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Tree mortality and snag dynamics in North American boreal tree species after a wildfire: a long-term study

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Abstract. Temporal patterns of tree mortality and snag dynamics after fire were investigated over 10 years in a permanent plot design established immediately after a wildfire in an eastern boreal forest landscape of north-western Quebec, Canada. Post-fire tree mortality, snag persistence, tree fall patterns and variables influencing snag dynamics were assessed in deciduous, mixed and coniferous stands that experienced low- and moderate-severity fires. Temporal patterns of tree mortality for the three species revealed that mortality was delayed through time. Most post-fire tree mortality occurred within 2 years following fire but continued until the end of the 10-year observation period. Jack pine was the most persistent snag species, followed by trembling aspen and black spruce. Factors influencing the persistence of snags were multi-scaled and generally species-specific. Fire severity was the only common factor influencing snag persistence among all species, with snags located in severely-burned stands being less susceptible to falling. Trembling aspen snag persistence increased with basal area and diameter. Salvage logging in the vicinity affected black spruce. Fall patterns also differed among species. Bypasses of the snag stage (i.e. when a living tree falls directly to the forest floor) as well as uprooting of snags were common.

Additional keywords: black spruce, delayed tree mortality, fire severity, jack pine, *Picea mariana* (Mill.) BSP, *Pinus banksiana* Lamb., *Populus tremuloides* Michx., Quebec, salvage logging, survival analysis, trembling aspen.

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Introduction

Wildfire is a major natural disturbance in North American boreal ecosystems (Johnson 1992; Payette 1992; Bergeron *et al.* 2004). Within large fires, burn severity may be highly heterogeneous as a result of stand, site, season and climate conditions (Turner *et al.* 1994; Kushla and Ripple 1997; Kafka *et al.* 2001; Oliveras *et al.* 2009). Initial tree mortality is usually massive and synchronous but its magnitude is influenced by fire severity (Hély *et al.* 2003). Some studies have highlighted the fact that tree mortality continues to occur in the mid- to long term (Brown and DeByle 1987; Ryan *et al.* 1988; Harrington 1993; Keyser *et al.* 2006), but few studies have addressed the issue in boreal ecosystems (but see Brown and DeByle 1987).

The large number of dead trees produced by fire is related to many ecosystem processes that range from carbon and nutrient cycling (Kasischke 2000; Boulanger and Sirois 2006) to habitat creation for a wide diversity of organisms (Saint-Germain *et al.* 2004; Chambers and Mast 2005; Nappi and Drapeau 2009). Although a growing body of knowledge on snag dynamics, i.e. the transition from standing dead trees to logs, is available for late-seral forests (Lee 1998; Garber *et al.* 2005; Boulanger and Sirois 2006; Taylor and MacLean 2007; Aakala *et al.* 2008), persistence of fire-killed snags has received limited attention, especially in the eastern boreal forest (but see Boulanger and Sirois 2006). Environmental conditions such as humidity, temperature and solar insulation influence dead wood degradation (Erickson *et al.* 1985; Harmon *et al.* 1986; Naesset 1999; Boddy 2001). As these environmental conditions differ drastically between post-fire and late-seral forest stands, snag dynamics are likely to differ within these two environments. Furthermore, the influence of surrounding salvage logging on snag

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dynamics of unsalvaged stands has only rarely been assessed (Russell *et al*. 2006).

In this study, we documented the fate of living and dead trees after a wildfire using a study design with permanent plots that offered a unique opportunity to follow simultaneously post-fire tree mortality and snag dynamics over a long period (10 years). First, we examined tree mortality at the stand scale with the specific objective of determining if and how temporal mortality patterns are related to stand composition and fire severity. Then, we analysed snag dynamics for three species: trembling aspen (*Populus tremuloides* Michx.), jack pine (*Pinus banksiana* Lamb.) and black spruce (*Picea mariana* [Mill.] BSP). For each tree species, our specific objectives were to: (1) generate survival curves of snags after fire; (2) quantify the effect of tree-, stand- and landscape-level explanatory variables on snag persistence; and (3) establish fall patterns, i.e. the different paths a tree may take from standing to lying on the forest floor.

Methods

Study area

Sampling was conducted in an area where a wildfire covering 12 557 ha occurred in June 1997 near Val-Paradis, north-western Quebec, Canada (49°09′N, 79°26′W). Lowland areas are covered by clay deposits originating from the proglacial Lake Barlow (Vincent and Hardy 1977) whereas tills and sandy fluvio-glacial deposits dominate uplands (Tremblay 1974). Elevation ranges from 440 to 537 m above sea level. The area is at the transition from mixed-wood to coniferous boreal forest (Gauthier *et al*. 2000) where black spruce (*Picea mariana* [Mill.] BSP), jack pine (*Pinus banksiana* Lamb.) and trembling aspen (*Populus tremuloides* Michx.) dominate. Paper birch (*Betula papyrifera* Marsh.) and balsam fir (*Abies balsamea* [L.] Mill.) were the main secondary species. According to the closest weather station located in La Sarre, climate is cold and continental, with a mean annual temperature of 0.7°C and mean total annual precipitation of 889.8 mm (1971–2000, Environment Canada, national climate data and information archive, see www.climate.weatheroffice.gc.ca/climate_normals/results_e.html, accessed 8 November 2010).

The fire was an intermittent crown fire and was extinguished on the third day (Hély *et al*. 2003). Various levels of fire intensity yielded highly variable degrees of severity within the fire. Intensive salvage logging by clear-cutting was conducted in 1997 and 1998 on 59% of the burned area and 92% of stands with commercial timber. Pre-fire stand age varied from 63 to >150 years (Greene *et al*. 2004).

Data collection

A series of permanent sample plots was established a few weeks after the fire. Thirty-six 0.04-ha plots (20 × 20 m) were established, with a stratified sampling protocol that covered a combination of three crown fire severity classes (low: 0–25% stand mortality, moderate: 25–75%, high: 75–100%) and three stand composition classes (deciduous, mixed, coniferous) based on the canopy composition (relative basal area) before the fire. Deciduous stands were dominated by trembling aspen (>70%), mixed stands were composed of 10–70% trembling aspen, with the rest being mostly jack pine and black spruce, and coniferous stands were dominated by jack pine, black spruce or a mix of these two species (see table 1 in Greene *et al*. 2004 for a full description of sites composition). All plots had a minimal buffer zone of 10 m from salvage cut areas. Unfortunately, in 1997, seven plots were inadvertently salvage logged. Seven new plots were thus established in 1998 of which one plot (severely burned coniferous) was logged in the following years, probably for firewood. Thus the final analysis was conducted on 35 plots.

All trees with diameter at breast height (DBH) greater than 5 cm were labelled. Standing dead trees (trees with no green foliage) were considered as snags when at least 1.3 m tall. A total of 2313 trees were surveyed over 10 years. Species, DBH, height, crown length, status (whether living or dead) and stem integrity (intact, broken, uprooted) were recorded in 1997, whereas these measurements were taken at the end of the summer for the re-established sites in 1998. Status and stem integrity of living trees and snags were reassessed in 1998, 1999, 2000, 2002, 2004 and 2006. In 2004 and 2006, the height of trees was measured and in 2004, percentage of residual bark was estimated.

Data analysis

In total, 2313 trees were surveyed from 1997 to 2006. To avoid any confusion regarding tree mortality and snag temporal dynamics, hereafter we will refer to the former as tree survival curves and to the latter as snag persistence curves. Survival time was calculated as the number of years from fire to tree death. As tree mortality rates varied between 98 and 100% per stand in the year of the fire in severely burned stands, we only considered lightly and moderately burned stands in our temporal analysis of tree mortality. Persistence time of each snag was calculated as the number of years from tree death to snag fall. Trees that eventually died during the observation period were included in the snag persistence analysis (43% of all snags). When an individual was not found, whether because it was accidentally cut, or the tag was lost or unreadable, or if a snag was still standing at the end of the observation period, the observation was considered as right-censored at the date of last census.

Survival analysis

Survival analysis provides an accurate and detailed representation of survival patterns. It has been used with tree mortality data (see Woodall *et al*. 2005 for a review) and more recently, in studies of snag dynamics (Lee 1998; Garber *et al*. 2005; Russell *et al*. 2006). Survival analysis makes it possible to compare whole survival distributions among different groups, handles censored data and can be interpreted as a function of independent variables (Allison 1995).

Given that some visits were separated by more than 1 year, we used three scenarios: minimum, median and maximum time since death or fall of trees to compute survival functions. These functions were computed at the stand scale for the six possible composition–severity combinations for tree mortality data and for each species in snags. Significance of differences was assessed using the log-rank test statistics using the SAS LIFETEST procedure (Allison 1995; SAS Institute Inc. 2002). This survival analysis allowed us to test the null hypothesis that the survival curves are the same in two or more groups. For tree mortality, there was no difference between survival curves of

Table 1. Stand and tree characteristics of main tree species
Note: within a given species, values followed by the same lowercase letter do not differ significantly ($P < 0.0001$). DBH, diameter at breast height

Species	Trembling aspen ($n = 551$) Mean ± s.e. (range)	Jack pine ($n = 298$) Mean ± s.e. (range)	Black spruce ($n = 1314$) Mean ± s.e. (range)
Tree-level variable			
DBH (cm)	$21.2^{a} \pm 0.3$ (5.0–48.0)	$13.9^{b} \pm 0.3$ (5.8–42.2)	$11.9^{c} \pm 0.1$ (5.0–38.0)
Height (m)	$19.1^{a} \pm 0.2$ (4.8–38.4)	$13.9^{b} \pm 0.2$ (4.7–23.3)	$11.2^{c} \pm 0.1$ (2.0–21.8)
Stand-level variable			
Pre-fire basal area ($m^2\,ha^{-1}$)[A]	$35.2^{a} \pm 2.1$ (20.3–57.0)	$33.0^{a} \pm 2.4$ (23.5–57.0)	$34.2^{a} \pm 1.6$ (23.5–57.0)

[A] All species included.

minimum, median and maximum survival time ($P \geq 0.2918$ in all groups). There was no significant difference between snag persistence curves of minimum, median and maximum time since fall for jack pine and trembling aspen ($P = 0.7873$ and 0.1870 respectively). Differences were more marked in black spruce ($P = 0.0006$) but this result had no major biological significance: divergences were concentrated between 3 and 5 years after death and the proportion of standing dead stems was the same or almost identical from the beginning to the end of the observation period. We thus assumed the date of the event to be the midpoint of the interval and based further analyses on this assumption.

Variables influencing tree survival and snag persistence

The SAS LIFEREG procedure and the log-rank test statistics were used to test the influence of fire severity and stand composition on tree survival at the stand scale (all species included). This procedure uses the method of maximum likelihood to produce estimates of parametric regression models. We assessed the effect of tree-, stand- and landscape-level variables on snag persistence for each tree species using the following procedure: first, predictive variables were identified and computed if necessary. Tree-level variables were DBH (cm), height and crown length. Stand-level variables included prefire basal area (BA, $m^2\,ha^{-1}$, all species included), composition (COMP, three classes) and fire severity (SEV, three classes). The landscape-level variable was the proportion of salvage-logged area within a 100-m radius from the centre of the permanent plots (SALVG). It was calculated using salvage report maps (ESRI 2000). Percentage of salvage-logged area within 100 m from the centre of our permanent plots ranged from 0 to 98.7% (average = 53.3%, s.e. = 4.5%).

Using multiple linear regressions, a list of models was then developed to assess the joint effect of tree-, stand- and landscape-level variables on snag persistence for each species. Models were based on variables known to be biologically meaningful with regard to snag fall (see Appendix for the list of models). Variables were considered independent and therefore used in models when Pearson's correlation coefficient between two given variables was less than 0.5. In all species, DBH, height and crown length were all strongly correlated with each other (Pearson's correlation coefficient >0.5, data not shown). As DBH is the tree-level variable most widely used in snag dynamics studies and given that its variance was slightly higher than other variables (Table 1), we decided to systematically include this variable in our models. For jack pine, stand composition was not included because this species was mostly only present in coniferous stands. Models including each individual variable were added to the list. DBH was the only variable determined by tree life history and has been shown to affect snag persistence in many instances (see Discussion), so we included it in many models. We considered SEV and SALVG as stand- and landscape-level factors likely to induce environmental changes following wildfire, and hence affect snag persistence in remnant habitats. These two variables were thus also frequently included in the models, together or separately.

Third, we used the LIFEREG procedure to investigate whether the models suggested by that procedure were included in the listed models for each species and added them if they were not. The null and full models were also included. Finally, Akaike's information criterion (AIC) was used to select the best model, i.e. the most simple and parsimonious one (Burnham and Anderson 2002). For black spruce and trembling aspen, the AIC is expressed by:

$$\mathrm{AIC} = -2(\text{log-likelihood}) + 2K$$

where K is the number of parameters in the model (including intercept, shape and scale).

For jack pine, the sample size was small relative to the number of parameters (i.e. $n/K < 40$). Hence, the second-order Akaike information criterion ($\mathrm{AIC_c}$) was used (Burnham and Anderson 2002), as expressed by:

$$\mathrm{AIC_c} = -2(\text{log-likelihood}) + 2K + 2K(K+1)/(n-K-1)$$

When several models competed for top rank ($\Delta\mathrm{AIC_c} < 2$), indicating uncertainty regarding the best model, we used multimodel inference (Burnham and Anderson 2002). By computing a weighted average of the regression coefficients of a given variable for all models including that variable, model-averaged estimates and unconditional standard errors were generated and used to build a 95% confidence interval, enabling us to assess the magnitude of the effect of this specific variable.

Tree fall pattern

After removal of dead trees that were still standing at the end of the observation period and individuals that were not followed throughout the entire observation period (i.e. censored data), we investigated detailed fall patterns for each individual to reconstruct the successive transit from one status to another. Any combination (double or multiple) of the following status was considered as a separate fall pattern class: living, standing dead intact, standing dead broken, fallen broken at the base, fallen uprooted (e.g. one fall pattern class is characterised by the successive following status: living to standing dead intact, to standing dead broken, to fallen broken at the base).

As broken snags have been found to be more persistent than intact ones, we compared the interval from death to fall in snags that fell after breaking at the base versus snags that exhibited other fall patterns using a Wilcoxon rank sum test because normality of variance was not met even when the data were transformed.

Results

Survival curves of trees after fire

In the year of fire (1997), tree survival varied between 76 and 93% in lightly burned stands and 52 and 63% in moderately burned stands, depending on stand composition (Fig. 1). Tree survival generally dropped considerably the second year (1998) and continued to decrease less drastically in the 3 following years, particularly in lightly burned stands (1998–2000).

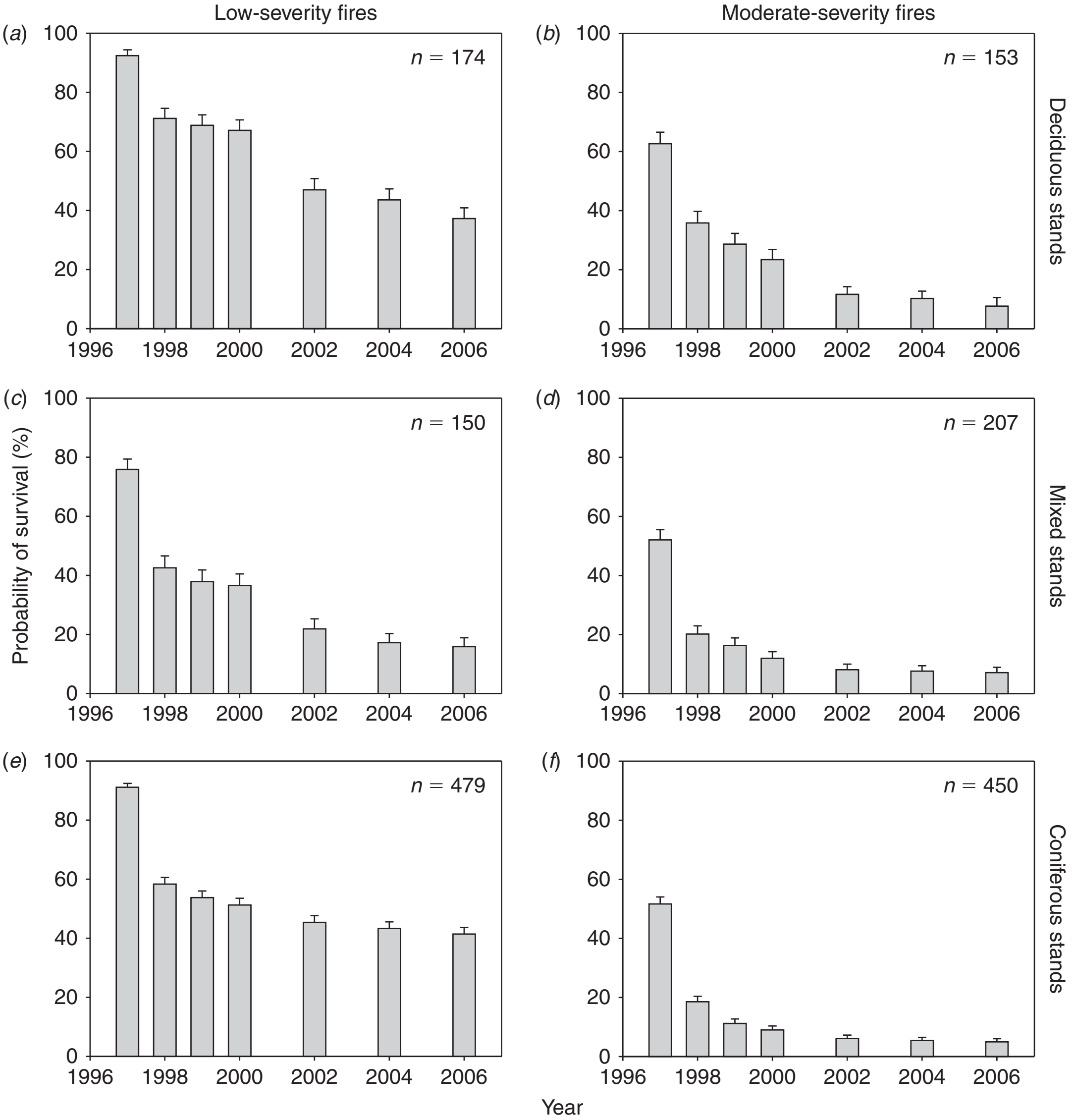

Fig. 1. Survival probability (±s.e.) of trees after fire in: (*a*) lightly burned deciduous stands; (*b*) moderately burned deciduous stands; (*c*) lightly burned mixed stands; (*d*) moderately burned mixed stands; (*e*) lightly burned coniferous stands; and (*f*) moderately burned coniferous stands (see Methods for a description of composition and fire severity classes). Different letters indicate significantly different survival curves among stand types as tested using the LIFEREG procedure and log-rank test (six combinations compared simultaneously). Survival probabilities are only presented for lightly and moderately burned stands as mortality was ≥98% the year of fire in severely burned stands.

Although trees continued to die every year during the observation period in every stand type, tree mortality tended to stabilise during the last 5 years of observation (2002–06), especially in moderately burned stands.

The differences between initial tree survival (1997) and survival at the end of the observation period (2006) varied between 45 and 60% in low- and mid-severity fires. Even though high tree mortality occurred in all stand types, survival at the end of the observation period remained higher in low-severity fires than in moderate-severity ones.

Both fire severity and stand composition influenced tree survival rates (LIFEREG procedure, log-rank test, $P \leq 0.0001$ and 0.0021 respectively). As expected, trees in lightly burned stands were more likely to survive than those in moderately burned stands, even in the long term (Fig. 1). Trees from deciduous stands generally had greater survival rates than those from mixed and coniferous stands whereas trees from mixed stands had lower survival rates than those from coniferous stands in which fire severity was low.

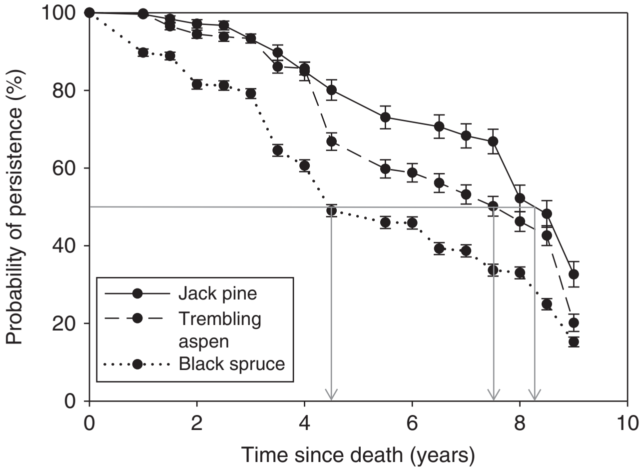

Fig. 2. Probability of post-fire snag persistence over time in three species using the LIFETEST procedure and log rank test. Grey arrows indicate half-lives.

Persistence curves of snags after fire

Snag persistence curves differed significantly for each species (LIFETEST procedure, log-rank test, $P<0.0001$, Fig. 2). Jack pine snags were the most persistent, black spruce the least, whereas trembling aspen snags were intermediate. Both jack pine and trembling aspen snags exhibited a reverse sigmoid function with evident time lags, i.e. initial periods of high snag persistence during the first 3 years (>85% persistence) followed by higher fall rates. Black spruce snags exhibited a more constant fall rate though time. Half-life of snags, the time required for half the stems to fall to the forest floor, was 4.4 years for black spruce, 7.5 years for trembling aspen and 8.3 years for jack pine. Survival analysis showed that 10 years after their death, 15.3% of black spruce snags, 20.1% of trembling aspen snags and 32.6% of jack pine snags were still standing. Given that tree mortality was delayed throughout the observation period, it is worth noting that these results are related to time since death, not time since fire. Moreover, these values must not be confused with the percentage of all dead trees that died during or after the fire and were still standing at the end of the observation period, which was somewhat higher. Specifically, 22.1% of black spruce snags, 44.8% of trembling aspen snags and 61.9% of jack pine snags were still standing at the end of the observation period.

Variables influencing snag persistence

Multimodel inference showed that fire severity was the only factor common to all tree species that influenced snag persistence: snag fall was less when stand fire severity was higher (Table 2). For trembling aspen and jack pine, the difference was significant among all severity classes. In black spruce, the difference was significant only when comparing lightly and severely burned stands. No significant differences occurred between lightly and moderately burned or between moderately

Table 2. Parameters associated with snag persistence according to multimodel inference

DBH, diameter at breast height; SEV, fire severity; L, low fire severity; M, moderate fire severity; H, high fire severity; BA, stand basal area (all species included); SALVG, proportion of salvage-logged area in a 100-m radius

Species	Parameter	Scale	Model-averaged estimate	Unconditional s.e.
Trembling aspen ($n=453$)	DBH (+)	Tree	0.01340	0.00330
	SEV (L *v.* H) (−)		−0.62727	0.08732
	SEV (L *v.* M) (−)	Stand	−0.45616	0.07853
	SEV (M *v.* H) (−)		−0.17111	0.05453
	BA (−)	Stand	−0.01888	0.00291
Jack pine ($n=244$)	SEV (L *v.* H) (−)		−0.57138	0.11133
	SEV (L *v.* M) (−)	Stand	−0.27186	0.07562
	SEV (M *v.* H) (−)		−0.35018	0.13229
Black spruce ($n=1039$)	SEV (L *v.* H) (−)	Stand	−0.12372	0.05620
	SALVG (−)	Landscape	−0.00677	0.00082

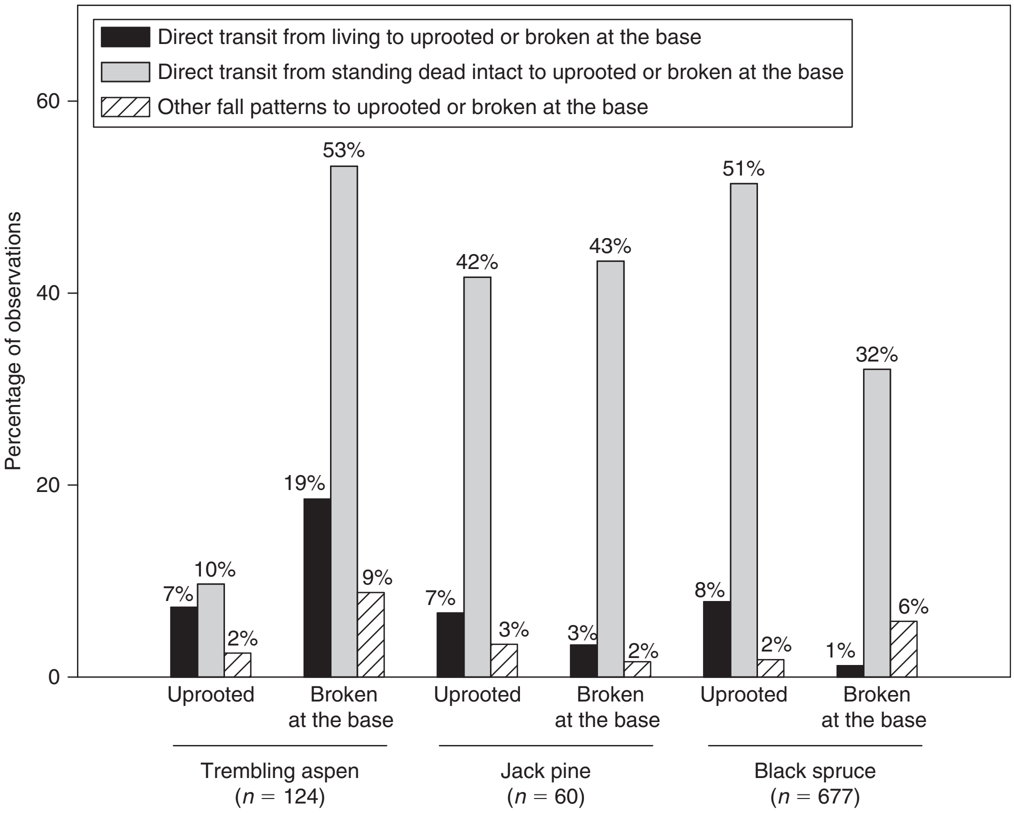

Fig. 3. Main fall patterns in fallen trembling aspen, jack pine and black spruce trees after fire.

Table 3. Persistence time as snags for fallen trembling aspen, jack pine and black spruce trees after fire according to specific fall patterns

Note: within a given species, values followed by the same lowercase letter do not differ significantly ($P < 0.0001$)

Mean interval from death to fall (years, mean ± s.e. (range))	Trembling aspen ($n = 124$)	Jack pine ($n = 60$)	Black spruce ($n = 677$)
Standing dead broken snags that fell after breaking at the base	$7.1^a \pm 0.5$ (3.5–8.5)	–[A]	$6.9^a \pm 0.4$ (1.0–8.5)
All other fall patterns	$2.9^b \pm 0.2$ (0.0–8.5)	4.2 ± 0.3 (0.0–8.5)	$3.4^b \pm 0.1$ (0.0–8.5)

[A] Only one stem that fell after breaking at the base was previously standing dead broken.

and severely burned stands. Fire severity was the only significant factor influencing snag persistence in jack pine.

Other factors influencing snag persistence were species-specific (Table 2). Variables from tree, stand and landscape scales were found to influence snag persistence in one species or another. For trembling aspen, large snags were more persistent than small ones, whereas snags located in stands with high basal area were more susceptible to fall. The only species for which the landscape-scale variable was significant was black spruce, with snags surrounded by a high proportion of salvage-logged burned stands being more susceptible to fall.

Tree fall patterns

All fall pattern classes representing at least 5% of stems in one species are presented in Fig. 3. In most cases, trees changed from a standing dead intact status to fallen, whether by breaking at the base or by uprooting (63 to 85% depending on species). Uprooting prevailed in black spruce (61%) whereas 81% of trembling aspen fell by breakage at the base. In jack pine, uprooting and breakage at the base were approximately equivalent (52 and 48% respectively). Direct transit from living to fallen status, whether by breakage at the base or uprooting, was common in trembling aspen (26%) whereas it was close to 10% for the two other species. Snags of trembling aspen and black spruce that were already broken at some point along the bole and that fell by breaking at the base were at least two times more persistent than snags that experienced any other fall pattern (Table 3, $P < 0.0001$ in both species).

Double breakage, i.e. breakage at the base of a snag already broken, although not prevalent, was observed in 9% of trembling aspen snags and in 6% of cases in black spruce. Multiple breakage values are, however, more frequent. Indeed, height of snags was only measured during the two last surveys (2004 and 2006). The status of a broken snag from which the stem would have been broken a second time was considered as the same (standing broken) throughout the survey. For broken snags still standing in 2006 for which height was estimated in 2004, 11% of black spruce snags and 14% of trembling aspen snags experienced a reduction in height. Multiple breakages were uncommon in jack pine, as only one snag out of 53 experienced a height reduction during that interval.

Discussion

This study provides a unique dataset of trees that were repeatedly surveyed over a long time frame following a wildfire. A large number of trees were monitored yearly or every second year over a 10-year period. Many forest cover types representative of the boreal ecosystems of eastern North America were included in our study design that combined forest cover composition with fire severity classes. To our knowledge, our study is the first to provide such a detailed assessment of tree mortality and snag dynamics in the first years following fire in the boreal forest. Moreover, no other study on post-fire tree mortality or fire-killed snag dynamics provides such a large number of permanent study sites surveyed over a long time period.

Survival curves of trees after fire

Our results clearly show delayed mortality of tree species in boreal forest ecosystems following low- and moderate-severity wildfires. To our knowledge, our study is the first to provide a quantitative assessment of this phenomenon in boreal ecosystems. In studies conducted on 4- to 10-year post-fire periods, delayed tree mortality has been reported in low- to moderate-severity wildfires in aspen (Brown and DeByle 1987) and ponderosa pine (*Pinus ponderosa* Dougl.) stands (Keyser *et al.* 2006) as well as in prescribed burns in Douglas-fir (*Pseudotsuga menziesii* Mirb.) (Ryan *et al.* 1988) and ponderosa pine (Harrington 1993) stands. In our study, we found approximately the same tree mortality pattern in all stand types: a strong pulse of mortality in the first 2 years after the fire, followed by a period of ongoing but low mortality in the following years. This pattern was also reported in the above studies.

For a given fire severity class, significant differences in survival curves were found across stand composition. However, these compositional differences were most likely attributable to the initial survival value. Indeed, when initial survival was higher in one stand type compared with another, survival at the end of the observation period was also usually higher. Furthermore, differential in survival (Δ initial – final survival value) was similar among severity classes (10% difference maximum).

Large boreal fires are generally considered to induce mortality of most trees (Johnson 1992). However, in the eastern Canadian boreal forest, partial tree mortality following wildfire has been shown to represent large proportions of area burnt (Kafka *et al.* 2001; Bergeron *et al.* 2002). When fire severity is heterogeneous, lightly and moderately burned stands exhibit an initial large amount of green tree retention. Nevertheless, delayed tree mortality may lead to a considerably lower rate of tree survival. For instance, in moderately burned stands in our study, mortality increased by an additional 44 to 50% during the 5 years after fire, resulting in survivorship of 6–11% (Fig. 1). Consequently, stands initially classified moderately burned would have been classified as severely burned stands (tree survival $\leq 25\%$) if classification had been done 5 years after fire. Hence, tree mortality following fire is an ongoing process in areas where fire severity is low to moderate at the time of the fire event.

Tree survival tended to stabilise in the last years of our census, suggesting that trees that survived 10 years after fire will generally remain alive. These legacy trees will contribute to maintaining a forest cover, increasing structural diversity and providing dead wood as they progressively die in the regenerating stands.

Snag persistence after fire

Few quantitative data exist on the persistence of snags after wildfire for the species under study. Most studies were conducted in the western United States and present half-lives similar to those found in our study, even though snags sometimes exhibited much larger sizes (Dahms 1949; Everett *et al.* 1999; Passovoy and Fulé 2006; Russell *et al.* 2006). In the eastern boreal forest, three studies assessed post-fire snag persistence for the studied species. Using a chronosequence approach in black spruce forests, Boulanger and Sirois (2006) found a half-life of 16.2 years in post-fire stands located 500 km north of our study area. In Manitoba, Canada, Bond-Lamberty and Gower (2008) found that only 23% of black spruce snags had fallen from year 1 to year 9 after fire. For jack pine, 86 to 100% of the snags were still standing 9 years after fire in burned stands located 350 km north-east of our study area (V. A. Angers, unpubl. data). All studies found much longer persistence than that we reported. This will be discussed in greater detail in the next section.

For both jack pine and trembling aspen, the nearly yearly monitoring of tree fall within the first 10 years following the fire showed a reverse sigmoid curve exhibiting a period of high retention in the first years after death before the onset of higher rates of snag fall. This pattern is consistent with other studies conducted on fire-killed snags (Chambers and Mast 2005; Russell *et al.* 2006) or snags that died of other causes (Keen 1929; Cline *et al.* 1980; Lee 1998; Garber *et al.* 2005; Mäkinen *et al.* 2006; Taylor and MacLean 2007; Angers *et al.* 2010). The 3-year lag time following death observed in our study is low but within the range of those obtained in other studies conducted on boreal tree species with similar DBH in mature forests (1–13 years; Lee 1998; Garber *et al.* 2005; Taylor and MacLean 2007; Angers *et al.* 2010).

Fire-killed snags are generally considered to be less persistent when compared with snags from the same species killed by causes other than fire (Morrison and Raphael 1993). In our study, this was the case for the three species under investigation. Trembling aspen's half-life was up to three times less than reported half-lives for aspen snags in late-seral forests (Lee 1998; Vanderwel *et al.* 2006; Angers *et al.* 2010). In black spruce, reported half-lives ranged from 18 to 40 years in late-seral forests (Aakala *et al.* 2008; Angers *et al.* 2010) compared with 4.4 years in our study. As observed with other mortality causes, jack pine post-fire snags were the most persistent. Angers *et al*. (2010) found half-lives of 26 years for jack pine snags sampled in late-seral forests, which is more than three times what was found in our study.

Factors influencing snag persistence

Variables from all scales (tree-, stand- and landscape-level) significantly influenced snag persistence in our study. However, explanatory variables differed among species.

Trembling aspen was the only species for which DBH had an influence on snag persistence, with larger DBH snags being more persistent than smaller ones. Numerous studies have reported that size is influential in post-fire snag persistence (Dahms 1949; Morrison and Raphael 1993; Everett *et al*. 1999; Chambers and Mast 2005; Russell *et al*. 2006). However, these studies were conducted in ecosystems where trees were much larger than those sampled in the present study. In our study, the lack of a relationship between snag persistence and size observed in jack pine and black spruce corroborates our results for these species in late-seral stands of the same region (Angers *et al*. 2010). This is probably related to the relatively narrow DBH range of jack pine and black spruce snags, which impedes the detection of a size effect (Johnson and Greene 1991; Lee 1998; Kruys *et al*. 2002; Storaunet and Rolstad 2002). Trembling aspen exhibited a much higher average DBH and, hence, a wider range of DBH size than jack pine and black spruce (Table 1). Sampling larger jack pine and black spruce snags could potentially provide a better test of the size effect on snag persistence for these species.

In trembling aspen, snags in stands with high basal area (all species included) were more susceptible to fall. Trees growing in stands with low stem density experience continuous wind exposure and develop physical characteristics for wind firmness compared with those that grow in denser stands where wind exposure is lower because surrounding stems provide shelter (Mitchell 1995). When a disturbance opens the stands, as is the case with fire and salvage logging, trees grown in low-basal area stands may better resist wind exposure. Alternatively, Chambers and Mast (2005) found that snags with higher basal area in ponderosa pine stands in Arizona were less prone to fall.

For all species, snags located in severely burned stands were less likely to fall compared with those in lightly burned stands. To our knowledge, no other published study has reported that fire severity influences snag persistence. A possible explanation for such a pattern may be that biological agents such as fungi and saproxylic insects that initiate and maintain decaying activities in wood are less active on severely burned snags (Rayner and Boddy 1988; Saint-Germain *et al*. 2004) given their lower moisture content (Boulanger and Sirois 2006). In addition, wood desiccation of snags in severely burned stands might be exacerbated by many factors including the relatively thin bark of the studied species (which does not provide sufficient insulation to protect subcortical tissues), the more rapid bark loss experienced by coniferous species compared with those from other fire severity classes ($P \leq 0.0015$, data not shown), and the sun- and wind-exposed conditions that occur when mortality is high.

Whereas we suggest that moisture level is likely to explain the differential persistence rates in post-fire snags observed in our study, it does not constitute a dominant factor in all situations. For instance, one could expect that the higher humidity levels in unburned mature stands would provide higher water content in snags that should lead to higher fall rates and shorter snag half-lives. This is not the case in unburned forests (Lee 1998; Vanderwel *et al*. 2006; Aakala *et al*. 2008; Angers *et al*. 2010). The study by Morrison and Raphael (1993) in burned and unburned forests of California's Sierra Nevada also documented shorter snag half-lives of snags in burns when compared with unburned stands. Their interpretation of such patterns includes the direct effect of fire that weakens the base of the snag and more direct exposure to wind in comparison with snags surrounded by live trees.

In addition to being more exposed to wind in a burned landscape, our permanent plots were embedded in a heavily salvage-logged matrix where more than 90% of commercial timber was salvage logged using clear-cuts. Hence, even though we did not measure wind conditions, the removal of surrounding snags likely increased wind exposure and fall susceptibility for retention trees and snags of our permanent plots, at least to a level that might be close to what has been documented in forest edges of remnant habitats in boreal ecosystems under clear-cutting (Esseen 1994; Harper *et al*. 2004; Mascarúa López *et al*. 2006; see Ruel 1995 for a review). This could explain the remarkably low snag persistence rates in our study, which were at least three times shorter than were observed in stands that experienced high-severity fires with either unsalvaged or lightly salvage-logged surroundings (Boulanger and Sirois 2006; Bond-Lamberty and Gower 2008; V. A. Angers, unpubl. data).

Influence of salvage logging on snag persistence in residual burned stands has seldom been addressed. The only other results were reported by Russell *et al*. (2006), who found no significant differences in persistence rates of snags sharing the same characteristics in salvage-logged or unlogged sites. Burned stands from the study of Russell *et al*. (2006) were salvage-logged using partial cuts and composed of Douglas-fir and ponderosa pine, two species that grow to larger diameters than the species in the current study and that are not particularly susceptible to windthrow.

In our study, we found that black spruce snag persistence was reduced by nearby salvage logging. Because of its lateral and very shallow root system (Viereck and Johnston 1990), black spruce is particularly vulnerable to uprooting compared with the other species (Ruel 1995), as seen in tree fall pattern results (Fig. 3). In addition, superficial root mortality induced by fire (Smirnova *et al*. 2008) may have amplified this vulnerability.

Our results enabled us to highlight the vulnerability of black spruce snags to fall in a salvage-logged context, but did not allow us to distinguish the effect of fire from salvage logging on snag persistence or to conclude that salvage logging has no effect on jack pine and trembling aspen. Both fire and salvage logging induce an opening of the canopy and a higher exposure to wind. In our study, in order to get enough variability to proceed with the modelling, we selected a 100-m radius around the plots to assess the influence of the surrounding landscape. However, a larger radius might be necessary to draw conclusions on the influence of the surrounding landscape. As much of the burned area was salvage logged, variability in the proportion of salvage-logged surroundings was low when considering a larger radius than that we used and no sites were located in a large, unsalvaged burned matrix. Sampling in a wildfire where spatial distribution of salvage-logged areas was more variable and included large patches of intact burns would allow us to assess the influence of fire alone as well as salvage logging on fall vulnerability. Unfortunately, extensive areas of burned forest that are accessible and have not been salvage logged are rare in Québec (Jayen 2004; Nappi *et al*. 2004).

Tree fall patterns

The classic degradation process presented in decay classifications, i.e. transition from a living tree to an intact standing dead tree, to a shortened snag following successive breakages, and ending in a stump (e.g. Maser *et al*. 1979) represented a low proportion of snags in our dataset (less than 10% in all species). This pattern was mostly observed in trembling aspen, a species with wood that decomposes more rapidly than coniferous species (Alban and Pastor 1993; Brais *et al*. 2006; Saint-Germain *et al*. 2007; V. A. Angers, P. Drapeau and Y. Bergeron, unpubl. data) and develops extensive columns of decay within the stem (Basham 1991) that favour successive breakage. A relatively large proportion of trees from all species bypassed the snag stage, as they were either uprooted or broken at the base (below 1.3 m) while alive. Trembling aspen was the species exhibiting the most important deficit in snag recruitment, with a quarter of the fallen stems that fell while alive (mostly broken at the base).

Uprooting has been extensively studied in living trees (e.g. Smith *et al*. 1987; Ruel 1995) but has only seldom been reported in snags (Taylor and MacLean 2007; Y. Bergeron, pers. obs.). Our results not only document this possibility, but clearly show that it may be a common fall pattern for the fire-killed coniferous species studied, particularly for black spruce where it is dominant. Uprooting in snags may prevail following a disturbance causing massive mortality because the opening of the canopy likely allows wind to enter more freely within stands. In such cases, salvage logging becomes a second disturbance that increases the vulnerability of trees and snags to wind.

As also found in unburned mature stands in the same region (Angers *et al*. 2010), jack pine consistently appeared to be highly breakage-resistant when compared with the other two species in burned plots. This might be explained by jack pine having the highest wood density, particularly in latewood, and the highest modulus of rupture of the studied species (Jessome 1977; Panshin and De Zeeuw 1980).

Several authors have reported that broken-topped snags are more likely to remain standing than others (Dahms 1949; Morrison and Raphael 1993; Chambers and Mast 2005). In our study, this was clearly the case for trembling aspen and black spruce (Table 3). Stability of broken-topped snags is likely enhanced because the loss of branches reduces wind stress and snow loading when the crown is partially or completely gone (Dahms 1949; Lee 1998; Huggard 1999).

Conclusion: ecological and management implications

Although fire provides a strong and synchronised pulse of tree mortality, delayed mortality in years following fire also occurs and represents a significant portion of total mortality in stands affected by low- and mid-severity fires. In this study, tree mortality was still ongoing 10 years after the fire. In managed ecosystems where green retention is implemented, managers often face the hastened death of several residual trees in the years following harvesting (Esseen 1994; Vanha-Majamaa and Jalonen 2001). This retention approach has been criticised as managers often consider legacy trees as a waste. However, our study shows that mid- and long-term tree mortality in partially burned stands is a common process in deciduous, mixed and coniferous stands. Green retention and the potential death of legacy trees in even-aged stands could thus be considered to a certain extent as a surrogate of tree mortality and snag dynamics in early post-fire stands. Moreover, the rates at which trees die and snags break and fall after fire can have tremendous implications for several ecosystem processes, including carbon balance and key habitat attributes recruitment.

Considering dead wood dynamics, i.e. inputs and decomposition rate of dead trees, in assessments of regional and global carbon budgets is crucial as dead wood represents an important source of carbon. This is especially important after wildfire in boreal forests as a considerable amount of dead wood is produced and because this disturbance affects large parts of that biome (Kasischke 2000; Bond-Lamberty *et al*. 2002). Delayed mortality following fire as observed in the present study does not only represent a larger total amount of carbon released than expected when considering initial mortality, but also influences the timing of the release by postponing some of it. Furthermore, as decomposition is more rapid in downed dead wood than in snags (Harmon *et al*. 1986; Yatskov *et al*. 2003; Boulanger and Sirois 2006), the variability in snag persistence can also greatly influence carbon balance (Bond-Lamberty and Gower 2008) and can even make the difference between the stand being a carbon sink or source (Bond-Lamberty *et al*. 2004).

Spatial and temporal tree mortality patterns may also have major implications for various structural habitat attributes for a wide range of species associated with decaying, standing and fallen dead wood (Drapeau *et al*. 2009). Delayed tree mortality in lightly and moderately burned stands involves a delayed recruitment of snags and downed dead wood. In a forest matrix where fire severity is heterogeneous, this continuous input of fresh dead wood creates the simultaneous availability of dead wood of different degradation stages. This diversity of dead wood substrate can have a marked influence on the occurrence of organisms associated with specific decay classes (Nappi 2009) while allowing the prolonged persistence of species associated with recently dead trees in burned systems (Nappi *et al*. 2010). In ecosystems where nurse logs are important to seedling establishment and development, the delayed mortality and the recruitment of fallen snags over time may also influence regeneration patterns (Harmon *et al*. 1986).

Only large trembling aspen snags were found to be more persistent than small ones, and this result is likely due to the fast-growing potential of this species compared with black spruce and jack pine. In this regard, in ecosystems where trembling aspen is a companion of species growing more slowly, particularly when in association with conifers, large trembling aspen snags may represent key elements owing to their greater persistence and to the fact that this species is preferentially used by primary excavators (Martin *et al*. 2004; A. Gasse, P. Drapeau and L. Imbeau, unpubl. data).

Finally, tree mortality and snag dynamics in this study were influenced by salvage logging, a management practice that is evolving worldwide in recently burned forests (Lindenmayer *et al*. 2004; Nappi *et al*. 2004; Schmiegelow *et al*. 2006). Hence, our results may be useful in a post-fire forest-management strategy where planning includes both harvesting operations and the conservation of burned patches to ensure biodiversity and regeneration functions through snag conservation and recruitment (Drapeau *et al*. 2002; Nappi *et al*. 2004; Hannon and Drapeau 2005).

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Appendix. Akaike's information criterion (AIC) and AIC_c parameters of the multiple linear regression models of snag persistence by species

DBH, diameter at breast height; COMP, stand composition; SEV, fire severity; BA, stand basal area; SALVG, proportion of salvage-logged area in a 100-m radius. *K* data are the number of parameters including intercept and variance; w_i, Akaike weight

Model	Model ID	log-likelihood	*K*	AIC	ΔAIC	w_i
Trembling aspen ($n = 453$)						
NULL (intercept only)	1	−367.75	3	741.49	110.32	0.00
DBH	2	−350.11	4	708.22	77.05	0.00
COMP	3	−367.35	4	742.70	111.53	0.00
SEV	4	−330.65	5	671.31	40.13	0.00
BA	5	−367.73	4	743.46	112.28	0.00
SEV + BA	6	−315.12	6	642.25	11.08	0.00
COMP + SEV + BA	7	−315.03	7	644.05	12.88	0.00
SALVG	8	−353.84	5	717.68	86.51	0.00
DBH + SEV	9	−327.57	6	667.13	35.96	0.00
DBH + SALVG	10	−343.71	6	699.41	68.24	0.00
SEV + SALVG	11	−330.07	7	674.14	42.97	0.00
DBH + SEV + SALVG	12	−327.05	8	670.10	38.93	0.00
FULL:DBH + COMP + SEV + BA + SALVG[A]	13	−305.59	10	631.17	0.00	0.99
Jack pine ($n = 244$)[B]						
NULL (intercept only)	1	−187.47	3	381.04	29.87	0.00
DBH	2	−186.91	4	381.99	30.82	0.00
SEV[A]	4	−170.46	5	351.17	0.00	0.49
BA	5	−186.55	4	381.26	30.10	0.00
SEV + BA[C]	6	−170.37	6	353.09	1.92	0.19
SALVG	8	−182.44	5	375.14	23.97	0.00
DBH + SEV	9	−170.44	6	353.24	2.07	0.17
DBH + SALVG	10	−181.60	6	375.55	24.38	0.00
SEV + SALVG	11	−169.97	7	354.42	3.25	0.10
DBH + SEV+SALVG	12	−169.96	8	356.54	5.37	0.03
FULL:DBH + COMP + SEV + BA + SALVG	13	−169.09	9	356.94	5.77	0.03
Black spruce ($n = 1039$)						
NULL (intercept only)	1	−1184.40	3	2374.81	72.27	0.00
DBH	2	−1183.66	4	2375.32	72.77	0.00
COMP	3	−1176.68	5	2363.36	60.82	0.00
SEV	4	−1180.50	5	2371.01	68.47	0.00
BA	5	−1183.29	4	2374.58	72.03	0.00
SEV + BA	6	−1179.87	6	2371.74	69.20	0.00
COMP + SEV + BA	7	−1165.86	8	2347.72	45.18	0.00
SALVG[C]	8	−1147.03	5	2304.06	1.52	0.19
DBH + SEV	9	−1179.82	6	2371.63	69.09	0.00
DBH + SALVG	10	−1146.41	6	2304.82	2.27	0.13
SEV + SALVG[A]	11	−1144.27	7	2302.54	0.00	0.40
DBH + SEV + SALVG[C]	12	−1143.67	8	2303.34	0.80	0.27
FULL:DBH + COMP + SEV + BA + SALVG	13	−1143.44	11	2308.89	6.34	0.02

[A] Best model according to Akaike model selection approach.

[B] Jake pine data presented for AIC and ΔAIC are in fact for AIC_c and ΔAIC_c.

[C] Models competing for best model according to Akaike model selection approach ($\Delta AIC_c < 2$).