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Carbon concentration of standing and downed woody detritus: Effects of tree taxa, decay class, position, and tissue type

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ABSTRACT

The degree to which carbon concentration (CC) of woody detritus varies by tree taxa, stage of decay, tissue type (i.e., bark versus wood), and vertical orientation was examined in samples of 60 tree species from the Northern Hemisphere. The mean CC of 257 study samples was 49.3% with a range of 43.4–56.8%. Angiosperms had a significantly lower CC than gymnosperms, with means of 47.8% and 50.6%, respectively. For whole-stems (i.e., wood and bark), the CC of gymnosperms significantly increased from 49.3% to 53.5% with decomposition, while angiosperms had no significant change. The CC of bark was higher than wood across all stages of decay by an average of ~1.0%. A similar magnitude of difference was found for standing versus downed dead wood in the later stages of decay, with the former having a higher CC than the latter. Differences between angiosperms and gymnosperms are hypothesized to be associated with initial lignin concentrations as well as subsequent decomposition by white- versus brown-rot fungal functional groups. The higher abundance of brown-rots in decomposing gymnosperms may lead to an increase in lignin concentrations, a compound that has higher CC than cellulose. As a result of these findings, uncertainties associated with forest carbon inventories may be reduced by using detrital CC specific to general taxa (angiosperms versus gymnosperms) and stage of decay rather than a single assumed value of 50% as commonly practiced.

1. Introduction

Wood detritus is an important component of forested ecosystems, serving as a habitat and food source; a store of energy, carbon (C), nutrients, and water; a fuel; and as geomorphic agent that regulates the flow of water and movement of sediments (Harmon et al., 1986). Woody detritus takes many forms: standing and downed stems and branches, stumps, and as dead coarse roots belowground (often collectively referred to as coarse woody debris, CWD). Recent concerns about greenhouse gas and wildfire management have motivated inventory of the mass of C stored in CWD at broad scales (Woodall et al., 2008). These efforts indicate that standing and down dead wood could account for an important share of forest C; for example, in the US, increase in woody detritus stores contributes ≈8% to national annual C sequestration (Heath et al., 2011). With the potential for increased frequency and severity of disturbances such as wildfire (Westerling et al., 2006), insect outbreaks (Kurz et al., 2008), and wind damage (Chambers et al., 2007), the abundance of woody detritus is likely to increase in the future. Therefore, improved C stock estimates of forest woody detritus are highly desirable.

The C stocks of woody detritus are rarely measured directly during standard forest inventories. Instead, C stocks are often estimated indirectly through use of volume estimators and associated biomass/C conversion constants (Woodall and Monleon, 2008). First, the volume of a piece of woody detritus is estimated using a general volume model (Woodall et al., 2011) or one specific to a species of dead wood (Fraver et al., 2007) with deductions where appropriate for missing tree components (e.g., tree tops; Domke et al., 2011). Second, biomass is derived from the unit of volume using a wood density constant specific to the tree taxa and decay class (i.e., stage of decay). Finally, estimates of biomass are converted to estimates of C stocks typically using just one carbon concentration (CC) constant of 50%. The accuracy of estimates of woody detritus C stocks could be improved through refining our understanding of how carbon concentration varies in woody detritus. The accuracy of woody detritus biomass estimates can be improved by incorporating wood density by decay class, species, position with respect to the soil surface, and tissue type (i.e., wood versus bark). Although more estimates of wood density would be desirable, considerable information exists on this variable, much of which was summarized by Harmon et al. (2008, 2011). In contrast, very little information exists on the CC of woody detritus, with a concentration of ≈ 50% often assumed (Woodall and Monleon, 2008). If variation in CC of live wood is any guide, dead

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wood CC is likely variable among species. Comparisons of fresh stem wood for angiosperms and gymnosperms indicate a range of 43.4–55.6% and 47.21–56.0%, respectively (Ragland et al., 1991; Lamlom and Savidge, 2003; Zhang et al., 2009). A few studies conducted on decomposing wood indicate variability commensurate with undecayed wood with CC ranging from 47.8% to 55.2% (Lambert et al., 1980; Lang and Forman, 1978; Harmon et al., 1987; Busse, 1994; Currie and Nadelhoffer, 2002). However, instead of readily apparent inter-specific differences, there appears to be an increase in CC along a continuum of increasing decomposition with a range of 47.8–51.5% for decay class 1 (i.e., little decay) versus a range of 50.8–55.2% for decay class 5 (i.e., extensive decay). The scarcity of decayed wood and bark CC data makes it difficult to assess systematic changes by decay class, the influence of piece position, or whether there are underlying differences between tree taxa.

The objective of this study was to determine the degree to which CC of woody detritus varies with tree taxa, decay class, tissue type, and position (i.e., vertical position). Based on the previous studies of undecayed and decayed wood CC cited above, we developed several hypotheses to guide our analysis. Given that angiosperms have lower live tree CC than gymnosperms, it is likely a similar pattern exists for decaying wood. These differences are caused by the lower lignin concentration of angiosperms relative to gymnosperms, a compound that has a higher CC than either cellulose or hemicellulose. As lignin generally decomposes more slowly than cellulose, CC is likely to increase as decomposition of wood proceeds. Although investigations of bark CC are lacking, we postulated that due to the higher ash content of bark compared to wood, bark CC should be comparatively lower. Standing dead wood is less likely to be in contact with mineral soil than downed wood which would lead to a lower ash content and subsequently higher CC in standing wood. We tested these hypotheses by examining the CC's of samples of dead wood and bark amassed over the last 25 years across the Northern Hemisphere by researchers associated with the Andrews Long Term Ecological Research site; these samples represent 60 tree species and five decay classes for pieces that were either standing or downed.

2. Methodology

2.1. Overview of CWD sample collection

The CWD samples used in this study were collected from 2825 individual standing dead and downed trees from a total of sixty different species (Appendix A) that had been collected in the past 25 years from a range of forest locations in the United States, Mexico, and Russia (Harmon et al., 1987; Harmon et al., 1995; Yatskov, 2000; Alvarez and Garcia, 2003; Yatskov and Krankina, 2003; Harmon et al., 2005; Harmon et al., 2008; Harmon et al., 2011; Fasth et al., 2011) (Appendix B). These samples were collected, processed, and archived in a similar manner (Harmon and Sexton, 1996). In all of the studies that contributed CWD samples to this study, individual pieces of CWD were selected to represent a full range of decay stages with at least three replicates of each of 4–5 decay classes per species. When possible, fresh undecomposed trees were also sampled. For each piece of CWD, key indicators of decay were recorded for subsequent decay classification. A chainsaw was used to remove cross sections (i.e., cookies) of wood and bark, 5–10 cm thick, along the length of each selected piece of CWD. For sound CWD, 3–4 cross-sections were removed per piece, whereas in the case of extremely decomposed or very short CWD, only two cross-sections were removed per piece. A number of attributes were measured and recorded for each cross-section: diameter; mean longitudinal thickness; circumference covered by bark; radial thickness of bark, wood, sapwood, and heartwood; and mean radial depth of decay. The total mass of the bark and wood for each cross-section was weighed on a portable electronic scale with a range of 1–6000 g (Ohaus Model CT6000). Then subsamples (50–200 g) were removed for subsequent moisture content analysis. When cross-sections had a range of decay or moisture conditions, samples were removed from the different areas in rough proportion to the area in each condition. Samples were dried at 55 °C to a constant mass and then weighed. Density (dry mass/fresh volume) and moisture content (water mass/dry mass expressed as a percent) of each cross-section was computed. An outlier analysis was performed to identify samples with excessively high or low density and moisture content. The mass and identity of these "outlier" samples were then checked and corrections made whenever possible. Four of these outliers were completely removed from the analysis. Once this quality control step was completed, samples from the multiple cross-sections were combined by tissue type (i.e., either bark or wood) to create one composite sample of each tissue type per piece of CWD. Dried and combined tissue samples were ground in a large Wiley mill to produce small chips (0.5 cm) and then ground again through a standard sized Wiley mill until particles passed through a fine screen (1 mm). These samples were then stored in sealed polycarbonate plastic vials until use.

The density of bark or wood was calculated as the total dry weight divided by the volume of each tissue within the cross-section. The overall cross-sectional density was calculated similarly, but using the total dry weight of all tissues and total volume. A weighted mean density for each log was calculated by weighting the densities from each cross-section in a piece by their cross-sectional area, so that the smaller cross-sections contributed less to the CWD piece average than the larger cross-sections. The radial thicknesses of wood and bark as well as bark cover were used to estimate the proportional volume of each tissue. The radial thickness of bark was linearly adjusted by bark cover, so that pieces completely covered with bark had the full radial thickness and those with lower amounts of bark cover had "thinner" bark.

2.2. Chemical analysis of samples

For each species, five samples representative of each decay class, position (standing or downed), and tissue type (bark, sapwood, or heartwood) were selected from the entire sample archive using a random number generator (SAS Institute). In cases where five samples were not available (i.e., more decomposed samples tend to have minimal bark and are more difficult to locate and identify to species in the field), the maximum available number of samples was used. In cases where sapwood and heartwood were separated during processing, these two tissues were pooled into a single wood sample using the average volume proportion of sapwood and heartwood for undecayed trees of the same species from the study's data set. Equal amounts of the five (or fewer when they were not available) representative samples were removed from their vials and mixed together into one pooled mixture. Our intent was to create a physical, rather than a statistical average of the species, tissues, positions, and decay classes the samples represented so that general trends could be examined rather than those within species. This pooled mixture was then split into three replicate samples of 0.5 g each to provide an indication of laboratory variability and to help spot outliers caused by the laboratory methods. In addition to the composite pool of five samples for each available study species, one softwood species (*Picea lutzii* (Little), PILU) and one hardwood species (*Quercus alba* (Lam.), QUAL) were chosen to test the range of CC variation among single logs (i.e., downed wood). Three samples each of bark and wood from single log samples for each of the two species for all available decay classes (fresh to highly decayed) were randomly selected for the determination of CC.

Whole-stem (i.e., bark and wood combined) CC for each species-position-decay class was calculated by multiplying the proportion of CWD that was either bark or wood by their CC and density (i.e., g/cm^3). This resulted in an average CC weighted by proportional volume and density. The uncertainty of whole-stem CC was calculated using a Monte Carlo approach with 10,000 replications drawn from standard errors estimated for each variable used to estimate the mean stem CC. The standard error of contributing variables was used because we were estimating the variance of the mean and not of individual mean attributes. To verify the calculated whole-stem CC, physical mixtures of bark and wood from individual samples of PILU and QUAL logs for each decay class were mixed in the same proportions as determined by the calculations of whole-stem value. These samples were analyzed for CC.

All samples were sent to the Central Analytical Lab (CAL) in the Crop and Soil Department of Oregon State University for C analysis with a Leco CNS-2000 Macro Analyzer (Leco Corporation, St. Joseph, MI). Sulfamethazine (51.8% carbon) and oatmeal (41.6% carbon) were used as standards, and run every six samples with an acceptable variation of 1.5%. To determine variability among laboratories for this analytical method, three replicated samples of *Pseudotsuga menziesii* (PSME) CWD wood representing three decay classes were sent to three laboratories (USGS Terrestrial Ecosystems Laboratory, Corvallis, OR; Department of Environmental Sciences, Western Washington University, Bellingham, WA; and USDA Forest Service Northern Research Station, Grand Rapids, MN) in addition to CAL for C analysis.

2.3. Statistical analysis

To adjust the CAL values to better reflect the mean values of all four labs, a linear regression was used to predict the mean value of all the laboratories (including CAL) from the mean values of CAL. This provided estimates of CC that are similar to those provided by multiple laboratories.

Comparisons of calculated versus physically combined whole-stem CC and individual versus pooled CC were carried out by analyses of variance (ANOVA) with the *F* test for CC.

Although CC is likely to vary among individuals within a species, our analysis focused on differences in major taxonomic levels, tissue type, decay classes, and position of the piece relative to the soil surface. The use of pooled samples would have caused a pseudoreplication problem if we had statistically analyzed for sample differences at the species level; however, since we did not, the species represented independent replicates from which to examine general trends. For the analysis at the lowest level of aggregation (see below), the mean value was used for the three replicates representing a species, position, tissue, and decay class.

Given that users of these data may make different decisions about how to compile CWD data for C inventories, we analyzed the data separately across a range of aggregation levels. When dependent variables were not part of the analysis, we used the mean of all the variables not used. For example, when analyzing the data without regard to position (standing or downed), a mean of all samples for each species, tissue, and decay was used. The first four levels examined CC for whole-stems: (1) by major tree taxa (angiosperm versus gymnosperm); (2) by decay class (from least to most decayed); (3) by position (standing and downed) and decay class; and (4) by major tree taxa, decay class, and position. The next four levels examined differences between the two tissue types, bark and wood: (1) by tissue type and decay class; (2) by tissue type, position, and decay class; (3) by tissue type, major taxa, and decay class and (4) by tissue type, position, decay class, and major taxa. The latter was the least aggregated level.

We used analysis of variance (ANOVA) to test how the dependent variable CC varied by the independent variables taxa (angiosperm/gymnosperm), decay class, tissue, and position. Depending on the level of variable aggregation multiple models were fit (Table 1). Because of the complexity inherent in this study, if a model's results showed a highly significant interaction between independent variables it was reported and the analysis was done again within one of the interaction variables to better understand the individual variables contributing to the interaction.

Examination of the residuals from the models were relatively symmetric and there was no indication of increasing variance with decreasing mean. Therefore, the ANOVA assumptions of normality and constant variance of residuals appeared to be adequately met. To determine which decay classes were significantly different in each analysis that included other main factors, Tukey's studentized range test was used.

Comparisons of CAL to all laboratories, pooled to individual samples, and physically combined to calculated whole-stem CC were carried out by fitting a two-way general linear model with fixed effects for the factors (and their interactions) and the *F* test to indicate significant differences in CC amongst the factors.

All statistical tests were performed by the MIXED and GLM procedures of SAS (SAS Institute Inc., Cary, N.C.). Statistical tests were judged to be significant if $0.05 > P > 0.01$ and highly significant if $P \leqslant 0.01$.

3. Results

3.1. Determining sampling and analysis variation

3.1.1. CAL compared to alternate labs

CAL values were found to be significantly lower than the mean of all laboratories (*P*-value 0.03) when comparing CC results for a standard material. Mean CC values for CAL were 46.5%, 51.3%, and 53.5% for decay classes 0, 3, and 5. Mean values for all laboratories combined were 48.0%, 52.8%, and 54.9%, respectively. The result of a linear regression used to adjust the CAL values and estimate an overall laboratory average for CC was:

$$\text{Adjusted C} = 0.9877 * (\text{CAL C}) + 2.0848$$

The adjusted values for carbon concentration of decay class 0 and 1 wood were similar to those found for fresh wood by others (Ragland et al., 1991; Lamlom and Savidge, 2003; Zhang et al., 2009).

Table 1
Models used in analysis of variance (ANOVA) testing of how the dependent variable carbon concentration varied by listed independent variables.

Independent variable	Model
Whole-stem	
Major taxa	$Y_{hi} = m + \alpha_h + c_k + \varepsilon_{hk}$
Decay class	$Y_{hi} = m + \alpha_h + a_i + \varepsilon_{hi}$
Decay class and position	$Y_{hjj} = m + \alpha_h + a_i + b_j + ab_{ij} + \varepsilon_{hjj}$
Decay class, position and major taxa	$Y_{hijk} = m + \alpha_h + a_i + b_j + c_k + abc_{ijk} + \varepsilon_{hijk}$
Tissue type	
Decay class	$Y_{hjl} = m + \alpha_h + a_i + d_l + ad_{il} + \varepsilon_{hil}$
Decay class and position	$Y_{hjj} = m + \alpha_h + a_i + b_j + ab_{ij} + \varepsilon_{hjj}$
Decay class and major taxa	$Y_{hjj} = m + \alpha_h + a_i + c_k + ac_{ik} + \varepsilon_{hjk}$
Decay class, position and major taxa	$Y_{hijl} = m + \alpha_h + a_i + b_j + c_k + abc_{ijk} + \varepsilon_{hijk}$

where m is the overall mean value of Y_{hijkl}, the average carbon concentration of the ith decay class of the jth position of the kth major taxa of the lth tissue in region h; α_h is the random effect of the region h where CWD was sampled, with $\alpha_{hh} \sim N(0, \sigma_b^2)$, and the assumption that α_h and $\alpha_{h'}$ are independent; a_i is the effect of the ith level of the independent variable decay class, with up to five classes; b_j is the effect of the jth level of the independent position which was either standing or downed; c_k is the effect of the kth level of the independent major taxa which was either angiosperm or gymnosperm; d_l is the effect of the lth level of the independent tissue type which was either bark or wood; $abcd_{ijkl}$ is the interaction of decay class and position and major taxa and tissue type including all interactions between combinations of a_i, b_j, c_k, and d_l; ε_{hijkl} is the random error term that adds variability to the value of Y, $\varepsilon_{hijkl} \sim N(0, \sigma^2)$ and ε_{hijkl} and $\varepsilon_{hijkl'}$ are independent.

3.1.2. Variation between pooled and individual sample carbon concentration

There was no significant difference between the pooled, composite samples and individual samples for both bark and wood in terms of CC (*P*-values 0.5002 and 0.2055 respectively). Pooled samples of QUAL wood ranged from 47.5% to 48.6% while individual samples ranged from 47.2% to 48.0%. Pooled samples of PILU wood ranged from 49.6% to 53.5% and individual samples ranged from 48.7% to 53.2%. Samples from individual pieces had a higher standard error than composite samples (0.0–1.5% compared to 0.0–0.8%, respectively), which would be expected since there is likely to be more variation among individual pieces than laboratory replicates of the composite samples.

3.1.3. Variation between hand-mixed individual whole-stem and calculated whole-stem carbon concentration

There was no significant difference between the individual samples that had their respective bark and wood physically combined for chemical analysis and calculated whole-stem CC (*P*-value 0.2247). Calculated values for PILU ranged from 49.7% to 53.2%, whereas physically combined samples ranged from 49.1% to 52.5% for decay classes 0–5. Calculated values for QUAL ranged from 47.8% to 47.1%, whereas physically combined samples ranged from 47.4% to 45.8% for decay classes 0–5.

3.2. Carbon concentration of coarse woody debris

3.2.1. Whole-stem differences between major taxa

The mean CC of all analyzed samples was 49.3%, with a range of 43.4–56.8% across 257 observations. Angiosperms had a significantly lower CC than gymnosperms, with means of 47.8% and 50.6%, respectively. Angiosperm values ranged from 43.4% to 51.9%, while gymnosperm values ranged from 45.8% to 56.8% (see Appendix C for individual species results).

3.2.2. Whole-stem differences among decay classes

The difference in whole-stem CC among decay classes was highly significant (*P*-value < 0.0001). The mean of all whole-stem CC (without regard to species or position) suggests a general trend of increasing CC with increasing decay class, although the largest changes occurred after decay classes 4 and 5 were reached. Fresh samples (decay class 0) had a mean CC of 48.1%. By the time decomposition had progressed to decay class 5 the mean CC had increased to 52.1% (Table 2).

3.2.3. Whole-stem differences among positions and decay classes

There was a significant interaction between decay class and position (*P*-value 0.0038). Differences among decay classes within a position remained highly significant (*P*-value < 0.0001), but the largest differences occurred in higher decay classes. For example, CC in downed dead material for decay classes 0–4 were similar, and significantly lower than decay class 5. In the case of standing dead, decay classes 1–3 were similar, and lower than decay class 4. When the position (downed or standing) was taken into account, there was a trend of whole-stem standing dead to be consistently higher in CC than whole-stem downed dead. Downed dead values ranged from 48.1% to 52.1% (decay classes 0–5), while standing dead values ranged from 49.0% to 52.9% (decay classes 1–4) (Table 2).

3.2.4. Whole-stem differences among major taxa, positions, and decay classes

There was a no significant interaction between taxa and position (*P*-value 0.1878). For angiosperms, neither decay class nor position was found to be statistically significant (*P*-values 0.9254 and 0.4826, respectively). Gymnosperms had highly significant differences in CC among decay classes (*P*-value < 0.0001), but no statistical significance of position (*P*-value 0.5375). For downed dead material, CC decay classes 0–3 were similar and significantly lower than decay classes 4 and 5. A similar trend was observed for standing dead with decay classes 1–3 having significantly lower CC than decay class 4. When the taxa of tree was taken into account (angiosperm or gymnosperm) for downed or standing CWD, there was a clear trend of gymnosperms having higher CC than angiosperms. The CC of downed gymnosperms increased from 49.3% to 53.5% from decay class 0 to 5, whereas angiosperms increased only slightly from 47.2 to 47.3 from decay class 1 to 5. The CC of standing dead gymnosperms increased with decay class from 49.2% to 53.7% for decay class 1–4 (Fig. 1). The CC of standing angiosperms increased from 48.4 to 49.4 for decay class 1–4 (Table 3).

3.2.5. Differences among tissue types and decay classes

The difference in CC between bark and wood was highly significant (*P*-value 0.0077), as was the difference among decay classes for wood. (*P*-value < 0.0001). Bark showed no significant difference among decay classes (*P*-value 0.0619). The CC of bark was higher than wood in by an average of ~1.0% (Fig. 2). The mean of all samples of bark and wood (without regard to tree taxa or position) showed a trend of gradually increasing CC with increasing decay class for bark, and a more delayed increase for wood occurring in decay classes 4 and 5 (Tables 4 and 5). Fresh samples (decay class 0) of bark and wood had mean CC of 48.6% and 48.3%, respectively. By the time decomposition had progressed to decay class 5, the mean CC had increased to 52.5% for bark and 51.9% for wood.

3.2.6. Differences among tissue types, positions, and decay classes

For both bark and wood there was a significant interaction between decay class and position (*P*-values 0.0039 and 0.0250, respectively) Differences in CC among decay classes were highly significant for both bark and wood (*P*-values 0.0004 and <0.0001, respectively) (Fig. 3). Bark exhibited a gradual increase in CC for downed dead, but a delayed increase until decay class 4 for standing dead material. Wood CC appeared to increase once decay class 4 was reached for downed dead, and decay class 3 for standing dead material. When the position (downed or standing) of bark and wood was taken into account there was a trend of consistently higher CC of standing dead bark and wood compared to downed dead bark and wood. Downed dead bark ranged in value from 48.6% to 52.4% (decay classes 0–5), whereas standing dead bark values ranged from 51.1% to 57.4% (decay classes 1–4). Downed dead wood values ranged between 48.3% and 51.9% (decay classes 0–5) and standing dead wood values were between 48.7% and 52.4% (decay classes 1–4) (Tables 4 and 5).

3.2.7. Differences among tissue types, decay classes, and major taxa

For both bark and wood there was a highly significant interaction between decay class and tree taxa (*P*-values 0.0082 and <0.0001, respectively) (Fig. 4). In general, gymnosperms had higher CC than angiosperms for both bark and wood. The CC of gymnosperm bark tended to remain constant among the decay classes (51.8–52.3%, decay classes 0–5) whereas it gradually increased for angiosperm bark (46.0–52.7%, decay classes 0–5) (Table 6). In contrast, the CC of gymnosperm wood gradually increased after decay class 2 (49.0–53.6% decay classes 0–5), and the CC of angiosperm wood decreased, particularly once decay class 5 was reached (47.9–46.2%, decay classes 0–5) (Table 6).

3.2.8. Differences among tissue types, decay classes, position, and major taxa

Examined at the lowest level of aggregation, there was a highly significant interaction between tissue type, decay classes, position, and major taxa (*P*-value < 0.0001). To unravel this complex set of

Table 2
Mean whole-stem carbon concentration by decay class (standard error in parenthesis) for combined positions, downed, and standing, with minimum and maximum values and count of species/position. The letters A and B denote no significance difference in carbon concentration among values with similar letters.

Decay class	Combined				Downed				Standing			
	C (%)	min	max	*n*	*C* (%)	min	max	*n*	*C* (%)	min	max	*n*
0	48.1 (0.4)A	45.9	49.7	14	48.1 (0.4)A[a]	45.9	49.7	14	48.1 (0.4)A[a]	45.9	49.7	14
1	48.7 (0.2)A	45.8	51.6	43	48.7 (0.2)A	45.8	51.6	42	49.0 (0.3)A	45.8	50.8	17
2	48.7 (0.2)A	43.4	51.4	48	48.7 (0.2)A	43.4	51.4	48	48.9 (0.3)A	46.2	50.5	14
3	49.1 (0.2)AB	45.5	53.8	54	49.0 (0.2)A	45.5	53.8	53	50.0 (0.6)A	46.8	53.1	9
4	50.2 (0.5)B	44.2	55.6	39	49.9 (0.5)A	44.2	55.4	37	52.9 (1.2)B	49.4	55.6	5
5	52.1 (0.9)C	43.8	56.8	18	52.1 (0.9)B[a]	43.8	56.8	18				
All classes combined	49.3 (0.2)	43.4	56.8	216								

[a] Values not used in position analysis.

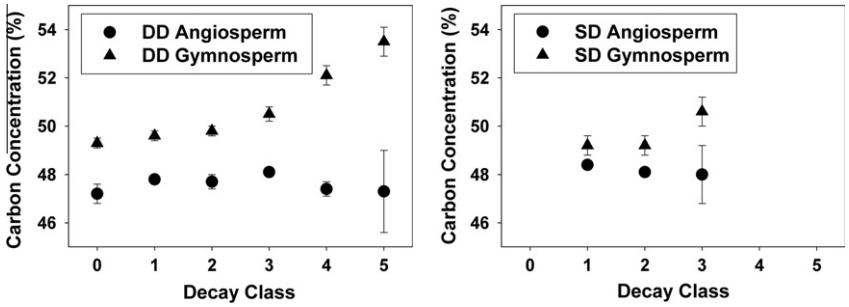

Fig. 1. Mean whole-stem carbon concentration for downed dead (DD) and standing dead (SD) by major taxa with bars representing the standard error.

Table 3
Mean whole-stem carbon concentration for downed and standing gymnosperms and angiosperms by decay class (standard error in parenthesis), with minimum and maximum values and count of species represented (*n*). The letters A, B, and C denote no significance difference in carbon concentration among values with similar letters.

Decay class	Downed				Standing			
	C (%)	min	max	*n*	*C* (%)	min	max	*n*
Gymnosperm								
0	49.3 (0.2)A[a]	48.7	49.7	6				
1	49.6 (0.2)A	48.1	51.6	21	49.2 (0.4)A	45.8	50.8	13
2	49.8 (0.2)A	47.9	51.4	23	49.2 (0.4)A	46.2	50.5	10
3	50.5 (0.3)A	48.7	53.8	21	50.6 (0.6)A	48.1	53.1	7
4	52.1 (0.4)B	47.7	55.4	20	53.7 (1.1)B	51.0	55.6	4
5	53.5 (0.6)B[a]	48.3	56.8	14				
Angiosperm								
0	47.2 (0.4)A[a]	45.9	48.6	8				
1	47.8 (0.2)A	45.8	48.8	21	48.4 (0.1)A	48.2	48.6	4
2	47.7 (0.3)A	43.4	50.4	25	48.1 (0.2)A	47.8	48.6	4
3	48.1 (0.2)A	45.5	51.3	32	48.0 (1.2)A	46.8	49.2	2
4	47.4 (0.3)A[a]	44.2	49.6	17	49.4 (0.0)A	49.4	49.4	1
5	47.3 (1.7)A[a]	43.8	52.0	4				

[a] Values not used in position analysis.

relationships we reran the analysis separately for each of the major taxa.

The CC of angiosperm bark increased with decay class for both standing and downed positions. In general, the CC value of standing dead angiosperm bark was consistently higher than downed values (49.1–58.3% and 46.0–52.7%, respectively). There was no significant interaction between decay class and position for angiosperm bark (*P*-value 0.9959); although there was a large increase in CC between decay classes 3 and 4 for standing dead bark. Angiosperm wood CC decreased slightly with decay class with values ranging from 48.2% to 47.4% for standing and 47.9–46.2% for downed (Table 7). Angiosperm wood showed no significant interaction between decay class and position, and no significant difference between standing and downed CC (*P*-value 0.8416). Decay

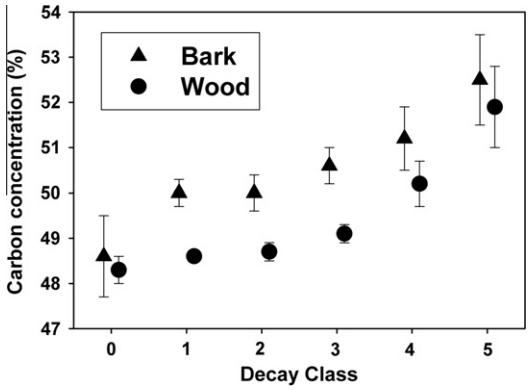

Fig. 2. Mean carbon concentration of bark and wood for all samples by decay class with bars representing the standard error.

class was not significant for angiosperm wood (*P*-value 0.9316) with downed dead decay class 5 CC lower than for decay classes 0–4 (Fig. 5).

Gymnosperm bark CC increased for both standing and downed positions, although for downed dead the increase was small. Gymnosperm bark showed no significant interaction between decay class and position (*P*-value 0.9856), with values ranging from 51.7% to 56.4% for standing and 51.8–52.3% for downed dead. Gymnosperm wood CC values increased with increasing decay class for both standing and downed positions. There was not a significant interaction between decay class and position. Decay class was significant (*P*-value < 0.0001) and position was not significant (*P*-value 0.9940) for gymnosperm wood with CC values ranging from 48.9% to 53.7% for standing and 49.0–53.6% for downed (Table 7). Both downed and standing gymnosperm wood gradually increased in CC, however, once decay class 3 was reached the increase for downed dead wood was greater than for standing dead wood (Fig. 5).

Table 4
Mean carbon concentration for combined, downed, and standing bark by decay class (standard error in parenthesis), with minimum and maximum values and count of pieces of CWD represented (*n*). The letters A, B, and C denote no significance difference in carbon concentration among values with similar letters.

Decay class	Combined bark *C* (%)				Downed bark *C* (%)				Standing bark *C* (%)			
	Mean	min	max	*n*	Mean	min	max	*n*	Mean	min	max	*n*
0	48.6 (0.9)A	41.1	53.0	14	48.6 (0.9)A[a]	41.1	53.0	14	48.6 (0.9)A[a]	41.1	53.0	14
1	50.0 (0.3)AB	44.0	54.3	59	49.5 (0.4)AB	44.0	54.3	42	51.1 (0.4)A	47.3	53.6	17
2	50.0 (0.4)AB	40.9	53.8	54	49.8 (0.5)AB	40.9	53.8	40	50.7 (0.5)A	45.5	53.5	14
3	50.6 (0.4)AB	44.7	54.3	44	50.6 (0.7)AB	44.7	54.3	36	51.5 (0.5)A	49.4	53.2	8
4	51.2 (0.7)AB	44.4	59.4	21	50.6 (0.7)AB	44.4	56.7	19	57.4 (0.9)B	47.4	59.4	2
5	52.5 (1.0)B	46.4	59.2	13	52.4 (1.0)B[a]	46.4	59.2	13				

[a] Values not used in position analysis.

Table 5
Mean carbon concentration for combined, downed, and standing wood by decay class (standard error in parenthesis), with minimum and maximum values and count of pieces of CWD represented (*n*). The letters A, B, and C denote no significance difference in carbon concentration among values with similar letters.

Decay class	Combined wood *C* (%)				Downed wood *C* (%)				Standing wood *C* (%)			
	Mean	min	max	*n*	Mean	min	max	*n*	Mean	min	max	*n*
0	48.3 (0.3)A	46.6	49.8	14	48.3 (0.3)A[a]	46.6	49.8	14	48.3 (0.3)A[a]	46.6	49.8	14
1	48.6 (0.1)A	44.2	51.7	59	48.6 (0.2)A	44.2	51.7	42	48.7 (0.3)A	45.0	51.4	17
2	48.7 (0.2)A	43.2	51.5	62	48.6 (0.2)A	43.2	51.5	48	48.8 (0.3)A	45.0	50.4	14
3	49.1 (0.2)AB	44.1	54.1	62	49.0 (0.2)AB	44.2	54.1	53	49.9 (0.7)AB	44.1	53.2	9
4	50.2 (0.5)B	42.8	56.4	42	49.8 (0.5)B	42.8	55.6	37	52.4 (1.5)B	46.2	56.4	5
5	51.9 (0.9)C	42.8	57.0	18	51.9 (0.9)C[a]	42.8	57.0	18				

[a] Values not used in position analysis.

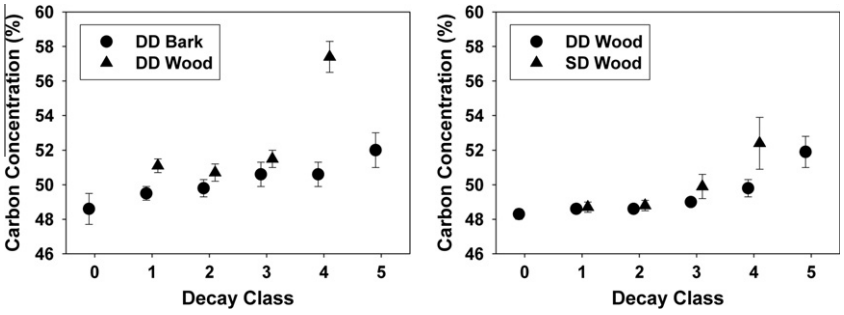

Fig. 3. Mean carbon concentration of bark and wood for downed dead (DD) and standing dead (SD) samples with bars representing the standard error.

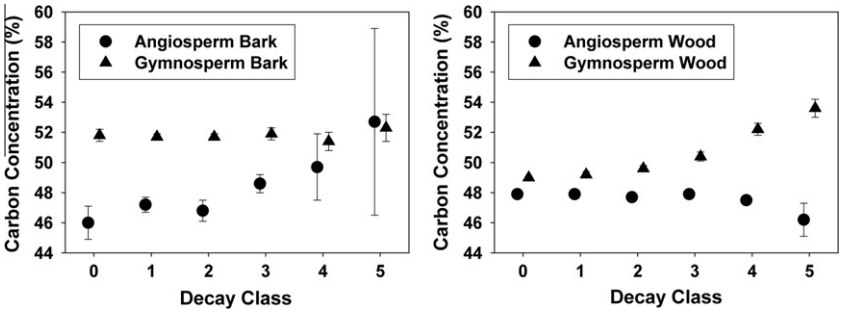

Fig. 4. Mean carbon concentration of bark and wood for angiosperm and gymnosperm samples with bars representing the standard error.

4. Discussion

The differences in CC we observed in dead wood across major taxa were quite similar to those observed by others for live wood (e.g., Ragland et al., 1991; Lamlom and Savidge, 2003; Zhang et al., 2009). Angiosperm wood tends to have lower lignin concentration and a higher ash content than gymnosperm wood (Harmon et al., 1986; Wilson et al., 1987). Higher ash content would lead to a ≈1% difference between these major taxa, if their lignin concentrations were identical. Given that lignin has an average CC of 63–72% compared to a value of ≈44% for cellulose and hemicellulose, an increase in lignin concentration leads to a greater CC. In addition, gymnosperms tend to have higher concentrations of phenol-based extractives than angiosperms; these extractives also tend to have a higher CC than cellulose.

We had hypothesized that bark would have a lower CC than wood based on its higher ash content (Wilson et al., 1987). However, we did not find this to be the case. The likely explanation is

Table 6
Mean carbon concentration for gymnosperm and angiosperm bark and wood by decay class (standard error in parenthesis), with minimum and maximum values and count of pieces of CWD represented (*n*). The letters A, B, C, and D denote no significance difference in carbon concentration among values with similar letters.

Decay class	Gymnosperm *C* (%)				Angiosperm *C* (%)			
	Mean	min	max	*n*	Mean	min	max	*n*
Bark								
0	51.8 (0.4)A	50.1	53.0	6	46.0 (1.1)A	41.1	49.7	7
1	51.7 (0.2)A	49.0	54.3	22	47.2 (0.5)A	44.0	50.8	20
2	51.7 (0.2)A	48.2	53.8	23	46.8 (0.7)A	40.9	52.4	16
3	51.9 (0.4)A	47.8	54.3	21	48.6 (0.6)A	44.7	53.3	15
4	51.4 (0.6)A	47.4	57.1	13	49.7 (2.2)A	44.4	59.4	5
5	52.3 (0.9)A	47.2	57.0	11	52.7 (6.2)A	46.4	59.2	2
Wood								
0	49.0 (0.1)A	47.8	49.8	6	47.9 (0.3)A	46.6	49.4	7
1	49.2 (0.2)A	45.0	51.7	22	47.9 (0.2)A	44.2	48.8	20
2	49.6 (0.2)A	45.0	51.5	23	47.7 (0.3)A	43.2	50.3	23
3	50.4 (0.3)A	48.0	54.1	22	47.9 (0.2)A	44.1	50.3	30
4	52.2 (0.4)B	46.0	56.4	22	47.5 (0.3)A	44.9	49.7	16
5	53.6 (0.6)B	47.2	57.0	14	46.2 (1.1)A	42.8	48.2	4

Table 7
Mean carbon concentration for down and standing angiosperm and gymnosperm bark and wood by decay class (standard error in parenthesis), with minimum and maximum values and count of samples represented (*n*). The letters A, B, C, and D denote no significance difference in carbon concentration among values with similar letters.

Decay class	Downed				Standing			
	(*C*%)	min	max	*n*	(*C*%)	min	max	*n*
Angiosperm bark								
0	46.0 (1.1)A[a]	41.1	49.7	7	46.0 (1.1)A[a]	41.1	49.7	7
1	47.3 (0.5)A	44.0	50.8	20	49.1 (0.7)A	47.3	50.5	4
2	47.0 (0.7)A	40.9	52.4	16	48.5 (0.9)A	45.5	50.1	4
3	48.7 (0.6)A	44.7	53.3	15	50.3 (0.8)A	49.4	51.3	2
4	49.5 (2.0)A[a]	44.4	56.7	5	58.3 (n/a)B[a]	58.3	58.3	1
5	52.7 (6.2)A[a]	46.4	59.2	2				
Gymnosperm bark								
0	51.8 (0.4)A[a]	50.1	53.0	6	51.8 (0.4)A[a]	50.1	53.0	6
1	51.7 (0.3)A	49.0	54.3	21	51.7 (0.3)A	49.0	53.6	13
2	51.8 (0.3)A	48.2	53.8	23	51.5 (0.4)A	48.5	53.5	10
3	51.8 (0.4)A	47.8	54.3	20	51.9 (0.5)A	50.3	53.2	6
4	51.3 (0.5)A[a]	47.7	54.3	13	56.4 (n/a)B[a]	56.4	56.4	1
5	52.3 (0.9)A[a]	47.2	57.0	11				
Angiosperm wood								
0	47.9 (0.3)A[a]	46.6	49.4	7	47.9 (0.3)A[a]	46.6	49.4	6
1	47.9 (0.2)A	44.2	48.8	20	48.2 (0.1)A	47.9	48.6	4
2	47.7 (0.3)A	43.2	50.3	23	48.1 (0.2)A	46.8	48.6	4
3	47.9 (0.2)A	44.2	50.3	30	47.7 (1.3)A	44.1	49.1	2
4	47.4 (0.3)A[a]	44.9	49.7	16	47.4 (n/a)A[a]	47.4	47.4	1
5	46.2 (1.1)A[a]	42.8	48.2	4				
Gymnosperm wood								
0	49.0 (0.1)A[a]	47.8	49.8	6	49.0 (0.1)A[a]	47.8	49.8	6
1	49.3 (0.2)A	46.5	51.7	21	48.9 (0.4)A	45.0	51.4	13
2	49.6 (0.2)A	46.6	51.5	23	49.1 (0.4)A	45.0	50.4	10
3	50.4 (0.3)A	48.2	54.1	21	50.6 (0.6)A	48.0	53.2	7
4	52.1 (0.4)B	46.0	55.6	20	53.7 (1.1)B	50.4	56.4	4
5	53.6 (0.6)B[a]	47.2	57.0	14				

[a] Values not used in position analysis.

that the concentration of phenol-based extractives in bark is generally much higher than in wood, and that this masks the effect of ash content. The high concentration of decay-resistant phenol-based extractives in outer bark is related to its function as a protective layer. Inner bark is also rich in extractives, but these compounds are likely to be carbohydrates such as sugars that are degraded more easily than the extractives found in outer bark. Inner bark is also rich in bast fibers, comprised mainly of cellulose and hemicellulose, both of which have a lower CC than lignin or the extractives found in bark. Variation in initial CC in bark may be influenced by bark thickness. It is likely that thin-barked species have a higher proportion of inner bark to outer bark than thick-barked species. This may mean that the bark of thinner barked species have proportionally more cellulose, less lignin and protective extractives than thicker barked species, leading to a lower initial bark CC.

The initial differences in CC in major tree taxa appear to persist as decomposition proceeds. In the case of gymnosperm wood, there is an increase in CC as it becomes more decayed. The inverse appears true for angiosperms. While these changes in CC are probably continuous, they were most noticeable after wood had proceeded through the decay class 3 and class 4 in gymnosperms and angiosperms, respectively. Given that the residence time of pieces remaining in a decay class increases roughly geometrically as decay class increases, the cumulative time for decomposition to change CC for decay classes 0–2 is much less than for decay classes 4 and 5. A possible cause of different temporal patterns in major tree taxa might be associated with the prevalence of white- versus brown-rot fungi. White-rots, which degrade lignin, are more common in angiosperms. This might lead to a decrease in CC as decomposition proceeds. In contrast, brown-rots, which are incapable of degrading lignin, are more prevalent in gymnosperms (Gilbertson, 1980) leading to an increase in CC as decomposition proceeds.

The causes of changes in bark CC over time are not clear. For gymnosperms there seems to be little change, whereas for angiosperms there is an increase. It is not clear why C rich compounds would be enriched with decomposition in one taxa, but not another. These trends may be related to the proportion of inner versus outer bark. If gymnosperms generally have thicker bark than angiosperms, then perhaps degradation of the inner bark has little overall effect on bark CC. In contrast, if angiosperms have thinner bark, then perhaps the proportion of inner and outer bark is similar, and degradation of cellulose and sugars in the inner bark lead to a C enrichment as decomposition proceeds. Many of the angiosperm genera sampled in this study (e.g., *Acer*, *Alnus*, *Fagus*, and *Populus*), and most tropical species, have relatively thin bark dominated by inner bark. Regardless of cause, these trends have an impact on the changes in CC for whole-stems by damping changes as decomposition proceeds. For gymnosperms, the lack of change of CC in bark dampened the CC increase observed in wood. For angiosperms, the increase in bark CC with decomposition was largely offset by the decrease in CC observed in wood. The end result for the whole-stems of angiosperms is that there little change in CC as decomposition proceeds.

The effect of piece position on CC is likely caused in large part by contact with the mineral soil. The chance of mineral soil contact is increased by several processes, the most obvious being falling to the ground, although that does not assure mineral soil contact. Many dead stems are suspended off the soil surface by either branches or other dead and downed stems, and as decomposition proceeds gradually have contact with the organic horizons of the soil. The presence of a dead stem can lead to the organic horizon thinning and this may expose the outer surface of the dead stem

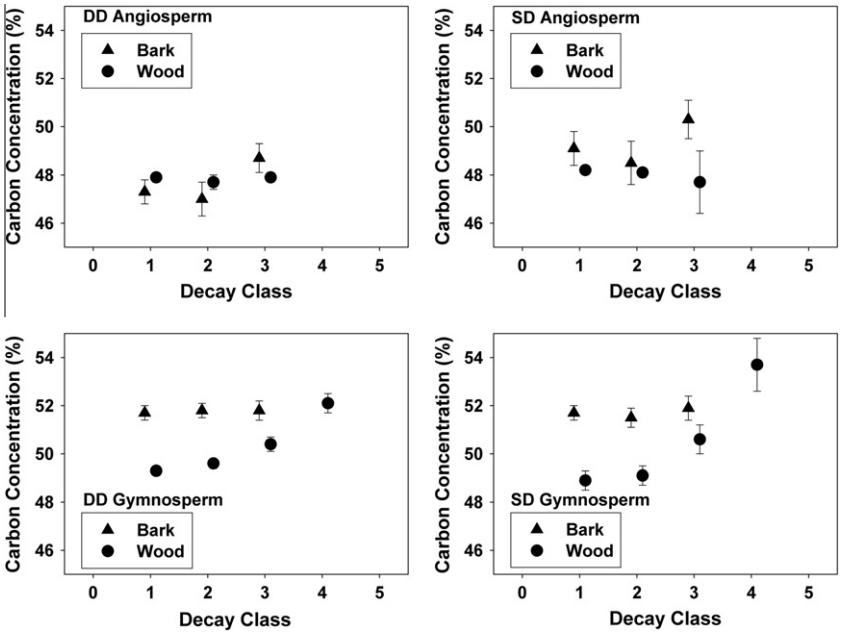

Fig. 5. Mean carbon concentration of downed and standing bark and wood by major taxa with bars representing the standard error.

to mineral soil. As bark fragments, it can also eventually lead to wood being exposed to mineral soil. However, mixing of mineral soil with wood is unlikely to be a solely passive contact process. Insects such as ants and termites actively bring soil into wood. During 25 years of data collection, we have anecdotal observations of ants and termites adding mineral soil to their nests within dead and downed wood. These insects are most common in warm temperate, subtropical, and tropical regions and could be altering the CC of wood and bark as it decomposes.

We analyzed CC data at different levels because the data we presented is likely to be applied in various ways by different users. Ideally, the CC of each species, tissue type, position, and decay class would be known when C stocks of woody detritus are being estimated; however, while this might be achieved at local scales, this is highly unlikely at broad scales. Application of CC values by individual piece species and decay classes may not be necessary. The situation can arise where the addition of estimation constants with greater uncertainty (e.g., CC of one species by decay class) can impart a false sense of increased certainty.

We adjusted our estimates of CC to represent the mean of analyses from four laboratories. These adjustments were conducted to accommodate the inherent variability in analytical equipment among individual laboratories, a variation almost as great as the range found among different decay classes (e.g., 3–4%). Replicates within laboratories were generally within 0.5%; hence considerable variability in CC is related to variation among laboratories. It is therefore important that future analyses of dead wood C use a common set of dead wood laboratory standards and that CC be adjusted to them.

Given that the purpose of our analysis was to examine trends above the level of species, we chose to physically mix samples for analysis. This allowed us to examine more combinations of species, tissues, positions, and decay classes than otherwise possible. However, because the laboratory replicates were of the same composite sample, an element of pseudoreplication (Hurlbert, 1984) entered our design. Had we analyzed CC's at the level of individual species, this might have been a substantial problem. However, species were grouped into major taxa (i.e., gymnosperms versus angiosperms) to examine general patterns of differences. Those wishing to use the data in Appendix C (see Supplemental Online data) at the species level, should be aware that these represent species level averages and not variation at the individual level which, based on our comparison of individual and pooled samples, would be about twice the value presented.

The common assumption of a CC of 50% is close to the mean of 49.3% that we estimated. If all decay classes were equally abundant in terms of mass, then assuming 50% as the CC would lead to an error of <1%. However, if dominated by either fresh wood or highly decayed wood, the estimate might be in error by as much as 3–5% if a CC of 50% is assumed. These errors would likely increase as one narrowed the focus to particular decay classes, positions, and species. At this level of detail, assuming a CC of 50% could cause estimates of C stocks to be potentially biased by 11–14% based on the range of values observed in this study. This range is likely to be far less than that caused by variation associated with sampling or density estimates. Woodall (2010) found standard errors associated with estimates of change in CWD C stores from forest inventories to be in excess of 100% for sparsely sampled forest types in regions of the US. In addition, Harmon et al. (2008) found that when density had been determined by field measurements, the measurement uncertainty associated with mass estimates was 4–7%. In contrast, when wood density had to be estimated as part of a modeling framework, the model uncertainty in mass estimates could rise to 50%, potentially far larger than associated sampling errors. Given that the maximum measurement uncertainty associated with CC was 20–33%, future research might be best focused on determining density conversion factors rather than CC. Assuming that woody detritus net accumulation may currently account for ≈8% of the US's total forest C sequestration (Heath et al., 2011), our data indicate that maximum variation of CC possible within woody detritus may only raise the uncertainty associated with current estimates of total sequestration across large scales less than 1%. In contrast, variation in wood density constants might cause estimates of total sequestration to be in error by as much 5%.

Despite the relatively minor reduction in uncertainty of total forest carbon stores and balances associated with adopting taxa-, decay class- and position-specific CC values for CWD, we

recommend the adoption of CC values at this level of aggregation (e.g., Tables 2 and 3) in future CWD C stock assessments. For one thing, many inventory systems currently aggregate data at this level and little additional work is required to use CC values at the taxa-, decay class- and position-specific level. For another, although the reduction in total C stock uncertainty gained by adopting more specific CC values may be relatively small, it does reduce one source of uncertainty, leading to more robust understanding of CWD dynamics.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2012.11.046.

References

Alvarez-Sanchez, J., Naranjo, Garcia E. (Eds.), 2003. Ecologia del Suelo en la selva tropical humeda de Mexico. Instituto de Ecologia, A.C., Instituto de Biologia y Facultad de Ciencias, UNAM, Xalapa, Mexico, 316 pp.

Busse, M.D., 1994. Downed bole-wood decomposition in lodgepole pine forests of central Oregon. Soil Sci. Soc. Am. J 58, 221–227.

Chambers, Jeffrey Q., Fisher, J.I., Zeng, H., Chapman, E.L., Baker, D.B., Hurtt, G.C., 2007. Hurricane Katrina's Carbon Footprint on U.S. Gulf Coast Forests. Science 318, 1107.

Currie, W.S., Nadelhoffer, K.J., 2002. The imprint of land-use history: patterns of carbon and nitrogen in downed woody debris at the harvard forest. Ecosystems 5, 446–460.

Domke, G.M., Woodall, C.W., Smith, J.E., 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, 14.

Fasth, B., Harmon, M.E., Sexton, J., 2011. Decomposition of fine woody debris in a deciduous forest in North Carolina. J. Torrey Bot. Soc. 138, 190–204.

Fraver, S., Ringvall, A., Jonsson, B.G., 2007. Refining volume estimates of down woody debris. Can. J. For. Res. 37, 627–633.

Gilbertson, R.L., 1980. Wood-rotting fungi of North America. Mycologia 72, 1–49.

Harmon, M.E., Woodall, C.W., Fasth, B., Sexton, J., Yatskov, M., 2011. Differences between Standing and Downed Dead Tree Wood Density Reduction Factors: A Comparison Across Decay Classes and Tree Species. Res. Pap. NRS-15. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northern Research Station, 40 pp.

Harmon, M.E., Woodall, C.W., Fasth, B., Sexton, J., 2008. Woody Detritus Density and Density Reduction Factors for Tree Species in the United States: A Synthesis. US For. Serv., Gen. Tech. Rep. 29, Northern Research Station, 65 pp.

Harmon, M.E., Fasth, B., Yatskov, M., Sexton, J., 2005. The Fate of Dead Spruce on the Kenai Peninsula: A Preliminary Report. US For. Serv. Gen. Tech. Rep. R10-TP-134. Anchorage, AK: U.S. Department of Agriculture, Forest Service State and Private Forestry, 23 pp.

Harmon, M.E., Fasth, B., Sexton, J., 2005. Bole Decomposition Rates of Seventeen Tree Species in Western U.S.A. Andrews LTER Web Report 2005. http://www.andrewsforest.oregonstate.edu/pubs/webdocs/reports/decomp/cwd_decomp_web.htm (accessed 30.06.11).

Harmon, M.E., Sexton, J., 1996. Guidelines for Measurements of Woody Detritus in Forest Ecosystems. US LTER Pub. No. 20. U.S. LTER Network Office, University of Washington, College of Forest Resources, Seattle, WA, 73 pp.

Harmon, M.E., Whigham, D.F., Sexton, J., Olmsted, I., 1995. Decomposition and mass of woody detritus in the dry tropical forests of the northeastern Yucatan Peninsula, Mexico. Biotropica 27, 305–316.

Harmon, M.E., Cromack Jr., K., Smith, B.G., 1987. Coarse woody debris in mixed-conifer forests, Sequoia National Park, California. Can. J. For. Res. 17, 1265–1272.

Harmon, M.E., Franklin, J.F., Swanson, F.J., Sollins, P., Lattin, J.D., Anderson, N.H., Gregory, S.V., Cline, S.P., Aumen, N.G., Sedell, J.R., Lienkaemper, G.W., Cromack Jr., K., Cummins, K.W., 1986. The ecology of coarse woody debris in temperate ecosystems. Recent Adv. Ecol. Res. 15, 133–302.

Heath, L.S., Smith, J., Skog, K., Nowak, D., Woodall, C.W., 2011. Managed forest carbon stock and stock-change estimates for the U.S. Greenhouse Gas Inventory, 1990–2008. J. For. 109, 167–173.

Hurlbert, S.H., 1984. Pseudoreplication and the design of ecological field experiments. Ecol. Monogr. 54, 187–211.

Kurz, W.A., Dymond, C.C., Stinson, G., Rampley, G.J., Neilson, E.T., Carroll, A.L., Ebata, T., Safranyik, L., 2008. Mountain pine beetle and forest carbon feedback to climate change. Nature 452, 987–990.

Lambert, R.L., Lang, G.E., Reiners, W.A., 1980. Loss of mass and chemical change in decaying boles of a subalpine balsam fir forest. Ecology 61, 1460–1473.

Lamlom, S.H., Savidge, R.A., 2003. A reassessment of carbon concentration in wood: variation within and between 41 North American species. Biomass Bioenergy 25, 381–388.

Lang, E.L., Forman, R.T.T., 1978. Detrital dynamics in a mature oak forest: hutcheson Memorial Forest, New Jersey. Ecology 59, 580–595.

Ragland, K.W., Aerts, D.J., Baker, A.J., 1991. Properties of wood for combustion analysis. Biores. Technol. 37, 161–168.

Westerling, A.L., Hidalgo, H.G., Cayan, D.R., Swetnam, T.W., 2006. Warming and earlier spring increase Western U.S. forest wildfire activity. Science 313, 940–943.

Wilson, P.L., Funck, J.W., Avery, R.B., 1987. Fuelwood characteristics of Northwestern conifers and hardwoods. Forest Research Lab Research Bulletin 60. Oregon State University College of Forestry, Corvallis, OR, 42 pp.

Woodall, C.W., Heath, L.S., Smith, J.E., 2008. National inventories of dead and downed forest carbon stocks in the United States: opportunities and Challenges. For. Ecol. Manage. 256, 221–228.

Woodall, C.W., Monleon, V.J., 2008. Sampling, Estimation, and Analysis Procedures for the Down Woody Materials Indicator. US For. Serv. Gen. Tech. Rep., NRS-22, Newtown Square, PA.

Woodall, C.W., Heath, L.S., Domke, G., Nichols, M., 2011. Methods and Equations for Estimating Volume, Biomass, and Carbon for Trees in the U.S. Forest Inventory, 2010. US For. Serv. Gen. Tech. Rep. NRS-GTR-88. 30 p.

Woodall, C.W., 2010. Carbon flux of down woody materials in forests of the north central United States. Int. J. For. Res. 2010, 1–9.

Yatskov, M.A., Krankina, O.N., Harmon, M.E., 2003. A chronosequence of wood decomposition in the boreal forests of Russia. Can. J. For. Res. 33, 1211–1226.

Yatskov, M.A., 2000. A Chronosequence of Wood Decomposition in the Boreal Forests of Russia. Corvallis, OR, Oregon State University, M.S. Thesis, 168 pp.

Zhang, Q., Wang, C., Wang, X., Quan, X., 2009. Carbon concentration variability of 10 Chinese temperate tree species. For. Ecol. Manag. 258, 722–727.