



Snag longevity of Douglas-fir, western hemlock, and western redcedar from permanent sample plots in coastal British Columbia

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ABSTRACT

Snags are important both as structural components and as animal habitat in forests, but abundance is often low and their dynamics poorly understood in young, managed stands. Using a large data set of 19,622 snags from permanent plots in second-growth forests of coastal British Columbia, we modeled snag longevity (time from tree mortality to snag fall) for three species: Douglas-fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), and western redcedar (*Thuja plicata*). Snag longevity was strongly related to species and snag size (diameter): the median snag longevity was 16 years for Douglas-fir, 11 years for hemlock and 5 years for redcedar. Western redcedar was predominantly in the subcanopy and its rapid fall rate was related to the small size of its snags. In addition to diameter, other attributes (height to diameter ratio, height, and live crown ratio before death) contributed significantly to models for one or two of the species. However, site level variables did not contribute significantly to any of the models. Snags greater than 50 cm diameter, especially Douglas-fir snags, have the potential for persistence well beyond 20 years in these second-growth forests, and could be important for wildlife.

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1. Introduction

Standing dead trees (snags) are an important component of forest structure. Snags are critical for the habitat of many animals (Harmon et al., 1986; Bull et al., 1997; Chambers and Mast, 2005; Smith et al., 2008) and have a functional role in nutrient cycling and the carbon budget of forests (Harmon et al., 1986). In natural forests, large volumes of coarse woody debris, including snags are present (Harmon et al., 1986; Spies et al., 1988; Aakala et al., 2008), whereas in managed forests snags can be sparse and are often of small size (Wilhere, 2003). However, snags of a wide variety of sizes may be used by wildlife: those as small as 10 cm diameter can provide nesting habitat for small birds whereas snags greater than 50 cm diameter provide nesting and foraging habitat for a wide array of species (Thomas, 1979). In general, animals that can use small snags are able to use large ones. Snag abundance and dynamics are functions of snag formation (tree mortality) and snag fall, both of which depend on species and on site factors (Schmid and Hinds, 1974; Franklin et al., 1987; Raphael and Morrison, 1987; Garber et al., 2005).

Forest type, tree size structure, species composition, site factors, and environmental conditions all influence snag formation. For example, mortality rates are linked to site productivity and are higher in high- than in low-productivity sites (Franklin et al., 1987). Silvicultural treatments such as fertilization, which boost growth, also increase the rate of mortality. In mature forests, causes of mortality vary greatly (Franklin et al., 1987; Maser, 1988; Guarín and Taylor, 2005; Papaik et al., 2005) and may depend on a single as well as a combination of factors, some of which affect large trees preferentially (some bark beetles), while others affect primarily small trees (suppression-related mortality). In young, developing stands, although wind, disease, and insect defoliation contribute to mortality, suppression-related mortality is likely to be the major cause.

Persistence (longevity) of snags is a key consideration in examining snag abundance and dynamics. Size, decay rates, and wind firmness, as well as various stand and site characteristics, control the rate of snag fall (Morrison and Raphael, 1993). Snag longevity can typically be portrayed by a reverse sigmoidal curve, with an initial lag period after which rates of fall increase rapidly (Harmon et al., 1986; Garber et al., 2005). The lag period can be short or last for many years for large trees (Cline et al., 1980; Harmon et al., 1986; Lee, 1998; Garber et al., 2005), and likely relates to rate of decay. Snag longevity generally increases with snag size (Keen, 1929; Dahms, 1949) and can also be affected

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substantially by stand characteristics such as tree density and thus silvicultural system (Garber et al., 2005; Russell et al., 2006). The cause of mortality will determine if snags are formed and can also influence their longevity (Keen, 1929; Dahms, 1949; Schmid et al., 1985; Taylor and MacLean, 2007). Windthrow that uproots green trees does not provide snags and forests in which windthrow represents a major proportion of the mortality can be expected to have low snag abundance; for example, Taylor and MacLean (2007) found that half of the trees dying did not contribute to snags.

Snags are abundant and often represent substantial volumes of wood in coniferous forests of coastal British Columbia and the Pacific Northwest (Spies et al., 1988). In old-growth forests, snags can be very large and persist for very long periods (Daniels et al., 1997); however, in managed stands harvesting usually occurs before trees reach these sizes. Large numbers of snags do occur in managed stands as small suppressed trees die during self-thinning, arguably the time of greatest individual tree mortality. Silvicultural treatments such as thinning remove overtopped and diseased trees, reducing snag formation. Stem breakage, windthrow, localized fires, insects, and pathogens may also cause mortality. Here we use a large set of permanent plots from Vancouver Island and the adjacent mainland to examine snag persistence in managed stands. Our specific objectives are to determine: (1) snag persistence or longevity since time of death, (2) how snag longevity relates to diameter, (3) if longevity differs among species, and (4) the effects of snag and stand characteristics on longevity.

2. Methods

2.1. The field experiment and data collection

For our analysis of snag longevity we used data from a long-term silvicultural experiment established between 1971 and 1975 (Stone, 1994). The original goal of the experiment was to examine the effects of nitrogen fertilization and thinning on the growth of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*) and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.). A total of 940 permanent sample plots were installed at 85 sites on Vancouver Island and the adjoining mainland of British Columbia, Canada. All stands were second growth and originated after logging, burning, or logging and burning; sites were either planted with Douglas-fir or left to regenerate naturally. Stands were typically even-aged; the youngest stand was 13 years-old and the oldest 81 years-old at the initiation of the study (Appendix 1).

The experiment was planned to examine three levels of fertilization (0, 225, 450 kg N/ha) and three levels of thinning (0, 20, 35% of basal area removed) in a fully replicated 3×3 factorial design (18 plots per site). The design was augmented at some sites to include increased treatment levels, whereas at other sites space was inadequate to apply all of the originally planned treatments. As a result, the number of plots per site ranged from 4 to 43. Plot sizes ranged from 0.05 to 0.1 ha. Trees were measured prior to treatment, in the first dormant season after treatment, and then four times at 3-year intervals; thereafter, measurements were

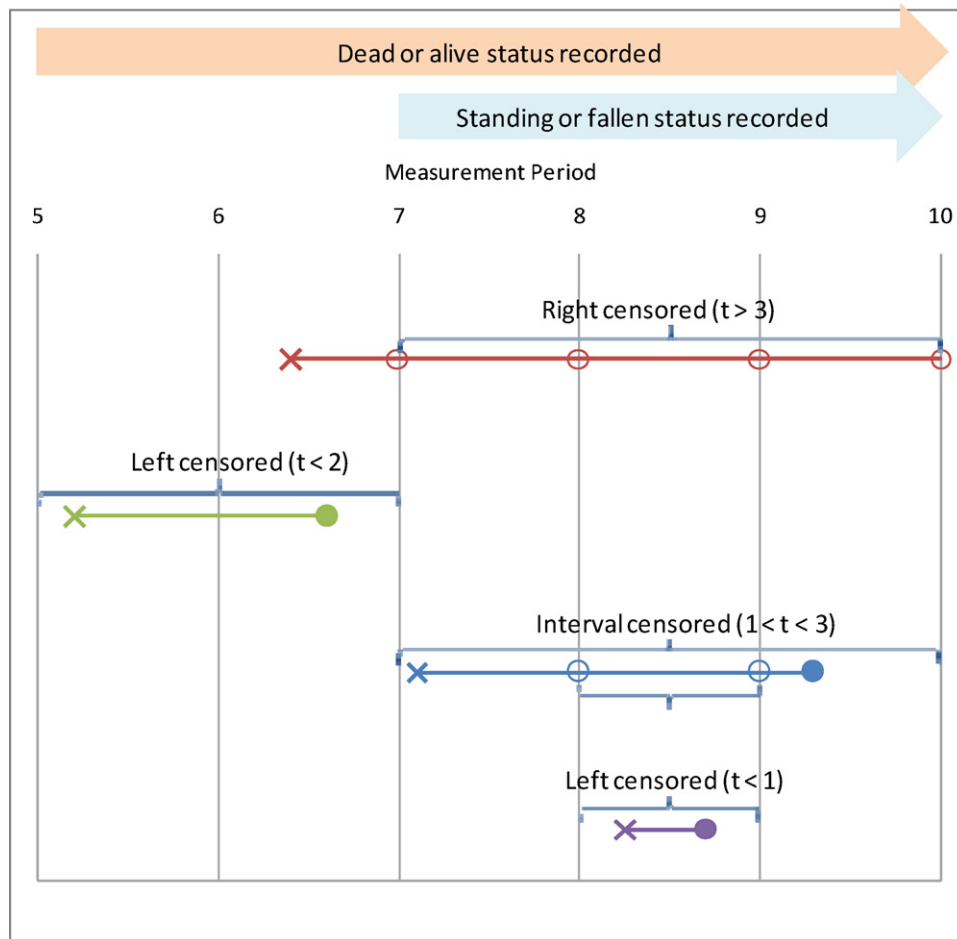


Fig. 1. Schematic diagram outlining how time until falldown was coded for the four observed scenarios. An X indicates when the tree died and a circle indicates whether the snag was observed as fallen (dark) or is still upright (open). The length of the braces conveys the interval assigned to the observation. Note that the number of years in a given interval was used in the calculations.

made at approximately 5–8-year intervals (depending on average height growth rate at the site). The total number of measurements ranged from 8 to 11 among sites, and occurred over 28 years on average (range 21–34 years).

In each plot, all trees above a minimum diameter at breast height (DBH) were tagged, DBH measured, and species and status (live or dead) recorded. The minimum DBH for measurement was 5 cm until to 1990, after which the minimum was lowered to 4 cm. On a subset of trees within each plot, crown class was recorded and total height, height to crown base, and maximum crown width was measured. Heights of trees not measured have been estimated from DBH using data from the subsets and a modification of the non-linear Møness function (J. Goudie, BC Ministry of Forests and

Range, pers. comm.). Relative height was calculated based on the ratio of each tree to the average of the tallest five trees in the plot. The live crown ratio of individual trees was predicted from the subsets using a linear equation based on individual tree characteristics (height, relative height, and slenderness (height/DBH)) and plot characteristics (plot basal area, site index, and dummy variable for thinning and fertilization).

Since 1996, the vertical status (standing or fallen) has been recorded for trees that died during the experiment. By 1996, some sites had been logged or deemed low priority and abandoned; hence, vertical status of snags was recorded at 76 of the original 85 sites. Because of variation in measurement time intervals, 41 sites had one measurement, 34 had two measurements, and 1 had three

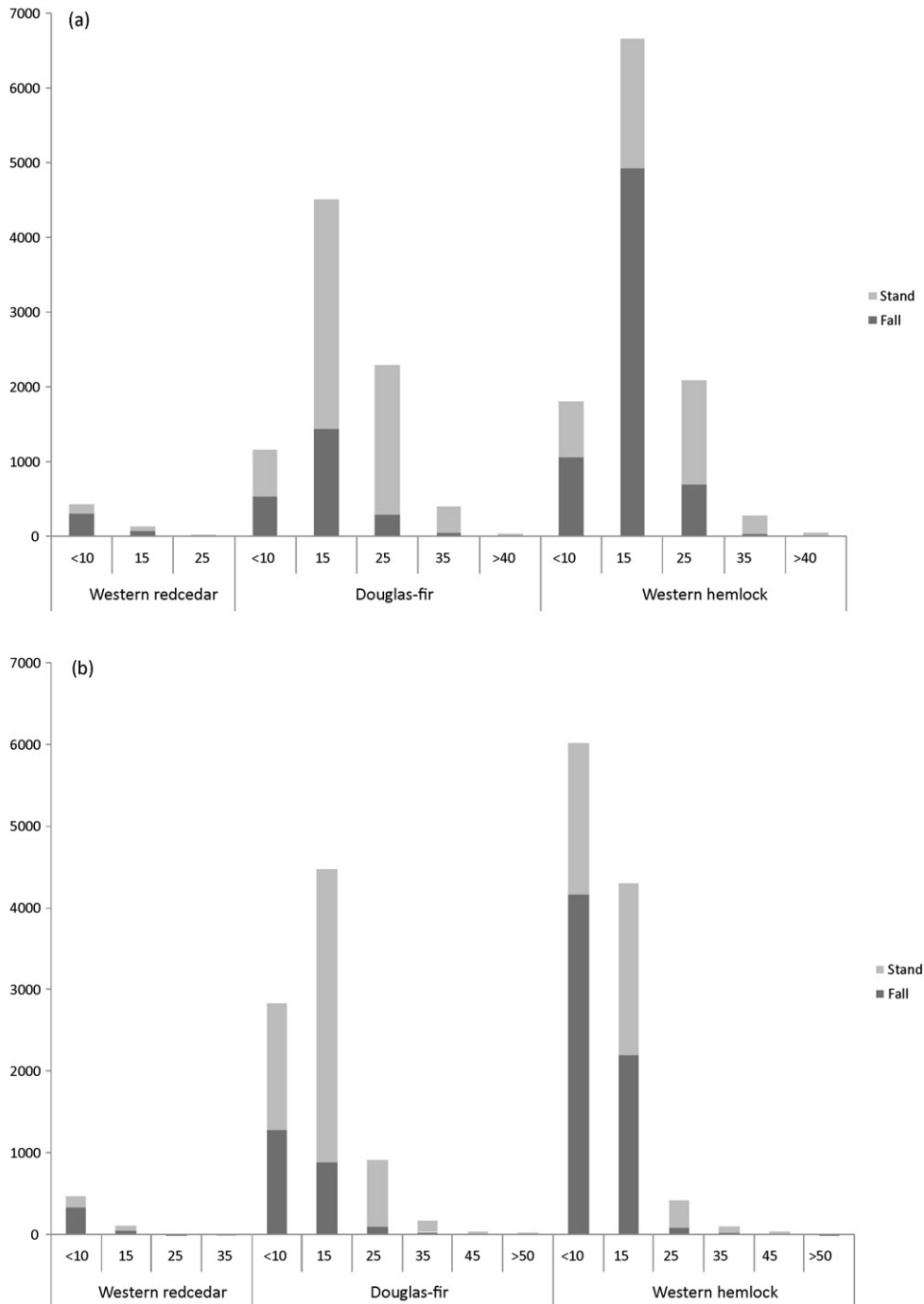


Fig. 2. The cumulative number of Douglas-fir, western hemlock, and western redcedar snags in (a) 10 m height classes and (b) 10 cm diameter classes summarized for a 34-year period of sampling on permanent sample plots. Black = fallen at the last measurement; grey = still standing at the last measurement.

measurements between 1996 and 2008. In total, there were 30,838 records of vertical status. Trees that died prior to the first post-treatment measurement were removed from analysis. The majority of snags were western hemlock (10,587), followed by Douglas-fir (8441), and western redcedar (594). The remaining snags were of other species, which had insufficient numbers for analysis.

2.2. Data analysis

Because the permanent plots were sampled periodically, the time of tree death was known to occur in the interval between two successive measurements but the exact time was unknown. The first time at which information was collected on whether dead trees were standing or fallen was the seventh measurement, approximately 20 years after the plots were installed. For each dead tree, the interval between death and falldown comprised of a lower and upper bound. For a snag still standing at its last measurement, the lower bound, or minimum time for remaining standing, was from year of the measurement when death was first recorded, i.e., the end of the measurement period during which the tree died. The upper bound was potentially infinite, and hence the time interval is right censored (Fig. 1). For a tree that had died and fallen before the first recording of vertical status, the lower bound of the time for remaining standing was unknown and the upper bound (maximum time) was the time from the beginning of the measurement period in which death occurred to the year of measurement; hence, the interval was left censored. For trees that died and then fell during one of the second or third recordings of vertical status, the lower bound was from the end of the measurement period in which death was recorded to the beginning of the next measurement period, and the upper bound was from the beginning of the interval in which death was recorded to the end of the measurement period, and hence these were interval censored. There were a number of trees that were first observed both dead and fallen at the same measurement period, and these were considered left censored with upper bound equal to the length of the measurement.

The accelerated failure time (AFT) model is a class of parametric models that handles right-, left- and interval-censored data (Allison, 1995; Hosmer et al., 2008). A general definition is to consider the distribution for time to failure (T) conditional on specified covariates x_1, x_2, \dots, x_k , as a probability distribution $f(\cdot)$ that involves at the minimum parameters describing scale (μ) and shape (σ):

$$T_i \sim f(\mu_i, \sigma) \quad \text{where } \mu_i = \exp(\theta_0 + \theta_1 x_{1i} + \dots + \theta_k x_{ki}) \quad (1)$$

The covariates (e.g. DBH) act multiplicatively on survival time, so conceptually time to failure or falling passes quickly or slowly depending on a tree's covariate values, hence the notion of

'accelerated' time. The scale parameter controls the general location of the distribution, whereas the shape parameter controls the spread of the distribution and is unaffected by covariates. Distributions for T in the LIFEREG procedure (SAS Institute Inc., 2004) include exponential, Weibull, gamma, log-logistic and log-normal. These distributions are fitted to the data using maximum likelihood, and the log-likelihood formulation distinguishes the four types of censored observations (Fig. 1).

We fit separate models for each of the three main species (Douglas-fir, western hemlock, and western redcedar). Our first step was to describe the underlying distribution of T . We tested four commonly used parametric distributions (exponential, Weibull, log-normal, and generalized gamma) and selected the distribution with the maximum log-likelihood. The maximum likelihood value for the distribution of T occurred with the Weibull model for Douglas-fir and western hemlock, but with the log-normal model for western redcedar. One way to differentiate these two distributions is by the shape of their hazard function, which describes the instantaneous probability of falling, given that a tree has survived up until that point (as a function of time). For the Weibull when the shape parameter $0 < \sigma < 1$, the hazard rate decreases with time (i.e. improvement), when $\sigma = 1$, the hazard is constant (as per the exponential distribution), and when $\sigma > 1$ the hazard increases with time (i.e. deterioration). For the log-normal, when $0 < \sigma < 1$, the initial hazard is low and it peaks at some intermediate time, when $\sigma \cong 1$ the hazard peaks early on and then subsides, and when $\sigma > 1$, the hazard peaks rapidly, and then subsides.

Initially, we included in the model a single covariate, DBH, which has long been found to have a major effect on the rate of snag fall (e.g., Keen, 1929). Then we examined other potential covariates. We tested four individual tree attributes (height, crown ratio at the measurement prior to death, slenderness (height/DBH), and relative height in the stand) and three stand-level attributes (basal area, fertilization, and thinning regime). Covariates were tested successively using likelihood-ratio tests and all final predictor variables were significant at $\alpha = 0.05$.

3. Results

Of the trees that died during the experiment (21–34 years), the percent that remained standing at the last measurement was approximately twice as high for Douglas-fir (72%) than for either western hemlock (39%) or western redcedar (33%). The median standing time of snags before falling was 16 years for Douglas-fir, 11 years for western hemlock, and 5 years for western redcedar. Snags of Douglas-fir and hemlock tended to be larger than those of redcedar (Fig. 2), which occurred mainly in the subcanopy in the plots. The most abundant height class for Douglas-fir and western

Table 1
Estimated parameters of the AFT model and sample size for each category for Douglas-fir, western hemlock, and western redcedar snag longevity in permanent sample plots.

Species	Parameter	Parameter ^a		Wald statistics		Sample size		
		Estimate	SE	χ^2	p-Value	RC	LC	IC
Douglas-fir	Intercept	-4.336	0.136	5838.5	<0.0001	6094	1793	553
	DBH	-0.068	0.004	198.3	<0.0001			
	Shape (σ)	1.7256	0.015					
Western hemlock	Intercept	-4.485	0.097	12935.7	<0.0001	4090	4333	2162
	DBH	-0.023	0.003	41.5	<0.0001			
	Shape (σ)	1.777	0.09					
Western redcedar	Intercept	1.112	0.187	35.33	<0.0001	195	266	133
	DBH	0.066	0.018	13.50	0.0002			
	Shape (σ)	1.152	0.104					

RC = right censored, LC = left censored, IC = interval censored.

^a The Lifereg procedure of SAS uses a slightly different parameterization than Eq. (1) for the Weibull models (i.e. Douglas-fir and western hemlock) that involves a scale parameter. To obtain estimates consistent with the notation of Eq. (1), Lifereg parameter estimates were divided by the negative of the estimated scale parameter.

hemlock snags was 10–20 m tall, whereas most western redcedar snags were <10 m tall (Fig. 2a). The vast majority of snags were <20 cm DBH and only a few exceeded 30 cm DBH for both Douglas-fir and western hemlock; most western redcedar were even smaller, <10 cm DBH (Fig. 2b).

For all species, snag longevity showed a strong positive, highly significant relationship to DBH at the time of death (Table 1). Small Douglas-fir snags fall fairly rapidly, but the probability of remaining standing to 50 years appears very high (>0.9) for large ones (Fig. 3a); however, only 26 Douglas-fir >50 cm DBH had died, which may distort longevity estimates for large snags. Most western hemlock <10 cm DBH fall within 10 years and the probability of surviving to 20 years is <0.15 (Fig. 3b). Although small western redcedar fall very quickly, snags of 20–30 cm DBH

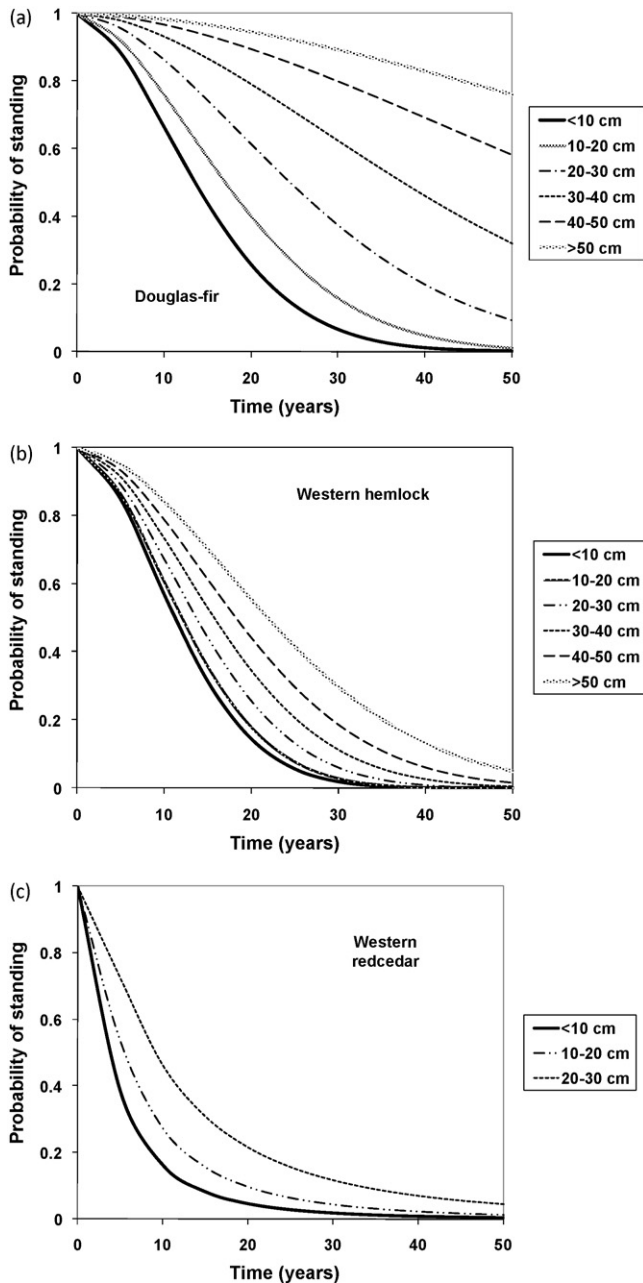


Fig. 3. The predicted probability of snag survival (remaining standing) by diameter class during a period of 50 years following tree death for Douglas-fir, western hemlock, and western redcedar on Vancouver Island and the adjacent mainland of British Columbia. Predictions are based on Eq. (1), using the median prediction from each diameter class.

Table 2

Fit statistics for the AFT model (Eq. (1)) describing time to failure model for three species, Douglas-fir, western hemlock and western redcedar in permanent sample plots.

Species	Model	Log-likelihood	Likelihood-ratio	p-Value
Douglas-fir	Null	-3638.4		
	DBH	-3494.9	287.1	<0.0001
	DBH, HT/DBH	-3442.7	104.3	<0.0001
	DBH, HT/DBH, HT	-3338.1	209.2	<0.0001
Western hemlock	Null	-6609.7		
	DBH	-6585.5	48.6	<0.0001
	DBH, HT _{REL}	-6412.4	346.1	<0.0001
	DBH, HT _{REL} , LCR	-6293.8	237.2	<0.0001
Western redcedar	Null	-313.6		
	DBH	-306.0	15.0	0.0001
	DBH, LCR	-298.0	16.1	0.0003
	HT _{REL} , LCR	-292.5	11.0	0.01

Covariates are diameter at breast height (DBH), height (HT), relative height in the plot (HT_{REL}), slenderness coefficient (HT/DBH), and live crown ratio prior to death (LCR). The null model contains no covariates, and for each species, the model is compared against the one in the previous row.

have a higher probability of standing than comparably sized hemlocks (Fig. 3c). For Douglas-fir and western hemlock snags, the value of the estimated shape parameters of the Weibull model ($\hat{\sigma} = 1.789$ and 2.021, respectively) indicates that the hazard increases over time. The estimated shape parameter for western redcedar snags ($\hat{\sigma} = 1.152$) indicates that the hazard peaks rapidly and then declines.

For each species, the inclusion of other covariates in addition to DBH improved the fit of the model (Table 2); however, the significance of covariates differed among the species. The slenderness coefficient, which has been associated with wind firmness and stability (e.g., Navratil, 1995), improved the model fit for Douglas-fir snags but not for the two other species. The addition of height also improved the fit for the Douglas-fir snag model.

The height of a western hemlock tree relative to the tallest trees in the plot was an important factor governing the longevity after death. Taller western hemlock snags in the stand stood longer than shorter, overtopped ones. The live crown ratio before death also had a positive effect on snag longevity; western hemlock snags that came from trees with long crowns relative to tree height stood longer than those from trees with short crowns. Stem diameter, although still a significant covariate, no longer had a positive effect on longevity once these two covariates were included (Table 3). The addition of relative height and live crown ratio prior death improved the fit of the model of western redcedar snag longevity, and DBH no longer had a significant effect; snags stood longer if prior to death, a tree had a long crown and was relatively tall compared to other trees in the stand.

The additional of stand variables, basal area and silvicultural treatments (thinning or fertilization) did not improve the fit of the models for any species.

4. Discussion

The median longevity of snags in permanent sample plots in second-growth stands in our study was similar to that reported in other studies (e.g., Garber et al., 2005; Russell et al., 2006; Vanderwel et al., 2006). The differences in median longevity among species, from 5 years for western redcedar to 16 years for Douglas-fir may be explained by size and resistance to rot. Most redcedars that died were small trees in the subcanopy and small snags have short persistence in all species. Western hemlock decays more quickly than Douglas-fir (Graham and Cromack, 1982), which accounts for its rapid deterioration and falldown. Our models

Table 3

Estimated parameters of final AFT models for snag longevity of Douglas-fir, western hemlock, and western redcedar in permanent sample plots.

Species	Intercept	DBH	Height/DBH	Height	Relative height	LCR	Shape (σ)
Douglas-fir	-8.891	0.158	3.325	-0.180			1.789
Western hemlock	-3.876	0.055			-3.247	-2.628	2.021
Western redcedar	0.631				2.751	2.783	0.932

For the two Weibull models (i.e. Douglas-fir and western hemlock), snag survival (remaining standing) is $S(t) = \Pr(T \geq t) = 1 - F(t) = \exp(-\mu t^\sigma)$ where $\mu = \exp(\theta_0 + \theta_1 x_1 + \dots + \theta_k x_k)$, and σ is the shape parameter. For the log-normal model (i.e. western redcedar), $S(t) = 1 - \Phi((\log(t) - \log(\mu))/\sigma)$ where $\Phi(\cdot)$ is the distribution function of a standard normal variate, and μ and σ are defined as above.

predict that large Douglas-fir snags are likely to persist for over 50 years, which is consistent with studies documenting that snags can persist in coniferous forests for more than 60 years (Everett et al., 1999; Storaunet and Rolstad, 2002; Newberry et al., 2004; Delong et al., 2005), and sometimes hundreds of years (Daniels et al., 1997). In many other systems, persistence of any snags beyond about 40 years seems unlikely (Lee, 1998; Garber et al., 2005; Passovoy and Fulé, 2006; Russell et al., 2006).

Data collected at periodic intervals precludes accurate modeling of lag time in snag falldown. Low rates of fall for a few years following tree death followed by rapidly increasing rates of fall have been found for snags resulting from disturbances such as fire (e.g., Chambers and Mast, 2005; Russell et al., 2006) and resulting from various mortality processes during stand development (e.g., Lee, 1998; Huggard, 1999). Because of the lag effect, snag falldown follows a negative sigmoidal shaped survival curve (Lee, 1998; Garber et al., 2005; Russell et al., 2006). Lag time prior to falling, however, can be short and not very pronounced (Garber et al., 2005), or undetectable (Storaunet and Rolstad, 2004). Fairly new snags that still have low amounts of decay can have lower fall rates than green trees (Huggard, 1999), which implies a period of stability following mortality. Our model is consistent with descriptions or models of snag survival, which show a decreasing rate of fall in large snags; thus our model resembles a Type III survival curve (Deevey, 1947).

We found large differences in persistence among size classes, similar to many studies (e.g., Keen, 1929; Dahms, 1949; Garber et al., 2005). The greater persistence of larger compared to smaller snags could relate to a variety of factors. For example, the ratio of the more decay-resistant heartwood to sapwood is generally higher in large snags; hence, decay may take longer to permeate a large snag, although this is not necessarily the case (Harmon, 1982). Given that large snags are often of more benefit to some animals (Chambers and Mast, 2005), the longer persistence of large snags is important.

Snag persistence differed substantially among Douglas-fir, western hemlock and western redcedar. The very short median fall time for redcedar (5 years) seems inconsistent with the high decay resistance of the heartwood and the potential for persistence documented for large redcedar snags (Daniels et al., 1997). The redcedar snags in our sample were in general smaller than those of the other two species; thus much of this species effect is actually a size effect and the low proportion of decay-resistant heartwood in small snags may be an important factor for snags of all species. In addition, redcedar is known for layering (Minore, 1990), which could result in weakly rooted, asymmetric stems when small and thus contribute to rapid structural failure following mortality. The high survival of Douglas-fir snags is consistent with previous

studies; for example, the greater longevity of Douglas-fir than of ponderosa pine snags may relate to its relatively thin sapwood (Russell et al., 2006).

Addition of other snag characteristics in addition to DBH improved the models, but significant variables differed among the three species. The slenderness coefficient, which improved the model for Douglas-fir, would be expected to be related to stability as breakage would be more likely in snags with high height to diameter ratios, as expected for live trees (Wilson and Oliver, 2000). Live crown ratio prior to death was also found to improve the models significantly for western hemlock and redcedar. A key consideration in evaluating snag persistence is that tree mortality may relate to different processes for different sized trees. In young stands, mortality of most small trees probably relates to self-thinning, with overtopped, weak trees having the highest mortality. In contrast, large trees were probably killed by damage or diseases that had little to do with position in the stand, i.e., not overtopped or shaded. The characteristics that we found significant (stem slenderness, relative height, and live crown ratio) relate to a general pattern of differences in mortality among trees of different sizes, and position in the competitive hierarchy.

Although silvicultural treatments affect mortality, neither thinning nor fertilization significantly contributes to our models of snag fall, in contrast to models developed for forests in Maine, USA (Garber et al., 2005). Silvicultural treatments increased the size of snags but did not influence the rate of fall for similarly size trees.

Snag persistence is a major determinant of snag abundance at any given time. The substantial differences we observed in fall rates and thus duration of snags of different size and species imply that these factors are relevant to predicting overall snag abundance. Although high input rates from self-thinning can yield high snag densities in young stands, these snags are mainly small and have low persistence relative to snags in old-growth forests. To obtain substantial numbers of large snags in managed stands will require deliberate attention during silvicultural planning; some of the largest trees will need to be retained and possibly killed. Viable options do appear to exist for maintaining some fairly large snags in managed systems.

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Appendix A. The number of plots, age of stands at first measurement and species composition after treatment of 76 installations on Vancouver Island and adjacent mainland

Installation	No. of plots	Plot size (ha)	Age of trees (years)	Percent Douglas-fir	Percent western hemlock	Percent other tree species ^a
1	18	0.05	34–39	95	4	1
2	18	0.05	28–32	83	16	1

Appendix A (Continued)

Installation	No. of plots	Plot size (ha)	Age of trees (years)	Percent Douglas-fir	Percent western hemlock	Percent other tree species ^a
3	18	0.05	41–46	94	3	3
4	18	0.05	29–37	97	2	1
5	18	0.05	27–29	90	8	2
6	8	0.10	36–49	95	2	3
7	10	0.05	37–40	97	0	3
8	14	0.05	36–42	80	4	16
9	8	0.05	27–29	73	24	3
10	10	0.05	28–31	90	7	3
11	8	0.05	24–25	99	1	
12	8	0.05	22–24	99	1	1
13	10	0.05	27–31	99	<1	<1
14	10	0.05	21–24	97	3	0
16	10	0.05	19–21	98	0	2
19	5	0.07	42–46	98	2	0
20	6	0.05	42–44	83	17	0
21	8	0.05	40–43	85	12	3
22	14	0.05	43–47	71	27	2
23	12	0.05	20–22	100	0	0
24	8	0.05	29–33	29	67	4
25	14	0.07	64–74	95	1	4
26	8	0.05	45–50	93	6	1
27	8	0.05	25–26	96	2	2
28	26	0.05	32–36	0	99	1
29	10	0.05	32–34	0	99	1
30	32	0.05	30–35	0	97	3
31	6	0.05	35–40	0	97	3
32	6	0.05	44–46	2	90	8
33	22	0.05	41–48	0	97	3
34	6	0.05	44–48	2	95	3
35	22	0.05	43–49	<1	97	2
36	16	0.05	45–49	1	98	1
37	12	0.05	45–56	23	73	4
38	22	0.10	55–68	50	50	0
39	12	0.05	50–56	3	96	1
40	30	0.07	48–63	47	49	4
41	4	0.05	30–31	94	1	5
42	4	0.05	32–36	74	16	10
43	10	0.05	33–37	75	18	7
44	14	0.05	32–32	78	16	6
46	14	0.07	52–55	92	6	2
47	18	0.07	60–64	100	0	0
48	6	0.05	34–40	95	1	4
49	4	0.05	32–35	81	16	3
51	6	0.05	31–37	68	28	4
52	6	0.05	22–24	93	7	<1
53	4	0.05	22–24	99	1	0
54	4	0.05	23–28	79	17	4
55	4	0.05	25–29	97	2	1
56	32	0.07	61–67	0	94	6
57	4	0.10	61–63	0	90	10
59	8	0.05	62–65	0	95	5
60	8	0.07	70–73	88	12	0
61	6	0.05	29–33	95	1	4
62	4	0.05	41–45	98	<1	2
63	4	0.05	77–81	62	38	<1
64	10	0.05	30–34	0	99	1
65	6	0.05	28–33	93	7	<1
66	4	0.05	45–50	11	89	<1
67	4	0.05	25–31	2	96	2
68	4	0.07	41–44	88	10	2
69	10	0.07	40–43	75	24	1
70	8	0.05	15–18	92	8	0
71	18	0.05	26–29	100	0	0
72	18	0.05	58–66	92	3	5
74	4	0.05	25–29	30	66	4
75	6	0.05	32–34	39	60	1
77	18	0.05	35–44	98	1	1
78	43	0.05	28–34	100	0	0
79	11	0.05	15–16	99	1	0
80	6	0.05	13	0	93	7
81	4	0.05	15–17	87	13	0
82	8	0.05	15	100	<1	0
83	8	0.05	14–16	100	0	0
85	4	0.05	15–16	83	17	0

^a Other species in western redcedar, Sitka spruce, western white pine.

References

- Aakala, T., Kuuluvainen, T., Gauthier, S., De Grandpré, L., 2008. Standing dead trees and their decay-class dynamics in the northeastern boreal old-growth forests of Quebec. *Forest Ecology and Management* 255, 410–420.
- Allison, P.D., 1995. *Survival Analysis using SAS®: A Practical Guide*. SAS Institute Inc., Cary, N.C.
- Bull, E.L., Parks, C.G., Torgersen, T.R., 1997. Trees and logs important to wildlife in the Interior Columbia River Basin. USDA Forest Service General Technical Report PNW-GTR-391.
- Chambers, C.L., Mast, J.N., 2005. Ponderosa pine snag dynamics and cavity excavation following wildfire in northern Arizona. *Forest Ecology and Management* 216, 227–240.
- Cline, S.P., Berg, A.B., Wight, H.M., 1980. Snag characteristics and dynamics in Douglas-fir forests, western Oregon. *Journal of Wildlife Management* 44, 773–786.
- Dahms, W.G., 1949. How long do Ponderosa pine snags stand? PNW For. Range Exp. Stn. Res. Note #57, Portland, OR.
- Daniels, L.D., Dobry, J., Klinka, K., Feller, M.C., 1997. Determining year of death of logs and snags of *Thuja plicata* in southwestern coastal British Columbia. *Canadian Journal of Forest Research* 27, 1132–1141.
- Delong, S.C., Daniels, L.D., Heemskerk, B., Storaunet, K.O., 2005. Temporal development of decaying log habitats in wet spruce-fir stands in east-central British Columbia. *Canadian Journal of Forest Research* 35, 2841–2850.
- Deevey, E.S., 1947. Life tables for natural populations of animals. *Quarterly Review of Biology* 22, 283–314.
- Everett, R., Lehmkühl, J., Schellhaas, R., Ohlson, P., Keenum, D., Riesterer, H., Spurbeck, D., 1999. Snag dynamics in a chronosequence of 26 wildfires on the east slope of the Cascade Range in Washington State, USA. *International Journal of Wildland Fire* 9, 223–234.
- Franklin, J.F., Shugart, H.H., Harmon, M.E., 1987. Tree death as an ecological process. *BioScience* 37, 550–556.
- Garber, S.M., Brown, J.P., Wilson, D.S., Maguire, D.A., Heath, L.S., 2005. Snag longevity under alternative silvicultural regimes in mixed-species forests of central Maine. *Canadian Journal of Forest Research* 35, 787–796.
- Graham, R.L., Cromack Jr., K., 1982. Mass, nutrient content, and decay rate of dead boles in rain forests of Olympic National Park. *Canadian Journal of Forest Research* 12, 511–521.
- Guarín, A., Taylor, A.H., 2005. Drought triggered tree mortality in mixed conifer forests in Yosemite National Park, California, USA. *Forest Ecology and Management* 218, 229–244.
- Harmon, M.E., 1982. Decomposition of standing dead trees in the southern Appalachian Mountains. *Oecologia* 52, 214–215.
- Harmon, M.E., Franklin, J.F., Swanson, F.J., Sollins, P., Gregory, S.V., Lattin, J.D., Anderson, N.H., Cline, S.P., Aumen, N.G., Sedell, J.R., Lienkaemper, G.W., Cromack Jr., K., Cummins, K.W., 1986. Ecology of coarse woody debris in temperate ecosystems. *Advances in Ecological Research* 15, 133–302.
- Hosmer, D.W., Lemeshow, S., May, S., 2008. *Applied Survival Analysis. Regression Modeling of Time-to-Event Data*, 2nd ed. John Wiley & Sons, Inc., Hoboken, NJ, 392 pp.
- Huggard, D.J., 1999. Static life-table analysis of fall rates of subalpine fir snags. *Ecological Applications* 9, 1009–1016.
- Keen, F.P., 1929. How soon do yellow pine snags fall. *Journal of Forestry* 27, 735–737.
- Lee, P., 1998. Dynamics of snags in aspen-dominated midboreal forests. *Forest Ecology and Management* 105, 263–272.
- Maser, C., 1988. *The Redesigned Forest*. R & E Miles, San Pedro, CA, 234 p.
- Minore, D., 1990. *Thuja plicata* Donn ex D. Don. In: Burns, R.M., Honkala, B.H. (Eds.), *Silvics of North America: I Conifers*. USDA Forest Service Agricultural Handbook 654, Washington, D.C., pp. 590–600.
- Morrison, M.L., Raphael, M.G., 1993. Modeling the dynamics of snags. *Ecological Applications* 3, 322–330.
- Navratil, S., 1995. *Minimizing Wind Damage in Alternative Silviculture Systems in Boreal Mixedwoods*. Publication Number Fo42-91/124/1995E. Canadian Forest Service and Alberta Forest Service, Edmonton, Alberta.
- Newberry, J.E., Lewis, K.J., Walters, M.B., 2004. Estimating time since death of *Picea glauca* × *P. engelmannii* and *Abies lasiocarpa* in wet cool sub-boreal spruce forest in east-central British Columbia. *Canadian Journal of Forest Research* 34, 931–938.
- Papaik, M.J., Canham, C.D., Latty, E.F., Woods, K.D., 2005. Effects of an introduced pathogen on resistance to natural disturbance: beech bark disease and wind-throw. *Canadian Journal of Forest Research* 35, 1832–1843.
- Passovoy, M.D., Fulé, P.Z., 2006. Snag and woody debris dynamics following severe wildfires in northern Arizona ponderosa pine forests. *Forest Ecology and Management* 223, 237–246.
- Raphael, M.G., Morrison, M.L., 1987. Decay and dynamics of snags in the Sierra Nevada, California. *Forest Science* 33, 774–783.
- Russell, R.E., Saab, V.A., Dudley, J.G., Rotella, J.J., 2006. Snag longevity in relation to wildfire and postfire salvage logging. *Forest Ecology and Management* 232, 179–187.
- SAS Institute Inc., 2004. *SAS OnlineDoc® 9.1.3*. SAS Institute Inc., Cary, NC.
- Schmid, J.M., Hinds, T.E., 1974. Development of spruce-fir stands following spruce beetle outbreaks. USDA Forest Service Research Paper RM-RP-131.
- Schmid, J.M., Mata, S.A., McCambridge, W.F., 1985. Natural falling of beetle-killed ponderosa pine. USDA Forest Service Research Paper RM-RN-454.
- Smith, C.Y., Warkentin, I.G., Moroni, M.T., 2008. Snag availability for cavity nesters across a chronosequence of post-harvest landscapes in western Newfoundland. *Forest Ecology and Management* 256, 641–647.
- Spies, T.A., Franklin, J.F., Thomas, T.B., 1988. Coarse woody debris in Douglas-fir forests of Western Oregon and Washington. *Ecology* 69, 1689–1702.
- Stone, J.N., 1994. *Extensive studies of fertilizing and thinning coastal Douglas-fir and western hemlock: an installation report*. FRDA Report 227. Research Branch, British Columbia Ministry of Forests, Victoria, B.C.
- Storaunet, K.O., Rolstad, J., 2002. Time since death and fall of Norway spruce logs in old-growth and selectively cut boreal forest. *Canadian Journal of Forest Research* 32, 1801–1812.
- Storaunet, K.O., Rolstad, J., 2004. How long do Norway spruce snags stand? Evaluating four methods. *Canadian Journal of Forest Research* 34, 376–383.
- Taylor, S.L., MacLean, D.A., 2007. Dead wood dynamics in declining balsam fir and spruce stands in New Brunswick, Canada. *Canadian Journal of Forest Research* 37, 750–762.
- Thomas, J.W., 1979. *Wildlife Habitats in Managed Forests: the Blue Mountains of Oregon and Washington*. Agricultural Handbook No. 553. USDA Forest Service, Portland, OR.
- Vanderwel, M.C., Caspersen, J.P., Woods, M.E., 2006. Snag dynamics in partially harvested and unmanaged northern hardwood forests. *Canadian Journal of Forest Research* 36, 2769–2779.
- Wilhere, G.F., 2003. Simulations of snag dynamics in an industrial Douglas-fir forest. *Forest Ecology and Management* 174, 521–539.
- Wilson, J.S., Oliver, C.D., 2000. Stability and density management in Douglas-fir plantations. *Canadian Journal of Forest Research* 30, 910–920.