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Temporal dynamics and decay of coarse wood in early seral habitats of dry-mixed conifer forests in Oregon's Eastern Cascades

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ABSTRACT

Early seral forest habitats are increasingly valued for the unique structural resources they provide in many western US forests. Coarse woody detritus (CWD) are a significant feature of this developmental stage and are highly dynamic, suggesting these environments exhibit temporally diverse structural conditions prior to forest canopy closure. In dry-mixed conifer forests, snags are hypothesized to decay slower than logs making long-term dynamics in these forests dependent on snag fall, breakage and the decay rates of both standing and surface CWD. We estimated snag fall and breakage rates for *Pinus ponderosa*, *Abies* sp., *P. menziesii* and *P. contorta* snags in three diameter classes (<23 cm, 23–41 cm and > 41 cm) from 6057 snags across a 24-year chronosequence of early seral environments. Snag and log decay rates were estimated by felling 60 *Abies* sp. and 60 *P. ponderosa* snags, and sampling 40 *P. ponderosa* logs. Half-life estimates for snags <23 cm, 23–41 cm, and >41 cm were 7, 12, and 17 years for *Pinus* sp., 10, 15, and 20 years for *Abies* sp., and 11, 17, and 23 years for *P. menziesii*. Breakage rates were lowest for small snags and not significantly different for medium and large snags, but did vary across species. We estimated an *Abies* sp. snag decomposition loss-rate constant of $k = 0.0179\ \mathrm{yr}^{-1}$ (SE = 0.00533, *p*-value = 0.0014) but *P. ponderosa* snags did not exhibit statistically significant decay ($k = 0.0024\ \mathrm{yr}^{-1}$, SE = 0.00518, *p*-value = 0.6414). *P. ponderosa* logs had an estimated decomposition loss-rate constant of $k = 0.0243\ \mathrm{yr}^{-1}$ (SE = 0.0073, *p*-value = 0.0023), confirming reduced decay rates in snags and variation among species. Following high-severity fire, dry-mixed conifer stands experience relatively rapid temporal changes in CWD resources largely dependent on snag species and diameter-at-breast-height (DBH). Variation in fall, breakage and decay rates among species and DBH suggests maintaining a diverse selection of snag species and diameters would meet multiple ecological needs across a broader temporal scale. Additionally, given the rapid temporal changes in CWD, defining early seral habitat as the period immediately following disturbance until canopy closure may not adequately account for the diversity in habitat structures and resources available over time.

1. Introduction

The ecological role of a tree is only partially fulfilled as a living organism (Franklin et al., 1987; Spies et al., 1988). Coarse woody detritus (CWD) provides structural habitat valuable to multiple vertebrate and invertebrate species as snags and logs in various decay states (Bull et al., 1997; Thomas et al., 1979). CWD also functions as a long-term nutrient and carbon store, are primary energy sources for saprophyte communities and contribute to soil development (Harmon et al., 1986; Triska and Cromack, 1980). Individual CWD can provide ecological functions for several hundred years, depending on the dynamic nature of its post-mortality existence.

Additions of CWD into ecosystems occur through multiple pathways at varying spatial and temporal scales. In western U.S. forests, individual tree mortality occurs mainly by competitive exclusion, insects, disease, wind, and lightning disturbance. At broader spatial and temporal scales, stand- and landscape-level tree mortality occurs in discrete pulse events caused by wind throw, insect outbreaks, and/or fire disturbance (Franklin et al., 1987; Spies et al., 1988).

Dry mixed-conifer forests in Oregon are fire adapted ecosystems with a mixed-severity fire regime, experiencing fire disturbance on intervals from 9–62 years. High-severity fire events at a given site may have fire free intervals >200 years (Agee, 1993). One of the most evident effects of fire disturbance is a pulse of tree mortality, dramatically increasing the amount CWD within the system. The magnitude of this transfer is most evident in high-severity fire areas where >75% of tree mortality occurs (Agee, 1993).

The availability of CWD to meet ecological needs is not only dependent on their creation but also on their decay rates (Harmon,

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2002). Decay rates are primarily controlled by moisture and temperature regimes of the substrate. Temperate dry-mixed conifer forests experience dry, hot summers and cold, moderately wet winters with precipitation occurring primarily as snowfall. In these systems, snags are hypothesized to have lower decay rates than logs, suggesting long-term CWD decay is partially controlled by the rate of fragmentation of snags into logs (Harmon et al., 1986).

In western U.S. forests, contemporary management strategies on public lands tend towards ecologically sustainable management practices that include retention of large dead wood resources as important structural components. Within dry-forest environments, much of these efforts have focused on retention of CWD while restoring forest structure to historical old-growth conditions (Brown et al., 2003), but early seral habitats are increasingly being recognized as important landscape features (Swanson et al., 2010). These environments contain a multitude of important habitat resources not as abundant in closed canopy forest environments, including CWD biological legacies. These habitats are highly dynamic stages of forest development, exhibiting relatively rapid structural changes as snags break and fall into logs and forest vegetation recovers. The rate of CWD structural change affects habitat quality because vertebrate and invertebrate species utilize CWD resources of various conditions (Thomas et al., 1979; Bull et al., 1997). No published study has explicitly evaluated snag dynamics and CWD decay rate changes in Oregon's dry-mixed conifer forests, and only one empirical study has tested this in other environments (Harmon and Fasth, 2005), even though they may lead to dramatic changes in the structural conditions of these environments.

In this study, we estimated snag fall and breakage rates for *Abies* sp., *P. ponderosa*, *P. menziesii* and *P. contorta* snags across a 24-year chronosequence of unmanaged high-severity fire sites in dry-mixed conifer forests of Oregon's Eastern Cascades. We also estimated decay rates of *P. ponderosa* and *Abies* sp. snags and *P. ponderosa* logs to further quantify the long-term presence of CWD on the landscape. Linking snag fall and breakage with decay provides a more comprehensive picture of the condition of CWD biological legacies during successional change of early seral environments. This information will improve land managers ability to plan for the presence of these important resources across landscapes over time.

2. Methods

2.1. Site and plot selection

We focused on snag and log dynamics in dry-mixed conifer forests of Oregon's Eastern Cascades consistent with the *Abies grandis* and *Abies concolor* zones of the Eastern Cascades (Franklin and Dyrness, 1988). Sample plots were selected from unmanaged high-severity fire (> 75% overstory mortality) sites occurring during the past 100 years within Deschutes and Winema National Forests and Crater Lake National Park. A total of 7 fire sites were suitable for this study and are displayed in Fig. 1, covering a chronosequence beginning 1 year and ending 24 years post-fire. The environmental conditions of these fires are summarized in Table 1. Thirty 0.25-hectare (50 m × 50 m) plots were randomly selected with equal probability point sampling across the seven fires, resulting in 3–6 plots per fire site. The sampling procedure constrained all plots so they were separated by a minimum of 200 meters. Climate data was obtained from PRISM Climate Group (PRISM Climate Group, 2010).

2.2. Snag dynamics sampling

All snags were marked and measured within each 50 × 50 m square plot using a systematic grid. We recorded species, diameter at breast height (DBH), total height, decay class, condition and time of death for each snag or log. A snag's condition was noted as standing whole, standing broken, or fallen. Broken snags had a visible break point greater than 2 m in height along the main stem. Snags broken below 2 m in height were considered fallen. Species was determined using characteristics described by Parks et al. (1997). Fire killed snags were separated from pre-fire killed snags when >5% of the sapwood was consumed or converted to char during the fire.

2.3. Snag and log decay rates

Randomly located 10 × 50-meter belt transects were used to select snags to sample for decay. The belt transects were located within the same GIS plot polygons as snag inventory plots but were outside of the snag plot boundaries for remeasurement considerations. The target DBH of snags was 41 cm, although samples ranging from 35–51 cm were considered acceptable. The first encountered snag from the random starting point, meeting the size and species requirements, was selected for felling. Twelve *Abies* sp. and *P. ponderosa* snags were randomly sampled from each of the recent fire sites (1–7 years post-fire) for a total of 60 snags of each species. After felling, total snag height was divided into 4 equal sections and 3 cross-sections were systematically removed at heights of 25%, 50%, and 75% of total height using a chainsaw. Each snag or log represents a sample unit in this study and we estimate decomposition loss-rate constants based on a change in weighted wood density over time.

We obtained estimates of surface decomposition loss rate-constants for *P. ponderosa* logs by opportunistically sampling logs felled as hazard trees during fire suppression operations. Limiting our sampling to these logs allowed us to confidently date their year of fall. Only *P. ponderosa* logs were found in sufficient quantity to warrant sampling. A total of 40 logs were found spanning a chronosequence from 2–7 years post-fire (Black Crater – 12, B & B Complex – 9, Davis Lake – 12 and Crane Complex – 7). The same information was collected for logs as snags and 3 cross-sections were removed from these logs using the same procedures described for snags.

Volume of each cross-section was calculated as the volume of a cylinder after removal of outer and inner bark. Diameter was determined using a diameter tape and longitudinal thickness (i.e. height of the cylinder) was estimated from the average of 6 longitudinal caliper measurements taken systematically around the outer edge of the cross-section. Each cross-section was weighed to the nearest gram. *P. ponderosa* sapwood and heartwood were separated with a hammer and chisel and analyzed separately in anticipation of their decay rate differences (Harmon et al., 1986). Subsamples were taken from each cross section to estimate moisture content and consisted of multiple small pieces removed in proportion to the observed variation in moisture content of the entire cross-section. Each aggregate subsample ranged between 100 and 150 g wet, weighed to the nearest 0.01 g. Subsamples were oven dried at 55 °C until reaching a low, stable moisture condition (~5 days) and compared to their wet weight to determine percent moisture content. Each cross-section was scaled by its subsample percent moisture content to obtain whole cross-section oven-dry weight (Harmon and Sexton, 1996). Wood density of each cross-section was calculated as oven-dry weight per unit pre-dried volume (g cm^{-3}).

Total snag and log wood densities were estimated as the weighted wood density of the three cross-sections removed from the sample. Each cross-section represents a different proportion of total snag or log mass since outerwood diameter decreases with tree height. We scaled each cross-section relative to the average area of all three cross-sections removed from an individual snag or log. Weighted density for the entire sample was the sum of the scaled cross-section wood densities (g cm^{-3}).

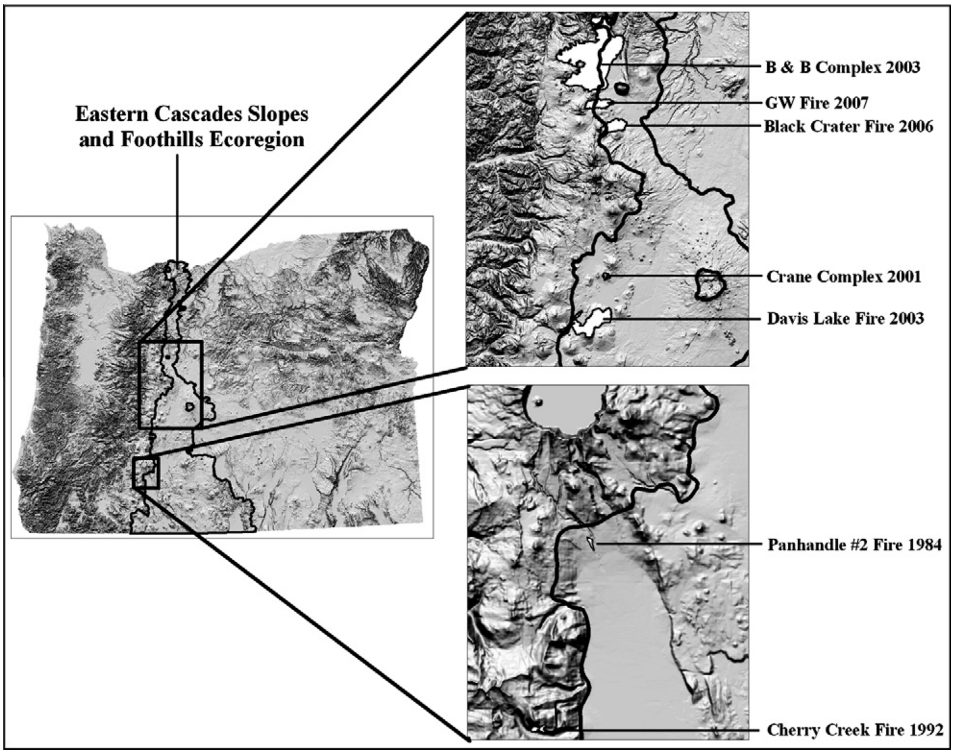

Fig. 1. A total of seven high-severity fire sites within dry-mixed conifer forests were sampled spanning a 24-year chronosequence. The "Eastern Cascades Slopes and Foothills Ecoregion" is consistent with ecoregions developed by the Western Ecology Division of the EPA (Omernik, 1987).

Table 1
The environmental characteristics of fires sampled for this study.

Fire site	Fire year	Location	Year Sampled	Total Hectares	Average Elevation (m)	Average PPT (mm)	Average T_{max} (°C)	Average T_{min} (°C)
GW Fire	2007	Deschutes N.F.	2008	2977	1301	1052.07	12.72	0.43
Black Crater Fire	2006	Deschutes N.F.	2008	3807	1445	909.54	11.82	−0.60
B & B Complex	2003	Deschutes N.F.	2008	36733	1159	1147.56	13.18	0.72
Davis Lake Fire	2003	Deschutes N.F.	2008	8572	1551	843.53	12.12	−0.84
Crane Complex	2001	Deschutes N.F.	2008	289	1478	804.73	12.82	−0.54
Cherry Creek Fire	1994	Winema N.F.	2007	134	1722	1418.16	11.20	−0.14
Panhandle 2	1984	Crater Lake N.P.	2008	49	1419	889.89	14.19	−1.13

3. Data analysis

3.1. Snag dynamics

Our study design resulted in a 3-level hierarchical spatial structure of 6057 snags nested within 30 random plots, nested within 7 fire sites. Dominant tree species sampled in this study included *Abies* sp., *P. ponderosa*, *P. menziesii* and *P. contorta*. Random environmental variables such as isolated high wind events or root rot pockets can simultaneously affect multiple snags within plots or across fire sites, potentially resulting in spatial autocorrelation of snag fall or breakage at the plot and/or site level. We tested for additional random variation not accounted for by years since fire and snag level predictors and found statistically significant random effects at the plot and site level, even with limited high level site replication (i.e. Davis Lake and B&B Complex at 5 years post-fire).

Separate analyses were conducted for snag fall and breakage at the individual snag level using a generalized-linear mixed model (PROC GLMMIX, SAS Institute Inc., 2008) with a binomial distribution and logit link function. Site level summaries for the proportion of snags fallen and broken are provided in Table 2 and 3. We used the RSPL estimation method and Kenward–Roger procedure for estimating degrees of freedom. Random error terms were included for plot and site as well as plot level predictor variables in the following full model:

$$\begin{aligned}\text{logit}(Y_{ijk}) = \mu + \beta_i + \gamma_j + \lambda_k + \beta_i\gamma_j + \beta_i\lambda_k + \gamma_j\lambda_k + \beta_i\gamma_j\lambda_k + \rho \\ + \nu + \omega + \eta + c + f + t + \varepsilon_m + \varepsilon_n + \varepsilon_{ijk}\end{aligned} \quad (1)$$

where,

Y_{ijk} is the proportion of fallen or broken snags in the *i*th year for the *j*th species in the *k*th diameter class

μ is the intercept

β_i is the effect of the *i*th year since the fire

γ_j is the effect of the *j*th species (*j = P. menziesii, P. ponderosa, P. contorta, Abies sp.)*

λ_k is the effect of the *k*th diameter class ($k \leqslant 23$ cm, 23–41 cm, $\geqslant$41 cm)

$\beta_i\gamma_j$ is the interaction effect of the *i*th year since fire and the *j*th species

$\beta_i\lambda_k$ is the interaction effect of the *i*th year since fire and the *k*th diameter class

$\gamma_j\lambda_k$ is the interaction effect for the *j*th species of the *k*th diameter class

Table 2
Summarized proportions of observed fallen snags for species and size classes by fire sites.

		Fire site and years since fire when sampled														
Species	Diameter Class	GW 1 year		Black Crater 2 years		B & B Complex 5 years		Davis Lake 5 years		Crane Complex 7 years		Cherry Creek 15 years		Panhandle 2 24 years		Total *N* (Sp/Size)
		Proportion Fallen (*N*)														
Abies sp.	<23 cm	0.000	(188)	0.051	(642)	0.197	(152)	0.293	(624)	0.337	(1497)	0.868	(91)	0.993	(141)	3335
	23–41 cm	0.000	(64)	0.019	(107)	0.055	(55)	0.109	(92)	0.025	(119)	0.654	(81)	0.881	(59)	576
	>41 cm	0.000	(47)	0.000	(45)	0.000	(19)	0.050	(20)	0.200	(5)	0.381	(21)	0.556	(9)	166
N (Sp/Site)			(299)		(794)		(226)		(736)		(1621)		(193)		(209)	4077
P. ponderosa	<23 cm	0.057	(228)	0.211	(19)	0.391	(23)	0.400	(10)	0.536	(56)	1.000	(9)	1.000	(4)	349
	23–41 cm	0.000	(16)	0.000	(9)	0.000	(23)	0.222	(9)	0.263	(19)	0.641	(39)	1.000	(4)	119
	>41 cm	0.024	(42)	0.000	(39)	0.000	(21)	0.058	(52)	0.219	(64)	0.346	(26)	0.680	(25)	269
N (Sp/Site)			(286)		(66)		(67)		(71)		(139)		(74)		(33)	737
P. menzesii	<23 cm	0.053	(19)			0.154	(13)	0.315	(222)	0.193	(456)	0.500	(18)			728
	23–41 cm					0.030	(33)	0.138	(29)	0.066	(91)	0.286	(14)			167
	>41 cm	0.000	(1)			0.000	(33)	0.000	(13)	0.333	(6)	0.167	(6)	1.000	(1)	60
N (Sp/Site)			(20)				(79)		(264)		(553)		(38)		(1)	955
P. contorta																
	<23 cm			0.048	(63)			0.217	(23)	0.521	(96)			1.000	(72)	254
	23–41 cm	1.000	(1)					0.200	(10)	0.200	(5)			0.938	(16)	32
	>41 cm													1.000	(2)	2
N (Sp/Site)			(1)						(33)		(101)				(90)	288
Total *N* (Site)			606		923		372		1104		2417		304		331	6057

Table 3
Summarized proportions of observed broken snags for species and size classes by fire sites.

		Fire site and years since fire when sampled														
Species	Diameter Class	GW 1 year		Black Crater 2 years		B & B Complex 5 years		Davis Lake 5 years		Crane Complex 7 years		Cherry Creek 15 years		Panhandle 2 24 years		Total *N* (Sp/Size)
		Proportion broken (*N*)														
Abies sp.	<23 cm	0.005	(188)	0.033	(609)	0.033	(122)	0.043	(441)	0.033	(993)	0.750	(12)	0.000	(1)	2366
	23–41 cm	0.000	(64)	0.076	(105)	0.269	(52)	0.829	(82)	0.112	(116)	1.000	(27)	0.857	(7)	453
	>41 cm	0.021	(47)	0.111	(45)	0.263	(19)	0.842	(19)	0.750	(4)	1.000	(13)	0.750	(4)	151
N (Sp/Site)			(299)		(759)		(193)		(542)		(1113)		(52)		(12)	2970
P. ponderosa	<23 cm	0.056	(215)	0.200	(15)	0.071	(14)	0.333	(6)	0.231	(26)	All Fallen		All Fallen		276
	23–41 cm	0.000	(16)	0.111	(9)	0.652	(23)	0.714	(7)	0.357	(14)	1.000	(14)	All Fallen		83
	>41 cm	0.049	(41)	0.128	(39)	0.571	(21)	0.224	(49)	0.220	(50)	0.882	(17)	0.625	(8)	225
N (Sp/Site)			(272)		(63)		(58)		(62)		(90)		(31)		(8)	584
P. menzesii	<23 cm	0.000	(18)			0.273	(11)	0.013	(152)	0.044	(368)	0.333	(9)			558
	23–41 cm					0.344	(32)	0.360	(25)	0.141	(85)	1.000	(10)			152
	>41 cm	0.000	(1)			0.303	(33)	0.308	(13)	0.500	(4)	1.000	(5)			56
N (Sp/Site)			(19)				(76)		(62)		(457)		(24)			766
P. contorta																
	<23 cm			0.000	(60)			0.111	(18)	0.087	(46)			All Fallen		124
	23–41 cm	0.000	(1)					0.000	(8)	0.000	(4)			0.000	(1)	14
N (Sp/Site)			(1)		(60)				(26)		(50)				(1)	138
Total *N* (Site)			591		882		327		820		1710		107		21	4458

$\beta_i\gamma_j\lambda_k$ is the interaction effect of the ith year since fire for the jth species of the kth diameter class

ρ is the total plot basal area

υ is the total trees per hectare

ω is the slope

η is the elevation

c is site average precipitation (mm)

f is site average maximum temperature

t is site average minimum temperature

ε_m represents random variation among plots

ε_n represents random variation among sites

ε_{ijk} is the random error term representing the variability among years within species and diameter classes

When analyzed using PROC GLIMMIX, the full model failed to converge even with adjustments to the optimization settings, so we reduced model complexity in a stepwise procedure to retain as much of the model structure as possible (Bolker et al., 2008). After removing the three-way interaction of years since fire, species, and size class the model successfully converged. No widely accepted model selection criteria is available for generalized linear mixed models with random effects (Bolker et al., 2008), so we continued with manual stepwise model selection identifying statistically significant predictor variables that minimized deviance and maintained good model fit (i.e. generalized chi squared/DF value close to 1). For comparison, this process was followed for a 2 and 3-level hierarchical model with an events/trials response variable pooled for each species and diameter class at the plot and site level.

Linear regression analysis was used to estimate break height as a function of years since fire, species and DBH (PROC MIX, SAS Institute Inc., 2008). A total of 484 snags were broken at the time of field sampling and used in this analysis with site and plot random effect terms to account for any positive correlations among residuals. Model assumptions for normality and equal variance were evaluated and break heights were log transformed to meet these assumptions (Ramsey and Shafer, 2002).

3.2. Decomposition

CWD mass loss occurs as wood decays via heterotrophic respiration and as wood fragments into smaller particles (Harmon et al., 1986). CWD fragmentation rates are beyond the scope of this study so our estimates represent decay rates from wood density loss only. The negative exponential model is the most commonly used and accepted decay model (Means et al., 1980; Harmon et al., 1986). In this model, density loss is described by the equation.

$$Y_t = Y_i * \exp^{(-kt)} \tag{2}$$

where,

Y_t = density at time t (g cm^{-3}),

Y_i = initial density (g cm^{-3}),

k = decomposition loss-rate constant (yr^{-1})

t = time in yearsDecomposition loss-rate constants (k-constants) were estimated for *Abies* sp. snags, *P. ponderosa* snags and logs, and *P. ponderosa* snag and log sapwood and heartwood in separate analyses using simple linear regression (PROC REG, SAS Institute Inc., 2008). Wood density values were log transformed so that the magnitude of the slope represented the k-constant for the negative exponential model (Harmon et al., 1986). Model assumptions of normality and equal variance were evaluated and met before continuing with interpretation of the parameter estimates and model results.

4. Results

4.1. Snag fall

The cumulative probability of snag fall increased with time for all snags but varied by species and DBH class. *Pinus* spp. were not statistically different from each other and had the most rapid increase in cumulative probabilities of snag fall over time for all DBH classes. The cumulative probabilities were slightly lower for *Abies* sp. snags indicating a slower fall rate for this species, but *P. menziesii* snags exhibited the slowest fall rate of all DBH classes sampled in this study. DBH class is negatively correlated with fall rate for all species, resulting in the largest DBH class having the slowest fall rate. Table 4 provides coefficients for the significant predictor variables and random error terms for estimating the cumulative probability of fallen snags on the logit scale. Plot and site random error terms were statistically significant, indicating additional environmental effects influence snag fall at the plot and landscape scale.

Table 5

Estimated snag half-lives and the percent of snags with broken tops in those years. A range is given when the model estimates half-life occurs between successive years.

Species	Size class	Half-life year	Percent broken
Abies sp.			
	<23 cm	10–11	9–11
	23–41 cm	15–16	67–70
	>41 cm	20–21	76–79
P. ponderosa			
	<23 cm	7–8	10–12
	23–41 cm	12–13	69–73
	>41 cm	17–18	77–80
P. menziesii			
	<23 cm	11–12	10–11
	23–41 cm	17–18	71–74
	>41 cm	23–24	81–84
P. contorta			
	<23 cm	7–8	3.5–4
	23–41 cm	12–13	0

Half-life estimates (i.e. year when 50% of the snag population has fallen) provide a metric for comparing fall rates across populations of interest and among studies. *Pinus* spp. have the fastest fall rates, resulting in the lowest half-life estimates among all species sampled in this study. For *Pinus* sp. small (<23 cm DBH) snags, half-life estimates are 7–8 years post-disturbance, increasing by 5 and 10 years for medium and large snags respectively. On average, *Abies* sp. half-life estimates occur three years later for all diameter classes. *P. menziesii* snags have the slowest fall rates so half-life estimates are 1, 2 and 3 years greater than *Abies* sp. snags for small, medium (23–41 cm DBH) and large (>41 cm DBH) snags respectively. The effect of DBH is greater for *P. menziesii* half-lives, increasing by 6 years for each diameter class increase. Estimated half-lives are provided in Table 5 along with the estimated percent of broken snags at that time for comparison.

The 3-level hierarchical model resulted in a ratio of the generalized chi-square statistic and degrees of freedom equal to 0.94, indicating limited overdispersion and adequate model fit (SAS Institute Inc., 2008). Fig. 2 is provided as an example of how the data distribution at the plot and site level results in our regression estimates and standard errors. Predictor variables remained the same when the data was pooled and analyzed at the plot and site level but these models did not capture all random effects or account for positive correlation of residuals at the plot and site levels. There was no statistically significant difference between the *Pinus* sp. analyzed in this data set but we had a limited sample size for *P. contorta.* We analyzed *P. contorta* individually to make sure the fall rate wasn't being masked by the larger data set and the resultant estimates were not significantly different, so we kept this

Table 4

Parameter estimates for predicting the mean proportion of fallen snags on the logit scale.

Fixed effect	Estimate	Std error	*p*-value
Intercept	−5.2536	0.4982	<0.0001
Years since fire	0.227	0.03805	0.0001
Abies sp.	0.5332	0.09955	<0.0001
P. ponderosa	1.3359	0.1764	<0.0001
P. contorta	1.4271	0.2008	<0.0001
<23 cm DBH	1.4092	0.3671	0.0001
23–41 cm DBH	0.04737	0.4175	0.9097
Years since fire ∗ <23 cm	0.1004	0.03262	0.0021
Years since fire ∗ 23–41 cm	0.07454	0.03186	0.0193

Type 3 tests of fixed effects

Fixed effect	Pr > F
Years since fire	0.0002
Species	<0.0001
Diameter class	<0.0001
Years since fire ∗ diameter class	0.007

Covariance parameter estimates

Cov parm	Estimate	Std error
Site	0.3222	0.2595
Plot	0.1623	0.07196

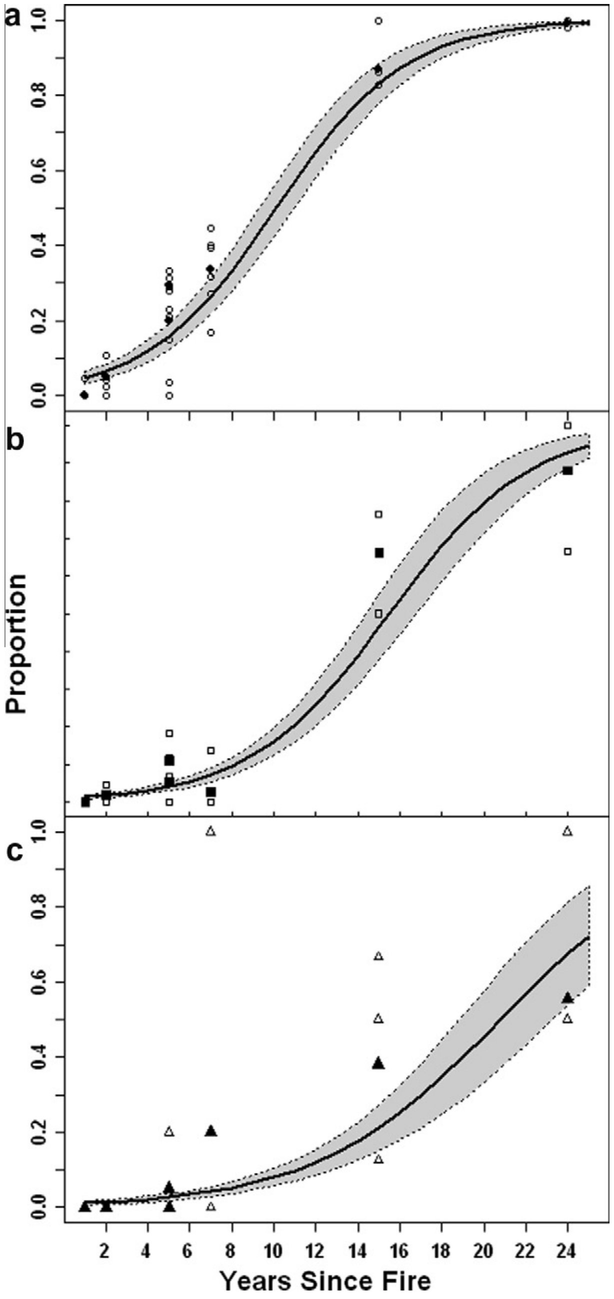

Fig. 2. An example illustrating the distribution of data at the plot and site level. Open points are plot level proportions and solid points are site level proportions. The solid line is the estimated mean and the shaded region is ±1 standard error. The data used for this example is from *Abies* sp. snag fall. $a \leqslant 23$ cm, $b = 23–41$ cm, $c \geqslant 41$ cm DBH.

species in the model. Fig. 3 depicts the back-transformed mean proportion of snags fallen during 24 years of early seral successional change following high-severity fire disturbance.

4.2. Snag breakage

The cumulative probability of snag breakage increased with time for all snags and also varied by species and DBH class. *P. ponderosa* snags break at the highest rate for all size classes, concurrent with high fall rates. In contrast, *P. contorta* snags have the slowest breakage rate for small snags and no observed breakage for medium snags, indicating these snags tend to fall intact. *Abies* sp. and *P. menziesii* have relatively moderate breakage rates and are not statistically different from each other. In contrast to fall rates, small DBH classes have a significantly slower breakage rate than other size classes but there is little difference between medium and large DBH classes within a sampled species. The majority of small DBH class snags fall before significant proportions break, increasing the variability in later years as depicted in Fig. 3. Table 6 provides coefficients for the significant predictor variables and random error terms for estimating the cumulative probability of snags with broken tops on the logit scale.

Snag breakage rates were estimated using a 3-level hierarchical model with site and plot random error terms. The ratio of the generalized chi-square statistic and degrees of freedom equaled 1.11, indicating limited overdispersion and adequate model fit (SAS Institute Inc., 2008). Relative to snag fall, there is a larger site effect for breakage indicating environmental factors at this spatial scale have a greater influence on snag breakage than snag fall. Plot level random environmental effects have similar magnitudes for fall and breakage. More variability occurs in our estimates of snag top breakage than snag fall as depicted in Fig. 3.

Break height was positively correlated with DBH and negatively correlated with years since fire. For each 1 cm DBH increase, median break height increased by 1.98% ($p < 0.0001$, 95% CI of 1.67% to 2.29%). A one year increase in time since fire decreased the median break height by 4.27% (p-value <0.0001, 95% CI of 2.24% to 6.27%). Statistical analysis indicated a slight species effect but the Bayesian Information Criterion was not significantly different (i.e. a difference of <2) between models with and without the species variable so we selected the simpler model. Site and plot covariance parameter estimates were small (0.01156 and 0.04951, respectively) and not statistically significant from zero, indicating snag break height is dominantly controlled by snag level factors.

4.3. Decomposition

Decomposition loss rate-constants varied by species and increased as snags fragmented into logs. *Abies* sp. snags had an estimated decomposition loss rate-constant of $k = 0.0179\ \mathrm{yr}^{-1}$ (SE = 0.00533, p-value = 0.0014) but *P. ponderosa* snags did not exhibit significant decay ($k = 0.0024\ \mathrm{yr}^{-1}$, SE = 0.00518, p-value = 0.6414). In contrast, we did find statistically significant decay of *P. ponderosa* logs ($k = 0.0243\ \mathrm{yr}^{-1}$, SE = 0.0073, p-value = 0.0023) confirming the hypothesized increase in CWD decay rates as snags fragment into logs. We also found *P. ponderosa* log sapwood decayed more rapidly than its heartwood, demonstrating the effect of decay resistant compounds on decay rates. Regression coefficients for estimating the decomposition loss rate-constants are provided in Table 7. The absolute values of the regression slopes are the decomposition loss-rate constants for each substrate and are the primary variable of interest in this analysis.

Although not directly sampled, the back-transformed intercepts are an estimate of mean wood density immediately following fire disturbance and are useful for providing a simple check on whether a decay lag exists. All of our intercept values are within the natural variability of green trees of these species indicating decay follows a negative exponential trend immediately following fire mortality (Bergman et al., 2010).

5. Discussion

5.1. Snag dynamics

Fire is a pulse disturbance creating stand- and landscape-level change in CWD abundance, removing existing CWD while simultaneously creating others. Early seral, post-fire environments are spatially and temporally dynamic systems with a gradient of eco-

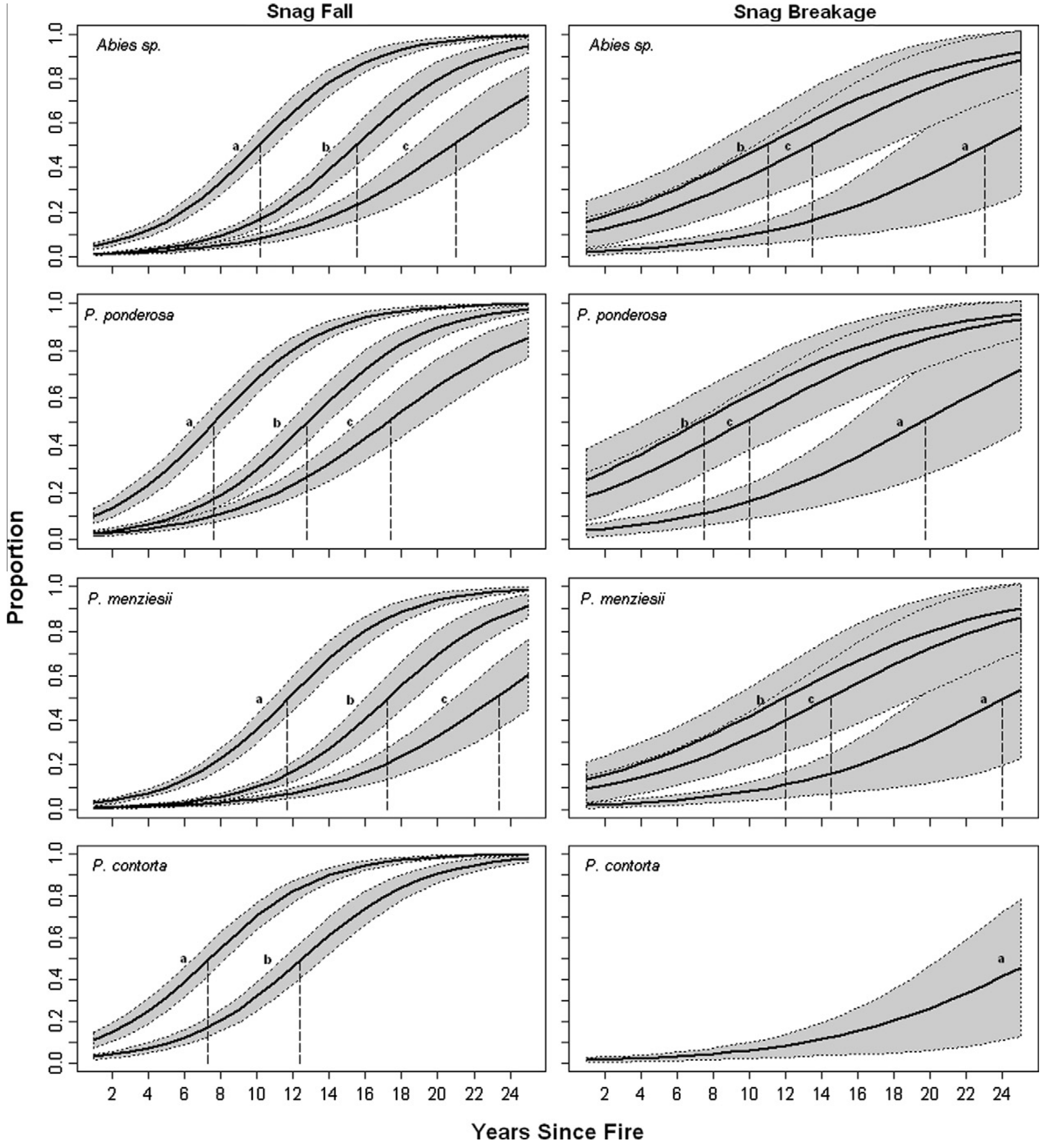

Fig. 3. Logistic regression curves of the proportion of fallen and broken snags by species, size class and year since fire. $a \leqslant 23$ cm, $b = 23$–41 cm, $c \geqslant 41$ cm DBH. Vertical dashed lines represent proportions of 0.50, or half-life estimates for snag fall and breakage. Solid lines are mean proportions and shaded areas represent ±1 standard error.

logical characteristics. Over time, the abundance of standing and surface CWD is dependent on successional changes that can be largely described by species composition and diameter distributions. Demographic characteristics of snag populations are dependent on pre-fire stand conditions, total mortality and the amount of time since the disturbance.

The initiation of snag fall varies by species and size class but in general, large snags have a longer lag period (Table 2). These trends are consistent with other studies with lag periods between 2 and 3 years and evidence of limited snag fall up to 5 years after death, particularly for larger size classes (Bull, 1983; Everett et al., 1999; Keen, 1955; Mitchell and Preisler, 1998; Schmid et al., 1985). Lag periods are followed by relatively slow rates of attrition for up to 10 years depending on species and DBH (Fig. 3). After initiation, small snags exhibit surprisingly similar fall rates among species and across broad geographic regions. The majority of published half-life estimates for small snags are ∼7 years (range 5–10 years), equivalent to our estimate for *Abies* sp., *P. ponderosa, P. contorta* and only slightly less than our observed estimate for *P. menziesii* snags. As DBH increases, fall rates decrease across species regardless of geographic region (Chambers and Mast, 2005; Dahms, 1949; Everett et al., 1999; Morrison and Raphael, 1993). DBH likely has a continuous effect on fall rates explaining some of the variation in our size-class estimates. In particular, very large snags (i.e. >70 cm DBH) could have much longer half-lives than our estimates, as suggested by studies reporting half-lives as great as

Table 6
Parameter estimates for predicting mean proportion of snags broken on the logit scale.

Fixed effect	Estimate	Std error	*p*-value
Intercept	−2.4618	0.7607	0.0212
Years since fire	0.1711	0.06691	0.0482
Abies sp.	0.1847	0.1671	0.2688
P. ponderosa	0.7864	0.2218	0.0004
P. contorta	−0.3252	0.4917	0.5084
<23 cm DBH	−1.6714	0.1873	<0.0001
23–41 cm DBH	0.4238	0.1806	0.019

Type 3 tests of fixed effects		Covariance parameter estimates		
Fixed effect	Pr > *F*	Cov Parm	Estimate	Std error
Years since fire	0.0482	Site	1.5991	1.1193
Species	0.0018			
Diameter class	<0.0001	Plot	0.1695	0.08242

Table 7
Regression coefficients for decay rates of *Abies* sp. snags and *P. ponderosa* snags and logs. Slopes represent the decomposition loss-rate constant for an exponential decay model.

Substrate	Estimate	Std error	*p*-value	LCL[1]	UCL[1]
Abies sp. snags					
Intercept	−1.06375	0.02427	<0.0001	−1.11236	−1.01515
Slope	−0.0179	0.00533	0.0014	−0.02857	−0.00722
P. ponderosa snags					
Intercept	−1.04721	0.02362	<0.0001	−1.0945	−0.9999
Slope	−0.00242	0.00518	0.6414	−0.0128	0.0079
P. ponderosa snag sapwood					
Intercept	−1.0498	0.02503	<0.0001	−1.09991	−0.99969
Slope	−0.00379	0.00549	0.493	−0.01477	0.0072
P. ponderosa snag heartwood					
Intercept	−0.98476	0.02835	<0.0001	−1.0452	−0.928
Slope	−0.01013	0.00622	0.1087	−0.02257	0.00231
P. ponderosa logs					
Intercept	−0.96224	0.03385	<0.0001	−1.0309	−0.89358
Slope	−0.0243	0.0073	0.0023	−0.388	−0.0092
P. ponderosa log sapwood					
Intercept	−0.98298	0.05229	<0.0001	−1.08884	−0.87712
Slope	−0.0373	0.01093	0.0015	−0.05946	−0.01522
P. ponderosa log heartwood					
Intercept	−0.91181	0.02989	<0.0001	−0.97244	−0.85119
Slope	−0.01642	0.00635	0.0139	−0.0293	−0.00354

[1] 95% Confidence limits.

or greater than 60 years post-disturbance (Everett et al., 1999). Unfortunately, large populations of snags of this size are difficult to find on the landscape so additional estimates could not be made for snags of this size in this study.

Although DBH has a significantly larger impact on fall rates, we did observe variation among species. Fall rates of *P. ponderosa* and *P. contorta* were not statistically different, similar to the results reported in a study of these species in northeastern Oregon (Bull, 1983). We rarely encountered *P. contorta* snags >41 cm so we would expect higher rates of attrition for populations of *P. contorta* snags than *P. ponderosa* since *P. ponderosa* snags may be larger. Somewhat unexpectedly, *Abies* sp. snags have slower fall rates than *P. ponderosa* even though *P. ponderosa* has greater wood strength (Bergman et al., 2010). Landram et al. (2002) reported half-lives for *Abies* sp. to be about 2 years longer than *P. ponderosa* snags in Southern Oregon. Morrison and Raphael (1993) reported similar effects. In contrast, *P. menziesii* snags have the slowest fall rates for all size classes (Everett et al., 1999; Russell et al., 2006). This species does have the greatest wood strength of all sampled species, suggesting snag fall rates are influenced by a complex interaction of snag decay, top breakage, wood strength and crown/stem weight.

Snag top breakage is positively correlated with time since fire (Bull, 1983; Chambers and Mast, 2005). The cumulative proportion of snags with broken tops follows consistent trends in diameter classes across all species although there is some variation (Fig. 3). Very little top breakage occurs in small snags (<23 cm DBH), partially a result of their reduced height and exposure to wind. For example, *P. contorta* snags do not readily break before falling and only snags <23 cm DBH showed any signs of top breakage (Bull, 1983; Everett et al., 1999). After 8 years of succession, 50% of small *P. contorta* snags will have fallen but only 3.5–4% will have broken tops, leaving snag fall as the dominant control of mass transfer. This species has the lowest breakage rates but all small snags have limited breakage (Table 5). Medium and large snags (i.e. 23–41 cm and >41 cm DBH) break at significantly higher rates with only slight difference between them. As the cumulative proportion of broken snags increases over time, median snag height continues to decrease. We believe the observed reduction in snag height is a result of multiple breakage events and increased fragmentation of the tops after they break (Everett et al., 1999). There is evidence that broken snags remain standing longer which could account for some of the observed height reduction (Chambers and Mast, 2005). Our study approach could not distinguish between the effects of these two factors since we did not track individual snags through time.

Variation in snag fall and breakage rates appears to arise from interactions of applied and resistive forces influenced by environmental factors and tree physiological characteristics. The total amount of applied horizontal and vertical force experienced by an individual snag is dependent on wind speed, crown position, crown architecture and upper bole/crown mass (Quine and Gardiner, 2007). Snag fall is resisted by the anchoring effect of coarse roots and is directly correlated with total aboveground biomass (Grier and Logan, 1977). Breakage is resisted by the tensile and compressive strength of the snag stem and is correlated with wood density (Bergman et al., 2010). Fall and breakage occur when a critical threshold of applied force is reached, dependent on the resistive forces of both roots and stem wood (Quine and Gardiner, 2007).

Although not explicitly tested, our data supports these physical controls on snag fall and breakage, offering plausible explanations for the variation observed. The effect of crown mass and wood strength on breakage rates is most evident with *P. contorta* snags. This species has relatively low crown mass, moderately-high wood density and experiences little crown breakage (Bergman et al., 2010; Jenkins et al., 2004). Whether wood density or crown mass is the dominant factor in determining breakage is difficult to discern. For example, *P. menziesii* has the slowest breakage rates even with relatively high crown mass. But, this species has the highest wood density of all sampled species and appears to be able to resist stem breakage. One dominant resistive force to snag fall is root anchorage. Since root biomass is positively correlated with aboveground biomass, total root resistance is higher in larger DBH snags, partially explaining their slower fall rates. Additionally, in this study many fallen snags resulted from stem failure below 2 m in height so we would expect similar factors to influence snag fall as snag breakage. The point of intra-stem snag failure is dependent on where maximum applied force occurs and the relative tensile and compression strength at that point. The thresholds of crown mass, wood density and root biomass at which breakage and fall occur is beyond the scope of this study, but there is suggestive evidence that they exhibit significant influence.

Environmental factors influence snag fall and breakage at both stand and landscape spatial scales. We found positive correlation among snag fall and breakage at both the plot and site scale. At the plot level, we tested for stand density influences on fall and breakage by including pre-fire total trees per hectare and total basal area, but neither was statistically significant. This isn't surprising since this study focused on high-severity fire sites with few survivors, limiting any potential wind-reducing effects of stand density. We also tested plot level topographic effects by including slope and elevation in the model but found no significant relationship. At the site level, we included environmental predictor variables for average annual precipitation, average maximum temperature and average minimum temperature but found no statistical relationship. This lack of significance could be the result of limited high-level replication, or the limited range of values from our sites.

Snag exposure to wind likely affects fall and breakage rates, but additional investigations are required to test this effect. For example, Chambers and Mast (2005) found that, at local scales, the basal area of live trees adjacent to snags reduced fall rates. At a broader scale, variation in fall and breakage rates has been reported across geographic regions due to climate and weather variability. For example, along the Front Range of Colorado, Chinook winds can exceed 75 mph increasing fall rates. Schmid et al. (1985) found half-lives to be as low as 5 years and as high as 10 years, depending on the landscape position of the snag population evaluated in this region. Wind events do not always lead to increased snag fall and breakage, but as snags become increasingly decayed or have snow and ice loads, a pulse of snag fall or breakage may result.

5.2. Snag and log decomposition

Many factors contribute to the observed variation in decay rates of snags and logs in dry-mixed conifer forests. Snags receive higher amounts of solar radiation than logs due to their vertical orientation and the shading of logs by residual snags and reestablishing vegetation, resulting in higher snag temperature and accelerated evaporation. Wind also accelerates evaporation by disrupting the boundary layer surrounding exposed material, affecting snags greater than logs. Additionally, logs absorb and retain moisture longer into the summer season because they are buried within the snow pack during winter and spring, have reduced water runoff, and are generally in direct contact with the soil surface. These factors reduce the decay rates of snags relative to logs by pushing the decomposition environment of this material beyond optimal moisture thresholds (Harmon et al., 1986). This effect has been suggested for *P. contorta* snags within the study region and is evident when comparing our *P. ponderosa* snag and log decay rates and our *Abies* sp. snag decay rates with reported log decay rates of *A. grandis* and *A. concolor* in this region (Busse, 1994; Harmon and Fasth, 2005).

Abies sp. snags exhibited statistically significant decay throughout the stem in contrast to *P. ponderosa* snag sapwood and heartwood. Bull et al. (1997) suggest *Abies* sp. snags retain bark longer than *P. ponderosa* snags, increasing moisture retention and improving the decomposition environment of this species. Additionally, the authors suggest *P. ponderosa* sapwood is slightly more decay resistant than *Abies* sp. wood resulting in decay rate differences. Comparisons of log and snag decay rates indicate an increasing decay rate as snags fall or break but the magnitude of this change is variable. *P. ponderosa* snags did not exhibit significant decay but *P. ponderosa* combined log sapwood and heartwood exhibited decay at a rate of $k = 0.0243\ \mathrm{yr}^{-1}$. This k-constant is only slightly less than that reported for *P. contorta* in Pringle Falls Experimental Forest of central Oregon but greater than those reported by others for *P. ponderosa* logs in the same forest type (Busse, 1994; Harmon and Fasth, 2005). *Abies* sp. snags decay at a rate $k = 0.0179\ \mathrm{yr}^{-1}$, which is less than reported decay rates for *A. grandis* and *A. concolor* logs in this region. An *A. grandis* log decay rate obtained in central Oregon was reported as $k = 0.038\ \mathrm{yr}^{-1}$ (Harmon and Fasth, 2005) and an *A. concolor* log decay rate on the Winema National Forest of southern Oregon was estimated as $k = 0.035\ \mathrm{yr}^{-1}$ (Harmon, unpublished data).

The influence of substrate quality is most evident when comparing *P. ponderosa* sapwood and heartwood decay rates. *P. ponderosa* heartwood contains decay resistant compounds such as tannins, resins, waxes, and polyphenols (Harmon et al., 1986). These compounds result in heartwood decaying at approximately 50% of the rate of its sapwood. Allometric equations are not available for estimating the proportion of heartwood present within *P. ponderosa* CWD, but it is positively correlated with DBH and age of a tree suggesting older, large trees will decay at a slower rate than younger, smaller trees after death (Bull et al., 1997). *P. ponderosa*'s sapwood k-constant is similar to other non-decay resistant woody necromass in this geographic region (Harmon and Fasth, 2005). The similarity in these estimates suggests non-decay resistant woody substrates decay at similar rates within a geographic region, regardless of species, after the necromass has transferred to the soil surface.

The higher decay rate but slower fall rate for *Abies* sp. than *P. ponderosa* snags contradicts the anticipated effects of decay on snag dynamics. There are plausible causes of this interaction that build off the previous discussion in snag dynamics. Our sampling methods investigated decay systematically across snag stems but always above 1.5 m in height. We expect moisture wicking to occur at least to this height, resulting in moisture conditions and decay rates equivalent to logs. A snag that breaks below 2 m in height is still considered fallen in this study. Since the outer portion of snag stems (i.e. sapwood) provide disproportionately more resistance to complete structural failure than the center, decay of this portion of the stem is more influential on fall rates (Quine and Gardiner, 2007). As previously discussed, *P. ponderosa* log sapwood decay rate is not significantly different than *Abies* sp. log decay rates resulting in similar reductions in tensile strength of these species. Since *P. ponderosa* has relatively higher stem and crown mass in these forest types, more force is applied on the lower stem tensile strength of *P. ponderosa* than *Abies* sp. snags, resulting in higher fall rates of *P. ponderosa* snags.

We believe additional factors might affect the observed difference in breakage rates of these species. *Abies* sp. snags have moderate crown mass, relatively low wood density and low breakage rates. We believe the increased vertical distribution of crown mass along the stem of this shade tolerant species distributes the applied force created by the crown mass to a broader region of the stem, reducing its stress to a particular point along the stem. In contrast, shade intolerant *P. ponderosa* snags have higher crown mass and a greater degree of concentration of this mass towards the upper bole, increasing stress on the stem. Additionally, *P. ponderosa* snags tend to have larger branch diameters that have a greater negative effect on the structural integrity of the stem, potentially reducing the strength of this species more than *Abies* sp. snags (Brown, 1978; Quine and Gardiner, 2007). This study cannot explicitly discern the driving mechanisms behind the interaction of decay and snag dynamics, but these are plausible explanations that could be explained with further investigation.

5.3. Management implications

Individual characteristics of CWD are important to consider in management strategies of dry-mixed conifer forests since temporal trajectories are variable among species and DBH classes. For example, large *P. menziesii* snags have the potential to stand longer with less top breakage than other snag species. They also have the lowest decay rates of any species in this forest type (Harmon and Fasth, 2005) and can be selected over other species to improve retention of sound CWD. But, longevity of sound snags and logs should not be the only characteristic incorporated into management regimes.

Top breakage appears to be important for primary cavity nesters. Bull (1983) reported that 13 of 15 of the *P. ponderosa* snags used for nesting had broken tops and that the cavities were excavated between 3 and 8 years following mortality. Chambers and Mast (2005) also reported that larger DBH snags with broken tops were more likely to be used as cavity nesting sites relative to unbroken, smaller snags. These habitat structures are more likely to be met by medium and large *P. ponderosa* snags. Additionally, some species prefer soft snags and logs that are more easily excavated, so selecting for *Abies* sp. snags promotes this type of CWD 10–20 years sooner than other species. Rapid decay of CWD may be particularly important for the timing of nutrient release and more rapid development of the soil profile (Triska and Cromack, 1980). Selection and retention of a variety of species and DBH will greatly improve the likelihood of meeting the various ecological functions CWD provides.

Early seral habitats have a distinct beginning point but are not static environments, continually changing over time as snags break, fall and decay while forest vegetation recovers. When considering retention of these habitats, the distribution of snag species and DBH within a stand can be used to predict the future trajectory of CWD and their ability to meet ecological and management needs. In dry-mixed conifer forests, stands can be composed entirely of *Abies* sp. that decay rapidly, not meeting the needs of primary cavity nesters beyond 5–10 years but providing good habitat for saprophyte communities sooner than other snag species. Eventually, a lag in CWD habitat will occur within a stand depending on the specific needs of the species utilizing the resource (Thomas et al., 1979). For example, cavity nesting species preferring large, broken snags with structural rigidity may lose this resource within 15–20 years. It could be >100 years before these structures develop again depending on site productivity and how quickly the next tree cohort establishes (Harmon, 2009). If several stands cannot be retained with various conditions, choosing stands with a mix of species and size classes has the potential to meet more ecological needs across a broader temporal scale.

6. Conclusions

Following high-severity fire in Oregon's Eastern Cascades, a pulse of CWD is created that persists as both snags and logs in predictable trends. Within these early seral environments, we found variation in fall and breakage rates among species and across diameter classes. Additionally, decay rates varied by species and between snags and logs that, when combined with snag fall and breakage, create diversity in habitat structure and resource availability over time. We recommend additional investigation into these complex, highly dynamic landscapes to better understand environmental controls on CWD dynamics. In particular, mixed-severity fires create spatially diverse landscapes with areas experiencing low- (<25% overstory tree mortality), moderate- (25–75% overstory tree mortality) and high-severity (>75% overstory tree mortality) disturbance (Agee, 1993). Early seral habitats only constitute a portion of the post-fire landscape, ranging from 40% to 70% of the fire areas we studied, an amount likely greater than historically occurred (Hessburg et al., 2005). Coarse wood is generated across post-fire landscapes but CWD dynamics and decay could vary across the fire severity gradient. Additionally, surrounding forest conditions are very different which may affect the quality of nesting, roosting or foraging resources, thus making these early seral environments unique (Fontaine et al., 2009; McComb, 2007). Obtaining a better understanding of variation across these landscapes would help link temporal dynamics to the spatial distribution of CWD at individual, stand and landscape scales ensuring adequate availability across broader spatial and temporal scales.

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