Mineralization rates and factors influencing snag decay in four North American boreal tree species

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Abstract: The rate at which the wood of dead trees decays has numerous ecological implications. Decay rates of fallen tree boles have been extensively documented. However, decay rates of snags and the factors that influence decay in snags have received much less attention, especially in boreal species of eastern North America. In this study, mineralization rates (measured as wood density loss) were assessed in snags of four boreal species: trembling aspen (*Populus tremuloides* Michx.), balsam fir (*Abies balsamea* (L.) Mill.), jack pine (*Pinus banksiana* Lamb.), and black spruce (*Picea mariana* (Mill.) BSP). Wood density and variables potentially influencing decay rates (time since death, age, average radial growth, diameter at breast height, cerambycid larvae activity, and scolytid larvae activity) were measured on discs of 207 snags in northwestern Quebec, Canada. Mineralization rates varied significantly among species. Trembling aspen exhibited a more rapid rate of loss than conifers ($k = 0.0274$). Jack pine was the second most rapid species to lose wood density ($k = 0.0152$), followed by balsam fir ($k = 0.0123$). Black spruce was particularly resistant to mineralization ($k = 0.0058$), and its wood density was not significantly influenced by time elapsed since death for the time period sampled in this study. Time since death coupled with cerambycid larvae activity was associated with lower wood densities in trembling aspen, balsam fir, and jack pine, whereas slower growth was associated with a decreased mineralization rate in black spruce.

Résumé : La vitesse à laquelle le bois des arbres morts se décompose influence plusieurs processus écologiques. Les taux de décomposition des billes au sol ont été largement documentés, mais les taux de décomposition des chicots et les facteurs qui les influencent ont reçu beaucoup moins d'attention, particulièrement dans le cas des espèces boréales des forêts de l'est de l'Amérique du Nord. Dans cette étude, nous avons mesuré le taux de minéralisation (c.-à-d. la perte de densité du bois) des chicots de quatre espèces boréales : le peuplier faux-tremble (*Populus tremuloides* Michx.), le sapin baumier (*Abies balsamea* (L.) Mill.), le pin gris (*Pinus banksiana* Lamb.) et l'épinette noire (*Picea mariana (*Mill.) Britton, Sterns, Poggenb.). La densité du bois et les variables qui pouvaient influencer le taux de minéralisation (temps écoulé depuis la mort, âge, croissance radiale moyenne, diamètre à hauteur de poitrine, activité des cérambycidés et des scolytes) ont été mesurées sur des disques prélevés sur 207 chicots dans le nord-ouest du Québec, au Canada. Le taux de minéralisation différait significativement selon l'espèce d'arbre. Le taux de minéralisation du peuplier faux-tremble était plus élévé que ceux des conifères ($k = 0,0274$). Le pin gris occupait le deuxième rang ($k = 0,0152$), suivi du sapin baumier ($k = 0,0123$). L'épinette noire s'est révélée particulièrement résistante à la minéralisation ($k = 0,0058$) alors que la densité de son bois n'était pas significativement influencée par le temps écoulé depuis la mort durant la période à l'étude. Le temps écoulé depuis la mort et l'activité des cérambycidés étaient associés à une densité du bois plus faible chez le peuplier faux-tremble, le sapin baumier et le pin gris, alors que la croissance plus lente de l'épinette noire était associée à des taux de minéralisation plus lents.

Introduction

In boreal ecosystems, the estimation of decay rates in fallen tree boles has received extensive attention, particularly in northern Europe (Næsset 1999; Yatskov et al. 2003; Mäkinen et al. 2006). The decay of snags (i.e., standing dead trees), in contrast, has been less frequently studied, especially for species occurring in the eastern boreal forest of North America (Boulanger and Sirois 2006; Saint-Germain et al.

2007). This apparent lack of interest may be, in part, because standing dead trees are in a transitory state and generally decay far more slowly than boles in contact with the forest floor (Yatskov et al. 2003; Boulanger and Sirois 2006). Together with tree mortality and snag fall rates, decay rates of snags represent, however, an important parameter of forest ecosystem dynamics because dead trees provide habitat for many organisms (Harmon et al. 1986; Saint-Germain et al. 2007; Drapeau et al. 2009). Furthermore, wood density influences

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breakage susceptibility and, therefore, plays an important role in snag dynamics (Basham 1991). Finally, because of their slow decay rates, snags also represent important slow-released or stored carbon and nutrient pools (Bond-Lamberty et al. 2002; Boulanger and Sirois 2006).

Decay rates of dead wood are often examined as a function of time since death (Lambert et al. 1980; Boulanger and Sirois 2006; Brais et al. 2006), but several interacting parameters have been found to influence decay rates and can be roughly divided into three categories: the substrate itself, environmental conditions, and decomposer organisms. Tree species, time since death, size, age, decay status at time of death, wood nutrients, and concentrations of organic compounds, together with paths of entry for fungi such as wounds or branch stubs, have all been identified as substrate parameters affecting decay rates to some extent (Harmon et al. 1986). Growth rates may also be influential, as chemical properties and wood anatomy can delay or slow down mineralization rates in slowly growing trees (Rayner and Boddy 1988). Environmental conditions that influence wood decay include temperature, humidity, slope, elevation, and contact with the forest floor (Erickson et al. 1985; Harmon et al. 1986; Næsset 1999). The composition of the decomposer community and interactions among decomposer species, which consist mainly of fungi in boreal ecosystems, can also affect decay rates (Harmon et al. 1986; Edmonds and Eglitis 1989).

The variables that influence decay in snags are likely to be different from those that influence downed woody debris, particularly in regard to the environmental context and the community of decomposer organisms. For instance, moisture content is more limiting in standing dead trees than in boles in contact with the forest floor, which in turn may influence the composition and activity of the decomposer community (Erickson et al. 1985; Harmon et al. 1986). The same argument applies when considering different parts of the bole: as temperature and humidity conditions close to the soil might favour biological activity responsible for wood decay and ground proximity might favour fungi colonization, one could expect higher decay rates at the base than in more distal parts of the bole (Tarasov and Birdsey 2001; Shorohova et al. 2008). Other agents such as saproxylic insects may also play an important role in wood decomposition of snags. Wood borers are particularly active in dead trees in boreal forest ecosystems (Saint-Germain et al. 2007). These agents have been suggested as decay accelerators because of the galleries that they excavate in the wood (Rayner and Boddy 1988; Edmonds and Eglitis 1989; Zhong and Schowalter 1989).

In this paper, we document mineralization rates of snags of four commonly occurring species in the northeastern North American boreal forest, i.e., trembling aspen (*Populus tremuloides* Michx.), balsam fir (*Abies balsamea* (L.) Mill.), jack pine (*Pinus banksiana* Lamb.), and black spruce (*Picea mariana* (Mill.) BSP). More specifically, for each tree species, our objectives were (*i*) to assess mineralization rates based on loss of wood density with time, (*ii*) to compare mineralization rates at the snag base and at breast height (1.3 m), and (*iii*) to assess the influence of factors related to the tree itself (time since death, size, growth, age) and to the activity of two wood-boring insect groups (cerambycids and scolytids).

Methods

Study area

The study was conducted in northwestern Quebec (Canada) in the transition zone between 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′N–48°29′N, 79°26′W–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, paper birch, and trembling aspen dominate. The disturbance regime includes recurrent wildfires (Dansereau and Bergeron 1993) and periodic spruce budworm (*Choristoneura fumiferana* [Clem.]) outbreaks (Morin et al. 1993).

For black spruce, sampling was conducted in coniferous forests 120 km further north (49°25′N–49°50′N, 79°18′W–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).

Detailed stand characteristics including tree composition, stand age, past harvesting activities, snag density, species-specific annual mortality, and snag fall rates are provided in Angers et al. (2010).

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 × 20 m plot was established in which every snag was identified. These were trees without green foliage that were at least 1.3 m tall and had a diameter at breast height (DBH) ≥ 5 cm. Additional snags were sampled in the surroundings of the plots to increase the number of samples of large-diameter stems and likely old snags based on their visual aspect (short broken bole, little bark remaining, soft wood). A total of 207 snags were sampled (Table 1). Characterization of snags included species, DBH (±0.1 cm), and activity of cerambycid, as well as scolytid larvae Cerambycidae (Coleoptera) and Scolytinae (Coleoptera: Curculionidae). These two groups of wood-boring beetles were selected because they are common xylophagous insects

Table 1. Characteristics of sampled snags.

Species	TSD (years)	DBH (cm)	Age (years)	Growth (cm·year^{-1})	SCOL activity (holes·m^{-2})	CER activity (holes·m^{-2})
Trembling aspen	8.6±0.9	16.6±1.0	63.9±2.8	0.26±0.00	53.8±22.4	9.5±2.5
($n = 50$)	(1–25)	(7.8–34.3)	(68–323)	(0.14–0.50)	(0–986.1)	(0–61.0)
Jack pine	17.5±1.5	14.3±0.8	53.9±1.6	0.26±0.01	31.1±8.0	17.2±4.4
($n = 37$)	(2–39)	(7.1–29.3)	(38–72)	(0.18–0.46)	(0–178.2)	(0–121.6)
Balsam fir	18.3±0.8	18.6±0.8	63.9±2.3	0.30±0.01	251.7±102.9	30.0±3.2
($n = 57$)	(4–31)	(6.1–33.4)	(37–170)	(0.11–0.55)	(0–5615.3)	(0–102.9)
Black spruce	16.4±1.4	12.2±0.5	156.5±5.5	0.08±0.01	13.2±6.0	6.6±2.6
($n = 63$)	(3–65)	(5.7–23.6)	(39–126)	(0.04–0.11)	(0–332.2)	(0–149.8)

Note: Values are expressed as mean ± SE (range). TSD, time since death; DBH, diameter at breast height; SCOL, scolytid larvae activity; CER, cerambycid larvae activity.

of boreal forests (Saint-Germain et al. 2007) and because their activity is easily identifiable based on the size, shape, and angle of the entry holes that they create (Vallentgoed 1991). Cerambycid larvae activity (CER) was measured as the density of entry and exit holes per unit area between 1 and 1.3 m in height along snags (holes·m^{-2}). Scolytid larvae activity (SCOL) was measured similarly, but for exit holes only.

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 (*i*) reduced the risk of crossdating failure due to advanced decay, (*ii*) validated year of death with multiple crossdated sections, and (*iii*) increased capture of the last ring produced, as growth rings may be partial or absent along the bole in the last years of life 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.

Sample manipulations

In this study, mineralization rates are expressed as wood density loss and were mostly due to respiration and leaching (sensu Harmon et al. 1986). Fragmentation was likely of minor importance as no external bole fragmentation occurred in bole sections where samples were taken. We assumed that fragmentation by invertebrates (Harmon et al. 1986; mainly cerambycid larvae) represented a negligible proportion of the sample volumes.

Following tree death, wood moisture often decreases in snags and fluctuates with environmental conditions (Johnson and Greene 1991; Boulanger and Sirois 2006). To avoid any bias related to influence of wood moisture on volume, we calculated sample volume on a dry-mass basis. In living trees, basic specific gravity (green volume, dry mass) is 7%–12% lower than dry specific gravity (dry volume, dry mass; Jessome 1977) for the studied species. As moisture content is usually lower in snags than in trees, density values presented in this study are likely to be somewhat higher than those from other studies presented on a green volume basis, but not as much when compared with live wood density.

Only cross sections collected at base and breast height of snags were used for density measures. They were oven-dried at 60 °C and weighed to the nearest 0.01 g until mass 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.

Tree-ring analysis

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 was 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. Cross sections from only one snag (trembling aspen) could not be successfully crossdated. Time since death (TSD, years) was calculated as the difference between the year of sampling and the year of death. Tree age (years) was usually assessed as the difference between year of death and year of production of the innermost ring at base height. When the inner part of the bole was decayed at base height, we estimated the number of missing rings based on averages made on discs taken at the base where all rings were visible. Average annual growth (growth, cm·year^{-1}) was measured as DBH/age.

Data analysis

The negative exponential model has been the most widely used in the literature to describe changes in dead wood den-

Fig. 1. Linear relationship between wood density and time since death (TSD) at the tree base (+, solid line) and at breast (●, broken line) height (Ht). Results from repeated-measures analysis of variance are presented in the upper right corner. Line slopes (*m*) are indicated.
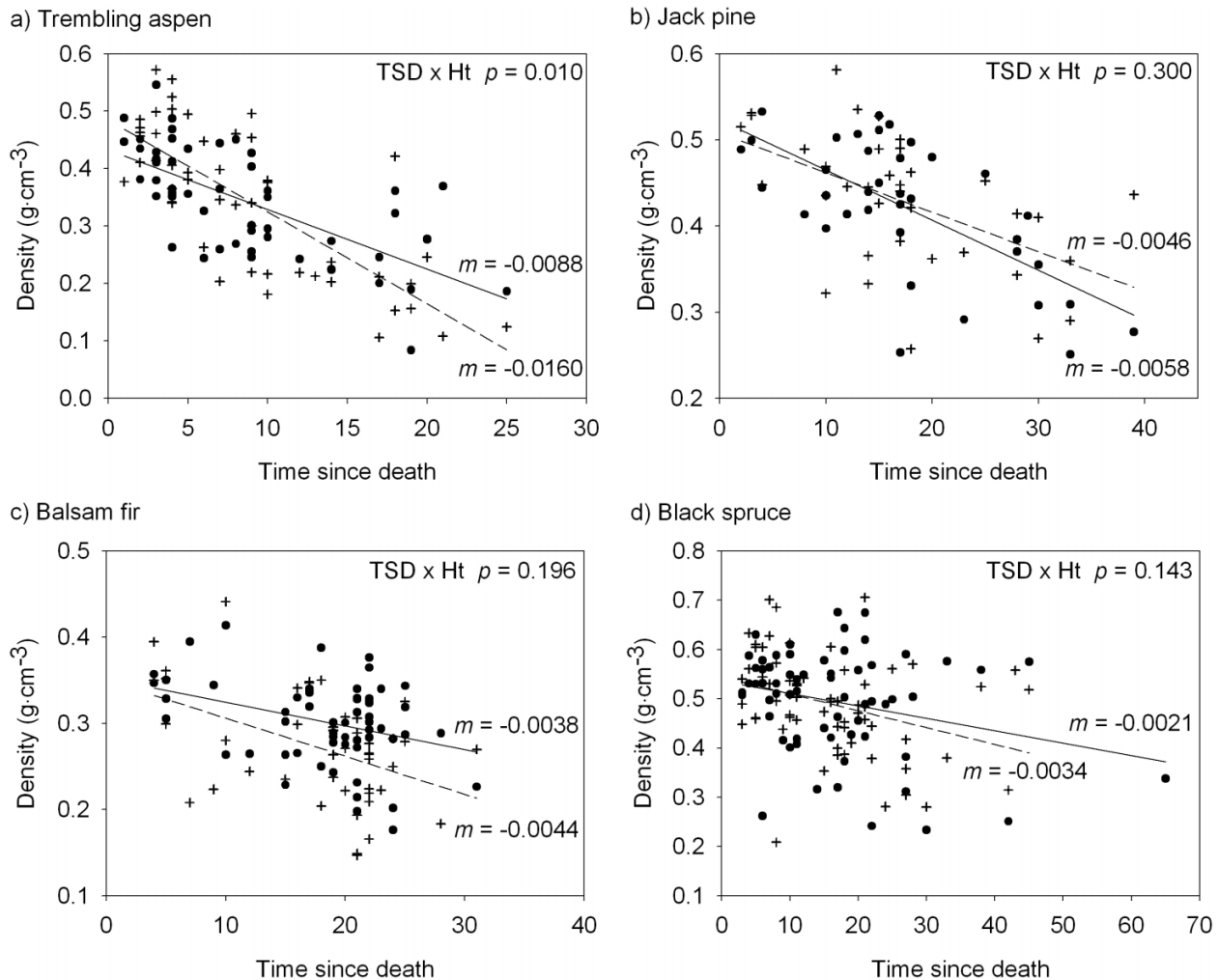
sity over time since tree death (e.g., Foster and Lang 1982; Yatskov et al. 2003; Brais et al. 2006):

$$[1] \qquad Y_t = Y_0 \, \mathrm{e}^{-kt}$$

where Y_t is wood density (g·cm^{-3}) t years after death, Y_0 is initial wood density, and k is the mineralization rate constant (year^{-1}) (Olson 1963). Despite some concerns about its ability to adequately represent mineralization in some cases (Laiho and Prescott 2004), this model provides the k constant that refers to the rate of mass loss each year, which is the typical benchmark used in most studies that compare mineralization rates.

The simple linear model has also been employed to describe decay, although to a lesser extent (e.g., Graham and Cromack 1982):

$$[2] \qquad Y_t = Y_0 + mt$$

where Y_t, Y_0, and t are as previously defined, and m represents the fraction of initial mass that is lost each year.

For each species separately, we first used both the negative exponential model and simple linear model, using the samples collected at breast height. In both cases, we added site

as a random effect to account for the between-site variance. Then, as wood density loss was well represented by the simple linear model in all species (see results), further analyses were based on that model. To assess if mineralization rates were different between species, analysis of covariance (AN-COVA) was used on wood density. To assess if mineralization rates were different between breast height and the base of snags, we used repeated-measures analysis of variance because of the nonindependence of those two measures.

Given verified or suggested relationships published in the literature (e.g., Edmonds and Eglitis 1989; Yatskov et al. 2003; Edman et al. 2006), we assessed the influence of six variables on wood mineralization (TSD, DBH, age, growth, SCOL, and CER; see Table 1) by building a series of models using multiple linear regressions. The rationale of model construction was based on the potential biological influence of variables on wood mineralization. For all modelling analyses, we used wood density at DBH. Because TSD was a significant factor influencing mineralization according to simple linear models (see Results), we considered it alone and included it in all models. DBH, age, and growth are tree-level characteristics that are determined by tree life history. Models including these individual variables were tested, as well as

Table 2. Mineralization rates of linear and negative exponential wood decay models.

Species	Linear model			Negative exponential model		
	$m \pm$ SE	p	r^2	$k \pm$ SE	P	r^2
Trembling aspen	-0.0088 ± 0.0002a	<0.001	0.494	0.0274 ± 0.0007	<0.001	0.510
Jack pine	-0.0058 ± 0.0002b	<0.001	0.564	0.0152 ± 0.0005	<0.001	0.537
Balsam fir	-0.0038 ± 0.0002c	0.006	0.283	0.0123 ± 0.0006	0.010	0.250
Black spruce	-0.0021 ± 0.0002	0.089	0.164	0.0058 ± 0.0003	0.038	0.062

Note: For linear model slopes (m), all values differed significantly among species ($p < 0.05$) according to ANCOVA. Black spruce was not included in species comparisons as its site conditions differed greatly from the others.

Table 3. Parameters associated with wood decay according to multimodel inference.

Species	Parameter	Model-averaged estimate	Unconditional SE
Trembling aspen ($n = 50$)	TSD	−0.0078	0.0020
	CER	−0.0013	0.0006
Jack pine ($n = 37$)	TSD	−0.0053	0.0011
	CER	−0.0009	0.0004
Balsam fir ($n = 57$)	TSD	−0.0024	0.0010
	CER	−0.0007	0.0002
Black spruce ($n = 63$)	Growth	−1.4258	0.6499
	DBH	−0.0080	0.0036

Note: TSD, time since death; CER, cerambycid larvae activity; growth, average growth; DBH, diameter at breast height.

models including combinations of them. Because growth is derived from DBH and age and is therefore strongly correlated to those variables, we did not include growth in the same models as age and DBH. Wood-boring insect effects (SCOL and CER) were considered separately. Finally, we ensured that models generated from standard least-square and stepwise (forward and backward) regressions were already included in the series of models and were added if not, as well as the null and full models. Two full models were tested to assess the effect of growth, as well as DBH and age. In jack pine, TSD and age were highly related to one another because all trees originated from the same postfire cohort. For this reason, models including those two variables were excluded. Prior to all regression models, assumptions of normality and homoscedasticity were verified. In black spruce, wood density data was squared to meet normality. A variance inflation factor (VIF) was also computed for each predictor to ensure that there was no collinearity between explanatory variables that were entered together in the models.

Akaike's information criterion (AIC) was then used to select the best model, i.e., the most simple and parsimonious among the candidate models (Burnham and Anderson 2002). Given that the sample size (n) for each species was rather small relative to the number of parameters K (i.e., $n/K < 40$), the second-order Akaike information criterion (AIC$_c$) was used, as expressed by

$$[3] \quad \text{AIC}_c = -2(\log - \text{likelihood}) + 2K \\ + [2K(K+1)/(n-K-1)]$$

where K is the number of parameters in the model, including the intercept and variance.

When several models competed for the topmost rank among the candidates (ΔAIC$_c$ < 2), indicating uncertainty regarding the best model, we used multimodel inference (Burnham and Anderson 2002). To assess the magnitude of a given variable's effect, we computed a weighted average of the re-

gression coefficients of that variable for all models that included it. Model-averaged estimates and unconditional standard errors were generated and used to build a 95% confidence interval.
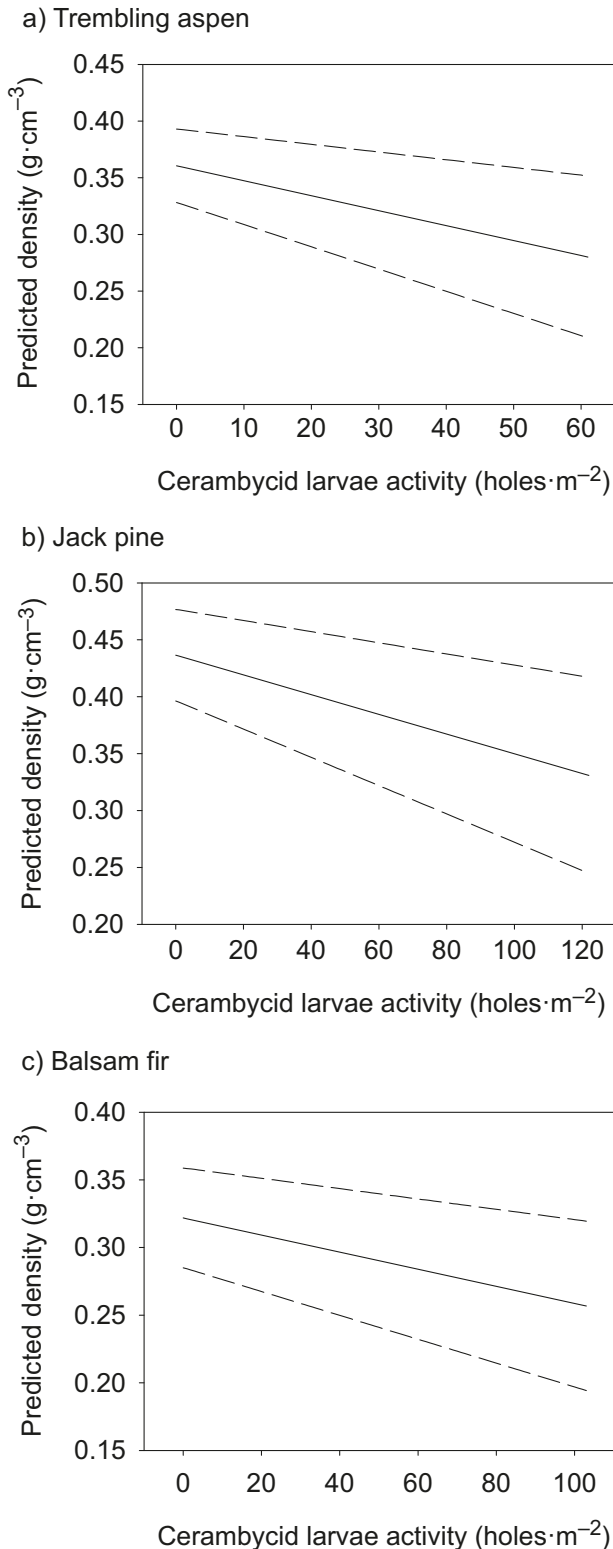
Results

The range and distribution of snag ages changed from species to species and were related to stand dynamics, disturbance history, and snag fall rates (Angers et al. 2010). Trembling aspen snag recruitment was mainly caused by self-thinning and senescence. As that species was the least persistent as a snag, the time frame for calculation of mineralization rates was limited to 25 years (Fig. 1). Jack pine mortality was relatively constant through time, and the time frame covered almost 40 years. In balsam fir, the 1970–1987 spruce budworm outbreak (Morin et al. 1993) was responsible for a large fraction of balsam fir mortality, as suggested by the high number of trees that had died ~20 years ago. Black spruce mortality was relatively constant over the last 30 years with some old snags (≥30 years old) still standing.

Mineralization rates

Regardless of model type (linear or negative exponential), wood density decreased significantly with time since death for all tree species sampled at LDRTF ($p < 0.05$; Table 2; Fig. 1), although stronger in trembling aspen and jack pine ($r^2 > 0.49$, linear models) than in balsam fir ($r^2 = 0.28$). Differences between linear and negative exponential models were so slight for these species (the difference in r^2 was always < 0.03) that they can be considered equivalent. This similarity indicates that the populations of snags studied experienced a relatively constant loss of wood density for each time interval for the time periods sampled in this study.

In black spruce, density was not significantly influenced by TSD according to the linear model. The negative expo-

Fig. 2. Contribution of cerambycid larvae to wood mineralization in (*a*) trembling aspen, (*b*) jack pine, and (*c*) balsam fir. Linear regressions presented were built with TSD kept constant at mean TSD for each species. Broken lines indicate 95% confidence intervals.

Fig. 3. Relationship between growth and squared wood density in black spruce. Broken lines indicate 95% confidence intervals.
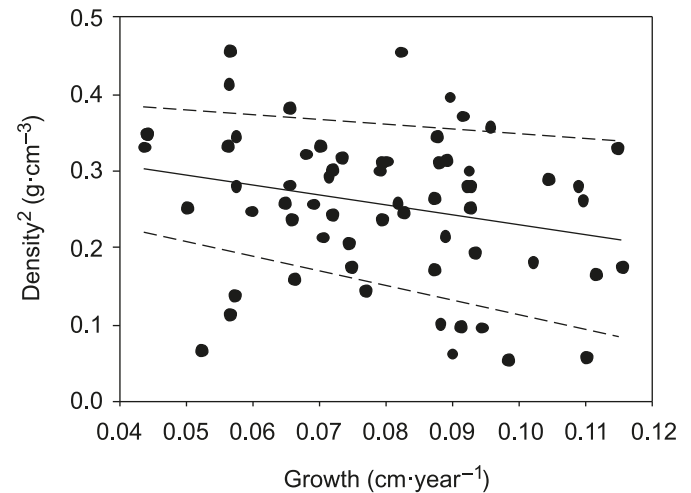
old, 20 years older than the second oldest snag) was removed.

Mineralization rates, whether represented by a negative slope in linear models (absolute value of *m*) or a mineralization rate constant in the negative exponential model (*k*), were fastest in trembling aspen, followed by jack pine and balsam fir (Table 2). ANCOVA on linear models indicated that the slope of trembling aspen was significantly steeper compared with that of the conifers. The jack pine mineralization rate was higher than that of balsam fir. As site conditions in black spruce stands differed from those of the other species (see Discussion), direct comparisons of mineralization rates can be misleading.

Loss in wood density also progressed with time since death at the base of the snag in every species (Fig. 1), but mineralization rates were not significantly different from those recorded at breast height in all coniferous species. In aspen, however, mineralization rates were significantly greater at the tree base than at breast height.

Factors associated with mineralization rates

Trembling aspen, jack pine, and balsam fir models all included TSD and CER as the most influential factors affecting wood mineralization. In all cases, TSD was clearly the most important factor. Increased cerambycid larvae activity was associated with lower wood densities but was three to six times less influential than TSD (Table 3; Fig. 2). The three species presented at least three competitive models that included other variables, but multimodel inference revealed that these additional variables did not add significant additional information regarding changes in wood density.

In black spruce, results from Akaike model selection revealed that of the five variables included in competing models, only growth, and to a much lesser extent DBH, influenced wood mineralization. Snags with slow growth and smaller DBH (Tables 1 and 3; Fig. 3) tended to decompose more slowly. As suggested by the very weak relationship between TSD and wood density, TSD did not emerge as a variable of influence in black spruce when compared with models that included other explanatory variables.

nential model, although indicating a significant influence of TSD, was very weak ($r^2 = 0.062$), and the decay rate did not significantly differ from 0 when the oldest snag (65 years

Table 4. Reported decomposition rates from other studies.

Species	Reference	k	m	Type of deadwood
Trembling aspen	This study	0.0274	–0.0088	Snags
	Alban and Pastor 1993	0.080		Logs
	Brais et al. 2006	0.060		Logs
	Miller 1983		–0.022	Logs
Jack pine	This study	0.0152		Snags
	Alban and Pastor 1993	0.042		Logs
	Brais et al. 2006	0.020		Logs
Balsam fir	This study	0.0123	–0.0038	Snags
	Lambert et al. 1980	0.0299		Logs
	Foster and Lang 1982	0.029		Logs
Black spruce	This study	0.0058	–0.0021	Snags
	Bond-Lamberty et al. 2002; Bond-Lamberty and Gower 2008	≈0.025		Snags and logs

Discussion

Mineralization rates of snags

Mineralization occurred in three out of the four snag species that we studied. We found little comparable information on snag mineralization rates for the studied species. The only mineralization rates that have been reported for snags were for trembling aspen and black spruce. In the same region, Saint-Germain et al. (2007) found results similar to those obtained in our study. Both tree species showed a significant negative linear relationship between wood density and time since death, and snags in trembling aspen decreased in density at a significantly faster rate ($m = –0.00746$) compared to black spruce ($m = –0.00319$; M. Saint-Germain, personal communication). In fire-killed black spruce snags, Boulanger and Sirois (2006) estimated a mineralization rate (k) of 0.00063, and this value did not significantly differ from 0 along a 29-year-long chronosequence. Their results were likely influenced, however, by differing disturbance, environmental, and geographical contexts that would impede direct comparison with our study.

Whether or not mineralization is detectable in snags seems to vary with both tree species and location. In boreal species, snag mineralization can be minimal, as wood density does not significantly change as a function of time (Johnson and Greene 1991; Yatskov et al. 2003; Boulanger and Sirois 2006). Other studies have shown that mineralization is detectable but it is slow (Yatskov et al. 2003; Saint-Germain et al. 2007).

As all snags were detected in the field and only one snag could not be crossdated, changes in wood density presented in this study represent the best possible estimation of the mineralization process occurring in standing dead trees given the methodological approach selected. However, as wood density influences breakage susceptibility (Putz et al. 1983; Basham 1991), more rapidly decaying snags might have fallen before we had a chance to sample them. This likely introduces an underestimation bias in mineralization rates, particularly for old snags (Storaunet and Rolstad 2002, 2004).

It is generally acknowledged that downed logs decompose faster than snags (Johnson and Greene 1991; Yatskov et al. 2003; Boulanger and Sirois 2006; but see birch in Yatskov et al. 2003) as a result of more favourable environmental conditions such as wood moisture for decay organisms and better connections to the forest floor for microorganisms to access logs. When compared with mineralization rates of dead wood (logs, occasionally snags and logs) reported in other studies, our data indicate that snag mineralization rates are consistently slower for trembling aspen, balsam fir, and jack pine logs and for snags and logs of black spruce (Table 4).

Among the species sampled at LDRTF, mineralization rates were up to two times slower for conifers than for trembling aspen. Mineralization rates are known to be higher in deciduous species than in coniferous species, as has been demonstrated in species of *Betula* and *Populus* (Yatskov et al. 2003; Mäkinen et al. 2006; Saint-Germain et al. 2007). Differences in anatomical structures and chemical composition are often cited to explain this trend (Harmon et al. 1986). When compared with conifers, the high carbohydrate and low lignin contents of aspen (Peterson and Peterson 1992) make this species more susceptible to decay.

The loss of wood density in black spruce exhibited a different response to TSD. In the Akaike model selection approach, TSD was not identified as a significant factor influencing mineralization rates, suggesting that influence of TSD is minimal or, at best, secondary when other parameters are considered for black spruce (see below). This was supported by the linear and negative exponential models results.

Modelling mineralization rates of dead wood

When modelling dead wood density loss over time (logs and (or) snags), most authors have used the exponential decomposition model, i.e., a relationship that assumes that mineralization rate is constant though time (Alban and Pastor 1993; Yatskov et al. 2003; Brais et al. 2006). To a lesser extent, linear models have also been used (Lambert et al. 1980; Graham and Cromack 1982; Yatskov et al. 2003), suggesting that snags experienced a constant loss of wood density at each time interval. Some studies have reported differential mineralization rates during the process of decay: sigmoid relationship (Tarasov and Birdsey 2001; Mäkinen et al. 2006) or multiphase decay process representing periods with distinct mineralization rates along the decay process (Yatskov et al. 2003). Those fits suggest that there is a lag time of slow wood density loss before mineralization becomes effective. This can be due to the time required for the decomposer community to colonize and establish in the substrate (Means

et al. 1985). In studies in which standing and fallen woody debris have been pooled, the lag phase could roughly correspond to the period when dead trees are still standing and experience slow mineralization (Mäkinen et al. 2006).

In our study, for the time frames sampled, linear and negative exponential relationships described density loss equally well, and relationships did not suggest any shift in mineralization rates throughout the sequence. However, we only considered standing dead trees. Considering the complete range of dead wood (snags and logs), which represent a longer time scale relative to snags alone, would probably have highlighted one type of model more clearly. However, caution is required before extrapolating these relationships to logs as mineralization rates are reported to be much higher when boles are in contact with the forest floor (Yatskov et al. 2003; Boulanger and Sirois 2006).

Differential mineralization rates within a snag

Studies have shown that density can be very heterogeneous within a dead bole and even within a single piece of wood (Creed et al. 2004). In snags, Harmon (1982) reported no difference in mineralization rates at the base of stems in fire-killed snags (mostly hardwoods). However, Shorohova et al. (2008) reported higher losses in wood density for stumps compared with logs and snags in Norway spruce (*Picea abies* L.), Scots pine (*Pinus sylvestris* L.), and two birch species. In our study, the only significant positional difference was found in trembling aspen, with more rapid loss of wood density at the base of the snag than at breast height. The lack of difference for conifers may be attributable, in part, to the base of conifer trees often being impregnated with phenolic compounds that slow down decay (Tarasov and Birdsey 2001).

Factors associated with mineralization rates

In boreal ecosystems, climate is the main factor that limits heterotrophic activity and, hence, wood decay (Trofymow et al. 2002). The very low mineralization rates in snags that were observed in both our study and elsewhere are attributable to two main factors. First, because snags eventually fall, the time frame available for sampling is shorter than in logs and might not allow detection of decreasing density (Yatskov et al. 2003). Second, the low moisture content of standing dead trees limits metabolic processes that control decomposer activity, particularly that of fungi (Erickson et al. 1985; Harmon et al. 1986; Johnson and Greene 1991). Other factors influence microclimatic conditions that, in turn, influence the presence and activity of the decomposer community and, therefore, mineralization rates.

Saproxylic insect colonization

A relationship between saproxylic insect colonization and wood mineralization has often been suspected but has rarely been quantified. In our study, the multimodel inference approach indicated that the activity of cerambycids, but not that of scolytids, contributed to wood mineralization. Edmonds and Eglitis (1989) found similar results in Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco). Greater influence of cerambycids than scolytids activity on decay might be due to differential impacts of the wood-boring behaviour of each group: cerambycid larvae make larger entry and exit holes, dig longer galleries, and penetrate deeper into the wood than

scolytids, thereby exposing more internal wood surface area to fungi. They may also carry different assemblages of decay agents (Zhong and Schowalter 1989).

Although fragmentation by gallery excavation of larvae likely exerts a minor effect on wood decomposition (Harmon et al. 1986; Zhong and Schowalter 1989), other aspects of this activity may more strongly influence the process. First, by penetrating the bark and (or) the wood, larvae provide access to carbohydrate resources for decomposer microorganisms such as fungi and bacteria. Second, these galleries also allow moisture to penetrate the bole, creating a more favourable environment for decomposition (Rayner and Boddy 1988; Zhong and Schowalter 1989). Lastly, insects may act as vectors of decomposer spores and directly inoculate wood (Rayner and Boddy 1988; Zhong and Schowalter 1989).

This said, the association between cerambycid larvae activity and mineralization rates found in three snag species (Fig. 2) has to be examined in the light of the colonization patterns of saproxylic insects on host trees. In conifers, colonization by cerambycids is mostly concentrated in dying or recently dead trees (Haack and Slansky 1987; Hanks 1999). The activity of cerambycids is concentrated at the beginning of the mineralization process, and it is thus likely that it may be a contributing factor in the mineralization process during the following years. In aspen, however, cerambycid larvae colonize snags in middle to late stages of decay, when wood density has already significantly decreased (Saint-Germain et al. 2007). In this situation, the association observed between higher cerambycid larvae activity and lower wood density (Table 3; Fig. 2) more likely reflects the colonization habitat requirements of cerambycid than a causal relationship with regard to snag mineralization.

Growth and DBH

Negative, positive, and insignificant correlations between diameter and dead wood decay rates have been documented in the literature. The vast majority of studies have concluded that large-diameter woody debris decay more slowly than smaller diameter material (Means et al. 1985; Harmon et al. 1986; Mäkinen et al. 2006). This relationship has mainly been highlighted in large-diameter trees but is more rarely observed in ecosystems with intermediate- or small-diameter trees (Foster and Lang 1982; Johnson and Greene 1991; Angers et al. 2010). In our study, this diameter effect was not detected given the relatively narrow DBH range that was measured for all tree species (Angers et al. 2010).

In black spruce, growth was the factor most strongly influencing mineralization (Table 3), with slowly grown trees being more resistant to decay than others. However, this result may be specific to sites where growth is strongly limited by climatic and edaphic conditions. In our study, black spruce was located in paludified and, therefore, very low productivity stands (Simard et al. 2007). This low productivity translates into slow growth, as individuals commonly sustained periods of growth for several years with radial increments of less than 1 mm·year^{-1} (Table 1). Slowly grown wood has a high density, with a high latewood-to-earlywood ratio and, thus, a higher concentration in lignin. This is often correlated with higher concentrations of defensive compounds, lower concentrations of nitrogen and amino acids, and lower porosity of the wood that limits penetration of fun-

gal hyphae through the tissue (for a review, see Edman et al. 2006). Lower rates of wood density loss in slowly grown wood were also found for *Picea abies* (Edman et al. 2006). Finally, within our low productivity stands, the slow growth of trees is linked with correspondingly smaller trees, which likely explains the counterintuitive relationship that we obtained between black spruce DBH and mineralization in which trees with smaller DBH decayed more slowly than larger ones.

Conclusion

Results from this study clearly show that most tree species did experience mineralization while standing dead. Snags can experience a considerable decrease in wood density, sometimes by as much as half their initial value, and still maintain enough mechanical resistance to remain upright. In addition, although they may share similar environments, snags of different tree species responded in an individualistic manner to mineralization. Our results also show that mineralization is not only influenced by the postmortem history of snags (time since death), but also by features acquired while the tree was living (growth).

The microclimatic context in which dead trees decompose also seems to be an important factor to consider and could explain why some studies have observed mineralization at the snag stage while others have not (Johnson and Greene 1991; Yatskov et al. 2003). In this study, only a limited number of factors were considered, whereas the main agents of decay, fungi, were not. Further studies are needed to understand more thoroughly the mineralization process in snags, particularly with regards to biotic decomposer agents such as fungi.

Acknowledgements

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