Progressive, idiosyncratic changes in wood hardness during decay: implications for dead wood inventory and cycling.

Authors: Brad Oberle[1,2]*, Kevin Dunham[3], Amy Milo[1], Maranda Walton[3], Darcy F. Young[1], Amy E. Zanne[1,2]

Author Affiliations:

[1]Department of Biological Sciences, George Washington University, 2023 G St. NW Washington DC 20052, USA

[2]Center for Conservation and Sustainable Development, Missouri Botanical Garden, St. Louis, MO 63166, USA

[3]Department of Biology, University of Missouri-St. Louis, St. Louis, MO 63166, USA

* Corresponding Author. brad.oberle@gmail.com; 1-314-640-0001

Department of Biological Sciences, George Washington University, 2023 G St. NW Washington DC 20052, USA

Abstract: Coarse woody debris (CWD) plays important roles in forests including carbon storage. Calculating the size of this carbon pool from survey data entails estimating the volume and density of dead wood. Density is highly correlated with other mechanical parameters in intact wood, explaining how penetrometers, which measure a mechanical parameter related to hardness, have proven useful for estimating dead wood density. However, the relationship between wood density and hardness varies with three key factors that vary in CWD: moisture content, tree species and degree of decay. We estimated how these factors influence penetrometer measurements across conditions ranging from lab standards to field conditions during a CWD survey. When measuring experimentally decayed wood under standard conditions, penetrometer distance was highly correlated with sample density and the effects of moisture content and interspecific variation were similar to those expected from analyses of intact wood. However, when we relaxed experimental controls and included samples that had decayed for different lengths of time, these relationships shifted such that penetrometer measurements no longer correlated with intact wood hardness and tended to increase relative to density and moisture content. The decoupling of mechanical properties in decaying wood is consistent with case hardening, which developed differently in different species and contributed to high variability in penetrometer measurements during the CWD survey. These results demonstrate temporal changes in decaying wood mechanical properties that have implications for surveying CWD and understanding carbon dynamics in temperate hardwood forests.

Highlights:

- Moisture, tree species and decay influence dead wood hardness and density
- Decayed wood penetrometer measurements reflect intact wood Janka hardness initially
- Hardness and density change differently during decay as case hardening develops

- Differences in the prevalence of case hardening may influence C cycling

Key Words: Penetrometer, Case hardening, Ozark forest

1. Introduction

Dead wood plays important roles in forest ecosystems. It provides habitat for wildlife and microbes, fuel for fire and contributes to nutrient cycles (Brown, 2002). In the forest carbon cycle, large pieces of dead wood, or coarse woody debris (CWD[1]), can represent a substantial pool that accounts for up to 45% of aboveground biomass and 20% of all carbon (Wilson et al., 2013). However, the absolute and relative size of the CWD pool varies in space and time (Woodall and Liknes, 2008) with important consequences for estimating forest carbon flux with global change (Woodall, 2010). Shifting climate has contributed to forest dieback events and huge influxes of carbon to the CWD pool (Adams et al., 2009). Whether this carbon feeds back into the climate system depends on how quickly it is released during the dynamics of CWD decay (Moore et al., 2013)

Because of the importance of dead wood, many forest inventories implement CWD surveys. Surveys that quantify dead wood biomass and its consequences for carbon cycling must estimate dead wood volume and density. Both values are difficult to measure accurately and efficiently in extensive surveys. One of the fastest and most widely used methods for estimating dead wood density is based on decay classification (Harmon et al., 1986). In this approach, surveyors assign pieces of CWD to ordered decay classes representing the degree of decay relative to intact wood by assessing the presence and extent of key indicators, such as bark retention or shape deformation (Pyle and Brown, 1998). A recent evaluation of a decay classification system in a Canadian forest found a high correlation with dead wood density

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[1] Abbreviations: coarse woody debris (CWD), specific gravity (SG), moisture content (MC), decay class (DC)

(Seedre et al., 2012). Using these relationships, inventory managers have estimated forest and decay class-specific biomass and C conversions (Harmon et al., 2013).

While decay classification systems can be fast and accurate, they also have several limitations. First, the number of classes and the criteria used can vary between surveys, impeding comparisons (Mäkipää and Linkosalo, 2011). Second, determining the decay class requires the judgment of a trained surveyor which can introduce subjectivity and variation depending on experience (Larjavaara and Muller-Landau, 2010). Finally, as an ordinal representation of a continuous process (decay), decay classification may lack the resolution necessary to parameterize important processes that govern CWD dynamics.

Noting these limitations, Larjavaara and Muller-Landau (2010) recommended an alternative method for quantifying dead wood density in permanent tropical forest plots based on a comparison of four methods. In addition to a decay classification system, they implemented three methods for measuring the resistance of CWD to a penetrating force. The most accurate and repeatable method in their system was based on a dynamic penetrometer: a steel stylus attached to a 1kg slide hammer. After repeatedly dropping the hammer from a fixed height, the penetration depth of the stylus was correlated to sample density and differed little among operators. Based on this result, the low cost of materials and minimal disruption of the wood during measurement, they recommended using a dynamic penetrometer to estimate dead wood density in CWD surveys for carbon accounting.

While developed as a more accurate and repeatable alternative to decay classification, the dynamic penetrometer does not directly measure density. Instead, it measures the volume of dead wood displaced by repeated application of a transverse penetrating force. This measurement principle is complementary to that of a routine materials science test. The Janka test quantifies the force necessary to embed a steel sphere 11.28 mm in diameter to half its length in another material (Green et al., 2006). The resulting value, hardness, is well known in the wood engineering literature for its effects on the performance of wood products such as flooring (Wiemann and Green, 2007). For intact wood, Janka hardness strongly correlates with density (Kretschmann, 2010). However, the relationship between hardness and density changes with several factors which are likely to vary during a CWD survey: wood moisture content, interspecific differences and degree of decay. Understanding how these factors influence penetrometer measurements could improve their accuracy and provide insights into how wood mechanical properties change during decay.

Moisture content (MC) can influence the relationship between wood hardness and density. The ratio of wood density to that of water (specific gravity, SG) tends to decrease linearly with increasing MC from oven dry (0% MC) to the fiber saturation point (typically near 28% MC). Janka hardness, in contrast, decreases as a power function of increasing MC up to an inflection point between 20% and 28% MC (Wiemann and Green, 2007). In natural settings, dead wood MC can vary across this range depending on air humidity, direct sun exposure, ground contact and saprobe activity (Glass and Zelinka, 2010). Consequently, changes in dead wood MC may change hardness and therefore penetrometer measurements independent of changes in density.

Second, interspecific differences in wood density explain most but not all variation in hardness. Hardness also depends on other features of wood chemistry and anatomy, from cellulose microfibril angle to void space distribution, that vary greatly among species (Tze et al., 2007; Winandy and Rowell, 2005; Zhang, 1997). For example, angiosperm wood tends to be denser and therefore harder than conifer wood (hence the common distinction of hardwood versus softwood). However, the empirical relationships between SG and hardness differs between these two groups (Wiemann and Green, 2007), reflecting division-level differences in wood construction. Taxonomic differences in wood construction may persist as wood decays through interactions with specialized saprobes contributing variation to the relationship between hardness and density depending on species composition.

Finally, mechanical properties can change idiosyncratically as wood decays. During the earliest stages of decay, wood may lose mechanical strength more quickly than density (Curling et al., 2002). Wooden stakes deployed in northern forests lost surface hardness after only three months even though mass loss was barely detectable (Jurgensen et al., 2006). While hardness may initially decline more quickly than density, CWD hardness can later increase. Under some conditions, dead wood develops an extremely hard, decay-resistant outer shell (Spaulding and Hansbrough, 1944). This phenomenon, known as case hardening, has been variously attributed to physical changes that result from exposure to sunlight and extreme temperature (Harmon et al., 1995), chemical properties of species with durable wood (Pyle and Brown, 1998), and the legacy effect of decay while suspended (Spaulding and Hansbrough, 1944). Whatever the cause, case hardened wood decays slowly and can be retained in forests much longer than other CWD (Harmon et al., 1986).

The impacts of moisture and species differences on the relationship between density and hardness as wood decays have important implications for estimating CWD biomass and understanding its dynamics. We examine how wood mechanical properties change during decay in a central North American hardwood forest by conducting penetrometer measurements across a range of settings. First, we conducted a lab experiment mimicking the standard conditions of the Janka test, but using experimentally decayed wood for samples and the penetrometer as the testing device. Then we conducted a field experiment during which we relaxed standards to more closely resemble the conditions likely to occur in the field. Finally, we conducted a field survey on naturally recruited and decayed wood.

Our tests shared two complementary goals: first to analyze how penetrometer measurements vary with factors known to influence hardness of intact wood and second to evaluate how well penetrometer measurements perform as indices of dead wood density. With respect to the first goal, we expected that variation in penetrometer depth depends on four predictors: (1) SG, (2) MC, (3) species and (4) degree of decay. Due to the complementarity of measurement principles (penetrometer measurement equals distance given fixed force, while hardness equals force given fixed distance), we expected that effects of the first three predictors are similar in magnitude but opposite in sign to their known effects on Janka hardness of intact wood. Specifically, we expected penetrometer depth to decrease in samples that are denser, drier and derived from species with harder intact wood. Furthermore, we expected the relationships among these factors to change through time as wood decays. With respect to the second goal, we expected that penetrometer depth explains more variation in dead wood density than other factors across a range of measurement conditions.

2. Material and methods

2.1. Study site

We investigated how mechanical properties change during wood decay at the Tyson Research Center near St. Louis Missouri, USA. This site is located on the northern border of the Ozark Highlands ecoregion of east central North America. Approximately 85% of the site consists of forests on steep limestone ridges that are dominated by oak (*Quercus*) and hickory

(*Carya*) species. Climate at the site is typical of a continental temperate deciduous forest, with average annual temperature and precipitation of approximately 14°C and 103 cm respectively.

2.2. Penetrometer construction

We constructed dynamic penetrometers at the University of Missouri-St. Louis machine shop following the specifications provided by Larjavaara & Muller-Landau (2010). During our initial trials, the grade 304 stainless steel stylus blunted quickly. To improve performance, we substituted a stylus of the same dimension made from hardened tool-grade steel. The replacement stylus maintained its shape during trials and was used for all measurements.

2.3. Experimental wood decay

We measured decayed wood from a common garden decay experiment that we began in 2009 and expanded in 2011. The experiment included wood from species that represent dominant taxa in Ozark forests and span a range of wood traits, including Janka hardness and SG. To generate starting material we felled living stems 5-9 cm in diameter and cut experimental replicates approximately 22 cm long. All samples decayed under field conditions with litter removed once per year in spring. We harvested material for penetrometer testing in 2010 and 2012.

2.4. Lab experiment

We measured how mechanical properties change in decayed wood by replicating key features of the Janka test in the lab using the penetrometer as the testing device.

2.4.1. Sample preparation

To test for the effect of species identity on penetrometer depth, we focused on eight species with the greatest variation in Janka hardness of intact wood (Table 1). The material from these species was deployed in 2009, harvested in 2010, dried at 105°C and stored in paper bags at room temperature until measurement in 2012. For measurement, we cut cross sections of

Table 1: Species measured, initial Janka Hardness[a] and samples sizes for both experiments and survey

		Hardness (N)		Lab Test	Field Test			Field Survey (DC)			
Species	symbol	12%MC	28%MC	n	1 year	3 years	1	2	3	4	5
Acer rubrum	*a*	.	3100	.	.	8	1	2	4	0	0
Aesculus glabra	*b*	1557	1290	16	.	8	0	0	0	0	0
Ailanthus altissima	.	.	3118	.	.	.	0	0	1	2	0
Amerlanchier arborea	*c*	8006	5515	16	.	8	2	1	7	3	1
Asimina triloba	*d*	.	.	.	.	8	0	0	0	0	0
Carya glabra	.	.	6800	.	.	.	1	5	4	2	1
Carya ovata	.	.	6500	.	.	.	0	2	0	0	0
Carya texana	.	.	6800	.	.	.	0	1	0	0	0
Carya tomentosa	*e*	8800	6400	19	.	8	0	0	1	1	0
Celtis occidentalis	*f*	.	3100	.	8	8	0	0	2	0	0
Cornus florida	*g*	9563	6272	16	.	8	2	4	94	19	1
Diospyros virginiana	*h*	10230	5693	16	.	8	0	0	1	1	0
Fraxinus americana	*i*	.	4300	.	8	.	0	6	5	2	1
Gleditsia triacanthos	*j*	7000	6200	16	.	.	0	0	0	0	0
Juglans nigra	*k*	.	4000	.	8	.	1	1	3	1	0
Juniperus virginiana	*l*	4000	2900	16	8	8	0	0	0	0	0
Morus rubra	.	.	7470	.	.	.	0	0	0	1	0
Lonicera mackii	*m*	.	.	.	8	.	0	0	0	0	0
Ostrya virginiana	.	.	5204	.	.	.	0	2	4	0	0
Pinus echinata	*n*	.	2000	.	8	.	0	0	0	0	0
Pinus strobus	*o*	.	1300	.	.	8	0	0	0	0	0
Platanus occidentalis	*p*	.	2700	.	.	8	0	0	0	0	0
Prunus americana	.	.	.	.	.	.	1	0	0	1	0
Prunus serotina	*q*	.	2900	.	.	8	0	0	0	0	0
Quercus alba	*r*	.	4700	.	8	.	0	19	15	15	1
Quercus marilandica	.	.	.	.	.	.	0	1	1	1	1
Quercus rubra	.	.	4400	.	.	.	1	7	38	25	0
Quercus stellata	.	.	.	.	.	.	0	0	1	1	0
Quercus velutina	*s*	5400	4700	16	8	8	1	11	9	2	2
Sassafras albidum	.	.	2800	.	.	.	0	6	12	4	1
Ulmus americana	.	.	2800	.	.	.	0	0	6	1	0
Ulmus rubrum	*t*	.	2900	.	.	8	0	0	27	0	0
Vitus vulpina	*u*	.	.	.	.	8	0	0	0	0	0

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[a] Janka Hardness values (N) as reported in (Kretschmann, 2010)

wood approximately 2 cm in length using an electric chop saw. After removing any remaining bark, we re-dried decayed wood disks at 105°C until their mass changed less than 1% on subsequent days. We then measured dry mass on a digital balance (Mettler Toledo PB3002-S/FACT) and immediately thereafter estimated volume using the water displacement method (Hughes, 2005). We calculated sample dry SG as the ratio of dry mass to dry displacement volume.

2.4.2. Moisture content

Janka hardness tests are typically conducted with wood at both 28% and 12% MC (Wiemann and Green, 2007). We first adjusted sample MC to near 28% by calculating the mass of water required and adding that mass to each sample in a sealed plastic bag which we left at room temperature for 5 days. At the end of this equilibration, we reweighed samples to check that they had attained the target MC within 1% and prepared them for initial penetrometer measurement (see 2.4.3). Following penetrometer measurement at high MC, we dried samples at 70°C until their mass corresponded to 14% MC and repeated the penetrometer trial on the same specimen.

2.4.3. Measurement procedure.

To stabilize our decayed wood subsamples, we secured specimens using two devices. First, we stabilized against radial failures by enclosing the circumference of the subsample using a steel hose clamp such that it contacted most of the circumference but did not compress the sample. Second, we stabilized samples against longitudinal failure by securing the transverse faces using a drill press vice using the minimal force necessary to contact most of both surfaces. We selected a trial location on the tangential surface while avoiding defects due to surface checking, knots and insect damage. We oriented the specimen in the vice such that the penetrometer would proceed vertically through a pre-drilled hole in the clamp towards the pith.

The trial followed the procedure proscribed by Larjavaara & Muller-Landau (2010). We dropped the 1kg slide hammer 20 times from 25 cm. Then, using digital calipers, we measured the cumulative distance traveled from the tip of stylus to the surface of the sample. During initial trials, some samples developed large cracks before the 20th strike. In cases where a radial crack extended to the pith, we interrupted the trial and recorded the distance traveled and the number of strikes to failure. For the measurement at low MC we repeated the procedure at a point on the opposite side of the same specimen.

2.5. Field experiment

To evaluate how results from the laboratory experiment generalized to conditions more representative of a field survey, we conducted a second experiment on samples from a broader range of species that had decayed for different lengths of time.

2.5.1. Sample preparation

In total, we measured samples from 21 species, including material that had decayed for one year (8 species), three years (16 species) and both one and three years (3 species) (Table 1). In contrast to the laboratory experiment, during which we measured bark-free, rehydrated and subsampled material, for the second experiment we measured the intact experimental replicate at field MC.

2.5.2. Measurement procedure

To stabilize samples during measurement, we wrapped their circumference in approximately two layers of food grade polyethylene film. After tightening the drill press vice against the tangential surfaces, we identified a measurement location near the midpoint of the sample while avoiding locations with major surface deformities. We cut a hole in the plastic film for the stylus and used the same penetrometer measurement procedure of stopping after 20 hits, radial failure or the stylus completely traversing the sample. In cases where the stylus traversed the sample, we recorded the penetrometer distance as the diameter of the sample at the measurement site and recorded the number of strikes up to and including the strike at which the tip of the stylus emerged from the opposite surface.

2.5.3. Sample specific gravity and moisture content

Immediately after the penetrometer measurement, we removed the plastic film and weighed the specimen using a digital balance. We then measured the volume of the sample using the water displacement method. After volume measurement, we dried samples at 105°C for three days and recorded their mass. We calculated sample wet SG as the ratio of dry mass to wet volume and sample MC as the difference between sample wet mass (pre-immersion) and dry mass divided by wet mass.

2.6. Field survey

To evaluate how penetrometers perform with naturally decayed wood, we used the device during a CWD survey of a 4 ha forest dynamics plot at the Tyson Research Center in July 2012. Our survey had two goals: first, to evaluate how species identity, degree of decay and stem diameter influence penetrometer measurements and second, to quantify the correspondence between penetrometer measurements and decay classification as alternative minimally destructive density indices.

2.6.1. Sample inclusion

Within the 4 ha plot, we measured dead wood that met either of two criteria: (1) pieces at least 7 cm in diameter for 1 m or (2) pieces with ID tags regardless of size. We cross referenced ID numbers against survey data to identify species for all tagged samples. We also measured the horizontal and vertical diameters of the stem at the widest point that was representative of its overall shape (i.e. above root flare or splintering).

2.6.2. Decay classification

We assigned every specimen to one of five ordered decay classes using standard criteria for hardwood dominated temperate forests (Pyle and Brown, 1998). Decay Class 1 (DC1) included the least decayed specimens that still retained fine branches or leaves. DC2 included more decayed specimens that had lost fine branches but still retained most of their bark. DC3 included specimens that had lost most of their bark but had mostly intact exposed wood. DC4 included specimens with major surface deformities but that otherwise supported their own weight. DC5 specimens were the most decayed and had lost structural integrity. Some specimens exhibited surface conditions representative of different decay classes. If different conditions characterized a contiguous portion of the specimen longer than 1m, we recorded the position and length of each decay class.

2.6.3. Measurement procedure

On each sample, after identifying the majority DC, we used the penetrometer at the most basal location that met diagnostic criteria and was at least 50 cm from the base of the stem. We oriented the penetrometer vertically and conducted the measurement without removing bark or affixing any stabilization device. We recorded the distance traveled through wood after 20 hits, structural failure or completely traversing the specimen. For tagged specimens with different decay classes, we repeated measurements in portions of the log representative of each class. In certain cases, we could not generate repeatable or comparable measurements. The smallest specimens moved during measurement and the most decayed tended to compress under the weight of the device before the first hit. We censored these measurements prior to analysis.

2.7. Statistical analyses

Penetrometer measurement generates two data points: distance embedded and number of strikes. In most cases, the number of strikes did not vary such that total distance indicated the amount of material displaced under a consistent application of force. In the remaining cases, where samples failed or were completely traversed, the applied force varied as did the condition of the material during the final strike. For an alternative measurement standardized by the amount of force applied, we calculated the logarithm of the ratio of distance traveled to number of strikes. We conducted all analyses on both indices of penetrometer measurements. Because the most adequate models for both responses (see 2.7.1) generally included the same predictors, we focused on total penetrometer depth and noted cases where these two indices support different inferences.

2.7.1. Penetrometer Depth as response

All four predictors that may influence hardness—SG, MC, species and decay—could interact. To explore this interaction space, we compared a series of linear models of different complexity, from saturated models including all possible interactions to simple bivariate models. In some saturated models, the number of parameters approached the number of data points, so we assessed model adequacy using the bias-corrected Akaike Information Criterion (AICc). To select the most adequate model for each dataset, we calculated the difference in AICc between each candidate model and the model with the lowest score (ΔAICc). We considered the model with ΔAICc of zero as the most adequate, those with ΔAICc < 2 as similar and those with ΔAICc > 5 as poorly fit to the data. We estimated linear models and checked diagnostic plots for violations of regression assumptions with the lm function in package stats using R v. 3.0.2. We tested specific hypotheses for the effects of each predictor in the context of the most adequate model. Species effects were coded using categorical predictors that represent unmeasured species-level effects (such as those due to wood construction or chemistry) that are independent of other predictors. Because decay class is an ordinal predictor, we coded its effect in the field survey as either continuous or categorical in separate models. If a predictor did not occur in the most adequate model, we considered its effect non-significant. If that predictor did occur, we tested marginal significance over all interactions using ANOVA.

Based on the most adequate models from the test at controlled conditions, we compared the estimated effects of SG and MC on penetrometer measurements of decayed wood to those expected from published Forest Products Lab (FPL) analyses of Janka hardness. Because penetrometer distance and Janka hardness are measured in different units (mm and N respectively) and because our analysis assumed a different functional relationships with predictor (linear versus power function), we calculated proportional effects at the mean value of each predictor. For the effects of SG, we calculated the expected proportional change in penetrometer measurement with a 0.01 increase in SG from its average value both using our estimated coefficients and the FPL formula for the change in Janka hardness (Wiemann and Green, 2007). We compared proportional effects for samples at high and low MC to the published formulae for wet and dry temperate hardwoods respectively. To compare the effects of changing MC, we calculated the percentage change in penetrometer distance between measurements at 14% and 27% to the percentage change in Janka hardness for dry versus wet samples of those species.

Across every dataset, we expected that species-level differences in penetrometer depth would correlate with the hardness of intact wood. To model these effects, for measurements of *i* samples from *j* species with known hardness, this expectation can be represented using linked hierarchical models as follows:

$$\text{Measurement}_i \sim \text{Normal}\ (\alpha_{measurment} + W_i * \theta + \text{Species}_i * \beta_j\ , \sigma_{measurement}) \qquad \text{Eq. 1}$$

$$\beta_j \sim \text{Normal}\ (\alpha_{species} + \text{Janka}_j * \beta_{janka}, \sigma_{species}) \qquad \text{Eq. 2}$$

Where Eq. 1. represents the measurement model as a typical multiple regression, such that measurements are normally distributed with a mean that is a linear function of an intercept, α_{depth}, a vector of covariate effects, θ, a matrix of covariate predictors, $W_{i,}$ a vector of species-level effects, β_j, and a standard deviation of errors, $\sigma_{measurement}$. Eq. 2 represents a second order model for variation in species-level effects (β_j) where $\alpha_{species}$ and $\sigma_{species}$ represent a species-level intercept and error terms and β_{janka} is a hyperparameter that quantifies the effect of species initial wood hardness on interspecific differences in measurement depth controlling for the effects of covariates.

A rudimentary approach to fit this model would involve two sequential regressions: the first to estimate species level effects (β_j) and the second to estimate the effect of variation in initial hardness (β_{janka}). However, this sequential approach ignores measurement error (σ_{depth}) when estimating the effect of initial hardness, inflating confidence in parameter estimates. A more accurate alternative involves estimating parameters in both models simultaneously. Doing so is straightforward in a Bayesian context where the full posterior distribution for parameters in Eq. 1, can depend on parameters in Eq. 2. We estimated the effect of initial interspecific differences in Janka hardness by fitting Eq. 1-2 in a Bayesian framework using OpenBUGS (Lunn et al., 2009). OpenBUGS estimates the posterior distribution of parameters using MCMC sampling. Our analyses used minimally informative priors and sampled the posterior distribution with three independent MCMC chains each run for 10,000 iterations. We used the Brooks Gelman Rubin statistic to diagnose convergence, discarded the first 100 samples as burn-in and retained every fifth sample to reduce within-chain autocorrelation. We then generated summary statistics (mean and 95% CI) based on at least 5000 independent samples from the posterior distribution. We concluded that species hardness significantly influenced penetrometer depth in any case where the 95% CI for β_{janka} in Eq. 2 excluded 0.

2.7.2. Penetrometer Depth as predictor

To assess how much variation in CWD condition can be explained by penetrometer depth and other predictors, we calculated coefficient of determination (R^2) for regression models in each dataset. For the first two experiments, we used SG as our measure of CWD condition and we calculated the R^2 for a series of models including each of the predictors for the best fit model from above. For the CWD survey, we used decay class as a continuous response and calculated coefficients of determination for models over the whole dataset and the subset consisting of samples identified to species.

3. Results

3.1. Specific Gravity

Penetrometers traveled further into less dense decayed wood. The most adequate models for both field and lab experiments included a main effect of SG on penetrometer distance (Supplementary tables 1-3). In the lab experiment, an increase in sample SG of 0.01 decreased penetrometer distance by 0.74 mm (±0.04 S.E.) in both dry and wet specimens (Fig. 1). This decrease corresponds to a 3.9% drop in penetrometer distance at the average SG of dry decayed specimens compared to an expected 3.7% increase in Janka hardness of dry intact temperate hardwoods. For wet specimens, this corresponds to a 2.9% decrease in distance compared to an expected increase of 3.8% in the Janka hardness of wet intact temperate hardwoods. While increasing SG decreased penetrometer distance in both experiments, the slope of the bivariate relationships differed depending on the measurement conditions, with a steeper decrease for samples measured during the field experiment than the lab experiment (Fig. 2. (a), ANOVA: Distance x experiment = -36.6, *F* = 30.13, $p<0.001$).

3.2. Moisture content

Penetrometers traveled further through more moist decayed wood. Based on our model adequacy criteria, MC had an additive main effect in both experiments (Supplementary tables 1-3). For paired measurements at high and low MC, the total embedded distance was 34.6% (6.57

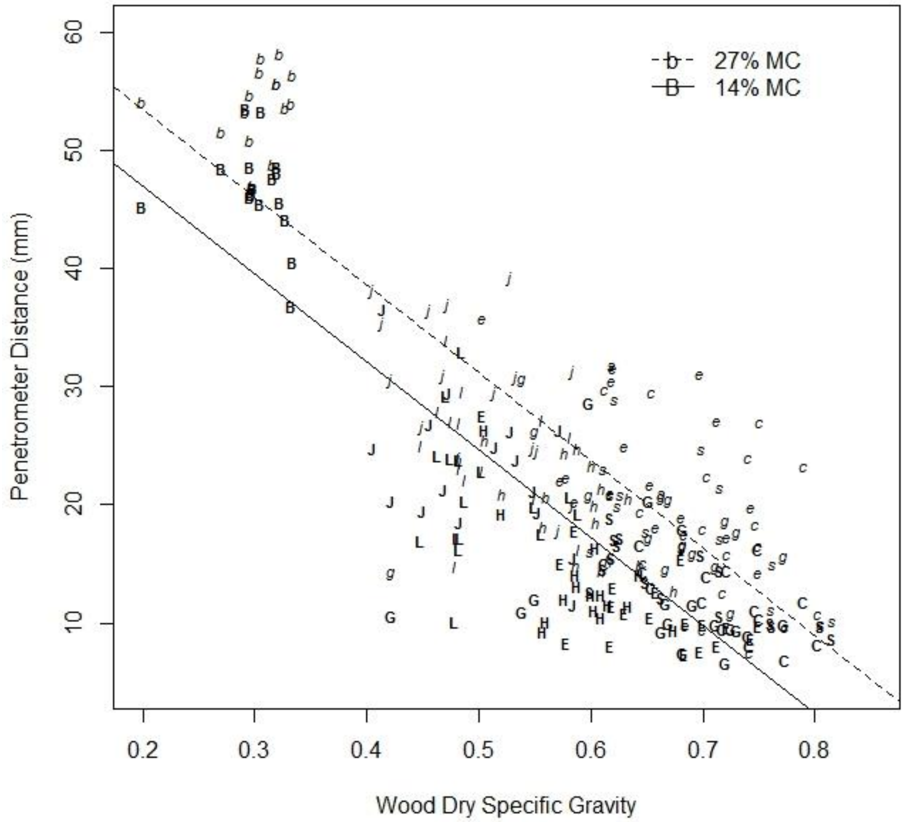


Fig. 1. Relationship between penetrometer distance and experimentally decayed wood dry specific gravity at two experimentally controlled moisture contents (MC). Letters reflect species as in Table 1.

mm) greater when measuring samples at 27% versus 14% MC (Fig. 1, paired *t*-test, Distance: t = 12.89, p<0.001). In comparison, increasing intact wood MC from 12% to 28% MC for these same eight species decreased average Janka hardness 37.7% (1948 N). In the field experiment, MC varied from 15.5% to 82.2% and was correlated with both penetration distance and SG (Fig. 2). The marginal relationship between penetrometer depth and MC showed no evidence for curvature across the observed range of MC (Fig. 2. (b)). Furthermore, MC and SG were correlated across samples in their condition at harvested from the experiment (Fig. 2. (c)).

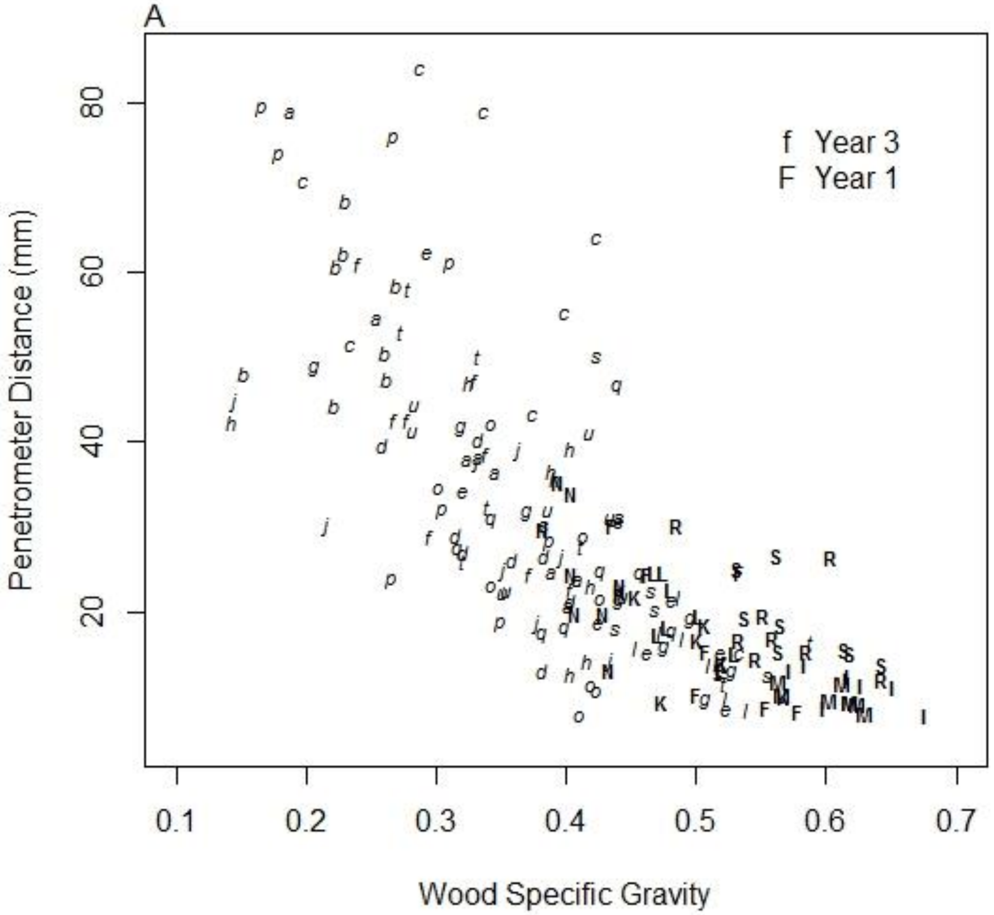
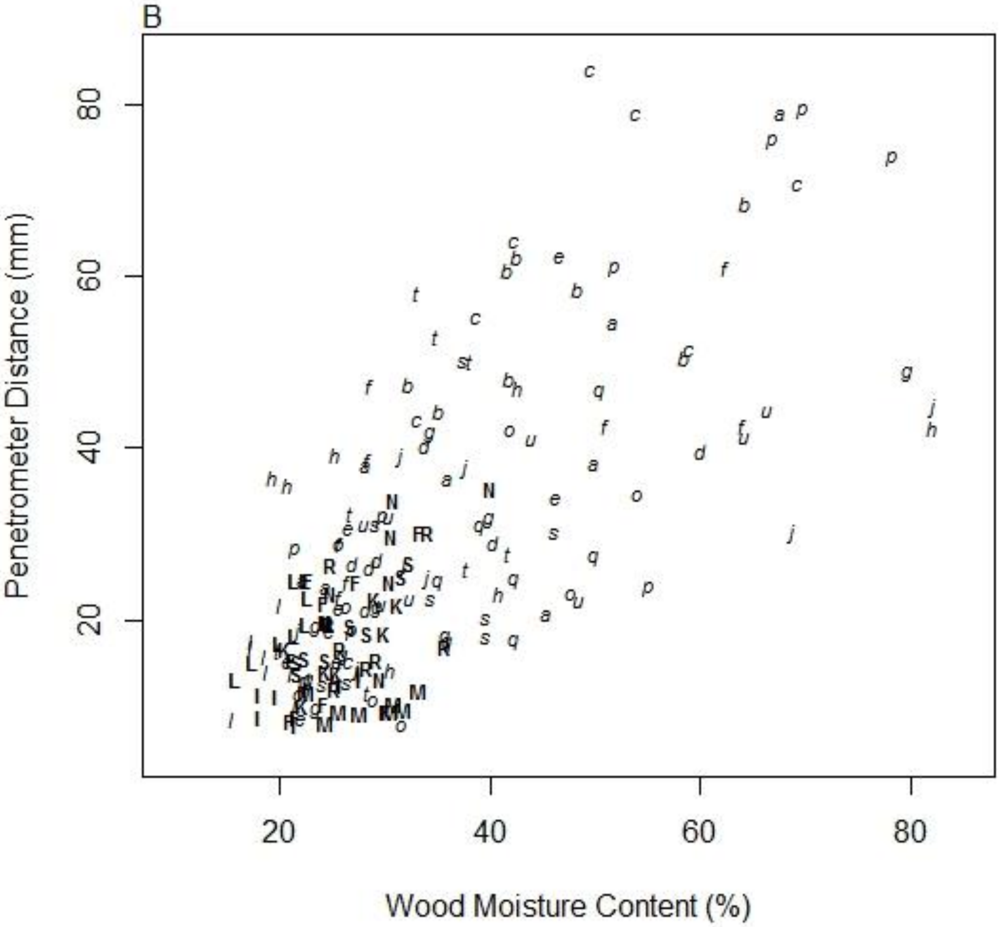
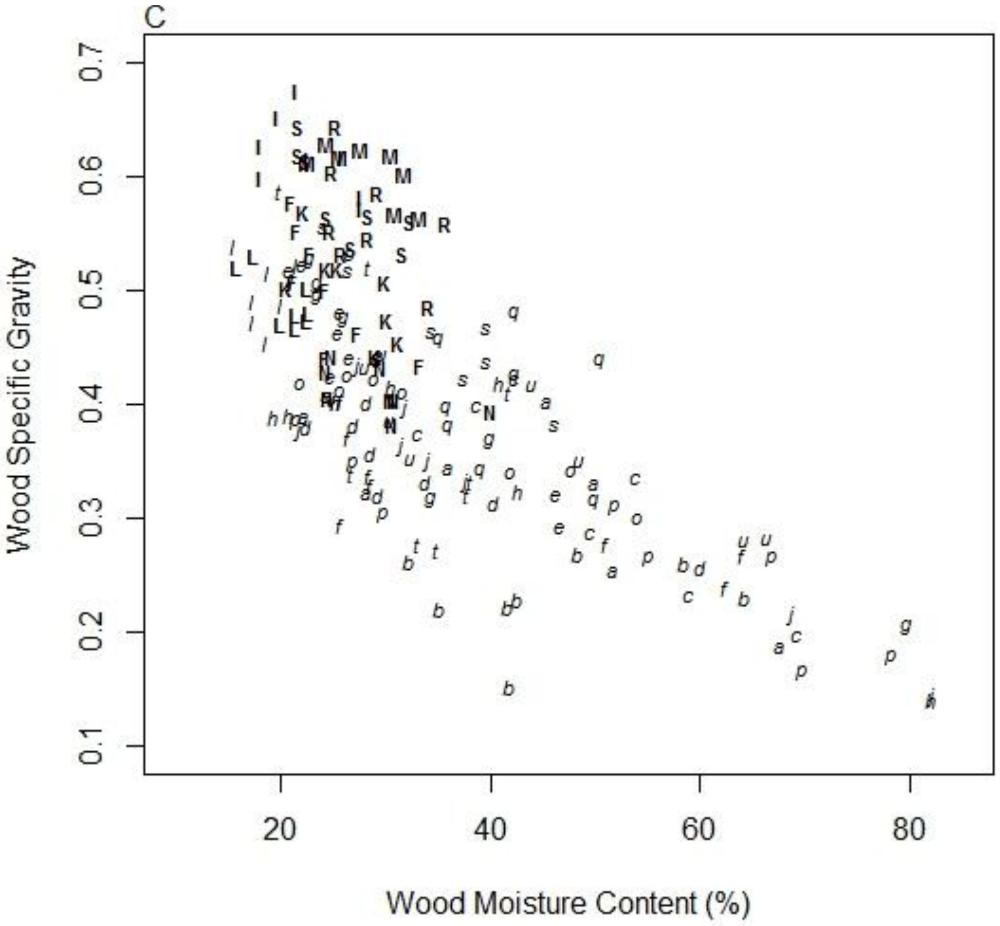


Fig. 2: Bivariate relationships between penetrometer distance, specific gravity and moisture content in experimentally decayed wood. Bold capital letters indicate species that have decayed for one year. Italic lowercase letters indicate species that had decayed for three years. Letters represent species as in Table 1.


B
Penetrometer Distance (mm)
20
40
60
80
Wood Moisture Content (%)
20
40
60
80


C
Wood Specific Gravity
0.1
0.2
0.3
0.4
0.5
0.6
0.7
Wood Moisture Content (%)
20
40
60
80

3.3. Species identity

Penetrometer measurements also varied among decayed wood samples from different species. Species effects were generally independent of other factors, corresponding to different species-level intercepts in more general relationships between penetrometer measurements and predictors like SG, MC and degree of decay (Supplementary tables 1-4). The field survey was an exception, with strong support for distinct relationships among the 23 different species identified using retained tags when total distance was the response (Supplementary table 4).

Interspecific differences in penetrometer measurements of less decayed samples tended to correlate with differences in intact wood hardness. Among the eight species in the lab experiment, the penetrometer stylus embedded further in dry decayed wood from species with less hard intact wood (Fig. 3). Controlling for the effect of SG in a multilevel model, the posterior mean for the slope of the relationship between species-level intercepts and dry Janka hardness was significantly less than zero for samples measured at low MC. Samples from the three species with low initial dry Janka hardness tended to deviate more from the overall relationship than samples from harder species such that the species with the

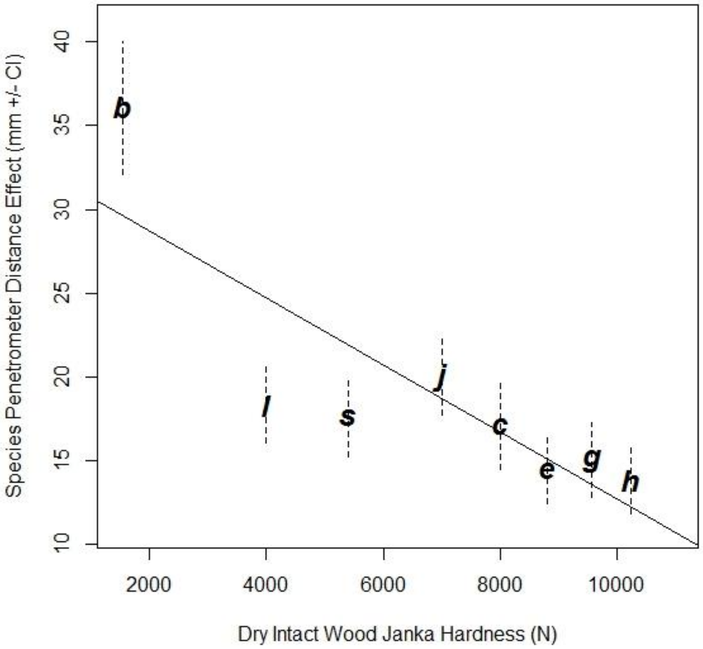


Fig. 3. Relationship between species-level effects on variation in penetrometer depth in dry experimentally decayed wood and dry intact wood Janka Hardness. Letters represent species as in Table 1. Dashed lines represent 95% CIs and solid line represents the posterior mean for the hierarchical regression relating intact wood hardness to decayed wood penetrometer depth (Eq. 2).

lowest Janka hardness, *Aesculus glabra*, had much greater penetrometer depth than expected. Posterior means for other subsets of the lab experiment tended to be negative but the 95% posterior CIs included zero (Table 2). In the field test and survey, variation in species-level effects did not consistently differ by intact wood hardness.

Table 2: Posterior summary statistics for heirarchical models explaining variation in penetrometer measurments as a function of variation in intact wood hardness. Bold indicates initial hardness effect (β_{janka}, Eq. 2) that is significantly different from 0.

				Posterior Summary Statistics		
Dataset	Species	Treatment	Measure	mean	2.5%	97.5%
lab	8	dry	distance	**-3.26E-03**	**-5.96E-03**	**-6.41E-04**
lab	8	dry	log(mm/hit)	-3.05E-05	-1.88E-04	1.28E-04
lab	8	wet	distance	-2.27E-03	-5.48E-03	7.66E-04
lab	8	wet	log(mm/hit)	-2.95E-06	-1.25E-04	1.10E-04
field	7	1 year	distance	6.26E-04	-3.07E-03	4.65E-03
field	7	1 year	log(mm/hit)	1.09E-04	-1.37E-04	3.59E-04
field	14	3 year	distance	1.73E-04	-2.43E-03	2.77E-03
field	14	3 year	log(mm/hit)	3.39E-05	-9.99E-05	1.68E-04
survey	13	DC2	distance	1.08E-03	-5.62E-03	7.48E-03
survey	13	DC2	log(mm/hit)	3.88E-05	-1.55E-04	2.33E-04
survey	17	DC3	distance	1.33E-03	-2.52E-02	2.93E-02
survey	17	DC3	log(mm/hit)	5.05E-05	-1.62E-04	2.94E-04
survey	12	DC4	distance	-1.35E-03	-1.38E-02	8.40E-03
survey	12	DC4	log(mm/hit)	-4.90E-05	-4.15E-04	2.68E-04

3.4. Degree of decay

Penetrometer measurements changed as species decayed for different periods of time. In the field experiment, the penetrometer stylus embedded an additional 16.3 mm into wood that had decayed for three years compared to one year (*t*-test, YR, $t = 6.947$, $p < 0.001$). The differences in penetrometer measurements largely reflected changes in SG and MC during decay. Across samples from all species, the relationships between penetrometer measurements and both SG and MC did not differ by the number of years of decay (ANOVA, distance: SG x YR $p = 0.30$, MC x YR $p = 0.55$). However, among the three species that had decayed for both one and three years, the most adequate model included an additive effect for the number of years of decay (Supplementary Table 3). Controlling for changes in SG and MC, penetrometer distance decreased after three years of decay (ANOVA, YR, *t* = -2.143, *p* = 0.038)

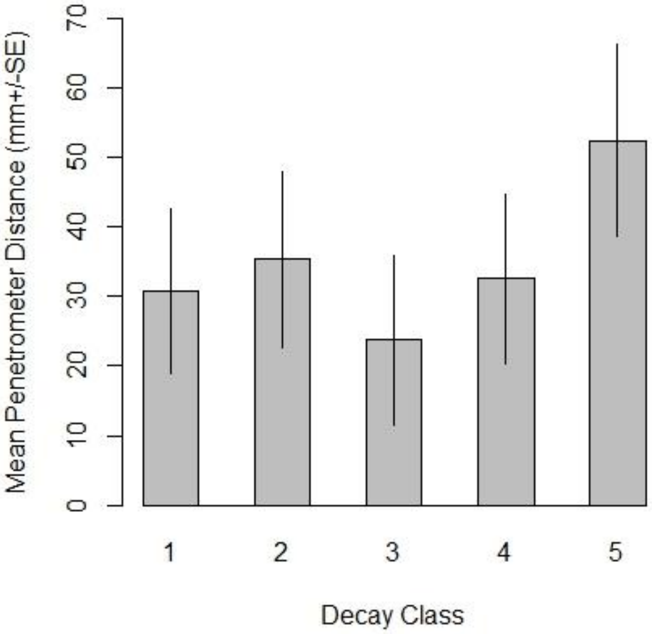


Fig. 4. Penetrometer distances across different decay classes in a coarse woody debris survey.

Penetrometer measurements also varied between pieces of coarse woody debris in different stages of decay. The most adequate models for all pieces and the subset identified to species included both DC and stem diameter as predictors (Supplementary tables 4-5). The effect of DC was best represented as categorical rather than continuous. Controlling for the effects of stem diameter, penetrometers embedded the furthest into samples at the most advanced stage of decay, DC 5, and the least into samples at the middle stage of decay, DC 3 (Fig. 4.). A similar pattern occurred among samples identified to species. Within individual identified logs, there were no consistent differences in penetrometer measurements between areas characterized by different decay classes (Supplementary table 6).

3.5 Explanatory power

As a tool for estimating dead wood density, the effectiveness of penetrometers depended on the number of measured covariates and the conditions under which wood decayed. For experimentally decayed wood, penetrometer measurements accurately predicted SG. In the laboratory experiment, penetrometer distance explained 67.8% of variation in sample SG. Adding sample MC as a covariate improved the R^2 of total penetration distance to 72.8% and including species identity improved the R^2 to 86.1%. In the field experiment, penetrometer distance alone explained 60.1% of the variation in sample SG. Including sample MC increased the R^2 to 66.9%, species identity to 88.1% and number of years decayed to 89.8%.

Compared to the highly predictive relationship between penetrometer measurements and SG of experimentally decayed wood, the relationships between penetrometer measurements and DC in a CWD survey were much weaker. Total penetration distance explained only 1.1% of the variation in DC in the CWD survey and only 0.5% of the variation in DC in the subset of pieces identified to species. By comparison, including species ID as a predictor in the CWD survey increased the amount of variation explained to 10.5%.

4. Discussion

Both the operating principle and the results of our experiments suggest that penetrometers measure a mechanical property of wood similar to hardness. Like the hardness of intact wood, penetrometer measurements of experimentally decayed wood are highly correlated with SG. Also like hardness, residual variation in penetrometer measurements depended on sample MC and species identity. However, the relationships between penetrometer measurements, SG, MC and species identity diverged as wood decayed and standardized measurement conditions were relaxed. These changes have important implications for understanding the dynamics of wood mechanical properties during decay and for using penetrometers to estimate density during CWD surveys.

The similarity between penetrometer measurements of decayed wood and hardness of intact wood was most clear in the results of the lab experiment. Like the standard Janka test, we conducted measurements at high and low MC on bark free, stabilized specimens with similar dimensions (Green et al., 2006). As expected, penetrometer distance decreased with SG and increased with MC. The proportional magnitudes of these effects were very similar to those expected based on analyses of variation in Janka hardness of intact wood. Furthermore, after controlling for variation in SG, penetrometers traveled further into decayed samples from species with softer intact wood. These results suggest that the relationships between these mechanical properties of wood are stable during the earliest stages of decay in central hardwood forests and differ from results of studies in boreal forests that found rapid initial changes in decayed wood mechanical properties (Curling et al., 2002; Jurgensen et al., 2006).

The same basic predictors influenced variation in measurements in the field experiment, but the relationships began to diverge from expectations based on analyses of intact wood. Compared to measurements taken at controlled MC, penetrometer depth of samples at field MC was even more strongly correlated with SG. The increase in the strength of the correlation under field conditions probably reflected the combined effects of SG and MC. At the time of sampling, the least dense samples also had the highest MC with both factors tending to increase penetrometer depth.

While penetrometer depth increased with MC in the field experiment, the shape of the marginal relationship differed from expectations based on analyses of Janka hardness of intact wood. In intact wood, the relationship between hardness and MC disappears at an inflection point at or below the fiber saturation point (Green et al., 2006). Across our samples, MC varied from below to well above the intact wood fiber saturation point but the increase in penetrometer measurements showed no evidence of curvature. This result suggests that the mechanical properties of decayed wood scale differently with MC, perhaps because saprobe activity modifies the chemical and anatomical structure of wood to change or eliminate the fiber saturation point (Griffin, 1977). For instance, white rot fungi tend to increase moisture content while reducing mechanical strength (Blanchette, 1991). These changes may occur at different rates in sapwood versus heartwood depending on the concentration of extractives and how they influence mechanical strength, moisture content and decomposition (Grabner et al., 2005). Future studies that examine how the fine-scale effects of fungi influence the scaling of bulk mechanical properties in decaying wood could illuminate the chemical and anatomical basis for shifts in wood strength and help assess the longevity of untreated wood structures.

Interspecific differences also influenced penetrometer measurements in the field experiment, but the differences among species no longer corresponded to the differences in intact wood hardness. Some of this discrepancy may reflect methodological differences between experiments. To simulate field conditions we measured through retained bark, while both the Janka test and our lab experiment removed bark and any effect associated with bark variation. Bark and wood properties may vary independently (Rosell et al., 2013), obscuring the strength of the relationship between penetrometer depth and intact wood hardness. The discrepancy may also reflect progressive changes in mechanical characteristics through time. Among the three species that we measured after both one and three years of decay, controlling for changes in SG and MC, penetrometer depth decreased after three years. This effect is consistent with case hardening (Spaulding and Hansbrough, 1944). Case hardening and related changes in mechanical strength could develop at different rates in different species and obscure the effects of initial differences in wood hardness.

The tendency for mechanical properties to diverge as dead wood decays under natural conditions may contribute to high variability we observed during the CWD survey. Decay class and species both influenced penetrometer depth, but both effects were weak and neither matched expectations based on relationships for intact wood. While specific gravity tends to decline monotonically with advancing decay class (Harmon et al., 2008 ; see also Fraver et al., 2013), the lowest average penetrometer measurements in our survey did not occur at DC1 but instead at DC3. The drop in penetrometer depth at DC3 could reflect the effect of bark loss which characterizes this decay class. However, penetrometer measurements of different portions of the same log in different decay classes did not show consistent differences in penetrometer measurements. Within log heterogeneity is common in hardwood decay (Pyle and Brown 1999) possibly reflecting fine-scale variation in decomposer colonization, dynamics and efficiency. Consequently, the hardness of different small areas of the same log may vary more strongly with local decay dynamics than aggregate features such as decay class. As with the experiments, penetrometer depth varied among species but species-level differences changed with decay class and were never correlated with intact wood hardness.

Because of the high variability we encountered during our CWD survey, we do not recommend using the protocol developed by Larjavaara and Muller-Landau (2010) for estimating CWD density in temperate hardwood forests. However, our results do suggest certain steps to improve penetrometer accuracy. First, dead wood hardness and SG varied with sample MC. Estimating sample MC during measurement based on wood electrical resistance or impedance would be a simple way to attribute variation in penetrometer distance to a highly variable and influential parameter (Brischke et al., 2008). Second, the varying presence of bark likely contributed variation to our survey results. Where permitted, removing bark prior to measurement would be a relatively fast and minimally destructive way to standardize sample conditions. Even with these improvements, extreme shifts in wood hardness relative to density due to case hardening and other idiosyncratic changes could make estimating dead wood density from penetrometers even more problematic than using decay classes in temperate forests.

Penetrometers were not an ideal CWD survey tool in the forest we studied. Yet, as a device for measuring hardness, they illustrated how mechanical properties change through time as wood decays and suggest biogeographic differences in the decay dynamics of CWD. In the forests that we studied, hardness tends to increase relative to SG at different rates for different species. This result is consistent with variation in rates of case hardening during decay. Previous studies of temperate forests have identified case hardening as an important process governing the physical structure and durability of CWD. In hardwood forests of the southern Appalachians, CWD pools were larger in habitats dominated by species that become case hardened (Webster et al., 2008). Variation in the species traits and physical circumstances contributing to case hardening may contribute to variation in the size of the CWD pool and the quality of habitat for the fungi insects and other saproxylic organisms that depend on CWD. In comparison to these results from temperate forests, the relative effectiveness of penetrometers for estimating density in the tropics suggests that wood mechanical properties may remain more strongly correlated during tropical wood decay. An experiment comparing decay of aspen stakes (*Populus tremuloides*) in boreal, temperate and tropical forests, found that mechanical traits changed differently with decay in colder sites but not in the tropics (González et al., 2008). If case hardening is less prevalent in the tropics, decay rates and CWD pool sizes may differ from those observed in the temperate zone. Understanding these differences may help predict regional variation in the carbon cycle consequences of climate change.

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References

Adams, H.D., Guardiola-Claramonte, M., Barron-Gafford, G. a, Villegas, J.C., Breshears, D.D., Zou, C.B., Troch, P. a, Huxman, T.E., 2009. Temperature sensitivity of drought-induced tree mortality portends increased regional die-off under global-change-type drought. Proc. Natl. Acad. Sci. U. S. A. 106, 7063–6.

Blanchette, R., 1991. Delignification by wood-decay fungi. Annu. Rev. Phytopathol. 29, 381–398.

Brischke, C., Rapp, A.O., Bayerbach, R., 2008. Measurement system for long-term recording of wood moisture content with internal conductively glued electrodes. Build. Environ. 43, 1566–1574.

Brown, S., 2002. Measuring carbon in forests: current status and future challenges. Environ. Pollut. 116, 363–72.

Curling, S., Clausen, C., Winandy, J.E., 2002. Relationships between and chemical composition of wood during incipient brown-rot decay. For. Prod. J. 52, 34–39.

Fraver, S., Milo, A.M., Bradford, J.B., D’Amato, A.W., Kenefic, L., Palik, B.J., Woodall, C.W., Brissette, J., 2013. Woody Debris Volume Depletion Through Decay: Implications for Biomass and Carbon Accounting. Ecosystems 16, 1262–1272.

Glass, S. V, Zelinka, S., 2010. Moisture relations and physical properties of wood, in: Wood Handbook, General Technical Report FPL-GTR-190. US Dept. of Agriculture, Forest Service, Forest Products Lab, Madison, WI, pp. 4–1 – 4–19.

González, G., Gould, W. a, Hudak, A.T., Hollingsworth, T.N., 2008. Decay of aspen (Populus tremuloides Michx.) wood in moist and dry boreal, temperate, and tropical forest fragments. Ambio 37, 588–97.

Grabner, M., Müller, U., Gierlinger, N., Wimmer, R., 2005. Effects of heartwood extractives on mechanical properties of larch. IAWA J 26, 211–220.

Green, D.W., Begel, M., Nelson, W., 2006. Janka hardness using nonstandard specimens., in: Research Note FPL-RN-303. US Dept. of Agriculture, Forest Service, Forest Products Lab, Madison, WI, p. 13.

Griffin, D., 1977. Water potential and wood-decay fungi. Annu. Rev. Phytopathol. 15, 319–29.

Harmon, M., Franklin, J., Swanson, F., Sollins, P., Gregory, S., Lattin, J., Anderson, N., Cline, S., Aumen, N., Sedell, J., Lienkaemper, G., Cromack, K., Cummins, K., 1986. Ecology of coarse woody debris in temperate ecosystems. Adv. Ecol. Res. 15, 133–302.

Harmon, M., Whigham, D., 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., Fasth, B., Woodall, C.W., 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, 259–267.

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., in: General Technical Report NRS-29. US Dept. of Agriculture, Forest Service, Northern Research Station, Newton Square, PA, p. 83.

Hughes, S.W., 2005. Archimedes revisited: a faster, better, cheaper method of accurately measuring the volume of small objects. Phys. Educ. 40, 468–474.

Jurgensen, M., Reed, D., Page-Dumroese, D., Laks, P., Collins, A., Mroz, G., Degórski, M., 2006. Wood strength loss as a measure of decomposition in northern forest mineral soil. Eur. J. Soil Biol. 42, 23–31.

Kretschmann, D., 2010. Mechanical properties of wood, in: Wood Handbook, General Technical Report FPL-GTR-190. US Dept. of Agriculture, Forest Service, Forest Products Lab, Madison, WI, pp. 5–1 – 5–46.

Larjavaara, M., Muller-Landau, H.C., 2010. Comparison of decay classification, knife test, and two penetrometers for estimating wood density of coarse woody debris. Can. J. For. Res. 40, 2313–2321.

Lunn, D., Spiegelhalter, D., Thomas, A., Best, N., 2009. The BUGS project: Evolution, critique and future directions. Stat. Med. 28, 3049–3067.

Mäkipää, R., Linkosalo, T., 2011. A Non-Destructive Field Method for Measuring Wood Density of Decaying Logs. Silva Fenn. 45, 1135–1142.

Moore, D.J.P., Trahan, N. a, Wilkes, P., Quaife, T., Stephens, B.B., Elder, K., Desai, A.R., Negron, J., Monson, R.K., 2013. Persistent reduced ecosystem respiration after insect disturbance in high elevation forests. Ecol. Lett. 16, 731–7.

Pyle, C., Brown, M., 1998. A rapid system of decay classification for hardwood logs of the eastern deciduous forest floor. J. Torrey Bot. Soc. 125, 237–245.

Rosell, J. a, Gleason, S., Méndez-Alonzo, R., Chang, Y., Westoby, M., 2013. Bark functional ecology: evidence for tradeoffs, functional coordination, and environment producing bark diversity. New Phytol. 201, 486–497.

Seedre, M., Taylor, A., Chen, H., Jogiste, K., 2012. Deadwood Density of Five Boreal Tree Species in Relation to Field-Assigned Decay Class. For. Sci. 59, 261–266.

Spaulding, P., Hansbrough, J.R., 1944. Decay of Logging Slash in the Northeast, in: Technical Bulletin 876. US Dept. of Agriculture, Washington, DC, p. 22.

Tze, W.T.Y., Wang, S., Rials, T.G., Pharr, G.M., Kelley, S.S., 2007. Nanoindentation of wood cell walls: Continuous stiffness and hardness measurements. Compos. Part A Appl. Sci. Manuf. 38, 945–953.

Webster, C., Huckins, C., Shields, J., 2008. Spatial distribution of riparian zone coarse woody debris in a managed northern temperate watershed. Am. Midl. Nat. 159, 225–237.

Wiemann, M., Green, D.W., 2007. Estimating Janka Hardness from Specific Gravity for Tropical and Temperate Species, in: Research Paper FPL-RP-643. United States Dept. of Agriculture, Forest Service, Forest Products Laboratory, Madison, WI, p. 21.

Wilson, B.T., Woodall, C.W., Griffith, D.M., 2013. Imputing forest carbon stock estimates from inventory plots to a nationally continuous coverage. Carbon Balance Manag. 8, 1.

Winandy, J.E., Rowell, R.M., 2005. Chemistry of Wood Strength, in: Rowell, R.M. (Ed.), Handbook of Wood Chemistry and Wood Composites. CRC Press, Boca Raton, pp. 303–347.

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.

Woodall, C.W., Liknes, G.C., 2008. Climatic regions as an indicator of forest coarse and fine woody debris carbon stocks in the United States. Carbon Balance Manag. 3, 5.

Zhang, S.Y., 1997. Wood specific gravity-mechanical property relationship at species level. Wood Sci. Technol. 31, 181–191.