Snag longevity under alternative silvicultural regimes in mixed-species forests of central Maine

Sean M. Garber, John P. Brown, Duncan S. Wilson, Douglas A. Maguire, and Linda S. Heath

Abstract: Predictions of snag longevity, defined here as the probability of snag survival to a given age, are key to designing silvicultural regimes that ensure their availability for wildlife and form an important component of carbon flow models. Species, diameter at breast height, stand density, management regime, and agent of tree mortality were assessed for their effect on snag longevity in a long-term silvicultural study on the Penobscot Experimental Forest in central Maine. Snag recruitment and fall data from USDA Forest Service inventories between 1981 and 1997 were analyzed using parametric survival analysis. A Weibull model fit the data best, indicating a significant lag time followed by rapid fall rates. Half-times varied among species, with *Thuja occidentalis* L. having the longest (10 years) and *Picea* species the shortest (6 years). Snag longevity was significantly greater with increasing diameter and decreased with increasing stand density. Agent of mortality and silvicultural treatment were also significant. Two models were developed for estimating probability of snag survival over time, one that included predictor variables unique to the silvicultural systems study on the Penobscot Experimental Forest and one using predictor variables available in most standard inventories. Snag survival models can easily be incorporated into comprehensive forest dynamics models to facilitate estimates of wildlife habitat structure and carbon flow.

Résumé : La prédiction de la longévité des chicots, définie ici comme étant la probabilité de survie des chicots, est un élément clé de la conception des régimes sylvicoles qui en assurent la disponibilité pour la faune et constitue une composante importante des modèles de flux de carbone. L'espèce, le diamètre à hauteur de poitrine, la densité du peuplement, le régime d'aménagement et la cause de mortalité des arbres ont été évalués pour connaître leur effet sur la longévité des chicots dans le cadre d'une étude sylvicole à long terme à la Forêt expérimentale de Penobscot située dans le centre du Maine, aux États-Unis. Les données d'inventaire de 1981 à 1997 du USDA Forest Service sur le recrutement et la chute des chicots ont été étudiées à l'aide d'une analyse paramétrique de survie. Un modèle de Weibull s'est le mieux ajusté aux données, ce qui indique qu'il y a une importante période de latence suivie par un taux de chute rapide. La demi-vie des chicots variait selon l'espèce, avec la plus longue (10 ans) associée à *Thuja occidentalis* L. et la plus courte (6 ans) à *Picea* spp. La longévité des chicots était significativement plus forte lorsque leur diamètre augmentait et plus faible lorsque la densité du peuplement augmentait. La cause de mortalité et le traitement sylvicole étaient également importants. Deux modèles ont été développés pour estimer la probabilité de survie des chicots en fonction du temps. Le premier inclut des variables de prédiction propres aux systèmes sylvicoles de la Forêt expérimentale de Penobscot et le deuxième utilise des variables de prédiction disponibles dans la plupart des inventaires standard. Les modèles de survie des chicots peuvent facilement être introduits dans des modèles détaillés de la dynamique forestière pour faciliter l'estimation de la structure des habitats fauniques et du flux de carbone.

[Traduit par la Rédaction]

Introduction

Coarse woody debris in forest ecosystems serves a number of ecological functions related to wildlife and nutrient cycling, including global carbon budgets (Harmon et al. 1986). Sources of coarse woody debris include tree mortality and branch or top loss from live trees. Snags resulting from tree mortality have become a major focal point for ensuring that managed forests include nesting, feeding, and perching habitat for many species of wildlife (Bull and Meslow 1977; Bull 1983; Neitro et al. 1985; Rosenberg et al. 1988; Bull et al. 1997). However, snags can also be a fire hazard, logging hazard, and epicenter for damaging biological agents (Neitro et al. 1985; Mitchell and Preisler 1991; Preisler and Mitchell 1993; Myers and Fosbroke 1995; Egan 1996).

Effective management of the forest snag resource requires a greater understanding and quantification of snag dynamics and, ideally, incorporation of this information into compre-

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S.M. Garber[1] and D.A. Maguire. Department of Forest Science, Oregon State University, Corvallis, OR 97331, USA.
J.P. Brown. USDA Forest Service, Northeastern Research Station, 241 Mercer Springs Road, Princeton, WV 24740, USA.
D.S. Wilson. Forestry Programme, University of Kwazulu-Natal, Private Bag X01, Scottsville 3209, South Africa.
L.S. Heath. USDA Forest Service, Northeastern Research Station, P.O. Box 640, Durham, NH 03824, USA.

[1] Corresponding author (e-mail: sean.garber@oregonstate.edu).

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hensive decision-making models. Several types of models are currently available in the Pacific Northwest, including the Snag Recruitment Simulator (SRS; Marcot 1992), the Coarse Woody Dynamics Model (CWDM; Mellen and Ager 2002), and the Snag Dynamics Protection Model (SDPM; McComb and Ohmann 1996). In addition, some traditional forest growth and yield models, which estimate the size and number of snags over time, also have a snag dynamics model (e.g., Forest Vegetation Simulator; TIPSY (Stone 1996)). These models assist managers in designing silvicultural regimes that ensure snag recruitment and availability from the perspectives of wildlife carrying capacity, but also allow foresters to predict and manage fuel loadings in fire-susceptible forests and scientists to understand storage and flow of carbon through ecosystems. A critical component of snag dynamics is how long snags remain standing, since this feature determines both snag availability as a wildlife resource and the time and decay stage with which it enters into the coarse woody debris pool on the forest floor.

Snag longevity, the probability of snag survival to a given age, has been described by a reverse sigmoidal curve. After tree mortality, snag fall rates are initially low, resulting in delayed snag fall or lag time (Keen 1929, 1955; Dahms 1949; Lyon 1977; Bull 1983; Landram et al. 2002). Documented lag times range from 1 to 15 years (McArdle 1931; Keen 1955; Lyon 1977). Following this initial delay, fall rates often increase for a period and then level off at a later time. The shape of the survival curve resulting from a variety of lag times, half-times (time required for 50% of the snags to fall), and longer term survival rates depends on many factors, including species, tree size, cause of tree death, soil type, climate, and disturbance regime (Morrison and Raphael 1993; Bull et al. 1997).

Most of the work on snag longevity has been completed in the Pacific Northwest and Rocky Mountains, with relatively little work in the northeastern United States. In the 1950s the USDA Forest Service in cooperation with private landowners initiated a long-term silvicultural study on the Penobscot Experimental Forest in central Maine. This long-term study provided an opportunity to quantify the dynamics of coarse woody debris, in particular the longevity of snags, in managed mixed-conifer and hardwood forests typical of the northeastern United States and southeastern Canada. The specific objectives of this study were to (*i*) determine the most important factors controlling snag longevity and (*ii*) develop a model to predict the probability of snag survival to a given age.

Materials and methods

Study site

The silvicultural systems study was established within spruce–fir–hemlock compartments on the Penobscot Experimental Forest (PEF) (Frank and Blum 1978). The PEF covers 1619 ha, is located within the town limits of Bradley and Eddington (southern Penobscot County, Maine, USA; 44°52′N, 68°38′W), and falls within the Central Maine Coastal and Interior Section of the Laurentian Mixed Forest Province (McNab and Avers 1994). Mean annual precipitation is 106 cm, with 48% falling as rain from May to October (Brissette 1996). Annual snowfall averages 239 cm (Sendak et al. 2003). Mean annual temperature is 6.6 °C, recorded in nearby Bangor, Maine. Maximum temperatures occur in July, averaging 20.0 °C, and the lowest temperatures occur in January, with an average temperature of –7.7 °C.

Soil parent material in the PEF is primarily glacial till. Soil types range from well-drained loams and sandy loams on glacial-till ridges to poorly drained and very poorly drained loams and silt loams in flat areas between these ridges. Study compartments are primarily underlain by somewhat well-drained to somewhat poorly drained loams and silt loams (Brissette 1996).

The forest canopy of the study areas is dominated by a mixture of species, primarily *Picea rubens* Sarg. (red spruce), *Abies balsamea* (L.) Mill. (balsam fir), and *Tsuga canadensis* (L.) Carr. (eastern hemlock), with lesser amounts of *Picea glauca* (Moench) Voss (white spruce), *Picea mariana* (Mill.) B.S.P. (black spruce), *Thuja occidentalis* L. (northern white cedar), *Pinus strobus* L. (white pine), *Acer rubrum* L. (red maple), *Betula papyrifera* Marsh. (paper birch), and *Betula populifolia* Marsh. (grey birch). *Picea rubens*, *Picea glauca*, and *Abies balsamea* dominate the relatively low-lying sites of poorer drainage; however, the proportion of *T. canadensis* and *Pinus strobus* increases as drainage improves.

Study design

The silvicultural systems study was initiated by the USDA Forest Service between 1952 and 1957. The primary objective was to investigate the effects of silvicultural treatments on growth, yield, and regeneration of *Picea rubens* and *Abies balsamea* (Frank and Blum 1978; Brissette 1996; Sendak et al. 2003). The study design is completely randomized with 10 treatments assigned to compartments at random and replicated twice. Each compartment or experimental unit averaged 10 ha. Treatments selected for the study were those that were recommended (even- and uneven-aged methods) or being used in practice (diameter-limit methods) in the early 1950s (Sendak et al. 2003): unharvested natural area; unregulated harvest; combination of single-tree and group selection systems with 5-, 10-, and 20-year cutting cycles; two-stage shelterwood; three-stage shelterwood without precommercial thinning; three-stage shelterwood with precommercial thinning; fixed-diameter-limit system; and modified-diameter-limit system (Table 1). This study addressed snag longevity on all but the two three-stage-shelterwood treatments. A detailed description of the treatments, harvests, and target stand structures were presented by Sendak et al. (2003).

Field procedures

A system of sample points along transects with a random start was established within each compartment. At each sample point, two nested subplots were used to measure the characteristics of the trees present. A fixed-area circular subplot of 0.08 ha (0.2 acres) was used to measure all trees with diameter at breast height (DBH) ≥ 11.43 cm (4.5 in.). A fixed area circular subplot of 0.02 ha (0.05 acres) was used to measure all trees with DBH ≥ 2.54 cm (1.0 in.) and <11.43 cm. All plots were remeasured at 5-year intervals and before and after each harvest. Compartment, plot, tree number, species, DBH, and condition have been recorded on

Table 1. Treatment abbreviations, names, and descriptions.

Treatment	Abbreviation	Description
Unharvested natural area	NAT	Control unit without harvesting
Unregulated harvest	URH	Removal of all merchantable trees
5-year selection	S05	Single-tree and group selection with a 5-year cutting cycle
10-year selection	S10	Single-tree and group selection with a 10-year cutting cycle
20-year selection	S20	Single-tree and group selection with a 20-year cutting cycle
Two-stage shelterwood	SW2	Shelterwood with two entries: a regeneration harvest and final harvest
Fixed diameter limit	FDL	Removal of all merchantable trees above a fixed diameter at variable time intervals
Modified diameter limit	MDL	Removal of all merchantable trees above a flexible diameter at fixed time intervals

Table 2. Predictor variables for estimating snag longevity.

Variable	Definition
SPP	Set of eight indicator variables for eight tree species
DBH	Diameter at breast height (cm)
TPH	Trees per hectare
PBA	Plot basal area ($m^2 \cdot ha^{-1}$)
SDI	Reineke's (1933) stand density index (no. 25-cm trees$\cdot ha^{-1}$)
RD	Curtis' (1982) relative density ($m^2 \cdot ha^{-1} \cdot cm^{-2}$)
CCF	Krajicek et al.'s (1961) crown competition factor
MANAGE	Set of seven indicator variables for eight silvicultural regimes (NAT or unharvested natural area is base-line regime): URH = 1 if unregulated harvest, 0 otherwise S05 = 1 if 5-year selection, 0 otherwise S10 = 1 if 10-year selection, 0 otherwise S20 = 1 if 20-year selection, 0 otherwise SW2 = 1 if two-stage shelterwood, 0 otherwise FDL = 1 if fixed diameter limit, 0 otherwise MDL = 1 if modified diameter limit, 0 otherwise
MORT	Set if mortality agent is recognizable (other mortality is considered base-line mortality): *Choristoneura fumiferana* = 1 if spruce budworm, 0 otherwise Breakage = 1 if stem breakage, 0 otherwise Suppression = 1 if suppression mortality, 0 otherwise
HARV	Indicator variable representing whether snag witnesses a harvest (0 = No, 1 = Yes)

all trees in each subplot since 1974 (T. Skratt, personal communication, 1997). Condition codes included merchantability and mortality. In 1981, the mortality code was expanded to include the following mortality agents: spruce budworm, uprooting, breakage, suppression, and unknown (indeterminate). Only one mortality agent was recorded per snag in the field. In May 1997, each plot within each compartment was revisited to determine whether snags found in inventories dating back to 1981 were still standing. Species, DBH, height, fragmentation state (broken or unbroken), and decay class were recorded on snags that were still standing. Decay classes were taken from Cline et al. (1980) and modified for application in central Maine to a four-class system (Heath and Chojnacky 2001; Chojnacky and Heath 2002): (1) sound and intact; (2) sound to somewhat rotten, with branch stubs firmly attached; (3) rotten, branch stubs pulled out; and (4) no structural integrity, branch stubs rotted down.

Analysis

Snag heights collected in 1997 were assessed across treatments using a mixed-effects analysis of variance for a completely randomized design with unbalanced subsamples. The Tukey–Kramer multiple-comparison procedure was used to differentiate between treatment pairs. This analysis was done using the MIXED procedure in SAS (SAS Institute Inc. 1999).

Previous work on snag longevity has shown that probability of snag survival over time follows a reverse sigmoidal shape (Keen 1929, 1955; Dahms 1949; Lyon 1977; Bull 1983). Therefore, a parametric modeling approach was taken on the PEF. Each snag i represented a single univariate observation with a theoretical lifetime (T_i, Lawless 1982; Cox and Oakes 1984) and a period of observation (c_i). T_i was considered a lifetime random variable with a given distribution. However, not all the trees had fallen during the period of observation, thus not all T_i were known. Consequently, snag longevity was modeled using survival analysis with censoring (Lee 1998). For snags that fell ($T_i = c_i$), censoring interval was defined as the time between two points: snag recruitment and the May 1997 inventory date. Date of snag recruitment was the midpoint of the interval between two inventories: where the tree was last found alive and where the tree was first found dead. For snags that did not fall ($T_i > c_i$), the right-censoring beginning point was defined as the midpoint between the time when the tree was last recorded alive and first found dead. Since other studies have shown low fall

Table 3. Means and ranges for diameter at breast height (DBH) and stand density index (SDI) by species grouping and position on the Penobscot Experimental Forest.

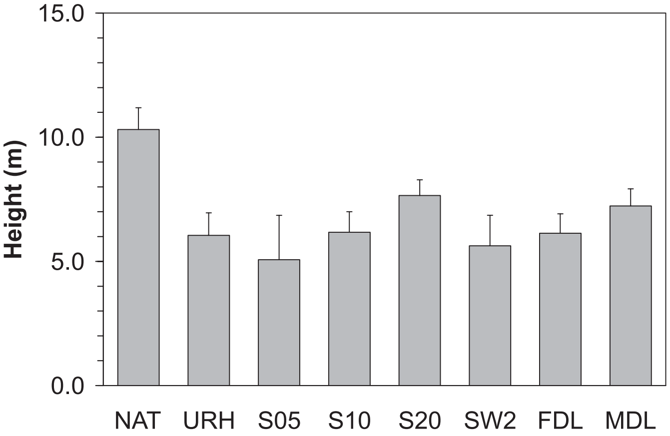
			DBH (cm)			SDI		
Species	Code	*n*	Mean	Min.	Max.	Mean	Min.	Max.
Softwood	Fallen	1840	14.8	7.6	41.7	717.0	40.3	1337.8
	Standing	270	16.0	7.6	47.0	683.1	287.2	1299.3
Hardwood	Fallen	162	14.9	7.6	40.6	800.7	285.5	1250.7
	Standing	30	16.0	8.1	29.5	804.8	355.7	1192.0

Table 4. Summary table for number of snags by species and silvicultural treatment.

	Silvicultural treatment[a]								
Species	NAT	URH	S05	S10	S20	SW2	FDL	MDL	Total
Abies balsamea	86	363	84	354	322	53	229	241	1732
Picea rubens and *Picea mariana*	7	11	17	28	48	1	36	52	200
Picea glauca	3	11	4	22	0	0	5	12	57
Tsuga canadensis	3	8	7	2	8	7	8	5	48
Thuja occidentalis	4	14	4	5	14	9	10	13	73
Acer rubrum	9	28	4	1	5	12	12	12	83
Betula papyrifera	4	10	0	0	1	8	11	7	41
Other species	4	27	0	0	4	11	11	11	68
Total	120	472	120	412	402	101	322	353	2302

[a] NAT, unharvested natural area; URH, unregulated harvest; S05, 5-year selection; S10, 10-year selection; S20, 20-year selection; SW2, two-stage shelterwood; FDL, fixed diameter limit; MDL, modified diameter limit.

Fig. 1. Average snag height for each silvicultural treatment. NAT, unharvested natural area; URH, unregulated harvest; S05, 5-year selection; S10, 10-year selection; S20, 20-year selection; SW2, two-stage shelterwood; FDL, fixed diameter limit; MDL, modified diameter limit. Bars represent 1 standard error.



rates in the first few years, a Weibull distribution model was fitted to the data (Lawless 1982):

$$[1] \qquad S(t) = e^{\lambda t^{\beta}}, \quad t > 0$$

where $S(t)$ is survival probability to time t, λ is the Weibull scale parameter, and β is the Weibull shape parameter. If β is not significantly different than one, the Weibull model simplifies to an exponential distribution, suggesting the absence of a lag time.

To assess the effects of tree, plot, and treatment variables, T_i was modeled as a function of species, DBH, and several alternative measures of average (average of initial and most recent inventories) plot density including trees per hectare (TPH), plot basal area (PBA), stand density index (SDI, Reineke 1933), Curtis' relative density (RD, Curtis 1982), and crown competition factor (CCF, Krajicek et al. 1961). In addition, the models considered the effects of management regime, mortality agent, and an indicator for snags that had experienced at least one harvest or stand entry (Table 2).

Lifetime models were fit by the method of maximum likelihood using the LIFEREG procedure in SAS. This procedure uses a log-link function, so [1] was reparameterized with $\lambda = \exp(-\mu)$ and $\beta = 1/\sigma$ (Lawless 1982). After algebraic manipulation, the reparameterized model was

$$[2] \qquad S(t) = e^{\left(-\left(e^{-\frac{\mu}{\sigma}}\right)\left(\frac{1}{t^{\sigma}}\right)\right)}$$

where $S(t)$ is the probability of survival to a given time t; σ is the shape parameter; and μ is a linear function of the covariates. Models with alternative sets of fixed covariates were compared using the log-likelihood statistic, starting with relatively simple models containing only species or species and DBH, and ending with models considering the full set of potential covariates. Covariates, including the shape parameter, were tested using likelihood ratio tests (Lawless 1982). All final predictor variables were significant at $\alpha = 0.05$.

Results

The database contained 2302 snags, including 2110 conifers and 192 hardwoods (Table 3). Eighty-seven percent of all snags fell during the 17-year period, with a slightly lower rate for hardwoods (84% vs. 87% for softwoods). Eleven species were represented, with *Abies balsamea* being the most abundant species and *Acer rubrum* being the most abundant hardwood (Table 4). Snag heights were about one-third higher in natural stands versus managed stands ($p < 0.001$; Fig. 1). However, among individual treatments, snag heights on the natural stands were only significantly taller than those on the S10 ($p = 0.016$), FDL ($p = 0.011$), SW2 ($p = 0.044$), and URH ($p = 0.019$). No other pairwise comparisons were significant.

The Weibull scale parameter was 1.34, significantly different from 1.0, suggesting a short but significant lag time (<2 years). The chosen model (log likelihood = –770.34) included DBH and SDI as continuous covariates, as well as indicator variables for species, management regime, and cause of mortality:

$$[3] \quad \mu = \alpha_0 + \alpha_1\mathrm{DBH} + \alpha_2\mathrm{SDI} + \alpha_{31}\mathrm{SPP}_1 + \ldots + \alpha_{38}\mathrm{SPP}_8 + \alpha_{41}\mathrm{MANAGE}_1 + \ldots + \alpha_{47}\mathrm{MANAGE}_7 + \alpha_{51}\mathrm{MORT}_1 + \ldots + \alpha_{53}\mathrm{MORT}_3$$

where

SPP_j is an indicator variable for species j, with $j = 1, 2, \ldots, 8$

MANAGE_k is an indicator variable for management regime k, with $k = 1, 2, \ldots, 7$

MORT_m is an indicator variable for cause of mortality m, with $m = 1, 2, 3$

α_0, α_1, α_2, α_{31} to α_{38}, α_{41} to α_{47}, and α_{51} to α_{53} are parameters to be estimated from the data

Parameter estimates and asymptotic standard errors for [3] are presented in Table 5.

Snag longevity was significantly influenced by a number of factors, including species, snag diameter, stand density, and silvicultural system. Species was a significant factor in snag longevity ($p = 0.0297$), with *Thuja occidentalis* having the longest half-times (approx. 10 years), while *Picea* species had the shortest half-times (approx. 6 years; Fig. 2).

All else being equal, snag longevity increased with increasing diameter (Fig. 3, $p = 0.0003$) and decreased with increasing stand density (Fig. 4, $p < 0.0001$). An increase in DBH from 5 to 50 cm resulted in an increase in snag half-time of over 6 years in all species. The different plot density measures were all highly significant and performed similarly in all fitted models. Number of trees per hectare (log-likelihood = –758.53) consistently performed slightly better than other density measures: RD (–767.55), CCF (–769.93), SDI (–770.34), and PBA (–774.88). SDI was selected for the final model due to its widespread use and expected better behavior in extrapolation. For a given species, an increase in SDI from 100 to 1000 resulted in half-time reduction of about 3–5 years. The agent of mortality was also a highly significant factor in all models tested ($p < 0.0001$). Mortality caused by *Choristoneura fumiferana* (Clem.) (eastern spruce budworm, *Abies balsamea* only) and suppression resulted in significantly greater longevity than mortality from other mechanisms including stem breakage.

Presented as a group of indicator variables, management regime had a significant effect on snag longevity ($p < 0.001$). Probability of snag survival in the NAT (control) treatment was greatest, followed by the SW2, FDL, S10, URH, S20, MDL, and S05 treatments (Fig. 5). Probability of survival in the S05 treatment was significantly shorter than all other treatments. The only other significant difference was the greater longevity in the MDL treatment than the URH treatment ($p = 0.029$). HARV, the indicator variable specifying whether the snag witnessed a harvest or not, was not significant as an additional covariate ($p = 0.191$).

Not all databases will include information on agent of mortality, and the range of possible silvicultural regimes is

Table 5. Parameter estimates and asymptotic standard errors for [2] and [3].

Covariate or parameter[a]	Parameter estimate	Standard error
Intercept	1.8262	0.3319
DBH	0.0190	0.0053
SDI	–0.0006	0.0000
Abies balsamea	–0.1270	0.2892
Picea rubens and *Picea mariana*	–0.2825	0.2978
Picea glauca	–0.2832	0.3261
Tsuga canadensis	–0.0431	0.3245
Thuja occidentalis	0.2540	0.3089
Acer rubrum	0.1121	0.3067
Betula papyrifera	–0.1034	0.3352
Other species	–0.0550	0.3243
URH	0.2054	0.1090
S05	–0.5125	0.1545
S10	–0.1306	0.1120
S20	–0.0913	0.1144
SW2	–0.0356	0.1458
FDL	–0.1623	0.1134
MDL	–0.0107	0.1163
Breakage	0.0077	0.0796
Suppression	0.3813	0.1201
Choristoneura fumiferana	0.3501	0.0775
σ	0.7451	0.0335

[a] DBH, diameter at breast height; SDI, stand density index; NAT, unharvested natural area; URH, unregulated harvest; S05, 5-year selection; S10, 10-year selection; S20, 20-year selection; SW2, two-stage shelterwood; FDL, fixed diameter limit; MDL, modified diameter limit.

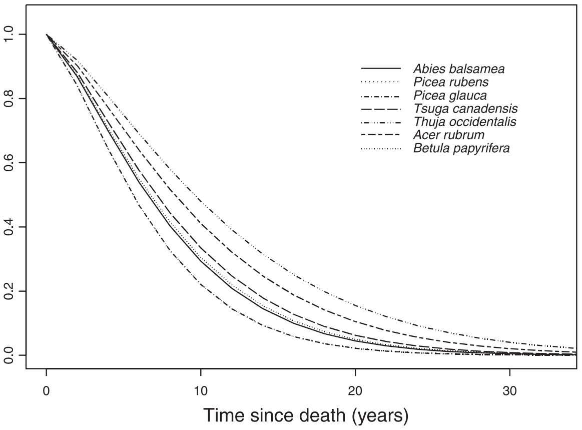


Fig. 2. Probability of snag survival over time for seven species. Estimates are based on model [2], with diameter, stand density, mortality agent, and treatment set at 15 cm, 700, suppression, and unharvested natural area, respectively.

Fig. 3. Probability of snag survival over time for four different initial diameters at breast height and four species: (*a*) *Abies balsamea*, (*b*) *Picea rubens*, (*c*) *Thuja occidentalis*, and (*d*) *Acer rubrum*. Estimates are based on model [2], with stand density index, mortality agent, and treatment set at 700, suppression, and unharvested natural area, respectively.

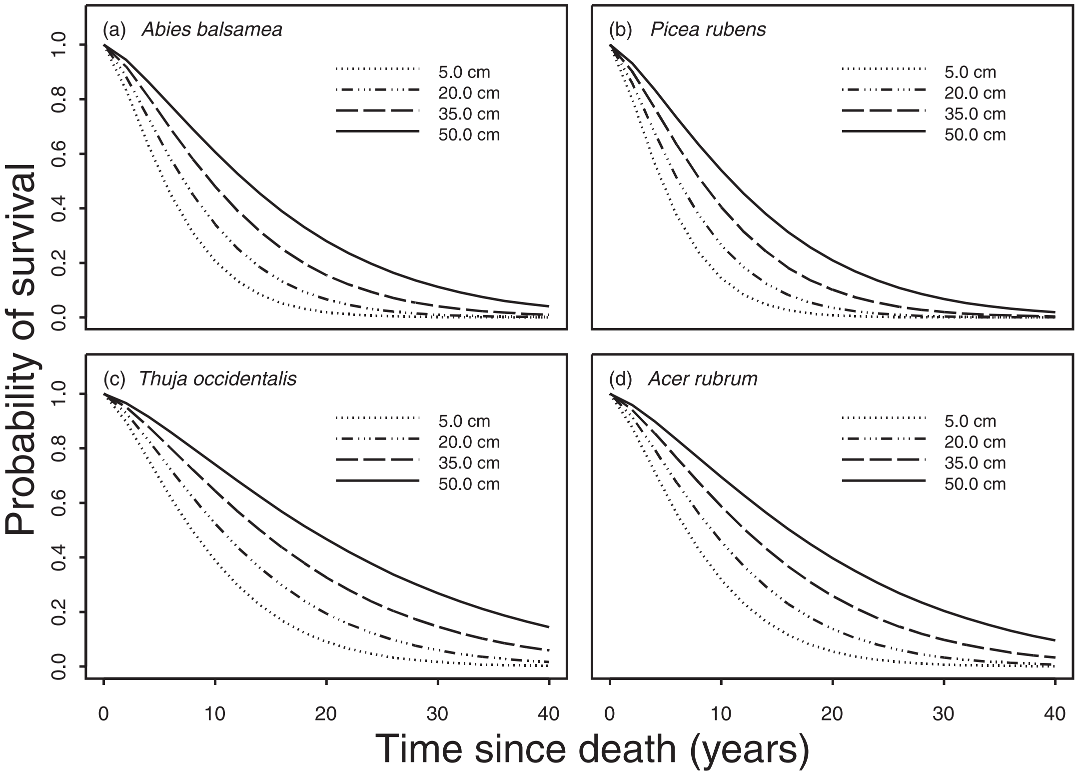


Fig. 4. Probability of snag survival over time for four different initial stand density indices and four species: (*a*) *Abies balsamea*, (*b*) *Picea rubens*, (*c*) *Thuja occidentalis*, and (*d*) *Acer rubrum*. Estimates are based on model [2], with diameter at breast height, mortality agent, and treatment set at 15 cm, suppression, and unharvested natural area, respectively.

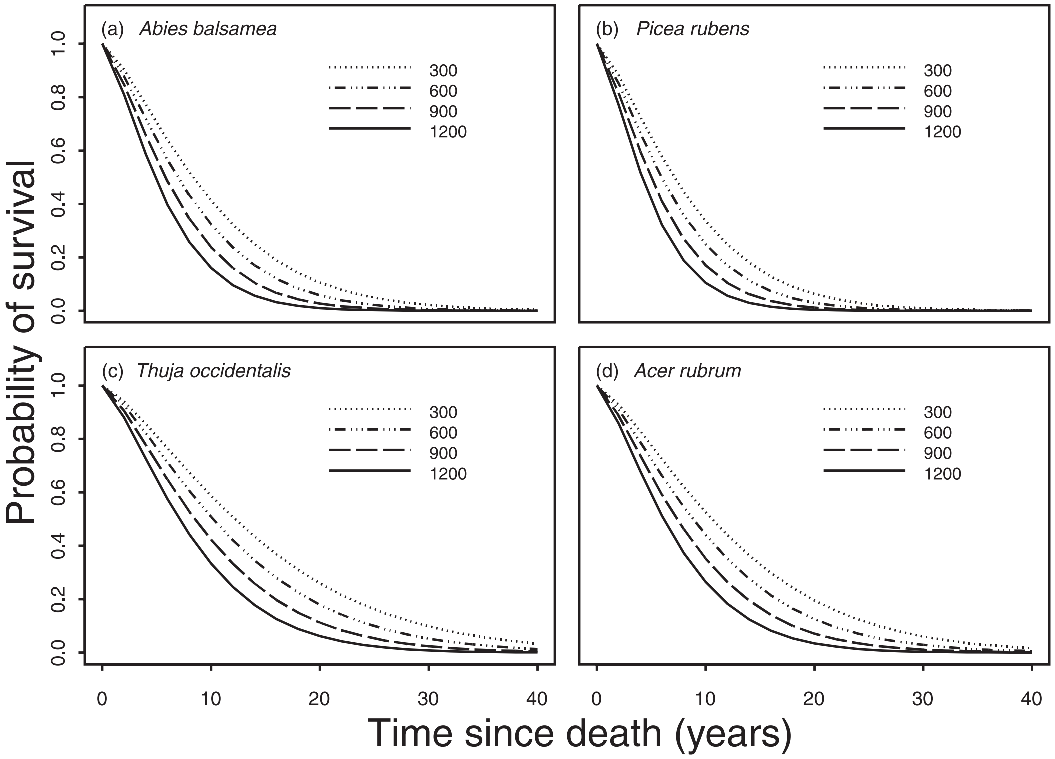


Fig. 5. Probability of snag survival over time for the eight silvicultural regimes and for four species: (*a*) *Abies balsamea*, (*b*) *Picea rubens*, (*c*) *Thuja occidentalis*, and (*d*) *Acer rubrum*. Estimates are based on model [2], with diameter, stand density index, and mortality agent set at 15 cm, 700, and suppression, respectively. NAT, unharvested natural area; URH, unregulated harvest; S05, 5-year selection; S10, 10-year selection; S20, 20-year selection; SW2, two-stage shelterwood; FDL, fixed diameter limit; MDL, modified diameter limit.

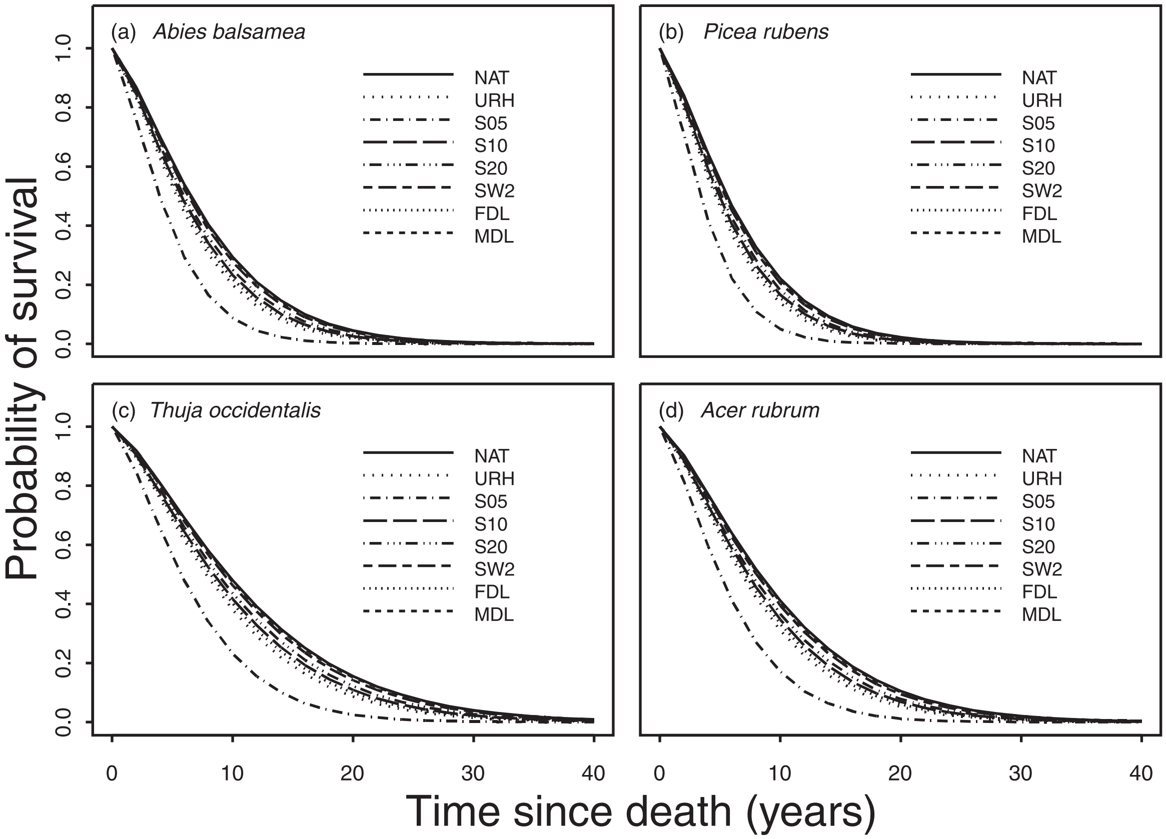


Table 6. Parameter estimates and asymptotic standard errors for [2] and [4].

Covariate or parameter[a]	Parameter estimate	Standard error
Intercept	2.0040	0.2953
DBH	0.0180	0.0050
SDI	–0.0006	0.0001
Abies balsamea	0.0684	0.2754
Picea rubens and *Picea mariana*	–0.3047	0.2893
Picea glauca	–0.2078	0.3201
Tsuga canadensis	–0.1317	0.3174
Thuja occidentalis	0.2005	0.2995
Acer rubrum	0.0587	0.2971
Betula papyrifera	–0.1108	0.3273
Other species	–0.1021	0.3158
σ	0.7610	0.0334

[a] DBH, diameter at breast height; SDI, stand density index.

much broader than the set tested at PEF. Therefore, model [2] was refit without indicator variables for silvicultural regime and agent of mortality (log likelihood = –787.13):

$$[4]\qquad \mu = \alpha_0 + \alpha_1\mathrm{DBH} + \alpha_2\mathrm{SDI} + \alpha_{31}\mathrm{SPP}_1 + \ldots + \alpha_{38}\mathrm{SPP}_8$$

where SPP_j is an indicator variable for species j, with $j = 1, 2, \ldots, 8$, and α_0, α_1, α_2, α_3, and α_{31} to α_{38} are parameters to be estimated from the data. Parameter estimates and asymptotic standard errors for [4] are presented in Table 6.

Discussion

A short lag time in snag fall was experienced by all species on the Penobscot Experimental Forest. This lag time has been reported in many other studies (Keen 1929; McArdle 1931; Dahms 1949; Keen 1955; Lyon 1977; Cline et al. 1980; Bull 1983; Lee 1998), although there have been exceptions (Riley and Skolko 1942; Storaunet and Rolstad 2004). The lag time may be due to a period of insect and fungal colonization that eventually leads to reduced structural stability of snags (Keen 1929). For example, moisture content has been shown to drop for a period after tree mortality before increasing (Lambert et al. 1980). A significant reduction in moisture may reduce fungal metabolic activity (Rayner and Todd 1979), consequently delaying the structural decay of snags.

Subsets of the species represented in the PEF data set had significantly different longevities from one another, but all were within the ranges reported for species in western North America covering the same diameter range (10–50 cm). Half-times have ranged from 5 to 12 years for *Pinus ponderosa* Dougl. ex Laws. (Dahms 1949; Keen 1955; Schmid et al.

1985; Bull and Partridge 1986; Landram et al. 2002) and from 5 to 10 years for *Pinus contorta* Dougl. ex Loud. (Lyon 1977; Bull 1983). These values are far smaller than the 20-year half-times extrapolated for *Picea engelmannii* Parry ex. Engelm. in the Rocky Mountains (Mielke 1950; Hinds et al. 1965; Schmid and Hinds 1974) and the nearly 35-year half-times suggested for *Pseudotsuga menziesii* (Mirb.) Franco in the Pacific Northwest (McArdle 1931; Graham 1982). Some of these differences may be the result of genuine species differences. For example, after accounting for DBH, *Pinus ponderosa* had slightly greater longevities than *Pinus contorta* on similar sites in northeastern Oregon (Bull 1983). *Pinus contorta* snags stood longer than *Abies lasiocarpa* (Hook.) Nutt. and *Picea engelmannii* snags in the northern (Lyon 1977) and southern (Schmid and Hinds 1974) Rocky Mountains, respectively. Likewise, *Tsuga heterophylla* (Raf.) Sarg. snags in the Pacific Northwest fell sooner than *Pseudotsuga menziesii* snags (McArdle 1931; Graham 1982).

Inherent differences in wood density and the concentration of lignin or other recalcitrant materials may result in differential rates of decay among species (Harmon 1982). The two densest species on the PEF, *Acer rubrum* and *Betula papyrifera*, have specific gravities around 0.55 (Hoadley 1990, determined at 12% moisture content) and had greater longevity than all the softwoods except *Thuja occidentalis* and *Tsuga canadensis* (specific gravities of 0.31 and 0.40, respectively). However, these two softwood species have greater lignin content than all the other species (Panshin and de Zeeuw 1980, p. 92) and, in the case of *Thuja occidentalis*, well-known decay resistance is conferred by several compounds in the wood (Scheffer and Cowling 1966).

To some extent, differences among the species may also be influenced by characteristics of the microsites they occupy and the interaction of microsite with species. While *Pinus ponderosa* survival was the same in southwestern and northeastern Oregon and Colorado, *Pinus contorta* survival was twice as long in the southern Rockies as in the northern Rockies and Blue Mountains of eastern Oregon (Schmid and Hinds 1974; Lyon 1977; Bull 1983; Schmid et al. 1985). Likewise, half-times of *Picea engelmannii* have been consistently reported near 30 years, yet at one site in southern Colorado, half-time reached only 15 years (Schmid and Hinds 1974). Wood decays at different rates in different climates (Harmon 1982; Erickson et al. 1985) and among different soil textures (Keen 1955). Climates characterized by greater moisture and soils having greater water-holding capacity support higher rates of wood decay and lower snag longevities (Keen 1955; Harmon 1982). Low humidity and higher winds reduce wood moisture content of snags to below 25% (Mielke 1950; Fahey 1983; Johnson and Greene 1991), low enough to prevent metabolic activity by most decay fungi (Rayner and Todd 1979).

Increasing snag DBH has been widely shown to lengthen snag survival (Keen 1929, 1955; Dahms 1949; Lyon 1977; Cline et al. 1980; Graham 1982; Bull 1983; Landram et al. 2002); however, there have been exceptions (e.g., Schmid et al. 1985). On the PEF, an increase in diameter from 5 to 50 cm at an SDI of 700 resulted in an increased snag half-time from 5 to 11 years for *Picea rubens* and from 8 to 19 years for *Thuja occidentalis*. It may take longer for decay fungi to completely colonize larger diameter trees, thus reducing decay rates. However, this was not supported by constant decay rates across diameter in Great Smoky Mountain National Park (Harmon 1982). Others have suggested that the higher proportion of decay-resistant heartwood found in larger trees may decrease the decay rate and lengthen snag longevity (Keen 1955).

Agent of mortality has been an important factor determining snag longevity in other species as well. *Pinus ponderosa* killed by fire remained standing longer than those killed by bark beetles in eastern Oregon (Keen 1929; Dahms 1949; Schmid et al. 1985). Likewise, fall rates differed among snags created artificially by several alternative methods in northeastern Oregon (Bull and Partridge 1986). Trees topped by either chainsaw or dynamite lasted longer than trees inoculated with fungi, baited with pheromones, or girdled. The shortest longevities were found in snags created by injection of herbicides or created by natural agents. All snags on the PEF study were created by natural means, with the most abundant source of snags being *Abies balsamea* killed by the eastern spruce budworm, *C. fumiferana*. Trees that died as a result of density-dependent mortality and *C. fumiferana* stood for the longest periods of time, while trees that died as a result of breakage had the shortest longevities. Differences were greater than 3 years for all species. Breakage provides an entry point for insects and decay fungi, whereas trees that died from density-dependent mortality or *C. fumiferana* had the advantage of starting out with intact boles and branches (*C. fumiferana* is a defoliating insect). Consequently, trees without breakage may resist decay for a longer duration than trees without breakage.

The effect of stand structure and forest management activities on snags has not been directly assessed in past studies. Snag longevity was strongly influenced by stand density on the PEF ($p < 0.001$). Although lower stand densities may be expected to result in shorter longevities because of exposure to wind and weather extremes (Hinds et al. 1965; Mielke 1950; Schmid and Hinds 1974; Schmid et al. 1985), lower stand density implied greater longevity on the PEF, all else being equal. Two possible mechanisms may explain this result. First, tree height to diameter ratio is commonly greater in denser stands, resulting in poorer mechanical stability. Second, the swaying of surviving trees in denser stands may facilitate direct contact with snags, causing them to break or uproot sooner.

Snag longevity was also significantly related to the silvicultural system by which the stand was being managed. Differences among silvicultural systems probably reflected differences in harvest frequency and intensity. On the PEF, harvest frequency appeared to have a greater impact than harvest intensity, since snag longevity was shortened by harvest entry of any type or intensity (as represented by silvicultural system). Snags in treatment units with more frequent cutting entries (e.g., S05) displayed shorter longevities, while snags in the units with the least frequent entries (NAT and SW2) had the greatest longevities. Despite removing proportionally less basal area or volume than that removed by even-aged systems, selection systems implemented to attain a negative exponential diameter distribution typically impact most of the stand area during each entry if all cohorts or size classes are properly regulated (Nyland 1996). Although current operational guidelines call for removal of snags for safety and liability reasons (Myers and Fosbroke 1995; Egan 1996), the snags in this study were never deliberately removed, and limited public access prevented removal by firewood cutters (R.M. Frank, personal communication, 2004). Therefore, the most likely cause of reduced snag longevity is mechanical disturbance by felling and skidding trees.

This study primarily focused on snag fall. However, snag fragmentation consists of snag height reduction as well (Harmon et al. 1986). Higher snag heights in the NAT treatment suggest a greater loss of snag height in the managed stands. Unfortunately, height data were not collected to determine whether there were initial differences in snag heights between compartments. However, just as with snag fall, mechanical disturbances associated with harvest are likely to accelerate the loss of snag height, and the residual stand is more exposed to wind.

Many contemporary growth models are individual-tree growth models (e.g., FVS; Stage 1973, Wykoff et al. 1982). These models can be combined with snag dynamics models using results such as those presented here to predict density, size, and fall rates of dead trees (e.g., Wilhere 2003) or the models can be modified slightly to track the creation and loss of snags internally. Mortality is generally tracked by reducing tree expansion factors, as mortality equations predict a specific probability or proportion of mortality (Ritchie 1999). This expansion factor can be transferred to a new tree in the tree list representing a snag, and can be diminished over successive growth periods, as the snag survival model describes the reduction in probability or proportion of snags remaining over time. The implications of various management or disturbance regimes on snag supply can be assessed with appropriate models and, where the predicted number of snags falls short of the target, it may be possible to alter management regimes to achieve the desired availability of snags over time (Wilhere 2003).

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