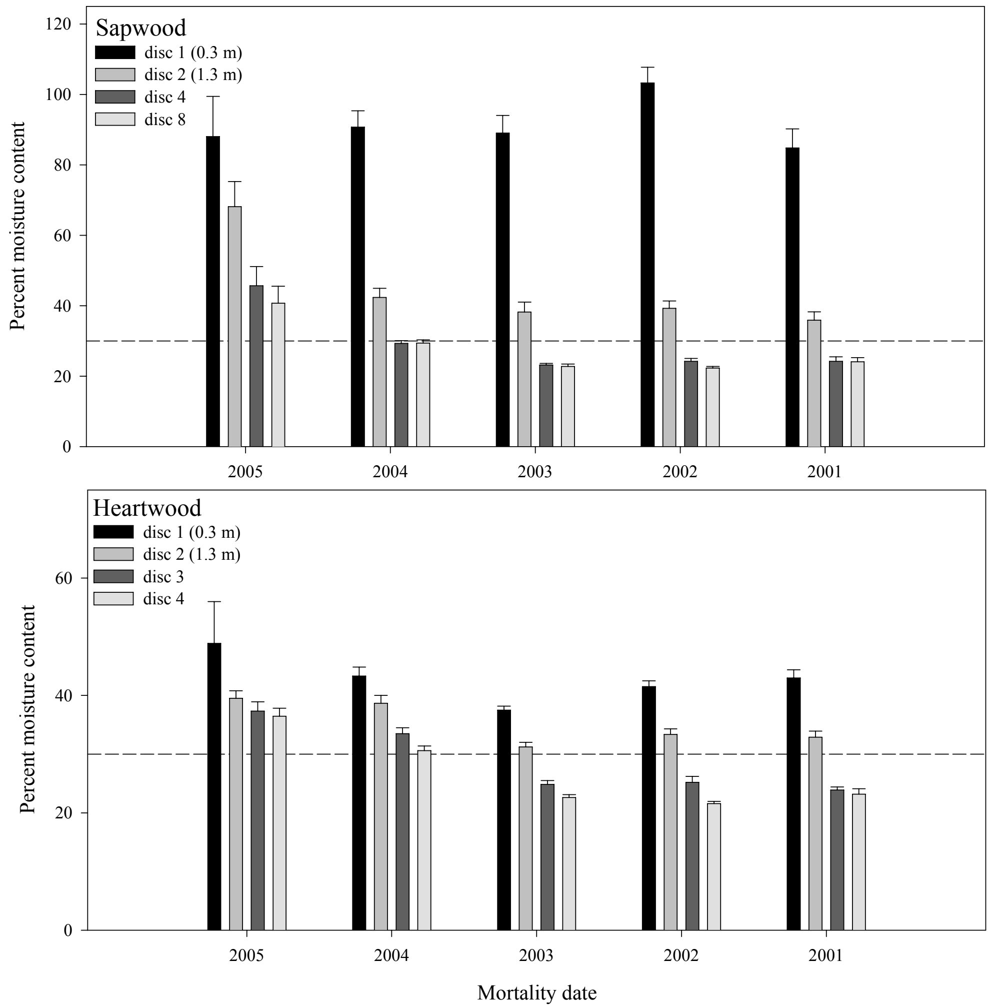

Figure 2. Percent moisture content means and standard errors within the sapwood (top) and heartwood (bottom), grouped by disc and mortality date. Dashed lines represent the fibre saturation point (approximately 30%).

Specific gravity measures grouped by sapwood and heartwood, and by discs 1, 2, 4 and 8, suggest a slight positive skew from normality; however, transformations of the data did not improved the distributions substantially. Lavene's tests of the raw data were not significant ($p > 0.01$) when grouped by biogeoclimatic unit, soil moisture regime or mortality date, suggesting equal variances across groupings. There was a significant effect of mortality date and disc height; however, there was a significant mortality date–disc height interaction (Table 7). In general, sapwood specific gravities decline over time and the apparent differences at different heights seen in 2005 decrease though time (Figure 3). The general linear model results for heartwood specific gravities revealed a different relationship, in which mortality date, biogeoclimatic unit, and the disc height–mortality date and disc height–biogeoclimatic unit interaction terms were significant (Table 8; Figure 3).

Table 7. Analysis of sapwood specific gravity within disc 1, 2, 4 and 8 by mortality date, biogeoclimatic unit and soil moisture regime nested within biogeoclimatic unit.

Source	df	Wilks' λ [1]	MS	F	P
Mortality Date	4		0.056	7.931	<0.001
Biogeoclimatic Unit	1		0.001	1	0.374
Soil Moisture Regime (Biogeoclimatic Unit)	4		0.001	0.141	0.967
Error	404		0.007		
Disc Height	3	0.889 (402)		14.981	<0.001
Disc Height × Mortality Date	12	0.939 (1063)		2.132	0.013
Disc Height × Biogeoclimatic Unit	3	0.994 (402)		0.833	0.476
Disc Height × Soil Moisture Regime (Biogeoclimatic Unit)	12	0.964 (1063)		1.248	0.244

[1] Wilks' λ is a multivariate test (with error df given in parentheses) applied to the repeated-measures factor, disc height and its interaction terms.

Table 8. Analysis of heartwood specific gravity within disc 1, 2, 4 and 8 by mortality date, biogeoclimatic unit and soil moisture regime nested within biogeoclimatic unit.

Source	df	Wilks' λ [1]	MS	F	P
Mortality Date	4		0.012	2.374	0.051
Biogeoclimatic Unit	1		0.046	23.000	0.009
Soil Moisture Regime (Biogeoclimatic Unit)	4		0.002	0.346	0.847
Error	402		0.005		
Disc Height	3	0.789 (400)		35.603	<0.001
Disc Height × Mortality Date	12	0.948 (1058)		1.805	0.043
Disc Height × Biogeoclimatic Unit	3	0.951 (400)		6.870	<0.001
Disc Height × Soil Moisture Regime (Biogeoclimatic Unit)	12	0.964 (1058)		1.219	0.264

[1] Wilks' λ is a multivariate test (with error df given in parentheses) applied to the repeated-measures factor, disc height and its interaction terms.

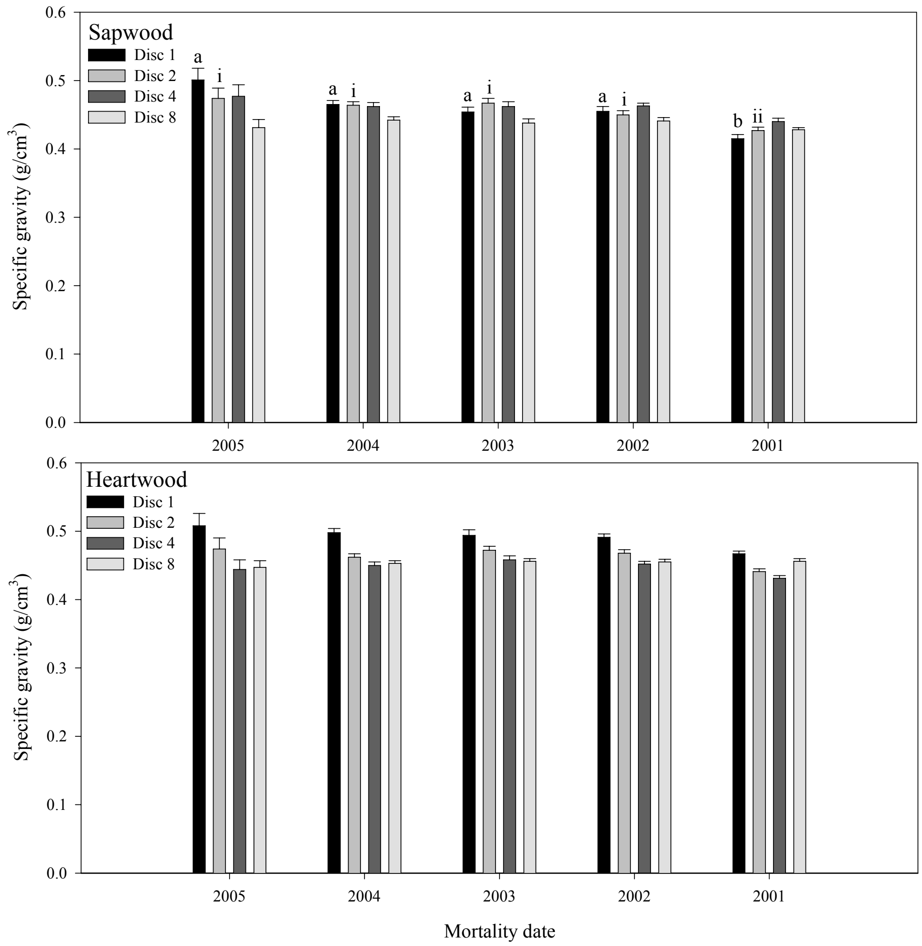

Figure 3. Specific gravity means and standard errors within the sapwood (top) and heartwood (bottom), grouped by mortality date.

Merchantable volume

The distribution of merchantable volume was positively skewed (data not shown). To meet assumptions of normality and homogeneity of variance, the data were transformed using the cube-root transformation. No significant differences were found in merchantable volumes due to biogeoclimatic unit or soil moisture regime nested within biogeoclimatic unit; however, significant differences in merchantable volumes were detected due to mortality dates (Table 9). Tukey multiple comparisons reveal that the mean merchantable volumes of sample trees with a mortality date of 2005 were smaller than those of trees with mortality dates from 2004 through 2001, and that merchantable volumes of sample trees with mortality dates of 2001 were larger than those of tree with mortality dates from 2002 to 2005 (Table 10). The between-group (i.e., mortality date) differences in merchantable volume suggest that variability due to tree size should be controlled for statistically.

Table 9. Analysis of merchantable volume by mortality date, biogeoclimatic unit and soil moisture regime nested within biogeoclimatic unit.

Source	SS	df	MS	F	p
Mortality Date	1.907	4	0.477	17.887	<0.001
Biogeoclimatic Unit	0.042	1	0.042	1.313	0.316
Soil Moisture Regime (Biogeoclimatic Unit)	0.128	4	0.032	1.204	0.309
Error	10.872	408	0.027		

Table 10. Summary statistics and Tukey multiple comparisons for merchantable volume grouped by mortality date.

Mortality date	Sample size	Mean	Standard error of the mean	Tukey multiple comparisons
2005	14	0.171	0.018	a
2004	98	0.484	0.039	b
2003	66	0.550	0.053	b
2002	134	0.423	0.023	b
2001	106	0.681	0.031	c

Blue-stain fungi

The depth of blue-stain penetration measured at breast height was positively correlated with the tree-diameter measure at breast height ($r = 0.482$, $p<0.001$). Further, the depth of blue-stain penetration was not significantly affected by the height along the merchantable stem, nor by mortality date, biogeoclimatic unit, and soil moisture regime nested within biogeoclimatic unit; however, diameter at breast height was a significant covariate, suggesting that the depth of blue-stain penetration could be predicted by diameter at breast height alone (Table 11).

Checking

The greatest percentage of checking occurred within the middle section, suggesting that the middle of the tree is most likely to check, followed by the bottom, with negligible checking occurring within the top (Table 12). Furthermore, within the bottom and middle sections, the percentage of checking increases with mortality dates further back in time, suggesting that these sections are more likely to develop checking the longer they remain standing dead; but this pattern does not exist for the top (Table 12). In sample trees with recorded checking (by stem section), there was significant difference in the number of checks by mortality date within the bottom section, but not within the middle and top sections (Table 13). There were significant differences in the depth of checking by mortality date within the bottom and middle sections, but not within the top section (Table 13). In general, the number of checks within the bottom-stem sections and the depth of checking within the bottom- and middle-stem sections increase with mortality dates further back in time (Figure 4).

Table 11. Analysis of blue-stain penetration depth within discs 1, 2, 4 and 8 by mortality date, biogeoclimatic unit and soil moisture regime nested within biogeoclimatic unit, and diameter at breast height as a covariate.

Source	df	Wilks' λ [1]	MS	F	P
Diameter at Breast Height	1		493.967	156.624	<0.001
Mortality Date	4		4.599	1.458	0.214
Biogeoclimatic Unit	1		31.270	4.386	0.104
Soil Moisture Regime (Biogeoclimatic Unit)	4		7.132	2.261	0.062
Error	407		3.154		
Disc Height	3	0.991 (405)		1.186	0.315
Disc Height × Diameter at Breast Height	3	0.966 (405)		4.748	0.003
Disc Height × Mortality Date	12	0.903 (1071)		3.508	<0.001
Disc Height × Biogeoclimatic Unit	3	0.946 (405)		7.744	<0.001
Disc Height × Soil Moisture Regime (Biogeoclimatic Unit)	12	0.949 (1071)		1.801	0.044

[1] Wilks' λ is a multivariate test (with error df given in parentheses) applied to the repeated-measures factor, disc height and its interaction terms.

Table 12. Percentage of sample trees, grouped by mortality date, with ≥ 1 check per stem section (i.e., bottom, middle and top).

		Mortality date				
		2005	2004	2003	2002	2001
Samples size per mortality date		15	98	66	135	106
Percentage of stem sections with checking	Bottom	0	4	33	24	48
	Middle	0	17	55	33	66
	Top	0	0	8	3	7

Table 13. Analysis of the number of checks and the depth of checking (cm) in the bottom-, middle- and top-stem sections, by mortality date (α' ≈ 0.02).

Test	Stem section	Kruskal-Wallis ($\chi 2$)	df	p
Number of checks	Bottom	11.347	3	0.010
	Middle	4.700	3	0.192
	Top	1.143	2	0.565
Depth of checking (cm)	Bottom	27.514	3	<0.001
	Middle	34.173	3	<0.001
	Top	3.610	2	0.164

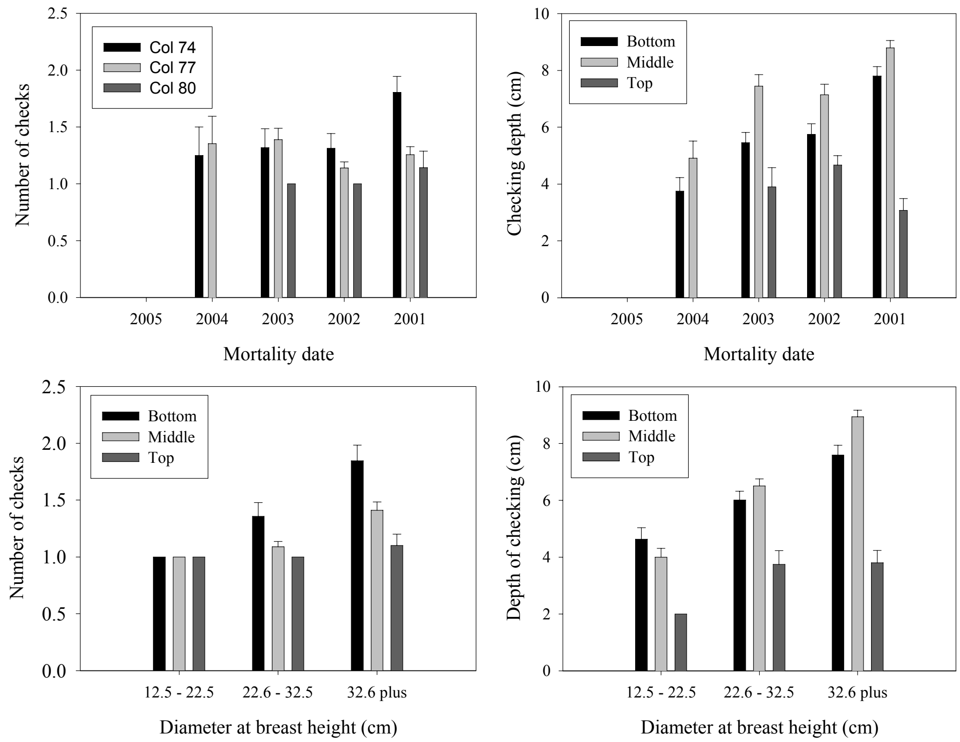

Figure 4. Number of checks (left) and checking depth (right) means and standard errors, within the bottom-, middle- and top-stem sections, grouped by mortality date (top) and diameter-at-breast-height class (bottom).

There were significant differences in the number of checks by diameter-at-breast-height class within the bottom- and middle-stem sections, but not within the top section (Table 14). Further, there are significant differences in the depth of checking by diameter-at-breast-height class within the bottom- and middle-stem sections, but not within the top stem sections, at the set alpha levels (Table 14). In general, with increasing diameter at breast height, there is an increase in the number of checks and an increase in the depth of checking within the bottom and middle sections (Figure 4).

Table 14. Analysis of the number of checks and the depth of checking (cm) in the bottom, middle and top-stem sections by diameter-at-breast-height class (i.e., 12.5 to 22.5 cm, 22.6 to 32.5 cm, and ≥32.6 cm; α' ≈ 0.02).

Test	Stem section	Kruskal-Wallis ($\chi 2$)	df	p
Maximum number of checks	Bottom	18.392	2	<0.001
	Middle	17.745	2	<0.001
	Top	0.500	2	0.779
Maximum depth of checking	Bottom	21.976	2	<0.001
	Middle	64.883	2	<0.001
	Top	1.987	2	0.370

Saprot

Within the first year after mortality, the percentage of trees with saprot detected in discs 1, 2, 4 and 8 is negligible (Table 15). By 2004, the percentage increased considerably with the smallest percentage recorded in discs 1; as mortality dates move further back in time, the percentage of trees with saprot increases, and the degree of increase is generally greater within lower discs, suggesting an interaction between the date of mortality, height along the stem and the likelihood of having saprot (Table 15).

Table 15. Percentage of samples with saprot detected within discs 1, 2, 4 or 8, grouped by mortality date.

Mortality date		2005	2004	2003	2002	2001
Samples size per mortality date		15	98	66	135	106
Percentage of samples with saprot detected	Disc 1	0	28	47	50	80
	Disc 2	0	43	57	63	73
	Disc 4	0	42	45	47	61
	Disc 8	7	46	38	33	43

Due to the negligible amount of saprot detected within trees that had died in 2005, the data was positively skewed (Figure 5). The data was square-root transformed and the repeated-measures analysis was limited to samples that had mortality dates from 2001 to 2004. Furthermore, the alpha level was set to 0.01 making the analysis conservative. The diameter-at-breast-height and mortality-date factors were both significant; biogeoclimatic unit and soil moisture regime nested within biogeoclimatic unit were not significant (Table 16). The repeated measures analysis did not find the depth of saprot penetration to be significantly different at varying heights along the stem; however, at conventional alpha levels there was slight height effect (Table 16). Furthermore, there is an interaction between height and mortality date, again at conventional alpha levels (Table 16). As indicated by depth of saprot penetration, saprot may be initiated sooner higher along the stem; however, as time advances, the depth of penetration at lower locations along the stem surpasses those at higher locations, resulting in the interaction (Figure 6).

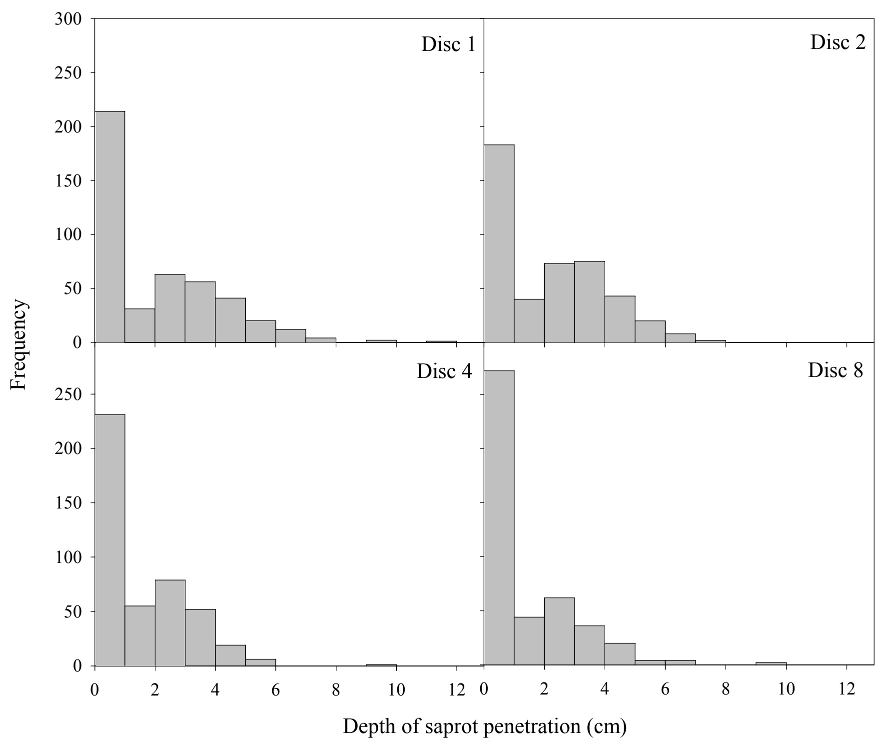

Figure 5. Frequency distributions of saprot-penetration depths (cm) within discs 1, 2, 4 and 8.

Table 16. Analysis of saprot-penetration depth within discs 1, 2, 4 and 8 by mortality date, biogeoclimatic unit and soil moisture regime nested within biogeoclimatic unit, and diameter at breast height as a covariate.

Source	df	Wilks' λ [1]	MS	F	P
Diameter at Breast Height	1		26.562	20.767	<0.001
Mortality Date	3		7.575	5.922	0.001
Biogeoclimatic Unit	1		1.555	0.701	0.449
Soil Moisture Regime (Biogeoclimatic Unit)	4		2.216	1.733	0.142
Error	394		1.279		
Disc Height	3	0.976 (392)		3.216	0.023
Disc Height × Diameter at Breast Height	3	0.992 (392)		1.039	0.375
Disc Height × Mortality Date	9	0.821 (954)		8.945	<0.001
Disc Height × Biogeoclimatic Unit	3	0.954 (392)		6.351	<0.001
Disc Height × Soil Moisture Regime (Biogeoclimatic Unit)	12	0.971 (1037)		0.964	0.482

[1] Wilks' λ is a multivariate test (with error df given in parentheses) applied to the repeated-measures factor, disc height and its interaction terms.

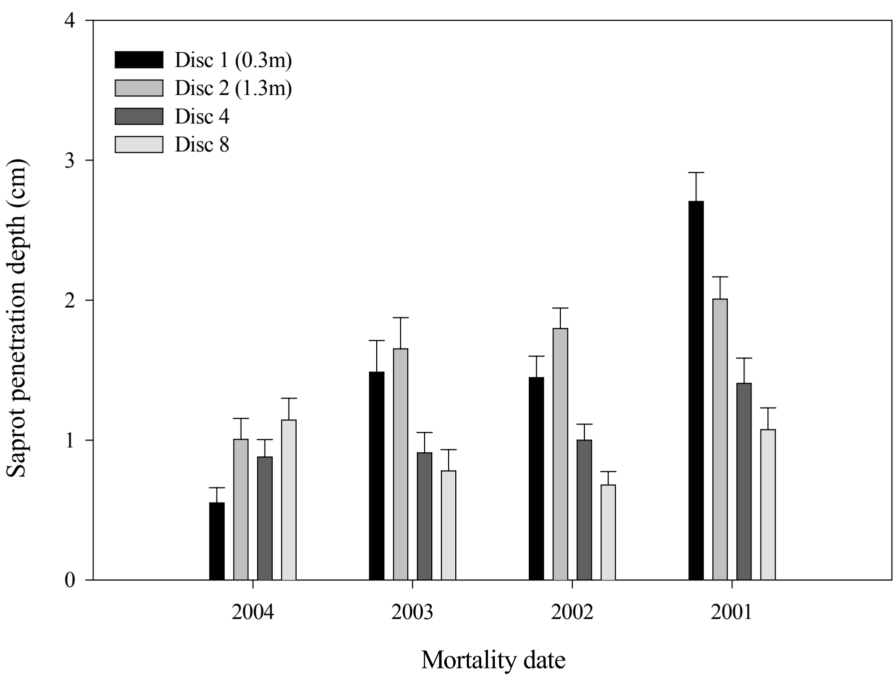

Figure 6. Saprot-penetration depth means and standard errors, within discs 1, 2, 4 and 8, grouped by mortality date.

Wood borer

With increasing time since death, a greater percentage of the samples had some level of wood-borer activity (Table 17). Approximately 29% of the samples had wood borer damage 2 years after mortality, and more than 50% of the sample trees had wood borer damage 3 years after mortality (Table 17). Based on the sample trees with detected wood borer, there was a strong positive correlation between average wood-borer depth and average blue-stain depth ($r = 0.706$, $p<0.001$).

Table 17. Percentage of sample trees with wood borer damage, grouped by mortality date.

Mortality date	2005	2004	2003	2002	2001
Samples size per mortality date	15	98	66	135	106
Percentage of samples with wood borer detected	7	29	65	67	59

Discussion

The use of dendrochronology to cross-date pine killed by mountain pine beetle allowed us to determine an exact year of mortality and to quantify change in the factors of wood quality and quantity over a 5-year period. Our study also demonstrated that an arbitrary classification of post-mortality tree conditions, based on external characteristics, is inaccurate in estimating year of mortality (Table 4).

Across all stands, five of the 1997 pine killed by mountain pine beetle had fallen (≈ 0.25%). Regardless of stand location, the predominant beetle activity within all 32 stands had occurred within the last 5 years. The recent nature of the outbreak within our study area is the most likely reason for observing such a small percentage of fallen trees. As a result, we conclude that in the first 5 years of an epidemic moving into an area, there is an insignificant volume loss related to falling pine. In support of our conclusion, Harvey (1986) found that 1 in 427 (≈ 0.23 %) pine trees had fallen in the first 5 post-mortality years in northeast Oregon. Mitchell and Preisler (1998) found that lodgepole pine killed by mountain pine beetle began to fall 3 years after death in thinned stands, and 5 years after death in unthinned stands. In thinned stands, 50% of the trees were down by 8 years, and 90% were down by 12 years, in central Oregon. In unthinned stands, 50% of the trees were down by 9 years, and 90% were by 14 years. Keen (1955) found that 85% of beetle-killed ponderosa pine were standing after 5 years, but fell at an increasingly rapid rate after that.

Our results clearly demonstrate that a small collection of biophysical variables can be used to explain variation in wood characteristics, except for specific gravity. First, we found that the biogeoclimatic unit and relative soil moisture regime rarely had an effect on the factors of wood quality or quantity. When tests for these explanatory variables were significant or even suggestive, the mean differences were small or resulting from increased power related to large sample size. Most changes in factors of wood quantity and quality occurred during the first 1 to 2 years after mortality, or were associated with height along the stem and size of the tree, which are indication of sapwood depth (Yang et al. 1985).

Although the overall sapwood and heartwood moisture contents decreased with greater time since death, the results of our study demonstrated that decreasing gradients in the moisture content exist vertically along the stem from bottom to top and horizontally from sapwood to heartwood. Significant interactions between height and mortality date suggest that the gradients varied with increasing time since death, therefore interpretation of changes in moisture content due to height or time since death independently are inaccurate (Tables 5 and 6). Figure 2 illustrates a similar interaction between sapwood and heartwood moisture contents and mortality date. Three studies within British Columbia (Reid 1961, Kim et al. 2005, Woo et al. 2005) have examined the relationship between moisture content and time since death in detail; to a lesser extent, the studies have attempted to characterize the variation in moisture content due to location within the tree. However, the previous studies tend to overlook the possible interactions between location within the tree and time since death. In a study completed by Kim et al. (2005), lodgepole pine from southern and southeastern British Columbia showed significant reductions in sapwood moisture content in red-attack and grey-attack stage trees compared to sapwood moisture content in green-attack stage trees. The designations of “green”, “red”, and “grey” refer to the general colour of the crown of attacked trees. and are similar to our external time-since-death categories (Table 1). Mean sapwood moisture content of red-stage trees ranged from 20% to 27%, and were between 40% and 80% at the end of the first year following attack. Heartwood moisture content, on the other hand, was significantly greater in green-stage trees compared to the red- and grey-stage trees. Woo et al. (2005) performed a small study in central British Columbia looking at one live tree and one dead tree of similar diameter that had been dead for 8 months. The sapwood moisture content of the dead tree was 85% less than that of the live tree, and 7% less within the heartwood. Further, Woo et al. (2005) did not find moisture content to vary with height. Our results differ considerably compared to those of previous studies, because we sampled at multiple locations along the length of each tree. Within our study, sapwood moisture content was generally greater than heartwood moisture content; however, the differences were not consistent, and by 3 to 4 years after mortality, the horizontal gradient had disappeared in all but the bottom discs (Figure 2). Reid (1961), studying beetle-killed lodgepole pine in southeastern British Columbia and southwestern Alberta over a 1-year period after attack, found that moisture content decreased horizontally from outer sapwood to inner sapwood in live trees, but the pattern was not apparent in dead trees. Reid (1961) also found that sapwood moisture content could decrease from 85% to 165% (oven-dry weight basis) in live trees to as low as 16% in dead trees. Further, moisture content decreased by 40% by the end of August following an attack in July, and then fell to fibre saturation point (approximately 30%) within the year. Within our study, the sapwood and heartwood moisture contents within the bottom two discs remained above the fibre saturation point, whereas the upper two discs dropped below the fibre saturation point after 1 to 2 years after mortality (Figure 2). Reid (1961) found that moisture content varied vertically in live trees, but no consistent pattern was found. Finally, mean sapwood and heartwood moisture content with discs 1 remained above 80% and 40%, respectively (Figure 2).

Blue-stain penetration depths are related to diameter at breast height and not to mortality date or height along the stem (Table 11). Previous studies have suggested that the onset of blue stain appears associated with a reduction in moisture content (Reid 1961), is initiated before drying, and the majority of the sapwood staining occurs within the first year after attack. Although we did not measure sapwood depth or area, sapwood depth generally increases with tree diameter (Smith et al. 1966; Nelson 1975, *in* Yang et al. 1985), and smaller diameter trees generally have lower ratios of sapwood to heartwood (Harvey 1979). Solheim (1995), studying beetle-killed lodgepole pine in southern British Columbia, found that blue stain was prevalent throughout the sapwood of trees examined 7 weeks after attack. Harvey (1979), in a study from Oregon, tracked the spread of blue stain in trees that had been successfully attacked by mountain pine beetle in August. Trees were sampled through November of that year, and again in June the following year. By 9 to 10 months following attack, more than 50% of the total volume and almost 100% of the sapwood volume were stained.

Within our study, the depth (cm) of wood-borer damage was caused primarily by ambrosia beetles, and the damage was complete by 2 to 3 years after mortality. According to Bob Hodgkinson (B.C. Ministry of Forests and Range, pers. comm. 2005), if they are in the vicinity, ambrosia beetles enter attacked trees during the spring following the year of attack. After two years since death, ambrosia beetles will not attack even if they are around. In general, the depth of wood-borer damage was limited to blue-stained wood.

Previous work suggests that checking is significant once wood moisture content falls below fibre saturation point, but there is little information as to whether checking worsens with time. Reid (1961), for example, showed that the trees attacked earlier in the season were the first to fall below the fibre saturation point, and that significant checking began at this point. In our study, mean sapwood and heartwood moisture content in discs 1 remained above 80% and 40% (Figure 2). Therefore, the point at which wood falls below fibre saturation point may not fully explain the onset of checking. Table 12 may suggest that the percentage of trees with checking worsens with time. However, both the number of checks and the depth of checking are most associated with the size of a tree, at least within the bottom- and mid-stem locations (Figure 4, Table 14). Table 13 and Figure 4 show an increase in the number of checks and depth of checking with increased time since death, however, mean merchantable volumes were significantly different within each cross-dated mortality date category (Table 9), generally increasing with greater time since death (Table 10). This most likely explains the significant differences in the number of checks and the depth of checking by mortality date.

Although saprot penetration was initiated within 2 to 3 years after mortality, and was detected within at least 46% of the sample trees that had died in 2004 (Table 15), the mean depths of saprot penetration at all disc heights were negligible, and only discs 1 exceeded 2 cm of saprot in trees that had died in 2001 (Figure 6). Harvey (1986), studying decay of mountain pine beetle-killed trees in Oregon, found that less than 1% of 226 m^3 (8000 ft^3) of wood sampled was lost to advanced decay 11 years after tree death, and decay was observed in 13.7% of sampled trees. Similar to observations made of blue-stain penetration depth, the size of a tree contributes significantly to the depth of saprot penetration (Table 16), most likely because of the proportion of its sapwood, which in dead trees is more susceptible to decay than is heartwood.

In conclusion, our research supports the findings of previous work where drying, blue stain and checking are the major causes of decline in wood quality and quantity in recently killed trees (1 to 2 years), with saprot and wood borers becoming more important in older dead material. Furthermore, location along the stem and tree size are major contributors to variation detected in factors of wood quality and quantity. Figure 7 is a composite conceptual model of the change in wood properties after mortality. It shows that significant change in moisture content-related variables (i.e., checking, blue stain and saprot) happens within the first 1 to 2 years after death, then tends to hold steady. The exception to this pattern is found in the lower, or base, portion of the tree, where moisture content remains higher, presumably due to absorption of moisture from the ground. Consequently, wood properties related to moisture content reflect this: saprot in the lower portion of the log tends to continue to increase, and check depth is generally less.

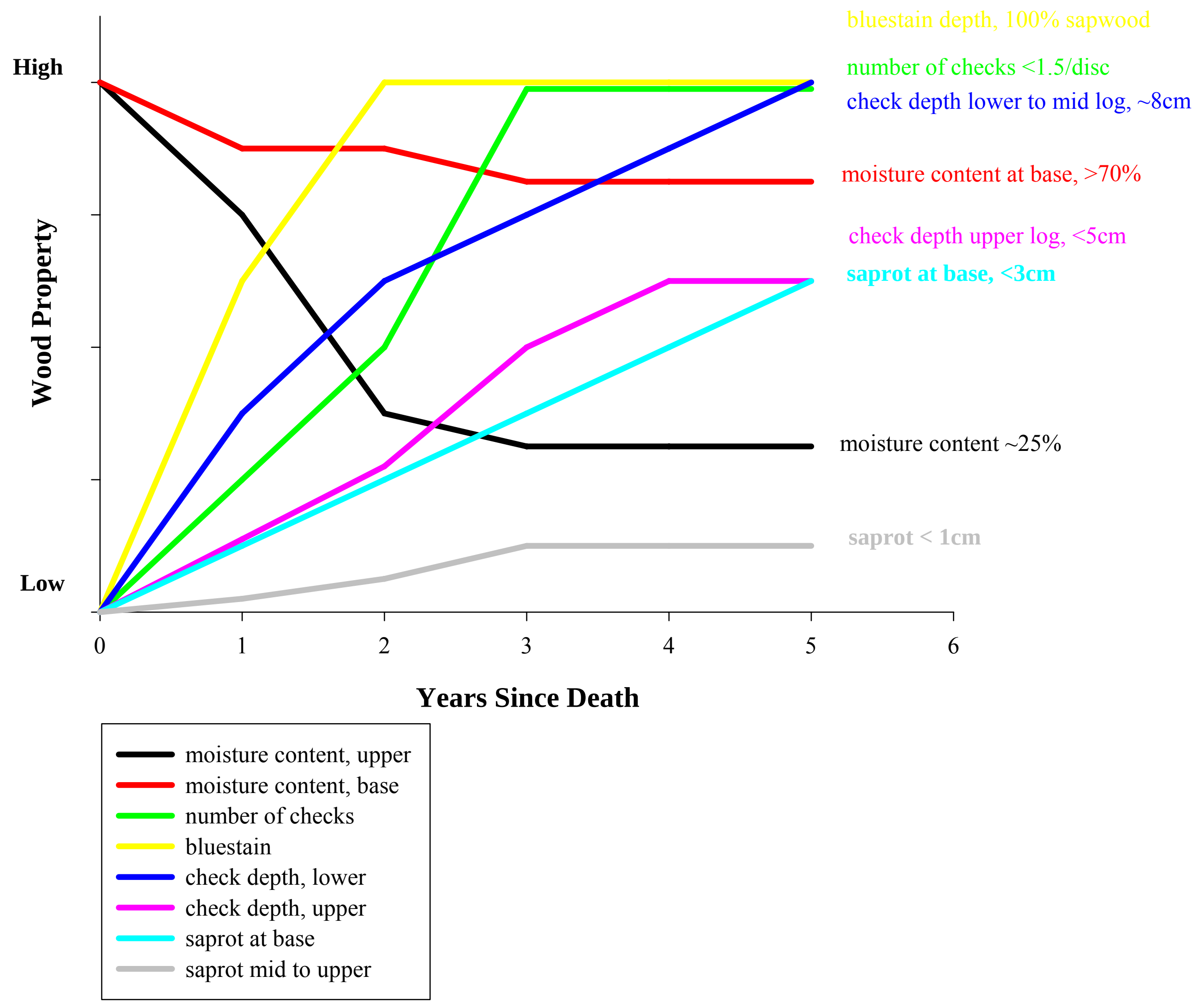

Figure 7. Conceptual model of wood properties with years after mortality. Text at the end of each line represents the final approximate mean values 5 years after mortality.

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