



Snag degradation pathways of four North American boreal tree species

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ABSTRACT

Many studies have highlighted the importance of deadwood, whether standing (snags) or fallen, in boreal ecosystems dynamics. However, a dearth of literature exists regarding the persistence and degradation pathways of these structures in northeastern American boreal species.

Degradation pathways were examined in four tree species of the eastern boreal mixedwood and conifer forests of Canada: Trembling aspen (*Populus tremuloides* Michx.), balsam fir (*Abies balsamea* (L.) Mill.), jack pine (*Pinus banksiana* Lamb.) and black spruce (*Picea mariana* (Mill.) BSP). Sampling was conducted in unharvested forests of northwestern Québec. Discs were collected on 363 snags and logs and dendrochronological analyses conducted to determine year of death by crossdating.

Survival curves were constructed for each species and degradation pathways were documented based on the shape of the relationship, lag time if applicable (time period from death to fall onset) and half-life (time required for half the stems to fall).

Most species survival curves exhibited a reverse sigmoid function. Trembling aspen, jack pine and to a lesser extent balsam fir presented significant lag times before initiation of a period with high fall rates. Black spruce experienced more snag losses during the first years following death. Jack pine was clearly the most persistent species due to snags high resistance to fall and stem breakage. Within the range of tree diameters in our study area, diameter *per se* did not significantly influence fall probability. Differential degradation pathways of the four species translate individualistic responses that are related to species autecology. This has important implications for all ecological functions related to deadwood and should be considered when planning retention strategies of legacy trees in an ecosystem management perspective.

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1. Introduction

Deadwood is a key component in many functions and processes of forest ecosystems (Harmon et al., 1986; Jonsson and Kruys, 2001). Whether standing (snag) or fallen (log), it provides nesting, denning, perching, sheltering, breeding and foraging sites for many vertebrates and invertebrates (Thomas et al., 1979; Harmon et al., 1986) as well as germination and growth substrates for many fungi, bryophytes and vascular plants (Harmon et al., 1986; Söderström, 1988; Renvall, 1995; Simard et al., 1998). Furthermore, deadwood plays an important role 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).

Deadwood dynamics, i.e. the rate at which dead trees degrade, decompose and fall, and the factors influencing how these processes occur (e.g. tree mortality patterns, tree-, stand- and landscape-level variables), has been studied extensively in coniferous forests of the North American West Coast (e.g. Harmon et al., 1986; Raphael and Morrison, 1987; Daniels et al., 1997) and Fennoscandia (e.g. Kruys et al., 2002; Storaunet and Rolstad, 2002, 2004). In the boreal forest of eastern North America, the amount of deadwood in different forest types relative to their age, successional status or disturbance history has been quantified in several studies (e.g. Sturtevant et al., 1997; Hély et al., 2000; Harper et al., 2003). Studies on deadwood dynamics of boreal tree species in this part of the boreal ecosystem, particularly the transition from standing dead trees to logs, are, however, more recent (Lee, 1998; Garber et al., 2005; Boulanger and Sirois, 2006; Taylor and MacLean, 2007; Aakala et al., 2008) and knowledge on the dynamics of individual tree species remains largely unknown. This is particularly true for jack pine (*Pinus banksiana* Lamb.). Indeed, despite its reported longevity as a snag (Dansereau and Bergeron,

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1993), no information exists on its snag–log dynamics to our knowledge.

Snag survival, i.e. the probability of a standing dead tree to remain standing after a given time, in opposition to the fall rate, i.e. the rate at which snags fall to the ground, is a major component in understanding deadwood dynamics. From a population dynamics' perspective, the fall rate represents both loss in the snag population and recruitment in the log population. Since functions and roles of deadwood change with its status and degradation stage, quantifying patterns of degradation, particularly the fall process of standing deadwood, is a primary step in the understanding of shifts in deadwood ecological functions. Probability of survival has been described with negative exponential (e.g. Storaunet and Rolstad, 2002, 2004) or reverse sigmoid functions (e.g. Keen, 1929; Garber et al., 2005). The former is observed when the survival is constant, whereas the latter results from an initial slow fall rate period expressed by a lag time, followed by a period where fall rate is more rapid and finally levels off.

Fall may take different degradation pathways and be the result of uprooting or of single or multiple bole breakages. Many factors are implied, including species, diameter, height, cause of death, bole condition at time of death, exposure to wind, climate, soil type, stand history and disturbance regime (Harmon et al., 1986; Raphael and Morrison, 1987; Garber et al., 2005).

In this study we document the degradation pathway of 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 and black spruce (*Picea mariana* (Mill.) BSP). Using empirical data from unharvested forests in both boreal mixedwood and conifer stands we develop and compare snag survival curves of each species and assess their degradation pathways. We discuss these findings with regards to stand dynamics and the autecology of each species.

2. Methods

2.1. Study area

The study was conducted in northwestern Quebec, at the transition between the mixedwood and coniferous boreal forest. For balsam fir, trembling aspen and jack pine, sampling was conducted in the Lake Duparquet Research and Teaching Forest (LDRTF), located 45 km northwest of Rouyn-Noranda (48°26'–48°29'N, 79°26'–79°18'W). Elevation ranges from 274 to 411 m above sea level. The area 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. Disturbance history includes recurrent fires (Dansereau and Bergeron, 1993), with spruce budworm (*Choristoneura fumiferana* (Clem.)) outbreaks when fire cycle is long enough (Morin et al., 1993).

For black spruce, sampling was conducted in the coniferous boreal forest, 120 km further north (49°25'–49°50'N, 79°18'–78°41'W), in the Lake Matagami Lowland ecological region, within the black spruce–feathermoss (*Pleurozium schreberi* (Brid.) Mitt.) bioclimatic domain (Robitaille and Saucier, 1998). Elevation ranges from 239 to 400 m above sea level. Disturbance regime is characterised by large stand-replacing fires (Bergeron et al., 2004) with return intervals long enough for successional paludification processes to take place, organic deposits to build up and low productive, open forests to develop (Simard et al., 2007).

Both areas are part of a broad physiographic unit known as the northern clay belt, an area characterised by fairly flat topography and clay deposits originating from the proglacial lakes Barlow and

Ojibway (Vincent and Hardy, 1977). According to the closest weather station located in La Sarre, climate is cold and continental, with mean annual temperature of 0.7 °C and mean annual precipitations of 950 mm (Environment Canada, 2002).

2.2. Data collection

Data collection was carried out during summers of 2004 and 2005. Seventeen stands were selected based on species composition, soil type, drainage and age. Site selection was further constrained by accessibility and absence or very few harvesting activities based on historical reconstructions (Bescond, 2002; Lecomte et al., 2006). In cases more sites fulfilled all requirements than what was necessary, sites were randomly selected. Sites were mesic and soils composed of glaciolacustrine clay in LDRTF whereas black spruce sites were subhydryc and soil composed of glacio lacustrine clay overlaid by an important organic layer. All stands were mature to late-successional. Stand origins and harvesting history are presented in Table 1.

In each stand, a 20 m × 20 m plot was established randomly, at least 50 m from any edge (road, cut, different stand). Every snag (tree without green foliage, at least 1.3 m tall and with diameter at breast height (DBH) ≥ 5 cm) and every log from which the stump was located within the plot (DBH ≥ 5 cm) was detected. Leaning dead trees were considered as logs if their angle from the ground was under 45° (Harmon and Sexton, 1996). Buried logs that were still judged datable, particularly those covered by mosses or sphagnum in black spruce stands, were also searched. Direction of fall of logs was measured to the nearest degree using a compass. Characterisation of snags and logs included species, DBH (±0.1 cm), height (in snags, ±0.1 m) and stem integrity (whether entire, broken or uprooted). Uprooted trees were considered as such when at least the basis of some coarse roots was still visible. A total of 363 dead trees were characterised.

Snags were felled and cross sections were taken from all dead trees that were sound enough to suggest potential use for dendrochronology analyses. Fragile samples were taped with thread-enforced tape and cut using a fine-toothed bow saw to hinder fragmentation. To optimise chances of successful cross-dating, three cross sections were taken from each bole when possible: at base height, breast height and near the top (around 3 m from top for intact trees and near breakage height 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. In boles with advanced decay, height at which cross sections were taken varied depending on bole periphery preservation to maximise crossdating success.

2.3. Tree ring analysis

All cross sections were dried and 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 (precision of 0.001 mm, Velmex incorporated, Bloomfield, New York, USA).

To establish year of death, each individual ring width series generated by all 756 cross sections was crossdated against master series built for balsam fir, jack pine and trembling aspen from nearby living trees in LDRTF (V.A. Angers, unpublished data) and from a master chronology built for black spruce by Simard et al.

Table 1
Stand composition, disturbance history and snag availability.

| Species | Stand | Composition ^a | Time since fire (years) ^b | Past harvesting activity ^c | Snag density (nb/ha) ^d | Snag basal area (m ² /ha) ^d | Nb of dead trees sampled |
|-------------------------|-------|--|--------------------------------------|---|-----------------------------------|---|--------------------------|
| Trembling aspen | ANI | Trembling aspen–white spruce | 134 | Potentially partially cut between 1926 and 1945 | 550 | 4.7 | 28 |
| | KAN | Trembling aspen | 88 | None | 275 | 6.4 | 14 |
| | ORA | Trembling aspen | 82 | None | 275 | 4.7 | 7 |
| | PET | Trembling aspen | 81 | None | 275 | 9.9 | 10 |
| | STI | Trembling aspen–eastern white cedar | 189 | Potentially partially cut between 1916 and 1926 | 225 | 11.1 | 6 |
| Balsam fir ^e | LAG | White birch–trembling aspen | 82 | None | 250 | 7.2 | 5 |
| | PET | Trembling aspen | 81 | None | 275 | 9.9 | 6 |
| | PHI | White birch–white spruce | 245 | Potentially partially cut between 1926 and 1945 | 250 | 6.8 | 23 |
| | STI | Trembling aspen–eastern white cedar | 189 | Potentially partially cut between 1916 and 1926 | 225 | 11.1 | 20 |
| | TBK | White spruce–white birch–eastern white cedar | 208 | Potentially partially cut between 1926 and 1945 | 175 | 5.2 | 20 |
| | TIM | White birch–white spruce | 82 | None | 325 | 5.4 | 31 |
| Jack pine | GUM | Jack pine | 82 | None | 275 | 4.9 | 16 |
| | MAC | Jack pine | 82 | None | 525 | 7.9 | 33 |
| | PLU | Jack pine | 82 | None | 425 | 6.1 | 6 |
| Black spruce | H1 | Black spruce | 350 | None | 300 | 3.2 | 23 |
| | N5 | Black spruce | 169 | None | 375 | 4.3 | 30 |
| | N6 | Black spruce | 710 ^f | None | 325 | 5.4 | 30 |
| | N16 | Black spruce | 1585 ^f | None | 375 | 4.0 | 25 |
| | N50 | Black spruce | 365 ^f | None | 150 | 2.6 | 18 |

^a Composition of living tree species based on prism sampling from the plot center.

^b At time of sampling. Based on fire reconstructions by Dansereau and Bergeron (1993, LDRTF) and Lecomte et al. (2006) and Fenton et al. (2005) in black spruce stands.

^c Based on historical reconstitutions by Bescond (2002, LDRTF) and Lecomte et al. (2006, black spruce stands).

^d All species included.

^e Composition of stands where balsam fir snags were collected was mainly balsam fir prior to the 1980s spruce budworm outbreak.

^f Based on calibrated ¹⁴C charcoal age (Lecomte et al., 2006).

(2007). Crossdating was performed using marker years, and with COFECHA (Holmes, 1983) and TSAP (Rinn, 1996) programs, the latter being used for visually comparing the pattern generated by each 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 363 stems detected in the field, only 12 have not been successfully crossdated. These trees either had cross sections that were too decayed to perform measurements or were too young (not enough rings) for reliable crossdating. Seventeen (17) stems had their periphery eroded and thus their outmost rings were possibly missing, impeding an accurate assessment of year of death (one stem of trembling aspen, seven of balsam fir, nine of black spruce). Given that this represented a small proportion of the sampled trees, those minimum death years were considered as the actual ones. Time since death was calculated as the difference between year of sampling and year of death.

2.4. Analysis of tree mortality data

To assess to what extent mortality was constant through time, we conducted survival analysis using the Kaplan-Meier estimator on uncensored data for each species. The survival curves generated were then compared to constant survival models using the Mantel-Haenszel and the Tarone-Ware tests. The Mantel-Haenszel test (also known as the Mantel-Cox or log-rank test) applies equal weighting to the whole time-series whereas the Tarone-Ware test gives less emphasis on the later part of the time-series (SYSTAT, 2004). In order to avoid bias potentially caused by undetected dead trees, we selected time frames where we assume that most trees that died during those periods were detected (1980–2004 for trembling aspen and balsam fir, 1970–2004 for jack pine and black spruce).

Uprooting occurrence was estimated as the ratio between uprooted logs to total fallen logs. Also, to assess if a massive fall event related to wind disturbance occurred, we used polar plots showing directions of fallen stems coupled with time of death for every site.

2.5. Analysis of snag survival data

Since sampling was carried out at one point in time, time since death and dead tree status (standing vs. fallen) are known. However, the time when fall occurred in logs or when it will occur in snags remains unknown. All data is therefore either right- or left-censored (Gore et al., 1985), which impedes the use of classical analyses such as logistic regression or survival analysis to build snag survival relationships.

To overcome this problem and in order to approximate event of fall, many authors have successfully used alternative methods such as dating fell scars on neighboring trees and age of seedlings growing on logs (Daniels et al., 1997; Storaunet and Rolstad, 2002; Yatskov et al., 2003; DeLong et al., 2008) or dating release growth on surrounding stems and reaction wood in stems bent over by a falling tree (Daniels et al., 1997), but these proxies were not transferable to the studied ecosystem given the small size, relatively rapid decay rates of trees and low reliability of these estimates.

Modelling approaches have also been suggested to estimate longevity of standing snags with right- and left-censored data. Krusys et al. (2002) proposed an approach which assumes that all snags are halfway through their total standing time and that there is a constant input of deadwood in the population. In most cases, this latter assumption was not met (see results). Gore et al. (1985), Johnson and Greene (1991), and more recently Richards and Johnson (2007) proposed snag survival modelling approaches based on maximum likelihood estimates that circumvent to some extent the assumption of constant mortality and that only require

time since death of dead trees and their status at time of observation (standing vs. fallen). However, these methods assume an exponential distribution of snag fall, i.e. a constant proportion of snags falling at each time interval and very little decomposition occurring within the standing dead boles. These two assumptions do not hold in the ecosystems under study (see results, Angers et al., submitted).

Given the limitations of both our data set and the statistical methods in use, we decided to document the degradation pathways of tree species with a descriptive approach that depicts survival curves of snags. First, for each species, survival relationships were constructed using the ratio between the cumulative number of trees still standing after at least a given number of years since death and the number of trees dead since at least that given time. Curves were then fitted to determine which function among linear, negative exponential and reverse sigmoid best described the relationship. Because standing time may be underestimated in all snags and time since fall overestimated in all logs, these relationships can at best be considered approximations of real survival probabilities. Whereas our descriptive curves cannot determine statistically the critical time period of snag fall, differences between standing and fallen dead trees can, however, be assessed statistically using one-way analysis of variance with deadwood status (standing and fallen) as a fixed factor. Analyses of variance on each tree species were thus conducted to assess if time since death differed in standing versus fallen dead trees.

As with other studies on snag dynamics' (e.g. Boulanger and Sirois, 2006; Aakala et al., 2008), uprooted trees were not included in the analyses since it is not possible to assess retrospectively whether an uprooted tree was living or dead prior to the event. However, uprooting can occur in dead standing trees of the species under study (Taylor and MacLean, 2007, V. Angers, pers. obs.). By excluding these trees we may overestimate snag survival rates given that some uprooted trees were snags. On the other hand,

trees that break off near the base are included in our analyses. Some of these trees may have been alive prior to the event. Thus, inclusion of these trees may underestimate snag survival rates. Consequently, our snag survival rates may be viewed as a coarse index of snags survival that incorporates these biases.

Survival probability curves can be described with regards to lag time, maximal longevity observed and half-life (Fig. 2a). Lag time corresponds to the delay from death to fall onset, maximal longevity observed designates the longest survival time observed, and half-life refers to the time required for half the stems dead at a given time to fall to the ground.

2.6. Analysis of degradation pathways

Linear regressions were used to assess the effect of time since death on snag height and DBH. Using 10 year periods in each species, analysis of variance was used to assess if DBH influenced the standing/fallen status. Prior to all analyses requiring it, assumptions of normality of variance and homoscedasticity were verified and data was transformed if necessary.

3. Results

3.1. Tree mortality

Graphical examination and survival analysis of temporal mortality pattern showed major difference between species (Fig. 1). Despite year to year variations in mortality, observed annual mortality and constant mortality did not significantly differ in jack pine and black spruce (jack pine: $p = 0.156$ [log-rank], $p = 0.152$ [Tarone-Ware]; black spruce: $p = 0.554$ [Mantel-Haenszel], $p = 0.734$ [Tarone-Ware]). In trembling aspen, increased mortality in the last decade induced a significant departure from constant mortality ($p = 0.012$ [Mantel-Haenszel], $p = 0.028$ [Tarone-Ware]). Balsam fir mortality also differed significantly from

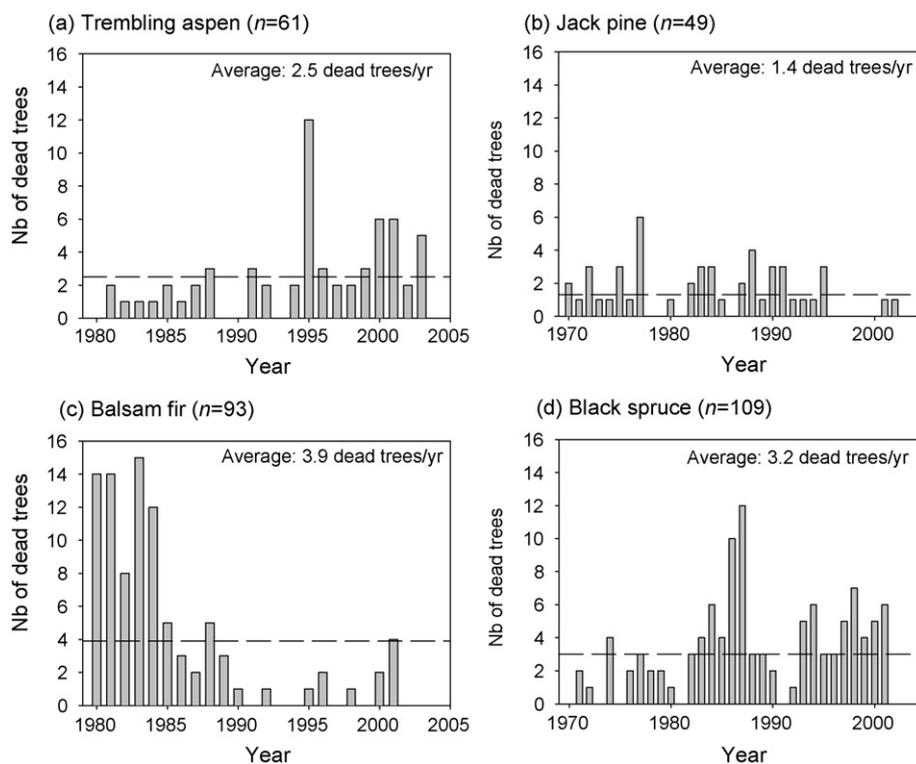


Fig. 1. Individual and average mortality (dotted lines) of sampled dead trees (standing and fallen) during specified periods.

Table 2

Time since death, diameter at breast height (DBH) and comparison between DBH of snags and logs sampled.

| Species ^a | | TRA | | JAP | | BAF | | BLS | |
|----------------------------|-----------------|----------------|------|----------------|------|----------------|------|----------------|------|
| | | Snags | Logs | Snags | Logs | Snags | Logs | Snags | Logs |
| Time since death | Average (years) | 8.0 | 18.0 | 18.8 | 29.1 | 18.2 | 22.3 | 16.5 | 24.0 |
| | S.E. (years) | 0.8 | 2.2 | 1.6 | 1.7 | 1.3 | 0.5 | 1.5 | 1.8 |
| | <i>n</i> | 49 | 14 | 31 | 19 | 28 | 69 | 59 | 55 |
| | <i>p</i> | <0.0001 | | <0.0001 | | 0.0004 | | 0.0018 | |
| DBH | Average (cm) | 14.8 | | 11.9 | | 14.5 | | 12.4 | |
| | S.E. (cm) | 0.8 | | 0.5 | | 0.4 | | 0.4 | |
| DBH 0–9 ysd ^b | <i>p</i> | – ^c | | – ^c | | – ^c | | 0.0160 | |
| DBH 10–19 ysd ^b | <i>p</i> | – ^c | | – ^c | | 0.8244 | | 0.7413 | |
| DBH 20–29 ysd ^b | <i>p</i> | – ^c | | 0.9672 | | 0.4020 | | 0.2935 | |
| DBH 30–39 ysd ^b | <i>p</i> | – ^c | | 0.2039 | | – ^c | | – ^c | |

p values shown are for comparison between average time since death among snags and logs belonging to the same species and for comparison between DBH of snags and logs by 10 year periods.

^a TRA: trembling aspen, JAP: jack pine, BAF: balsam fir, BLS: black spruce.

^b ysd: years since death.

^c Sampling size was insufficient to proceed with comparison of means (less than 5 individuals per group).

constant mortality ($p \leq 0.001$ [Mantel-Haenszel and Tarone-Ware]): 68% of trees died between 1980 and 1984 and tree deaths were sporadic between 1990 and 2005, a pattern typical of mortality caused by a severe spruce budworm outbreak.

Uprooting occurred in all species. Balsam fir appeared to be less susceptible, with only 10.4% of logs uprooted. Trembling aspen showed a slightly higher proportion of uprooting (12.5%) whereas black spruce and jack pine had similar values, with 17.9% and 20.8%, respectively. Whereas wind certainly plays a major role in live tree and snag fall by breaking or uprooting already weakened stems, polar plots showing directions of fallen stems (not shown) coupled with time of death for every site did not indicate any massive mortality or fall occurrence that would be related to a particular windstorm.

3.2. Snags survival

For all species, average time since death was significantly shorter in snags than in logs (Table 2). Survival probability curves clearly showed different patterns among tree species (Fig. 2). Trembling aspen followed two distinct stages that are best described by two linear functions representing those two stages. First, the species exhibited a short but distinct lag time, followed by a very rapid and linear fall rate that suggests that once snags start falling, the time window within which all snags are on the ground is relatively short compared to the other species studied. Jack pine survival exhibited a reverse sigmoid relationship with high retention of snags in the first years after death (no log observed among the 8 trees dead in first 13 years), suggesting that there is an

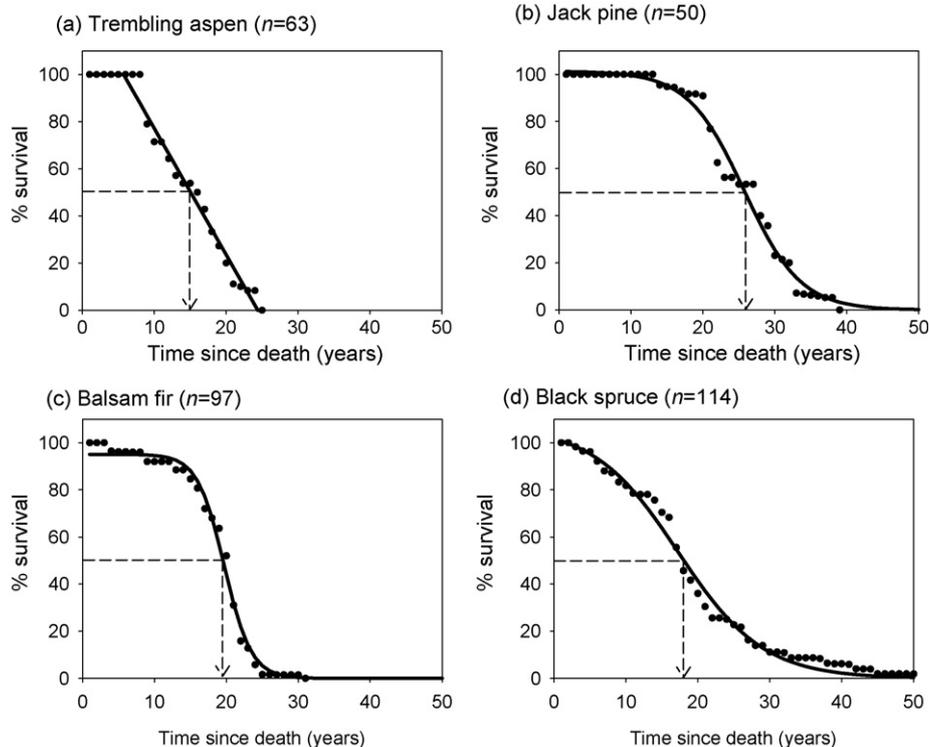


Fig. 2. Cumulative percentage of survival over time. Dots represent the annual standing/fallen cumulative ratio observed (see Section 2) whereas curves represent the general trend. Half-life, the time required for half the stems dead at a given time to fall to the ground, is represented by the dashed arrows.

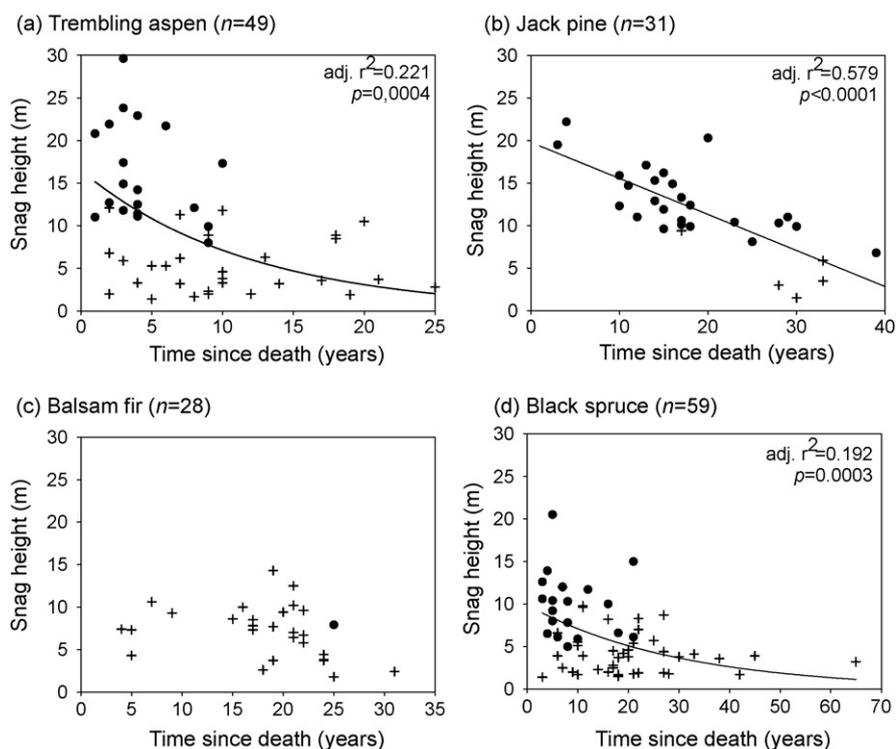


Fig. 3. Relation between snag height and time since death. Dots represent unbroken stems and crosses, broken stems.

important delay from death to fall of first snags. Balsam fir also showed this reverse sigmoid relationship but lost a significant amount of snags in the very first years after death, followed by a relative constant survival for the next few years. Black spruce survival was also best expressed as a reverse sigmoid function, but the fall rate was too rapid in the first years to observe a lag time.

Trembling aspen had a 15.1 year half-life, the shortest of all species, meaning there is a 50% chance that a snag of either species will have fallen within the first 15 years after death (Fig. 2). Jack pine showed the greatest persistence as a snag, with a 25.8 year half-life. Balsam fir and black spruce were in an intermediate position with similar half-lives of 19.5 and 18.1 years, respectively.

3.3. Degradation pathway

Stem integrity of snags (broken vs. unbroken) was highly variable among species but, as one would expect, broken snag's relative abundance generally increased with time since death (Fig. 3). This was particularly evident for trembling aspen and black spruce, although black spruce snags seemed to stay intact longer: In trembling aspen, the oldest unbroken snags died 10 years before sampling whereas in black spruce, the oldest unbroken snag was 21 years old.

Fig. 3 also shows that snag height rapidly decreased to less than 5 m in both trembling aspen and black spruce, two species for which the relationship between snag height and time since death was curvilinear. Jack pine and balsam fir exhibited opposite patterns relative to each other. As in survival probability, jack pine showed the greatest resistance to breakage, with the youngest broken snag dead 17 years before sampling and only 5 out of 31 snags broken (Fig. 3b). Although balsam fir seemed to be the most breakage-prone species, with only one out of 28 snags unbroken, snags remained quite tall with most taller than 5 m 20 years after death (Fig. 3c).

Height was used as a proxy to assess the degradation pathway of trees following their death. Prior to this analysis, the possibility

that height was biased by stand age was investigated. Many stands were relatively young (≥ 81 year-old) and mortality due to stem exclusion in the first cohort after fire might introduce a bias towards snags being taller with time since disturbance. To explore this, height of unbroken stems was related to time since death. When few stems were unbroken, DBH was also used as an indicator. In jack pine, and to a lesser extent in trembling aspen, this analysis revealed a bias induced by the cohort effect (data not shown), making assessments on degradation pathways based on snag height hazardous. However, there was no such cohort effect in black spruce and balsam fir. In black spruce, snags were significantly shorter as time since death increased (Fig. 3d) whereas in balsam fir, no transformation allowed both a significant relationship and respect of the normality of residuals assumption (Fig. 3c).

In all species, looking at successive periods of 10 years since death where sample size was sufficient, DBH had no influence on the probability of a dead tree to be standing or fallen (Table 2).

4. Discussion

4.1. Tree mortality, snag recruitment and influence of stand dynamics

Along with fall and decomposition rates, deadwood recruitment is a major component in the study of deadwood dynamics. Therefore, mortality patterns that model deadwood input have to be considered when studying snag dynamics. In this regard, mortality generated by a factor such as uprooting is important to consider in snag dynamics since it bypasses the snag stage when occurring in living trees and because uprooted trees create different habitats than other logs (Schaetzl et al., 1989). Episodic and relatively severe disturbance events provide pulses of snags whereas mortality induced by succession processes is usually less severe and more continuous in time (Everett et al., 1999; Harper et al., 2003). Moreover, cause of death may have an effect on the

temporal pattern in fall rates of trees after death (Harmon et al., 1986; Raphael and Morrison, 1987; Renvall, 1995).

4.1.1. Trembling aspen

In aspen our results indicate that mortality was induced by a set of different causes. Based on harvesting history, stand age (Table 1) and results of Harvey and Brais (2007), the aspen stands studied are in a transitional stage between stem exclusion and decline. Self-thinning and senescence were thus presumably two important sources of mortality. In addition, the Abitibi region experienced a forest tent caterpillar (*Malacosoma disstria* Hbn.) outbreak that lasted from the late 1990s to the early 2000s (Cooke and Lorenzetti, 2006, Fig. 1). Although less lethal than other defoliators, the forest tent caterpillar can trigger decline and eventually death in trembling aspen (Churchill et al., 1964; Candau et al., 2002), especially in suppressed trees that are more susceptible (Churchill et al., 1964). High mortality in 1995 is essentially due to synchronized mortality in one stand (ANI, Table 1) that might be attributed to competition (all stems were suppressed), drought at the end of summer 1995 and successive years of low intensity defoliation by the forest tent caterpillar (F. Lorenzetti pers. comm.).

The low uprooting occurrence found in our study (12.5%) was a little less than that reported by Hill et al. (2005) in northeastern Ontario (18%). Trembling aspen is a likely wind firm species given that stands of clonal origin are characterised by suckers issued from a developed lateral network of roots that are anchored to the soil by vertically penetrating roots (Peterson and Peterson, 1992).

4.1.2. Jack pine

For jack pine snags, height (most <15 m), as well as DBH (most <15 cm) and stand age, suggests that most snags were recruited via self-thinning mortality. This mortality process was fairly constant (Fig. 1). We found a high rate of uprooting among jack pine logs (20.8%). This was unexpected since jack pine usually features a tap root or at least a vertical root system (Rudolph and Laidly, 1990), that root rot is not prevalent in this species (Basham, 1991) and that sampling was conducted on fine-textured deposits that do not restrict root development (Béland et al., 1999). Part of these stems might be old snags that felled many years after death, when rotten roots broke as suggested by coarse and very short root fragments still connected to the stumps.

4.1.3. Balsam fir

Balsam fir stands experienced the 1970–1987 spruce budworm outbreak (Morin et al., 1993), which was likely responsible for a large part of our sample set of dead trees (Fig. 1) as supported by suppressed or missing rings indicative of severe defoliation in the early 1980s (data not shown). Thus most dead stems came from stands where balsam fir dominated the forest cover before the outbreak and experienced high mortality (Bergeron et al., 1995). Spruce budworm-related mortality in balsam fir usually begins 3–4 years after the first severe defoliation (MacLean and Ostaff, 1989) and is mostly completed with a similar time delay after defoliation ceases (Blais, 1981), which corresponds well with the mortality distribution observed in our study and in Bergeron et al. (1995).

Because of its shallow root system, balsam fir is generally considered an uprooting-prone species (Frank, 1990) and commonly uproot after death (Taylor and MacLean, 2007). We found, however, a relatively low level of uprooting (12.5%) in comparison with Taylor and MacLean (2007) who observed a 20% mortality rate caused by uprooting in living balsam fir. This is likely explained by the spruce budworm being the predominant cause of mortality.

4.1.4. Black spruce

Most black spruce deaths were presumably due to senescence. Indeed, all black spruce stands were initiated by old fires (≥ 169

years, Table 1), average tree age was 165 years, and stands were relatively open, thus reducing stem competition. The observed mortality peak in the late 1980s may be, however, partly related to the spruce budworm outbreak (Fig. 1). Growth reduction and tree mortality in black spruce that are linked with spruce budworm outbreaks (based on dendrochronological reconstructions) have been observed elsewhere (Simard and Payette, 2001; Lussier et al., 2002; Morin et al., 2008) as well as in the study area (M. Simard and others, unpublished data). Although not as severe as in balsam fir-dominated stands, mortality due to the spruce budworm in black spruce can significantly contribute to deadwood recruitment.

Uprooting has been documented to be a major cause of death of black spruce in the clay belt region, especially in old stands (Smith et al., 1987; Harper et al., 2003), which is supported by our results (17.9% of fallen trees uprooted). This is explained in part by the lateral and very shallow root system of the species, combined with poorly drain organic and gleysolic soils with high water table, limits rooting depth (Smith et al., 1987) as well as infection by root decay (Basham, 1991; Whitney, 1989).

4.2. Snag survival

For the four species under study, snags died significantly more recently than logs, on average, indicating that snag fall is not a random process and that time since death influences snag survival. All species had a different temporal pattern in fall rates, but trembling aspen, jack pine and to a lesser degree balsam fir exhibited a reverse sigmoid curve with a lag time before onset of snag fall indicating high snag retention in the first years after death. Such functions have also been reported in other studies (e.g. Keen, 1929, 1955; Cline et al., 1980; Lee, 1998; Garber et al., 2005; Mäkinen et al., 2006). Lag times following death vary from 1 to 5 years in other studies conducted on boreal species with similar DBH (Lee, 1998; Garber et al., 2005; Taylor and MacLean, 2007), which is a little less than what was found in this study. In Alberta's midboreal ecoregion, Lee (1998) found very similar results in the sequence of fall of trembling aspen: most snags remained standing during the first 5 years after death and fall rate increased strikingly 10–20 years after death.

Other authors found negative exponential survival functions, implying a constant fall rate through time (Everett et al., 1999; Storaunet and Rolstad, 2004). In these studies, the absence of lag time may simply be explained by the studied species pattern of degradation or because lag time was too short to be detectable given the interval between observations (no observations in the first years following death).

Half-life patterns in our study were generally similar to what was found in other studies. Trembling aspen snags half-life values were between results reported by Vanderwel et al. (2006) in southern Ontario, who modelled a 9 year half-life at 25 cm DBH, and those from Lee (1998) in Alberta, who observed a half-life of 22 years. For balsam fir, the half-life found in this study was slightly higher than the 16 years found by Taylor and MacLean (2007) but was much greater than the 6–10 year reported by Garber et al. (2005). In black spruce stands located about 500 km north of our study area, Boulanger and Sirois (2006) observed a comparable half-life for post-fire black spruce snags (16.2 years). In eastern Québec, Aakala et al. (2008) modelled considerably higher half-lives in balsam fir and black spruce (30–35 years and 35–40 years, respectively), but these high values are likely due to the fact that their models were based on a more limited range of dead trees than was the case in our study (e.g. DBH > 19 cm, rejection of very decayed samples, transition model based on decay classes with highly variable times since death).

The absence of a significant influence of DBH on snag survival is generally consistent with what has been reported in other studies

that documented snag survival within the DBH range we analysed. Higher survival probabilities in large snags have mostly been observed in ecosystems where trees were much larger than those sampled in this study (Keen, 1929, 1955; Dahms, 1949; Raphael and Morrison, 1987; Everett et al., 1999; Morrison and Raphael, 1993), except for Garber et al. (2005) in Maine, who had slightly larger but still similar DBH values. In our study, the size effect might have been undetectable given the relatively narrow DBH range observed (Table 2, Johnson and Greene, 1991; Lee, 1998; Kruys et al., 2002; Storaunet and Rolstad, 2002).

Snapshot sampling, or retrospective reconstruction based on observations made in a given year, as compared to continuous sampling over time, might introduce biases (Harmon and Sexton, 1996; Kruys et al., 2002; Storaunet and Rolstad, 2002, 2004). First, as deadwood pieces age, they decompose and collapse as a result of decay, thus becoming harder to detect or to date retrospectively and hence impossible to include in the reconstruction. Because slow-decaying individuals are more likely to be detected than individuals that died during the same period but decayed more rapidly, the reliability of the reconstruction period diminishes as one goes back in time and is a function of decay rates. Since snags generally decay more slowly than logs, this could lead to an overestimation of survival probability in old snags (right end of survival curves, Fig. 2) and thus overestimated half-lives. This possible overestimation is likely in rapidly decaying species, such as trembling aspen in our case (Alban and Pastor, 1993, Angers et al., submitted). Second, causes of death were roughly estimated. However, these causes varied between stands and through the observation period and introduced spatial and temporal variability, both in the mode of death (died standing, snapped, broken at the base) and in the degradation pathways that is difficult to assess retrospectively. Survival curves might thus have been different if other causes of mortality were involved, if sampling had been conducted in other stands or if sampling had been conducted in the same stands but at a different time.

4.3. Specific degradation pathway

As opposed to uprooting, breakage decreases the height of snags but does not necessarily bypass the snag stage. Factors that influence breakage susceptibility include wood density, wood mechanical properties, cause of death, stem integrity and condition at time of death, and exposure to wind and snow (Putz et al., 1983; Morrison and Raphael, 1993; Storaunet and Rolstad, 2002; Taylor and MacLean, 2007). Although many studies found that wood density loss is low as long as dead trees remain standing (Johnson and Greene, 1991; Krankina and Harmon, 1995; Boulanger and Sirois, 2006), others found that wood density effectively decreases in snags over time (Yatskov et al., 2003; Saint-Germain et al., 2007). Breakage can induce feedback effects on future snag degradation, whether positive, through opening passages for decay agents that increase decay rates for the rest of the bole and thus hasten breakage likelihood (Everett et al., 1999), or negative, by partially or completely removing crown, making snags less susceptible to wind breakage (Dahms, 1949; Huggard, 1999; Lee, 1998). Degradation pathways are related to species autecology and, hence, are treated separately for each species.

4.3.1. Trembling aspen

Most trembling aspen seem to die standing (Senecal et al., 2004) and degradation pathway of *Populus* snags is generally considered to pass by bole breakage at various heights along the bole rather than uprooting (Peterson and Peterson, 1992). The aspen root system being well anchored, wind stress is concentrated along the

bole. Stems are commonly colonized and weakened by wood-decaying fungi prior to death, especially in the upper part of the bole, reducing competitive abilities and making stems very prone to breakage, whether living or dead (Basham, 1991; Harvey and Brais, 2007). In our study, more than 61% of snags were broken and no snag older than 10 years remained unbroken (Fig. 3a). Susceptibility to breakage has also been reported for *Populus tremula*, for which Hytteborn et al. (1991) found that 75% of gap makers died by snapping off at some point along the bole. Once the crown is decimated, snags offer less resistance to the wind and likely reduce risk of breakage (Lee, 1998). However, as decay migrates downwards, successive breakages may occur before the snag finally collapses, resulting in snag shortening instead of snag fall. Multiple breakages were not directly observed in our study, but the presence of many boles segments on the floor is consistent with this interpretation.

Forest tent caterpillar outbreak has probably been a decisive factor in the recent death of aspen trees in our study area. Compared to pathogen-killed snags for which mechanical properties of the wood are already altered prior to death or broken trees that offer an entry to decay fungi, forest tent caterpillar mortality leaves an intact stem with fresh and solid wood. These snags might therefore follow a delayed degradation process (Huggard, 1999; Storaunet and Rolstad, 2004; Garber et al., 2005), as suggested by the fact that all snags that died during the seven years prior to sampling were still standing.

4.3.2. Jack pine

Jack pine was the most persistent species in our study. Many boreal *Pinus* species also display high resistance to degradation and decomposition relatively to the *Abies* and *Picea* genus (Alban and Pastor, 1993; Yatskov et al., 2003). As compared with other coniferous species, the relatively high wood density (Angers et al., submitted), vertical root system (Rudolph and Laidly, 1990) and the low susceptibility to stem and butt decay of jack pine in the first 100 years (Basham, 1991) all contribute to its longevity, whether as snags or logs.

Jack pine was also the most breakage-resistant species. Indeed, breakage is lagged by about 30 years after tree death and is likely to be more pronounced beyond the time scale considered in this study. Its tangled branches and the relatively high stem density of the sampled stands might contribute to postpone fall and breakage by enhancing resistance to wind penetration in the stand. Furthermore, the scarcity of breakage might have delayed further breakage and fall due to lack of entry for decay fungi. The very low amount of broken snags observed in our study (Fig. 3b) suggests that jack pine snags fall directly to the forest floor by breaking below 1.3 m or uprooting. As examined by Angers et al. (submitted) on the same samples, this is apparently not related to a higher decay rate of the wood at the base of snags than at DHB.

Even though jack pine snags are clearly the most persistent of the four studied species, their persistence time is likely to be underestimated given the relatively young age of our sampled stands (~80 years). In older stands, the reconstruction period would have been extended, leading to longer persistence at the snag stage. In the same study area, Dansereau and Bergeron (1993) noted that fire-killed jack pine snags can remain standing for over 100 years. Older jack pine stands were not available in the region but dendrological reconstruction of pre-fire mortality and snag dynamics over 70 years in three 120 year-old stands burned in 1996 located 350 km north-east of LDRTF showed a similar lag time, though a half-life of 38.5 years (V.A. Angers, data not shown). Even though fire might have influence snags dynamics during an eight years period between fire and sampling, the half-life is considerably longer.

4.3.3. Balsam fir

Even though the survival curve of balsam fir snags did not exhibit a lag time as obvious as trembling aspen or jack pine, there was a clear high initial retention period (more than 90% of snags standing 12 years after death, Fig. 2c). This represents a higher survival rate than reported by Bergeron et al. (1995) in the same study area, who noted that 25% of spruce budworm-killed balsam firs had fallen within 7–8 years after the mortality peak occurred. This difference may be related to a temporal issue as sampling of our study was conducted almost 20 years after the mortality peak occurred. Recent mortality causes may not be directly related to the spruce budworm outbreak and probably induced a different degradation pathway.

Data from our study corroborate results from other studies that balsam fir is prone to breakage. Of all snags observed, only one remained intact (Fig. 3c). In Ontario, 5 years after the mortality peak induced by the spruce budworm, Stocks (1987) observed top breakage in 70% of dead trees. In New-Brunswick, Taylor and MacLean (2007) observed successive breakage over time in balsam fir snags. Of the three coniferous species studied, balsam fir had the least dense wood (Angers et al., submitted, same samples as in this study), which likely contributed to its reduced mechanical resistance.

Balsam fir is moreover the most susceptible eastern boreal species to stem decay (Basham, 1991) which, combined with butt rot, enhances its susceptibility to breakage. The environmental context of our study sites probably also contributed to breakage vulnerability: the strong and synchronized opening of the canopy caused by the severe mortality of balsam fir resulted in higher exposure of snags to wind and this might have hastened snag breakage and fall as compared to snags that would have been surrounded by live trees.

4.3.4. Black spruce

The temporal pattern in fall rate of black spruce may seem contradictory. Considering its half-life, this species is the least persistent of the three coniferous species studied due to the absence of a lag time following death. On the other hand, the slope of its survival curve is the least pronounced, with snags falling more constantly than in other species (Fig. 2d) and the oldest snags observed in this study (>40 year-old).

This contrasting pattern may be reconciled by a twofold explanation. Some snags fall quite rapidly following their death. Infection by root and butt decay, especially by *Armillaria* sp., is common in the region (Basham, 1991) and given that the average minimal age at death is 165 years and that extensive decay gets more common as trees age, snags were likely highly susceptible to stump breakage (Basham, 1991; Whitney, 1989). On the other hand, snags that remained standing for decades may be particularly decay resistant. Black spruce stands were paludified and low productive (Simard et al., 2007). Trees therefore experienced a very slow growth which in turn generated high density wood with physiological and chemical properties that limit fungi decay capacity (Angers et al., submitted, see Edman et al., 2006 for a review).

5. Conclusion

This study provides original baseline information on patterns of degradation of individual tree species following death in mature and late-successional stands under natural disturbances in North America's eastern boreal forest. Even though our approach was based on a single sample in time combined with dendrochronological reconstruction, it appeared to be robust and comparable with results from approaches based on chronosequence (Boulanger and Sirois, 2006) as well as modelling and/or

repeated measures designs (Lee, 1998; Garber et al., 2005; Vanderwel et al., 2006; Taylor and MacLean, 2007). Our approach is not limited by assumptions that are difficult to verify or meet, as occurs in modelling studies, or by the shortcomings of chronosequence approaches, e.g. differences in deadwood dynamics due to site characteristics and small sample sizes. As compared to repeated measures designs, it does not require waiting for years before data is available and time since death is estimated to the annual level and is not an approximation based on the midpoint of the interval between two inventories when the tree was last found alive and was first found dead (e.g. Garber et al., 2005; Taylor and MacLean, 2007). Nevertheless, the study of deadwood dynamics would benefit from a regularly measured permanent sampling design coupled with a monitoring of abiotic factors and decomposer organisms that would provide a more comprehensive understanding of deadwood degradation patterns, especially regarding fall, and underlying mechanisms (see Morrison and Raphael, 1993; Lee, 1998; Garber et al., 2005; Vanderwel et al., 2006; Mäkinen et al., 2006; Taylor and MacLean, 2007).

Similar to the paradigm that species exhibit individualistic responses to their environment during their life time (Gleason, 1926; Whittaker, 1957), this individualistic way of responding extends after death and is expressed through differential degradation pathways between species. The propensity for trees to remain standing after death, the differential steepness of survival curves of snags, and the differences in susceptibility to uprooting or stem breakage all represent individualistic responses that have important implications for different ecological functions of deadwood, ranging from habitat and species conservation to resource allocation (e.g. light transmission in gaps) to nutrient and carbon cycling.

Three species, trembling aspen, jack pine and to a lesser extent balsam fir, exhibited a high retention of snags in the first years after death. This delay is of great biological importance for organisms that use fresh standing dead wood, meaning that this resource is largely available during a given time period. In systems where mortality patterns generate a relatively constant recruitment of dead trees, continuity in habitat availability though time would be ensured for long periods of time. Since black spruce snags have low persistence, companion species, even low in density, are particularly important in providing snag availability in systems dominated by black spruce. This is especially true for species that can attain larger diameter than black spruce.

From an ecosystem management perspective, maintenance of biological legacies (*sensu* Franklin et al., 2002) through key structural attributes such as snags is often presented as an approach to mitigate habitat alteration by conventional forest management. Development of natural-based silviculture approaches that incorporate deadwood management will necessarily require baseline data on fall rates of snags for long-term planning of deadwood recruitment in managed forest landscapes (DeLong et al., 2008). The fact that snags of tree species respond in an individualistic manner will require flexibility in live and deadwood retention strategies with regards to the dominant tree species or forest cover types under management. Moreover, differential degradation status and decay stages are used by different species (Harmon et al., 1986; Saint-Germain et al., 2007; Drapeau et al., 2009). Wildlife managers will need to consider habitat dynamics and therefore snag demography in order to propose recommendations and guidelines related to deadwood-dwelling species conservation (e.g. Bull et al., 1997). Finally, this study was conducted in unharvested stands. To effectively include deadwood legacies in forest management strategies, deadwood dynamics also needs to be studied more thoroughly in managed systems.

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