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Morphological attributes and snag classification of four North American boreal tree species: Relationships with time since death and wood density

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A B S T R A C T

Snag degradation classification systems based on external morphological attributes are widely used in ecology but have rarely been related to elapsed time since death (TSD) or wood density. Furthermore, these classification systems rely on the overall aspect of snags, and the predictive ability of specific attributes has rarely been investigated.

We examined which morphological attributes best predicted TSD and wood density in snags of four major boreal species in eastern North America: trembling aspen (*Populus tremuloides* Michx.), balsam fir (*Abies balsamea* [L.] Mill.), jack pine (*Pinus banksiana* Lamb.) and black spruce (*Picea mariana* [Mill.] BSP). We also investigated how a commonly used snag degradation classification system relates to TSD and wood density. Sampling was conducted in northwestern Quebec, Canada. For each species, 37–65 snags were sampled and TSD was determined using dendrochronology.

Bark cover was the only morphological attribute common to models of all species and was the sole predictive variable of TSD in balsam fir. As for TSD, the combination of predictors for wood density was species-specific and wood penetrability was a common predictor in all species. Degradation stages provided rough approximations of TSD and wood density.

This study shows that the degradation classification system used can be helpful when rough estimates are needed. However, species-specific models built according to significant morphological attributes do not represent more time- and resource-consuming field assessments and they provide more precise measurements of TSD and wood density.

1. Introduction

Degradation classification systems of dead wood, i.e. deterioration classifications that are based on external morphological attributes, are used in a wide range of ecological studies in forest ecosystems. As different degradation stages are used by different organisms associated with dead wood, degradation classification has been extensively employed to assess habitat availability and quality (Kruys et al., 1999; Drapeau et al., 2002; Saint-Germain et al., 2007). It is has also been used to characterize forest ecosystems and assess ecosystem integrity (Spies et al., 1988; Rouvinen et al., 2002; Desponts et al., 2004). Dead wood plays important roles in physical and chemical processes such as carbon sequestration and nutrient cycling (Krankina and Harmon, 1995; Brais et al., 2006, but see Laiho and Prescott, 2004) and represents an important component of the aboveground biomass in disturbed and older forest ecosystems (Harmon et al., 1986). Consequently, degradation classification systems have also been used to assess the contribution of coarse woody debris to the biogeochemical dynamics and carbon balance in forest ecosystems (Means et al., 1992; Krankina and Harmon, 1995; Bond-Lamberty et al., 2002; Creed et al., 2004). In many instances, degradation classification systems have been used as tools to roughly reconstruct temporal patterns of past tree mortality or disturbance events retrospectively (Lertzman and Krebs, 1991; Groven et al., 2002; Rouvinen and Kouki, 2002; Pham et al., 2004). Finally, snag dynamics have been modelled using transition rates between degradation stages based on residence time of snags in each degradation stage (Morrison and Raphael, 1993; Kruys et al., 2002; Aakala et al., 2008).

In many instances, degradation classification systems are used to describe the general external characteristics of dead trees. On

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other occasions, they are used as proxies for time since tree death (TSD) or for assessing wood decomposition, where one assumes that degradation stages are correlated to these response variables. In this regard, several studies explored the relationship between degradation stages and TSD, with correlations ranging from very weak (Mast and Veblen, 1994; Daniels et al., 1997) to relatively strong (Huggard, 1999; Campbell and Laroque, 2007; DeLong et al., 2008). The same conclusions were reached regarding wood density (Yatskov et al., 2003; Creed et al., 2004; Saint-Germain et al., 2007).

Degradation classification systems for standing dead trees (snags) are based on a visual assessment that combines several morphological attributes, such as presence of branches, twigs and leaves, bark cover, stem integrity (intact, broken), and wood hardness. In most cases, these classifications are not species-specific and, on some occasions, they have been used across a wide range of ecosystems. For instance, the system developed by Thomas et al. (1979) has been used for coniferous species in the Pacific Northwest region of the United States, but it has since been applied to species from the eastern boreal forest of Canada (e.g. Harper et al., 2005; Taylor and MacLean, 2007). This broad use of snag degradation classification systems suggests that all species roughly follow a common degradation pattern, starting from an intact dead tree that gradually loses its leaves, twigs and bark, and which eventually breaks at some point above ground level.

When assigning a snag to a degradation stage in the field based on its external appearance, observers are frequently challenged by the impossibility of selecting a single category for which all criteria are met. For instance, a snag may be broken and its wood may be relatively soft, which indicates an advanced degree of degradation or decomposition (i.e. degree of wood density loss), while it also bears all its bark, which suggests that the snag is not very old. This example suggests that some criteria may be more indicative than others. Relatively few studies have evaluated the relevance of specific criteria to predict TSD or wood density, but those that did found significant differences in the contribution of different morphological attributes (Yatskov et al., 2003; Newberry et al., 2004; Storaunet, 2004; Waskiewicz et al., 2007). Among these authors, only Yatskow et al. (2003) included more than two species and deciduous species.

This study examined relationships between external appearance, wood density, and TSD in snags of four of the main boreal species in eastern North America: trembling aspen (*Populus tremuloides* Michx.), balsam fir (*Abies balsamea* [L.] Mill.), jack pine (*Pinus banksiana* Lamb.) and black spruce (*Picea mariana* [Mill.] BSP). The specific objectives were to: 1 – investigate which readily observed external morphological attributes are the best predictors of TSD and wood density, 2 – assess to what extent a commonly used degradation classification system in the eastern boreal forest (Imbeau and Desrochers, 2002) was appropriate to the studied species, 3 – evaluate the relationship between TSD and wood density with degradation stages of Imbeau and Desrochers' (2002) degradation classification system.

2. Methods

2.1. Study area

Our study was conducted in northwestern Quebec (Canada), in the transition zone between the mixedwood and coniferous boreal forest. The region is part of a broad physiographic unit known as the northern Clay Belt, which is characterized by flat topography and clay deposits originating from the proglacial lakes Barlow and Ojibway (Vincent and Hardy, 1977). Climate is cold and continental, with a mean annual temperature of 0.7 °C and mean annual total precipitation of 889.8 mm (weather station of La Sarre, Environment Canada, 2010). Two distinct areas were sampled.

For balsam fir, trembling aspen, and jack pine, sampling was conducted in the Lake Duparquet Research and Teaching Forest (LDRTF; 48°26′–48°29′N, 79°26′–79°18′W), which is located 45 km northwest of Rouyn-Noranda. The research forest is located in the Rouyn-Noranda ecological region, within the balsam fir-white birch (*Betula papyrifera* Marsh.) bioclimatic domain (Robitaille and Saucier, 1998), where associations of balsam fir, black spruce, white spruce (*Picea glauca* [Moench] Voss), paper birch, and trembling aspen dominate. The disturbance regime includes recurrent wildfires (Dansereau and Bergeron, 1993) and periodic outbreaks (Morin et al., 1993) of spruce budworm (*Choristoneura fumiferana* [Clem.]).

For black spruce, sampling was conducted in coniferous forest 120 km further north (49°25′–49°50′N, 79°18′–78°41′W), in the Lake Matagami Lowland ecological region. This area is within the black spruce–feathermoss (*Pleurozium schreberi* [Brid.] Mitt.) bioclimatic domain (Robitaille and Saucier, 1998). The disturbance regime is characterized by large stand-replacing fires (Bergeron et al., 2004), with return intervals long enough for successional paludification processes to take place, organic deposits to accumulate, and low productivity open forests to develop (Simard et al., 2007).

Stand age, past disturbance history and stand dynamics suggest that mortality causes were different from species to species (Angers et al., 2010). In jack pine, most snags were recruited via self-thinning mortality. Trembling aspen mortality was also related to self-thinning, but senescence and possibly defoliation by the forest tent caterpillar (Malacosoma disstria Hbn.) also played a role. In balsam fir, most snags originated from the 1970–1987 spruce budworm outbreak (Morin et al., 1993). Most black spruce deaths were presumably due to senescence. Detailed stand characteristics are provided in Angers et al. (2010), and include tree composition, stand age, past harvesting activities, snag density, species-specific annual mortality, and snag fall rates.

2.2. Field methods

Data collection was conducted during the summers of 2004 and 2005. Seventeen stands were selected, based on species composition, surficial material type (glaciolacustrine clay in LDRTF, glaciolacustrine clay overlain by a thick organic layer in black spruce stands), drainage class (mesic sites in LDRTF, subhydric sites in black spruce stands), and age (mature to overmature stands).

In each stand, a 20 m $\times$ 20 m plot was established randomly, at least 50 m from any edge (road, cut, different stand). Every snag was identified. These were trees without green foliage that were at least 1.3 m tall, and which had a diameter at breast height (DBH) $\geqslant$ 5 cm. Leaning dead trees were considered as snags if their angle from the ground was >45° (Harmon and Sexton, 1996). To fulfill sampling requirements for some specific attributes (e.g. snags of advanced degradation stages based on their external appearance), additional snags were sampled in the area surrounding the plots. A total of 216 snags were sampled (see Table 2 for distribution among species). Characterization of snags included species, DBH (±0.1 cm), height (±0.1 m), stem integrity (whether intact or broken), presence of dead leaves, twigs and branches (three categories: abundant, partial, absent), and bark cover (10% categories). Wood penetrability was also assessed, using a knife that was pushed into the wood in several locations around the bole between 1 and 1.3 m, always by the same observer to limit bias (four categories: 1 – hard wood, blade can not penetrate into the sample; 2 – blade can only slightly penetrate the sample [$\leqslant$0.5 cm]; 3 – blade penetrates the periphery of the bole, center hard; 4 – soft wood, blade easily penetrates the bole). Mean snag DBH ranged from 12.2 ± 0.5 (SE) cm (black spruce) to 18.6 ± 0.8 cm (balsam fir). Jack pine and trembling aspen were intermediate with average DBH of 14.3 ± 0.8 cm and 16.6 ± 1.0 cm, respectively.

Cross-sections that were ≈ 5 cm thick were taken from all snags. Fragile samples were taped with thread-enforced tape and cut using a fine-toothed bow saw to minimize fragmentation. To optimize the chances of successful crossdating, three cross-sections were taken from each bole when possible: at the base, breast height and near the top (around 3 m from top for intact trees and near the point of breakage for broken trees). This sampling procedure 1 – reduced the risk of crossdating failure due to advanced decay, 2 – validated year of death with multiple crossdated sections, and 3 – increased capture of the last ring produced in stressed trees (Mast and Veblen, 1994; V.A. Angers, unpublished data). For broken trees, if the fallen tree top was reliably identifiable, a cross-section was also taken to maximize crossdating success. In boles with advanced decay, heights at which cross-sections were taken varied, depending on bole periphery preservation to maximize crossdating success.

2.3. Wood density analysis

All cross-sections were oven-dried at 60 °C and weighed to the nearest 0.01 g until weight was stable for at least 24 h. Bark was stripped and dry volume (cm^3) was calculated assuming a cylindrical shape averaging maximum and minimum diameters and thicknesses of the cross-section. Wood density ($g\ cm^{-3}$) was calculated as the ratio of dry mass to dry volume.

2.4. Tree ring analysis

After wood density measures, all cross-sections were sanded until xylem cells were clearly visible. When necessary, hot glue was used to consolidate fragmented samples prior to sanding. Ring width was measured for each cross-section along two radii (one when decay impeded ring visibility elsewhere on the cross-section) using a Velmex micrometer (0.001 mm precision; Velmex incorporated, Bloomfield, New York, USA).

Year of death was considered as the year of the last ring produced. To establish year of death, each individual tree ring series that was generated by all sampled cross-sections was crossdated against master series constructed for balsam fir, jack pine, and trembling aspen from nearby living trees in LDRTF (Angers et al., 2010) and from a master chronology developed for black spruce (Simard et al., 2007). Crossdating was performed using marker years, and verified with COFECHA (Holmes, 1983) and TSAP (Rinn, 1996) programs, with the latter being used for visually comparing the pattern generated by each tree ring series and the average of the master series. When discrepancies in years of death were obtained for cross-sections belonging to the same dead tree, the most recent year was retained. Of the 216 snags collected in the field, only five could not be successfully crossdated. These were excluded from the analysis because cross-sections were too decayed to perform measurements (one aspen), cross-sections were too young (not enough rings) for reliable crossdating (one aspen), or because snags had their periphery eroded and, thus, their outmost rings were possibly missing, impeding an accurate assessment of year of death (two firs, one spruce). TSD was calculated as the difference between year of sampling and year of death.

2.5. Data analysis

2.5.1. Morphological attribute predictors of TSD and wood density

Several discrete variables (i.e. dead leaves, twigs, branches) lacked observations in some classes in some species. When there were fewer than five observations in a given class, we merged adjacent classes and reconfigured that variable classification into a condensed classification system for data analysis (See "Condensed classification" column in Table 2). For bark cover, we used the median of the original classes being merged to designate the resulting class. In all discrete variables, this merging step yielded a two- or three-class system. Classification reconfiguration was done separately for each species. Most discrete data were transformed to a binary form. In cases where observations were almost all concentrated in one class, the variable was excluded from the analysis (i.e. presence of dry leaves in all species, stem integrity in balsam fir, presence of branches in jack pine). In balsam fir, all bark cover classes (10%) were represented and that variable was thus considered to be continuous.

To evaluate residual height in broken snags, we first estimated the original height by regressing DBH against height of unbroken snags and surrounding living trees ($n = 25$ to 69, depending on species). Using the logarithmic relationships generated from these data (all r^2 were $\geqslant 0.67$, data not shown), the percentage of estimated original height (%Height) was computed as the ratio of observed snag height to estimated original height.

For each species, two sets of multiple linear regressions were conducted to examine the ability of these variables to predict (a) TSD and (b) wood density of snags. Candidate variables that were tested are presented in Table 2. When preliminary observations of the data indicated non-linear relationships between variables, the response variable was transformed or a morphological attributes classification was adapted. Forward and mixed stepwise procedures were used and yielded the same models. A variance inflation factor (VIF) was calculated for each predictor to ensure that there was no collinearity between explanatory variables introduced together in models. All resulting VIF values were <4.0.

2.5.2. Linkages between degradation classification system, TSD, and wood density

After assessing all morphological attributes that were observed in the field, snags were assigned to a degradation stage according to Imbeau and Desrochers' classification system (Imbeau and Desrochers, 2002, adapted from Bergeron et al., 1997, Table 1, Fig. 1). When different variables suggested assignment to two or more degradation stages, we classified the snag into the median class suggested by all attributes.

To assess to what extent Imbeau and Desrochers' (2002) degradation classification system was adequate to characterize external morphological attributes of the studied species, an inconsistency index was calculated for each species. This index corresponds to the percentage of snags that could have been placed in more than one degradation stage if each criterion was considered individually, and varied from 0 to 100. We also calculated the inconsistency index for each degradation stage to examine if some stages were more problematic than others.

As very few observations occurred in degradation stages 7 and 8 (the last snag stages), we merged them.

For each species, the relationship between TSD and degradation stage was tested using a one-way analysis of variance (ANOVA), followed by post hoc Tukey's HSD tests. Relationships between wood density and degradation stage were tested in the same way.

All statistical analyses were done using JMP 7.0 software (SAS Institute Inc.). Prior to all regressions and analyses of variance, assumptions of normality and homoscedasticity were verified and the data were transformed if necessary.

3. Results

3.1. Morphological attribute predictors of TSD and wood density

To predict TSD, four models corresponding to the four species studied were generated. All models were significant ($p < 0.0001$)

Table 1
Imbeau and Desrochers' decay classification system for snags (Imbeau and Desrochers, 2002, adapted from Bergeron et al., 1997). Classes 1–3 refer to living trees and are not shown.

Snag decay class	Criteria
4	Recently dead, hard wood, firm bark cover, 0% green foliage, small twigs still remaining
5	Hard wood, no dead foliage, no small twigs
6	Hard wood, loose bark cover, broken top, height still more than 50% of what is observed on trees with the same DBH
7	Soft, decomposed wood, broken top with height less than 50% of what is observed on trees with the same DBH
8	Height < 2m

and the percentage of variance explained by models varied from 29% to 64%, depending on species (Table 3). All models included different combinations of morphological attributes which best predicted TSD (Table 4). The number of predictive variables also differed among species: trembling aspen model included as many as four variables, whereas balsam fir included only one (Table 4). For all models, confidence intervals varied as a function of TSD (Fig. 2).

Bark cover was the only variable common to all species models predicting TSD (Table 4). Bark cover alone explained almost 45% of variance in balsam fir (Table 3), and no other variable significantly contributed to the model. Balsam fir was the only species for which the whole bark cover gradient was covered. In this case, the relationship between bark cover and TSD was nonlinear (bark cover remained almost entire until about 15 years after death and then declined rapidly), and TSD was thus square-transformed (i.e. TSD^2). In addition to the models proposed, some shortcuts could be derived from observed bark loss patterns. For example, all snags that still bore at least 90% of their bark had been dead for less than 10 years in trembling aspen and for less than 15 years in balsam fir. In jack pine, bark cover did not generally decrease below 80% until more than 20 years had elapsed following death.

Wood penetrability was included in models for trembling aspen and jack pine (Table 4). Twig presence was a significant predictor for jack pine and black spruce. Stem integrity and presence of branches were included in only one model (trembling aspen).

When investigating morphological attributes that best predicted wood density, most models explained a large proportion of variance, ranging from 53% to 65% in jack pine, trembling aspen, and black spruce (Table 5). In balsam fir, the model explained a significant but much lower percentage of the variance (17%). As with TSD, species generally featured different combinations and numbers of variables, ranging from one in balsam fir and black spruce to three in jack pine (Table 5). Wood penetrability was a significant predictor for all species, whereas bark cover was significant for trembling aspen and jack pine, and stem integrity for jack pine only (Table 5).

3.2. Adequacy of Imbeau and Desrochers' degradation classification system

Application of Imbeau and Desrocher's degradation classification system appeared to be problematic. In most instances, a single snag included characteristics of two or more adjacent classes, placing the onus on the observer to decide the final assignment. The

Table 2
Synthesis of candidate morphological attributes tested in models predicting time since death and wood density, together with discrete variable condensed classification.

Species	Morphological attributes	Number of classes	Condensed classification[a]	*n*
Trembling aspen (n = 52)				
	Stem integrity	2	Intact, broken	19, 33
	Wood penetrability	3	1, 2, 3–4	17, 23, 12
	Bark cover	3	50%[b], 90%, 100%	7, 6, 39
	Branches	2	Absent, partial or abundant	22, 30
	Twigs	2	Absent, partial or abundant	34, 18
	%Height	Continuous	–	52
Balsam fir (n = 57)				
	Wood penetrability	2	1–2, 3–4	46, 11
	Bark cover	Continuous	–	57
	Branches	2	Partial, abundant	8, 49
	Twigs	2	Absent or partial, abundant	26, 31
	%Height	Continuous	–	57
Jack pine (n = 37)				
	Stem integrity	2	Intact, broken	32, 5
	Wood penetrability	3	1, 2, 3–4	15, 15, 7
	Bark cover	3	45%[b], 90%, 100%	10, 13, 14
	Twigs	2	Absent or partial, abundant	7, 30
	%Height	Continuous	–	37
Black spruce (n = 65)				
	Stem integrity	2	Intact, broken	20, 45
	Wood penetrability[c]	3	1, 2, 3–4	21, 26, 18
	Wood penetrability[d]	2	1–2, 3–4	47, 18
	Bark cover	3	50%[b], 90%, 100%	8, 14, 43
	Branches	2	Absent or partial, abundant	11, 54
	Twigs	2	Absent or partial, abundant	31, 34
	%Height	Continuous	–	65

[a] After grouping of the initial classes to eliminate classes lacking observations.
[b] Based on the median of the original classes being merged.
[c] Used in modelling of best predictors of TSD.
[d] Used in modelling of best predictors of wood density. Classes 1 and 2 were merged because wood density of both classes was so similar that no transformation could linearize relationship between wood density and degradation classes.

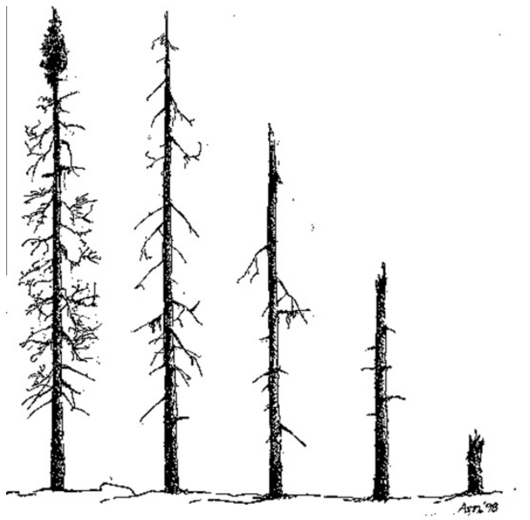

Fig. 1. Visual representation of Imbeau and Desrochers' decay classification system for snags (Imbeau and Desrochers, 2002, adapted from Bergeron et al., 1997). Classes 1–3 refer to living trees and are not shown. Reproduced with permission of the authors and The Journal of Wildlife Management, The Wildlife Society, Allen Press Publishing Services.

inconsistency index varied from 49% in black spruce to 95% in balsam fir. Trembling aspen and jack pine were in an intermediate position with 60% and 76% of inconsistencies, respectively. Except for balsam fir, the inconsistency index was generally lowest in degradation stage 4 (first snag stage, Fig. 1), varying between 0% (trembling aspen and jack pine) and 19% (black spruce).

3.3. Linkages between Imbeau and Desrochers' degradation classification system, TSD, and wood density

Degradation stages of Imbeau and Desrochers' (2002) degradation classification system provided rough approximations of TSD. For each species, analysis of variance showed that significant differences in mean TSD existed among degradation stages ($p \leqslant 0.0004$ in all species, Fig. 4), with average age generally increasing with degradation stages. However, overlap in TSD between adjacent degradation stages occurred in all species, as Tukey's tests indicated that there was no significant difference in average age between adjacent classes on many occasions. Indeed, when grouping degradation stages to create significantly distinct groups, the number of classes decreased. Three grouped degradation stages were significantly distinct in balsam fir (stages 4, 5, 6–7) and jack pine snags (stages 4, 5, 6–8) whereas only two groups were significantly distinct in trembling aspen and black spruce (4–5, 6–8; $p \leqslant 0.0001$ in all species).

Table 3
Summary of multiple linear regression statistics predicting time since death and wood density in four boreal tree species.

	Trembling aspen	Balsam fir	Jack pine	Black spruce
Time since death				
n	52	57	37	65
F-ratio	13.0	45.6	22.1	14.1
p	<0.0001	<0.0001	<0.0001	<0.0001
r^2 adj.	0.540	0.443	0.638	0.291
Wood density				
n	52	57	37	64[a]
F-ratio	32.22	12.38	14.56	115,22
p	<0.0001	0.0009	<0.0001	<0.0001
r^2 adj.	0.647	0.169	0.530	0.644

[a] One observation was excluded from the analysis because of erroneous wood density.

Table 4
Multiple linear regression results predicting time since death (TSD) in four boreal tree species.

Morphological attributes	Coefficient	SE	*t*-Value	*p*
Trembling aspen				
Intercept	12.057	0.190	8.78	<0.0001
Stem integrity	−8.432	0.254	−4.60	<0.0001
Wood penetrability_1[b]	−6.166	0.245	−3.49	0.0011
Wood penetrability_2[b]	−4.234	0.220	−2.67	0.0104
Branches	5.388	0.227	3.29	0.0019
Bark cover_50%[b]	4.686	0.249	2.61	0.0121
Balsam fir				
Intercept	602.926	0.263	15.59	<0.0001
Bark cover[a]	−4.096	0.004	−6.75	<0.0001
Jack pine				
Intercept	26.504	0.393	11.09	<0.0001
Wood penetrability_1[b]	−6.748	0.310	−3.57	0.0011
Twigs	−10.183	0.412	−4.07	0.0003
Bark cover_45%[b]	7.305	0.351	3.42	0.0017
Black spruce				
Intercept	20.582	0.244	10.45	<0.0001
Twigs	−9.460	0.317	−3.70	0.0005
Bark cover_50%[b]	9.850	0.482	2.54	0.0138

[a] TSD was square-transformed to fit a linear relationship with bark cover.
[b] Wood penetrability_1 and 2 as well as Bark cover_45% and 50% refer to binary variables of the condensed classification presented in Table 1.

Although trembling aspen exhibited a consistently lower average age in all degradation stages when compared with other species (Fig. 4), the difference was not always significant, suggesting that this deciduous species did not progress through degradation stages much more rapidly than did the coniferous species. Among coniferous species, the progression through degradation stages was similar, with no significant distinction in TSD, regardless of the degradation stage considered.

Significant differences in wood density were observed between the extreme stages of degradation within a given species, but the intermediate stages overlapped (Fig. 5). As with TSD, grouping degradation stages to create significantly distinct groups also reduced the number of classes. Three grouped degradation stages were significantly distinct in trembling aspen (4, 5–6, 7–8) and balsam fir (stages 4, 5–6, 7) whereas only two groups were significantly distinct in jack pine (4–5, 6–8) and black spruce (4–6, 7–8; $p \leqslant 0.0003$ in all species). Within a given degradation stage, wood density often varied from species to species, with the species-specific differences lessening with progression through degradation stages.

When compared to average fresh wood densities reported for black spruce (ex.: 0.445 g cm^{-3}, Jessome, 1977), the measures presented in this study (Fig. 5) may seem rather high. Those high wood density values are due to the very slow growth that characterize paludified and low productivity stands of our study area (see Simard et al., 2007; Angers, 2011).

4. Discussion

4.1. Morphological attribute predictors of TSD and wood density

To our knowledge, this is among the first studies to examine what combinations of individual morphological attributes best predict TSD in snags of species from the eastern boreal forests of North America. Our models clearly show that the morphological attributes related to TSD of snags differ from one species to another.

Bark cover was, however, a common predictor of TSD for all species and this single criterion was found to be a better predictor

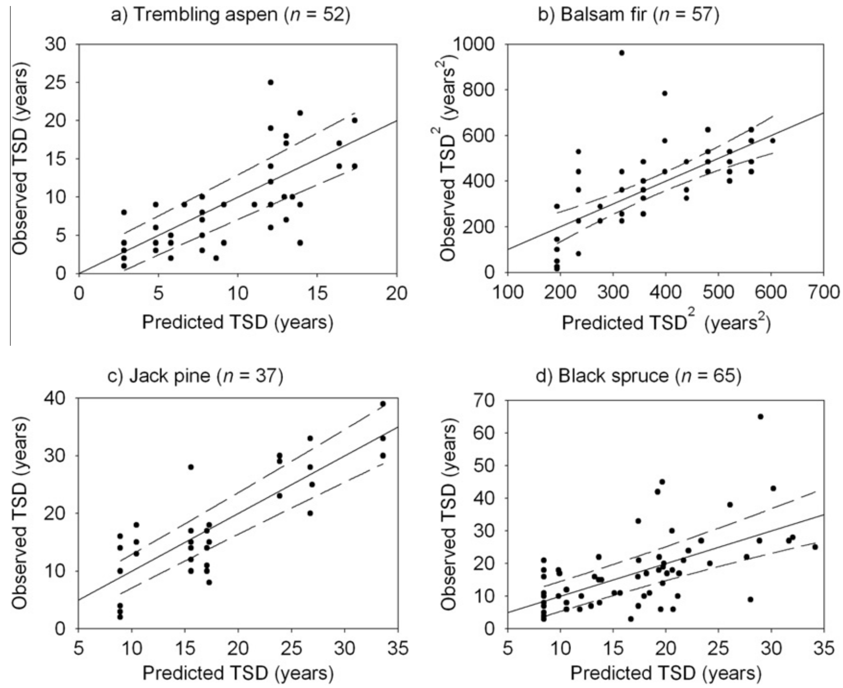

Fig. 2. Regression between observed and predicted time since death (TSD, full line) and 95% confidence bands (dashed lines) in four boreal tree species.

Table 5
Multiple linear regression results predicting wood density in four boreal tree species.

Morphological attributes[a]	Coefficient	SE	*t*-Value	*p*
Trembling aspen				
Intercept	0.332	0.002	26.49	<0.0001
Wood penetrability_1	0.106	0.026	5.71	<0.0001
Wood penetrability_3–4	−0.077	0.003	−3.83	0.0004
Bark cover_50%	−0.058	0.003	−2.42	0.0194
Balsam fir				
Intercept	0.312	0.007	46.69	<0.0001
Wood penetrability	−0.053	0.015	−3.52	0.0009
Jack pine				
Intercept	0.324	0.004	12.63	<0.0001
Stem integrity	0.105	0.005	3.77	0.0006
Wood penetrability_1	0.054	0.003	2.82	0.0080
Bark cover_45%	−0.057	0.003	−2.81	0.0082
Black spruce				
Intercept	0.362	0.015	24.47	<0.0001
Wood penetrability	0.187	0.017	10.73	<0.0001

[a] Wood penetrability_1 and 3–4 as well as Bark cover_45% and 50% refer to binary variables of the condensed classification presented in Table 1.

than any combination of morphological attributes in balsam fir. Waskiewicz et al. (2007) also found that bark loss was the most useful predictor of age in ponderosa pine (*Pinus ponderosa* Dougl.) snags from northern Arizona, and Newberry et al. (2004) reported that bark-related variables were included among the variables predicting TSD in interior spruce (*P. glauca* × *P. engelmannii* Parry ex Engelm.) and subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.) found in sub-boreal spruce forests in British Columbia.

Bark cover was a good predictor of TSD when compared with other morphological attributes because trees that die of causes unrelated to fire usually enter the snag stage with all their bark intact, and residual bark cover can be estimated regardless of stem integrity or residual height of a snag. This type of relationship is not always as simple with other variables. For instance, the presence of branches and twigs can be irrelevant when a snag is broken below crown height (Storaunet, 2004).

Presence of branches and presence of twigs were not consistently significant in our models, but one or the other was significant for three species. Examining morphological attributes predicting TSD, Newberry et al. (2004) reported that branch remains (four categories) and fine branch flexibility (three categories) significantly contributed to predicting TSD. Storaunet (2004), using Norway spruce (*P. abies* [L.] Karst) in Norway and DeLong et al. (2008), studying the same species and region as Newberry et al. (2004), found branch order classification (five classes) to be a better predictor of TSD than bark cover. In our study, branches and twigs were classified into two categories, which may not have been sufficiently refined for these variables to be significant predictors in our models.

Percentage of estimated original height (%Height) did not emerge as a predictive variable of TSD, while stem integrity was a significant predictive variable of TSD in trembling aspen only (Table 4). Stem integrity appeared to be a straightforward indicator of TSD in trembling aspen: of all snags observed in this species, intact snags were always 10 years old or younger (Angers et al., 2010, Fig. 3a). This is consistent with previous findings suggesting that trembling aspen was resistant to breaking at the base (Angers et al., 2010) and prone to successive breakages along the bole (Angers et al., 2011) in the first years following death.

Stem integrity and %Height act as important criteria in a number of degradation classification systems, including that of Imbeau and Desrochers (Thomas et al., 1979; Cline et al., 1980). However, these variables must be used with caution as they can be misleading. For instance, young snags that are broken in the lower part of the stem before death, at the moment of death, or shortly after death, which are not in an advanced level of external degradation, could be classified in an "advanced" degradation stage based on stem integrity and %Height. This early low breakage pattern did not seem to occur in jack pine and balsam fir. In the case of jack pine, this response is probably due to its high breakage resistance and to the fact that snags seemed to fall by breaking under 1.3 m or uprooting instead of decreasing their height progressively through intermediate breakages (Angers et al., 2010; 2011). In balsam fir, spruce-budworm induced mortality left most balsam fir trees in-

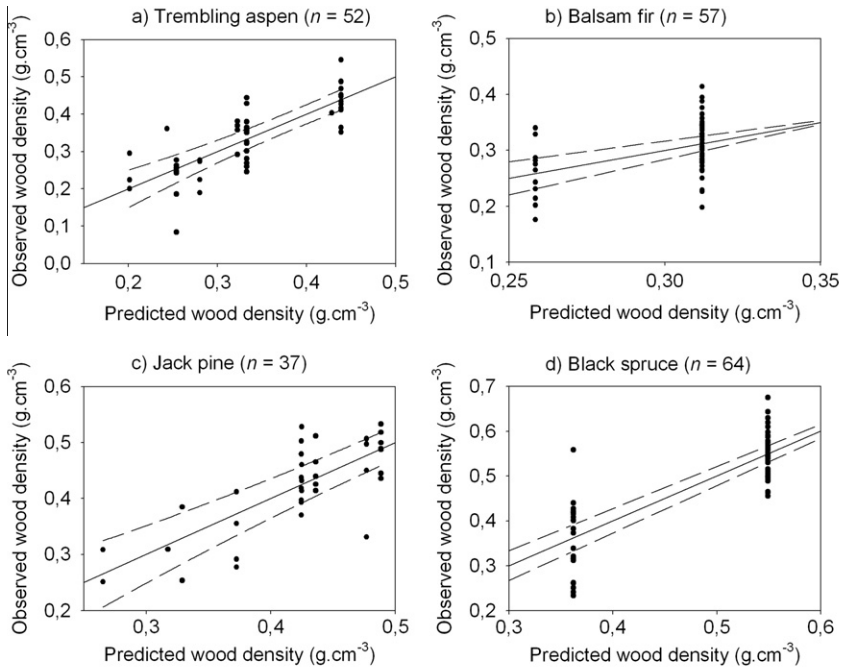

Fig. 3. Regression between observed and predicted wood density (full line) and 95% confidence bands (dashed lines) in four boreal tree species. One observation was excluded from the analysis in black spruce (erroneous wood density, $n = 64$).

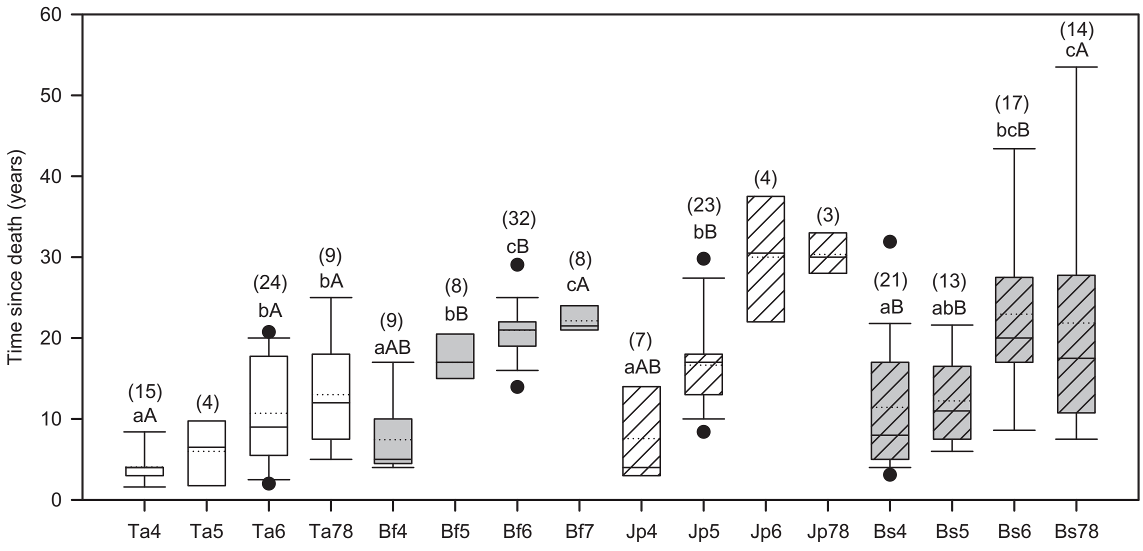

Fig. 4. Box plots showing time since death according to degradation stages for four boreal tree species. Boundaries of the box indicate the 25th and 75th percentiles, the full line within the box marks the median, the dotted line within the box marks the mean, the error bars indicate 90th and 10th percentiles and the dots indicate 5th and 95th percentiles. Numbers in parenthesis indicate sample size. Different lower-case letters indicate significantly different values among degradation classes within a given species while different upper-case letters indicate significantly different values among species within a given degradation class, following ANOVA and Tukey's HSD post hoc tests ($p < 0.05$). When n included fewer than four observations, no means comparisons were conducted. Decay classes 7 and 8 were merged because of low number of observations. There were no snags in degradation class 8 for balsam fir.

tact (Angers et al., 2010). In other situations involving balsam fir, the pattern of early breakage in the lower part of the bole could be observed in trees with mechanical weakness caused by advanced butt rot (Basham, 1991). Waskiewicz et al. (2007) also reported that bole breakage may not be related to TSD.

In this study, the cause of tree death was relatively homogenous within each species (Angers et al., 2010). Relevant criteria for classifying snags found in this study may become irrelevant when the cause of death alters the external appearance of snags. For instance, in this study, jack pine retained most of its bark in the first 20 years after death, with 89% of snags bearing 90% or more of their bark. In fire-killed trees, this variable would become useless and misleading as fire often causes the bark to shed and fall rapidly (Boulanger and Sirois, 2006). In a site located about 70 km north of the study area (Angers et al., 2011), only 20% of fire-killed snags still bore 90% or more of their bark seven years after fire.

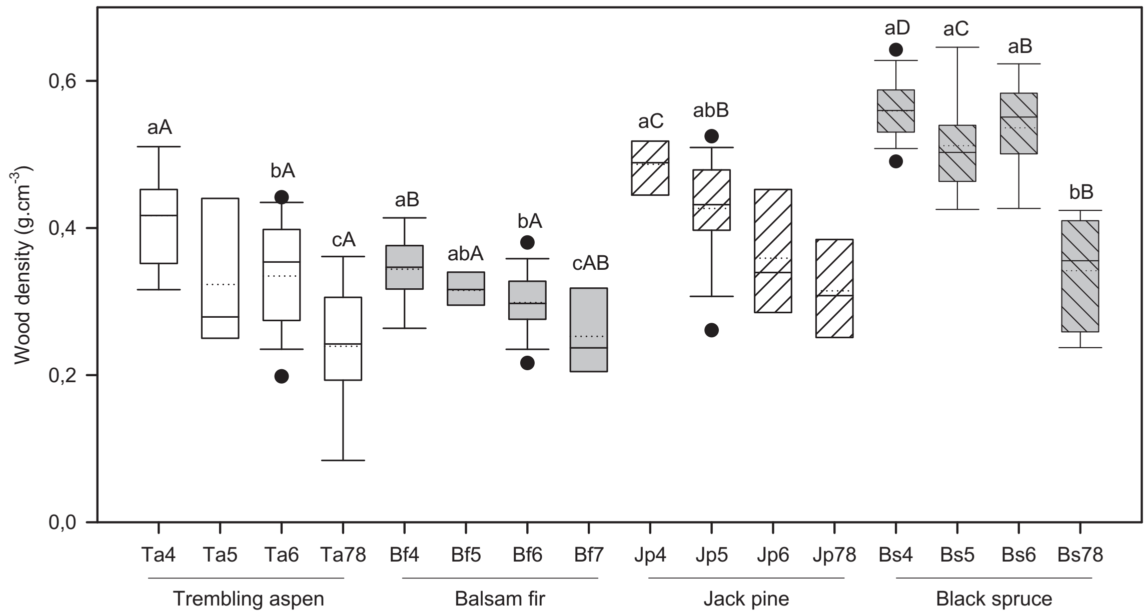

Fig. 5. Box plots showing wood density according to degradation stages for four boreal tree species. Boundaries of the box indicate the 25th and 75th percentiles, the full line within the box marks the median, the dotted line within the box marks the mean, the error bars indicate 90th and 10th percentiles and the dots indicate 5th and 95th percentiles. Different lower-case letters indicate significantly different values among degradation classes within a given species while different upper-case letters indicate significantly different values among species within a given degradation class following ANOVA and Tukey's HSD post hoc tests ($p < 0.05$). One observation was excluded from the analysis (erroneous wood density, $n = 64$ in black spruce). Sample sizes (n) are the same than in Fig. 4, excepted for Bs5 where it is 12. When n included fewer than five observations, no means comparisons were conducted. Degradation classes 7 and 8 were merged because of low number of observations. There were no snags in degradation class 8 for balsam fir.

In the only other study that examined predictive morphological attributes of wood density in coarse woody debris (including snags), Yatskov et al. (2003) also found predictors of wood density to change from taxon to taxon among five major taxa from the boreal forest of Russia. As expected, wood penetrability was the common predictive variable of wood density of the four studied species. Of all variables assessed in our study, wood penetrability is the only one that relates to the internal properties of a snag. This variable emerged even though the sampling procedure only assessed penetrability of the peripheral part of the bole. Wood density can be very heterogeneous within a bole (Creed et al., 2004) and even within a single piece of wood (Boddy, 2001); our sampling procedure was not designed to detect inner decay that may occur in many species, whereas wood density measurements do. In balsam fir, the low degree of variability in wood density as compared to other tree species partly explains the poor predictive ability of the model. Indeed, wood density of almost all of the samples ranged between 0.2 and 0.4 g cm^{-3} (Angers, 2011). Accordingly, balsam fir shared the narrowest range of wood penetrability classes of all species with black spruce (only two classes after merging, Table 2). Also, a great majority of observations were concentrated in wood penetrability class 1–2 (75% of observations, Table 2), as a result of a relatively synchronous spruce budworm-related mortality (Angers et al., 2010). Bark cover was the second most represented variable in models and also emerged as an important predictor for coniferous species in Russia (Yatskov et al., 2003).

4.2. Adequacy of Imbeau and Desrochers' degradation classification system

The high inconsistency index in snags classification suggests that assigning a snag to a degradation stage may often be subjective, as it leaves a lot of room for interpretation (Creed et al., 2004; Waskiewicz et al., 2007). This situation also likely means that some criteria may not be appropriate for some species. It is surprising to note that, although initially designed for coniferous species, Imbeau and Desrochers' degradation classification system describes fairly well the degradation of the only deciduous species sampled in this study, trembling aspen. The low inconsistency index found in the first degradation stage in most species is likely due to the relatively low variation in morphological attributes found at this stage.

4.3. Linkages between Imbeau and Desrochers' degradation classification system, TSD, and wood density

In our study, relationships found between Imbeau and Desrochers' (2002) degradation stages and TSD, as well as wood density, were generally consistent with other studies. In many tree degradation classification systems worldwide, several authors have found a rough correspondence between degradation stages and TSD. Snags classified in first degradation stages are generally dead for a shorter period of time than those in more advanced stages (Mast and Veblen, 1994; Daniels et al., 1997; Huggard, 1999; Mäkinen et al., 2006; Taylor and MacLean, 2007; Aakala et al., 2008; DeLong et al., 2008). Relatively good relationships have been reported (Huggard, 1999; Campbell and Laroque, 2007; DeLong et al., 2008), but the variation in TSD within each category and overlap between categories were commonly so high (Mast and Veblen, 1994; Daniels et al., 1997; Huggard, 1999; Waskiewicz et al., 2007; Aakala et al., 2008; DeLong et al., 2008) that some authors consider degradation classifications based on external appearance of snags as poor indicators of TSD (Mast and Veblen, 1994; Daniels et al., 1997).

Most studies regarding decomposition of wood along a degradation gradient have been performed on logs (Bond-Lamberty et al., 2002; Creed et al., 2004, see Yatskov et al., 2003 for a review). Different patterns that are influenced by tree species morphology and physiology emerge from these studies, from linear wood density loss to differential decomposition rates that depend on degradation stages (Yatskov et al., 2003). Snag wood decomposition, however, has been less frequently studied, especially in the eastern boreal forest of North America (Boulanger and Sirois, 2006; Saint-Germain et al., 2007). This paucity of data is mostly because standing dead trees are in a transitory stage and generally decompose far more slowly than boles that are in contact with the forest floor (Krankina and Harmon, 1995; Yatskov et al., 2003; Boulanger and Sirois, 2006). In our study as well as in the two reported studies that examined the relationship between wood density and degradation stages in snags, results are generally similar to those regarding TSD: Degradation stages of snags provide a rough approximation of wood density but so much overlap exists between degradation stages (Mäkinen et al., 2006; Saint-Germain et al., 2007) that classification systems are often reduced to two or three distinct classes, which may be of little help in the end when more precise estimations are needed. This is in large part due to the fact that a degradation classification represents a discrete tool to assess a continuous phenomenon, i.e. density loss (Creed et al., 2004), and that the range of wood densities in snags is much narrower than in logs.

In all species, relatively few snags in degradation stages 7 and 8 were observed. Many dead trees fall to the forest floor before they reach these stages, as the mechanical stability of snags usually decreases with the progression of time and snags are thus more susceptible to falling (Aakala et al., 2008). Also, in our case, stand history might explain their scarcity in jack pine. Indeed, jack pine stands were relatively young (≈80 years, Angers et al., 2010) and, as jack pine is the most fall-resistant snag species of those studied (Angers et al., 2010), few snags were old enough to have developed characteristics of later degradation stages. The same rationale applies when considering the very low representation of jack pine snags with wood penetrability class 4 (Table 2).

Snags of boreal deciduous species are generally known to deteriorate faster than coniferous species. This has been documented with respect to fall rates (i.e. the rates at which snags fall to the forest floor, Mäkinen et al., 2006) and wood decomposition rates (i.e. the rates at which snag wood loses its density; Alban and Pastor, 1993; Yatskov et al., 2003; Mäkinen et al., 2006). Mäkinen et al. (2006) also reported lower average TSD of silver birch (*Betula pendula* Roth.) snags when compared with Scots pine (*Pinus sylvestris* L.) and Norway spruce snags in each degradation stage, but did not present comparison tests. Examining the same species as in the present study, the authors found that trembling aspen snags fall (Angers et al., 2010) and decompose (Angers, 2011) more rapidly than the other conifer species sampled at LDRTF. Differences in progression rates through the degradation stages between species or groups of species were not that straightforward in the present study. As the degradation classification system that we used integrates both degradation and, indirectly, wood decomposition through penetrability class, one would expect the system to adequately expose differences between species. Nevertheless, trembling aspen did not progress faster through degradation classes with respect to TSD or density loss. This might be due to the limitation of the degradation system to express this process, but also to the high variability in TSD and wood density as well as the low number of observations in certain classes, which may have prevented clear differences from emerging.

5. Conclusion

The inclusion of multiple species in this study enabled us to highlight the differences in the response of each species throughout their degradation. Although common morphological attributes were significant predictors for the two sets of models that we developed, the combinations of predictive variables and the rates at which these attributes changed were species-specific. Our results suggest that each species exhibits an individualistic response (sensu Gleason, 1926; Whittaker, 1957) when it decomposes after its death. In this regard, the development of species-specific decay classification systems or predictive models that combine significantly related predictive variables would be beneficial to all studies where a rapid and relatively accurate approximation of TSD or residual density in snags is required.

Results from this study clearly showed that the degradation classification of Imbeau and Desrochers (2002), which is similar to many other systems, is limited in terms of its power to predict TSD and wood density. Assignment to a single degradation stage that was based on several criteria appeared to be problematic. Furthermore, only two to three classes were distinct, and these varied among species. These problems are of minor importance when rough approximations are required, but such a classification tool rapidly becomes ineffective when more precise estimations are needed and that resources limit snag sampling for crossdating or wood density measurements purposes. Species-specific models built according to significant morphological attributes do not require more time- and resource-consuming field assessments but provide continuous and as well as more precise estimates of TSD and wood density.

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