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Woody Debris Volume Depletion Through Decay: Implications for Biomass and Carbon Accounting

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ABSTRACT

Woody debris decay rates have recently received much attention because of the need to quantify temporal changes in forest carbon stocks. Published decay rates, available for many species, are commonly used to characterize deadwood biomass and carbon depletion. However, decay rates are often derived from reductions in wood density through time, which when used to model biomass and carbon depletion are known to underestimate rate loss because they fail to account for volume reduction (changes in log shape) as decay progresses. We present a method for estimating changes in log volume through time and illustrate the method using a chronosequence approach. The method is based on the observation, confirmed herein, that decaying logs have a collapse ratio (cross-sectional height/width) that can serve as a surrogate for the volume remaining. Combining the resulting volume loss with concurrent changes in wood density from the same logs then allowed us to quantify biomass and carbon depletion for three study species. Results show that volume, density, and biomass follow distinct depletion curves during decomposition. Volume showed an initial lag period (log dimensions remained unchanged), even while wood density was being reduced. However, once volume depletion began, biomass loss (the product of density and volume depletion) occurred much more rapidly than density alone. At the temporal limit of our data, the proportion of the biomass remaining was roughly half that of the density remaining. Accounting for log volume depletion, as demonstrated in this study, provides a comprehensive characterization of deadwood decomposition, thereby improving biomass-loss and carbon-accounting models.

Key words: carbon cycle; coarse woody debris; deadwood; decay constant; decay rate; decomposition; forest dynamics; forest biomass; forest fuels; habitat structure.

INTRODUCTION

Woody detritus plays a crucial role in forest ecosystem structure and function, influencing biodiversity, nutrient cycling, soil development, and the spread and severity of wildfire (Harmon and others 1986; Schoennagel and others 2004; Stokland and

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others 2012). Down woody debris (DWD) in particular constitutes a substantial carbon pool in forests worldwide, often representing approximately 20% of the total aboveground biomass (Laiho and Prescott 1999; Bradford and others 2009). DWD abundance on a given site changes continuously through time, the result of additions (tree mortality, branch fall) and depletions (wood decomposition, combustion). Understanding DWD dynamics, particularly changes in abundance due to wood decomposition, has recently grown in importance, given the growing interest in temporal changes in forest carbon stocks (Cornwell and others 2009; Woodall 2010), the persistence of DWD as a habitat structure (Tikkanen and others 2007), and the longevity of forest fuels and fuel-reduction treatments (He and others 2004).

Quantifying wood decomposition presents considerable challenges, owing in part to the long time scales required for complete decomposition—hundreds of years in some situations (Kueppers and others 2004). Thus, attempts to quantify decomposition by following individual logs over time are practical only for portions of the decay process (Laiho and Prescott 1999). As an alternative, researchers may assemble information obtained from a set of logs with varying mortality dates spanning long time periods (that is, the chronosequence approach) to describe decay dynamics and estimate decay rates (Means and others 1985; Aakala 2010; van Geffen and others 2010).

A large number of deadwood decay chronosequences have been conducted, and the resulting decay rate constants for many tree species are readily available in the published literature. However, most of these constants have been derived from reductions in wood density (see Laiho and Prescott 2004; Rock and others 2008), using when necessary standard green wood (that is, non-decayed) densities as initial values. In contrast, decay rates based on direct measurements of biomass loss are uncommon because the initial biomass of samples is rarely known. In the absence of true biomass depletion rates, researchers may rely on density-derived depletion rates to model temporal changes in biomass and carbon. However, this practice is known to underestimate rate loss, because DWD volume reductions are not taken into account (Harmon and others 1987; Krankina and Harmon 1995; Næsset 1999; Beets and others 2008; Grove and others 2009; Zell and others 2009). Thus, when DWD biomass depletion is assessed using a chronosequence approach, it is best accomplished by combining density depletion and volume depletion (recall that mass is the arithmetic product of density and volume). However, quantifying volume depletion (that is, progressive changes to log size and shape) retrospectively has also long posed a methodological challenge.

To address this issue, we present a method that overcomes the challenge of estimating DWD volume depletion. The method is based on the observation that the gradual collapse of logs through decay provides a reliable means of assessing volume loss over time. Specifically, we demonstrate that under typical conditions, a decaying log's cross-sectional width (horizontal diameter) remains relatively stable even through the most advanced stages of decay, whereas the cross-sectional height (vertical diameter) diminishes as decay progresses and structural integrity is weakened. The resulting collapse ratio (current height/current width) thus provides a reliable estimate of the proportion of the log's volume remaining. Combining volume depletion (via the collapse ratio) with wood density from the same logs allows us to estimate biomass depletion. We note that the collapse of logs through decay has been long recognized; in fact, cross-sectional shape is an important characteristic in assessing decay in numerous decay-stage classifications (for example, Maser and others 1979; Müller-Using and Bartsch 2009; Stokland and others 2012). Our contribution is the demonstration that the collapse ratio provides a means of estimating the initial volume and hence the volume lost.

A number of long-term studies in forests of the north-central U.S. provide an excellent opportunity to demonstrate these concepts and to quantify temporal changes in DWD density, volume, and biomass using a chronosequence approach. Though not the original intent of these studies, they provide mortality dates, pre-mortality diameters, and locations for many logs of three common tree species in the region. We have relocated these logs, recorded their current dimensions, and collected samples for density determination in the laboratory. Our objectives were to (i) demonstrate that the cross-sectional width of decaying logs remains relatively stable through time, thereby providing a method (that is, the collapse ratio) for characterizing volume depletion; (ii) correctly quantify biomass depletion by combining volume depletion and wood density depletion for each of these three species; and (iii) evaluate the impact of our approach for modeling temporal changes in DWD biomass in forest ecosystems. Our results highlight the important distinction between density, volume, and biomass depletion and thus have implications for a wide range of forest ecology studies and carbon-accounting efforts.

MATERIALS AND METHODS

Long-Term Studies

The study sites lie within the Laurentian Mixed Forest Province (Aaseng and others 2003) of north-central Minnesota, USA. The climate is cold–temperate continental, characterized by short cool summers and long severe winters, with mean annual temperature of 3.6°C and precipitation of 67.8 cm (McNab and Avers 1994).

A large number of long-term, permanent-plot studies provide pre-mortality diameters, mortality dates, and locations for 89 mapped and/or individually tagged logs of the three most abundant species in these studies: *Pinus resinosa* Ait., *Populus tremuloides* Michx., and *Picea glauca* (Moench) Voss. These studies include long-term, repeatedly measured permanent plots, experimental silvicultural thinnings with felled trees left on site, decomposition studies following the fate of placed logs, and allometric studies that required detailed measurements of trees that were felled and left on site. The diameter at breast height (1.4 m) was measured less than one year before tree death for all but two *P. resinosa* samples, for which diameters had been measured 3 years before felling; for these, we augmented diameters based on the known average growth rates (the result of dendrochronological analyses from the same plot). We also obtained 46 decayed wood samples from additional sites with known tree mortality dates, but without pre-mortality diameter measurements. These studies include documented timber harvests, documented blowdowns (with windthrow of individual trees confirmed when necessary by the onset of reaction wood in displaced saplings), and a chainsaw certification course. We sampled only those stems that fell to the forest floor during a discrete disturbance (windthrow or chainsaw felling), thereby avoiding the confounding factor of residing as a snag before falling (Storaunet and Rolstad 2002).

Only logs greater than 10 cm in diameter were sampled, as this is a common minimum DWD diameter in resource assessments (Woodall and others 2009). We measured log height (perpendicular to forest floor) and width (parallel to forest floor) at former breast height on log cross sections carefully exposed when necessary by sawing and excavation. Each log was assigned a decay class in the field, using a five-class system (Maser and others 1979), with class 1 being least and class 5 most decayed. To obtain ''green'' (non-decayed) wood densities, we used 54 logs (18 of each species) from a recently initiated companion study of decomposition in which logs of two species (*P. resinosa*, *P. tremuloides*) used in the present study were felled and placed within an intact forest, with the intent of following them over time. This companion study included *Picea mariana*, which we used in place of *P. glauca* for ''green'' density, justified because the two species co-occur and have identical wood densities in all five decay classes (Harmon and others 2008). Table 1 provides details of the sampled logs.

Locating sufficient numbers of logs with known fell dates proved to be challenging. We located and sampled logs from 52 stands across 25 upland sites, an average of 2.6 logs per stand. Although stand conditions likely influenced decay rates, the large number of distinct stands, as well as the fact that stand conditions necessarily changed over the past decades as our samples decayed, makes it impractical to consider details of each stand or site.

Field and Laboratory Sampling

Field collection of wood samples for density determination varied according to the state of decay. For intact or relatively intact samples, we obtained radial cross sections by sawing, and samples were collected a minimum of 0.5 m from the log end to avoid possible excessive decay at exposed cross sections. Well-decayed, friable samples (for example, decay class 5) were collected using a sharpened

Table 1. Attributes of the Decayed Sample Logs (that is, Excluding the 54 Recent, Non-decayed Logs from Our Companion Study)

Species	Initial diameter known			Initial diameter unknown			Earliest sample
	N	Mean (cm)	Max (cm)	*N*	Mean (cm)	Max (cm)	
P. resinosa	19	23.7	45.0	23	18.3	50.0	1941
P. tremuloides	32	25.9	50.1	21	23.4	39.2	1959
P. glauca	38	17.4	44.0	2	15.5	20.0	1986

''Initial diameter known'' metrics refer to the diameter immediately prior to felling; ''initial diameter unknown'' metrics refer to diameters at time of sampling.

steel core (5.3 cm internal diameter) of known volume inserted into the sample perpendicular to the exposed cross section to avoid crumpling wood fibers (Tarasov and Birdsey 2001; Aakala 2010). All samples were sealed in plastic and frozen until processed in the laboratory. Intact or relatively intact samples included heartwood, sapwood, and bark; however, for samples in extremely advanced decay, this distinction could not be confirmed. One sample was collected from each log.

Laboratory methods for determining sample volume also varied according to decay state. For intact samples (that is, radial cross sections), we relied on multiple direct measurements to arrive at volume. For partially decayed pieces, we vacuum sealed (FoodSaver® model V2040) the sample and determined volume by water displacement, using hydrostatic weighing based on Archimedes' principle (Hughes 2005) and adjusting for tap water density. The volume of the standard-sized polyethylene vacuum-sealed bag was then subtracted from the fresh (that is, undried) volume before analyses, and adjustments due to an imperfect vacuum seal were made following Fraver and others (2002). For well-decayed, friable samples (those collected with a metal core), internal core volume was taken as the sample volume. Following volume determination, samples were oven dried at 75°C for eight days and weighed. From these data, we calculated density (g dry mass cm^{-3} fresh volume) for each sample. Finally, these samples were ground in a Wiley mill and analyzed for percent carbon content using a Leco TruSpec (model 630-100-400).

Depletion curves for density, volume, biomass, and carbon were based on proportions of the initial attribute remaining through time. For initial density, we used the means of the 18 recently felled trees for each species, obtained from our companion study. Density of the decayed samples was then divided by these initial densities to arrive at the proportion of the density remaining. For volume depletion, the collapse ratio (current cross-sectional height/current cross-sectional width) of the decayed log was used as a surrogate for the proportion of volume remaining. Our calculations of biomass remaining began with a standard 1-m-long cylinder (any length or rotated solid would produce the same result) using the tree's initial breast height diameter when available or the current cross-sectional width when initial not available, to calculate initial volume. This volume was multiplied by the initial density (above) for each species to arrive at initial biomass. Remaining biomass was then calculated as the product of the sample density and the proportion of volume remaining. Biomass of the decayed log was then divided by the initial biomass to determine the proportion of biomass remaining. Percent carbon values from individual samples were multiplied by their corresponding biomass values and expressed as proportions remaining for analyses.

Statistical Analyses

We assessed potential changes in log cross-sectional width through decay by regressing the current field-measured horizontal diameters (that is, log width) against initial diameters, using the 89 samples for which initial diameters were known. We reasoned that if the one–one line representing initial diameter fell within the 95% confidence limits of the linear regression, the cross-sectional width could be considered relatively stable through decay. This relationship was further explored by subsetting the data by decay class and species. These tests were followed by a more robust test of the difference between the fitted regression slope and a one–one line (based on 89 samples), using the one-sample, ordinary least squares (OLS) slope test within the R smatr package, version 2.1 (Warton and others 2006). Because the results from these tests ultimately showed the width to be relatively stable, we used the current diameters as surrogates for the initial diameters for the 46 samples for which initial diameters were unknown, thus allowing us to use all decayed samples ($N = 135$) in subsequent analyses.

For each species and DWD attribute (density, volume, biomass, carbon), we compared a set of candidate statistical regression models that represent the proportion remaining as a function of time since tree death. Model functional forms included linear, asymptotic, sigmoidal, logarithmic, logistic, power, rational, negative exponential, Weibull, Gompertz, and Chapman-Richards (see Appendix A in supplementary material). We compared candidate models using corrected Akaike's information criterion (AICc) as well as Akaike model weights, which allowed us to determine which models were best supported by the data (Burnham and Anderson 2002). For each species–attribute combination, the model with the lowest AICc score was selected as the best, and for each of these, we insured that the distribution and normality of residuals were acceptable.

RESULTS

The regression of the current horizontal diameters (cross-sectional width) against the initial diameters revealed a significant linear relationship (Figure 1; linear regression: current = −0.03 + 0.93 × initial; $P < 0.0001$; $R^2 = 0.88$). The fact that the one–one line representing initial diameter fell within the 95% confidence limits of the regression suggests that the cross-sectional width remains relatively stable through decay. This finding held in all cases when data were subset by decay class and by species. Similarly, the one-sample slope test (Warton and others 2006) provided reasonable evidence that the regression did not differ from the one–one line (test statistic $r = -0.20$, $P = 0.06$), and it confirmed that the one–one line fell within the regression confidence limits (tested at $\alpha = 0.05$). Although the cross-sectional width remains relatively stable, the cross-sectional height becomes greatly reduced as the log progressively collapses upon itself through decay (Figure 1 inset and Figure 2).

The depletion curves for wood density, log volume, and biomass differed from each other and varied by species (Figure 3), with AICc scores distinguishing the best-fitting curves. As expected, of the attributes examined, biomass depletion occurred at the fastest rate: at the temporal limit of our data, the biomass remaining was roughly half that of the density remaining (Figure 3). Its depletion was best described by a rational function for *P. resinosa* and *P. glauca* and a Weibull function for *P. tremuloides* (Table 2; Figure 3). Volume depletion for *P. resinosa* and *P. tremuloides* was best described by a Weibull function, which suggested an early lag in depletion, whereas volume depletion for *P. glauca* was best approximated by a rational function (Table 2; Figure 3). We note that the volume depletion shown in Figure 3 is equivalent to that of the reduction in the collapse ratio, as the ratio is used as a direct surrogate for the volume remaining. Each species had a different best-approximating form to describe density depletion; depletions for *P. resinosa*, *P. tremuloides*, and *P. glauca* were best described by Weibull, rational, and power functions, respectively (Table 2; Figure 3). Carbon depletions for *P. resinosa* and *P. glauca* were best described by the rational function (as with biomass); however, an asymptotic function best described *P. tremuloides* carbon depletion (Table 2; Figure 3). Shapes of the carbon depletion curves are very similar to those of biomass because carbon represented roughly one-half of the biomass (48.5% for *P. resinosa*, 47.6% for *P. tremuloides*, and 49.7% for *P. glauca*, averaged across samples). Appendix B in the supplementary material shows the ranking of all model forms for each species–attribute combination.

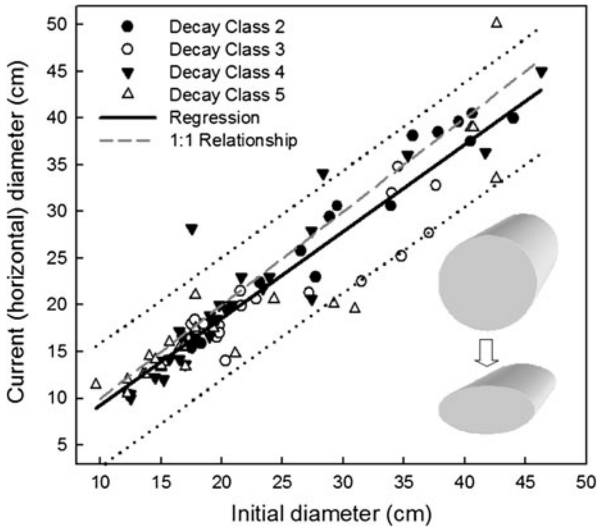

Figure 1. Relationship between the current horizontally measured log diameter (cross-sectional width) and its initial diameter at time of death, derived from permanent-plot data. The strong linear relationship even across decay classes suggests that width remains relatively stable through decay, even though the height is diminished as the decaying log collapses upon itself (*inset*). Dotted lines represent 95% confidence intervals of the regression.

Figure 2. Partial excavation (*foreground*) of a decayed *P. tremuloides* log revealing an elliptical cross section (*white outline*), which results from progressive collapse as decay proceeds. The relative stability of the cross-sectional width through time (even as the height is being reduced) permits an estimation of the log's initial diameter and hence initial volume.

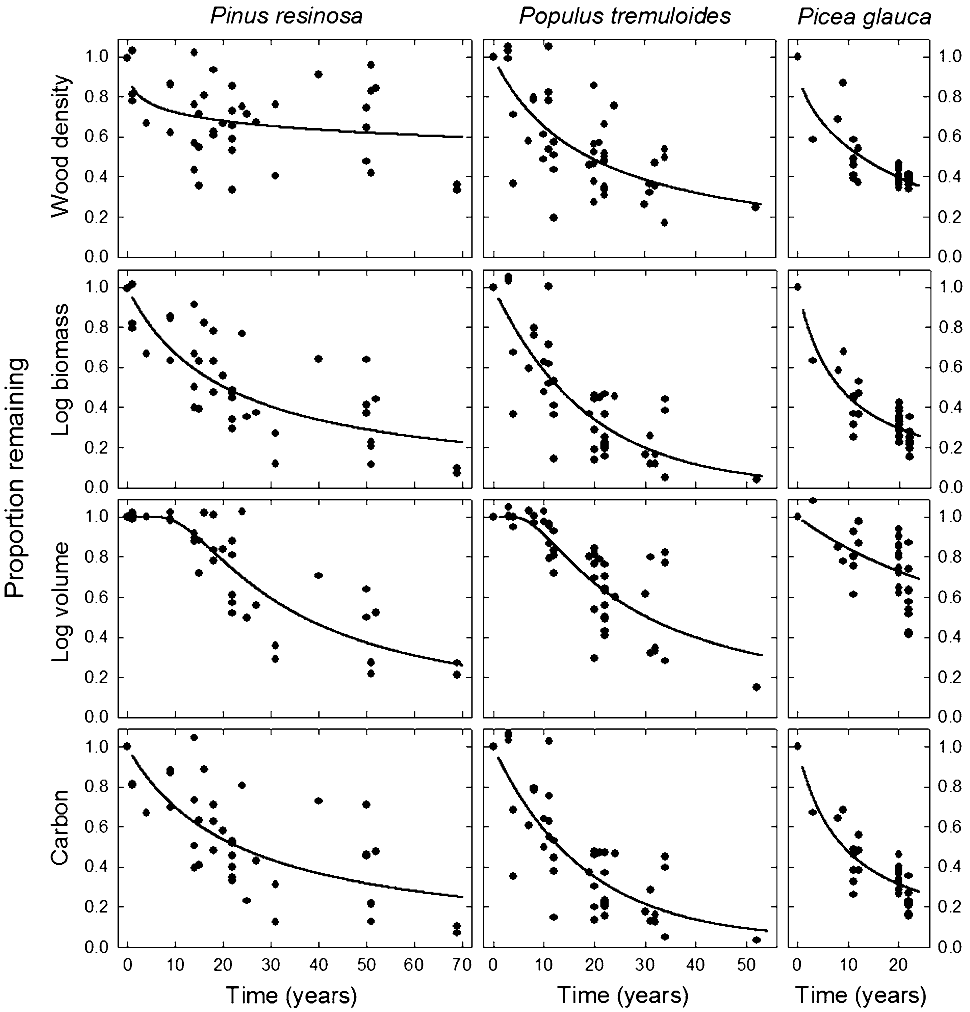

Figure 3. Depletion curves for wood density, log biomass, log volume, and carbon for the three species evaluated. Curves represent best-fitting models for each species–attribute combination. We note that volume depletion is equivalent to the reduction in the collapse ratio (cross-sectional height/width), as the ratio is used as a direct surrogate for volume remaining. ''Log'' refers to the decaying stem, not a logarithm. See Table 2 for model form and coefficients.

Table 2. Top Model Forms (Based on the Corrected AIC) and Coefficients Describing the Depletion for Each Species–Attribute Combination

Species	Attribute	Model	Model form	*a*	*b*
P. resinosa	Density	Weibull	$Y = 1 - \mathrm{EXP}(-a * (\mathrm{TIME} ** b))$	1.911	−0.174
	Volume	Weibull	$Y = 1 - \mathrm{EXP}(-a * (\mathrm{TIME} ** b))$	74.382	−1.297
	Biomass	Rational	$Y = 1/(1 + (a * \mathrm{TIME}))$	0.049	–
	Carbon	Rational	$Y = 1/(1 + (a * \mathrm{TIME}))$	0.043	–
P. tremuloides	Density	Rational	$Y = 1/(1 + (a * \mathrm{TIME}))$	0.053	–
	Volume	Weibull	$Y = 1 - \mathrm{EXP}(-a * (\mathrm{TIME} ** b))$	32.919	−1.132
	Biomass	Weibull	$Y = 1 - \mathrm{EXP}(-a * (\mathrm{TIME} ** b))$	7.689	−0.986
	Carbon	Asymptotic	$Y = a + ((1 - a) * \mathrm{EXP}(-b * \mathrm{TIME}))$	0.031	0.056
P. glauca	Density	Power function	$Y = 1 - a * \mathrm{TIME} ** b$	0.163	0.437
	Volume	Rational	$Y = 1/(1 + (a * \mathrm{TIME}))$	0.019	–
	Biomass	Rational	$Y = 1/(1 + (a * \mathrm{TIME}))$	0.121	–
	Carbon	Rational	$Y = 1/(1 + (a * \mathrm{TIME}))$	0.110	–

Time in years.

For convenience of use, model forms are presented as they would appear in a typical programing language. See Appendix B in the supplementary material for the full ranking of candidate model forms for each species and attribute.

DISCUSSION

Log Collapse Through Time

Our results demonstrate that a decaying log's cross-sectional width remains relatively stable even through the most advanced stages of decay (Figure 1). Although the relationship between initial and current cross-sectional width is not perfect—the fitted regression falls slightly below the one–one line (Figure 1) and the slope test provided only modest support for similarity—we believe it is sufficient for estimating the former from the latter. Stone and others (1998) also recognized that log widths had not changed after 65 years of decay in British Columbia, a finding they used to confirm the relocation of individual logs on permanent plots, and Henry and Swan (1974) similarly used outlines of well-decayed logs to estimate their former living diameters. Cross-sectional height, however, diminishes as decay progresses because internal voids created by insects and other wood-decay organisms (Stokland and others 2012), as well as the fungal-mediated breakdown of xylem cells themselves (Blanchette 1980; Boddy and Watkinson 1995), lead to a log's gradual collapse upon itself under the force of gravity. We emphasize that the resulting elliptical shape is not the result of the decaying log spreading out on the forest floor, but rather collapsing vertically upon itself. The horizontal stability may be enhanced by colonization by bryophytes and ground-layer vascular plants (Figure 2). Given this relative stability, the collapse ratio (current height/current width) provides a reliable surrogate for the proportion of the log volume remaining; that is, a ratio of 0.6 indicates that 40% of the log's field-measured volume has been lost to decay. Our confirmation of this relationship has important implications for accurately predicting long-term dynamics of DWD volume, biomass, and carbon content.

Characterizing decay-mediated volume loss has long presented a methodological challenge, although this metric is needed to properly estimate biomass depletion in chronosequences (Harmon and others 1987; Krankina and Harmon 1995; Næsset 1999; Beets and others 2008; Grove and others 2009; Zell and others 2009). Previous studies have attempted a variety of methods to estimate initial log volume for this purpose (Grier 1978; Brown and others 1998; Krankina and others 1999; Müller-Using and Bartsch 2009); however, none have done so using the readily available collapse ratio. Volume loss of decayed logs has been attributed primarily to fragmentation (Harmon and others 1987; Yin 1999; Grove and others 2009; Müller-Using and Bartsch 2009), a term that implies breakage into smaller pieces by gravity or other physical forces. Our findings support the suggestion by Krankina and others (1999) that volume depletion through heterotrophic decomposition may be more prevalent than losses by fragmentation.

The use of collapse ratios to assess volume and biomass depletion functioned well for these species and in this setting; however, it may not apply universally. First, logs or portions of logs that have been truly fragmented by physical force or excavated by mammals have had their dimensions altered by factors other than heterotrophic decomposition. Second, hollow case-hardened logs, often the result of residing as a snag for an extended period before falling (Yatskov and others 2003), may not show the collapse described here. Third, because our results were derived from northern temperate forests, where fungi are the primary agents of wood decomposition, they may not hold in other regions where insects dominate as decomposers, as insect activity may cause excessive breakage and deformation (personal observation). Finally, because our decay rates were derived from lower stem sections, in most cases at breast height, they do not apply to upper canopy or branch wood, which would be expected to decay more quickly (Müller-Using and Bartsch 2009).

Depletion Curves

Combining DWD volume depletion (via the collapse ratio) with wood density values from the same logs allowed us to model biomass depletion through time. Ours is one of the few chronosequence studies to simultaneously assess temporal changes in these three DWD attributes (see Harmon and others 2000; Mäkinen and others 2006). Our results corroborate those of previous studies, showing that the three attributes follow distinct depletion curves (Figure 3), which suggests caution when using density-depletion curves as surrogates for changes in biomass and carbon (see ''Implications of Findings'' section). In addition, volume depletion may show an initial lag of 10 years or more during which volume remains constant (log dimensions remained unchanged), even while wood density and biomass are being reduced (see also Harmon and others 1987; Brown and others 1998; Mäkinen and others 2006). For example, *P. resinosa* lost approximately 35% of its mass, but none of its volume after 10 years of decay (Figure 3). Once volume depletion begins, biomass loss, being the arithmetic product of density and volume depletion, occurs much more rapidly than density alone. The initial lag simply suggests that structural integrity had not been sufficiently compromised to initiate collapse.

The fact that biomass loss for any species was not best described by the negative exponential (which assumes a constant decay rate) suggests that the rate varies through time. Forms of the top models for each species showed a more rapid early stage and a slowing in later stages of decay when compared to the negative exponential (not shown). Similar rate changes through time are well reported (for example, McFee and Stone 1966; Means and others 1992; Harmon and others 2000; Mäkinen and others 2006; Freschet and others 2012) and can be explained by a rapid early phase in which the most labile compounds are consumed, transitioning to a slow phase where more recalcitrant compounds persist for prolonged periods. This shift in wood chemical composition both contributes to and results from corresponding shifts in fungal community composition as decay advances (Boddy 2001; Stokland and others 2012).

Decomposition rates showed considerable variability both within and between species, as evidenced by the wide scatter of sample points seen in Figure 3. This variability may be expected given the large number of biotic and abiotic factors at play. Among the more important may be the composition of the fungal community acting within the log itself, as fungal species vary greatly in their capacity to degrade wood (Boddy 2001; Lindner and others 2011; Clinton and others 2009). Other biotic factors that affect within-log, within-species, and between-species variability include (i) initial wood density, as density is inversely correlated with decay rates (Chambers and others 2000); (ii) anomalous anatomical features, such as reaction wood or fire-affected wood, which are more resistant to decay (Verrall 1938; Blanchette and others 1994); (iii) growth rate of the stem prior to death, given that slow-growing trees tend to decay more slowly (Edman and others 2006); (iv) the time elapsed before falling and coming in direct contact with the forest floor, as ground contact hastens decomposition (Næsset 1999); (v) stem diameter, because large-diameter logs typically decay more slowly (Beets and others 2008); (vi) species-specific wood anatomical and chemical traits, as these dramatically influence decay rates (Cornwell and others 2009); and (vii) overgrowth of logs by bryophytes, which may retard decomposition (Hagemann and others 2010). Related abiotic factors, such as temperature, humidity, and exposure, exert their influence primarily by regulating biotic agents (Boddy 2001; Stokland and others 2012). For example, the activity of wood-decay fungi becomes negligible when logs dry below mass moisture contents of 25–30% as well as when overly saturated (Panshin and de Zeeuh 1980).

Our models do not allow us to predict longevity of decaying logs as doing so would require undue extrapolations beyond the range of our empirical data. Nevertheless, for *P. tremuloides* and *P. resinosa*, roughly 30% of the volume remained at the temporal limit of our data, at a time when the instantaneous decay rate has slowed dramatically (Mäkinen and others 2006; Freschet and others 2012), suggesting that longevities far exceed 52 and 70 years, respectively (see Figure 3). Others have noted that determining the endpoint of the DWD decay process may be an intractable task, given the gradual transition to relatively stable soil organic matter (McFee and Stone 1966; Mackensen and others 2003).

Implications of Findings

Our results have implications both for how decomposition rates are derived and how the resulting rates are applied. For example, DWD decay rates derived from chronosequence studies are typically based on depletions in wood density (Laiho and Prescott 2004; Rock and others 2008), with rate constants (*k*, derived from negative exponential models) for many tree species readily available in the published literature. In the absence of true biomass depletion rates, researchers may rely on density-derived depletion rates to assess temporal changes in biomass and carbon. However, this practice is known to overestimate these attributes through time, because DWD volume reductions are not taken into account (Harmon and others 1987; Krankina and Harmon 1995; Næsset 1999; Beets and others 2008; Grove and others 2009; Zell and others 2009). Our approach provides an estimate of the magnitude of this overestimate: at the temporal limit of our data, the proportion of biomass remaining was roughly twice that of density remaining (Figure 3). We thus recommend caution in applying published decay rates to metrics from which they were not derived. We further recommend that future chronosequence field studies where samples are collected for density determination also record collapse ratios to account for volume loss. Combining volume loss with wood density reduction, as we have shown in the present study, would improve characterizations of biomass and carbon depletion, thereby improving mass-loss and carbon-accounting models. Further, because forest fuel inventories are typically reported in mass units (Brown 1974), our approach could improve modeling of the longevity of coarse forest fuels and fuel-reduction treatments.

Up to this point, we have emphasized correct assessments of DWD biomass and carbon depletion. However, DWD volume—more than density, biomass, or carbon—is the metric of choice in studies of forest structure and complexity (Spies 1998), and given the importance of DWD to numerous dead-wood-dependent organisms (Stokland and others 2012), volume is often used as a direct surrogate for biodiversity (Lassauce and others 2011). When used in a chronosequence, our collapse ratio provides a reliable means of estimating and modeling temporal changes in DWD volume.

Our results also highlight the importance of adjusting for log collapse when calculating static DWD volume, biomass, or carbon stocks from typical field inventory data, where decayed log width, but not height, is recorded using calipers (Figure 2). Field measurements of logs in advanced decay stages (classes 4 and 5 in our system) can be easily reduced via decay class-specific collapse ratios. This recommendation has been made previously (for example, Means and others 1985; Spies and others 1988; Fraver and others 2007); when overlooked, it may result in overestimates of DWD volume, biomass, and carbon stocks. Mean collapse ratios from the current study were 0.800 (SD = 0.192, median = 0.859) and 0.412 (SD = 0.172, median = 0.407) for decay classes 4 and 5, respectively. Fraver and others (2002) found that collapse ratios did not differ between hardwood and softwood species, suggesting wide applicability of such ratios.

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