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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.