NRC Research Press

NOTE

Woody material structural degradation through decomposition on the forest floor

Shawn Fraver, Mehdi Tajvidi, Anthony W. D'Amato, Daniel L. Lindner, Jodi A. Forrester, and Amy M. Milo

Abstract: Dead woody material (DWM) plays numerous important roles in forest ecosystems; however, through the process of decomposition, it undergoes structural and chemical changes that progressively alter its function in these roles. Much remains unknown about how DWM mechanical strength and structural integrity change through decomposition in natural forest settings. We assessed changes in wood strength (bending strength, compressive strength, and surface hardness) using standard wood stakes of known initial mass from three species. The stakes were placed in forested settings for two and four years before collection for laboratory analyses. All three strength metrics decreased as stakes lost mass due to decay; however, bending strength had the strongest relationship with mass loss, a result that was consistent for all species, as well as species-pooled data. Results for all strength-loss metrics indicate that stakes had experienced ca. 10% strength loss before any detectable mass loss had occurred. Further, our results suggest that the decay class system typically used during field inventories — based in large part on tactile assessments of wood structural integrity — may provide a reasonable characterization of DWM mass loss, which is a critical assumption for carbon accounting and modelling based on inventory data.

Key words: carbon accounting, decay class, decay stakes, forest fuels, wood decay, woody debris.

Résumé : Le matériel ligneux grossier (MLG) joue plusieurs rôles importants dans les écosystèmes forestiers. Cependant, durant le processus de décomposition il subit des changements structuraux et chimiques qui modifient progressivement les fonctions associées à ces rôles. Beaucoup de choses demeurent inconnues au sujet de la façon dont la résistance mécanique et l'intégrité structurale du MLG changent durant sa décomposition en forêt naturelle. Nous avons évalué les changements dans la résistance du bois (résistance à la flexion, résistance à la compression et dureté superficielle) à l'aide de baguettes de bois standards dont on connaissait la masse initiale de trois espèces. Les baguettes ont été laissées en forêt pendant deux et quatre ans avant d'être récoltées pour les analyses en laboratoire. Les résultats des trois mesures de résistance ont diminué à mesure que progressait la perte de masse due à la décomposition des baguettes. Cependant, la résistance à la flexion était le plus étroitement reliée à la perte de masse, un résultat constant chez toutes les espèces ainsi qu'avec les données des espèces regroupées. Les résultats pour toutes les mesures de perte de résistance indiquent que les baguettes avaient subi une perte de résistance d'environ 10 % avant que survienne une perte de masse détectable. De plus, nos résultats confirment que le système de classes de décomposition normalement utilisé lors des inventaires terrestres, fondé en grande partie sur des évaluations tactiles de l'intégrité structurale du bois, fournit une approximation raisonnable de la perte de masse du MLG, laquelle est essentielle pour la modélisation et la comptabilisation précise du carbone sur la base des données d'inventaire. [Traduit par la Rédaction]

Mots-clés : comptabilisation du carbone, classe de décomposition, baguettes de bois servant à mesurer la décomposition, combustibles forestiers, décomposition du bois, débris ligneux.

Introduction

Dead woody material (DWM) plays a crucial role in forest ecosystems where it contributes to carbon storage, nutrient cycling, and biodiversity maintenance (Harmon et al. 1986; Stokland et al. 2012). However, as woody material decomposes, it undergoes structural and chemical changes that strongly influence its function in these roles. Progressive changes in wood mechanical strength, in particular, influence a number of ecological processes. For example, wood mechanical strength governs nest selection by cavity-nesting birds such that their community structure depends on the distribution of trees containing zones of suitable hardness (Lorenz et al. 2015). Woody material strength is also closely related to foraging selection by bears, given that their food source (carpenter ants) is more likely to occur in logs of intermediate hardness (Frank et al. 2015). Similarly, the structural integrity and prevalence of internal voids in decaying wood dictate its use by Plethodontid salamanders for foraging and oviposition (Heatwole 1962) and influence the likelihood of stem breakage in snags (Angers et al. 2010).

Wood loses mechanical strength through decomposition as the structural components of cell walls — lignin, cellulose, and hemicellulose — are progressively degraded by fungi. Insects hasten

Received 7 May 2017. Accepted 12 October 2017.

S. Fraver and M. Tajvidi. School of Forest Resources, University of Maine, 5755 Nutting Hall, Orono, ME 04469, USA.
A.W. D'Amato. Rubenstein School of Environment and Natural Resources, University of Vermont, 81 Carrigan Drive, Burlington, VT 05405, USA.
D.L. Lindner. USDA Forest Service, Northern Research Station, Center for Forest Mycology Research, Madison, WI 53726, USA.
J.A. Forrester. Department of Forestry and Environmental Resources, North Carolina State University, Jordan Hall 3108, Raleigh, NC 27695, USA.
A.M. Milo. Department of Biological Sciences, George Washington University, Washington, DC 20052, USA.
Corresponding author: Shawn Fraver (email: shawn.fraver@maine.edu).

structural degradation by introducing additional decomposing microbes and creating internal voids (Harmon et al. 1986). Several recent studies have shown various metrics of wood strength to be sensitive indicators of decay in natural forest settings (Larjavaara and Muller-Landau 2010; Oberle et al. 2014); in fact, in the earliest stages of decay, reduction in mechanical strength may occur before measurable reductions in wood mass (Curling et al. 2002; Venäläinen et al. 2014).

Despite the large body of research addressing dead woody material (DWD) in recent decades (Russell et al. 2015), much remains unknown about the changes in DWM strength and structural integrity through decomposition in natural forest settings. This knowledge gap is especially important given that the criteria for assigning decay classes (evaluation of how far decay has advanced; Sollins 1982) during forest inventories rely in large part on field assessments of wood strength (Woodall and Monleon 2008). It also has relevance in the context of postdisturbance salvage logging operations, given that wood may partially degrade and thus lose value before salvage operations can commence (Ruel et al. 2010). Thus our objectives were to (*i*) assess changes in wood mechanical strength (i.e., bending strength, compressive strength, and surface hardness) caused by decomposition on the forest floor and (*ii*) test the relationship between these strength metrics and mass loss, a critical metric used in ecological studies, including forest carbon accounting and modelling. We accomplished these objectives by using standard wood stakes of three common tree species, for which initial density and dry mass were known, deployed in natural forest settings (in the US Lake States) for two to four years before collection for laboratory analyses.

Wood mechanical strength loss owing to fungal decay is well known in the forest products literature (e.g., Brischke et al. (2008) and Witomski et al. (2016)). Such studies typically involve inoculation of sound wood with selected fungi, followed by laboratory incubation for specified periods and ultimately strength tests (Witomski et al. 2016). Our study differs in that wood samples were placed in natural forest settings and thus were colonized by a range of resident wood-decay fungi known from these sites (Brazee et al. 2012, 2014).

Methods

Study design

The sites used in this study are part of a larger experiment aimed at assessing the impacts of intensive biofuel harvesting on site productivity and nutrient cycling (see Kurth et al. 2014). As part of that study, ca. 1400 decay stakes — standard-sized wood stakes for which initial density and dry mass were known — of three species were placed in various sites and treatments to assess variability in stake decay rates as a function of site conditions and local fungal communities. Sites and treatments included a continuum of open- to closed-canopy conditions, creating a range of moisture and light availability; for details, see Kurth et al. (2014) and Brazee et al. (2014). Multiple stakes at each site–treatment location were deployed in 2010 with the intent of collecting subsets of them at two-year intervals over eight years. Study sites are located in northern Minnesota and northern Wisconsin, USA.

Stakes were manufactured to 2.54 × 2.54 × 20 cm from locally harvested balsam fir (*Abies balsamea* (L.) Mill.) and aspen (*Populus tremuloides* Michx.) for the Minnesota sites and from sugar maple (*Acer saccharum* Marsh.) for the Wisconsin sites, representing the common overstory tree species for each location. Only select, knot- and defect-free wood was used. Before being deployed, all stakes were oven dried for 8 days at 75 °C to achieve constant mass (Fraver et al. 2013), and each was weighed while dry. Each stake was uniquely numbered and tagged. Stakes were placed on the forest floor on permanently monumented plots in June 2010 (Minnesota) and July 2010 (Wisconsin).

This current study of wood strength made use of a predetermined, randomly drawn subset of the larger pool of decay stakes at these sites. At one site in Minnesota (Pelican Lake), we used 34 stakes for each of *Abies balsamea* and *Populus tremuloides* (two stakes from each of 17 permanent sample plots), and at one site in Wisconsin (Flambeau State Forest), we used a similar sample size of 33 stakes of *Acer saccharum*. In addition, 10 nondecayed stakes of each species, randomly chosen from the complete pool of stakes, were initially set aside for strength tests. Sample sizes were chosen to provide adequate confidence in our estimates of strength loss, based on data presented in Jurgensen et al. (2006). Analyses of variance revealed that the initial densities, within a species, did not differ significantly between the deployed and nondeployed stakes (tested at $\alpha = 0.05$). Stakes used in this study were collected in early July of 2012 and 2014, that is, after two and four years of decay on the forest floor. Samples were limited to this four-year period because, as decay advances, pieces become irregular in shape and lose volume (Fraver et al. 2013), making them unsuitable for use on the testing equipment (below), which requires samples of uniform size. Indeed, several samples had deformities making them admittedly less than ideal for these tests; we return to this topic in the Results and discussion. In the laboratory, stakes were cleaned of soil and debris and oven dried for 8 days at 75 °C before being weighed. Stakes were kept at equilibrium humidity and temperature for at least two weeks prior to the strength tests that followed.

Strength tests and analyses

We selected three wood strength tests — static bending, compression perpendicular to grain, and surface hardness — intended to best represent the range of tactile criteria typically employed in field inventories of woody material. The tests are described here in the order in which they were performed on each decay stake. Center-loading static bending (flexure) tests, with samples centered in the test machine (using the entire stakes), were conducted with supports spanning 16.5 cm, resulting in modulus of rupture (MOR, a measure of stress required to cause failure) for each sample. Though this span distance differs from the American Society for Testing and Materials standard (14 inches, or 35.6 cm) (ASTM 2014), it allows comparisons of the relative flexural strength across these samples. Compression tests were conducted using a 2.54 × 2.54 cm plane compression platen, recording a stress at proportional limit for each test, which depicts the greatest force that the stake can withstand before losing shape. Surface hardness tests were conducted using the Janka method, which measures the force required to embed a small steel sphere (11.3 mm in diameter) half way into the sample (Green et al. 2006). Two compression tests and two surface hardness tests were conducted for each stake choosing portions of the stake unaffected by the static bending fracture and least affected by decay-related deformities, rotating the stake 90° radially, with results averaged for each stake (Hoadley 2000; Green et al. 2006). All tests were conducted on an Instron® (model 4202) system, using forces applied at 2.54 $mm \cdot min^{-1}$ (flexure and surface hardness) and 5.0 $mm \cdot min^{-1}$ (compression test).

For analysis, we expressed the three strength metrics as percent reductions relative to the mean of nondecayed samples, and we expressed mass loss as a percentage relative to the stake's initial dry mass before deployment. Following Jurgensen et al. (2006), we chose to analyze the nontransformed percentages because we were particularly interested in the value of the intercepts. Expressing these measures as percentages also allowed us to combine the analyses for the three species, which have rather different properties when expressed in absolute terms. We used nonlinear mixed-effects models to assess the relationship between strength-loss metrics (the response variables) and mass loss, for a total of three tests. Initial screening of linear and three candidate nonlinear models using Akaike's corrected information criterion

(AICc) indicated that a power function ($y = a{\cdot}x^b$) was best supported by data for all three strength metrics, using the pooled data. Species was treated as a random effect in these models, allowing a random intercept. In addition, we analyzed the relationship between strength-loss metrics and mass loss separately by species, also using the power function model form. All models were evaluated in the nlme package (Pinheiro et al. 2016) for R (R Core Team 2016). Goodness-of-fit (pseudo R^2) was expressed as the correlation between observed and predicted strength reductions (cf. Canham et al. 2004).

Results and discussion

All three strength-loss metrics showed strong positive relationships with mass loss for each species, as well as species-pooled data (Fig. 1; Table 1). Similar findings using decay stakes in forested settings have been reported (Jurgensen et al. 2006; González et al. 2008). Our findings suggest that bending strength had the strongest relationship with mass loss for each species individually, as well as for the pooled data (Table 1, R^2 values). For the pooled data, bending strength had an R^2 of 0.860, followed by surface hardness ($R^2 = 0.824$) and compressive strength ($R^2 = 0.718$) (Table 1; Fig. 1). In contrast to our findings, Jurgensen et al. (2006) found that radial compressive strength better represented mass loss when compared with surface hardness or longitudinal shear. This contrasting result might be explained by the greater range of densities represented by our three species when compared with the two used by Jurgensen et al. (2006).

All individual species models, as well as species-pooled models, from the three strength metrics had positive intercepts, indicating that stakes had lost strength before any detectable mass loss had occurred (Fig. 1; Table 1). For the pooled data, these intercepts were 13.7, 7.2, and 6.9 for bending strength, compressive strength, and surface hardness, respectively. This finding has been previously reported from laboratory incubation studies (Curling et al. 2002; Venäläinen et al. 2014), as well as from a field trial similar to our own (Jurgensen et al. 2006). In fact, the latter study reports a ca. 9% loss in compressive strength before detectable mass loss, a value quite close to our estimate of 7.2% (above). Curling et al. (2002) conclude that the initial strength-loss results from the fungal degradation, but not consumption, of the galactan and arabinan components of hemicellulose. Although these findings may suggest that strength tests could be used to assess incipient wood decay in situations where rapid estimates of decay are needed (Jurgensen et al. 2006) or when assessing species with inherently slow decay, we caution that early strength-loss rates do not necessarily translate to higher decay rates (i.e., mass loss) over longer time periods. We recommend additional research on this topic, as a demonstrated strong relationship between early strength reduction and long-term decay rates would be quite beneficial (in terms of time efficiency) in studies addressing controls of wood decay. Properly addressing this topic would require strength tests using a large number of species (capturing a range of functional traits) and spanning a range of initial decays.

The three strength metrics were strongly correlated within *Acer saccharum* and *Populus tremuloides* and were moderately correlated within *Abies balsamea* (Table 2), suggesting that decay affected various aspects of strength in similar ways and implying that any of these metrics could function reasonably well as indicators of decay progression within a species.

Here, we add cautionary notes regarding the strength tests themselves. As mentioned above, partial decay had at times rendered our samples less than ideal for use on the testing equipment. For example, one sample had broken in half upon field collection, making it unusable for the static bending test, although we chose to perform the remaining two tests. A number of samples had deformities resulting from the general loss of volume, which admittedly compromised their suitability for such tests. Though such deformities would clearly be unacceptable for testing commercial forest products, we allowed ourselves flexibility in this regard, reasoning that we could not simultaneously use partially decayed material (the objective of our study) and have perfectly preserved samples. Interestingly, the vast majority of deformed samples were those of *Populus tremuloides*, the species

Fig. 1. Relationship between three strength-loss metrics (bending strength, compressive strength, and surface hardness) and mass loss of decaying wood. Colored dots and lines represent the three species tested (*Abies balsamea* = green, *Acer saccharum* = blue, *Populus tremuloides* = red); the grey line represents pooled species data. R^2 values refer to pooled data. Model parameters for individual species are shown in Table 1. Intercepts of the fitted curves are positive for all three metrics, meaning that strength is reduced before any mass loss has occurred.

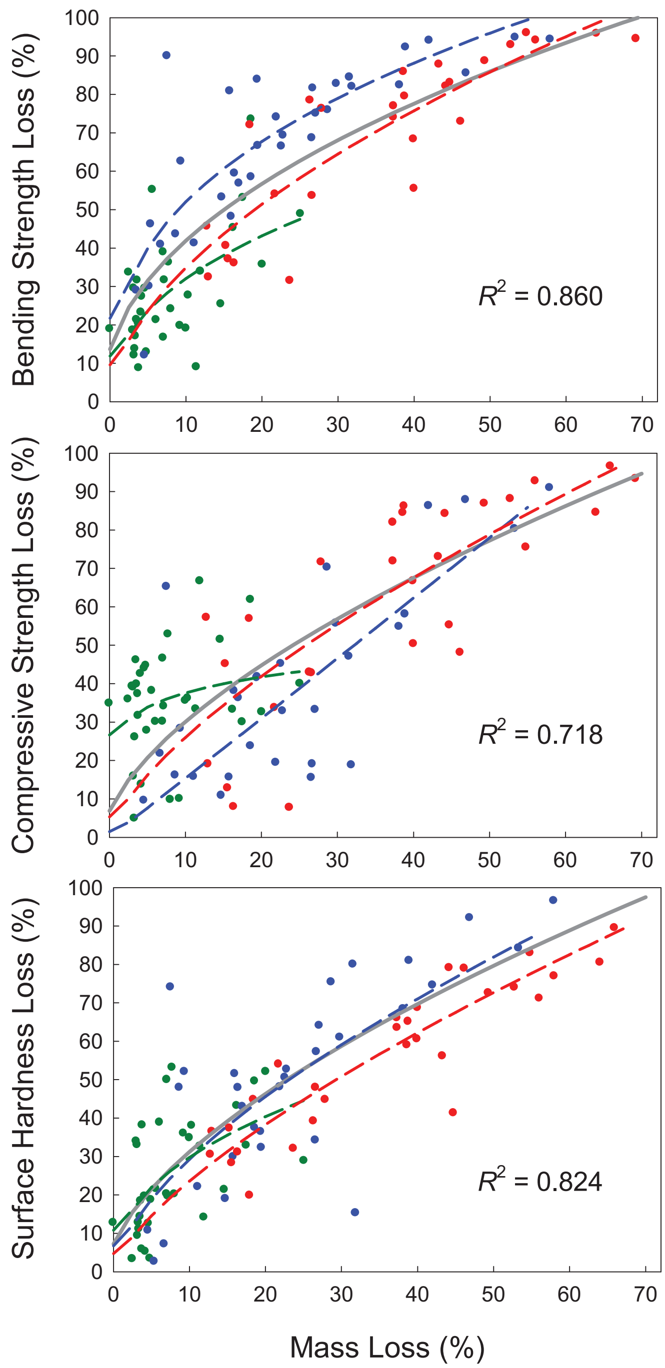

Table 1. Parameter estimates (with standard errors in parentheses) and fit statistics for models relating strength loss metrics (y) to mass loss (x), in the form $y = a{\cdot}x^b$.

	Species	a	b	R^2	RMSE
Bending strength	*A. saccharum*	21.7 (3.6)	0.38 (0.05)	0.84	12.0
	A. balsamea	11.9 (3.2)	0.43 (0.11)	0.56	12.3
	P. tremuloides	9.6 (2.3)	0.56 (0.06)	0.87	10.9
	Species pooled	13.7 (2.0)	0.47 (0.04)	0.86	13.7
Compressive strength	*A. saccharum*	1.5 (0.9)	1.01 (0.16)	0.79	16.7
	A. balsamea	26.6 (5.9)	0.15 (0.10)	0.25	13.8
	P. tremuloides	5.3 (2.4)	0.69 (0.12)	0.77	16.6
	Species pooled	7.2 (1.8)	0.61 (0.07)	0.72	18.3
Surface hardness	*A. saccharum*	6.7 (2.7)	0.64 (0.12)	0.74	17.3
	A. balsamea	10.8 (3.3)	0.44 (0.13)	0.55	12.7
	P. tremuloides	4.7 (1.5)	0.70 (0.09)	0.86	10.3
	Species pooled	6.9 (1.3)	0.62 (0.05)	0.82	14.0

Note: RMSE, root mean square error.

Table 2. Pearson coefficients indicating the correlation among three strength metrics (bending strength, compressive strength, and surface hardness) in dead woody material for each of the three species tested.

	A. saccharum		*P. tremuloides*		*A. balsamea*	
	Bending	Compression	Bending	Compression	Bending	Compression
Compression	0.79	—	0.89	—	0.59	—
Hardness	0.86	0.87	0.90	0.87	0.53	0.61

that ultimately showed the strongest relationship between strength loss and mass loss for two of the three strength metrics. We note too that, unlike bending strength, the compressive strength and surface hardness tests were conducted at specific stake locations and thus may not capture the variability within the entire stake. The uncertainty thus introduced could partially explain the poorer model fit (lower regression R^2; Table 1) for these metrics when compared with that of bending strength.

Although our intent was not to compare species, we note that the conifer species (*Abies balsamea*) showed the least strength loss (all three metrics) and the least mass loss when compared with the hardwood species (Fig. 1). This finding reflects the fact that conifers generally decay more slowly than hardwoods, despite their lower initial wood densities (Russell et al. 2014), which is often attributed to higher concentrations of extractives in softwoods.

Mechanical strength of dead woody material (DWM) has important implications for interpreting and processing forest inventory data, particularly for estimating forest biomass and carbon stocks. During DWM field inventories, decay classes are assigned to each DWM piece to depict how far decay has advanced (Sollins 1982). The various field protocols for assigning decay classes include tactile assessments of wood strength and structural integrity such as surface hardness (Maser et al. 1979), the depth that a sharp object can penetrate the log (Larjavaara and Muller-Landau 2010; Jacobs and Work 2012), the ability of the piece to hold its own weight (Sollins 1982; Stokland et al. 2012), and resistance to forced breakage (Larjavaara and Muller-Landau 2010). Decay classes thus assigned are used to convert field-measured DWM volumes to biomass, using published decay-class-specific and species-specific density reduction factors (e.g., Harmon et al. 2008), reflecting the fact that DWM mass diminishes as decomposition advances. Although we were unable to assign decay classes to our samples (the criteria also include characteristics such as bark features and cross-sectional shape that do not apply to our stakes), our results suggest that the wood strength loss, as assessed by the decay-class system, may provide a reasonable characterization of mass loss, which is a critical assumption for carbon accounting and carbon modelling based on field inventory data (Fraver et al. 2013).

Strength loss following tree death also has relevance in the context of postdisturbance salvage logging operations, given that wood may partially degrade and thus lose value before salvage operations can commence. Ruel et al. (2010) found that static bending became variable for *Abies balsamea* and was reduced for *Picea mariana* (black spruce) logs that had remained on site for four years after windthrow. Somewhat similarly, Mochan (2002) found gradual declines in bending strength the longer windthrown Sitka spruce (*Picea sitchensis* (Bong.) Carrière) trees were left on site, for up to three years. Our results show significant reductions in static bending for all three species tested after two years, with further reductions at year four only for *Acer saccharum* (not shown). We note that unlike the two studies mentioned above, our samples were located directly on the forest floor (not partially elevated following windthrow), which would have increased their moisture content and hastened their decay (Næsset 1999). Their small size, relative to the material used in the studies mentioned above, as well as the lack of bark, also likely contributed to more rapid decay and accompanying strength loss.

Our study adds to the growing number of decay-stake experiments worldwide that are providing insights into aspects of wood decomposition that had been previously underappreciated. For example, Bradford et al. (2014) demonstrated the greater importance of local drivers such as fungi and termites, relative to regional climatic factors, in governing wood decay rates in eastern US forests. Similarly, Meier et al. (2010) pointed to the strong influence of fungal richness and community composition, as well as temperature, in controlling wood decay rates in the Peruvian Andes, and Risch et al. (2013) demonstrated the importance of land use on wood decay rates, presumably through altered temperature regimes, in central Europe. Crockatt and Bebber (2014) reported that decay rates increased along a gradient of forest edge to interior forest, following a similar gradient of increasing moisture; González et al. (2008) reported a similar positive influence of moisture on wood decay rates in boreal and temperate forests.

In summary, our study demonstrates that the three strength metrics were moderately to strongly correlated with each other over the range of decay found in our samples. Reductions in all three metrics closely paralleled reductions in wood mass, consistent with findings of Jurgensen et al. (2006) and González et al. (2008). Our results suggest that the wood strength assessments — similar to the ones tested here — employed in decay-class systems may provide a reasonable characterization of mass loss from decaying wood in natural forest settings, which is a critical assumption for carbon accounting based on inventory data.

Acknowledgements

We thank M. Curzon, J. Kragthorpe, C. Kuehne, M. Russell, R. Seavey, T. Smith, and A. Teets for assistance in the laboratory or field. Comments from K. Costanza and three anonymous reviewers substantially improved the manuscript. This work was improved through discussions with B. Oberle. This project was supported by the USDA/DOE Biomass Research and Development Initiative (No. 2009-10006-05948), the Minnesota Environment and Natural Resources Trust Fund, and the Minnesota Forest Resources Council.

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