

Residence Times and Decay Rates of Downed Woody Debris Biomass/Carbon in Eastern US Forests

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ABSTRACT

A key component in describing forest carbon (C) dynamics is the change in downed dead wood biomass through time. Specifically, there is a dearth of information regarding the residence time of downed woody debris (DWD), which may be reflected in the diversity of wood (for example, species, size, and stage of decay) and site attributes (for example, climate) across the study region of eastern US forests. The empirical assessment of DWD rate of decay and residence time is complicated by the decay process itself, as decomposing logs undergo not only a reduction in wood density over time but also reductions in biomass, shape, and size. Using DWD repeated measurements coupled with models to estimate durations in various stages of decay, estimates of DWD half-life (T_{HALF}), residence time (T_{RES}), and decay rate (k constants) were developed for 36 tree species common to eastern US forests.

Results indicate that estimates for T_{HALF} averaged 18 and 10 years for conifers and hardwoods, respectively. Species that exhibited shorter T_{HALF} tended to display a shorter T_{RES} and larger k constants. Averages of T_{RES} ranged from 57 to 124 years for conifers and from 46 to 71 years for hardwoods, depending on the species and methodology for estimating DWD decomposition considered. Decay rate constants (k) increased with increasing temperature of climate zones and ranged from 0.024 to 0.040 for conifers and from 0.043 to 0.064 for hardwoods. These estimates could be incorporated into dynamic global vegetation models to elucidate the role of DWD in forest C dynamics.

Key words: carbon flux; decomposition; forest inventory; forest fuels; decay class; coarse woody debris.

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INTRODUCTION

Forest ecosystems and their associated carbon (C) stocks have become an important consideration of global strategies aimed at reducing greenhouse gas (GHG) concentrations and possibly mitigating future climate change effects (Ryan and others 2010; Malmshheimer and others 2011; McKinley and others 2011). An important component of forest C is dead wood, of which a major component is downed woody debris (DWD; defined hereafter as

downed dead wood ≥ 7.62 cm in diameter and ≥ 0.91 m in length). This DWD may be a large component of overall stocks, accounting for approximately 20% of total C in primary (that is, old growth; Harmon and others 1990) and secondary (Bradford and others 2009) forests.

The decomposition of DWD has emerged as a knowledge gap hampering our ability to quantify changes in C pools (Birdsey and others 2006). Improved estimates of DWD decay rates have a direct use in process-based (for example, Aber and others 1995) and empirical (for example, Rebasin and others 2010) ecosystem dynamic models, while a refined understanding of the DWD decay process has important implications for forecasting forest fuel loads (Rollins and others 2004), assessing potential habitat for dead wood-dependent organisms (Stokland and others 2012), and addressing the implications of utilization of logging slash for bio-energy production (for example, forest harvest residues) on C balances and net GHG emissions (Schlamadinger and others 1995; Sathre and Gustavsson 2011; Zanchi and others 2012). By coupling estimates of DWD decay with climate information, it may be possible to estimate changes in DWD decomposition rates under future climate scenarios. Ultimately, a clearer understanding of the variability of DWD decay rate and associated C flux estimates is essential for predicting ecosystem responses to global change (Weedon and others 2009).

Methodologies for sampling and quantifying the volume, biomass, and C content of DWD, and their associated stocking levels have greatly improved in recent years (Fraver and others 2007, 2013; Woodall and others 2009; Gove and Van Deusen 2011; Gove and others 2012; Ritter and Saborowski 2012). However, studies that investigate the temporal dynamics of DWD are limited, yet urgently needed to determine the role of woody forest detritus in regional C cycles. Specifically, few studies have quantified DWD mass loss through time. Most studies that investigate DWD decay rates estimate changes in wood density, which is often used as a surrogate for mass. As an example, of the 37 studies reviewed by Laiho and Prescott (2004; their Table 4), only five addressed DWD mass loss; the remainder focused on density depletion. However, the use of density depletion is known to underestimate mass loss because it fails to consider log volume loss as decay progresses (Harmon and others 1987; Næsset 1999; Zell and others 2009; Fraver and others 2013).

In routine DWD inventories in the US, a five-class system is commonly used to denote the decay

class (DC) of individual DWD pieces (Woodall and Monleon 2008), based on physical characteristics of the piece. Obtained through a synthesis of North American DWD density data, the ratio of the density of a decayed DWD piece to that of a non-decayed piece, termed a DC reduction factor (Harmon and others 2011), can be used to estimate density reduction that occurs as pieces advance through subsequent DCs. Because estimates of DWD mass based on density alone will underestimate mass loss (as above), additional reduction factors can subsequently be incorporated to account for DWD structural changes (that is, volume loss) as decay progresses (for example, Means and others 1985; Spies and others 1988; Fraver and Palik 2012), an approach that has recently been applied to standing dead wood (Domke and others 2011).

For studies that have meticulously measured C flux on decaying DWD, methodologies have been restricted to logs of intermediate decay. For example, DC 2 pieces were only investigated by Hagemann and others (2010), whereas Noormets and others (2012) examined DC 2 and 3 pieces. Stage of decay has been shown to influence DWD C flux (Wang and others 2002), hence, including pieces in all stages of decay is essential to accurately depict DWD mass loss dynamics. Chronosequence studies have been used as one approach to capture these dynamics over a range of DC (for example, Mattson and others 1987; Mackensen and Bauhus 2003; Noormets and others 2012); however, the time and effort required for such studies have generally restricted their application to a specific forest type under a controlled set of stand conditions. Given the limitations to these various approaches, the use of DC simulations could be a powerful alternative for estimating mass loss rates of DWD. Using a DC transition model (for example, Kruijs and others 2002; Aakala 2010; Russell and others 2013), simulations allow one to quantify the degree of uncertainty surrounding estimates of DWD mass loss. By quantifying uncertainty attributed to both model performance and inventory measurements, confidence intervals can be constructed to assist in our understanding of DWD mass-loss dynamics. Given the various decomposition pathways and factors influencing wood degradation (Stokland and others 2012), simulation-based models aimed at accurately estimating DWD decomposition at large regional scales need to account for species and forest type differences, climatic regimes, and DWD physical attributes such as DC and piece size.

As a quantitative measure of decay rates, investigators have defined DWD half-life to be the

number of years for a DWD piece of a specific size to lose 50% of its initial biomass. As an example, Radtke and others (2009) reported DWD half-lives to range between 5 and 8 years for *Pinus taeda* L. in southeastern US plantations. In contrast, measures of DWD residence times are much more multifaceted and have been given several definitions. Early estimates for DWD residence time assumed a linear decay of woody debris over a 10-year period (IPCC 1997), a default value which was found to be a tremendous overestimate of DWD decomposition for common species in southeastern Australia (Mackensen and others 2003). Some define DWD residence time as the number of years in which 10% (Hérault and others 2010), 5% (Mackensen and Bauhus 2003), or 1% (Lambert and others 1980) of initial DWD biomass remains, while others approximate DWD residence times based on experimental observations (Mackensen and others 2003).

The primary goal of this study was to estimate the decay rate and residence time of DWD across the major forest types of the eastern US using Forest Inventory and Analysis data. Specific objectives were to: (1) estimate DWD biomass depletion through time by coupling DC transition simulations with associated DC and volume reduction factors (VRFs) and (2) quantify DWD decay rate, half-life, and residence time for the primary species, and associated DWD C flux for common forest types in the eastern US. A Monte Carlo-based simulation approach was used to determine the effectiveness of estimating DWD residence time for individual species to address questions regarding C accounting.

METHODS

Study Area

Forest types of the eastern US are diverse, ranging from hemlock-pine-northern hardwood (north), oak-hickory (west), and southern pine forests (south and east) (Smith and others 2009). The study area investigated here ranged eastward from the state of Minnesota to Maine in the north and Louisiana and Georgia in the south, spanning approximately 18° latitude and 29° longitude. Whether observing the Köppen climate regions (Kottek and others 2006) or Bailey (1980) ecoregions, each forest type varies in terms of its potential productivity and species assemblage. Across the study area, mean annual temperatures (MAT) range from 1.4 to 19.8°C and precipitation from 55 to 201 cm (Rehfeldt 2006; USFS 2012). More than

75 forest types have been identified by the USDA Forest Service's Forest Inventory and Analysis (FIA) program across the study area, which represent 14 broader forest type groups (Woudenberg and others 2010).

Modeling DWD Decay Class Transitions

During field inventories, DC was assigned to each DWD piece using a five-class system, with 1 being least and 5 being most decayed. Estimates of DWD DC transition, defined as the probability that a DWD piece will remain in the same DC or advance to subsequent DCs in 5 years, have recently been quantified across the eastern US (Russell and others 2013). Downed woody debris DC transitions were estimated by predicting the cumulative probabilities of pieces advancing in decay using a cumulative link mixed model [Russell and others 2013; using matched data (their Table 3)] with forest type (ForType) specified as the random effect. As DWD C loss is likely linked to its unique attributes and endemic climate (Herrmann and Bauhus 2013), the number of degree days greater than 5°C (DD5), coupled with the length of the DWD piece (LEN; m) and initial DC, was used to indicate decomposition potential across the eastern US and thus estimate DWD DC transitions (Russell and others 2013):

$$\text{logit}(\gamma_{ikj}) = \theta_k - \beta_1 DD5 - \beta_2 LEN - u_{\text{ForType}_j} + \epsilon, \quad (1)$$

where θ_k is the intercept term for DC k (that is, DC 1, DC 2, DC 3, DC 4, or DC 5), γ is the cumulative probability for DWD piece i moving through each of the successive k decay classes within each ForType j , β_i are the parameters estimated for conifer and hardwood species separately, and ϵ is the random residual term. The random effect u was specified to represent forest type-specific effects on the transition process. Models were fit using paired DWD piece observations (measured once between 2002 and 2007, then remeasured 5 years later) from a national forest inventory database (FIA) of eastern US forests (Woodall and others 2012). Other variables representing climate, including mean annual precipitation did not reduce Akaike's information criteria and log-likelihood statistics (Russell and others 2013). The data used for simulation in this analysis were a DWD inventory collected across 23 eastern US states in 2001 and are independent of datasets used in related studies (Table 1; Appendix A; Woodall and others 2012; Russell and others 2013).

Table 1. Summary of DWD Data Employed in This Analysis Collected by the US Forest Inventory and Analysis Program Across 23 Eastern US States in 2001, for Conifer ($n = 32$) and Hardwood Species ($n = 87$)

	Variable ¹	Mean	SD	Min	Max
Conifers					
Plot ² ($n = 275$)	DD5 ($> 5^{\circ}\text{C}$) ³	2,861.8	1,331.2	1,233.0	5,669.0
	MAT ($^{\circ}\text{C}$)	9.7	6.3	1.5	20.6
DWD piece ($n = 2,138$)	DIA _{SM} (cm)	9.9	4.6	7.6	76.2
	DIA _{LG} (cm)	17.9	8.2	7.6	101.6
	LEN (m)	7.9	5.9	0.9	73.2
Hardwoods					
Plot ² ($n = 454$)	DD5 ($> 5^{\circ}\text{C}$) ³	2,924.2	1,106.0	1,233.0	5,655.0
	MAT ($^{\circ}\text{C}$)	10.3	5.3	1.5	20.5
DWD piece ($n = 2,246$)	DIA _{SM} (cm)	10.4	5.3	7.6	76.2
	DIA _{LG} (cm)	18.4	10.0	7.6	111.8
	LEN (m)	6.0	4.8	0.9	61.0

¹ Variables: number of degree days (DD5); mean annual temperature (MAT); DWD large- (DIA_{LG}) and small-end diameter (DIA_{SM}); length (LEN).

² Climate data obtained from USFS (2012).

Monte Carlo Simulations of DWD Decay

As DWD DC transition models predict the five-year probability of remaining in the same DC or advancing to subsequent DCs, we used a DC reduction factor (DCRF; Harmon and others 2011) to estimate changes in DWD wood density through time. Recognizing that employing the DCRF alone may underestimate the true rate of mass loss (Harmon and others 1987; Zell and others 2009; Fraver and others 2013), we similarly incorporated the DCRF with a VRF to account for structural reductions in DWD volume as decay progresses. We applied a VRF of 0.800 and 0.412 for DC 4 and 5 pieces, respectively, to all species as observed by Fraver and others (2013) for three species in Minnesota. As no difference was observed in VRFs for hardwood and conifer species (Fraver and others 2002), and others have observed similar VRF values in contrasting forest types (for example, 0.439 and 0.431 for DC 5 pieces observed by Spies and others (1988) and Means and others (1985), respectively, in *Pseudotsuga menziesii* Mirb. Franco logs; and 0.82 and 0.42 for DC 4 and 5 pieces, respectively, for *Pinus* species in Minnesota [(Fraver and Palik 2012)]), we assumed the VRFs chosen would have wide applicability for species across the eastern US. Hence, estimates of DC transition and ultimately DWD biomass represented decay estimated from both density and volume reduction, thus providing a realistic assessment of mass depletion.

Predictions were accomplished by applying the DWD DC transition equations (Russell and others 2013; fixed-effects only) to the 2001 data described above using a Monte Carlo simulation framework,

as follows. First, the independent variables DD5 and LEN were used to represent climate regime of the plot location and DWD piece size, respectively, and were subsequently applied to estimate the DWD DC transition. Then, a random number was drawn from a uniform probability density function $U \sim (0,1)$ and compared with the cumulative five-year probability predicted using the DC transition model. If the random number was less than or equal to the predicted probability of remaining in the same DC, it remained in the same class. If the random number fell between the predicted probability of remaining in the same DC and the cumulative probability of remaining in the same DC or advancing one DC, it advanced one class. Similarly, if the random number fell between the predicted probability of remaining in the same DC and the cumulative probability of remaining in the same DC, advancing one DC, or advancing two DCs, it advanced two classes (for example, from DC 1 to 3), and so on (Appendix B). Equations provided predictions in five-year increments, and simulations were applied iteratively until all DWD pieces reached DC 5. For each of the 4,384 DWD pieces, a 1,000-run Monte Carlo simulation was performed up to 200 years.

The volume (*Vol*) and biomass (*Mass*) were computed for all DWD pieces at each five-year step. DWD *Vol* was estimated assuming a conic-paraboloid form (Fraver and others 2007). Initial density (*ID*; kg m^{-3}) for an individual species *m* (Harmon and others 2008), the appropriate DCRF for DWD of a given species group *n* in a DC *k* (Harmon and others 2011; Table 6), and the appropriate VRF for DC *k* was multiplied by *Vol* to estimate *Mass*:

$$Mass = ID_m * DCRF_{kt} * VRF_k * Vol, \quad (2)$$

where VRF is 1, 1, 1, 0.800, and 0.412 for DC 1, 2, 3, 4, and 5, respectively. The proportion of biomass remaining compared to initial (that is, non-decayed) biomass, denoted as $Mass_{(R)}$, was estimated at each five-year step.

The DWD data and DC transition models were used in a simulation to quantify three measures of biomass loss: DWD half-life and two measures of residence time (one liberal and one conservative estimate). We considered the number of years when the mean value of $Mass_{(R)}$ for a species group of interest reached 0.50 as the DWD half-life, denoted T_{HALF} . Determining DWD residence time was more complex, as the process represents a gradual transition and is not necessarily marked by a distinct end point (Mackensen and Bauhus 2003). We determined DWD residence time using an empirical assessment of the reduction factors involved for a DC 5 piece, as follows. After an algebraic manipulation of equation (2), one will notice that $Mass$ will reach a lower asymptote at the minimum value for its DCRF. This value is 0.29 and 0.22 for DWD pieces of DC 5 for conifer and hardwood species, respectively (Harmon and others 2011; Table 6). However, if the statistical variability presented in these DCRF values are considered (Harmon and others 2011), these same values are 0.29 ± 0.02 (mean \pm two standard errors) and 0.22 ± 0.04 , respectively. One also needs to consider the variability surrounding the VRF for a DC 5 piece, which is 0.412 ± 0.172 (mean \pm SD; Fraver and others 2013). If the statistical variability presented in both the $DCRF$ and VRF are computed, the lower asymptote values for $Mass$ are 0.119 ± 0.100 (mean \pm two standard errors) and 0.091 ± 0.078 , for conifers and hardwoods, respectively, after computing the variance of the product of two random variables.

Hereafter, we define a liberal estimate of DWD residence time (T_{LIBRES}) as the number of years in which the mean proportion of biomass remaining for all DWD pieces falls within two standard errors of the mean for a DC 5 piece. Similarly, we define a conservative estimate of DWD residence time (T_{CONRES}) as the number of years in which the mean proportion of biomass remaining for all DWD pieces falls within one standard error of the mean for a DC 5 log. From a biological perspective, these residence times might be used as a surrogate for the number of years until a DWD piece loses all structural integrity and transitions to another population (that is, another carbon pool). At this

point, the DWD piece may be incorporated into the soil organic horizon, and thus no longer meets the criteria for being inventoried as DWD (exclusive of combustion or harvest removal). In summary, three key metrics of DWD biomass loss were assessed: (1) T_{HALF} , (2) T_{LIBRES} , and (3) T_{CONRES} .

Means and standard deviations of $Mass_{(R)}$ at each five-year step were summarized from the simulation results for (1) all conifer and hardwood DWD pieces, (2) DWD pieces by DWD length (that is, short, medium, and long pieces), and (3) DWD pieces by DIA_{LG} classes (that is, small, medium, and large pieces). Based on the means estimated for $Mass_{(R)}$, inverse linear interpolation was used to approximate the number of years that T_{HALF} , T_{LIBRES} , and T_{CONRES} were attained.

Finally, we used these simulation results to calculate decay rates for the species and climate regions of interest. The annual rate of decomposition was determined using the negative exponential model (Olson 1963) to supplement the developed half-lives and residence times. Here, the annual decay rate parameter k was obtained from $Mass_t = Mass_0 \exp(-kt)$, where $Mass_t$ is DWD biomass at time t (years), and $Mass_0$ is initial biomass. Summaries were made for conifers and hardwoods grouped according to MAT of plot location and for individual species that contained 20 or more observations.

Comparisons with Published Estimates

We compared our estimates of T_{HALF} and k for several species with previous investigations that estimated similar DWD attributes using chronosequence and/or direct studies primarily through the use of density-loss curves. To validate the predictions from our simulation approach to previous empirical studies, the percentage of predictions accurate to within $\pm 50\%$ of reported estimates (Rykiel 1996) was calculated for all species and/or where DWD half-lives and k parameters were reported. The $\pm 50\%$ value was chosen because of the tremendous variability in how these studies estimate decay parameters (for example, chronosequence versus direct measurements; density-versus mass-loss curves).

Ecosystem-Level C Flux

To investigate the performance of our simulation approach and associated estimates of DWD decay rates and residence times, we forecasted ecosystem-level DWD C estimates. This was accomplished by projecting current DWD stocks inventoried from

2007 to 2011 (hereafter termed “year 2010”) by the FIA program in 29 eastern US states (Woodall and others 2013). These data were collected in a similar manner to the 2001 data, with the primary difference being that DWD were sampled along three 7.32-m transects at each of four subplots, totaling 87.8 m for a complete FIA plot (Woodall and Monleon 2008).

Current DWD C stocks were first estimated by multiplying plot-level biomass values by a C concentration constant of 0.5 (Mg/ha), followed by a simulation of DWD pieces. Carbon stocks in the DWD pool were then estimated in 5-year time steps from 2010 onward. Assuming no inputs into the DWD pools over a 100-year span, C flux was defined as the amount of C lost for each 5-year span (Mg/ha/5-year). If the estimate of T_{CONRES} (that is, the conservative DWD residence time) for a given species was exceeded by the number of simulation years, then it was assumed that the piece had completely decomposed (that is, biomass was set equal to zero). Means for C flux were summarized by forest type group following multiple simulation runs.

RESULTS

Monte Carlo Simulations of DWD Decay

For the 32 conifer species in this study’s simulation dataset, mean DIA_{LG} and LEN averaged 17.9 ± 8.2 cm and 7.9 ± 5.9 m (mean \pm SD), respectively, on 275 inventoried plots. For the 87 hardwood species, these same attributes measured on 454 plots averaged 18.4 ± 10.0 cm and 6.0 ± 4.8 m, respectively (Table 1).

Based on the proportions of biomass remaining for all DWD pieces, conifers exhibited relatively slow decay, whereas hardwoods displayed a rapid decay to their observed T_{HALF} (Figure 1A, B). Estimates of DWD half-lives and residence times were shorter as MAT increased, which was observed along with an increase in the decay rate parameter k (Table 2; Appendix C). Values for the decay rate parameter k ranged from 0.024 for conifers in the coolest climate zones ($\text{MAT} < 2.8^\circ\text{C}$) to 0.064 for hardwoods in the warmest climate zones ($\text{MAT} > 13.7^\circ\text{C}$). Estimates of T_{HALF} averaged 18 and 10 years for conifers and hardwoods, respectively. For conifers, estimates of T_{HALF} ranged from 12 years for *Pinus elliotii* Engelm. to 22 years for *Pinus banksiana* Lamb. For hardwoods, T_{HALF} ranged from 8 years for two species in the *Quercus* genus and *Liquidambar styraciflua* L. to 11 years for two species in each of the *Betula* and *Populus* genera

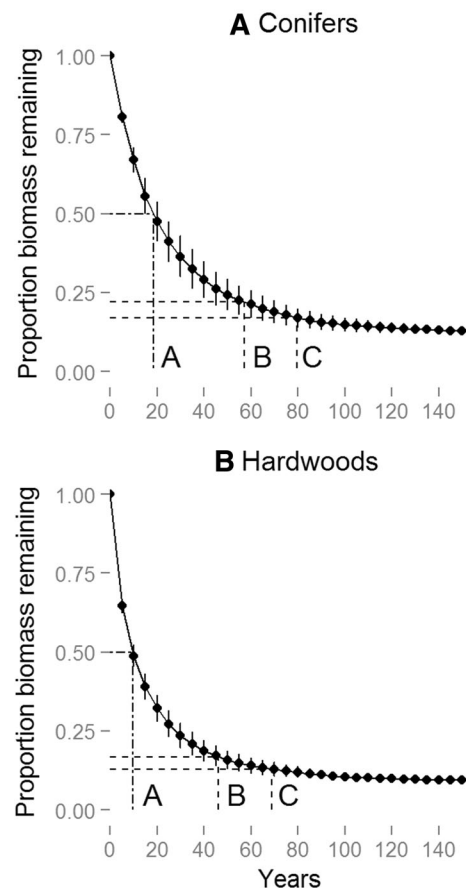


Figure 1. Proportion of original biomass remaining for DWD pieces across eastern US forests using a decay class and VRF approach. Segments within each figure denote the half-life (A), and liberal (B), and conservative (C) estimates of residence time, where B and C are defined as the number of years when the biomass curve falls to within two and one standard error(s), respectively, of the reduction factor for a decay class 5 piece. Error bars denote $\pm 1\text{SD}$.

and *Fraxinus nigra* Marsh. Similar trends were evident in decay rates: values for the decay rate parameter k ranged from 0.023 to 0.048 and from 0.043 to 0.076 for conifers and hardwoods, respectively (Table 3; Appendix D).

Estimates of T_{CONRES} averaged 80 and 69 years for conifer and hardwood species, respectively. Species with short half-lives tended to display short residence times, with some exceptions (Table 3). For example, *Prunus serotina* Ehrh. and *Quercus prinus* L. displayed estimates for $T_{\text{HALF}} \leq 10$ years, yet showed some of the longest residence times among the hardwood species examined (≥ 63 years when considering T_{CONRES}). Relative to DWD residence time (as measured by T_{CONRES}), T_{HALF} occurred at approximately the 25th and 15th percentiles for conifers and hardwoods, respectively,

Table 2. Estimates of DWD Half-Life (T_{HALF}), Liberal (T_{LIBRES}), and Conservative (T_{CONRES}) Residence Time (years), and Associated Decay Rates (k ; standard errors in parentheses) Predicting the Annual Decomposition for Conifer and Hardwood Species Groups Found in Eastern US Forests by Climate Regime

Species group	Climate regime ¹	n^2	T_{HALF}	T_{LIBRES}	T_{CONRES}	k (SE) ³
Conifers	MAT < 2.8	546	22	66	95	0.024 (9.2×10^{-5})
	$2.8 \leq \text{MAT} < 4.2$	648	21	64	93	0.024 (9.1×10^{-5})
	$4.2 \leq \text{MAT} < 7.3$	390	20	58	83	0.025 (9.3×10^{-5})
	$7.3 \leq \text{MAT} < 13.7$	122	17	45	63	0.038 (1.5×10^{-4})
	MAT ≥ 13.7	415	14	35	48	0.040 (1.1×10^{-4})
Hardwoods	MAT < 2.8	178	11	59	75	0.043 (4.9×10^{-4})
	$2.8 \leq \text{MAT} < 4.2$	345	11	56	72	0.043 (3.6×10^{-4})
	$4.2 \leq \text{MAT} < 7.3$	493	11	52	66	0.045 (2.2×10^{-4})
	$7.3 \leq \text{MAT} < 13.7$	736	9	36	55	0.052 (1.9×10^{-4})
	MAT ≥ 13.7	464	8	26	47	0.064 (2.9×10^{-4})

¹ Mean annual temperature (MAT; °C) obtained from USFS (2012); group cutoffs are the 0.2, 0.4, 0.6, and 0.8 quantiles of the data.

² Number of downed woody debris piece observations (n).

³ R^2 ranged from 0.88 to 0.98 (conifers) and from 0.67 to 0.93 (hardwoods).

indicating that hardwoods took relatively longer to reach residence time after achieving their initial 50% mass loss.

Differences in estimates of half-lives and residence times were noted when DWD pieces were analyzed across three corresponding length classes (Figure 2A–F). For example, T_{HALF} for *Abies balsamea* (L.) Mill. pieces was predicted to be 23, 24, and 27 years for short, medium, and long DWD pieces, respectively. Similar relationships were observed when pieces were analyzed across three corresponding DIA_{LG} classes.

Comparisons with Published Estimates

Eighty percent of the species- or genus-specific estimates for T_{HALF} reported here was within $\pm 50\%$ of the half-lives reported for the same species in other studies found across eastern US states (Figure 3A). Estimates were most similar for *Picea rubens* Sarg. (Foster and Lang 1982) in New Hampshire and *Pinus resinosa* Ait. in Minnesota (Fraver and others 2013), each which displayed a T_{HALF} within $\pm 5\%$. The largest percent difference in reported estimates for T_{HALF} was for *Pinus taeda* (Moblely and others 2013) and *Quercus* spp. (MacMillan 1988). Similarly, 42% of the species- or genus-specific estimates for the decay rate parameter k reported here was within $\pm 50\%$ of the values for k reported for the same species in other studies (Figure 3B).

Ecosystem-Level C Flux

Generally, hardwood-dominated and mixed forest types experienced higher initial rates of DWD C flux than conifer-dominated ecosystems (for example, the first 10 years; Figure 4A–C).

Although oak-gum-cypress forest types had the largest current DWD stocking levels (1.78 ± 3.46 Mg C/ha), DWD stocks on these plots were projected to deplete the fastest assuming no future inputs. Current DWD C stocks were forecasted to undergo 99%-depletion in 80 years for plots found in white-red-jack pine, spruce-fir, and aspen-birch forest type groups (the maxima observed) and in 53 years for loblolly-shortleaf pine forest types (the minimum observed).

DISCUSSION

DWD Decay Rates

The Monte Carlo simulation approach served as a viable tool to test the validity of the probability-based DC transition model to characterize DWD biomass dynamics through time. Methods outlined here generated estimates of DWD decay rate, half-life, and residence time that are biologically-reasonable based on comparisons to published estimates for common species found in eastern US forests. The approach presented here could be applied to any DWD inventory with repeated measurements, including national forest inventories, to produce decay rates, half-lives, and residence times for a wide range of species and forest types. As such, our approach has direct implications for tasks such as refining dead wood C flux rates in forest ecosystem models (Aber and others 1995), forecasting forest fuel loads (Rollins and others 2004), assessing habitat dynamics for dead wood-dependent organisms (Stokland and others 2012), understanding the role of forest residue in a C accounting framework, and informing forest bioenergy policies. Moisture, temperature, C concentration, forest floor contact, and

Table 3. Estimates of DWD Half-Life (T_{HALF}), Liberal (T_{LIBRES}), and Conservative (T_{CONRES}) Residence Time (years), and Associated Decay Rates (k) Predicting the Annual Decomposition for Common Conifer and Hardwood Species Found in Eastern US Forests

Species	n^1	T_{HALF}	T_{LIBRES}	T_{CONRES}	k (SE) ²
Conifers					
<i>Abies balsamea</i>	527	20	63	87	0.023 (1.0×10^{-4})
<i>Juniperus virginiana</i>	51	17	50	70	0.027 (2.3×10^{-4})
<i>Picea glauca</i>	28	20	63	86	0.025 (3.5×10^{-4})
<i>Picea mariana</i>	281	21	66	90	0.025 (1.1×10^{-4})
<i>Picea rubens</i>	75	20	61	84	0.027 (1.4×10^{-4})
<i>Pinus banksiana</i>	301	22	68	94	0.025 (1.2×10^{-4})
<i>Pinus echinata</i>	46	14	37	50	0.039 (2.9×10^{-4})
<i>Pinus elliotii</i>	36	12	30	40	0.048 (3.1×10^{-4})
<i>Pinus resinosa</i>	48	20	63	87	0.023 (3.3×10^{-4})
<i>Pinus strobus</i>	77	19	59	82	0.024 (2.9×10^{-4})
<i>Pinus taeda</i>	222	13	35	47	0.041 (1.4×10^{-4})
<i>Pinus virginiana</i>	132	15	41	57	0.037 (1.7×10^{-4})
<i>Thuja occidentalis</i>	184	20	61	83	0.026 (1.1×10^{-4})
All conifers	2,097	18	57	80	0.028 (6.4×10^{-5})
Hardwoods					
<i>Acer rubrum</i>	167	10	47	71	0.048 (4.2×10^{-4})
<i>Acer saccharinum</i>	22	9	43	61	0.058 (9.6×10^{-4})
<i>Acer saccharum</i>	113	10	50	75	0.045 (6.9×10^{-4})
<i>Betula alleghaniensis</i>	36	11	56	84	0.045 (6.5×10^{-4})
<i>Betula papyrifera</i>	219	11	56	84	0.045 (3.4×10^{-4})
<i>Fagus grandifolia</i>	44	10	48	72	0.047 (6.7×10^{-4})
<i>Fraxinus nigra</i>	30	11	54	81	0.045 (7.4×10^{-4})
<i>Liquidambar styraciflua</i>	48	8	32	44	0.063 (9.2×10^{-4})
<i>Liriodendron tulipifera</i>	21	9	40	56	0.057 (1.0×10^{-3})
<i>Populus balsamifera</i>	39	11	53	80	0.046 (8.4×10^{-4})
<i>Populus grandidentata</i>	44	10	51	77	0.046 (7.9×10^{-4})
<i>Populus tremuloides</i>	218	11	61	89	0.043 (4.6×10^{-4})
<i>Prunus serotina</i>	20	10	48	76	0.053 (1.7×10^{-3})
<i>Quercus alba</i>	84	9	38	54	0.048 (6.4×10^{-4})
<i>Quercus falcata</i>	34	8	33	45	0.057 (9.2×10^{-4})
<i>Quercus nigra</i>	34	8	29	39	0.076 (1.2×10^{-3})
<i>Quercus prinus</i>	40	9	44	63	0.049 (7.8×10^{-4})
<i>Quercus rubra</i>	124	10	49	73	0.053 (5.2×10^{-4})
<i>Quercus stellata</i>	27	9	36	50	0.060 (1.0×10^{-3})
<i>Quercus velutina</i>	94	9	40	57	0.054 (5.8×10^{-4})
<i>Sassafras albidum</i>	27	9	42	59	0.055 (9.7×10^{-4})
<i>Tilia americana</i>	21	10	47	70	0.047 (1.4×10^{-3})
<i>Ulmus americana</i>	74	9	44	64	0.050 (5.8×10^{-4})
All hardwoods	2,212	10	46	69	0.050 (1.4×10^{-4})

¹ Number of observations (n).² R^2 ranged from 0.86 to 0.99 (conifers) and from 0.68 to 0.94 (hardwoods).

composition of the decomposer fungal community all influence DWD decomposition rates (Harmon and others 1986, 2013; Stokland and others 2012), but are not necessarily measurements influencing residence time as defined here. To refine conversions of DWD volume into biomass and C, estimates of DWD stocks can likely be improved by investigating the assumption of 50% C content. For example, Weggler and others (2012) observed that default values for C

concentrations overestimated DWD C when compared to species-specific C concentrations for common species in Switzerland, and Lamblom and Savidge (2003) concluded that C content varied substantially within individual trees and across species, including many of the species analyzed in this study. Harmon and others (2013) suggest that the C content of recalcitrant DWD components (for example, lignin) varies through the decay process in

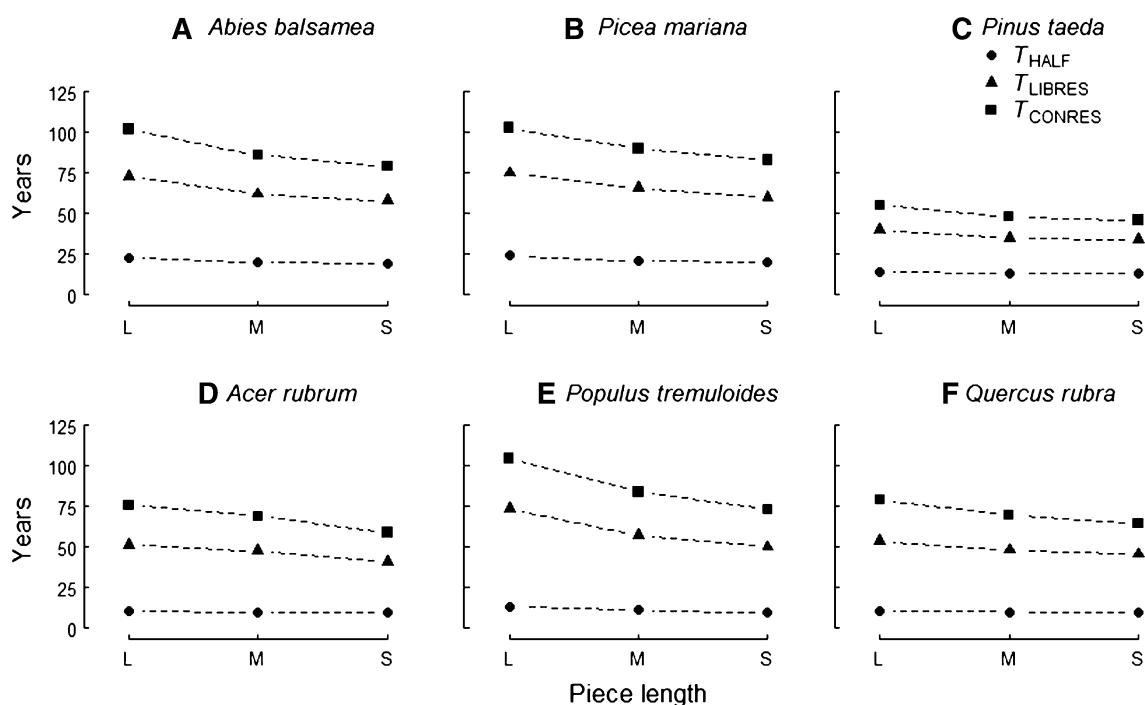


Figure 2. Estimated DWD half-life (T_{HALF}) and liberal (T_{LIBRES}) and conservative (T_{CONRES}) estimates of residence time for selected conifer and hardwood species for long- (*L*), medium- (*M*), and short- (*S*) length pieces. Length class cutoffs were taken as the 0.33 and 0.67 quantiles of the data within a species.

concert with differences in fungal colonization, thus increasing the complexity of modeling such systems. Incorporating these ecological factors and seeking improvements in volume-to-biomass-to carbon conversion factors, through detailed measurements at experimental sites, could help to refine mass/C loss estimates within a given forest type and/or at regional scales.

As suggested by Harmon and others (2011), the methodologies that rely on density-loss estimates alone should serve only as a preliminary assessment for analyses that quantify DWD decay processes. We suggest that the density- plus structural-loss approach applied here provides a more realistic assessment of mass loss through decay, as it avoids the underestimation inherent in the commonly-used density-only approach. Nevertheless, it is important to note the various assumptions involved in implementing this approach, including applying VRFs to all species across the region, using fixed C concentration and *ID* values, and accepting the idea that DC transition models can be used to infer decomposition parameters (for example, *k*). Future studies that examine the uncertainty associated with these assumptions should refine our understanding of DWD decomposition temporal dynamics.

Comparisons with Published Estimates

Despite the variability across studies and different-sized DWD pieces examined, 80% of the estimates for T_{HALF} reported here was within $\pm 50\%$ of the half-lives reported for the same species in other studies. For example, Lambert and others (1980) observed a half-life for *Abies balsamea* logs of 23 years, whereas we found a T_{HALF} of 20 years. In the US southern Appalachian region, Harmon (1982) found the following three species to decay fastest to slowest: *Quercus prinus* > *Acer rubrum* L. > *Pinus virginiana* Mill., and we similarly observed these species to decay from fastest to slowest when considering T_{HALF} . Through direct measurements, Alban and Pastor (1993) found that species that decayed fastest at two sites in Minnesota were in the order of *Populus tremuloides* Michx. > *Picea glauca* (Moench) Voss > *Pinus resinosa* > *Pinus banksiana*, which we also observed, although estimates of T_{HALF} were approximately equal for *P. glauca* and *P. resinosa*. The largest discrepancy for a hardwood species was between our estimates for *Quercus* spp. (approximately 9 years) and the value reported by MacMillan (1988; 40 years). This difference likely arises because of the relatively large diameter logs (mean of 36 cm) sampled by MacMillan (1988), when compared to ours

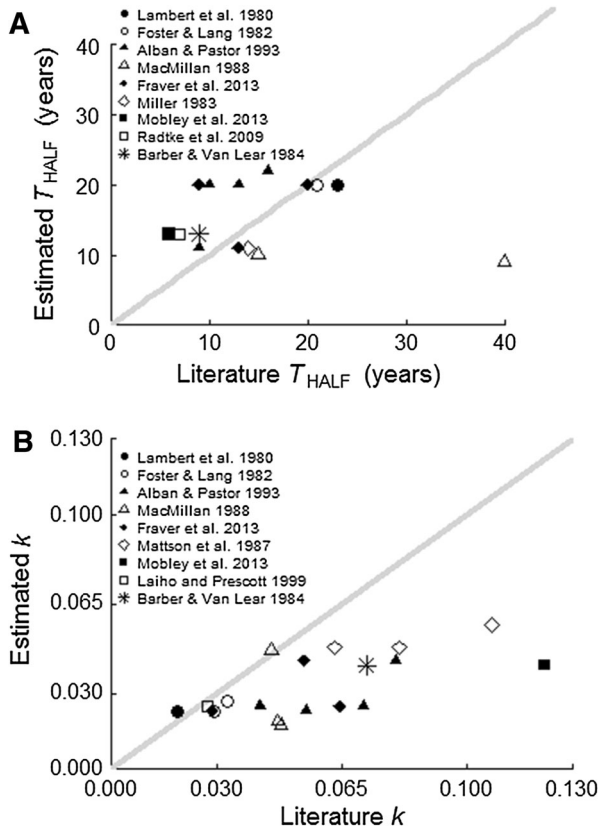


Figure 3. Comparisons of DWD half-lives (T_{HALF} ; **A**) and decay rate parameters (k ; **B**) determined in this study with published estimates for individual species in eastern US forests. For detailed discussion of individual species, see text.

(mean of 18 cm), assuming that large diameter logs decay more slowly (Harmon and others 1987). Values for the k parameters calculated here generally were less than those reported in the literature (Figure 3B), which could be related to differences among studies that solely use mass loss to estimate decomposition or from our sample containing larger-diameter DWD from the FIA inventory (>7.6 cm). We hesitate to make similar quantitative estimates of T_{LIBRES} and T_{CONRES} with other studies due to the large variability in how DWD residence time is defined across studies. For example, the number of years it takes for 95% of DWD to decompose is commonly reported (for example, Alban and Pastor 1993; Mackensen and Bauhus 2003) and could be considered a metric of DWD residence time. Common to many of these studies is the use of a density depletion curve fitted using the negative exponential model, but this may not appropriately account for lags in decomposition, water-logged pieces, and/or may contain decay-resistant wood (Harmon and others 2000; Hérault and others 2010; Fraver and others 2013). Similarly, if structural losses are not taken into account for DWD in advanced stages of decay, studies may overestimate the true biomass and C content of DWD. Despite the differences in definitions of DWD residence time and difficulties in quantifying biomass at advanced stages of decay, the T_{LIBRES} and T_{CONRES} estimates reported here provide a limited range of DWD residence times for the

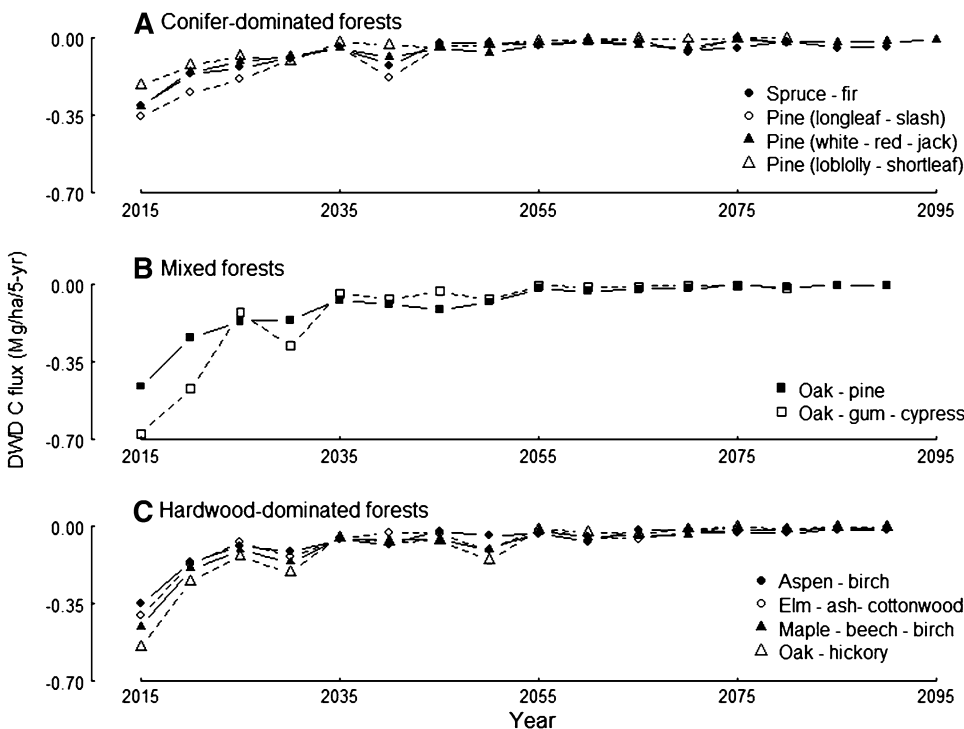


Figure 4. Projected DWD C flux for current (2007–2011) DWD C stocks in various forest type groups across the eastern US.

common species in the eastern US. Results indicate that estimates of DWD residence time could range from as rapid as 44 years for short (< 3.9 m) *Acer rubrum* logs to as extensive as 161 years for long *Abies balsamea* (> 7.6 m) and *Pinus banksiana* (> 14.0 m) logs.

Similar estimates were obtained when pieces were analyzed across three corresponding DIA_{LG} classes, indicating that measures of DWD length may be equally beneficial to estimating DWD decomposition as diameter. Although some studies have found diameter to influence the decay rate of DWD (MacKensen and others 2003; Zell and others 2009), others have not (Harmon and others 1987; Radtke and others 2009). The finding that DWD half-lives and residence times were similar whether using length or diameter is important for two primary reasons. First, not all inventories measure end diameters, especially in line-intercept sampling, however, DWD piece length is routinely collected (Woodall and others 2008). Second, DWD length reflects the degree of nonfragmentation and soundness of pieces in all stages of decay, whereas long-axis diameter measurements will overestimate volume for DWD in advanced decay stages (Fraver and others 2007).

Ecosystem-Level C Flux

Through predicting the decay dynamics of individual pieces, stand-level DWD stocks can be projected. This analysis demonstrated such an approach for projecting C flux rates into the future. The fact that oak-gum-cypress and oak-hickory forests displayed some of the highest rates of DWD C flux was not surprising given that those forest types are located at lower latitudes with warm climates and are dominated by hardwoods that display short residence times. Using the eastern US as a study area, our estimates of short residence times for hardwoods agrees with others that have found conifers to decompose more slowly than hardwoods (Weedon and others 2009). It is important to note that we did not account for future DWD inputs in these simulations; however, future work coupling our simulation approach with ecosystem simulation and dynamic global vegetation models could allow for an array of C flux projections. Given the importance of climate in DWD DC transition models, such projections could also be designed to account for the influence of future climate regimes on DWD dynamics.

Conclusions and Management Implications

The approach outlined has the ability to quantify a variety of ecosystem functions related to forest

detritus. For example, our estimates of DWD residence time can directly inform the question as to how long delineated populations of DWD are expected to reside in forest ecosystems. This could help in quantifying C stocks for future climate scenarios (for example, Aber and others 1995) and can aid in estimating net GHG emissions over time associated with burning of logging slash for energy (for example, Schlamadinger and others 1995; Sathre and Gustavsson 2011; Zanchi and others 2012). Values presented for the decay rate parameter k could be used as parameters in forest ecosystem models of various scales and resolutions, including empirical [for example, the Fire and Fuels Extension to the Forest Vegetation Simulator (Rebain and others 2010)], process-based [for example, CENTURY (Kirschbaum and Paul 2002), CenW (Kirschbaum 1999), and BIOME-BGC (White and others 2000)], and dynamic global vegetation models such as LPJ (Sitch and others 2003) to represent decomposition rates of plant material.

The rates of DWD C depletion presented here could be used as a benchmark when quantifying the influence of alternative climate scenarios on DWD decay processes. Similar estimation techniques that quantify the C implications of contrasting emissions scenarios with those that are focused on forest-derived biomass are only allowable through regional-scale analyses such as those presented here. Estimates of DWD half-lives, residence times, and decay rates can similarly serve as a baseline for assessing future forest ecosystem responses to global changes.

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REFERENCES

- Aakala T. 2010. Coarse woody debris in late-successional *Picea abies* forests in northern Europe: variability in quantities and models of decay class dynamics. *For Ecol Manage* 260:770–9.
- Aber JD, Ollinger SV, Federer CA, Reich PB, Goulden ML, Kicklighter DW, Melillo JM, Lathrop RG. 1995. Predicting the effects of climate change on water yield and forest production in the northeastern United States. *Clim Res* 5:207–22.
- Alban DH, Pastor J. 1993. Decomposition of aspen, spruce, and pine boles on two sites in Minnesota. *Can J For Res* 23:1744–9.
- Bailey RG. 1980. Description of the ecoregions of the United States. USDA Misc. Pub. 1391. Washington, DC: U.S. Department of Agriculture. 77 pp.

- Barber BL, Van Lear DH. 1984. Weight loss and nutrient dynamics in decomposing woody loblolly pine logging slash. *Soil Sci Soc Am J* 48:906–10.
- Birdsey R, Pregitzer K, Lucier A. 2006. Forest carbon management in the United States: 1600–2100. *J Environ Qual* 35:1461–9.
- 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* 39:802–13.
- Domke GM, Woodall CW, Smith JE. 2011. Accounting for density reduction and structural loss in standing dead trees: implications for forest biomass and carbon stock estimates in the United States. *Carbon Balance Manage* 6:1–11.
- Foster JR, Lang GE. 1982. Decomposition of red spruce and balsam fir boles in the White Mountains of New Hampshire. *Can J For Res* 12:617–26.
- Fraver S, Milo AM, Bradford JB, D'Amato AW, Kenefic L, Palik BJ, Woodall CW, Brissette J. 2013. Woody debris volume depletion through decay: implications for biomass and carbon accounting. *Ecosystems* 16:1262–72.
- Fraver S, Palik B. 2012. Stand and cohort structures of old-growth *Pinus resinosa*-dominated forests of northern Minnesota, USA. *J Veg Sci* 23:249–59.
- Fraver S, Ringvall A, Jonsson BG. 2007. Refining volume estimates of down woody debris. *Can J For Res* 37:627–33.
- Fraver S, Wagner RG, Day ME. 2002. Dynamics of coarse woody debris following gap harvesting in the Acadian forest of central Maine, U.S.A. *Can J For Res* 32:2094–105.
- Gove JH, Ducey MJ, Valentine HT, Williams MS. 2012. A distance limited method for sampling downed coarse woody debris. *For Ecol Manage* 282:53–62.
- Gove JH, Van Deusen PC. 2011. On fixed-area plot sampling for downed coarse woody debris. *Forestry* 84:109–17.
- Hagemann U, Moroni MT, Gleissner J, Makeschin F. 2010. Disturbance history influences downed woody debris and soil respiration. *For Ecol Manage* 260:1762–72.
- Harmon ME. 1982. Decomposition of standing dead trees in the southern Appalachian mountains. *Oecologia* 52:214–15.
- Harmon ME, Cromack K Jr, Smith BG. 1987. Coarse woody debris in mixed-conifer forests, Sequoia National Park, California. *Can J For Res* 17:1265–72.
- Harmon ME, Fasth B, Woodall CW, Sexton J. 2013. Carbon concentration of standing and downed woody detritus: effects of tree taxa, decay class, position, and tissue type. *For Ecol Manage* 291:259–67.
- Harmon ME, Ferrell WK, Franklin JF. 1990. Effects on carbon storage of conversion of old-growth forests to young forests. *Science* 247:699–702.
- Harmon ME, Franklin JF, Swanson FJ, Sollins P, Gregory SV, Lattin JD, Anderson NH, Cline SP, Aumen NG, Sedell JR, Lienkaemper GW, Cromack K, Cummins KW. 1986. Ecology of coarse woody debris in temperate ecosystems. *Adv Ecol Res* 15:133–302.
- Harmon ME, Krankina ON, Sexton J. 2000. Decomposition vectors: a new approach for estimating woody detritus decomposition dynamics. *Can J For Res* 30:76–84.
- Harmon ME, Woodall CW, Fasth B, Sexton J. 2008. Woody detritus density and density reduction factors for tree species in the United States: a synthesis. USDA For. Serv. Gen. Tech. Rep. NRS-29. 65 pp.
- Harmon ME, Woodall CW, Fasth B, Sexton J, Yatkov M. 2011. Differences between standing and downed dead tree wood density reduction factors: a comparison across decay classes and tree species. USDA For. Serv. Res. Pap. NRS-15. 40 pp.
- Hérault B, Beauchêne J, Muller F, Wagner F, Baraloto C, Blanc L, Martin J-M. 2010. Modeling decay rates of dead wood in a neotropical forest. *Oecologia* 164:243–51.
- Herrmann S, Bauhus J. 2013. Effects of moisture, temperature and decomposition stage on respiratory carbon loss from coarse woody debris (CWD) of important European tree species. *Scand J For Res* 28:346–57.
- Intergovernmental Panel on Climate Change (IPCC). 1997. Revised 1996 IPCC guidelines for national greenhouse gas inventories, volume 3—reference manual. Prepared by the National Greenhouse Gas Inventories Programme. Japan: IGES. <http://www.ipcc-nggip.iges.or.jp/public/gl/invs6.html> (last accessed 14 Jan 2013).
- Kirschbaum MUF. 1999. CenW, a forest growth model with linked carbon, energy, nutrient and water cycles. *Ecol Model* 118:17–59.
- Kirschbaum MUF, Paul KI. 2002. Modelling C and N dynamics in forest soils with a modified version of the CENTURY model. *Soil Biol Biogeochem* 34:341–54.
- Kottek M, Grieser J, Beck C, Rudolf B, Rubel F. 2006. World map of the Köppen–Geiger climate classification updated. *Meteorol Z* 15:259–63.
- Kruys N, Jonsson BG, Ståhl G. 2002. A stage-based matrix model for decay-class dynamics of woody debris. *Ecol Appl* 12:773–81.
- Laiho R, Prescott CE. 1999. The contribution of coarse woody debris to carbon, nitrogen, and phosphorus cycles in three Rocky Mountain coniferous forests. *Can J For Res* 29:1592–603.
- Laiho R, Prescott CE. 2004. Decay and nutrient dynamics of coarse woody debris in northern coniferous forests: a synthesis. *Can J For Res* 34:763–77.
- Lambert RL, Lang GE, Reiners WA. 1980. Loss of mass and chemical change in decaying boles of a subalpine balsam fir forest. *Ecology* 61:1460–73.
- Lamlom SH, Savidge RA. 2003. A reassessment of carbon content in wood: variation within and between 41 North American species. *Biomass Bioenergy* 25:381–8.
- Mackensen J, Bauhus J. 2003. Density loss and respiration rates in coarse woody debris of *Pinus radiata*, *Eucalyptus regnans* and *Eucalyptus maculata*. *Soil Biol Biogeochem* 35:177–86.
- Mackensen J, Bauhus J, Webber E. 2003. Decomposition rates of coarse woody debris—a review with particular emphasis on Australian species. *Aust J Bot* 51:27–37.
- MacMillan PC. 1988. Decomposition of coarse woody debris in an old-growth Indiana forest. *Can J For Res* 18:1353–62.
- Malmsheimer RW, Bowyer JL, Fried JS, Gee E, Izlar RL, Miner RA, Munn IA, Oneil E, Stewart WC. 2011. Managing forests because carbon matters: integrating energy, products, and land management policy. *J Forest* 109:57–50.
- Mattson KG, Swank WT, Waide JB. 1987. Decomposition of woody debris in a regenerating, clear-cut forest in the southern Appalachians. *Can J For Res* 17:712–21.
- McKinley DC, Ryan MG, Birdsey RA, Giardina CP, Harmon ME, Heath LS, Houghton RA, Jackson RB, Morrison JF, Murray BC, Pataki DE, Skog KE. 2011. A synthesis of current knowledge on forests and carbon storage in the United States. *Ecol Appl* 21:1902–24.

- Means JE, Cromack K Jr, MacMillan PC. 1985. Comparison of decomposition models using wood density of Douglas-fir logs. *Can J For Res* 15:1092–8.
- Miller WE. 1983. Decomposition rates of aspen bole and branch litter. *For Sci* 29:351–6.
- Mobley ML, Richter DD, Heine PR. 2013. Accumulation and decay of woody detritus in a humid subtropical secondary pine forest. *Can J For Res* 43:109–18.
- Næsset E. 1999. Decomposition rate constants of *Picea abies* logs in southeastern Norway. *Can J For Res* 29(3):372–81.
- Noormets A, McNulty SG, Domec J-C, Gavazzi M, Sun G, King JS. 2012. The role of harvest residue in rotation cycle carbon balance in loblolly pine plantations. Respiration partitioning approach. *Glob Change Biol* 18:3186–201.
- Olson JS. 1963. Energy storage and the balance of producers and decomposers in ecological systems. *Ecology* 44(2):322–31.
- Radtke PJ, Amateis RL, Prisley SP, Copenheaver CA, Chojnacky DC, Pittman JR, Burkhart HE. 2009. Modeling production and decay of coarse woody debris in loblolly pine plantations. *For Ecol Manage* 257:790–9.
- Rebain SA, Reinhardt ED, Crookston NL, Beukema SJ, Kurz WA, Greenough JA, Robinson DCE, Lutes DC. 2010 (Revised 18 December 2012). The Fire and Fuels Extension to the Forest Vegetation Simulator: updated model documentation. Internal Report. Fort Collins, CO: USDA Forest Service Forest Management Service Center. 398 pp.
- Rehfeldt GE. 2006. A spline model of climate for the western United States. USDA For. Serv. Gen. Tech. Rep. RMRS-165.
- Ritter T, Saborowski J. 2012. Point transect sampling of deadwood: a comparison with well-established sampling techniques for the estimation of volume and carbon storage in managed forests. *Eur J Forest Res* 131:1845–56.
- Rollins MG, Keane RE, Parsons RA. 2004. Mapping fuels and fire regimes using remote sensing, ecosystem simulation, and gradient modeling. *Ecol Appl* 14:75–95.
- Russell MB, Woodall CW, Fraver S, D'Amato AW. 2013. Estimates of coarse woody debris decay class transitions for forests across the eastern United States. *Ecol Model* 251:22–31.
- Ryan MG, Harmon ME, Birdsey RA, Giardina CP, Heath LS, Houghton RA, Jackson RB, McKinley DC, Morrison JF, Murray BC, Pataki DE, Skog KE. 2010. A synthesis of the science on forests and carbon for U.S. forests. *Ecol Soc Am* 13:1–16.
- Rykiel EJ. 1996. Testing ecological models: the meaning of validation. *Ecol Model* 90:229–44.
- Sathre R, Gustavsson L. 2011. Time-dependent climate benefits of using forest residues to substitute fossil fuels. *Biomass Bioenergy* 35:2506–16.
- Schlamadinger B, Spitzer J, Kohlmaier GH, Ludeke M. 1995. Carbon balance of bioenergy from logging residues. *Biomass Bioenergy* 8:221–34.
- Sitch S, Smith B, Prentice IC, Arneth A, Bondeau A, Cramer W, Kaplan J, Levis S, Lucht W, Sykes M, Thonicke K, Venevsky S. 2003. Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic global vegetation model. *Glob Change Biol* 9:161–85.
- Smith WB, Miles PD, Perry CH, Pugh SA. 2009. Forest resources of the United States, 2007. USDA For. Serv. Gen. Tech. Rep. WO-78. 336 pp.
- Spies TA, Franklin JF, Thomas TB. 1988. Coarse woody debris in Douglas-fir forests of western Oregon and Washington. *Ecology* 69:1689–702.
- Stokland JN, Siitonen J, Jonsson BG. 2012. Biodiversity in dead wood. Cambridge, UK: Cambridge University Press. 509 pp.
- United States Forest Service. 2012. Research on forest climate change: potential effects of global warming on forests and plant climate relationships in western North America and Mexico. Rocky Mountain Research Station, Moscow Laboratory. <http://forest.moscowfsl.wsu.edu/climate/> (last accessed 28 June 2012).
- Wang C, Bond-Lamberty B, Gower ST. 2002. Environmental controls on carbon dioxide flux from black spruce coarse woody debris. *Oecologia* 132:374–81.
- Weedon JT, Cornwell WK, Cornelissen JHC, Zanne AE, Wirth C, Coomes DA. 2009. Global meta-analysis of wood decomposition rates: a role for trait variation among tree species? *Ecol Lett* 12:45–56.
- Wegler K, Dobbertin M, Jüngling E, Kaufmann E, Thürieg E. 2012. Dead wood volume to dead wood carbon: the issue of conversion factors. *Eur J Forest Res* 131:1423–38.
- White MA, Thornton PE, Running SW, Nemani RR. 2000. Parameterization and sensitivity analysis of the BIOME-BGC terrestrial ecosystem model: net primary production controls. *Earth Interact* 4:1–85.
- Woodall CW, Monleon VJ. 2008. Sampling protocols, estimation procedures, and analytical guidelines for down woody materials indicator of the Forest Inventory and Analysis program. Forest Service Gen. Tech. Rep. NRS-22. Washington, DC: U.S. Department of Agriculture. 68 pp.
- Woodall CW, Rondeux J, Verkerk P, Ståhl G. 2009. Estimating dead wood during national inventories: a review of inventory methodologies and suggestions for harmonization. *Environ Manage* 44:624–31.
- Woodall CW, Walters BF, Oswalt SN, Domke GM, Toney C, Gray AN. 2013. Biomass and carbon attributes of downed woody materials in forests of the United States. *For Ecol Manage* 305:48–59.
- Woodall CW, Walters BF, Westfall JA. 2012. Tracking downed dead wood in forests over time: development of a piece matching algorithm for line intercept sampling. *For Ecol Manage* 277:196–204.
- Woodall CW, Westfall JA, Lutes DC, Oswalt SN. 2008. End-point diameter and total length coarse woody debris models for the United States. *For Ecol Manage* 255:3700–6.
- Woudenberg SW, Conkling BL, O'Connell BM, LaPoint EB, Turner JA, Waddell KL. 2010. The Forest Inventory and Analysis Database: database description and users manual version 4.0 for phase 2. Forest Service Gen. Tech. Rep. RMRS-245. Washington, DC: US Department of Agriculture. 339 pp.
- Zanchi G, Pena N, Bird N. 2012. Is woody bioenergy carbon neutral? A comparative assessment of emissions from consumption of woody bioenergy and fossil fuel. *GCB Bioenergy* 4:761–72.
- Zell J, Kändler G, Hanewinkel M. 2009. Predicting constant decay rates of coarse woody debris—a meta-analysis approach with a mixed model. *Ecol Model* 220:904–12.