Assessing and modeling snag survival and decay dynamics for the primary species in the Acadian forest of Maine, USA

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ABSTRACT

Snags are an important component of forest structure and a key carbon pool, but there is currently a limited understanding of their survival and decay in the Acadian region of North America. Using standing and fallen snag observations collected from permanent sample plot (PSP) remeasurements at a long-term, replicated silviculture methods experiment in central Maine, USA, the objective of this analysis was to develop quantitative models to better understand snag survival and decay dynamics. Species examined included the conifers Abies balsamea, Picea rubens, Thuja occidentalis, and Tsuga canadensis, and the hardwoods Acer rubrum and Betula papyrifera. Proportional hazards regression models that estimate the 5-year probability (Pr) of snag survival indicated that observed decay class (a measure of snag decomposition) could be used as a surrogate for years since death given the difficulties and errors associated with determining years since death for standing snags. Averaged across all species, Pr (5-year snag survival) estimated as a function of snag diameter at breast height (dbh) in decay classes 1, 2, 3, and 4 were predicted as 0.69 ± 0.09 (mean ± standard deviation), 0.36 ± 0.09, 0.16 ± 0.05, and 0.06 ± 0.02, respectively. Where snag dbh was significant in estimating survival (3 of 6 species), hazard ratios indicated that snag survival would increase by as much as 24% for each 10 cm increase in dbh, but was dependent on species. Probability matrices predicting the 5-year likelihood of snags transitioning to advanced decay classes or falling showed that T. canadensis and T. occidentalis snags were slowest to decay, as measured by the average time it takes for a snag to progress from decay class 1–4. Probability of snag height-loss, predicted using snag dbh and the harvest interval of the stand, was estimated to be highest for larger dbh snags found in stands with frequent harvest intervals (e.g. 40 cm dbh and every 5 years). Models predicting the amount of volume reduced in standing snags through time were related to the estimated total volume of a live tree with the same dbh, mode of death, and general decay stage (i.e. soft versus hard). When used together, these models quantifying snag dynamics and associated species and size differences can serve as tools for managers to estimating standing deadwood stocks in mixed-species stands found throughout the Acadian region.

1. Introduction

Monitoring coarse woody debris levels in managed forests is an essential component of determining forest carbon stocks, gauging forest fuel loads, and quantifying biodiversity potential. Specifically, snags (standing dead trees) are key elements for maintaining forest biodiversity and providing a heterogeneous forest structure (Harmon et al., 1986). Whether standing or fallen, decaying snags and logs store carbon and are an important process in forest carbon dynamics as they release carbon through decomposition (Harmon et al., 2011).

Managing for snags and deadwood attributes (i.e. their size, mode of death, and decay stage) has recently become a requirement for many forest certification programs (e.g. Sustainable Forestry Initiative, 2004). In the northeastern USA and eastern Canada, site-specific management guidelines have been established that seek to institute a baseline for maintaining healthy snag densities (Woodley, 2005; Elliot, 2008; Benjamin, 2010). However, the shortfalls of models depicting snag characteristics was recently highlighted by Woodall et al. (2012), who found that models predicting carbon stocks for standing snags in the USA were overestimated by 100% when compared to observed field measurements.

From a probabilistic perspective, snag survival rate (defined as the probability of a standing dead tree to remain standing for a

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given duration) is considered the complement to snag fall rate. Understanding the dynamics of both provides insight into losses in snag population and recruitment of downed wood populations (Angers et al., 2010). A common approach in many analyses has been to fit curves employing a reverse sigmoid function to estimate the probability of snag survival (e.g. Garber et al., 2005; Aakala et al., 2008; Angers et al., 2010), which has been shown to be related to a host of variables including species, snag size, agent of mortality, decay stage, stand age, stand density, and type of forest management (Lee, 1998; Garber et al., 2005; Vanderwel et al., 2006; Aakala et al., 2008; Smith et al., 2009; Angers et al., 2010). Larger diameter snags may (Garber et al., 2005; Yamasaki and Leak, 2006) or may not (Vanderwel et al., 2006; Holeksa et al., 2008) display greater longevity than smaller diameter snags, or their longevities may be approximately equal (Lee, 1998). Forest management practices may reduce snag abundance and recruitment through removing trees deemed to be unacceptable growing stock (Cline et al., 1980).

To estimate snag decay dynamics Kruys et al. (2002), presented an approach to calculate the 5-year probability of snags advancing in decay stage, while Aakala et al. (2008) furthered this work by including the probability of a snag falling when characterizing snag decomposition. They also found the decay class of snags to be a useful predictor in estimating the proportion of snags remaining standing (Aakala et al., 2008).

Estimating the amount of volume reduced through time as snags decay is important in understanding the dynamics between snag and downed wood fluxes. Snag height loss, and ultimately snag volume loss, has been related to species and whether or not a snag displays a broken or intact top (Ganey and Vojta, 2005). Modeling efforts predicting the proportion of snags remaining through time have employed reverse sigmoid curves using years since death (Radtke et al., 2009) and decay stage (Aakala et al., 2008) as predictors. Little research has been conducted for the primary species in the Acadian forest region assessing the degree to which snags lose volume. Current snag height-loss equations within the Forest Vegetation Simulator–Fires and Fuels Extension (FVS–FFE), a widely-used growth model throughout the Acadian region, assume a fixed proportion of height lost annually (Rebain et al., 2009). In addition, FVS–FFE uses an equation originally parameterized for Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) in the US Pacific Northwest for modeling the decay of snags for all species nationwide (Rebain et al., 2009).

Storaunet and Rolstad (2004) concluded that using years since death is most feasible for developing snag survival functions, however, the actual time when a tree died and entered the snag population is often unknown. This is an important variable because snags are required to be specified as either right- or left-censored when developing survival equations (Gore et al., 1985). There are several limitations in using years since death to estimate snag survival. First, years since death cannot be directly measured on a snag in the field. Commonly, analyses will assign the year of death as the midpoint between the last year the tree was observed alive and the first year the tree was observed dead (e.g. Garber et al., 2005). This interpolated year of death is a strong assumption, especially when studies that employ permanent sample plots (PSPs) are inventoried on a 10-year cycle (a common cycle used throughout the Acadian region) and when half-times for snag survival can be as short as 6 years, as was shown for some *Picea* species in the region (Garber et al., 2005). Second, method of tree death is not taken into account when determining years since death. As an example, severe wind events such as microbursts may create an immediate pulse of snags through breakage of stems, while a forest stand beginning to undergo self-thinning may lead to a gradual accretion of snags that will die through suppression. Third, years since death is difficult to quantify for snags in advanced decay stages,

especially for studies that determine years since death through extracting tree cores and analyzing tree rings (e.g. Aakala et al., 2008; Angers et al., 2010). These reasons necessitate the investigation of surrogates for years since death such as stage of decay and mode of tree death. This would be advantageous for trees growing in mixed-species stands in the Acadian region because numerous agents of mortality affect trees and the multitude of conifer and hardwood species display varying wood densities, which when coupled with measures of snag size and other factors, could influence snag survival.

The primary objective of this analysis was to develop quantitative tools to better understand the dynamics between the survival and decay of snags in the Acadian forest region. Specific objectives of this analysis were to: (1) determine differences in snag attributes for six common species found across the Acadian region using remeasurement data from PSPs located in central Maine, (2) estimate the probability of snag survival using snag decay stage as a surrogate for years since death, and (3) predict height and volume reduction in decaying snags as a function of decay stage and mode of death.

2. Methods

2.1. Study area

The Acadian forest region falls in the transition zone between the conifer-dominant boreal forests to the north and the broadleaf forests to the south (Braun, 1950; Rowe, 1972). Three Canadian Maritime Provinces (New Brunswick, Nova Scotia, and Prince Edward Island) are found in the region, along with southern portions of Québec and much of the US state of Maine. Specifically, this study was conducted on the 1619 ha Penobscot Experimental Forest (PEF) located in the towns of Bradley and Eddington, Maine (44°52′N, 68°38′W). Mean annual temperature and annual precipitation are 6.2 °C and 110 cm, respectively. The principal soil material of the PEF is glacial till. Soils range from well-drained loams and sandy loams found on glacial till ridges to poorly- and very poorly-drained silt loams found in flatter areas between ridges (Sendak et al., 2003). The PEF is characterized by a mixture of northern conifer and hardwood species that dominate its forest cover. Conifer species include red (*Picea rubens* Sarg.), black (*P. mariana* (Mill.) BSP), and white spruce (*P. glauca* (Moench) Voss), balsam fir (*Abies balsamea* (L.) Mill.), eastern hemlock (*Tsuga canadensis* (L.) Carr.), and eastern white pine (*Pinus strobus* L.). Hardwood species include red maple (*Acer rubrum* L.), paper (*Betula papyrifera* Marsh.) and gray birch (*B. populifolia* Marsh.), and quaking (*Populus tremuloides* Michx.) and bigtooth aspen (*P. grandidentata* Michx.).

An operational scale experiment to compare nine silvicultural treatments was established by US Forest Service (USFS) researchers between 1952 and 1957. Experimental units were laid out primarily in red spruce–balsam fir-eastern hemlock cover types on the PEF (Frank and Blum, 1978). The treatments, each with two replicates, were randomly assigned to experimental units averaging 10 ha in size.

Uneven-aged treatments included selection cutting with 5-, 10-, and 20-year cutting cycles that were managed to target residual basal areas goals of 26.4, 23.0, and 18.4 m² ha⁻¹, respectively. Selection treatments included some cultural treatments like pruning, where spruce, hemlock, and fir species were favored. Even-aged treatments included a commercial clearcut and two-stage shelterwood treatment. In the clearcut treatment, all commercial value was removed but undesirable species and cull trees were left scattered or in small patches. Most recent harvests occurred in 1987. For the shelterwood treatment, initial cuts occurred in the mid-1950s and the overstory removed approximately 10 years

later, leaving a residual basal area of approximately 7.0 m^2 ha^{-1}. Exploitive cutting was represented by a fixed and flexible (or modified) diameter limits treatment. In these treatments, (1) all merchantable trees of desired species that exceeded diameter limits were removed and (2) undesirable species, culls, and desirable trees below minimum diameter limits were retained. A nonharvested reference area was established which serves as the experiment's control. A detailed description of the types of removals and structural goals for the various treatments can be found in Sendak et al. (2003).

2.2. Data collection

Sample plots were established along transects nested within each experimental unit, averaging 18 PSPs per experimental unit. PSPs consisted of a nested design with 0.081, 0.020, and 0.008 ha circular plots sharing the same plot center. The USFS routinely inventoried these plots: all pole- and sawtimber-sized trees ⩾11.4 cm diameter at breast height (dbh) were measured in the 0.081 ha plot, large saplings (6.4 cm ⩽ dbh < 11.4 cm) were measured on the 0.020 ha plot, and small saplings (1.3 cm ⩽ dbh < 6.4 cm) were measured on the 0.008 ha plot. Since 2000, plots switched from being measured every 5 to every 10 years, and if harvesting occurred, immediately pre- and post-harvest. Beginning in 1974, trees were uniquely numbered in these plots and experimental unit, plot number, tree number, species, dbh, tree status (e.g. alive versus dead), and agent of mortality were recorded. In 1981, codes for agent of mortality were initiated to include the following: spruce budworm (*Choristoneura fumiferana*), uprooting, breakage, suppression, and unknown.

Although snags were recorded since 1981, decay stage began to be recorded on standing snags in 1996. A four-class system was used to designate the decay of snags (Table 1). Shortly thereafter in 1997, each plot within each management unit was revisited to collect information on standing snags that were first observed from 1981 to 1996. These observations comprised the data presented in Garber et al. (2005). Tree species, dbh, height, and decay class were recorded on snags previously inventoried. Snags were recorded as either standing or downed. Recruited snags not previously inventoried by USFS were excluded in the 1997 measurement.

In 2010 and 2011, previous snags inventoried by USFS in addition to recruited snags not previously inventoried were recorded in a complete inventory of snags at the PEF. Each plot was revisited and all snags ⩾11.4 cm dbh were measured in the 0.081 ha plot, while snags ⩾2.5 cm dbh were measured in the 0.020 ha plot. Tree species, dbh, height, agent of mortality, and decay class were recorded on all snags. Snag conditions were recorded as either standing (height ⩾ 1.37 m), leaning (<45° from terrain), downed (a snag that was standing at some earlier inventory), or nonlocatable (a snag that was standing at some earlier inventory but could not be located). For leaning snags, height was measured perpendicularly from the ground to the top of the leaning snag. Years since death was calculated for each snag observation. The year of snag

recruitment was defined as the midpoint between the year when the tree was last measured alive and the first year when the tree was measured dead, similar to Garber et al. (2005).

Various measures of density were computed for each plot. These included basal area ha^{-1} (BAPH), trees ha^{-1} (TPH), additive stand density index (SDI; Ducey and Larson, 2003), relative density for mixed-species stands (RD; Woodall et al., 2005), and crown competition factor (CCF) as well as percent canopy cover (PCC) estimated using crown width equations developed for the region (Russell and Weiskittel, 2011). Depth-to-water table (DWT), defined as the distance from soil surface to the normal high level of the water table, was obtained from a GIS raster layer based on the algorithm of Murphy et al. (2011). To represent the various silvicultural treatments, the average harvest interval (AHI) of each experimental unit was calculated in years to reflect the general management intensity occurring in a stand. For uneven-aged and commercial clearcut treatments, AHI was calculated by averaging the durations of the multiple harvest intervals. For the shelterwood treatment and nonharvested control, AHI was calculated as the number of years since the experiment began. AHI ranged from 5 years in the 5-year selection cutting treatment to 55 years in the nonharvested control and two-stage shelterwood treatments.

2.3. Modeling snag survival

Previous work in modeling snag survival has been accomplished through fitting survival models with censoring (Lee, 1998; Garber et al., 2005; Aakala et al., 2008). Proportional hazards (PH) regression models are a class of survival models that differ from others in that they describe how a unit increase in a covariate changes survival with respect to a baseline hazard rate (Cox, 1972). The PH model is considered semiparametric because no assumption is placed on the shape of a baseline hazard (nonparametric component), but it assumes a linear effect of the covariates on the hazard (parametric component). A hazard function $h(t|X)$ assesses the risk of failure at some time t, conditioned on the probability of survival to time t:

$$h(t|X) = h(t)\exp(X_1\alpha_1 + \ldots + X_p\alpha_p) \tag{1}$$

where $h(t)$ is the baseline hazard, X_i's are the covariates, and α_i's are the estimated parameters. The PH model was chosen for modeling snag longevity at the PEF for several reasons. First, it allows for independent variables that can change through time. This could be advantageous when a plot-level metric such as stand density is used, which has been shown to influence snag survival (Garber et al., 2005) and can change as a stand develops as a snag is subject to varying stand structures. Second, the PH model ensures that probabilities and subsequent estimates of those probabilities are constrained between 0 and 1 (O'Quigley, 2008). Third, since the effect of covariates is the same at all times t, hazard ratios can be developed which compare the changes in probability of snag survival for each unit increase in a covariate.

Snag survival was modeled by censoring snag observations that fell. Given the usefulness of snag dbh in estimating snag survival (Garber et al., 2005; Vanderwel et al., 2006; Aakala et al., 2008), dbh was used as a predictor in the PH model. Mean years since death within each decay class for each species was correlated with years since death (Fig. 1), hence, snag decay class was used as the censoring variable as a surrogate. Hence, the initial snag survival model was fit to each species as:

$$h(dcy|dbh) = h(dcy)\exp(a_1 dbh) \tag{2}$$

where $h(dcy|dbh)$ is the hazard function predicting snag decay class conditioned on snag dbh. Additional covariates were also tested in the models to reflect stand density (BAPH, TPH, CCF, PCC, RD), site conditions (DWT), and differences in the average harvest interval

Table 1
Decay class designations for snags used in this analysis (adapted from Heath and Chojnacky, 2001).

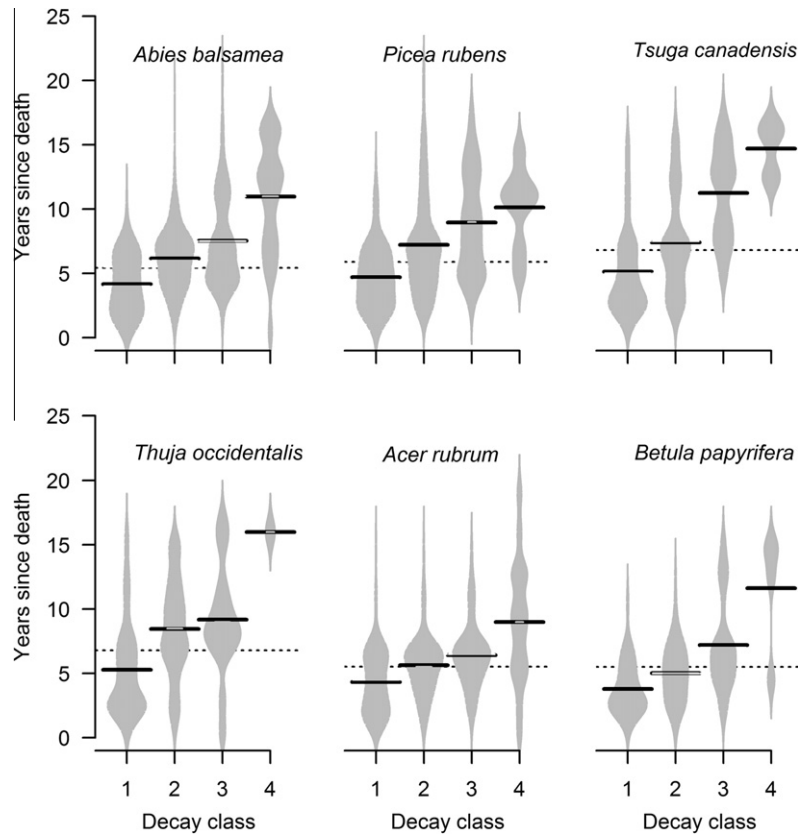| Decay class	Characteristics
1	Structurally sound; bark intact; fine branches
2	Sound but somewhat rotten; branch stubs attached; partially soft texture
3	Rotten; branch stubs mostly pulled out; heavy bark peeling; soft texture
4	No structural integrity; bark detached or absent

Fig. 1. Beanplot (Kampstra, 2008) of years since death by decay class for six species measured at the Penobscot Experimental Forest. Black lines indicate means within decay class; dashed lines represent mean within species.

(AHI) for the various experimental units, but were not significant in estimating snag survival. The developed models for each species in Eq. (2) were also compared to models that were developed that used years since death as the hazard function.

2.4. Quantifying snag decay dynamics

Upon quantifying the probability of snag fall, decay class dynamics were quantified to better understand the temporal aspects of snag decay. These matrix models predicted the 5-year probability of snags advancing in decay (Kruys et al., 2002; Aakala et al., 2008). In this approach, a snag in decay class i can either (1) remain in the same class i, (2) move to decay class $i + 1$, (3) move to decay class $i + 2$, or (4) fall (snag height reduced to <1.37 m). Residence times estimating the duration that snags remain in a certain decay class i were calculated by averaging the years since death for each decay class i for each species dating back to the 1997 inventory. Mean residence times and methodologies for estimating the annual and 5-year probabilities of decay class transitions were calculated as outlined in Aakala et al. (2008). Probability of snag fall was calculated from Eq. (2) and divided by the mean residence time in the appropriate decay class to determine an annual probability. Five-year transitions were obtained by multiplying the annual fall probability by five. Snags in decay class 1 were assumed to have zero probability of falling during the first 5-year time period, as these species generally display a half-life greater than 5-years, a more parsimonious transition model was favored, and catastrophic disturbances to this site were absent.

2.5. Modeling snag volume reduction

Determining the amount of volume reduced through decay would aid managers in accurately estimating standing deadwood stocks. Models for predicting snag reduction were estimated in two stages: first the probability of a snag experiencing height loss was modeled with logistic regression. Second, the volume remaining in snags (provided that snag height loss has occurred) was modeled using a nonlinear form with the constraint that decayed snag volume could not exceed the volume of an equivalent size tree with no decay (i.e. a live tree).

Volumes of snags were estimated using numerical integration of the species-specific taper equations of Li et al. (2012). This permitted the ability to calculate snag volume that accounts for the reduction of volume for snags that have broken and suffered height loss, without requiring the measurement of diameter at breakage (Aakala et al., 2008). Estimating the volume of snags prior to breaking was derived by first estimating total (e.g. nonbroken) height using dbh and the species-specific allometric equations of Saunders and Wagner (2008) developed at the PEF, then computing the total nonbroken volume using the taper equation.

A logistic regression model predicting the probability of a snag experiencing no height loss ($\hat{\pi}_{nohtloss}$) was fit to each species and was related to snag dbh and the average harvest interval (AHI) of the stand:

$$\hat{\pi}_{nohtloss} = \frac{1}{1 + \exp[b_0 + b_1 \text{dbh} + b_2 \text{AHI}]} \tag{3}$$

Additional covariates representing stand density and site conditions did not aid in predicting $\hat{\pi}_{nohtloss}$.

Snags were assumed to have decayed if predicted snag volume was less than volume predicted assuming no height loss (or total snag volume, denoted vol_{total}). If height loss occurred, the volume of the decayed snag (vol_{dcy}) was modeled as the dependent variable:

$$\text{vol}_{dcy} = \frac{\text{vol}_{total}}{1 + \exp[c_0 + c_1 \text{mort}_S + c_2 \text{mort}_B + c_3 \text{dcy}_{hard}]} \tag{4}$$

where vol$_{dcy}$ is decayed snag volume (m^3), mort$_S$ and mort$_B$ are indicator variables representing whether or not a snag's mode of death (from Gale and Barfod, 1999) was suppression or breakage, respectively, and dcy$_{hard}$ is an indicator variable representing whether or not a snag was recorded as hard (decay classes 1 and 2) or soft (decay classes 3 and 4; dcy$_{soft}$). Separate values for the c_i parameters in Eq. (4) were estimated for conifers and hardwoods as few observations in decay classes 3 and 4 were recorded for many species.

2.6. Bayesian estimation

Parameters were estimated for Eqs. (2)–(4) using the PHREG, GENMOD, and MCMC procedures, respectively, available in the SAS/STAT® software system (SAS Institute Inc., 2010). The BAYES statement was used in the PHREG and GENMOD procedures to set the conditions for the Monte Carlo simulations. For each of the equations and species, 100,000 iterations were run through a Markov chain to achieve convergence and estimation of posterior distributions. These iterations were conducted following a 10,000 iteration burn-in, where sample estimates were discarded. To reduce autocorrelations between successive Markov chain samples, the thinning parameter was set to three. A normal distribution was selected as the prior for each of the parameters such that $\sim N(0.0, 1.0e^{-6})$. Final selection of the parameters for each equation for each species were chosen after an assessment similar to an approach outlined by McCarthy (2007; pp. 252–253). This included requiring the trace plots to be well-mixed, inspecting graphs to ensure that successive Markov chains were not correlated, and ensuring that the value zero was not included in the highest posterior density (HPD) interval (akin to the frequentist approach of accepting a value of a parameter at the $\alpha = 0.05$ level). Effective sample sizes (Kass et al., 1998) for each of the parameters were examined to assess Markov chain mixing.

3. Results

3.1. Snag measurements and snag fall

The data collected comprised 3538 measurements of standing and fallen snags, which included 2778 measurements on conifers, 735 measurements on hardwoods, and 25 measurements of unknown species. The most abundant conifers were *A. balsamea* and *P. rubens* (1468 and 665 measurements, respectively) and the most abundant hardwoods were *A. rubrum* and *B. papyrifera* (353 and 195 measurements, respectively). Together, the following six species comprised 90% of all snag observations at the PEF: *A. balsamea*, *A. rubrum*, *B. papyrifera*, *P. rubens*, *Thuja occidentalis*, and *T. canadensis*. Eighty-nine percent of all snag observations were standing. Twenty-four snags (300 total) that were standing in the 1997 inventory presented in Garber et al. (2005) were found to still be standing in the 2010–2011 inventory.

As measured in 2010–2011, mean dbh for standing snags ranged from as small as 7.7 ± 6.4 cm (mean ± SD) for *A. rubrum* to as large as 18.5 ± 6.9 cm for *T. occidentalis*, while mean snag height ranged from 5.3 ± 3.2 m for *T. occidentalis* to 7.7 ± 4.7 m for *T. canadensis* (Table 2). Suppression was the most common mode of death for four of the primary species measured (54% of all snags), while breakage was the most common mode of death for *B. papyrifera* and *P. rubens*. Eighty-five percent of all snags were found to be in decay classes 1 or 2 (Table 3). Mean years since death differed depending on species and the decay class of individual snags (Fig. 1).

3.2. Modeling snag survival and decay

Models predicting snag survival were found to be dependent on species and snag dbh (Fig. 2). Averaged across all species, the

Table 2
Snag summary statistics for six species measured in 2010–2011 at the Penobscot Experimental Forest[a].

Species	Statistic	dbh (cm)	Height (m)	Years since death
Abies balsamea	Mean	8.1	5.6	5.2
(n = 741)	SD	6.7	3.4	2.8
	Min	2.5	0.6	0.5
	Max	41.9	25.1	20.5
Acer rubrum	Mean	7.7	5.7	5.6
(n = 225)	SD	6.4	3.2	2.8
	Min	2.5	1.3	1.0
	Max	32.0	19.0	19.0
Betula papyrifera	Mean	12.4	6.7	6.2
(n = 83)	SD	8.8	4.5	3.1
	Min	2.5	1.2	1.0
	Max	33.3	20.4	15.0
Picea rubens	Mean	12.1	6.7	6.2
(n = 285)	SD	10.9	4.0	3.4
	Min	2.5	1.3	1.0
	Max	51.0	18.7	20.5
Thuja occidentalis	Mean	18.5	5.3	9.2
(n = 57)	SD	6.8	3.2	4.6
	Min	3.0	1.8	0.5
	Max	38.9	18.2	17
Tsuga canadensis	Mean	18.1	7.7	8.6
(n = 90)	SD	10.2	4.7	4.6
	Min	2.5	1.4	1.0
	Max	45.0	19.3	17.5
All species	Mean	10.2	6.0	5.9
(n = 1,645)	SD	8.8	3.8	3.4
	Min	2.5	0.6	0.5
	Max	53.3	29.6	20.5

[a] dbh, Diameter at breast height.

estimated probability of snag survival for a 20 cm dbh snag in decay classes 1–4 was 0.69 ± 0.09, 0.36 ± 0.09, 0.16 ± 0.05, and 0.06 ± 0.02, respectively. Snag half-life, defined as the probability of snag survival equal to 0.5, varied depending on species. The hardwood species *A. rubrum* and *B. papyrifera* predicted half-lives at an approximate decay class of 2, while *P. rubens* displayed the shortest half-life at a decay class between 1 and 2. For models that used years since death, half-times were predicted somewhere between 7 and 10 years, depending on species. Interspecific differences from using years since death or decay class were generally similar for the six species examined, although differences were apparent for *A. balsamea* (Fig. 2).

The coefficient for the PH model showed either that (1) the probability of snag survival increased as snag dbh got larger (e.g. *A. balsamea*, *A. rubrum*, and *P. rubens*), or (2) dbh was insignificant in predicting snag survival (e.g. *B. papyrifera*, *T. occidentalis* and *T. canadensis*; Table 4). Predicted hazard ratios indicated that the influence of snag dbh varied across species (Table 5). For example, for each 10 cm increase in snag dbh, survival was predicted to be 24.0% greater for *A. rubrum* snags, with a 95% highest probability density (HPD) interval of [8.7, 38.7]. In contrast, survival was predicted to be 14.0% greater for *P. rubens* snags for each 10 cm increase in dbh with a 95% HPD interval of [5.3, 22.5].

Species fastest to decay, as measured by the average time it takes for a snag in decay class 1 to reach decay class 4, were *A. rubrum* (4.7 years) and *P. rubens* (5.4 years). Species slowest to decay were *T. canadensis* (9.6 years) and *T. occidentalis* (10.7 years). Mean residence times were longest for snags in decay classes 1 and 4. Averaged across all species, mean residence times (±SD) for decay classes 1–4 were 10.6 ± 2.3, 3.5 ± 1.0, 3.7 ± 1.8, and 8.4 ± 3.2 years, respectively. Between-species differences in residence times resulted in differences in the 5-year transition rate from one decay class to another (Table 6). By including both the probability of a snag advancing in decay class and falling, the 5-year probability of snags remaining in decay class 1 was highest for *T. occidentalis* and *T. canadensis*. Snags beginning in

Table 3
Decay class and mode of death by species (percent of total observations in parentheses) for snags measured in 2010–2011 at the Penobscot Experimental Forest.

Species	Count of decay class				Count of mode of death		
	1	2	3	4	Breakage	Suppression	Other
Abies balsamea	393 (53%)	259 (35%)	77 (10%)	12 (2%)	233 (31%)	451 (61%)	57 (8%)
Acer rubrum	85 (38%)	100 (44%)	37 (16%)	3 (1%)	77 (34%)	123 (55%)	25 (11%)
Betula papyrifera	14 (17%)	37 (45%)	28 (34%)	4 (5%)	56 (67%)	16 (19%)	11 (13%)
Picea rubens	196 (69%)	76 (27%)	11 (4%)	2 (1%)	99 (35%)	159 (56%)	27 (9%)
Thuja occidentalis	20 (35%)	27 (47%)	9 (16%)	1 (2%)	39 (68%)	2 (4%)	16 (28%)
Tsuga canadensis	43 (48%)	31 (34%)	13 (14%)	3 (3%)	28 (31%)	34 (38%)	28 (31%)
All species	800 (49%)	606 (37%)	213 (13%)	26 (2%)	596 (36%)	839 (51%)	210 (13%)
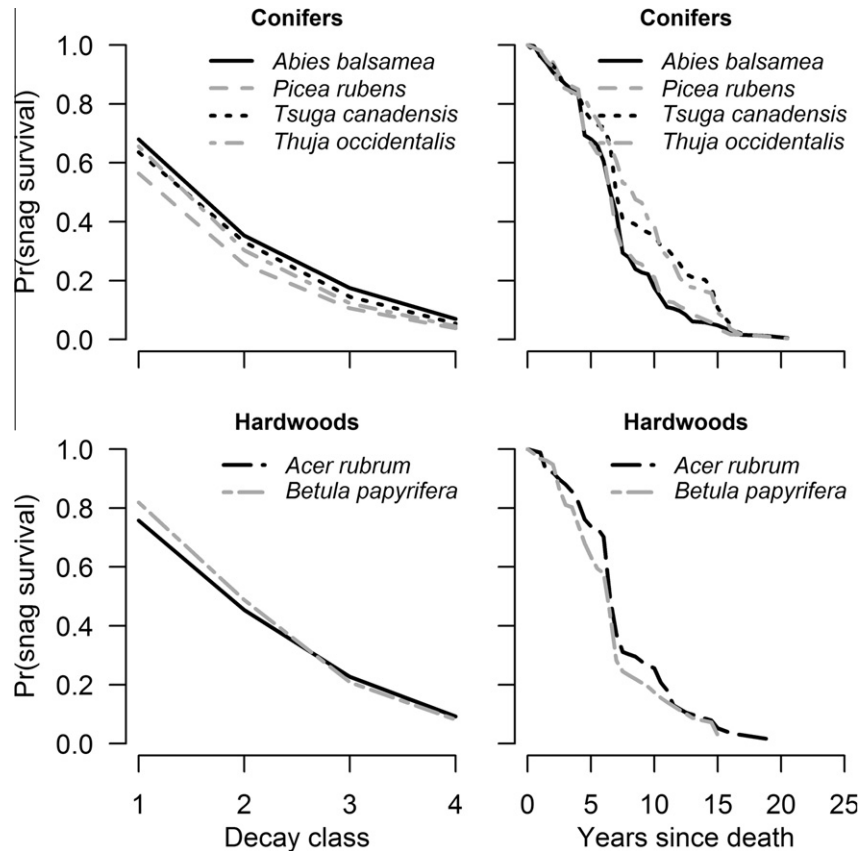
Fig. 2. Probability of snag survival by decay class and years since death for six common Acadian species with a diameter at breast height of 20 cm.

decay classes 1 and 2 were predicted to progress quickly through subsequent decay classes or fall. Snags observed in decay class 4 would likely fall in 5 years for *P. rubens* ($Pr = 0.854$), but would likely remain standing for *A. rubrum* ($Pr = 0.621$) and *T. occidentalis* ($Pr = 0.596$).

3.3. Modeling snag volume reduction

Average predicted 5-year height loss calculated assuming non-broken height and measured snag height (±SD) ranged from 2.7 ± 6.4 m for *A. balsamea* to 8.1 ± 16.5 m for *T. occidentalis*. Snag

Table 4
Mean posterior estimates (standard deviations in parentheses) estimating the probability of snag survival (Eq. (2)) and snag height loss not occurring (Eq. (3)) for six common Acadian species.

Species	Parameter				
	Eq. (2)		Eq. (3)		
	a_1		b_0	b_1	b_2
	Decay class	Years since death			
Abies balsamea	−0.0193 (0.0048)	−0.0382 (0.0053)	−0.00968 (0.21)	−0.158 (0.017)	0.0267 (0.0045)
Acer rubrum	−0.0279 (0.010)	−0.0424 (0.011)	−0.237 (0.47)	−0.296 (0.066)	0.0278 (0.013)
Betula papyrifera	−0.0104 (0.011)	−0.0364 (0.0125)	0.871 (0.55)	−0.253 (0.076)	–
Picea rubens	−0.0152 (0.0052)	−0.0385 (0.0059)	−0.167 (0.51)	−0.159 (0.024)	0.0435 (0.0098)
Thuja occidentalis	−0.00142 (0.016)	−0.0215 (0.017)	4.21 (3.08)	−0.523 (0.24)	–
Tsuga canadensis	0.00157 (0.011)	−0.0234 (0.012)	−2.94 (1.3)	−0.333 (0.097)	0.129 (0.039)

Table 5
Predicted hazard ratios (HR) of snag fall for each additional cm unit increase (5, 10, or 20 cm) in snag dbh with mean percent increase and 95% highest probability density (HPD) intervals for six common Acadian species.

Species	dbh unit	HR	Mean (%)	HPD$_{LOW}$ (%)	HPD$_{HIGH}$ (%)
Abies balsamea	5	0.908	9.2	5.0	13.4
	10	0.826	17.4	9.7	25.0
	20	0.683	31.7	18.4	43.7
Acer rubrum	5	0.871	12.9	4.4	21.6
	10	0.760	24.0	8.7	38.7
	20	0.584	41.6	17.8	63.3
Betula papyrifera	5	0.951	4.9	−5.6	15.5
	10	0.907	9.3	−10.8	29.2
	20	0.833	16.7	−22.4	50.2
Picea rubens	5	0.927	7.3	2.6	11.9
	10	0.860	14.0	5.3	22.5
	20	0.741	25.9	10.7	40.5
Thuja occidentalis	5	0.996	0.4	−15.0	15.5
	10	0.998	0.2	−31.5	29.3
	20	1.020	−2.1	−66.5	54.6
Tsuga canadensis	5	1.009	−0.9	−11.6	9.3
	10	1.022	−2.2	−23.8	18.4
	20	1.055	−5.5	−50.5	35.6

Table 6
Transition matrices for six common Acadian species predicting the 5-year probability of snags advancing in decay class or falling[a].

From class	To class				
	1	2	3	4	Fall
Abies balsamea					
1	0.547	0.126	0.327	–	–
2	–	0.147	0.294	0.560	0.000
3	–	–	0.043	0.598	0.359
4	–	–	–	0.454	0.546
Acer rubrum					
1	0.560	0.121	0.319	–	–
2	–	0.046	0.458	0.496	0.000
3	–	–	0.041	0.554	0.405
4	–	–	–	0.621	0.379
Betula papyrifera					
1	0.537	0.130	0.333	–	–
2	–	0.018	0.528	0.455	0.000
3	–	–	0.113	0.357	0.530
4	–	–	–	0.524	0.476
Picea rubens					
1	0.607	0.104	0.289	–	–
2	–	0.229	0.232	0.539	0.000
3	–	–	0.163	0.351	0.487
4	–	–	–	0.146	0.854
Thuja occidentalis					
1	0.689	0.077	0.234	–	–
2	–	0.135	0.297	0.568	0.000
3	–	–	0.128	0.385	0.487
4	–	–	–	0.596	0.404
Tsuga canadensis					
1	0.668	0.083	0.249	–	–
2	–	0.113	0.340	0.547	0.000
3	–	–	0.414	0.156	0.430
4	–	–	–	0.432	0.568

[a] Transitions assumed to be biologically impossible denoted as "–".

dbh and AHI were significant covariates in predicting the probability that a snag would experience height loss. Parameter estimates from the logistic model in Eq. (3) indicated that larger dbh snags would experience a higher probability of height loss. Assuming a constant dbh, models indicated that snags found in stands with a longer AHI displayed a lower probability of experiencing a reduction in height (Table 4). For small dbh snags, models predicted increasing AHI would lower the probability of a snag experiencing height reduction. For large dbh snags, AHI played less of a role in helping to predict the probability of snag height loss, especially for *A. rubrum* and *T. canadensis* (Fig. 3). For AHI of the nonharvested control treatment, Eq. (3) was fit using multiple years to represent AHI: this included 0 (assuming no harvest), 55 (assuming no harvesting since the beginning of the experiment), and 120 (assuming last harvest occurred sometime in the late 1800s). We found all three values to produce consistent curves when plotted across various values for dbh, indicating that dbh was the primary driver when predicting the probability of height loss.

Models indicated that snag volume was related to indicators for mode of death and the general decay class (hard versus soft) of the snag (Table 7). Ranked in order, the highest proportion of intact volume for conifers displaying hard decay classes was from snags dying from (1) suppression, (2) other modes of death, and (3) breakage. The highest proportion of intact volume for hardwoods displaying hard decay classes was from snags dying from (1) other modes of death, (2) suppression, and (3) breakage. Snags with soft decay classes were predicted to display a lower proportion of intact volume than their hard decay class counterparts. Differences were more pronounced in conifers as opposed to hardwoods for models that predicted the proportion of intact volume (Fig. 4).

4. Discussion

4.1. Snag measurements and snag fall

Snag characteristics from an inventory of 300 snags in 1997 presented in Garber et al. (2005) were comparable to the 2010–2011 inventory presented here. *A. balsamea* and *A. rubrum* were the most abundant conifer and hardwood snags, respectively. Approximate mean snag height between 5 and 10 m across the various silvicultural treatments presented in Garber et al. (2005) agrees with the means presented here, which ranged between 5.3 m and 7.7 m for the six species under investigation. Mean dbh was smaller than the

average of 16.0 cm reported for conifers and hardwoods by Garber et al. (2005) for some species, but likely arises due to the smaller minimum dbh measurement for snags (2.5 cm) used in this present analysis, in addition to measuring recruited snags. After analyzing data 42 and 55 years after initial silvicultural treatment, findings show that individual snag dimensions for the common species occurring at the PEF remain comparable. These similarities provide evidence that prescribed silvicultural treatments are continuing to produce snags with similar dimensions through time.

Distributions of the number of standing snags across decay classes were generally left-skewed, with many snags observed in decay class 1 and fewer in decay class 4, providing support that snag survival can be captured through modeling with a reverse-sigmoid curve. Suppression was observed as the most common mode of death for four of the species examined, which has been similarly reported in other species (Runkle, 2000; Vanderwel et al., 2006). Stem breakage was observed as the most common mode of death for the two other species. Whether or not stems broke initially causing tree death, or if they died from some other method such as suppression and stem breakage followed, remains to be known. Given the long duration between successive measurements for some PSPs (up to 10 years), snags may have suffered height loss through breakage prior to being recorded as a snag. The 1997 inventory sampled snags that died from a recent spruce budworm (*C. fumiferana*) outbreak, however, no trees were designated as suffering mortality due to insect or disease in 2010–2011. Such differences highlight the need for having flexible data collection protocols to assign mortality to new or reoccurring agents. Incorporating morphological attributes of snags such as wood penetrability, percent bark cover, and presence/absence of foliage (see Angers et al., 2012) would likely provide a more comprehensive
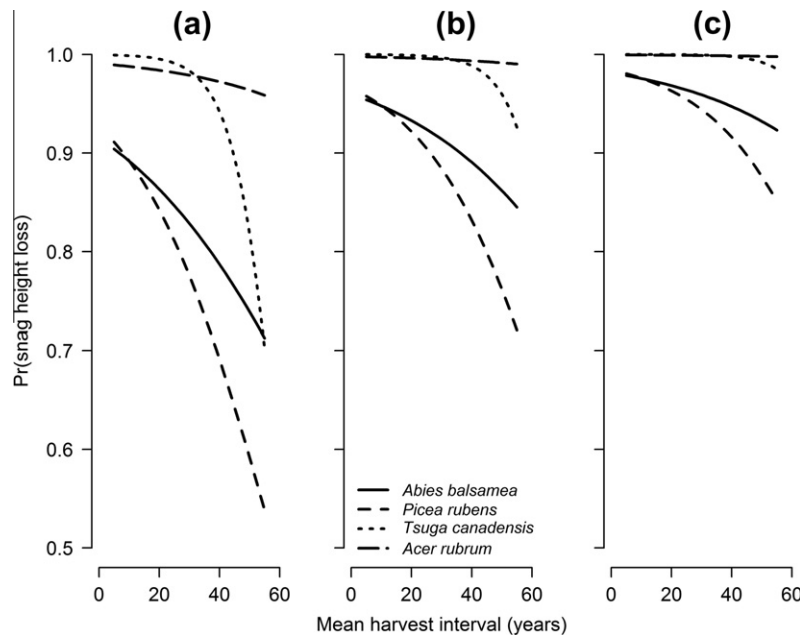
Fig. 3. Probability of a snag experiencing height loss for common Acadian species with diameter at breast height set at 15 cm (a), 20 cm (b), and 25 cm (c).

Table 7
Mean posterior estimates (standard deviations in parentheses) for estimating the volume remaining in snags following height loss (Eq. (4)) for conifers and hardwoods in the Acadian region, given that snag height loss has occurred.

Species group	Parameter			
	c_o	c_1	c_2	c_3
Conifers	0.814 (0.21)	−0.818 (0.31)	0.948 (0.11)	−1.21 (0.20)
Hardwoods	−0.652 (0.16)	0.980 (0.39)	0.959 (0.15)	−0.215 (0.14)

assessment of snag decomposition and mode of death for the six species examined here.

4.2. Modeling snag survival and decay

The fact that *P. rubens* displayed the shortest half-life using decay class as the censoring variable agreed with what Garber et al. (2005) found using years since death. A primary difference in the survival curves developed here was that dbh was not a significant predictor for estimating the survival for *B. papyrifera*, *T. occidentalis*, and *T. canadensis* (Table 4). These species similarly displayed some of the longest mean residence times within decay class 1 (Table 6). Results for these species were similar to those of Cline et al. (1980) who showed that snag longevities did not differ across a range of dbh. For other species (*A. balsamea*, *A. rubrum*, and *P. rubens*), results here agree with Garber et al. (2005) and Yamasaki and Leak (2006) who showed that snag survival was greater for larger diameter snags. Species-specific equations were developed in this analysis, whereas Garber et al. (2005) fit snag survival curves to all snag observations, then used indicator variables to account for species differences. We withheld from using indicator variables to account for species as they tend to lead to large standard errors in the snag survival equation.

It was unanticipated that snag survival was related only to dbh for some species. Other covariates such as stand structure (e.g. BAPH, CCF), forest management intensity (AHI), and site conditions (e.g. DWT) offered no improvement in predicting the survival of snags for the six species examined here. Snag height could be a useful predictor for survival, but height was only measured in two inventories (1997 and 2010–2011) and Angers et al. (2012) did not observe any correlation between height and years since death for *A. balsamea* snags in northwestern Québec. In determining decomposition for standing snags and fallen logs Storaunet and Rolstad (2002), suggest separating snag survival and snag failure components, a practice which can aid in determining which covariates relate to decomposition of snags depending on their status (i.e. standing or fallen). As the focus here was in modeling survival and decay of individual snags, there is much room for exploration into the role that stand-level disturbances play in snag recruitment, especially in datasets gathered from PSP remeasurements.

Transition matrices reflected the differences of species as they relate to snag decay dynamics. For snags in decay class 1, models predicted a more than even-chance that they would remain in decay class 1 in 5 years (Table 6). Models then predicted snags to progress at varying rates through the remaining decay classes. Results highlighted the usefulness of mean residence times (Kruys et al., 2002) to account for differences in decomposition for the various species measured. The two hardwood species analyzed (*A. rubrum* and *B. papyrifera*) were the two densest species in terms of wood density and displayed the longest half-life for snag survival, but this did not equate to longer durations of mean residence times in hard decay stages. *T. occidentalis* and *T. canadensis* displayed the longest durations in hard decay stages, likely due to the high lignin content for these species (Panshin and de Zeeuw, 1970; Garber et al., 2005). As found by Hofmeyer et al. (2009), site quality influences the probability of heart rot decay in *T. occidentalis*, indicating that site and/or microsite characteristics could aid in modeling efforts that depict decay dynamics. Compared to this analysis, Aakala et al. (2008) observed a more uniform progression of decomposition into intermediate decay classes for *A. balsamea* in boreal forests in Québec, but they also observed a half-time at a much more advanced decay stage and collected data from old-growth stands.

Proportional hazards models fitting survival curves with Markov chain Monte Carlo methods were flexible to account for the variability observed between species. Hazard ratios with appropriate highest probability density intervals (Table 5), which estimate the percent increase in snag survival as dbh increases can serve as useful management tools for quantifying snag dynamics in these mixed-species stand types.
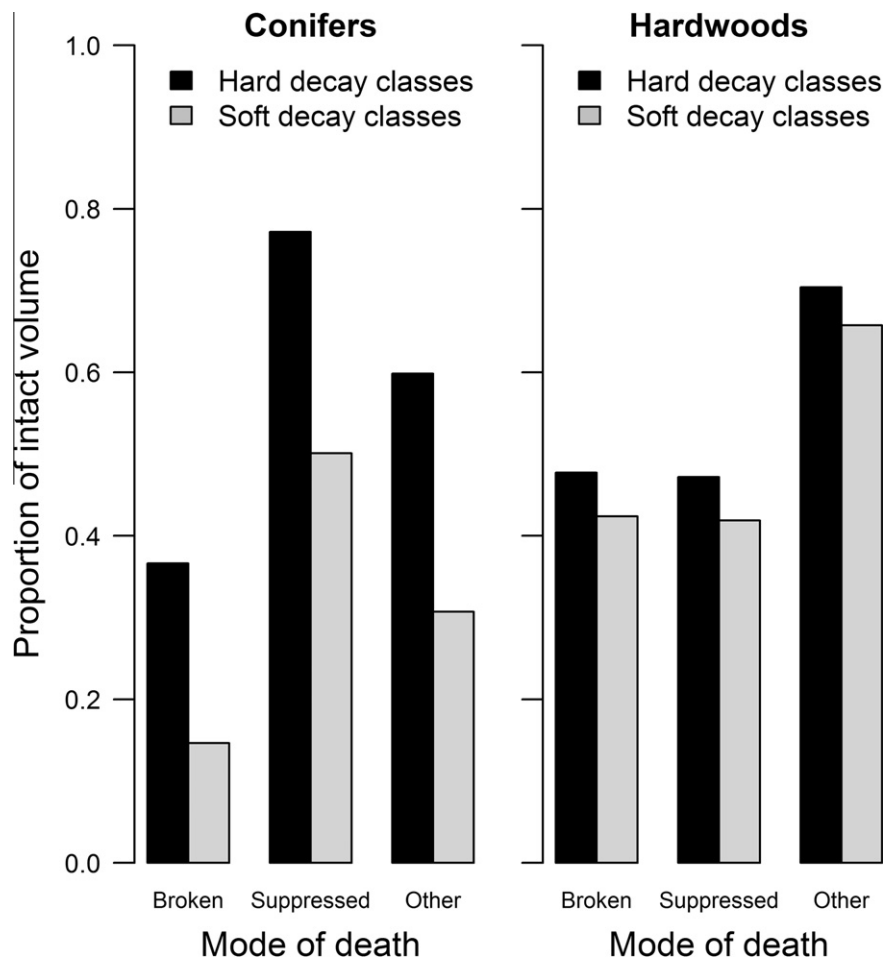
Fig. 4. Predicted proportions of intact volume by mode of death assuming a tree volume prior to mortality of 0.40 m^3.

4.3. Modeling snag volume reduction

By first estimating the total height of a live tree using observed snag dbh, the probability of snag height loss was found to be related to snag dbh and the average harvest interval (AHI) of the stand. Results show how one might use allometric equations from live trees to estimate intact snag height, and then estimate the probability that a snag loses height. The model predictions showing that larger dbh snags would experience a higher probability of height loss could be related to snag longevity, as large dbh snags were predicted to have longer survival times for several species. These larger-sized snags would be subject to more agents influencing height loss if they remain standing longer, such as swaying of live trees and high wind events. Similarly, results showing that stands managed on a more frequent harvest interval (e.g. an AHI of 5 years) have a higher probability of snag height lost agree with the findings of Vanderwel et al. (2006) who showed that harvesting influenced snag survival, as harvesting brushes snag tops during felling operations. Removals as part of the experiment were not generally heavy in the uneven aged selection treatments, which could minimize the role that exposure to wind plays in predicting snag survival at this site. For the commercial clearcut and shelterwood (even-aged treatments), cuttings may have occurred recently enough to form complex stand structures when compared to selection stands. This might lend further investigation into measures other than AHI to depict snag dynamics in contrasting silvicultural regimes.

Aakala (2010) related the proportion of intact snag volume to decay class, while this analysis also found that mode of death and predicted total snag volume provided biologically sensible estimates of decayed snag volume. Tree taper equations which employ integral estimates for determining volume were flexible and robust, as volume can be estimated for any snag with a broken stem and can also be used for determining the volume for live trees. The observation that broken and suppressed trees displayed similar amounts of intact volume for hardwoods could be due to the fact that differences in mode of death were observed (Table 3). For example, suppression was the most common mode of death for *A. rubrum*, while breakage was most common for *B. papyrifera*. Models indicate that snags in soft decay stages were predicted to contain less volume than snags in hard decay stages, which can be related to the snag survival and snag height loss equations developed.

Site differences have been shown to provide fluctuations in mean residence times, even for the same species (Aakala, 2010). Future efforts in modeling the decay dynamics of snags for these species could focus on employing data collected across more expansive geographic areas under a variety of site conditions. In doing this, additional variables such as those reflecting climate and geographic locale (e.g. Radtke et al., 2009) could be useful covariates for assessing snag and coarse woody debris decay rates. PSPs that traditionally focus on measurement of live trees should continue to be used for monitoring the characteristics of individual snags and their decay dynamics through time.

5. Conclusions

To further our understanding on snag dynamics in the Acadian region, this analysis lends insight into quantifying snag survival and decay transitions for the primary species in the region. Our results from four conifer and two hardwood species indicate snag survival and decomposition could be attributed to snag dbh and mean residence time in a given decay class. As problems are encountered when years since death is used as the censoring variable to estimate snag survival, observed decay class was found to provide similar results to using years since death for most species. The hardwood species *A. rubrum* and *B. papyrifera* displayed the longest half-lives for all species, while the conifers *T. occidentalis* and *T. canadensis* were the slowest to transition from the lowest to highest stages of decay. As managers are likely interested in overall stocking levels of standing deadwood, a more thorough assessment of snag dynamics than merely survival is needed. By quantifying the probability of a snag experiencing height loss for individual species groups, estimates of standing deadwood stocking levels can become more refined. Results here indicate that height loss is almost certain for larger dbh snags found in stands with a frequent harvest interval. Coupled together, snag survival and height loss estimates indicated that snags in soft decay stages would contain less volume than snags in hard decay stages.

Models depicting snag decay dynamics using tree variables can help to bridge the gap between traditional forest growth and yield models like the Forest Vegetation Simulator (Crookston and Dixon, 2005) and their model extensions such as the Fires and Fuels Extension (Rebain et al., 2009), which provides estimates of forest carbon stocks and their dynamics. Results here made use of a network of established PSPs to guide investigations into snag dynamics. Most investigations have used dendrochronological methods to inform snag decay dynamics (e.g. Aakala et al., 2008; Angers et al., 2010), however, PSP data collected from long-term studies like the PEF can help to inform not only snag dynamics, but a host of other processes related to forest dynamics.

Acknowledgments

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