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Change in wood quality and fall rate of trees up to ten years after death from mountain pine beetle

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Abstract

Despite the history of mountain pine beetle outbreaks in British Columbia, including the outbreak in the mid 1980s that affected timber supply in the Quesnel Timber Supply Area, little was known about the post-mortality rate of deterioration of wood quality and quantity, and the rate of change in stand structure due to fall of dead trees. In this stuidy, we used dendrochronology to crossdate pine killed by mountain pine beetle. We determined the exact year of mortality and characterized decay and degradation in factors of wood quality and quantity over time. Over 550 trees were sampled and successfully cross-dated, 126 of these had been dead for more than 6 years. At the stand level, 0.25% of the pine that had been dead for 5 years or less had fallen. In stands where trees were killed between 6 and 10 years ago, the average fall rate was 28%, ranging from 0 to 60% per plot. Most trees did not start to fall until 8 years post-mortality. No relationship was found between rate of fall and tree size, although dry sites had a higher rate of tree fall than wet sites. We found that change in moisture content of the wood was the main driver behind the changes in wood properties. Dependent variables included checking (number and depth), bluestain depth, saprot, and damage caused by wood borers. A small collection of biophysical variables (time-since-death, tree size (DBH), height of sample, and growth rate) explained the variation in dependent variables, and a number of regression models were built to predict the dependent variables. Biogeoclimatic unit and soil moisture regime were not important predictors of decay and degrade in this study, except for development of saprot at the base of the trees. Significant change in the above factors occurred within the first 1-2 post-mortality years and varied with position along the stem and with the size of the tree, followed by a period of relative stability in wood properties until 8 or more years post-mortality, when dead trees start to fall.

Keywords: post-mortality, decay, check, saprot, time-since-death, moisture content

Résumé

Malgré l'historique des infestations de dendroctone du pin ponderosa en Colombie-Britannique, y compris le foyer du milieu des années 1980 qui a touché la région d'approvisionnement en bois de Quesnel, on sait peu de choses sur le taux de détérioration des facteurs de qualité et de quantité du bois après mortalité et sur l'évolution de la structure des peuplements en raison de la chute des arbres morts. Dans la présente étude, nous avons eu recours à des techniques de dendrochronologie pour dater les pins tués par le dendroctone du pin ponderosa. Nous avons déterminé l'année exacte de la mort et nous avons caractérisé la détérioration des facteurs de qualité et de quantité du bois sur une période donnée. Nous avons échantillonné et daté avec succès plus de 550 arbres, dont 126 étaient morts depuis plus de six ans. À l'échelle du peuplement, 0,25 % des pins morts depuis cinq ans ou moins étaient tombés. Dans les peuplements dont les arbres avaient été tués entre six et dix ans plus tôt, le taux de chute moyen s'établissait à 28 %, et se situait entre 0 et 60 % par placette. La plupart des arbres ne sont tombés que huit ans et plus après leur mort. Nous n'avons établi aucun lien entre le taux de chute et la taille des arbres. Les sites secs présentaient toutefois un taux de chute plus élevé que les sites humides. Nous avons découvert qu'un changement du taux d'humidité est le principal facteur qui a une influence sur les propriétés du bois. Les variables dépendantes incluent la gerçure (nombre et profondeur), la profondeur de bleuissement, la pourriture de l'aubier et les dommages causés par les perce-bois. Quelques variables biophysiques (temps depuis la mort, taille de l'arbre (DHP), hauteur de l'échantillon et taux de croissance) expliquent la variation des variables dépendantes. Nous avons développé un certain nombre de modèles de régression afin de prédire les variables dépendantes. L'unité biogéoclimatique et le régime d'humidité du sol n'étaient pas des indicateurs prévisionnels de dégradation et de pourriture du bois dans le cadre de la présente étude, sauf dans le développement de la pourriture de l'aubier à la base des arbres. Des changements importants se sont produits dans les facteurs mentionnés plus haut durant les deux premières années après la mort. Les changements variaient le long de la tige et en fonction de la taille des arbres. Nous avons constaté une certaine période de stabilité dans les propriétés du bois jusqu'à huit ans et plus après la mort des arbres, alors qu'ils commençaient à tomber.

Mots-clés : Après mortalité, dégradation, gerçure, pourriture de l'aubier, temps depuis la mort, taux d'humidité.

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1 Introduction

Despite a history of mountain pine beetle outbreaks, including the outbreak in the mid 1980s that affected timber supply in the Quesnel TSA (Timber Supply Area), the post-mortality rate of deterioration of wood quality and quantity, and the rate of change in stand structure due to the fall of dead trees has not been well-studied. A few studies have examined deterioration of beetle-killed wood over time, using samples from the current outbreak in British Columbia (e.g., Lewis et al. 2006, Trent et al. 2006), and other studies have focused on changes in specific wood product recovery from beetle-killed wood (e.g., Orbay and Goudie 2006, Feng and Knudson 2005, Oliveira et al. 2005, Byrne et al. 2005). Lewis et al. (2006) characterized the post-mortality rate of deterioration of wood quality and quantity, and the fall rate of trees dead for up to 5 years. They found that drying, bluestain and checking were the major causes of decline in wood quality and quantity in recently killed trees (1 to 2 years after death), and that time-since-death (TSD) was a good predictor of these variables. Saprot fungi and ambrosia beetles became established during the first 2 years post-mortality, but the depth of penetration did not change with increasing TSD, 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 were also major contributors to variation detected in the factors of wood quality and quantity. Trent et al. (2006) examined fine-scale wood quality variables, such as fibre length, and their relationship with TSD. Like Lewis et al. (2006), they found a significant negative relationship between TSD and moisture content; however, none of the other variables tested were significant. Time-since-death in Trent et al. (2006) was determined from external indicators and local knowledge, which Lewis et al. (2006) found was very inaccurate at the tree level. Recent work has shown that tests of wood deterioration over time at the tree and stand level must employ accurate measures of TSD, such as cross-dating (Stokes and Smiley 1968).

The magnitude of the current outbreak is such that significant reductions in wood supply are anticipated in the mid-term. These reductions can be limited by economically efficient use of beetle-killed wood for as long as possible, but in order to do this, it is necessary to know the relationship between time-since-death, time since fall, and wood quality and quantity variables beyond 5 years. This information will add to what we have shown in previous work and is essential to plan 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 the area affected by beetle. Further, the rate of change in stand structure (e.g. fall-down rate) is essential to understand and plan for impacts on wildlife habitat and other non-timber values.

1.1 Objectives

As a continuation of our previous work (Lewis et al. 2006), our objective was to expand the time frame to examine pine that has been dead for 6-10 years and beyond. We examined the frequency of tree fall in beetle-affected stands (i.e., stand-level study) to determine if there was an increase in the frequency of tree fall resulting from the mortality of trees killed by mountain pine beetle. Secondly, we determined, in depth, the biophysical factors that affected wood quantity and quality in individual trees (i.e., tree-level study) following mortality. The tree-level study on wood decay and degrade focused on standing trees.

The scope of this study was limited to the biophysical variables that affect wood quality and quantity after mortality caused by mountain pine beetle. There are a number of other factors that significantly influence economic efficiency when dead wood is processed. These include cost of the raw product (stumpage rates and delivered wood cost), the technology used to process the wood, the actual product made, demand for the product and selling price, and the opportunity to harvest and process green wood with the dead wood. These variables were not addressed in this study.

Specific research objectives for the stand-level study were to determine:

1. The incidence of tree-fall in each sample plot and;
2. Tree fall as a function of time-since-death.

Specific research objectives for the tree-level study were to determine:

1. The relationship between moisture content and specific gravity in the heartwood and sapwood to the date of mortality;
2. The relationship between the penetration depth of saprot and the date of mortality;
3. The frequency and magnitude of checking relative to the date of mortality;
4. The rate and magnitude of infestation by wood borers relative to the date of mortality; and
5. The effect of ecosystem characteristics, tree size and location along the stem on the above factors of wood quality and wood quantity.

2 Material and Methods

2.1 Sampling area

The sampling area for the 2006 study (phase I) and this one (phase II) was in the Sub-boreal spruce biogeoclimatic zone (SBS), and included two subzones: the Dry Cool Sub-Boreal Spruce (SBSdk) and the Kluskus Moist Cold Sub-Boreal Spruce (SBSmc3) biogeoclimatic variant. Phase I sampling was located approximately 150 km southwest of Vanderhoof in two general areas – the Fawnie Range, and Nechako River area. Thirty-one stands were selected during phase I sampling. Phase II sampling was located along the north slope of Tetachuck Lake, adjacent to Tweedsmuir Park and the Entiako Protected Area (Figure 1). This area was affected by the earliest stages of the current outbreak (~1995), and sample areas were identified using a chronosequence of air photos to identify areas with red trees from the period 1996 to 2000 and not harvested at some later date. We accessed the study area by boat to identify sample stands during a reconnaissance trip. Candidate stands were located using the air photo information, and selected trees within those stands were cored and a preliminary, visually cross-dated year of death was assigned in the field. Cores were held in a field mount, cut with a scalpel to expose the cross-section, and then sanded by hand. We used known pointer years from existing master chronologies in the same general area (developed during Phase I) to cross-date the sample trees. Fifteen stands were selected during phase II sampling.

2.2 Stand-level study

Within each stand, the following independent variables (IVs) were measured: (1) aspect, (2) slope, (3) elevation, (4) moisture regime, (5) species composition, (6) stand density, (7) diameter class distribution and (8) number of standing trees in time-since-death categories (by external indicators). Within each stand, the following dependent variables (DVs) were also measured: (1) number of fallen trees and (2) diameter of fallen trees.

2.3 Tree-level study

The identification of sample trees took place during the stand-level surveys. The target populations were trees killed by mountain pine beetle, still standing and dead for 1-5 years (phase I), and 6-10 years (phase II). We selected 474 and 150 trees during phases 1 and II respectively, across the range of diameter at breast height classes (DBH, measured at 1.3 m from the ground: 12.5-22.5 cm, 22.6-32.5 cm, 32.6+cm), soil moisture regimes (SMR: dry = 1, mesic = 2, and wet = 3), and time-since-death (TSD: 0-10 years). Selected trees were free of defects along the merchantable stem (e.g., fire scars, double tops, crooks or burls). From each tree, the following DVs were measured: (1) moisture content (%), (2) specific gravity (g/cm3), (3) bluestain penetration depth (cm), (4) number and depth of checking (cm), (5) saprot penetration depth (cm), and (6) depth of woodborer damage. For each tree, the following IVs were also measured: (1) the mortality date, (2) sample height, (3) soil moisture regime and (4) diameter-at-breast-height (DBH). Mortality dates were determined using standard dendrochronological procedures (Stokes and Smiley 1968), and existing master chronologies for the area developed during Phase I.

Each sample 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 the stump and breast height. Discs 3 to 12 were cut at equal distances between breast height and the height at which the stem diameter equaled 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.

One half of disc 1 was returned to the lab for cross-dating against a local master chronology. Small samples of the sapwood and heartwood from discs 1, 2, 4 and 8 were removed, and fresh weights were measured in the field. Percent moisture contents (ovendry basis) and specific gravities were measured for each disc, based on the methods of Haygreen and Bowyer (1996).

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 (i.e., a cone with the tip cut off), estimated using equation 1.

$$[1] \qquad V = \pi h/3 * (R^2 + R * r + r^2)$$

Where h = height of the frustum, R = the bottom radius and r = the top radius.

In addition to trees selected for intensive sampling during Phase II, we also searched the surrounding area of each stand to locate 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 disc from between stump height and DBH on the dead tree to determine year of mortality, and by removing a disc 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 the dead tree). Thirty pairs of trees were sampled.

2.4 Data analysis

The samples collected during phases I and II were pooled. Analyses performed during phase I (Lewis et al. 2006) demonstrated that there was no difference in wood moisture content and other response variables among the two sampled subzones, with the exception of measurements taken from the basal disc which have been addressed in the analysis. Therefore, data from the two subzones were also pooled. Time-since-death in all analyses was treated as a continuous variable, in part because of the differences in sample size among different mortality years due to 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 ($p = .522$). Diameter at breast height was treated as a covariate for some of the following analyses.

Percent moisture contents for both the sapwood and the heartwood were natural-log transformed to meet the 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 dataset, with sapwood to heartwood (wood type) and disc height as the repeated measures. Following that, a multi-variate general linear model was developed with the 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 different locations on the tree: disc 1 (0.3m), disc 2 (1.3m), disc 4 (1/3 of the merchantable height) and disc 8 (2/3 of merchantable height), and interactions among independent variables (disc, TSD, SMR, and heartwood/sapwood) were examined with analysis of variance. Hypotheses and error SSCP (sums-of-squares and cross-products) matrices were used to test the effects of the models. Mean moisture content was plotted against TSD separately by wood type, SMR, and disc.

Specific gravity was analyzed using identical procedures as moisture content.

To identify independent variables that may explain variation in dependent variables that are influenced by sapwood proportion and/or tree size (i.e., bluestain penetration depth, number of checks, depth of checks), we developed a Pearson correlation matrix for all DVs for each disc against IVs, including: TSD, SMR, stand density, mean stand DBH, stand basal area, DBH, diameter growth over the last 10, 20 and 50 years, and change in diameter over the last 10, 20 and 50 years relative to the DBH of the tree at the start of the period, and specific gravity in the sapwood and heartwood at each disc.

The percent tree volume occupied by blue-stained wood was calculated for each tree using equation 2, and mean values were plotted by TSD to examine the rate of colonization by bluestain fungi.

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

Where r = radius of the section, b = depth of bluestain in the section, and L = length of the section.

Rapid colonization to the limit of the sapwood, and a decline in blue-stained sapwood volume with TSD were observed, the latter most likely due to smaller trees being attacked at later stages of the outbreak. Further, bluestain penetration is limited to sapwood; therefore, we expected measures of growth to be important predictors of bluestain depth. Results from the Pearson correlations of bluestain depth on measures of growth were most significant for the 20-year growth period. This led us to test the hypothesis that bluestain penetration depth was a function of absolute growth over the last 20 years, and/or the DBH of the tree at the beginning of the last 20-year growth period. Both independent variables were natural-log transformed. A multiple linear regression model was developed that included both variables, and these were tested for significance with ANOVA. Bluestain penetration depth was plotted as a function of DBH 20 years before tree mortality, and the growth rate of the tree over the last 20 years.

2.5 Abundance and prediction of checking, saprot and woodborer damage

Percentage of trees with no measurable damage caused by breast height checking (disc 2), and basal saprot and woodborer (disc 1), were plotted against TSD.

The following analytical procedures were used to assess the importance and ability of key biophysical independent variables (IVs) to predict the response in the following dependent variables (DVs): number and depth of checking at breast height and depth of saprot and woodborer damage at basal height. Although recorded as a count, the number of checks was treated as a continuous variable and all depths were measured in cm. Independent variables included TSD, SMR, DBH, average stand density, diameter growth over the last 10, 20 and 50 years, the percent change in DBH relative to estimated

DBH 10, 20 and 50 years ago, and specific gravity of sapwood and heartwood in basal and breast height discs.

Pearson correlation and scatter-plot matrices were used to statistically and visually identify potential links between IVs and DVs. Significant correlations ($\alpha \leq 0.001$) were selected as potential predictor variables for further analysis. A strict alpha level was used due to the large sample size (i.e., $n >> 500$). Multicolinearity and singularity tests between IVs were assessed using SPSS version 16.0 (SPSS 2008), and if present, IVs of greatest ease in field collection were retained for further analysis. Based on the above procedures, TSD, DBH and average stand density consistently established themselves as the most practical IVs to predict damage caused by checking, saprot and woodborer.

Separately for each DV, consecutive linear mixed-effects (LME) models were used to identify the best collection of IVs to predict the level of damage using Program R (2008). Additional IVs were entered in the following order: TSD, DBH, and then average stand density. The above IVs were treated as fixed effects and the random effect of stand was added to account for variation associated with groups of trees being sampled within randomly selected stands across the study area.

Both DBH and average stand density remained untransformed. All DVs were natural-log transformed, as was TSD. These transformations were justified based on previous work by Lewis et al. (2006). First, the rate of advancement in checking, saprot and wood borer damage is non-linear. Damage typically established within the first two to three years, followed by a marginal diminishing rate in further advancement as TSD increased and as the wood moisture content (%) decreased. Second, a maximum in damage will eventually be attained.

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. The un-transformed DVs were predicted and plotted against model IVs.

The number and depth of checks was plotted as a function of TSD and location on the tree. The number of checks in the basal disc (1) was less than in other discs due to the increased wood moisture content, and disc 2 usually had the most checks (Figure 2). Therefore, the number of checks was modeled using only disc 2, as the basal portion of the log would require a different model, and the effect of the increased moisture content disappears by disc 2. Check depth was also greatest in discs 2 and 3 (Figure 3); therefore check depth was modelled using data from disc 2.

3 Results

3.1 Stand-level study

Table 1 lists the stand attributes grouped by biogeoclimatic unit. In phase I samples, 0.25 % of lodgepole pine had fallen with mountain pine beetle as the cause of mortality. In phase II, the mean fall rate at the plot level was 28% with a range of 0-60%.

Table 1. Total number of plots measured, average stand densities, species compositions, downed pine killed by mountain pine beetle (MPB), grouped by biogeoclimatic (BEC) unit.

BEC unit	Time-since-death	Number of plots	Stems/ ha	Approximate % pine in stand	Downed pine killed by MPB (%)
SBSdk	0-5	102	980-1225	68-90	<1
	6-10	15	500-1450	60-100	28 (range = 0-60)
SBSmc3	0 -5	81	1000-1350	84-94	0

3.2 Tree-level study

Table 2 outlines the frequency of sample trees by biogeoclimatic unit and soil moisture regime. In total, 624 trees were identified for the tree-level study, 578 were felled and measured, and 562 trees were successfully cross-dated. Interseries correlations ranged from 0.22-0.71 with a mean of 0.49. In phase I sampling (0-5 years post-mortality), 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. External indicators were not used during phase II sampling for trees that died 6-10 years ago.

Table 3 shows the frequency of sample trees by sampling phase (I and II) and by geographic area. Table 4 has the distribution of cross-dated sample trees by TSD. Some years (e.g., 5 and 6 years post-mortality) have a small sample size because most of the trees in a stand would be killed during the first 2 years of the beetle's arrival in the area, followed by a significant drop in attack rate because of reduced availability of host trees.

Table 2. Frequency of sample trees and cross-dating statistics, grouped by biogeoclimatic (BEC) unit and soil moisture regime (SMR).

BEC unit	SMR	Trees identified	Trees Felled	Trees cross-dated	Correlation of cross-dating		
					Min.	Max.	Mean
SBSdk 0-5 years	Dry	86	85	85	0.22	0.69	0.48
	Mesic	98	81	81	0.25	0.68	0.50
	Wet	104	102	99	0.28	0.71	0.50
SBSdk 6-10 years	Dry	39	39	37	.23	.57	.40
	Mesic	77	65	63	.27	.65	.41
	Wet	34	27	26	.26	.66	.43
SBSmc3 0-5 years	Dry	62	57	55	0.34	0.68	0.49
	Mesic	61	60	58	0.28	0.71	0.49
	Wet	63	59	58	0.26	0.68	0.45

Table 3. Frequency and percent of sample trees by sampling phase (I = 0-5 years post-mortality, II = 6-10 years post-mortality) and by geographic area.

Grouping	Frequency	Percent
Phase I	474	76
Phase II	150	24
Fawnie Range	213	34.1
Nechako River	261	41.8
Tetachuk Lake	150	24
Total	624	100

Table 4. Frequency and percent of cross-dated sample trees by time-since-death.

TSD (years)	Frequency	Percent
0	15	2.4
1	98	17.4
2	66	11.7
3	135	24
4	106	18.9
5	5	0.9
6	7	1.2
7	26	4.6
8	17	3.0
9	63	11.2
10	24	4.3
Total	562	100

3.3 Fall-down rate

In addition to the stand-level results, which provided some data on fall-down rates, we sampled live trees that were damaged by the fall of a dead tree (either scarred or had compression wood). Cross-dating of the dead tree provided date of death, and scars or initiation of compression wood were also dated to provide date of tree fall. Figure 4 shows a distribution of mortality dates and a distribution of years to fall for the paired samples. Most of the sample trees died 9 years prior to sampling, and most of these remained standing for over 6 years post-mortality.

Trees sampled during phase II had been dead for 6-10 years, and had a higher fall-down rate compared to trees dead for 0-5 years (<1%). Fall down rate by diameter class showed no apparent effect of tree diameter on fall rate (Figure 5). However, a pattern with soil moisture regime was evident, with 51.3%, 25.3% and 18.7% of trees down in plots in soil moisture regimes dry, mesic and wet respectively.

3.4 Moisture content

Percent moisture content measures, grouped by sapwood and heartwood, and by discs 1, 2, 4 and 8, are shown separately for the two subzones in Figures 6 and 7. Moisture content of the sapwood declined sharply within the first 2 years post-mortality, becoming stable at approximately fibre saturation point (~25%) after 2 years post-mortality. One exception is found at the base of the tree where moisture content remains above 80% for 5 or more years. Figure 6 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 fibre saturation point within 2 years post-mortality, although the heartwood started with lower moisture content than the sapwood (30-50% depending on sample disc) (Figure 7).

The analysis of variance on the entire dataset, with wood type and disc height as repeated measures, determined that both TSD and SMR are significant explanatory variables, but the amount of variation explained by SMR was very low (under 2%), when the entire dataset was analyzed (Table 5).

Table 5. Analysis of variance of all data pooled, with wood type (sapwood and heartwood) and disc height as repeated measures. SS = sum squares, MS = mean squares, F = F statistic, p = probability

Source	**SS**	**df**	**MS**	**F**	**p**	**Partial Eta Squared**
Intercept	5927.799	1	5927.799	15190.605	<.001	.965
TSD	292.176	1	292.176	748.731	<.001	.577
SMR	3.005	1	3.005	7.699	0.006	.014
Error	213.845	548	.390			

As both TSD and SMR were found to be significant parameters, but Figure 6 and 7 showed that moisture contents depended on wood type and disc height, linear regressions were developed to predict % moisture content separately, in heartwood and sapwood, by disc, using the following model:

[3] $$\text{Percent moisture content} = e^{(\text{intercept} + \beta 1 * \text{TSD} + \beta 2 * \text{SMR})}$$

Table 6 provides regression parameters and descriptive statistics for each of the eight regression models developed (2 wood types x 4 disc locations). It is evident from the parameters that moisture contents in disc 1 and 2 vary differently with TSD than moisture contents in the upper discs (4 and 8). Soil moisture regime makes a significant contribution to the moisture contents at discs 1 and 2, although the importance of that contribution (as estimated by partial eta squared) is much less than the TSD factor. Table 7 provides converted equations for moisture contents of each wood type and at each sample (disc) height.

Table 6. Regression parameters and model statistics for each of the eight regression models. Two wood types (sapwood, sw; heartwood, hw) and four disc heights (1 = 0.3m, 2 = 1.3 m, 4 = 1/3 of the merchantable height, 8 = 2/3 of merchantable height). DV = dependent variable. P = probabilty

DV	β-parameter	β-value	P	Partial Eta Squared
lnswmc1[1]	Intercept	4.423	<0.001	.82
	TSD	-.153	<0.001	.299
	SMR	.145	<0.001	.029
lnhwmc1	Intercept	3.789	<0.001	.952
	TSD	-.062	<0.001	.294
	SMR	.026	.074	.006
lnswmc2	Intercept	3.696	<0.001	.879
	TSD	-.121	<0.001	.379
	SMR	.073	.002	.017
lnhwmc2	Intercept	3.638	<0.001	.952
	TSD	-.088	<0.001	.474
	SMR	.033	0.019	.010
lnswmc4	Intercept	3.412	<0.001	.935
	TSD	-.081	<0.001	.394
	SMR	.001	.971	.000
lnhwmc4	Intercept	3.459	<0.001	.956
	TSD	-.075	<0.001	.443
	SMR	-.006	.650	.000
lnswmc8	Intercept	3.371	<0.001	.936
	TSD	-.082	<0.001	.405
	SMR	.004	.774	.000
lnhwmc8	Intercept	3.376	<0.001	.957
	TSD	-.068	<0.001	.416
	SMR	-.012	.313	.002

[1] lnswmc1 = natural log of sapwood moisture content at disc 1

Table 7. Regression equations to predict % wood moisture content by time-since-death and soil moisture regime.

Wood x Disc height	Regression model
Sapwood, disc 1	% mc = e $^{(4.23 - .153 * TSD + .145 * SMR)}$
Heartwood, disc 1	% mc = e $^{(3.789 - .062 * TSD + .026 * SMR)}$
Sapwood, disc 2	% mc = e $^{(3.696 - .121 * TSD + .073 * SMR)}$
Heartwood, disc 2	% mc = e $^{(3.638 - 088 * TSD + .033 * SMR)}$
Sapwood, disc 4	% mc = e $^{(3.412 - .081 * TSD + .001 * SMR)}$
Heartwood, disc 4	% mc = e $^{(3.459 - .075 * TSD - .006 * SMR)}$
Sapwood, disc 8	% mc = e $^{(3.371 - .082 * TSD + .004 * SMR)}$
Heartwood, disc 8	% mc = e $^{(3.376 - .068 * TSD - .012 * SMR)}$

Figure 8 shows plots of mean % moisture content (heartwood and sapwood) against TSD by disc and soil moisture regime. The plots show a steady decline in % moisture content (natural log), with disc 1 consistently higher in moisture content than other discs, and moisture regime having little effect on the moisture content of discs 4 and 8.

Predicted moisture contents based on the equations in Table 4 and displayed by TSD and disc height are plotted in Figure 9, with SMR being held constant at 2.

3.5 Specific gravity

The repeated measures ANOVA using the total dataset for specific gravity with disc and wood type as the repeated measures showed no significant effect of TSD and SMR on specific gravity ($p = .849$ and .345 respectively). When wood type and disc height were separated, and regression models built using the general linear model procedure, multivariate tests showed that although some variables had a significant relationship with specific gravity, none of the variables tested (disc height, wood type, TSD and SMR) or their interactions, explained more than 6% of the variation in specific gravity.

3.6 Bluestain fungi

Within the first year of attack, blue-stained wood volume reached near maximum levels then remained steady showing a minor decline from 0-5 years post-mortality, and again from 6-10 years post-mortality (Figure 10), which is explained by beetles attacking smaller trees at later stages of the epidemic in each locality. Based on Pearson correlations as explained above in the methods, the absolute growth over the last 20 years (ABS20), and the DBH at the beginning of the 20-year period (PRE20DBH) were selected for regression analysis with bluestain penetration depth as the dependent variable. Box plots of these two variables showed that the natural log of each was normally distributed (Figure 11). These variables were built into the following multilinear regression model:

[4] Bluestain depth (cm) = -1.26 + .917 * ln (ABS20) + 1.115 * ln (PRE20DBH)

The model was significant with an adjusted R squared of .533 (Table 8).

Table 8. Regression analysis of bluestain depth in cm on absolute growth over the past 20 years and DBH of the tree at the start of the 20-year period. SS = sum squares, MS = mean squares, F = F statistic, p = probability

Model	SS	df	MS	F	p
Regression	258.940	2	129.47	318.664	<0.001
Residual	225.098	554	.406		
Total	484.038	556			

Predicted bluestain penetration depths (cm) were contour plotted against DBH at the beginning of the 20-year growth period, and absolute growth over the past 20 years (Figure 12).

3.7 Checking, saprot and woodborer damage

The percentage of trees with detectable signs of checking, saprot and woodborer damage generally increased with advanced time-since-death; however, the trend was neither linear nor consistent, with large year-to-year fluctuations likely due to sample size (Figure 13) and DBH.

The greatest number of checks occurred within the middle section of trees, followed by the bottom, and negligible checking occurs within the top (Figure 2). Furthermore, within the bottom and middle sections, the number of checks 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 the pattern does not exist for the top (Figure 2).

Figure 14 demonstrates that checking occurs relatively quickly and that by year 2 the percent of trees that have developed checks in the region of the tree most likely to check (middle section) is above 80. Check depth appears to continue to increase with time-since-death at most disc heights, but is particularly notable at the basal disc (Figure 3).

The number of checks and depth of checks, saprot and woodborer were consistently predicted by TSD and DBH (Table 9). Average stand density was not retained in any of the final models, likely due to variation associated with stand being played-down as a random-effect. Equations [5-8] can be used to estimate each dependent variable. In general, the number of checks, and the depth of checking, saprot and woodborer damage, all increase with increasing TSD. With greater scrutiny, the variation in the response variables increases with increasing TSD, as a function of DBH. Therefore, stands with less variation around mean TSD or DBH will be characterized by more consistent profiles of decay and degradation (Figures 15-18).

Table 9. Linear mixed-effects model parameter estimates and statistics for each dependent variable (DV).

DV	IV	β-parameter	SE	t [a]	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 woodborer 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] n = 516 for all models.

[5] $$NC = e^{(-0.429 + 0.317 * \log_e(TSD + 1) + 0.014 * DBH)} - 1$$

[6] $$DC = e^{(-0.932 + 0.629 * \log_e(TSD + 1) + 0.034 * DBH)} - 1$$

[7] $$DS = e^{(-0.666 + 0.746 * \log_e(TSD + 1) + 0.019 * DBH)} - 1$$

[8] $$DW = e^{(0.536 * \log_e(TSD + 1) + 0.011 * DBH)} - 1$$

4 Discussion

This study examined the biophysical variables that influence change in properties of wood quality and wood quantity. The study design had some limitations due to mountain pine beetle population dynamics, and the need to collect data and develop models within a short time period. To limit unexplained variation due to geographic location of sample trees, and a preference by the beetle for larger trees as host, the best sample design would be to select sample areas and sample trees from the same area over 10 or more years to monitor change in wood properties over time from the same stand of trees and trees from the same size class. This was not possible given the time frame. As a result, we had to select sample trees that were killed at different stages of the beetle outbreak, and we had an uneven sample size at various years-since-death. For example, the samples from the SBSdk subzone were taken from two different areas due to the dynamics of the beetle outbreak. In the statistical analysis, we were able to control for the autocorrelation between tree size and time-since-death, 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 the variation associated with differences in geographic area was addressed by treating stand as a random effect when appropriate.

Subzone was not a significant factor in this study, although the two subzones sampled were adjacent to each other and plant communities identified in the SBSmc3 variant suggest that some of the areas we sampled may have been more transitional to the SBSdk. Given the strong positive relationship between high moisture content in the base of the tree and development of saprot and wood-borer damage, the influence of subzone, as expressed in the soil moisture regime, is likely important in this regard. We expect that very dry subzones will have a significantly slower rate of tree fall, and harvested trees will require less trimming at the base (butt cull), than relatively wetter subzones. Results from the plot level measurements during phase II sampling do not support this hypothesis however. We found a higher fall-down rate on “dry” plots compared to “wet” plots. This could be an artifact of little difference in actual soil moisture content between the different regimes. Dry plots may also 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. In addition, carpenter ants could be more prevalent on dry sites which could contribute to a higher fall rate (our data combined all damage by wood borers so we are not able to test this hypothesis).

Our results indicate that moisture content in the wood has a major role in determining wood quality over time. Moisture content affects the degree and depth of checking, and the development of saprot and carpenter ant damage at the base of the tree. Moisture content was influenced primarily by TSD, with some influence by soil moisture regime, but this was significant only for discs 1 and 2 (up to 1.3m). Regression equations to predict sapwood and heartwood moisture content by TSD and SMR were created (Table 7). Equations for disc 4 and 8 were sufficiently similar that they could be combined for operational purposes.

The best estimators of bluestain penetration depth were variables that are linked with the amount of sapwood – the growth over the last 20 years, and the DBH of the tree at the beginning of the 20-year period. Bluestain fungi are limited to sapwood (Solheim 1995); therefore the depth of bluestain penetration should vary with the amount of sapwood. Vigorous trees have a greater amount of sapwood compared to declining trees (Munster-Swendsen 1987) and therefore faster growing trees are expected to have a greater proportion of sapwood. We did find a significant relationship between these indicators of tree growth and penetration depth by bluestain, and this was described with a regression model on the natural logs of the growth factors.

The most important variable to estimate the number and depth of checks, saprot depth, and depth of damage by woodborers, were TSD and DBH. Average stand density had a weak relationship with the number of checks, and 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. There was a low predictive value for stand density, therefore it was left out of our models, but biologically the relationship makes sense. Open-grown trees tend to be more vigourous due to reduced competition, and therefore have a greater proportion of sapwood, which has a higher moisture content than heartwood. Once dead, the open-grown trees would undergo a more dramatic change in moisture content in the sapwood during the drying process, resulting in more checks.

Most of the change in the wood properties occurred within the first two years of mortality, with a slower reduction in wood quality thereafter (Figure 13). Therefore there is a short window of opportunity to utilize recently dead trees that have wood characteristics similar to green trees, with the exception of bluestain which becomes established within 6-8 months. This window is about 1 year long, as the number of checks increases substantially by the second year post-mortality. Following year 2, there is a period of stability in the wood properties, with little change occurring, although existing checks deepen with time. Saprot continues to develop at the base of the tree due to the higher moisture content in the wood which supports decay fungi. Most trees remain standing until year 8 (in our study – this will vary in different regions with different soil moisture regimes), at which time the system becomes less stable and predictable as trees start to fall. This general relationship is diagramed in Figure 19.

5 Acknowledgments

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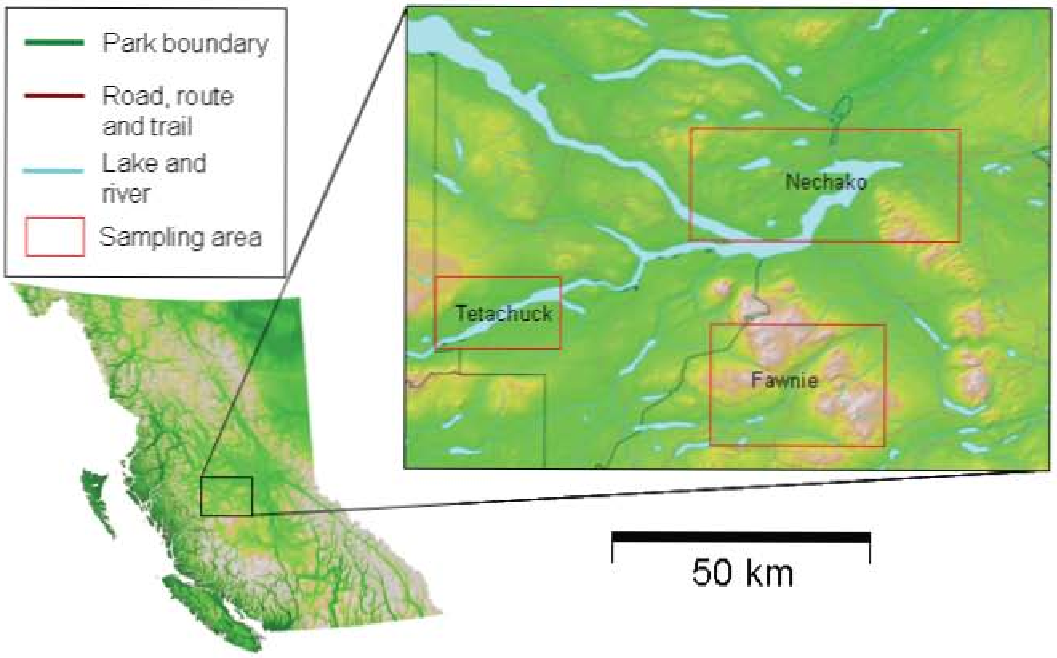

Figure 1. Map of the sample area, located approximately 150 km southwest of Vanderhoof, BC. Phase I samples were from the Fawnie and Nechako areas, Phase II samples were from Tetachuck Lake.

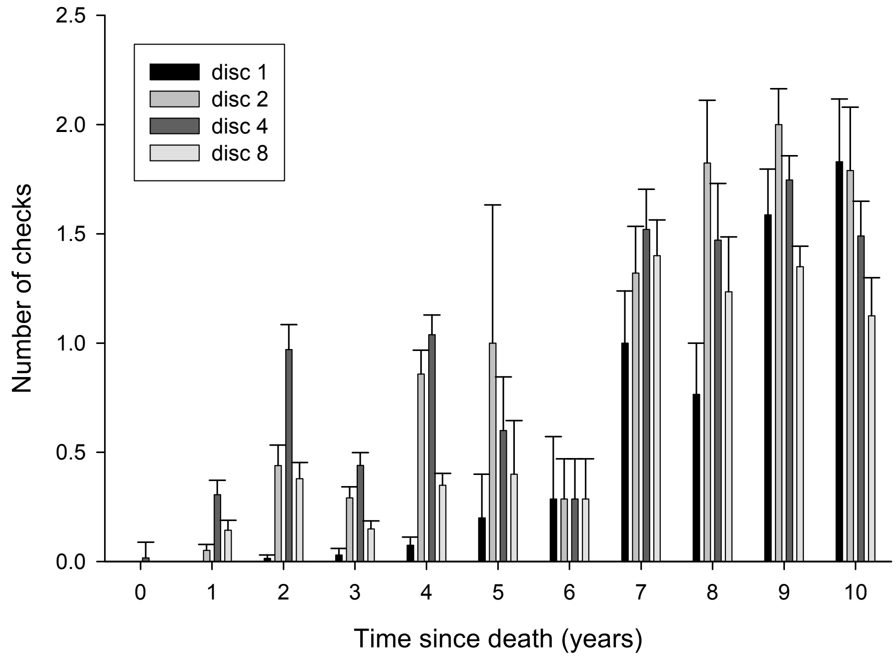

Figure 2. Number of checks by time-since-death and disc height. Disc 1 = 0.3m, disc 2 = 1.3m, disc 4 = 1/3 merchantable height, disc 8 = 2/3 merchantable height.

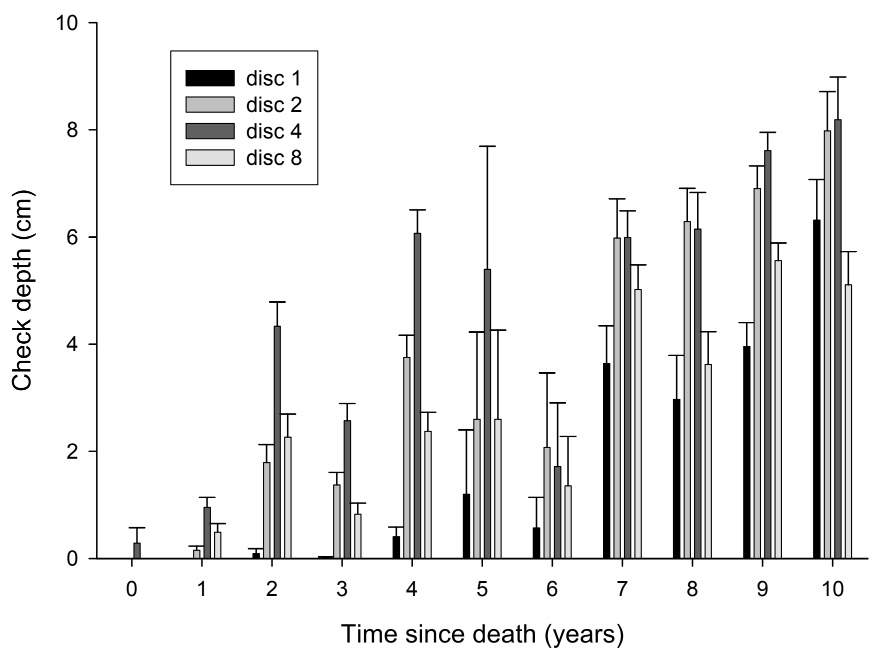

Figure 3. Depth of checks (cm) by time-since-death and disc height. Disc 1 = 0.3m, disc 2 = 1.3m, disc 4 = 1/3 merchantable height, disc 8 = 2/3 merchantable height.

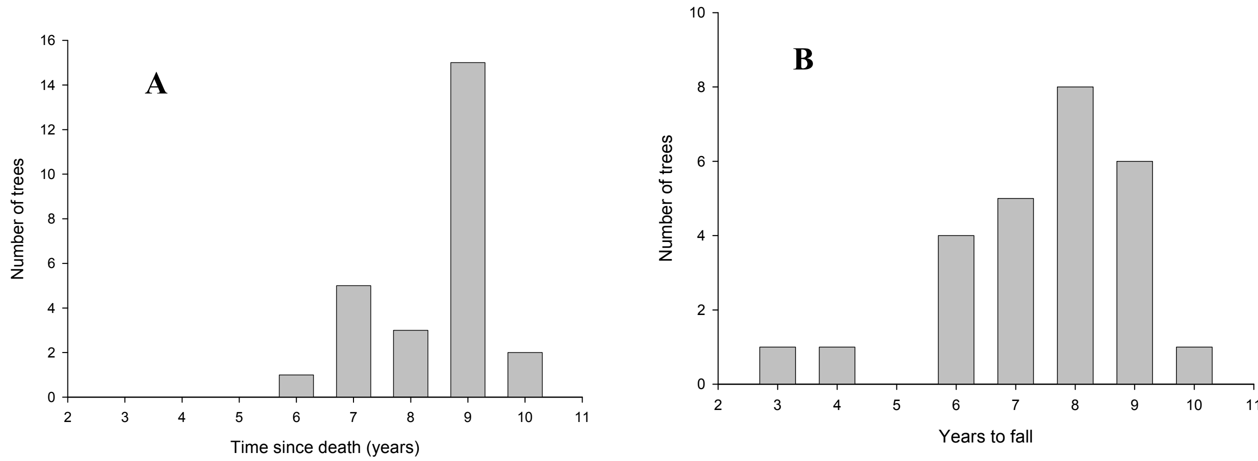

Figure 4. Frequency distributions of time-since-death of fallen sample trees killed by mountain pine beetle (A), and years to fall of the same trees (B). Date of fall was determined by dating scars on live adjacent trees damaged when the beetle-killed tree fell over.

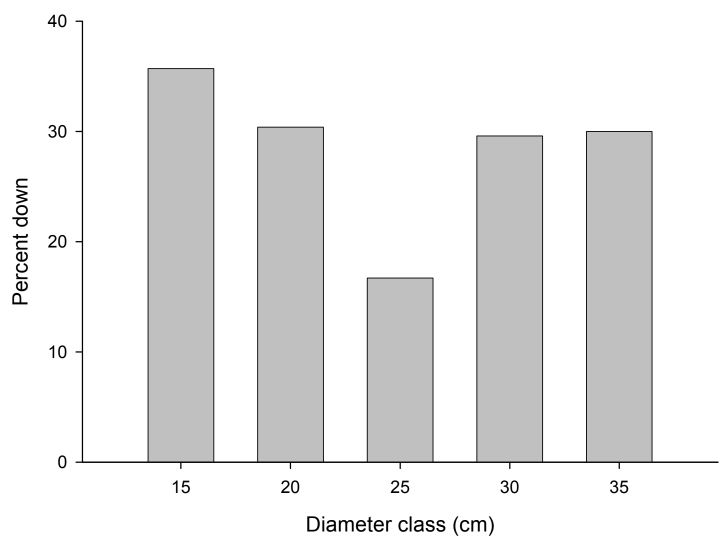

Figure 5. Percent of dead pine trees, killed 6-10 years ago that were down by diameter class.

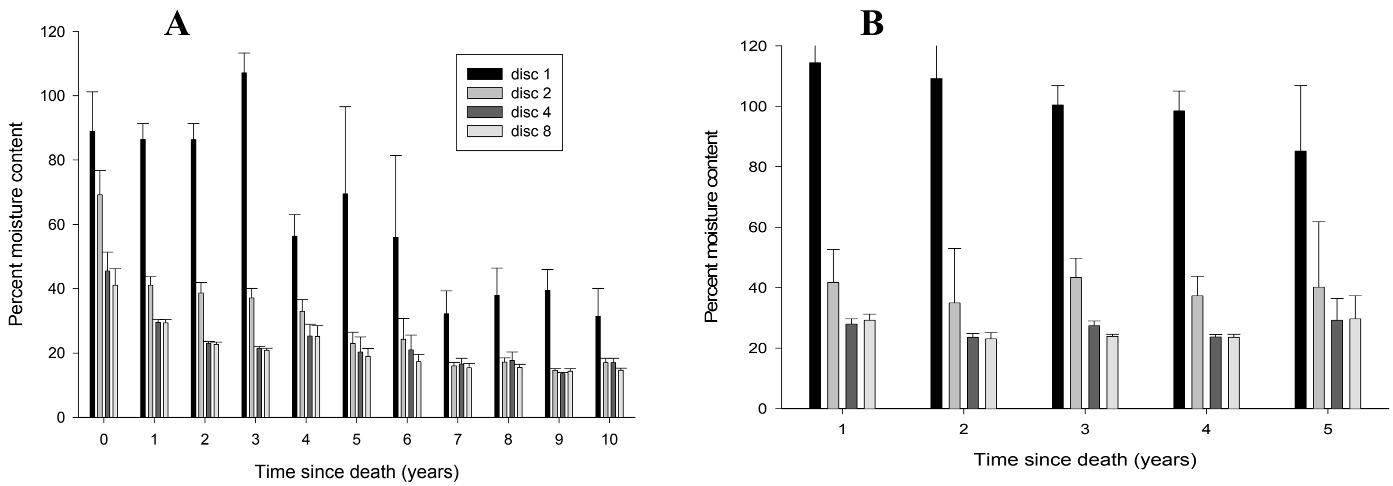

Figure 6. Percent moisture content in the sapwood versus years since death for the SBSdk (A) and the SBSmc3 (B), by disc. Bars equal standard error. Disc 1 = 0.3m, disc 2 = 1.3m, disc 4 sampled at 1/3 merchantable height, and disc 8 sampled at 2/3 merchantable height.

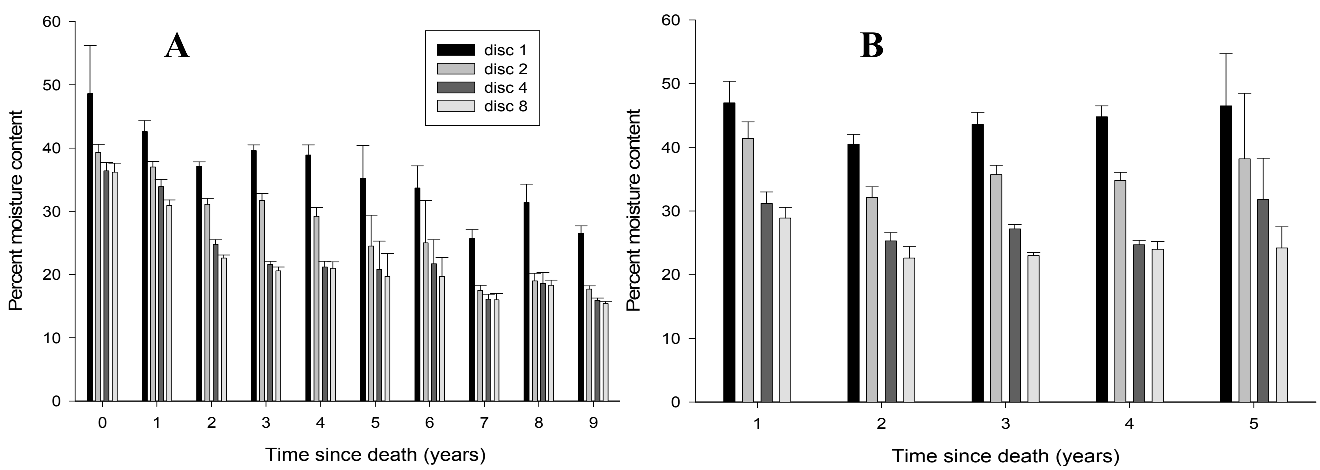

Figure 7. Percent moisture content in the heartwood versus years since death for the SBSdk (A) and the SBSmc3 (B), by disc. Bars equal standard error. Disc 1 = 0.3m, disc 2 = 1.3m, disc 4 sampled at 1/3 merchantable height, and disc 8 sampled at 2/3 merchantable height.

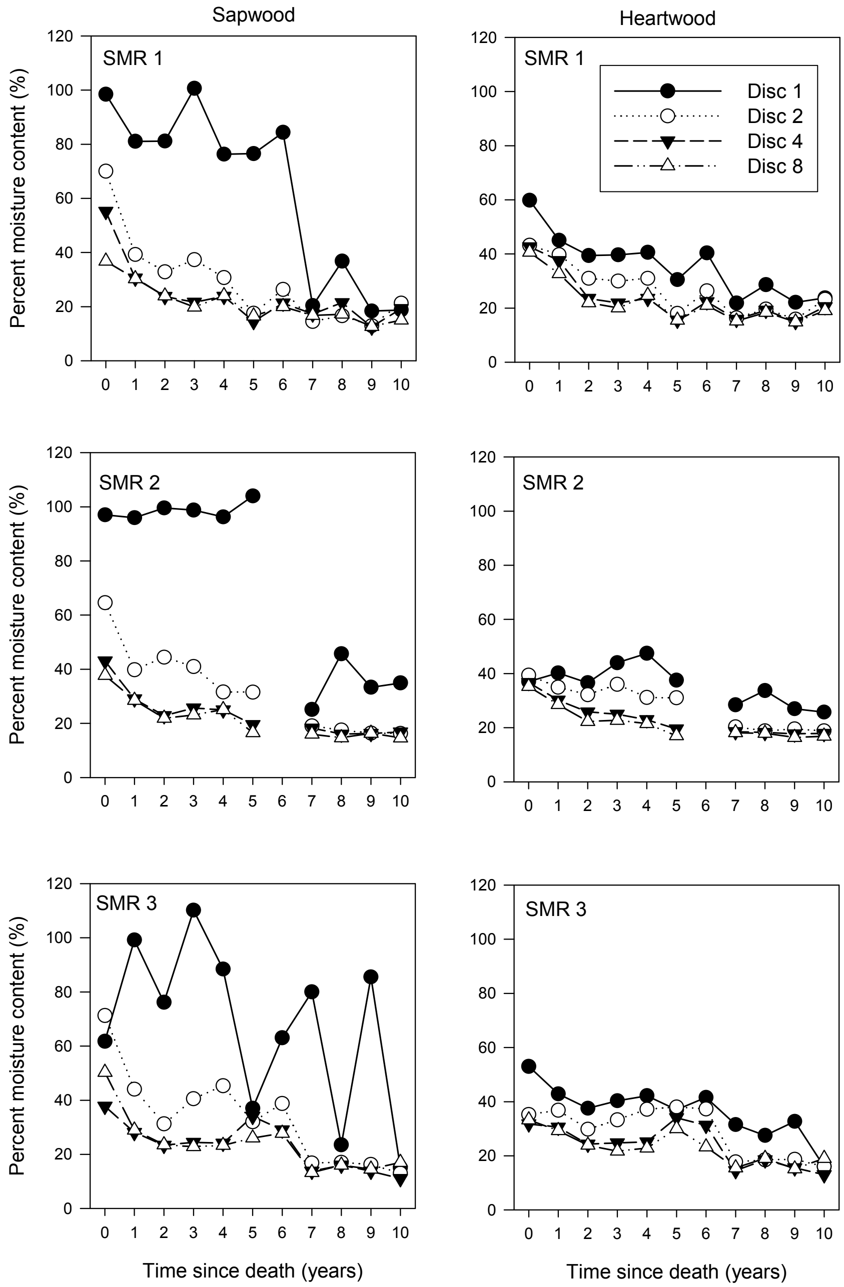

Figure 8. Mean moisture content by sapwood (left) and heartwood (right), SMR, disc and TSD. Disc 1 = 0.3m, disc 2 = 1.3m, disc 4 sampled at 1/3 merchantable height, and disc 8 sampled at 2/3 merchantable height.

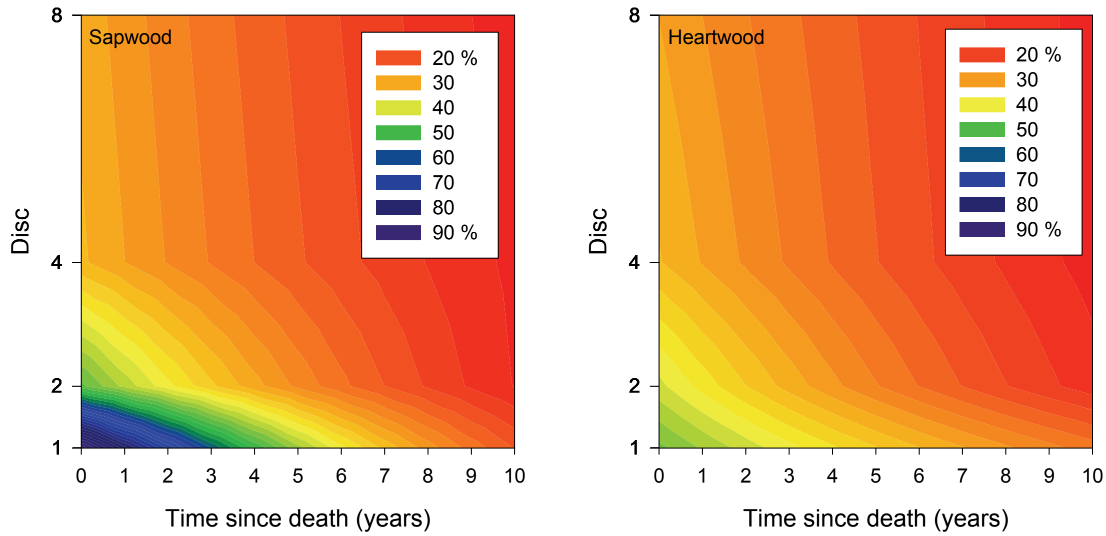

Figure 9. Sapwood (left) and heartwood (right) moisture content (%) predicted as a function of TSD and location along the stem, holding SMR constant at 2 (mesic).

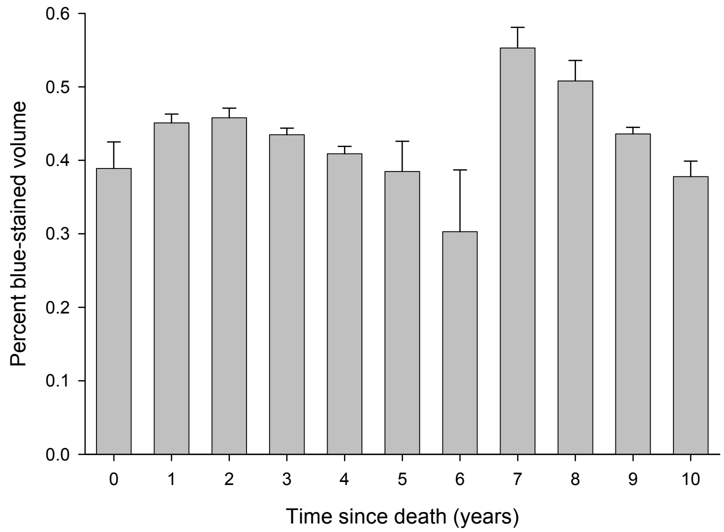

Figure 10. Percent blue-stained wood volume plotted against years since death. Bars represent standard error.

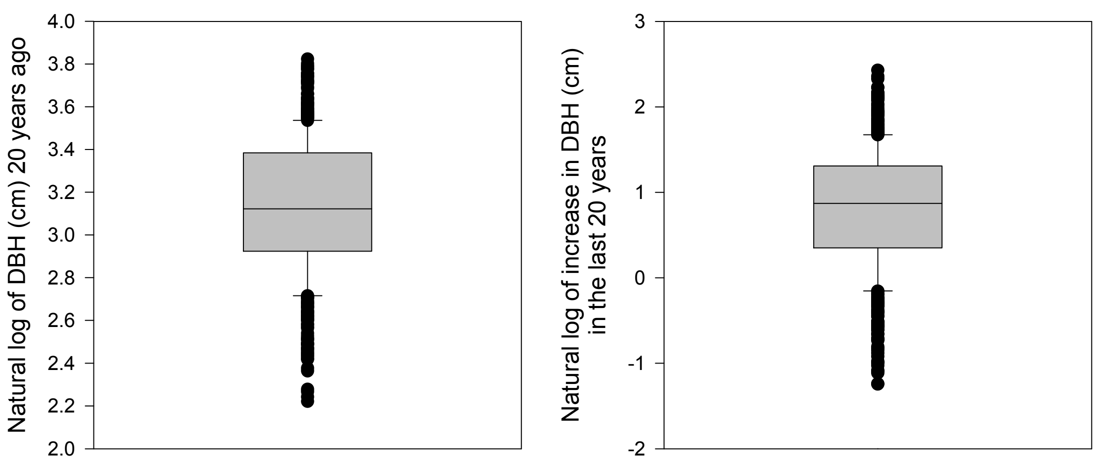

Figure 11. Box and whisker plots of absolute growth over the last 20 years prior to mortality (ABS20) and dbh at the beginning of the 20-year growth period (PRE20DBH). Both variables are natural-log transformed.

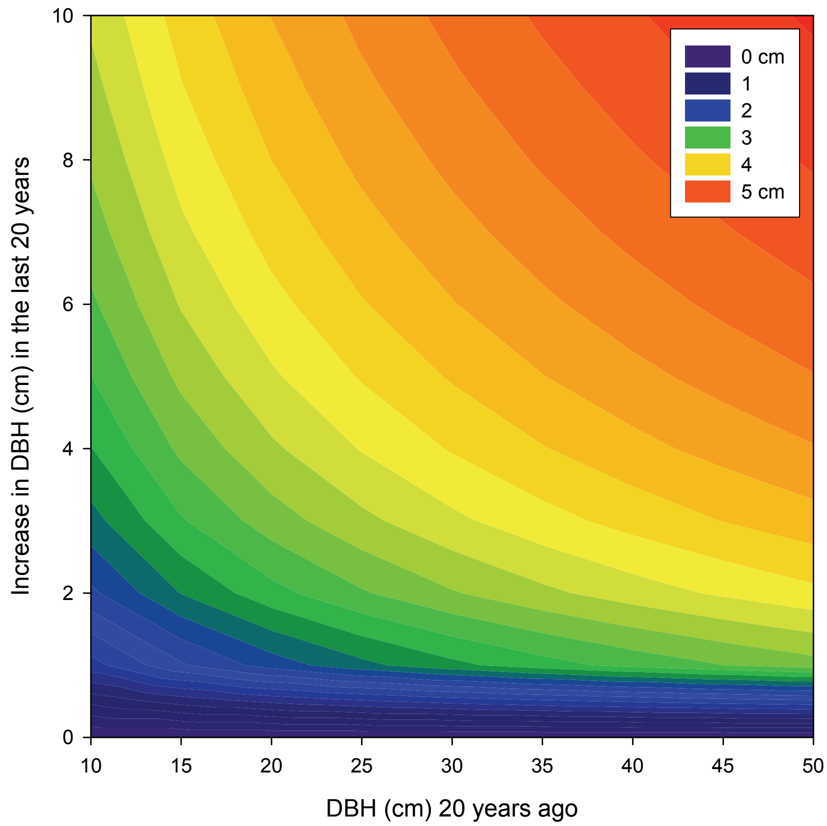

Figure 12. Predicted depth of bluestain fungi (cm) by diameter at breast height 20 years before mortality and absolute growth (cm) in the last 20 years.

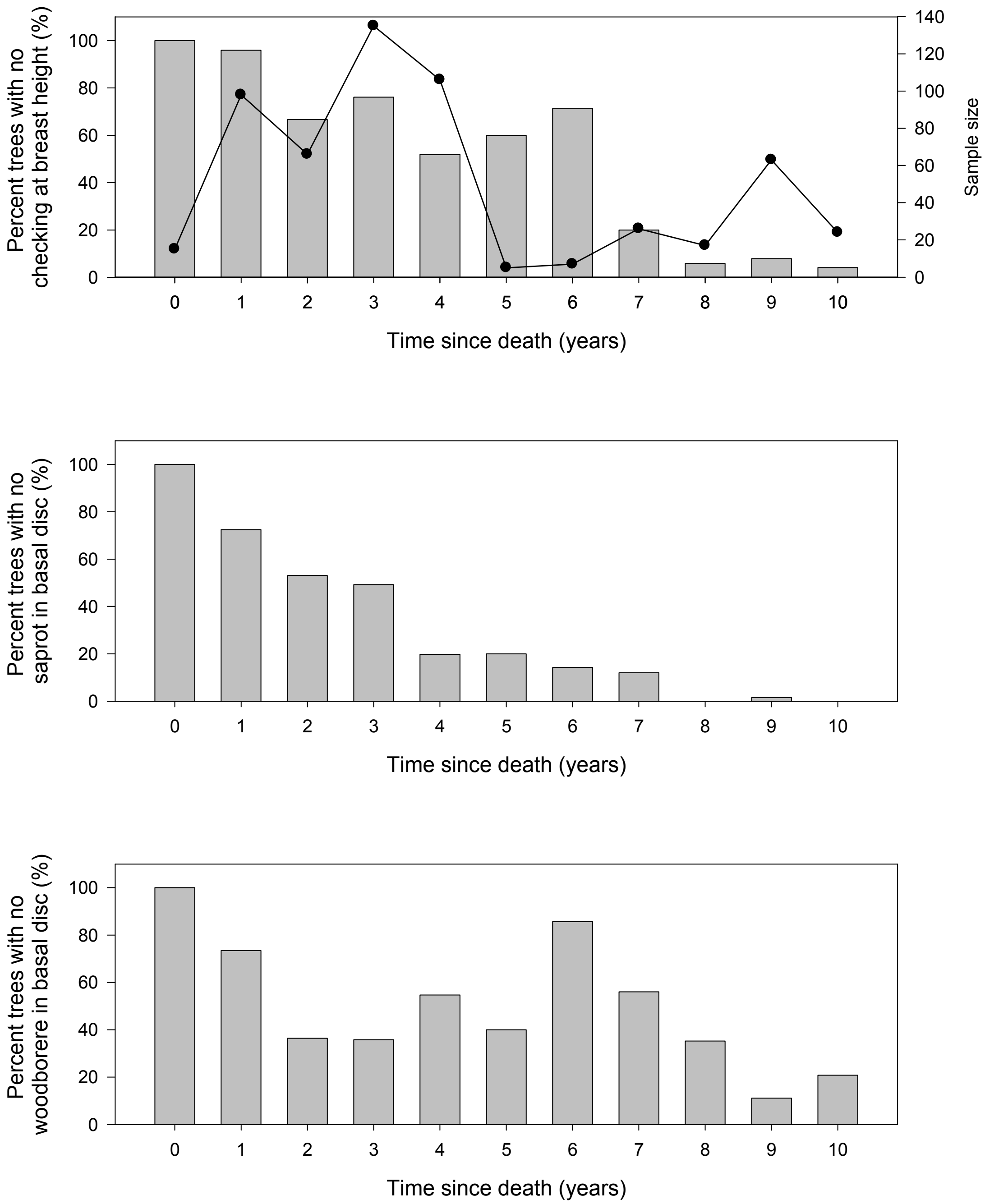

Figure 13. Percent trees with no detectable checking, saprot or woodborer damage by time-since-death. Line graph at top refers to axis at the right.

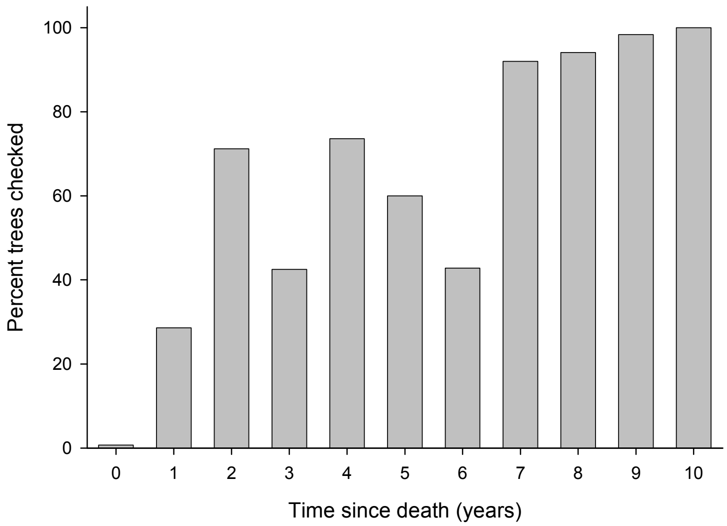

Figure 14. The percent of trees showing checks for all data combined, against time-since-death.

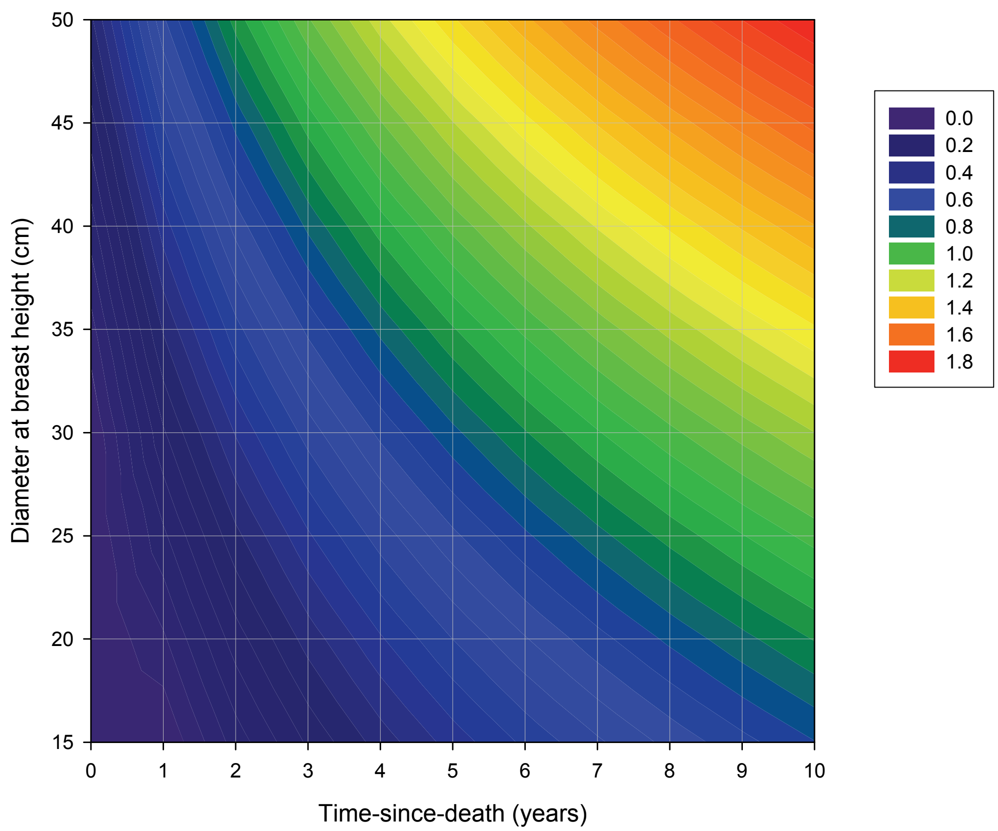

Figure 15. Number of checks at breast height predicted as a function of time-since death and diameter at breast height.

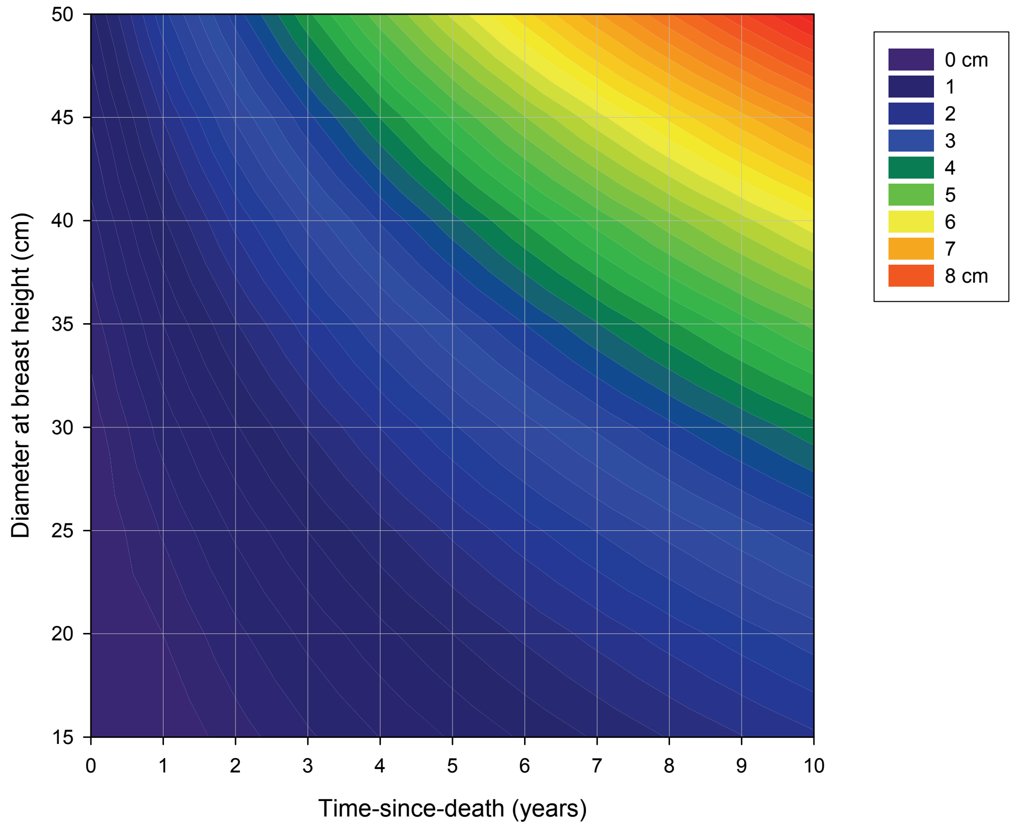

Figure 16. Depth of checking at breast height predicted as a function of time-since death and diameter at breast height.

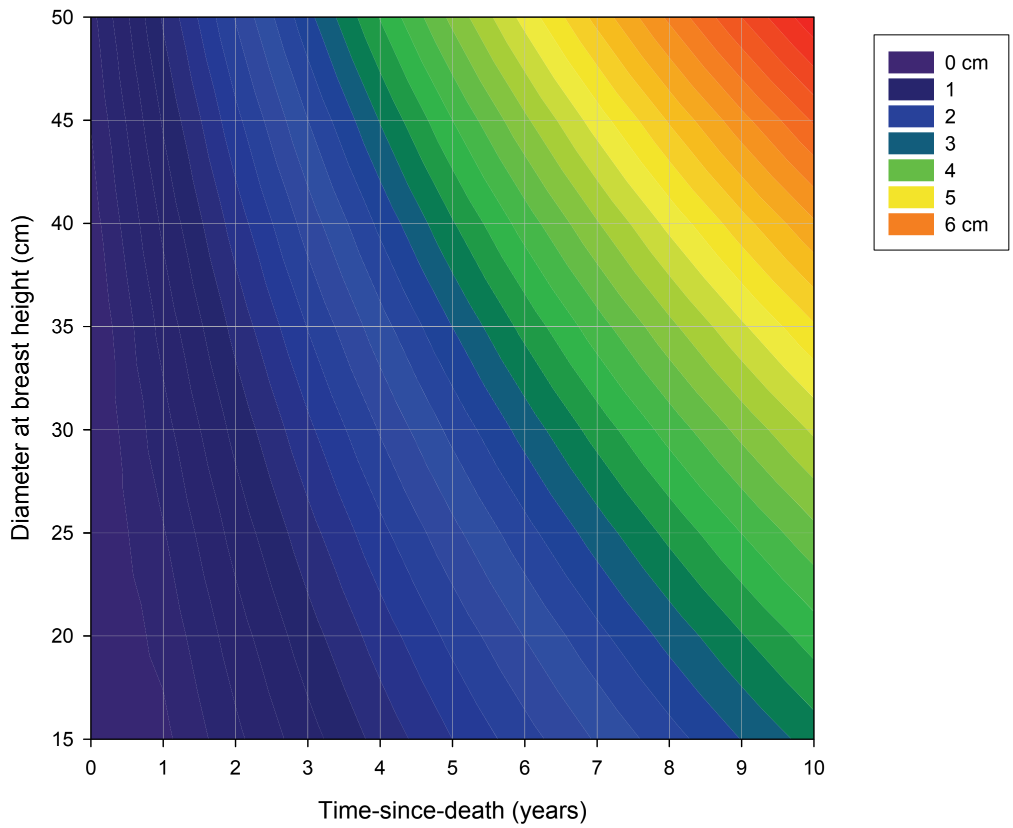

Figure 17. Depth of saprot at basal height predicted as a function of time-since death and diameter at breast height.

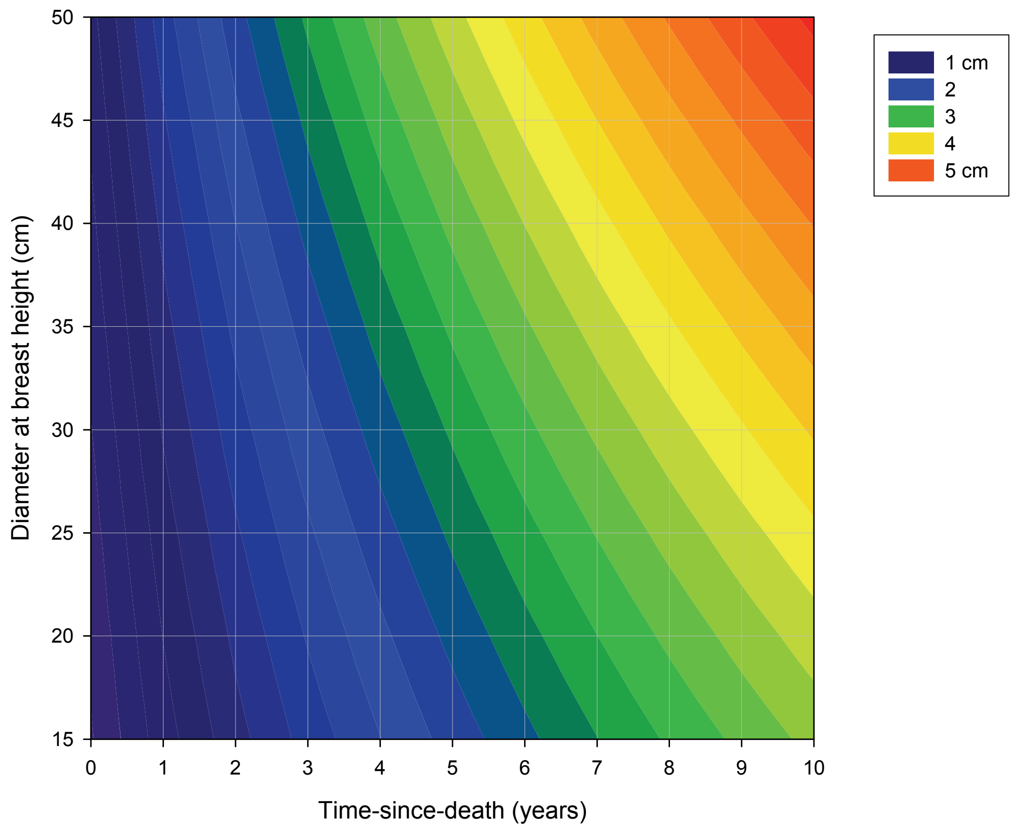

Figure 18. Depth of wood borer damage at basal height predicted as a function of time-since death and diameter at breast height.

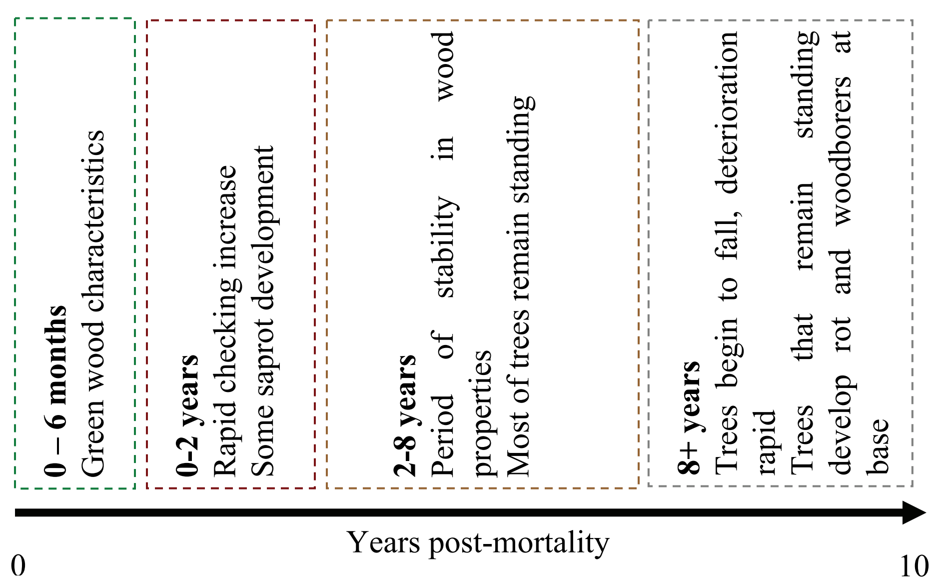

Figure 19. Diagram of changes to wood properties as a function of TSD.