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Standing dead trees and their decay-class dynamics in the northeastern boreal old-growth forests of Quebec

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Abstract

In unmanaged boreal forests standing dead trees are an important component of stand structure, but knowledge on their quantities and dynamics is limited. We characterized the populations of standing dead trees, and modeled their decay-class dynamics in the northeastern boreal old-growth forests of Quebec, Canada. Using 40 m × 400 m plots, we sampled five *Picea mariana*-dominated, five mixed *P. mariana-Abies balsamea*, and five *A. balsamea*-dominated stands. We classified dead trees into five decay classes, extracted sample disks, and crossdated the year of death of 190 trees. Mean times since death in each decay class were used to construct a matrix model for transition dynamics between the classes. Standing dead trees were abundant in all stands, but with large between-stand variation (density, 89.4–229.4 trees ha^{-1}; volume, 8.3–49.2 m^3 ha^{-1}). On average, dead trees represented 21.4% of the number of all standing trees in *P. mariana*-dominated stands, 34.0% in mixed *P. mariana-A. balsamea* stands, and 33.7% in *A. balsamea*-dominated stands. Modeling indicated lower transition rates between decay classes for *P. mariana* than for *A. balsamea*. Half-life as standing dead trees was 35–40 years for *P. mariana* and 30–35 years for *A. balsamea*. Our results showed that standing dead trees are an important and long-lasting structural component of the stands studied. To retain stand structural complexity and the associated species diversity in managed forests of this region, strategies for managing standing dead trees need to be developed.

Keywords: Coarse woody debris; Standing dead trees; *Abies balsamea*; *Picea mariana*; Decay class; Transition matrix

1. Introduction

Standing dead trees are an important structural component of many forest ecosystems (Harmon et al., 1986). They are significant for biodiversity, as a large number of dead wood dependent organisms are confined to standing dead trees during their life cycle (Nilsson et al., 2001). Standing dead trees may serve, for example, as habitat for a variety of vertebrates, invertebrates, fungi, and lichens (Harmon et al., 1986; Jonsell et al., 1998; Kruys et al., 1999). In ecosystems, where trees die and remain standing they form an important part of the overall cycle of coarse woody debris, influencing the cycling and storage of nutrients and carbon (Harmon et al., 1986), and seedbed availability (Hofgaard, 1993). If the dead trees remain standing for extended periods of time, they undergo changes in their quality before eventually falling. This makes their rates of decay and fall important determinants for the quality of new logs entering the pool of down dead wood (Vanderwel et al., 2006).

In order to develop forest management strategies that mimic natural processes and structures, baseline information on standing dead trees in natural forests is needed (Kuuluvainen, 2002). As the absolute amounts of dead trees vary along with stand productivity (e.g. Sippola et al., 1998), it is important to relate the information on standing dead trees to the living trees in the same forest type (cf. Krankina and Harmon, 1995; Nilsson et al., 2002). However, considering dead wood dependent organisms and their adaptations, focusing on the relative quantities of standing dead trees is insufficient. These organisms are often confined to certain qualities of standing dead wood, of which decay stage is considered one of the most important (Jonsell et al., 1998). Thus, to fully take standing dead trees into account in forest management, information is required also on their dynamics, i.e. their longevity, and the rates at which their quality changes.

Studies on the rates of coarse woody debris decay have traditionally focused on down wood, employing Olson (1963) negative exponential model of plant litter decomposition, or its

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variants (Mackensen et al., 2003). Contrary to this, research on the dynamics of standing dead trees has focused on their population dynamics, concentrating on fall rates as a function of time since death (e.g., Keen, 1955; Cline et al., 1980; Lee, 1998; Huggard, 1999; Garber et al., 2005). As the decay stage is considered an efficient surrogate measure for the quality of a dead tree, several studies have taken into account the change in the quality of standing dead trees by estimating transition rates from one decay class to another (Raphael and Morrison, 1987; Morrison and Raphael, 1993; Vanderwel et al., 2006). Recent studies have employed similar methods also on down dead wood either by calculating transition rates (e.g., Kruys et al., 2002; Vanderwel et al., 2006) or by estimating residence times (Zielonka, 2006) in different decay classes.

Despite their recognized importance and the growing number of studies, the dynamics of standing dead trees in boreal forests is not well known. This also applies to North America where relatively few studies have reported the properties of standing dead tree populations, and even fewer have considered their processes of decay (Lee, 1998; see, however, Vanderwel et al., 2006).

The return intervals of stand-replacing fires in the northeastern boreal forests of Quebec are long (Cyr et al., unpublished). As a consequence the landscape naturally contains a high proportion of old stands. The dynamics of these stands, dominated by *Picea* spp. or *Abies balsamea*, are driven mainly by the spruce budworm (Choristoneura Fumiferana (Clemens)) outbreaks and by small-scale mortality of individual or small groups of trees (De Grandpre et al., 2000; Pham et al., 2004). In an earlier study (Aakala et al., 2007), we showed that standing tree mortality formed an important part of overall mortality in these stands. As a result, standing dead trees were abundant, distributed either randomly or occurring in smaller clusters throughout the stands. Explicit studies on the importance of standing dead trees in these ecosystems are rare (see, however, Imbeau and Desrochers, 2002; Vaillancourt, 2007). However, the importance of standing tree mortality implies that in a natural state standing dead trees are a significant structural component, thus an essential part of the overall dynamics of dead wood, and important for the maintenance of biodiversity.

In addition to the recruitment through standing tree mortality the dynamics of standing dead trees are determined by their current populations, and the rates of standing dead tree decay and fall. In this study, we aimed at describing these components of dead tree dynamics in the boreal old-growth forests of northeastern Quebec. The objectives were (1) to describe in detail the populations of standing dead trees, comparing them with characteristics of the living stand, and (2) to develop a model for decay-class dynamics of standing dead trees to assess their overall longevity and availability as a structural component of the ecosystems.

2. Materials and methods

2.1. Study areas

The study areas were located in the North-Shore region of Quebec, Canada. Field data were collected from two areas: from the vicinity of Lac Dionne (50 km north of Baie-Comeau), and from the Rivière Pentecôte area (100 km northeast of Baie-Comeau), between 49°30′–50°00′N and 67°30′–69°00′W. Dominant tree species in the areas are *Picea mariana* and *Abies balsamea*, along with *Picea glauca*. *Betula papyrifera* and *Populus tremuloides* are occasional deciduous co-dominants. Forest fires are rare (Cyr et al., unpublished data), and the main disturbances are spruce budworm and wind (De Grandpre et al., 2000; Bergeron et al., 2001; Harper et al., 2002). The study areas are described in more detail in Aakala et al. (2007).

The study was conducted in stands of three different species compositions: *P. mariana*-dominated, *A. balsamea*-dominated, and mixed stands co-dominated by these (hereafter referred to as *P. mariana* stands, *A. balsamea* stands, and mixed stands; see Aakala et al., 2007 for details on stand classification). *P. glauca* occurs as a co-dominant in the *A. balsamea* and mixed stands, but due to difficulties in distinguishing the two species in the field, they were treated as one group, referred hereafter to as *P. mariana*. The species composition was assumed to follow a site productivity gradient; *P. mariana* dominating the poorer sites, *A. balsamea* the more fertile sites, and mixed stands the intermediate sites (Bergeron and Dubuc, 1989; Boucher et al., 2006). Five stands in each species composition group were selected for field sampling, which was conducted in the summer of 2004.

2.2. Sampling

In each stand, a 40 m wide and 400 m long transect was sampled. The starting points and the directions of the transects were selected randomly, taking into account the size and shape of the stands as defined on the ecological forest maps of the Ministry of Natural Resources of Quebec. The starting points were located in the forest interior to avoid edge effects. All standing dead and living trees with a diameter at breast height (1.3 m, DBH) of over 19 cm were measured. A standing dead tree was defined as a dead tree over 1.3 m tall and standing at an angle >45° (they were distinguished from stumps less than 1.3 m tall, although both were recorded). Species, DBH, height, condition (intact or snapped), and decay class (Table 1, from Aakala et al., 2007, modified from Imbeau and Desrochers, 2002) were recorded. In addition to large trees, smaller standing dead trees with DBH between 9 and 19 cm were measured, but using 20 m as the width of the transect. The same information was otherwise recorded as for larger trees.

Sample disks from standing dead *P. mariana* and *A. balsamea* with DBH over 19 cm were extracted for determining their year of death using dendrochronological crossdating, as described in Aakala et al. (2007). An effort was made to collect three sample disks in each decay class (classes 4–7, decay class 8 being too decayed for crossdating) from the dominant species in *P. mariana* and *A. balsamea* stands, and from both species in mixed stands. Only sample disks that were deemed datable (i.e. relatively intact disks, with no apparent weathering of the outer rings) were accepted. In practice this meant that a large part of the stems in decay class 7 were rejected in the field. Samples

Table 1
Decay classes (from Aakala et al., 2007; modified from Imbeau and Desrochers, 2002)

Decay-class	
4	Recently dead, small branches and at least some foliage still attached. Wood hard
5	Foliage absent, small twigs still present. Cambium dried or absent, Wood hard
6	Some of the larger branches still present. Wood hard
7	Snapped, only largest branches possibly present. Some softening of wood detectable
8	Snapped, less than 2 m high. Wood soft

Note: In the classification, classes 1–3 are reserved for living trees, and were not used in this study. Trees in classes 4–6 may be intact or snapped, in classes 7–8 trees are always snapped.

were extracted from trees in different decay classes as they were encountered, by starting from the point of easiest access to the transect for practical reasons.

2.3. Volume calculations

Tree volumes were estimated using volume integrals of taper equations. The equations have the advantage that they provide volume estimates that account for the reduction of volume for snapped trees, without additional measurements on the diameter at snapping point. The equations of Sharma and Zhang (2004) were used for *P. mariana* and *A. balsamea*. Laasasenaho (1982) equations for Fennoscandian *Betula pendula* were used for deciduous trees. The calculations were performed using Mathematica$^{\text{TM}}$ 4.0 software. Estimating the volume of snapped trees required information on total tree height (prior to snapping), which was derived through regression between DBH and tree height, acquired from the measurements of intact living trees.

2.4. Fall rates

Estimates on decay class-specific fall rates of standing dead trees were based on the observed proportions of dead trees still standing in each decay class, compared with the combined number of stumps and standing dead trees in the same decay class. We assumed that the proportion of standing dead trees falling in each decay class remains constant, irrespective of the total number of dead trees. Standing dead trees were also assumed to eventually fall due to stem breakage, not uprooting. A standing dead tree was considered fallen when its height was reduced to below 1.3 m. Height reductions above 1.3 m, i.e. fragmentation of standing dead trees, were not considered when estimating fall rates.

2.5. Modeling decay-class dynamics

Decay-class dynamics were modeled using a matrix model similar to that of Kruys et al. (2002), by parameterizing the model specifically for standing dead *P. mariana* and *A. balsamea*. In the model of Kruys et al. (2002), a dead tree in decay class i can either (1) remain in the same class i or (2) move to decay-class $i + 1$ or (3) move to decay class $i + 2$. In this study, annual probabilities for these transitions were calculated using the mean residence times in each class (m_i). The residence times were estimated from the crossdating results by assuming time since death to represent the midpoint of a tree's residence in that class. The residence time in the first decay class (DC 4) was thus calculated by multiplying the mean time since death by two. The residence times in the other decay classes were then derived by subtracting the residence times in the previous classes from the mean time since death in that class (from the beginning to the midpoint of the class) and multiplying the result by two (from the midpoint to the end of the class).

The model of Kruys et al. (2002) was developed for coarse woody debris in general. To study the dynamics of standing dead trees in particular, the model was modified by adding the possibility of trees to leave the system by falling (stem height reduced to below 1.3 m) prior to decaying to decay class 8. This was done by adding a new class to the model, and assigning a transition probability from each decay class to the new class. The probability of a tree falling in a certain decay class was modeled by fitting a reverse sigmoid curve to the observed proportions of trees still standing in each class (survival curve), a model found suitable in earlier studies (Garber et al., 2005, and references therein). Additionally, it was assumed that trees in decay class 4 have a zero probability of falling, and stumps observed in this class are the result of trees having died snapping from the base of the stem. Thus, when the fall rates were calculated for the model, the proportion of stumps from standing dead trees in decay class 4 was considered zero, and the probabilities in decay class 5 calculated as deviation from the zero.

Decay-class specific probabilities of standing dead trees falling (r_i) were calculated from the fitted survival curve, by subtracting the proportion of fallen trees in decay class $i - 1$ from the proportion in decay class i. For annual probabilities of falling ($p_{i,f}$), the derived class-specific probability was divided by mean residence time (m_i) in that class:

$$p_{i,f} = \frac{r_i}{m_i}$$

Including the possibility of trees falling affects the transition probabilities to other classes as well, and the equations of Kruys et al. (2002) were modified accordingly. The transition probability from decay-class i to $i + 1$ was calculated as:

$$p_{i,i+1} = \frac{1 - p_{i,f}}{m_i}$$

and the probability of remaining in the same class

$$p_{i,i} = 1 - (p_{i,i+1} + p_{i,f})$$

The transitions, denoted as q in the following equations, were calculated at 5-year intervals (modified from Kruys et al., 2002):

Trees falling:

$$q_{i,f} = (p_{i,f})^5$$

Transition from class i to class $i + 1$:

$$q_{i,i+f} = \sum_{x=1}^{5} (p_{i,i+1})^{x-1} p_{i,i+1} (p_{i+1,i+1})^{5-x}$$

Remain in the same class i:

$$q_{i,i} = (p_{i,i})^5$$

Transition from i to $i + 2$:

$$q_{i,i+2} = 1 - (q_{i,f} + q_{i,i+1} + q_{i,i})$$

The equations above describe the population dynamics of the standing dead trees. To study only the decay rates, i.e. the transition rates from one class to another, the equations can be modified by removing the terms $p_{i,f}$ and $q_{i,f}$ that describe the probability of fall.

2.6. Statistical analyses

The Kruskall–Wallis test was used to evaluate the statistical significance of differences in stand type means of tree densities, basal areas, and volumes. The differences in time since death between decay classes and species were analyzed using one-way analysis of variance (ANOVA) and Tukey's test. Pearson's correlation coefficients were calculated to test the dependence of quantities of standing dead on the amount of living trees. The analyses were performed with SPSS$^{\text{TM}}$ 12.0.1, with a p-value of 0.05 set as the limit for statistical significance.

3. Results

3.1. Living trees

The mean quantities of living trees (DBH > 19 cm) on each stand type varied considerably (Table 2). However, the variation was large also within the stand types, and the differences in mean values between stand types were not significant (Kruskall–Wallis $\chi^2 = 2.34$, $p = 0.310$ for densities, $\chi^2 = 4.02$, $p = 0.134$ for basal areas, and $\chi^2 = 4.02$, $p = 0.134$ for volumes). Average tree sizes followed the same trend as mean quantities, with the smallest trees found in *P. mariana* stands (DBH = 23 cm, volume = 0.31 m^3), intermediate trees in mixed stands (DBH = 25 cm; volume = 0.35 m^3), and the largest trees in *A. balsamea* stands (DBH = 28 cm; vol = 0.47 m^3).

The species compositions were analyzed with stands pooled by stand types (Table 3). *P. mariana* stands consisted almost solely of *P. mariana* (97.9% of trees), mixed stands had almost an equal share of *P. mariana* (47.9%) and *A. balsamea* (46.3%), and *A. balsamea* clearly dominated that stand type (77.3%). Diameter distribution of living trees (DBH > 19 cm), with stand types pooled, followed a negative exponential distribution (not shown).

3.2. Standing dead trees

The shapes of the pooled diameter distributions of large standing dead trees (DBH > 19 cm) were similar to those of living trees (not shown). However, including the smaller dead trees (DBH 9–19 cm) changed the shape of the distribution from negative exponential to unimodal, with a peak occurring

Table 2
Densities, basal areas (BA), and volumes (Vol) of living (DBH1 >9 cm) and standing dead trees (DBH9 >cm) in each stand, followed by stand type means ± standard deviations

Stand	Type	Living trees density (trees ha^{-1})	BA (m^2 ha^{-1})	Vol (m^3 ha^{-1})	Standing dead trees density (trees ha^{-1})		BA (m^2 ha^{-1})		Vol (m^3 ha^{-1})	
		DBH > 19	DBH > 19	DBH > 19	DBH > 9	DBH > 19	DBH > 9	DBH > 19	DBH > 9	DBH > 19
2	*A. Balsamea*	113.1	5.7	38.3	205.1	116.3	7.4	5.6	28.8	22.8
6	*A. Balsamea*	189.4	9.3	68.1	221.9	135.6	8.8	7.3	38.2	32.8
9	*A. Balsamea*	230	19.6	168.4	104.4	79.4	8.9	8.5	41.7	40.2
14	*A. Balsamea*	351.9	22.9	181.3	220	135.0	15.6	10.9	49.1	47.8
15	*A. Balsamea*	328.8	19.7	140	183.1	150.6	11.2	10.6	49.2	47.1
3	Mixed	135.63	6.4	41.4	229.4	113.1	7.8	5.5	29.9	22.4
7	Mixed	65.6	2.8	18.1	175.1	58.8	4.9	2.8	16.7	10.3
8	Mixed	138.1	6.1	43.7	188.8	73.8	5.3	3.3	20.5	13.0
10	Mixed	243.1	11.5	91.5	125	77.5	5.1	4.2	21.1	17.6
12	Mixed	291.3	16	131.7	195	127.5	8.8	7.6	39.3	34.6
1	*P. Mariana*	117.5	4.7	34.3	134.4	23.1	2.6	0.9	12.5	4.5
4	*P. Mariana*	198.1	8.3	60.4	133.8	55.0	3.8	2.3	17.5	10.9
5	*P. Mariana*	186.9	8.5	60	204.4	59.4	5.2	2.6	22.1	11.0
11	*P. Mariana*	146.3	6.5	54.7	89.4	46.9	2.9	2.3	15.7	12.4
13	*P. Mariana*	78.1	2.9	19.6	97.6	13.8	1.8	0.5	8.3	2.6
Mean	*A. Balsamea*	242.6 ± 98.9	15.4 ± 7.5	119.2 ± 63.0	186.9 ± 48.7	123.4 ± 27.4	10.4 ± 3.2	8.6 ± 2.2	41.4 ± 8.5	38.1 ± 10.5
Mean	mixed	174.7 ± 90.9	8.6 ± 5.2	65.3 ± 45.7	182.7 ± 37.9	90.4 ± 28.9	6.4 ± 1.8	4.7 ± 1.9	25.5 ± 9.1	19.6 ± 9.6
Mean	*P. Mariana*	145.4 ± 49.5	6.2 ± 2.4	45.8 ± 18.1	131.9 ± 45.4	39.6 ± 20.1	3.3 ± 1.3	1.7 ± 0.9	15.2 ± 5.2	8.3 ± 4.4

Quantities of large standing dead trees (DBH >9 cm) are given for comparison with living trees.

Table 3
Species compositions of living trees (DBH > 19 cm), large dead trees (DBH > 19 cm), and small dead trees (DBH 9–19 cm), stand types pooled

Stand type	*A. Balsamea* (%)		*P. Mariana* (%)		*B. Papyrifera* (%)	
	No. of trees	Volume	No. of trees	Volume	No. of trees	Volume
Living (DBH > 19 cm)						
A. balsamea	77.3	70.9	15.6	23.6	7.1	14.5
Mixed	46.3	43.7	47.9	52.3	5.9	4.0
P. mariana	1.6	1.5	97.9	97.9	0.5	0.6
Large dead (DBH > 19 cm)						
A. balsamea	59.3	59.5	15.1	21.0	23.5	17.7
Mixed	39.3	40.8	34.8	37.0	24.0	20.4
P. mariana	3.2	2.9	92.1	93.0	3.2	2.1
Small dead (DBH 9–19 cm)						
A. balsamea	76.0	72.1	6.3	9.6	14.6	15.7
Mixed	51.9	45.0	23.5	33.9	23.0	19.6
P. mariana	6.8	5.3	90.8	93.0	2.4	1.7

in the diameter class 13–15 cm in *P. mariana* stands, 13–21 cm in mixed stands, and in 22–24 cm in *A. balsamea* stands.

As with living trees, the variation in standing dead tree quantities between stands was large (Table 2). *P. mariana* stands had, on average, the smallest quantities of dead trees, and A. balsamea the highest. The differences in mean quantities between stand types were not significant for the number of trees (Kruskall–Wallis, $\chi^2 = 3.50$, $p = 0.174$). However, the differences were significant for basal area and volume ($\chi^2 = 10.58$, $p = 0.005$ for basal area; $\chi^2 = 9.26$, $p = 0.010$ for volume). The average proportions of standing dead trees to the number of all standing trees (DBH > 19 cm) were 21.4, 34.0, and 33.7% in *P. mariana*, mixed, and *A. balsamea* stands, respectively.

The dependence of quantities of standing dead trees on the quantities of living trees was analyzed with Pearson's correlation coefficient (r). For tree numbers (trees with DBH > 19 cm), with all transects pooled, r was 0.66 ($p = 0.007$, $n = 15$) (Fig. 1a). Analyzed by stand types ($n = 5$ in each group), the correlation was highly significant in *P. mariana* stands ($r = 0.962$, $p = 0.009$), but not in mixed ($r = 0.63$, $p = 0.255$) or in *A. balsamea* stands ($r = 0.409$, $p = 0.494$).

When volumes were analyzed, the relationship between living and dead trees was more apparent than with tree numbers (Fig. 1b). With all 15 transects pooled, the correlation was 0.88, which was significant ($p = 0.000$). Analyzed as stand types ($n = 5$ in each group), *P. mariana* stands showed a slightly stronger correlation ($r = 0.96$, $p = 0.011$) than *A. balsamea* stands ($r = 0.907$, $p = 0.034$). The correlation in mixed stands was not significant ($r = 0.83$, $p = 0.08$).

The species composition of large standing dead trees (DBH > 19 cm) was similar to that of living trees only in the *P. mariana* stands (Table 3). In mixed and *A. balsamea* stands significant differences between species composition of living and dead trees were mainly caused by the higher proportion of *B. papyrifera* (Pearson's $\chi^2 = 155.7$, $p = 0.000$ in mixed; $\chi^2 = 300.5$, $p = 0.000$ in *A. balsamea* stands). In addition, a few *P. tremuloides* were found standing dead in *A. balsamea* stands, but none alive.

The species composition of the smaller standing dead trees (DBH 9–19 cm; Table 3) corresponded to what was expected from the stand type classification: *P. mariana* dominated *P. mariana* stands, and *A. balsamea* dominated *A. balsamea* stands. However, mixed stands had a clearly higher proportion

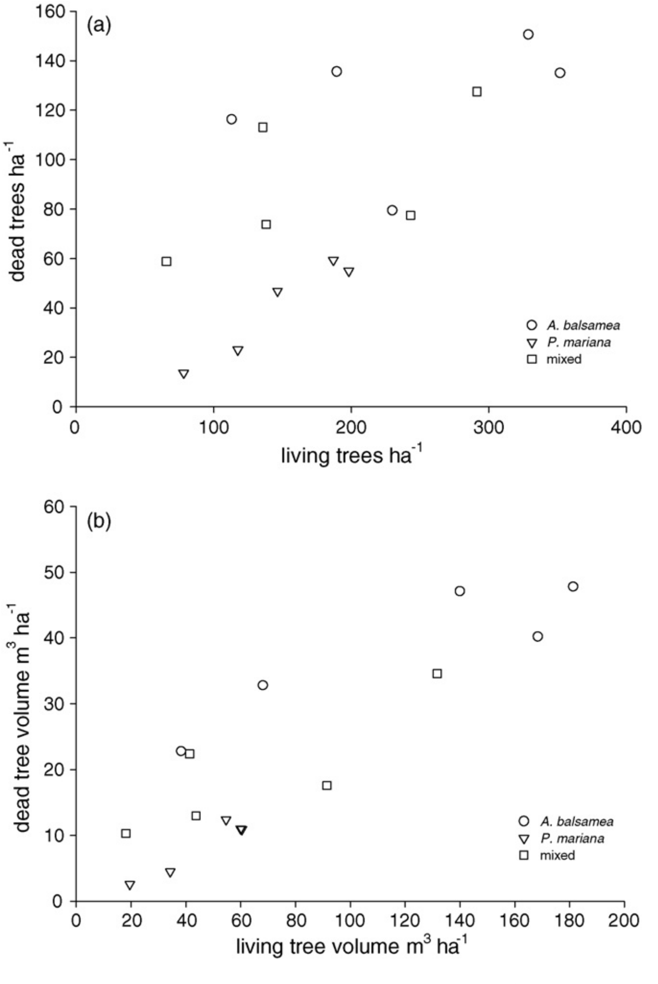

Fig. 1. Relationship between densities (a) and volumes (b) of living and dead standing trees in each stand.

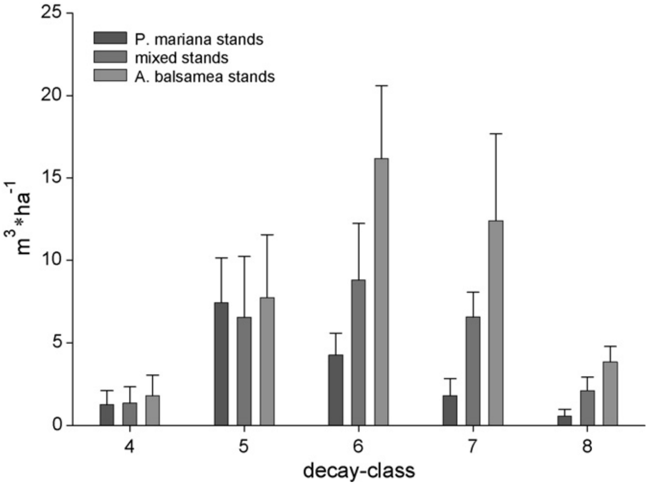

Fig. 2. Decay-class distributions of standing dead tree volume.

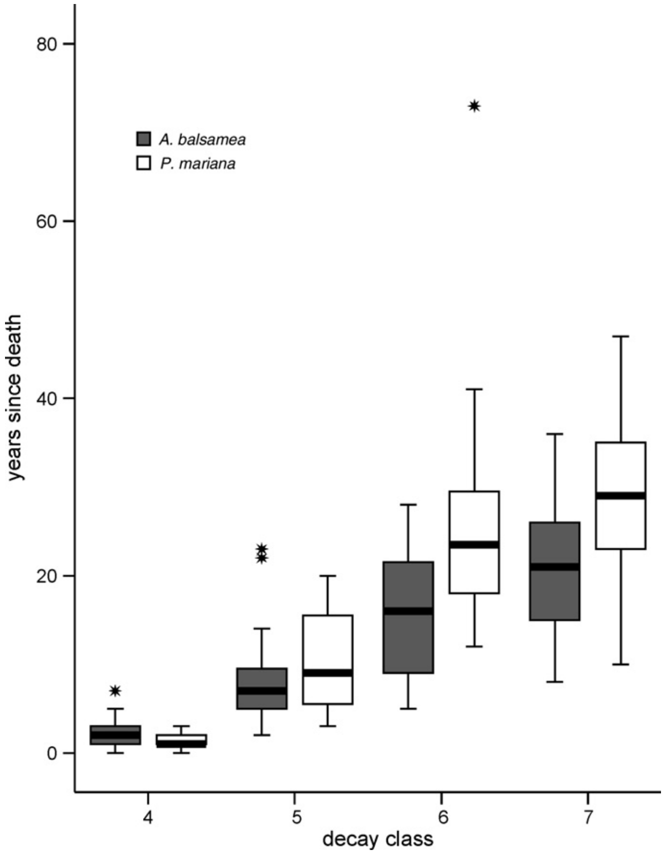

Fig. 3. Box-plot of times since death in each decay class for *A. balsamea* and *P. mariana*. Asterisks represent extreme values.

of *A. balsamea*, compared to what was found in living and large dead trees.

The decay-class distributions showed some stand-type specificity (Fig. 2). The peak in both numbers and volume occurred in *P. mariana* stands in decay class 5, with 51 and 7.5 m^3 ha^{-1}, respectively. In *A. balsamea* and mixed stands, the highest number of trees was in decay class 7, with 65 and 63 trees ha^{-1}, respectively. Volumes peaked in decay class 6, with 8.8 m^3 ha^{-1} in mixed and 16.2 m^3 ha^{-1} in *A. balsamea* stands.

3.3. Time since death

Year of death was crossdated for 190 trees. Time since death in each decay-class followed, on average, the expected trend: decay-class 4 had the shortest mean time since death, and decay class 7 the longest (Fig. 3). The variation within each class was large, but comparing each class to the neighboring classes, the results indicated significant differences between all decay classes for *A. balsamea*. For *P. mariana*, the differences between decay classes 6 and 7 were not significant (Tukey's test, $p = 0.118$). For *A. balsamea*, analysis of time since death and decay classes between samples from *A. balsamea* and mixed stands revealed no differences. The same was true of *P. mariana*. Thus, for further analyses and to parameterize the decay-class dynamics model, the samples were grouped by species (Fig. 3).

Between-species differences in times since death in each decay class were not significant in classes 4 and 5, but were significant in classes 6 and 7. In other words, standing *A. balsamea* stems reached decay classes 6 and 7 significantly faster than *P. mariana* stems.

3.4. Standing dead trees vs. stumps in decay-classes

The proportion of stumps from the combined number of stumps and standing dead trees in each decay class differed between *P. mariana* and *A. balsamea* (Fig. 4). The proportion of *A. balsamea* stumps remained relatively constant until decay class 7, whereas for *P. mariana* the proportion of stumps increased after decay class 6. Moreover, the starting level (proportions in decay class 4) differed, as very few *A. balsamea* stumps were observed, compared with 13% for *P. mariana*.

3.5. Modeling decay-class dynamics

Transition probability matrices were constructed separately for *P. mariana* and *A. balsamea*. To study the population dynamics of standing dead trees, the matrices were constructed with the probability of trees falling (Table 4; fall rates from the reverse sigmoid curve, Fig. 4). To study the rates of transition between classes, another set of matrices was constructed without trees falling (Table 5). The calculated mean residence times were very short for the trees in the advanced decay class 7, most likely due to only the least decayed part of that class being accepted for crossdating. To have a more realistic value for modeling, the mean residence time used for decay class 6 was used for decay class 7.

In the model, the between-species differences in the mean residence times of trees in each decay class caused differences in the transition rates from one class to another, and in the longevity of dead trees standing. The overall effect can be seen as generally steeper transition probability curves for faster decaying *A. balsamea*, as compared with *P. mariana* (Fig. 5, including the possibility of trees falling). The age at which the probability of remaining in the system was equal to the

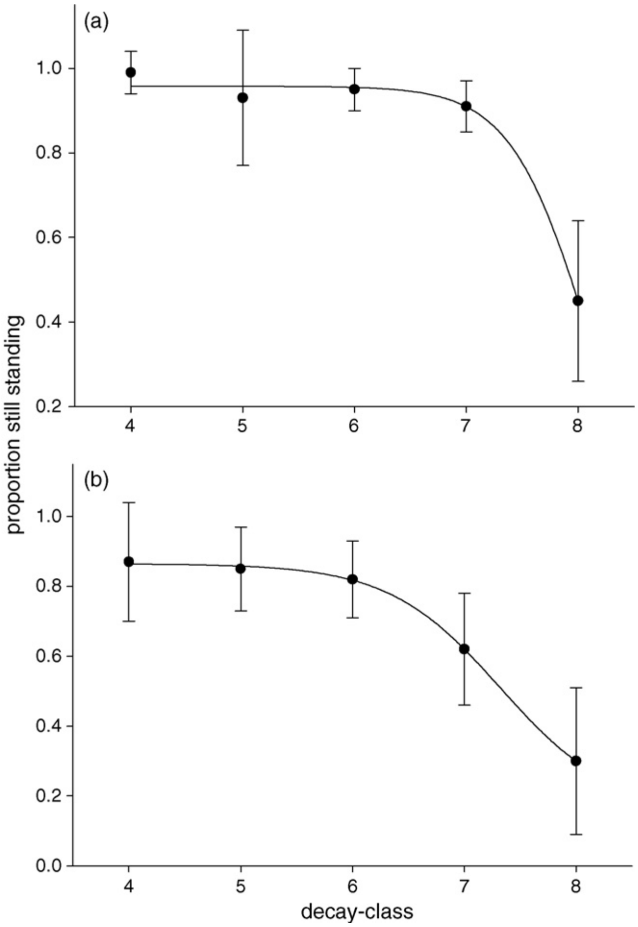

Fig. 4. Proportion of trees still standing (error bars 1 ± S.D.) of the total number of stumps and standing dead trees in each decay class for *A. balsamea* (a) and *P. mariana* (b). Solid line represents the reverse sigmoid curve fit.

probability of leaving the system (half-life) was between 30 and 35 years for *A. balsamea*, and between 35 and 40 years for *P. mariana*. The time since death at which the probability of still standing lowers below 0.01 (1%) for *A. balsamea* was reached between 70 and 75 years (after the 14th transition), whereas with *P. mariana* it was not reached until 115–120 years (after the 23rd transition).

Table 4
Transition probability matrix for 5-year intervals with the possibility of trees falling

From class	To class				
	4	5	6	7	Out
Picea mariana					
4	0.051	0.672	0.276	–	0.000
5	–	0.697	0.219	0.084	0.000
6	–	–	0.641	0.248	0.110
7	–	–	–	0.602	0.397
Abies balsamea					
4	0.343	0.442	0.214	-	0.000
5	–	0.417	0.429	0.153	0.000
6	–	–	0.540	0.304	0.155
7	–	–	–	0.470	0.529

Transitions considered biologically impossible are marked with "–".

Table 5
Transition probability matrix for 5-year intervals without the possibility of trees falling

From class	To class				
	4	5	6	7	Out
Picea mariana					
4	0.067	0.776	0.156	–	–
5	–	0.730	0.229	0.040	–
6	–	–	0.674	0.276	0.049
7	–	–	–	0.674	0.325
Abies balsamea					
4	0.343	0.447	0.208	–	–
5	–	0.427	0.445	0.126	–
6	–	–	0.569	0.339	0.091
7	–	–	–	0.569	0.430

Transitions considered biologically impossible are marked with "–".

Decay class-specific probabilities of standing dead trees falling were modeled with the reverse sigmoid curve, using the observed proportions of stumps of the combined number of stumps and standing dead trees within each decay class. When these probabilities were removed, only slight changes were observed in the modeling results (not shown). Half-life increased to 40–45 years (8th transition) for *P. mariana*. For *A. balsamea*, no clear changes occurred. The <1% probability

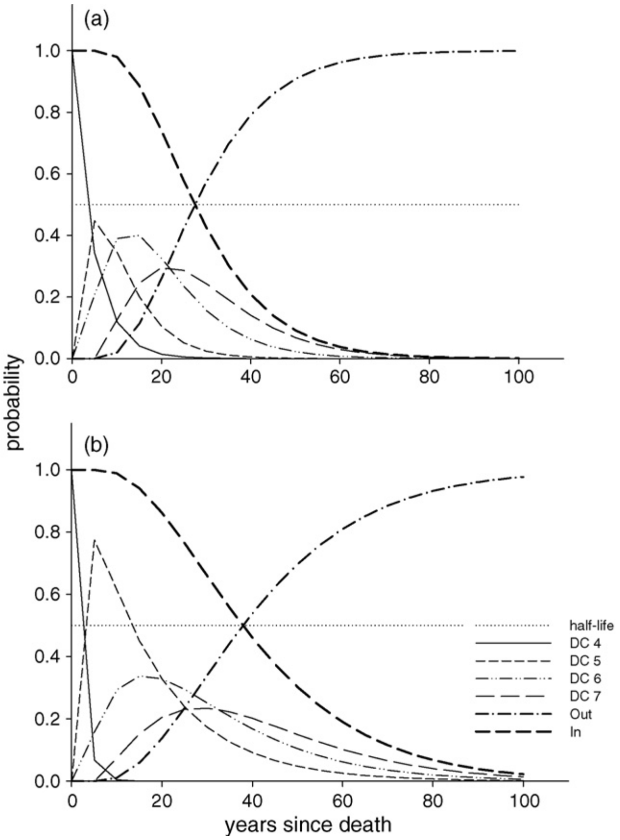

Fig. 5. Transitions between decay-classes for *A. balsamea* (a) and *P. mariana* (b). "In" and "Out" represent the probabilities of a dead tree still standing, and a probability that a standing dead tree has fallen, respectively. Horizontal dotted line represents the 50% probability of a dead tree standing.

of still residing in the system increased to 120–125 years (24th transition) for *P. mariana*, and to between 75–80 years (15th transition) for *A. balsamea*.

4. Discussion

4.1. Quantities of standing dead trees

The quantities of standing dead trees measured are in accord with the previously reported range of values for boreal coniferous forests, although volumes in the *A. balsamea* stands are among the highest found in comparable areas (reviewed by Nilsson et al., 2002). In addition, the proportion of dead trees to the number of all standing trees were clearly higher in all stand types than the 10% that has often been found in boreal old-growth forests (Nilsson et al., 2002). The last spruce budworm outbreak that began in the 1970s (Blais, 1983) explains this high proportion in mixed and *A. balsamea* stands, but the proportion was higher also in the *P. mariana* stands that generally suffer lower and more diffuse mortality from the outbreaks (MacLean, 1980; Bergeron et al., 1995). The notion by Nilsson et al. (2002) that the proportion also depends on the minimum DBH used could explain the findings here, as the minimum DBH of 19 cm in this study represents the higher end of tree sizes in the *P. mariana* stands.

The influence of the disturbance history of the stands was shown also on the dependence of standing dead tree quantities from the living trees (Fig. 1). Mixed and *A. balsamea* stands that were influenced more strongly by the last outbreak showed weaker or nonsignificant correlations between the quantities of living and dead trees. The correlation was clearly stronger in the *P. mariana* stands that had experienced more constant mortality in the past (Aakala et al., 2007).

4.2. Species and decay classes of standing dead trees

The species compositions of living and dead trees were similar in *P. mariana* stands. Previous studies on the development of these stands have shown minimal changes in species composition over time (De Grandpre et al., 2000; Harper et al., 2002). The differences between living and standing dead trees were clear in mixed and *A. balsamea* stands. The higher proportion of *B. papyrifera* among the dead trees in these two stand types is indicative of its role as transient successional species. These dead trees were obviously remnants from earlier stages of stand development, their regeneration having been unsuccessful later in the sere. Thus, in the old-growth stage, the proportion of deciduous species appears to be diminishing. However, De Grandpre et al. (2000) found that *B. papyrifera* is able to regenerate in old mixed and *A. balsamea* stands in the North Shore, thus continuing to contribute to species, and eventually to dead tree diversity.

The decay-class distributions showed some stand-type specificity (Fig. 2). The distribution peaked in *P. mariana* stands in decay class 5, whereas in mixed and *A. balsamea* stands the number of trees was highest in decay class 7. The peak occurring later in decay-stage succession in mixed and *A. balsamea* stands was likely the result of the last spruce budworm outbreak; the outbreak-killed trees had reached the more advanced stages of decay. Thus, the shape of the decay class distribution that can be observed is heavily dependent on the proximity in time to an epidemic mortality event, such as the spruce budworm outbreak. In the less decomposed classes, the quantities were smaller mainly due to the lower mortality rate afterwards, but also due to the differences in the residence times (i.e. the time-window of mortality each class represents).

4.3. Decay-class dynamics and overall standing times

P. mariana and *A. balsamea* both showed relatively similar behavior with respect to the distribution of the residence times in different decay classes out of total longevity. The residence times in the earliest decay class 4 were clearly the shortest, which is shown in the modeling results as a rapidly declining probability of occurrence for that class with increasing time since death. This was not surprising, as the needle loss and drying out of cambium (criteria for transition from decay class 4 to 5) occur relatively rapidly. The residence times in the intermediate classes 5 and 6 were clearly longer than in decay class 4, leading to less rapid changes in the probability of occurrence in these classes. In these classes the wood material was still considered hard. Thus, it appears that the condition of wood surface remains relatively unchanged for extended periods of time, which is well in line with results of earlier studies (e.g., Zielonka, 2006). Estimates on the residence times in decay class 7 are somewhat suspect because the most decayed samples from that class were rejected. Thus, the small differences between mean times since death for classes 6 and 7 are likely a sampling artifact, and, proper estimates for the residence times in decay class 7 cannot be given. Because of this, in the model the residence time in decay class 6 was used also for class 7, which means that the residence times in that class were arbitrarily increased to obtain a more realistic value.

The mean times since death in decay classes 6 and 7 were significantly different between *P. mariana* and *A. balsamea*. That the differences were observed only in the later stages of decay was probably due to too short residence times in the earlier classes for them to become visible. When only the decay rates were considered (i.e. the modeling results without trees falling) the shorter decay class residence times of *A. balsamea* led to a slightly shorter half-life compared to *P. mariana*. The larger between-species differences in classes 6 and 7 had a greater impact on the model results later, which led to larger differences in the $<1\%$ probability of still residing as a standing dead tree (Fig. 5).

The differences between the two species would indicate that species-specific properties, such as density and chemical composition of the wood material, affect the decay rates. However, as with many of the factors that influence decomposition, the results from earlier studies on the reported species-specific differences have been contrasting (Harmon et al., 1986; Mackensen et al., 2003). One reason for this is that the effects of species-specific differences on decay rates are often difficult to discern from variation in environmental conditions (Harmon et al., 1987). In a recent study in Atlantic Canada, Campbell and Laroque (2007) concluded that climatic factors are probably more important determinants for the differences in decay rates between *P. mariana* and *A. balsamea* than the species properties. In the present study, the microclimatic conditions between the open *P. mariana* stands, and under the closed canopy of the two other stand types are probably large enough to influence the rates of decay. However, as these factors were not explicitly considered, it is impossible to say whether the main determinant for the differences were due to environmental differences, or the properties of the species.

Other studies on the decay-class dynamics of standing dead trees are rare and direct comparisons not possible due to differences in the classification (e.g. Raphael and Morrison, 1987; Morrison and Raphael, 1993; Vanderwel et al., 2006). However, studies reporting total longevities of standing dead trees are more readily available. In southern boreal Russia, Krankina and Harmon (1995) estimated that dead *Picea abies* rarely stand longer than 10 years. Storaunet and Rolstad (2002, 2004) found half-lives of 22 and 26 years for Fennoscandian *P. abies* (DBH $\geq$20 cm). Lee (1998) reported half-lives of 16 years for *B. papyrifera* and 19 years for *P. glauca* and *P. tremuloides* (all with DBH $>$ 10 cm). Based on these examples, the half-lives found in the present study appear to be relatively high among those reported from boreal forests. Moreover, it should be noted that the half-lives in this study are underestimates of the total, as trees in decay class 8 were not included in the modeling, even though they were considered as standing dead wood.

The small differences in the model results without the possibility of falling illustrate the observed patterns of trees falling. Decreases in the probability of dead trees still standing occurred after reaching class 6 for *P. mariana*, and after reaching class 7 for *A. balsamea*. The reason for this was that in classes 4, 5, and 6 the wood material is still considered hard. As the wood starts to soften (criterion for transition to decay class 7), it weakens the mechanical durability of the stem, thus increasing the probability of the tree falling. That fall rates of *P. mariana* increased already in class 6 could be caused by the differing decay rates along the bole: faster decay at the base may have increased the probability of falling, although the majority of the wood material is still hard. In addition, previous studies have reported faster decaying trees to exhibit a pronounced pattern of top-deterioration and breakdown compared to more decay resistant trees (e.g. Landram et al., 2002; Hennon and McClellan, 2003). The deterioration of the top lowers the center of gravity of the tree, making it less susceptible to falling (Vanderwel et al., 2006). Such a difference between the species would explain the observed differences in fall rates. The faster decaying *A. balsamea* fragments from the top, reducing pressure on the lower stem. *P. mariana*, by contrast, remains intact longer and falls over as an entire tree.

The reliability of the used approach to determine fall rates is hampered by the difficulty in assigning decay classes to stumps that are comparable with those of standing trees. Re-measuring permanent sample plots would enable assessments of fall rates without difficulties related to classifying stumps into decay classes (e.g., Keen, 1955), but such information is rarely available. Some authors have developed other methods for assessing fall rates without the need for re-measuring plots, but these have generally relied on the assumption of constant recruitment of standing dead trees (e.g. the life-table approach of Huggard, 1999; methods presented by Storaunet and Rolstad, 2004), which was not a valid assumption in our study.

4.4. Evaluation of the decay class dynamics model

The reliability of the results of the decay class dynamics model depend on the accuracy of establishing the mean time since death in each decay class, which involves several uncertainties. First, determining the year of tree death by crossdating is subject to error. Although the crossdating success was high (190 out of 194 collected samples), it is possible that the last rings do not conform to the actual year of tree death due to lack of production of annual rings caused by the weakening of the tree prior to death. Second, when sampling a chronosequence, slower decaying trees have a higher probability of being included in the sample compared to faster decaying trees (Kruys et al., 2002). Kruys et al. (2002) devised a correction for this second bias, but it assumes constant input of dead trees (Storaunet and Rolstad, 2004), which was not a valid assumption in our study. Third, the higher number of trees killed during the years of the spruce budworm outbreak increases the probability of those years being included in the sample, but not necessarily conforming to the midpoint of time since death in that class. Because of these uncertainties, the results on the model results should be interpreted with care, and perhaps best treated as descriptive estimates. Proper generalizations and model validation for longer time periods and larger areas would require further testing with a larger (independent) data set. Despite these shortcomings, we believe that the model results provide valuable information on the dynamics of standing dead trees in the studied stand types that is useful in building a more detailed understanding of stand dynamics.

4.5. Management implications

If mimicking natural structures is a management objective, two different processes should be taken into account: First, the spruce budworm outbreaks infrequently create large amounts of standing dead trees (Blais, 1983; Kneeshaw and Bergeron, 1998; Aakala et al., 2007) that were visible as peaks in the decay-class distribution. This ‘‘pulse’’ of dead trees moves through the stages of decay, as described by the model in the present study, dampening slowly with time as the result of the trees falling. Second, outside of the episodic events, smaller-scale mortality continuously creates smaller quantities of standing dead trees (Aakala et al., 2007), apparent in the presence of trees across all decay-classes. Both of these processes need to be considered in management, as they have implications concerning the role of standing dead trees in the ecosystem. In addition, the presented model results provide forest management planning important information on how long standing dead trees in different stages of decay may act as habitat structure (cf. Campbell and Laroque, 2007). Because of their fairly long standing times, standing dead trees should also be taken into account when considering the role of forests in carbon dynamics.

5. Conclusions

This study demonstrated the importance of standing dead trees as long-lasting components of boreal old-growth forests of the North Shore region. Standing dead trees were abundant in all stand types studied, and a prominent component of stand structure. Sustaining natural structural diversity in managed forests would thus require management considerations for retention of standing dead trees.

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