

# Do larger snags stand longer?—snag longevity in mixed conifer–hardwood forests in Hokkaido, Japan

Kensuke Onodera<sup>1</sup> · Sawako Tokuda<sup>1</sup>

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## Abstract

• **Key message** More than half of the dead trees fell down within decade. Besides, DBH effect on snag longevity varied by tree species and was not detected for some species. Management of long-lived snags in temperate mixed forests should be reconsidered.

• **Context** Snags (standing dead trees) provide essential habitats for many species. Those with large diameter at breast height (DBH) are prioritized for retention; one of the reasons is that snag longevity (recruitment to falling down) increases with increasing DBH in conifer-dominated forests. Despite its importance, the DBH effect on hardwood snags is inadequately understood.

• **Aims** The aim of this study is to investigate whether and how the DBH effect varies by tree species in mixed conifer–hardwood forests.

• **Methods** We checked the current status (standing or falling) of dead trees that had been recorded in 37 permanent plots and applied a generalized linear mixed model. We used tree species, time since death, DBH, and interaction terms as variables.

• **Results** Half of the dead trees with a DBH of 25 cm were estimated to have fallen down within 1–6 years for most of the species. While snag longevity increased with increasing DBH

in *Abies sachalinensis* and *Phellodendron amurense*, we detected no such effect in *Picea* and three hardwood species.

• **Conclusions** For highly decayed or long-lived snags, retaining large snags is not always effective. Managers of species-rich mixed forests should consider the variability of the DBH effects and management of dead wood before and after tree mortality.

**Keywords** Dead wood · Forest management · Retention harvesting · Temperate zone · Wood decay

## 1 Introduction

Snags (standing dead trees) are important resources for biodiversity conservation in forests. They provide essential habitats for many species. Saproxylic invertebrates and their predators and parasitoids depend on dead woods, and many of them prefer snags to downed logs (Jonsell and Weslien 2003). Snags provide foraging sites for birds such as the three-toed woodpecker, *Picooides tridactylus*, which requires a number of snags to maintain their populations (Bütler et al 2004). Many fungal species colonize in snags, and fungivorous insects rely on them (Kaila et al. 1994; Stokland et al. 2012). In addition, snags play a key role in global carbon budget and nutrient cycling in forest ecosystems (Bradford et al. 2009; Holub et al. 2001). Snags usually decay more slowly and store carbon over longer periods than downed logs. As snags decay, essential nutrients such as nitrogen are slowly released (Lambert et al. 1980; Yatskov et al. 2003). Snags finally fall down and supply coarse woody debris to the forest floor. Coarse woody debris influences seedbed availability (Takahashi et al. 2000), the amount of soil organic matter (Graham et al. 1994), and wildfire disturbance (Metz et al. 2011).

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✉ Kensuke Onodera  
onodera-kensuke@hro.or.jp

Sawako Tokuda  
tokuda-sawako@hro.or.jp

<sup>1</sup> Forestry Research Institute, Hokkaido Research Organization, Koshunai, Bibai, Hokkaido 079-0198, Japan

Recruitment and fall down drive the dynamics of snags in forests. The duration of time from recruitment to falling down, which is often referred to as snag longevity, not only determines snag abundance but also is closely related to the quality of the habitats provided to species associated with snags. The assemblage of species associated with snags varies by several factors, including tree species, diameter, sun exposure, burn treatment, and decay condition of snags (Drapeau et al. 2009; Gibb et al. 2006; Jonsell et al. 1998; Saint-Germain et al. 2007; Ulyshen and Hanula 2009). Snag longevity influences the succession of the species assemblages through progression of the decay stage, and the process is usually categorized into five or more stages (Stokland et al. 2012). The first stage is the period immediately after tree death. From the second to fourth stages, bark is gradually loosening and falling and wood decomposition is spreading into heartwood. Finally, at the fifth stage, wood is heavily collapsing and partially disintegrated into fragments. Among the few studies available, the species richness of saproxylic beetles was shown to be highest at the first and second stages for conifer snags (Ulyshen and Hanula 2010). In contrast, species richness was highest at the middle stage for hardwood snags (Hammond et al. 2004; Saint-Germain et al. 2007). The provision of snags in different decay stages is crucial for conserving biodiversity in forests, and enlightened management requires a full understanding of snag longevity.

Snag longevity has been examined in several forests, particularly in conifer-dominated forests of North America and Scandinavia (e.g., Keen 1929; Storaunet and Rolstad 2004). Longevity varies among forests under the influences of a variety of biotic and abiotic factors, e.g., tree species, diameter at breast height (DBH), cause of mortality, soil type, and site conditions (Garber et al. 2005; Keen 1955; Mielke 1950; Storaunet and Rolstad 2002; Aakala et al. 2008). Forest management practices also influence snag longevity (Garber et al. 2005). Forestry for timber production typically results in a reduction in the abundance of snags (Graves et al. 2000). Harvest frequency (cutting cycle) had a negative impact on snag longevity in forests managed under the selection system (Garber et al. 2005; Vanderwel et al. 2006a).

For conifers, increasing DBH had a positive effect on snag longevity (Garber et al. 2005; Keen 1955; Lyon 1977; Parish et al. 2010). For example, for *Tsuga heterophylla* (Raf.) Sarg. in British Columbia (Canada), an incremental increase in DBH class from 20–30 to 40–50 cm increased the half-life of snags (expected age when half of the snags will have fallen down) from 14 to 19 years (Parish et al. 2010). Studies on hardwood snags are few, and the DBH effects on hardwood snag longevity are inadequately understood. Lee (1998) found no significant DBH effect in *Populus tremuloides* Michx. -dominated forests of Alberta, Canada. He suggested that this was likely the case because only small-diameter snags were included in the analysis. However, Vanderwel et al. (2006a)

identified a significant DBH effect among small-diameter snags, but not among large-diameter snags in hardwood forests dominated by *Acer saccharum* Marsh., *Ostrya virginiana* (Mill.) K. Koch., *Quercus rubra* L., *Fraxinus americana* L., and *Acer rubrum* L. in Ontario, Canada. Russell and Weiskittel (2012) developed the snag longevity models for six tree species separately. They found a significant DBH effect for *Abies balsamea* (L.) Mill., *Acer rubrum*, and *Picea rubens* Sarg., but not for *Betula papyrifera* Marshall, *Thuja occidentalis* L., and *Tsuga canadensis* (L.) Carrière. Accordingly, the DBH effects on snag longevity likely differ among tree species. However, Russell and Weiskittel (2012) withheld to use tree species as an indicator variable in their modeling because of a decline of statistical power and did not examine whether the DBH effect varied significantly by tree species.

Snag size is a practical criterion for selecting those that are to be retained in forests. Conifer snags with large DBH are currently prioritized for retention in managed forests to provide snag habitats over protracted periods and to compensate for the lack of large woody debris for biodiversity conservation (Watt and Caceres 1999). It is worth examining whether such criteria can be adapted similarly to hardwood snags for managing temperate mixed forests. In general, the durability to wood decay is heterogeneous among hardwoods compared with the durability of conifers (Harmon 1982). The differences in durability could be attributed to differences in lignin and phenolic compounds in dead wood cells (Scheffer and Cowling 1966; Witzell and Martín 2008) and could correlate with differences in snag longevity among tree species. Heterogeneity of durability to wood decay may also relate to the variation in the DBH effect on snag longevity. Therefore, we hypothesized that the DBH effect on snag longevity varies by tree species and developed models for estimating snag longevity, i.e., the probability of a snag still be standing at a given point in time since tree death using data obtained from permanent plots.

## 2 Materials and methods

### 2.1 Study area

We used data from 37 permanent plots located in mixed conifer–hardwood stands in Hokkaido, northern Japan, which is in a cool–temperate zone (Nakashizuka and Iida 1995). Mean annual precipitation and mean annual temperature in the period 1971–2000 at observation stations nearest to each of the plots (18 stations in total) ranged from 1205 to 2221 mm and from 3.3 to 7.2 °C, respectively (Japan Meteorological Agency 2002). Elevation of the plots ranged from 100 to 670 m a.s.l. The plots were typically snow-covered from December until May. The crowns of the forests were dominated

by boreal conifers, *Abies sachalinensis* (F. Schmidt) Mast., *Picea jezoensis* (Sieb. et Zucc.) Carrière, and *Picea glehnii* (F. Schmidt) Mast., and temperate hardwoods, including *Acer pictum* Thunb. subsp. *mono* (Maxim.) H. Ohashi, *Quercus crispula* Blume, and *Tilia japonica* (Miq.) Simonk. The forest floor was broadly dominated by dwarf bamboos, *Sasa kurilensis*, *Sasa senanensis*, and *Sasa nipponica*. Other features of the vegetation, such as understory species that co-occurred with the dominant species, were described by Uemura (1994).

## 2.2 Field data

The Hokkaido prefectural government had established the permanent plots and collected data on tree growth and mortality before we began our study. The area of most plots was 0.25 ha, although one covered 0.5 ha and another four covered 1 ha (Online resource 1) because these five plots were established especially to study tree growth in preserved forests (most of the plots were established in nonpreserved forests). All live trees in the plots with a DBH >5 cm had been identified to species, marked, and numbered using paint and vinyl or aluminum tags. DBH was measured to the nearest 2 cm (e.g., when DBH was >5 cm but <7 cm, a value of 6 cm had been recorded). Measurement intervals were generally around 5 years (2–7 years), but for three of the plots, the intervals exceeded 7 years (8–10 years) on one occasion (Online resource 1). Trees that died between measurements had also been recorded.

Most of the plots had not been harvested since their establishment, but selective cutting was conducted in two of the plots (Online resource 1). Garber et al. (2005) analyzed the negative effect on snag longevity by logging practices and discussed that the most likely cause was mechanical disturbance by felling and skidding. Thus, we used only data collected after the last harvest to exclude the effects of logging practices. As some of the older data had been lost, we used data collected between 1970 and 2011. As a result, measurements were taken on three to nine occasions among the plots within the measurement periods that we employed for the analyses (Online resource 1).

## 2.3 Current status of dead trees

In the 37 permanent plots, 1446 dead trees (410 conifers and 1036 hardwoods) with a DBH  $\geq 12$  cm had been recorded before our study (Online resource 1). During the period 2008–2011, we visited each of the 37 study plots once and checked the current status (still standing or already fallen) of these dead trees. Although a large number of dead trees with a DBH <12 cm had been recorded in the plots (2142 trees), we did not include such small dead trees in our study because we considered that analyzing the data of such small trees is less

effective to examine the DBH effect, even though checking all the small dead trees will be laborious. We calculated time since death (TSD) of dead trees as the elapsed time from the year of tree death to the year that we visited the plots. The year of tree death was defined as the midpoint in the interval between two measurements made when the tree was last found alive and when the tree was first found dead. Therefore, there are errors ranging from 1 to 3.5 years for most of the plots with measurement intervals of 2–7 years (Online resource 1). In addition, we were unable to distinguish the dead trees killed by uprooting or base snapping (i.e., those that had died and fallen down on the same occasion and therefore never achieved snag status) from dead trees that died and later fell down before the next measurement occasion (i.e., short-lived snags). These limitations inherent in interval measurement data were inevitable, and thus, we must be aware that they affect the estimation of snag longevity. The effect of this error on the estimation of snag longevity should be larger at smaller TSD, because not a few dead trees would have died and fallen simultaneously and our definition of TSD assumed that these dead trees stood 1–3.5 years after their mortality.

## 2.4 Data analysis

In the first step, we applied a generalized linear mixed model (GLMM) (link function=logit, error distribution=binomial) to the data on the dead trees in the permanent plots. GLMM is an extension of the generalized linear model (Zuur et al. 2007). GLMM can deal with unobserved heterogeneity in response variables and unexplained sources of variation which account for lack of fit. If we ignore such sources of variation, it might affect standard errors and *p* values, although adding regression parameters concerning this variation (e.g., the sampling areas) can lead to the loss of degrees of freedom. GLMM can deal with the sources of variation as random effects and has advantages in an analysis of overdispersed data. Snag longevity would be affected by several unobserved effects in each plot, such as microclimate. Additionally, we focused on the interaction between the tree species and the DBH effects, leading to the loss of degrees of freedom. Thus, GLMM was considered to be effective for our analysis. The response variable in our modeling exercise was current dead tree status (standing or fallen). Fixed effects were tree species (SP), TSD, and DBH on the last occasion when the tree was living and measured. Seven tree species groups were considered in our model (1: *Abies sachalinensis*, 2: *Picea jezoensis* and *Picea glehnii*, 3: *Q. crispula*, 4: *Phellodendron amurense* Rupr., 5: *Acer pictum*, 6: *Tilia japonica*, 7: other hardwoods). We gathered the data of *Picea jezoensis* and *Picea glehnii* to achieve adequate sample size; the two *Picea* species had almost similar trends in wood decay experiments (Odajima 1964; Wood technology and wood utilization division 1982). We also employed two-way interaction terms between

the fixed effects TSD and SP, and DBH and SP (referred to hereafter as TSD×SP and DBH×SP) to determine whether the effects varied among tree species. The random effect in the model was the plot. To select the best model, we compared all combinations of the fixed effects and interaction terms using the Akaike information criterion (AIC). In general, a model containing interaction terms should include fixed effects appearing within interaction terms; we permitted a model containing only interaction terms to be a candidate model in our model selection. If a model with only interaction terms is selected as best, we can consider that TSD or DBH would have only an effect by varying with tree species and a model may lack a main effect of tree species.

For the second step, we applied GLMM to each species group separately to focus on the traits of each species more explicitly. Fixed effects were TSD and DBH, and the random effect was the plots. We did not use interaction terms in this step. We selected the best model with the method in the same way as the first step.

All statistical analyses were performed in R version 3.0.1 (R Core Team 2013) and the package lme4 (Bates et al. 2014).

### 3 Results

Among the 1446 dead trees that had been recorded in the plots, 128 conifers and 166 hardwoods were still standing when we visited the permanent plots. Among the dead trees still standing, *Abies sachalinensis* was the most abundant in conifer snags, and the four species *Q. crispula*, *Phellodendron amurense*, *Acer pictum*, and *Tilia japonica* were the dominants in hardwood snags (Table 1). We found only one snag of *Pinus parviflora* Siebold et Zucc. var. *pentaphylla* (Mayr) A. Henry. We could not identify nine conifer and 12 hardwood snags because of tag or data losses; we excluded these snags from further analysis.

In the first step, a model containing the two interaction terms (TSD×SP and DBH×SP) was selected as the best,

indicating that the TSD and DBH effects varied among tree species (Table 2). Adding the other fixed effects did not decrease AIC values (Table 2). Parameters of the best model for TSD and DBH interaction with species are presented in Table 3.

In the second step, both of the fixed effects, TSD and DBH, were included in the best models for *Abies sachalinensis*, *Phellodendron amurense*, *Q. crispula*, and other hardwoods (Table 4). However, the confidence interval of the estimated parameter of DBH for *Q. crispula* contained the value of 0 and the *p* value was greater than 0.05 (Table 5), and thus, the DBH effect on snag longevity was not obvious. For *Picea* spp. and *Tilia japonica*, only TSD was included in the best models (Table 4). For *Acer pictum*, although the interaction term DBH×SP was significant in the first step, only TSD was included in the best model in the second step. Parameters of the best models incorporating both TSD and DBH are shown in Table 5.

The probability of a snag still be standing decreased with increasing TSD for all species (Table 5, Fig. 1). The slope of the decrease by TSD varied among species; it was most sharply for *Acer pictum* and most gently in *Q. crispula* across species (Fig. 1). The half-lives to falling down of dead trees with a DBH of 25 cm were 6 years for *Abies sachalinensis* and *Phellodendron amurense* and 1–5 years for other species, except for *Q. crispula* in which more than half of the dead trees fell down when TSD=0.

The probability of a snag still be standing increased with increasing DBH in *Abies sachalinensis*, *Phellodendron Amurense*, and “other hardwoods” (Table 5, Fig. 2). The slope of the increase by DBH was steepest in *Phellodendron amurense*, showing an increase in probability to 0.5811 when DBH increased to 40 cm (TSD=10) (Fig. 2).

### 4 Discussion

As the TSD increased, the probability of a snag still be standing declined most sharply in *Acer pictum*, whereas the slopes

**Table 1** Number and diameter at breast height (DBH) of trees with DBH ≥12 cm that had died between measurement occasions in the permanent plots and number of those still standing when the current status of the dead trees was checked in the period 2008–2011

Species	Number of dead trees		DBH of dead trees (cm)		
	All	Standing	Mean (SD)	Median	Max.
<i>Abies sachalinensis</i>	335	110	35 (17.0)	34	74
<i>Picea</i> spp.	72	17	37 (24.7)	30	104
<i>Quercus crispula</i>	95	19	25 (24.0)	16	156
<i>Phellodendron amurense</i>	110	18	19 (7.1)	16	44
<i>Acer pictum</i>	146	15	24 (13.5)	19	78
<i>Tilia japonica</i>	158	17	24 (15.7)	16	74
Other conifers	3	1	25 (5.8)	24	36
Other hardwoods	527	97	21 (10.7)	18	86

Thirteen unidentifiable snags were not included

**Table 2** AIC and delta AIC values of the best ten candidate and full models describing probability of a snag still be standing in the permanent plots in mixed forests in Hokkaido, Japan

Model	AIC	ΔAIC
TSD <sup>a</sup> ×SP <sup>b</sup> +DBH <sup>c</sup> ×SP	1160.667	0
TSD×SP+DBH×SP+TSD	1160.668	0.001
TSD×SP+DBH×SP+DBH	1160.668	0.001
TSD×SP+DBH×SP+TSD+DBH	1160.668	0.001
TSD×SP+DBH	1161.269	0.602
TSD×SP+TSD+DBH	1161.269	0.602
TSD×SP+TSD+DBH+SP	1165.597	4.930
TSD×SP	1167.737	7.070
TSD×SP+TSD	1167.737	7.070
TSD×SP+DBH×SP+SP	1169.998	9.331
TSD×SP+DBH×SP+TSD+DBH+SP	1169.999	9.332

<sup>a</sup> Time since tree death  
<sup>b</sup> Tree species (categorical)  
<sup>c</sup> Diameter at breast height

of the decrease were intermediate in *Phellodendron amurense* and *Tilia japonica* (Fig. 1). The differences in the TSD effect among tree species may relate to wood resistance to decay after tree death. Snags with wood most resistant to decay probably remain standing longer. Field tests of wood decay by Odajima (1964) and the Japan Wood Protection Association (2012) demonstrated that timber stakes of *Picea* spp., *Phellodendron amurense*, *Acer pictum*, and

**Table 3** Estimated parameters of the best model describing the probability of a snag still be standing in permanent plots located in mixed forests on Hokkaido, Japan

Variable	Estimate	Standard error	Confidence interval		p value
			2.5 %	97.5 %	
Intercept	-0.118	0.232	-0.571	0.337	
TSD <sup>a</sup> × <i>Abies sachalinensis</i>	-0.096	0.016	-0.128	-0.064	<0.001
TSD× <i>Picea</i> spp.	-0.127	0.042	-0.208	-0.045	0.002
TSD× <i>Quercus crispula</i>	-0.090	0.026	-0.141	-0.039	<0.001
TSD× <i>Phellodendron amurense</i>	-0.192	0.046	-0.281	-0.102	<0.001
TSD× <i>Acer pictum</i>	-0.419	0.116	-0.646	-0.192	<0.001
TSD× <i>Tilia japonica</i>	-0.179	0.038	-0.253	-0.103	<0.001
TSD×other hardwoods	-0.171	0.021	-0.212	-0.130	<0.001
DBH <sup>b</sup> × <i>Abies sachalinensis</i>	0.020	0.006	0.007	0.032	0.002
DBH× <i>Picea</i> spp.	0.010	0.009	-0.007	0.027	0.239
DBH× <i>Quercus crispula</i>	-0.011	0.014	-0.037	0.016	0.429
DBH× <i>Phellodendron amurense</i>	0.051	0.024	0.003	0.099	0.037
DBH× <i>Acer pictum</i>	0.051	0.023	0.007	0.095	0.025
DBH× <i>Tilia japonica</i>	0.015	0.014	-0.013	0.042	0.309
DBH×other hardwoods	0.027	0.010	0.007	0.046	0.008

Confidence intervals were calculated by the Wald method

<sup>a</sup> Time since tree death  
<sup>b</sup> Diameter at breast height

**Table 4** AIC values of candidate models developed for each species separately, describing probability of a snag still be standing in the permanent plots in mixed forests in Hokkaido, Japan

Species	Model		
	TSD+DBH	TSD	DBH
<i>Abies sachalinensis</i>	362.8	366	404.7
<i>Picea</i> spp.	71.8	70.1	75.1
<i>Quercus crispula</i>	94.8	95.1	99.8
<i>Phellodendron amurense</i>	77.8	79.7	96.5
<i>Acer pictum</i>	60.9	59.7	96.3
<i>Tilia japonica</i>	89.8	89.1	109.3
Other hardwoods	423.5	426.4	503

Italicized numbers indicate minimum AIC values.

*Tilia japonica* had low resistance to decay. Although other factors, such as differences in fungal species among forests, may also affect decaying speed (Wood technology and wood utilization division 1982), our data clearly show that snags of *Acer pictum* have low resistance to wood decay across a broad area of Hokkaido.

The DBH effects on snag longevity were not obvious in some species (Table 5). Parish et al. (2010) and Vanderwel et al. (2006a) suggested that the positive DBH effects could relate to the higher ratio of heartwood to sapwood in larger snags because heartwood is more decay-resistant and provides the most structural support. Thus, snag longevity will be

**Table 5** Estimated parameters of the best model describing the probability of a snag still be standing in permanent plots located in mixed forests in Hokkaido, Japan

Species	Variable	Estimate	Standard error	Confidence interval		p value
				2.5 %	97.5 %	
<i>Abies sachalinensis</i>	Intercept	0.102	0.452	-0.783	0.987	
	TSD <sup>a</sup>	-0.114	0.020	-0.153	-0.075	<0.001
	DBH <sup>b</sup>	0.020	0.009	0.003	0.038	0.025
<i>Picea</i> spp.	Intercept	0.057	0.895	-1.696	1.810	
	TSD	-0.112	0.057	-0.223	-0.000	0.049
<i>Quercus crispula</i>	Intercept	0.378	0.684	-0.962	1.718	
	TSD	-0.086	0.035	-0.155	-0.018	0.013
	DBH	-0.023	0.017	-0.056	0.011	0.193
<i>Phellodendron amurense</i>	Intercept	-0.934	0.996	-2.886	1.018	
	TSD	-0.178	0.051	-0.278	-0.079	<0.001
	DBH	0.076	0.038	0.002	0.150	0.043
<i>Acer pictum</i>	Intercept	1.735	1.107	-0.436	3.905	
	TSD	-0.531	0.218	-0.958	-0.103	0.015
<i>Tilia japonica</i>	Intercept	0.257	0.524	-0.770	1.283	
	TSD	-0.170	0.044	-0.256	-0.084	<0.001
Other hardwoods	Intercept	-0.301	0.360	-1.006	0.405	
	TSD	-0.163	0.023	-0.208	-0.118	<0.001
	DBH	0.028	0.012	0.004	0.052	0.023

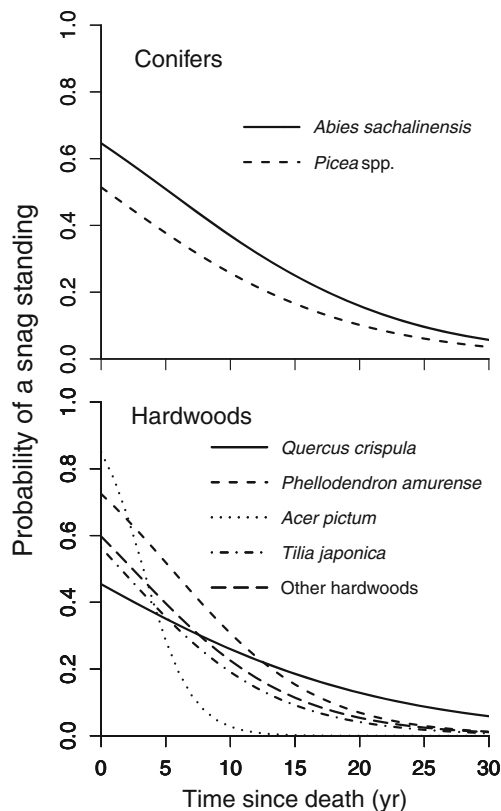
Confidence intervals were calculated by the Wald method

<sup>a</sup> Time since tree death

<sup>b</sup> Diameter at breast height

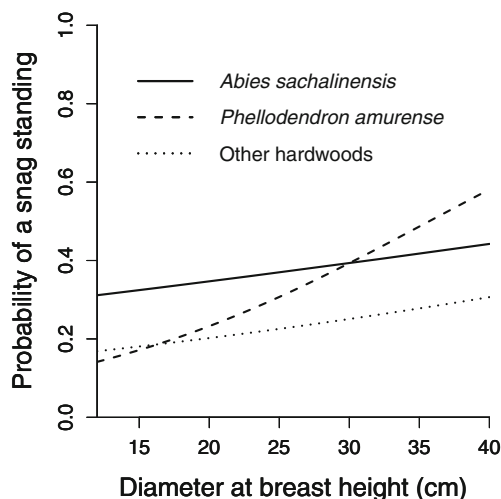
shorter in trees with extensive heartwood decay. Living trees with large DBH often have a large cavity (hollow trunk) resulting from extensive heartwood decay (Onodera et al. 2013). The DBH effect may be offset by the spread of heartwood decay in living trees and may decrease in species with low resistance to wood decay before they die. Among *Populus tremuloides* trees in Alberta, 30–42 % of individuals had wood decay in stands exceeding 50 years of age (Hiratsuka and Loman 1984), and no DBH effects were apparent (Lee 1998). We found obvious DBH effects in *Abies sachalinensis* and *Phellodendron amurense*, but not in *Picea* spp., *Q. crispula*, *Acer pictum*, and *Tilia japonica* in the second step (Table 5, Fig. 2). Heartwood decay has been observed frequently in old trees of *Abies sachalinensis*, *Picea* spp., *Q. crispula*, and *Acer pictum* in Hokkaido (Imazeki 1965; Onodera et al. 2013). The nonsignificant effect of DBH on snag longevity in some of the species that we studied is consistent with observations of heartwood decay in *Picea* spp., *Q. crispula*, and *Acer pictum*, but not in *Abies sachalinensis*. Trotsiuk et al. (2012) found that more than 47 % of all the upper-story trees had decayed heartwood, but the percentage of trees with decay per plot ranged from 7 to 41 % in virgin beech forests. The variability in the percentage of trees with decay may be one of the reasons for this inconsistency. Explicit explanations of the DBH effect on snag longevity will require further studies of wood decay in living trees.

Some dead trees die and fall simultaneously and never become snags. To link snag dynamics models with forest growth models, measurements of the probability that a dead tree will become a snag are required, in addition to measurements of tree mortality rates. The probability of a snag still be standing when TSD=0 in our model could be inferred as the probability that a dead tree will become a snag (Fig. 1). The probabilities of a snag with a DBH of 25 cm still standing when TSD=0 were 0.85 for *Acer pictum*, 0.72 for *Phellodendron Amurense*, and 0.45–0.65 for the other species that we studied (Fig. 1). Although these values could be overestimated by the limitations of our interval measurement as described before, these probabilities were a little lower than those for Ontario, Canada, where more than 69 % of newly dead trees became snags (Vanderwel et al. 2006a). The probability of a tree still be standing at the moment of death may largely depend on the major agents of tree mortality in the forests. Typhoons are the main cause of tree falls in cool-temperate forests of Japan (Nakashizuka and Iida 1995), and strong winds were likely the prevailing agents of tree mortality at our study sites. In contrast, competitive suppression is the major agent of mortality for trees in Ontario, where wind has a relatively minor role (Vanderwel et al. 2006b). We suggest that mortality by strong wind in Hokkaido reduces the chance of trees becoming snags, compared with mortality by suppression.



**Fig. 1** Probabilities of a snag still be standing estimated from time since tree death and species. Values of diameter at breast height have been set to 25 cm

Our estimated half-lives of dead trees with a DBH of 25 cm were within the range of 1–6 years, except for *Q. crispula* (Fig. 1). We analyzed all dead trees, including those that had never achieved snag status, but many other studies examined only snag data and were therefore unable to calculate the



**Fig. 2** Probabilities of a snag still be standing estimated from diameter at breast height and tree species. Values of time since tree death have been set to 10 years

probability that a dead tree will become a snag. For comparison purposes, we considered that the probability value when TSD=0 in our model was the probability that a dead tree will become a snag (as described above). We subsequently corrected the values of the probability of a snag still be standing by dividing them by the probability that a dead tree will become a snag (when TSD=0); this procedure removed the proportions of dead trees that did not become snags from the estimated probabilities (i.e., the probabilities of a snag still be standing when TSD=0 was set to 1). After applying this correction, we calculated that the half-lives of snags with a DBH of 25 cm were 13, 12, 11, and 4–9 years for *Q. crispula*, *Abies sachalinensis*, *Picea* spp., and other species, respectively. These half-lives are generally similar to those of other studies. For example, the half-lives of snags were 8.5 years for beetle-killed *Pinus ponderosa* Dougl. ex Lawson et C. Lawson in Oregon and California, USA (Keen 1955), 5.5 years for fire-killed *Pinus contorta* Dougl. ex Loudon in Montana, USA (Lyon 1977), 6–10 years for conifer and hardwood snags with a DBH of 15 cm in central Maine, USA (Garber et al. 2005), and 4–13 years for conifer and hardwood snags with a DBH of 25 cm in Ontario (Vanderwel et al. 2006a). In contrast, snags stood longer in some forests; the half-lives to falling down were 16–21 years for *Picea abies* (L.) Karst. in Norway (Storaunet and Rolstad 2004) and 30–35 and 35–40 years for *Abies balsamea* and *Picea mariana* (Mill.) Britton, Sterns, and Poggenburg, respectively, in Quebec, Canada (Aakala et al. 2008). The half-lives of snags with a DBH of 20–30 cm were 24, 13, and 9 years for *Pseudotsuga menziesii* (Mirbel) Franco, *Tsuga heterophylla*, and *Thuja plicata* Donn ex D. Don, respectively, in British Columbia (Parish et al. 2010).

## 5 Management implications

Our study emphasized that snag management in temperate mixed forests will become more complex. The richness of tree species in temperate forests is a necessary consideration for snag management. Assemblages of saproxylic beetles vary among the species of snags (Ulyshen and Hanula 2009), and almost all tree genera have some monophagous species of saproxylic invertebrates (Jonsell et al. 1998). Therefore, we should retain snags of diverse tree species, and they should be conserved according to the probabilities that a dead tree will become a snag and snag longevity as influenced by TSD and DBH effects.

We must devise alternatives to the DBH criterion in attempts to provide appropriate numbers of highly decayed snags of some species. Highly decayed snags are rare and essential substrate for biodiversity conservation in forests. Therefore, we should retain snags with the greatest potential longevity, thereby providing highly decayed snags. Although

the DBH criterion has been widely used for selecting snags with greatest longevities, our study showed that snags fall down at rates unrelated to their DBH values for some species in temperate mixed forests. In this regard, reconsidering the importance of living trees with decay may be worthwhile. Although trees with extensive decay will have decreased snag longevity after death, they will function like snags before they die. Thus, living trees with decay will maintain dead wood substrate for protracted periods both before and after their deaths and will provide highly decayed wood. To provide highly decayed snags of some species, retaining living trees with decay may be more effective than retaining large snags.

It is difficult to control wood decay in living trees because heartwood decay spreading inside the trunk and large branches is usually difficult to identify by external appearances. We must balance timber production and biodiversity conservation; therefore, too much wood decay is not appropriate. Our study suggested that tree species susceptible to wood decay before tree death may be considered not to have the DBH effect on snag longevity. Thus, if forest managers intend to harvest a sufficient volume of logs, once they select the retaining trees of *Picea* spp., *Acer pictum*, and *Tilia japonica*, the other trees should not be managed by long rotation forestry that may extend wood decay.

When combined with models of tree growth and mortality for forests in Hokkaido (Umeki 2001, 2002), the models presented herein should contribute to predicting snag dynamics there. In addition, combining them with models estimating the wood density of snags and fallen logs (Sakai et al. 2008) should make it possible to estimate carbon storage in dead wood. The results of this study cannot be applied to snags retained in clear-cuts because greater wind exposure in open sites reduces snag longevity. For forest management aiming to balance timber production and biodiversity conservation, further studies about the relationships between snag dynamics and environmental conditions, including the effects of various forest management practices, are needed.

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## 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. *For Ecol Manag* 255:410–420. doi:10.1016/j.foreco.2007.09.008

- Bates D, Maechler M, Bolker B, Walker S (2014) lme4: linear mixed-effects models using Eigen and S4. R package version 1.1-7. <http://CRAN.R-project.org/package=lme4>
- Bradford J, Weishampel P, Smith ML, Kolka R, Birdsey RA, Ollinger SV, Ryan MG (2009) Detrital carbon pools in temperate forests: magnitude and potential for landscape-scale assessment. *Can J For Res* 39: 802–813. doi:10.1139/X09-010
- Büttler R, Angelstam P, Schlaepfer R (2004) Quantitative snag targets for the three-toed woodpecker *Picoides tridactylus*. *Ecol Bull* 51:219–232
- Core Team R (2013) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Drapeau P, Nappi A, Imbeau L, Saint-Germain M (2009) Standing dead-wood for keystone bird species in the eastern boreal forest: managing for snag dynamics. *For Chron* 85:227–234. doi:10.5558/tfc85227-2
- Garber SM, Brown JP, Wilson DS, Maguire DA, Heath LS (2005) Snag longevity under alternative silvicultural regimes in mixed-species forests of central Maine. *Can J For Res* 35:787–796. doi:10.1139/x05-021
- Gibb H, Pettersson RB, Hjältén J, Hilszczański J, Ball JP, Johansson T (2006) Conservation-oriented forestry and early successional saproxylic beetles: responses of functional groups to manipulated dead wood substrates. *Biol Conserv* 129:437–450. doi:10.1016/j.biocon.2005.11.010
- Graham RT, Harvey AE, Jurgensen MF, Jain TB, Tonn, JR, Page-Dumroese DS (1994) Managing coarse woody debris in forests of the Rocky Mountains. Res Pap INT-RP-477, USDA For Serv Intermount Res Sta, Ogden
- Graves AT, Fajvan MA, Miller GW (2000) The effects of thinning intensity on snag and cavity tree abundance in an Appalachian hardwood stand. *Can J For Res* 30:1214–1220. doi:10.1139/x00-051
- Hammond HEJ, Langor DW, Spence JR (2004) Saproxylic beetles (Coleoptera) using *Populus* in boreal aspen stands of western Canada: spatiotemporal variation and conservation of assemblages. *Can J For Res* 34:1–19. doi:10.1139/X03-192
- Harmon ME (1982) Decomposition of standing dead trees in the southern Appalachian Mountains. *Oecologia* 52:214–215. doi:10.1007/BF00363839
- Hiratsuka Y, Loman AA (1984) Decay of aspen and balsam poplar in Alberta. Info Rep NOR-x-262, North For Res Cent Can For Serv Env Can, Edmonton. 19 pp
- Holub SM, Spears JDH, Lajtha K (2001) A reanalysis of nutrient dynamics in coniferous coarse woody debris. *Can J For Res* 31:1894–1902. doi:10.1139/x01-125
- Imazeki R (1965) Stem and butt rot diseases of forest trees. *Ann Phytopathol Soc Jpn* 31:248–253 (in Japanese)
- Japan Meteorological Agency (2002) Mesh climatic data of Japan 2000. Japan Meteorological Business Support Center, Tokyo
- Japan Wood Protection Association (2012) Introduction to wood protection science third edition. Japan Wood Protection Association, Tokyo, 283 pp, (in Japanese)
- Jonsell M, Weslien J (2003) Felled or standing retained wood—it makes a difference for saproxylic beetles. *For Ecol Manage* 175:425–435. doi:10.1016/S0378-1127(02)00143-3
- Jonsell M, Weslien J, Ehnström B (1998) Substrate requirements of red-listed saproxylic invertebrates in Sweden. *Biodivers Conserv* 7:749–764. doi:10.1023/A:1008888319031
- Kaila L, Martikainen P, Punttila P, Yakovlev E (1994) Saproxylic beetles (Coleoptera) on dead birch trunks decayed by different polypore species. *Ann Zool Fenn* 31:97–107
- Keen FP (1929) How soon do yellow pine snags fall? *J For* 27:735–737
- Keen FP (1955) The rate of natural falling of beetle-killed ponderosa pine snags. *J For* 53:720–723



- Lambert RL, Lang GE, Reiners WA (1980) Loss of mass and chemical change in decaying boles of a subalpine balsam fir forest. *Ecology* 61:1460–1473. doi:10.2307/1939054
- Lee P (1998) Dynamics of snags in aspen-dominated midboreal forests. *For Ecol Manag* 105:263–272. doi:10.1016/S0378-1127(97)00286-7
- Lyon LJ (1977) Attrition of lodgepole pine snags on the Sleeping Child Burn, Montana. Res Note INT-219, USDA For Serv Intermountain For Range Exp Sta, Ogden
- Metz MR, Frangioso KM, Meentemeyer RK, Rizzo DM (2011) Interacting disturbances: wildfire severity affected by stage of forest disease invasion. *Ecol Appl* 21:313–320. doi:10.1890/10-0419.1
- Mielke JL (1950) Rate of deterioration of beetle-killed Engelmann spruce. *J For* 48:882–888
- Nakashizuka T, Iida S (1995) Composition, dynamics and disturbance regime of temperate deciduous forests in Monsoon Asia. *Vegetatio* 121:23–30. doi:10.1007/BF00044669
- Odajima T (1964) Decay resistance of Todo-fir and Yezo-spruces. *Month Rept Hokkaido For Prod Res Inst* 155 (in Japanese)
- Onodera K, Tokuda S, Abe T, Nagasaka A (2013) Occurrence probabilities of tree cavities classified by entrance width and internal dimensions in hardwood forests in Hokkaido, Japan. *J For Res* 18:101–110. doi:10.1007/s10310-011-0327-9
- Parish R, Antos JA, Ott PK, Di Lucca CM (2010) Snag longevity of Douglas-fir, western hemlock, and western redcedar from permanent sample plots in coastal British Columbia. *For Ecol Manag* 259:633–640. doi:10.1016/j.foreco.2009.11.022
- Russell MB, Weiskittel AR (2012) Assessing and modeling snag survival and decay dynamics for the primary species in the Acadian forest of Maine, USA. *For Ecol Manag* 284:230–240. doi:10.1016/j.foreco.2012.08.004
- Saint-Germain M, Drapeau P, Buddle CM (2007) Host-use patterns of saproxylic phloeophagous and xylophagous Coleoptera adults and larvae along the decay gradient in standing dead black spruce and aspen. *Ecography* 30:737–748. doi:10.1111/j.2007.0906-7590.05080.x
- Sakai Y, Takahashi M, Ishizuka S, Inagaki Y, Matsuura Y, Unno A, Nakata K, Nagasaka A, Niwa H, Sawata S, Houjyou Y, Tamaki Y, Kasetani T, Takeda H, Aiura H, Yamanouchi M, Shimada H, Iwatsuki T, Yamaba A, Yamada T, Maeda H, Muro M (2008) Estimating decay rates of dead wood by changes in wood density in coniferous plantations in Japan. *Jpn J For Environ* 50:153–165 (in Japanese with English summary)
- Scheffer TC, Cowling EB (1966) Natural resistance of wood to microbial deterioration. *Annu Rev Phytopathol* 4:147–168. doi:10.1146/annurev.py.04.090166.001051
- Stokland JN, Siitonen J, Jonsson BG (2012) Biodiversity in dead wood. Cambridge University Press, Cambridge
- Storaunet KO, Rolstad J (2002) Time since death and fall of Norway spruce logs in old-growth and selectively cut boreal forest. *Can J For Res* 32:1801–1812. doi:10.1139/x02-105
- Storaunet KO, Rolstad J (2004) How long do Norway spruce snags stand? Evaluating four estimation methods. *Can J For Res* 34:376–383. doi:10.1139/x03-248
- Takahashi M, Sakai Y, Ootomo R, Shiozaki M (2000) Establishment of tree seedlings and water-soluble nutrients in coarse woody debris in an old-growth *Picea–Abies* forest in Hokkaido, northern Japan. *Can J For Res* 30:1148–1155. doi:10.1139/x00-042
- Trotsiuk V, Hobi ML, Commamot B (2012) Age structure and disturbance dynamics of the relic virgin beech forest Uholka (Ukrainian Carpathians). *For Ecol Manag* 265:181–190. doi:10.1016/j.foreco.2011.10.042
- Uemura S (1994) Climatic preferences and frequent co-occurrence of boreal and temperate plants in Hokkaido Island, northern Japan. *Vegetatio* 112:113–126. doi:10.1007/BF00044686
- Ulyshen MD, Hanula JL (2009) Habitat associations of saproxylic beetles in the southeastern United States: a comparison of forest types, tree species and wood postures. *For Ecol Manag* 257:653–664. doi:10.1016/j.foreco.2008.09.047
- Ulyshen MD, Hanula JL (2010) Patterns of saproxylic beetle succession in loblolly pine. *Agr For Entomol* 12:187–194. doi:10.1111/j.1461-9563.2009.00467.x
- Umeki K (2001) Growth characteristics of six tree species on Hokkaido Island, northern Japan. *Ecol Res* 16:435–450
- Umeki K (2002) Tree mortality of five major species on Hokkaido Island, northern Japan. *Ecol Res* 17:575–589
- Vanderwel MC, Caspersen JP, Woods ME (2006a) Snag dynamics in partially harvested and unmanaged northern hardwood forests. *Can J For Res* 36:2769–2779. doi:10.1139/x06-173
- Vanderwel MC, Malcolm JR, Smith SM (2006b) An integrated model for snag and downed woody debris decay class transitions. *For Ecol Manag* 234:48–59. doi:10.1016/j.foreco.2006.06.020
- Watt WR, Caceres MC (1999) Managing for snags in the boreal forests of northeastern Ontario. OMNR, Northeast Science and Technology TN-016. 20 pp
- Witzell J, Martín JA (2008) Phenolic metabolites in the resistance of northern forest trees to pathogens—past experiences and future prospects. *Can J For Res* 38:2711–2727. doi:10.1139/X08-112
- Wood technology and wood utilization division (1982) Properties of the important Japanese woods. Table of the properties of woods. *Bull For For Prod Res Inst* 319:85–126, in Japanese
- Yatskov M, Harmon ME, Krankina ON (2003) A chronosequence of wood decomposition in the boreal forests of Russia. *Can J For Res* 33:1211–1226. doi:10.1139/x03-033
- Zuur AF, Ieno EN, Smith GM (2007) Analysing ecological data. Springer, New York