

Decomposition rates of American chestnut (*Castanea dentata*) wood and implications for coarse woody debris pools

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Abstract: Observations of the rapid growth and slow decomposition of American chestnut (*Castanea dentata* (Marsh.) Borkh.) suggest that its reintroduction could enhance terrestrial carbon (C) sequestration. A suite of decomposition models was fit with decomposition data from coarse woody debris (CWD) sampled in Wisconsin and Virginia, U.S. The optimal (two-component exponential) model was integrated with generic growth curves and documented longevity and typical stem density to evaluate how CWD and biomass pools relate to decomposition. CWD decomposed faster in Wisconsin ($4.3\% \pm 0.3\%$ per year) than in Virginia ($0.7\% \pm 0.01\%$ per year), and downed dead wood decomposed faster ($8.1\% \pm 1.9\%$ per year) than standing dead wood ($0.7\% \pm 0.0\%$ per year). We predicted considerably smaller CWD pools in Wisconsin (maximum 41 ± 23 Mg C·ha⁻¹) than in Virginia (maximum 98 ± 23 Mg C·ha⁻¹); the predicted biomass pool was larger in the faster growing Wisconsin trees (maximum 542 ± 58 Mg C·ha⁻¹) compared with slower growing trees in Virginia (maximum 385 ± 51 Mg C·ha⁻¹). Sensitivity analysis indicated that accurate estimates of decomposition rates are more urgent in fertile locations where growth and decomposition are rapid. We conclude that the American chestnut wood is intermediate in resistance to decomposition. Due to the interrelatedness of growth and decomposition rates, CWD pool sizes likely do not depend on species alone but on how the growth and decomposition of individual species vary in response to site productivity.

Key words: American chestnut, coarse woody debris, decomposition, carbon cycling, carbon sequestration, forest carbon simulations, forest growth, modeling, plantation development.

Résumé : Les observations ayant trait à la croissance rapide et à la décomposition lente du châtaignier d'Amérique (*Castanea dentata* (Marsh.) Borkh.) indiquent que sa réintroduction pourrait accroître la séquestration terrestre du carbone. Une série de modèles de décomposition ont été ajustés aux données de décomposition de débris ligneux grossiers (DLG) échantillonnés au Wisconsin et en Virginie, aux États-Unis. Le modèle optimal (exponentiel à deux composantes), des courbes génériques de croissance, la longévité documentée et la densité typique de la tige ont été intégrés pour évaluer comment les DLG et les réservoirs de biomasse sont reliés à la décomposition. Les DLG se décomposaient plus rapidement au Wisconsin ($4,3 \pm 0,3 \%$ ·an⁻¹) qu'en Virginie ($0,7 \pm 0,01 \%$ ·an⁻¹) et les débris au sol se décomposaient plus rapidement ($8,1 \pm 1,9 \%$ ·an⁻¹) que les débris sur pied ($0,7 \pm 0,0 \%$ ·an⁻¹). Nous avons prédit que les réservoirs de DLG seraient considérablement plus petits au Wisconsin (maximum de 41 ± 23 Mg C·ha⁻¹) qu'en Virginie (maximum de 98 ± 23 Mg C·ha⁻¹); nous avons aussi prédit que le réservoir de biomasse serait plus gros chez les arbres du Wisconsin qui croissent plus vite (maximum de 542 ± 58 Mg C·ha⁻¹) comparativement à ceux de la Virginie (maximum de 385 ± 51 Mg C·ha⁻¹). Une analyse de sensibilité a indiqué qu'il était plus urgent d'obtenir des estimations précises du taux de décomposition dans les endroits fertiles où la croissance et la décomposition sont rapides. Nous arrivons à la conclusion que le bois du châtaignier d'Amérique a une résistance intermédiaire à la décomposition. Étant donné l'interdépendance des taux de croissance et de décomposition, la taille des réservoirs de DLG ne dépend probablement pas seulement de l'espèce mais de la façon dont la croissance et la décomposition de chaque espèce varie en réponse à la productivité de la station. [Traduit par la Rédaction]

Mots-clés : châtaignier d'Amérique, débris ligneux grossiers, décomposition, recyclage du carbone, séquestration du carbone, simulations du carbone forestier, croissance forestière, modélisation, développement des plantations.

Introduction

Forested ecosystems sequester atmospheric CO₂ in living biomass, dead wood, leaf litter and other detritus, and soil carbon (C). Once disturbances are controlled for, the magnitude of C fluxes, from the atmosphere to living biomass and then to decomposing dead biomass, are largely determined by life-history traits gov-

erning growth rates, longevity, and resistance to decomposition (Weedon et al. 2009). Hence, forests that are dominated by fast-growing, long-living trees that produce decay-resistant wood are expected to store more C in the absence of disturbance.

American chestnut (*Castanea dentata* (Marsh.) Borkh., hereafter "chestnut") is an eastern North American hardwood species that once dominated much of its native range but was functionally

Received 6 June 2014. Accepted 9 September 2014.

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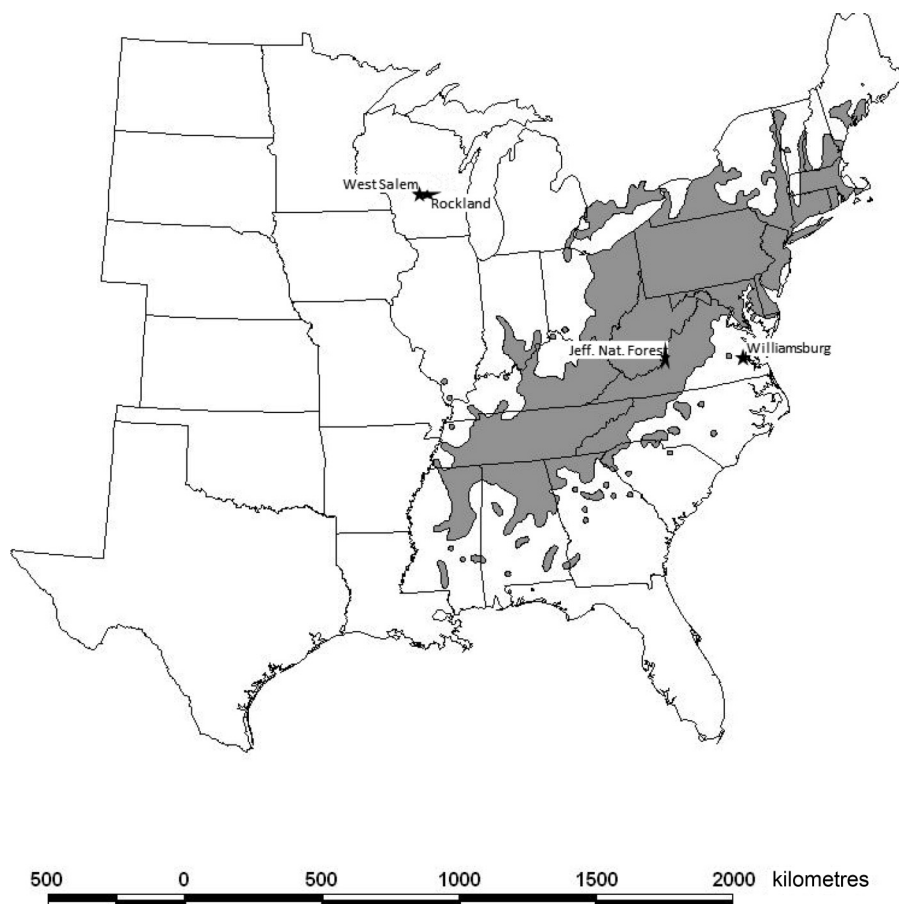
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Fig. 1. Locations where chestnut wood samples or growth data were collected. West Salem and Rockland are in Wisconsin, and Jefferson National Forest (Jeff. Nat. Forest) and Williamsburg are in Virginia. Shading indicates historical chestnut range.



extirpated by chestnut blight (*Cryphonectria parasitica* (Murrill) M.E. Barr), which is a fungal pathogen introduced from northeastern Asia (Jacobs et al. 2013). Chestnut may have been among the fastest growing eastern deciduous tree species, with growth rates comparable with those of trembling aspen (*Populus tremuloides* Michx.; Jacobs et al. 2009). Unlike aspen wood, chestnut wood is thought to have an intermediate to high resistance to decay, and chestnut trees are long lived (Brown and Panshin 1940; Mattson et al. 1987; Moss 1973; Smith 2000; Youngs 2000). Because of these qualities, forests dominated by chestnut trees may have been important sinks of C within their historical range that covered most of Appalachia (Fig. 1; Ellison et al. 2005; Jacobs et al. 2009).

Current efforts to reintroduce a blight-resistant chestnut in eastern North American forests emphasize the C storage characteristics of chestnut trees as one of the rationales for its re-introduction (Dalglish and Swihart 2012; Diskin et al. 2006; Griffin 2000; Jacobs et al. 2009, 2013; Ronderos 2000). However, many uncertainties hamper the estimation of the C storage potential of chestnuts. Historical C inventories of old-growth chestnut forests are unavailable, and the modern rarity of chestnut on the landscape precludes the estimation of C uptake by chestnut-dominated forests through common methods such as flux measurements (Paillet 2002; Baldocchi 2008) or repeated inventories (Harmon and Hua 1991; Muller and Liu 1991; Jacobs et al. 2009). In the case of chestnut, C storage potential can only be estimated in a modeling framework.

Forest carbon models need to account for the processes of growth, death, and decomposition (Masera et al. 2003; Scheller et al. 2007). However, although the fast growth of young chestnut trees and their high longevity are relatively well documented, the only

available quantitative estimate of the decomposition rates of chestnut wood (i.e., $k = 4.2\%$ loss of biomass per year) was measured on a single log in North Carolina (Mattson et al. 1987). Moreover, there is an ongoing discussion about the usefulness of the single-component decomposition model (i.e., $Y_t = Y(0)e^{-kt}$, Olson 1963) that is presupposed when decomposition rates are reported in terms of k values that express annual mass reductions (Harmon et al. 1986; Fraver et al. 2013; Manzoni et al. 2012). In particular, Fraver et al. (2013) fitted six decomposition models through sets of decomposition measurement data and found that a single-component decomposition model never performed well.

Ultimately, we seek to model the potential of chestnut to influence C storage and dynamics in natural forests within its former range. The present study includes the following two objectives necessary to reach that ultimate goal: (i) to evaluate a suite of decomposition models to simulate the decomposition of chestnut wood samples and derive a first approximation of parameter values for these models, and (ii) to assess the importance of accurate estimates of decomposition rates given the uncertainties in stand dynamics associated with growth and self-thinning in the chestnut-dominated forest types.

Materials and methods

Study sites

Two chestnut plantations (15 km apart) near West Salem, Wisconsin (43°90'N, 91°09'W), and Rockland, Wisconsin (43°91'N, 90°92'W), are located in the "driftless" area of southwestern Wisconsin, approximately 600 km west of the historical chestnut range (Fig. 1). The soil is generally fertile with a pH of 5.6–7.0;

Table 1. Locations and types of measurements.

Location	Age (years)	P_a (mm)	T_a (°C)	SI	Slope (%)	Aspect (°)	Measurements used	References
West Salem, Wisconsin	1–17	838	8.3	18.3	12	255	Dead wood samples	n/a
West Salem, Wisconsin	19	838	8.3	19.2–22.9	24	85	Crowns and boles (%C)	Jacobs et al. (2009)
Rockland, Wisconsin	8	838	8.3	20.1	17	40	Crowns and boles (%C)	Jacobs et al. (2009)
Rockland, Wisconsin	12	838	8.3	19.8	4	30	Crowns and boles (%C)	Jacobs et al. (2009)
Williamsburg, Virginia	10	1200	14.8	n/a	n/a	n/a	Dead wood samples	n/a
Jefferson National Forest, Virginia	18–58	1200	8.9	n/a	25.2±2.2	217±21	Biomass (dbh)	Reynolds and Burke (2011)

Note: Variable abbreviations: age, ages of the trees; P_a , annual precipitation; T_a , annual temperature; SI, site index; dbh, diameter at breast height. n/a means not available.

mean annual precipitation is 838 mm (National Oceanographic and Atmospheric Administration (NOAA) 2003). Chestnut was interplanted with black walnut (*Juglans nigra* L.) and red oak (*Quercus rubra* L.) in both plantations (Table 1; Jacobs and Severeid 2004; Jacobs et al. 2009). The trees in West Salem and Rockland were never fertilized or irrigated. The young chestnut trees grew extraordinarily fast (Jacobs and Severeid 2004; Jacobs et al. 2009) until chestnut blight occurred in both plantations around 2010. Currently almost all of the chestnut trees have died. Some of the trees were harvested after 12 years, and untreated tree stems were used for fence posts.

Locations in Virginia were the Jefferson National Forest (JNF) and the College Woods, Williamsburg, within the historical range of chestnut (Fig. 1). JNF is located in the foothills of the southern Appalachians in Craig County, Virginia (37°47'N, 80°23'W). Elevations of the chestnut sampling plots range from 600 to 800 m, with slopes from 14% to 50%. Aspect varies from northeast to southwest. Mean annual precipitation in nearby New Castle, Virginia, is 965 mm. The soils are mostly Typic Hapludults, coarse textured, siliceous, shallow, and with gravel-sized fragments common throughout the profile. The inherent nutrient content is low (Meiners et al. 1984). Chestnut blight reached the JNF around 1930. The Williamsburg College Woods are located on deep, well-drained soils on coastal plain fluvial sediments, classified as fine-loamy, thermic Ultic Hapludalfs, with slopes ranging from 0% to 15%. Mean annual temperature is 15 °C and mean annual precipitation is 1200 mm. Wood fences were constructed from untreated chestnut tree stems as part of a series of trail-improvement projects by the Civilian Conservation Corps between 1933 and 1934.

Growth and decomposition data

The primary source of growth data that was used in our simulations came from Reynolds and Burke (2011) and Jacobs et al. (2009). Reynolds and Burke (2011) estimated growth rates of chestnut trees in the JNF during the first and the last 10 years of the lifespans of chestnuts that died between the age of 1 and 58 years by measuring growth rings ($n = 78$). Jacobs et al. (2009) reported growth from 8-year-old chestnuts in Wisconsin ($n = 186$). The decomposition of chestnut wood was estimated using samples from Wisconsin and Virginia. Wisconsin samples came from the fence posts and from standing and downed dead trees on the hills. Approximately three crosssections were taken from each fence post; one at the ground subsurface, one at the soil surface, and a third at approximately 1 m above the surface. Both standing and downed dead trees were sampled at variable stem heights. Fence posts were sampled from the College Woods, Williamsburg, with a similar method.

All samples were weighed and dried to a constant mass at a temperature of 60 °C. In total, 67 samples were taken from West Salem and 39 samples were taken from Williamsburg. Decomposition rates were estimated from the current mass (W_t) and the estimated mass at the time of death of the trees (W_0). The time since the tree (sample) died (t) was determined either according to the planting dates and the age of the tree at the time of death or

from the documented time of fence construction (fence posts were assumed to have come from newly felled timber). W_t was associated with the measured dry mass of the samples. W_0 was derived from the estimated initial volume of the samples (V_0) and the initial density (ρ_0) according to $W_0 = \rho_0(V_0)$. V_0 was estimated from the current volume (V_t) of the samples, based on judgments of the sizes of abrasions. For example, V_0 of the more decomposed (typically ground contact) samples at the time of death was derived by estimating how volume differed with the better conserved (aboveground) parts of the same logs. For well-conserved samples, it was assumed that $V_t = V_0 \cdot Y_t$ of more intact, cylindrical-shaped samples was estimated from diameter and length, and the V_t of decomposed samples was measured by water displacement (Hughes 2005). A linear relationship was derived to relate sample volumes that were measured according to a water displacement method to volumes that were estimated from dimensions ($n = 10$; $y = 44.8 + 0.96x$, $R^2 = 0.92$). Decomposition was estimated according to $Y_t = W_t/W_0$, where Y_t is the fraction of remaining mass. Water content was estimated as the difference between fresh and dry mass. The climate for the Wisconsin sites was taken from Jacobs et al. (2009). Climate data was taken from Reynolds and Burke (2011) for the JNF and from NOAA (2003) for the Wisconsin plantations.

Decomposition modeling

We confronted alternative candidate models of decomposition with our data. Six curve shapes were combined with four variations of driving variables that take into account different climate conditions (Table 2). Functional response curves were selected from those proposed by Fraver et al. (2013) and Manzoni et al. (2012) because they have performed well for other tree species.

Each decomposition model predicts the fraction of initial mass that remains at time t (Y_t) from the initial sample mass ($Y_0 = 1.0$) and on the effective exposure time of a sample (τ). In the simplest models, we used a time-dependent driving variable (Table 2). More complex formulations of τ account for the effects of environmental factors such as moisture or temperature by increasing or reducing τ (Côtéaux et al. 2002). For example, a sample exposed to both high humidity and high temperature might reach a mass Y_{ref} faster, which is represented by a higher τ at a given chronological time. Generally, more complex decomposition models account for temperature and moisture by expressing τ as the integral of the correction factors, λ , for temperature or moisture over time. Correction factors are close to 1.0 when conditions are favorable for decomposition, and τ will be larger than when conditions are unfavorable for decomposition and the λ are closer to 0.0. We used a correction factor that depends on temperature, λ_t , to correct the effective exposure time according to a Q_{10} model of the response of decomposition kinetics to temperature (Table 2). Additionally, we used two variations of a correction factor that account for moisture, one that depends on water content in a sample, and one that depends on the precipitation deficit of a site. Finally, the temperature and moisture correction candidate models were combined to form more complex climate correction

Table 2. Model notations listed according to the process they were used to quantify.

Notation	In the text or in Table 3	φ_{init}	Units	Ref*
$Y_t = e^{-bt}$	Exponential (decomposition curve)	—	% DW	1, 2
$Y_t = f_{\text{labile}}(e^{-(a\tau)} + (1 - f_{\text{labile}})e^{-(b\tau)})$	TwoCompExp (decomposition curve)	—	% DW	3
$Y_t = e^{-\gamma t}$, where $\gamma = -(a/b)(t/b)^{a-1}$	FengAndLI (decomposition curve)	—	% DW	3, 4
$Y_t = 1/(1 + a\tau)$	Rational (decomposition curve)	—	% DW	2
$Y_t = 1 - (1 - e^{-bt})^b$	ChaRi (decomposition curve)	—	% DW	2
$Y_t = 1 - e^{-(a/t)^b}$	Weibull (decomposition curve)	—	% DW	2
A	Shape parameter in decomposition equation	$U[-\infty, \infty]$	—	
B	Shape parameter in decomposition equation	$U[-\infty, \infty]$	—	
f_{labile}	Initial labile fraction of dead material	$U[0, 1]$	—	
$\tau = \int \delta t$	Time dependent driving variable	—	Year	
$\tau = \int \lambda_{m,\text{msat}} \cdot \delta t$	Time- and $\lambda_{m,\text{msat}}$ -dependent driving variable	—	Year	
$\tau = \int \lambda_{m,\text{pdef}} \cdot \delta t$	Time- and $\lambda_{m,\text{pdef}}$ -dependent driving variable	—	Year	
$\tau = \int \lambda_t \cdot \delta t$	Time- and λ_t -dependent driving variable	—	Year	
$\tau = \int \lambda_t \cdot \lambda_{m,\text{pdef}} \cdot \delta t$	Time-, λ_t , and $\lambda_{m,\text{pdef}}$ -dependent driving variable	—	Year	
$\tau = \int \lambda_t \cdot \lambda_{m,\text{msat}} \cdot \delta t$	Time-, λ_t , and $\lambda_{m,\text{psat}}$ -dependent driving variable	—	Year	
$\lambda_{m,\text{msat}} = m/m_{\text{sat}}$	Factor that depends on water content in a sample	—	—	
$\lambda_{m,\text{pdef}} = P/\text{PET}$	Reduction actor depends on precipitation deficit	—	—	
$\lambda_t = Q_{10}^{[(T - T_{\text{opt}})/10]}$	Correction factor depends on temperature	—	—	5
P	Mean daily precipitation	—	mm·year ⁻¹	
PET	Mean potential evapotranspiration	—	mm·year ⁻¹	
T	Mean annual temperature	—	°C	
m_{sat}	Optimal sample water content for decomposition	$U[0, 1]$	g·g ⁻¹	
T_{opt}	Optimal temperature for decomposition	$U[20, 30]$	°C	
Q_{10}	Decomposition rate response to 10°C higher temperature	$U[1.5, 3]$	10 °C ⁻¹	
ρ	Initial wood density	$U[0.44, 0.48]$	—	
$d(\text{dbh})/dt = \alpha/(a - \beta) \cdot [e^{-\beta(\text{dbh})} - e^{-\alpha(\text{dbh})}]$	Diameter breast height (dbh) model	—	cm	6, 7
dbh_i	Initial dbh (cm)	1	cm	n/a
α	Growth curve parameter	$U[0.3, 0.5]$	—	
β	Growth curve parameter	$U[0, 0.2]$	—	n/a
c_1	Allocation coefficient (biomass from dbh)	0.075	—	8
c_2	Allocation coefficient (biomass from dbh)	2.417	—	8
g_1	Allocation coefficient (boles:stem)	-0.3065	—	8
g_2	Allocation coefficient (boles:stem)	5.424	—	8
$\text{TO} = \text{ANPP}/(\varepsilon + 1)$	Turnover from self-thinning	—	Mg·ha ⁻¹ ·yr ⁻¹	2
N_i	Initial stem density	$U[3000, 5000]$	—	10
ε	Thinning parameter	$U[1.71, 2.22]$	—	2

Note: Y_t is the fraction of initial mass as a function of time or a climate-corrected driver. DW is the dry mass in Mg·ha⁻¹. The correction factor is λ_c , where c is a climate factor. ANPP is the sum of biomass increments of individual trees and determines turnover (TO in Mg·ha⁻¹·year⁻¹), which is used to predict the reduction of stem density in the next year.

*Numbered references are as follows: 1, Olson (1963); 2, Fraver et al. (2013); 3, Manzoni et al. (2012); 4, Feng and Li (2001); 5, van't Hoff (1884); 6, Lucas 1959; 7, Huang and Titus 1995; 8, Zhou and Hemstrom (2009); 9, Franklin et al. (2009); 10, Jansen et al. 1996.

models that account for both temperature and moisture according to the two moisture dependency candidates.

The optimal decomposition model was selected by a maximum likelihood model (L_m), calculated for each candidate model in a Metropolis–Hastings variant of a Markov Chain Monte Carlo procedure (MCMC-MH: Metropolis et al. 1953). MCMC-MH is a method of directed searching for performance optima by sampling a parameter space that is defined a priori through likelihood distributions of the parameters (φ_{init} ; Table 2) that are derived from the literature or are uninformative (Table 2; $\varphi_{\text{init},i} \sim U[-\infty, \infty]$). Additionally, MCMC-MH can be used to determine confidence intervals in outputs, given the variability of the measurements. This is done through “acceptance sampling”, which singles out parameter sets that are associated with good model performance.

MCMC-MH was applied for each model and for all of the decomposition measurements to determine the optimal decomposition model. The Akaike weights (AIC_w) of the optimized decomposition models were used as a criterion for model selection (Akaike 1973). AIC_w was calculated from the L_m found in the MCMC-MH procedure. In addition to the AIC_w , coefficients of variation (R^2) were used to evaluate model performance. MCMC-MH was applied for the decomposition data from West Salem, Wisconsin, and Williamsburg, Virginia, separately. These applications were used to estimate the site-specific parameters.

We tested for significantly different means (Tukey's HSD test) in annual mass loss in Wisconsin samples that had soil contact during decomposition (i.e., downed dead trees and fence post cross sections taken from the soil surface), and Wisconsin samples that decomposed without touching soil, and Virginia samples (none of which touched the soil). We found that there was a significant difference between decomposition rates of wood that had decomposed on or below the surface and wood that decomposed without soil contact. The importance of this effect was analyzed in more detail by applications of MCMC-MH to appropriate subsets of decomposition data.

Modeling stand dynamics to project CWD

We simulated stand dynamics (stem growth and mortality) to project CWD pools in Wisconsin and Virginia separately, pooling the sites in West Salem and Rockland, Wisconsin, for simulation 1 and JNF and the College Woods, Virginia, for simulation 2. Simulations accounted for the growth and death of individual stems within a stand. Dead trees are added to the CWD pool, and decomposition reduces that pool over time. Similar to the methods used for fitting decomposition parameters, we used MCMC-MH procedures to fit the additional growth and thinning parameters to available stand data (Jacobs et al. 2009; Reynolds and Burke 2011). All simulations tracked dry biomass (DW) as the state variable.

C is inferred from the dry mass using a fixed concentration ($0.45 \text{ kg C} \cdot (\text{kg DW})^{-1}$).

Each simulation describes quantitative dynamics of stem growth, mortality, and consequent CWD accumulation and decay during one generation of two hypothetical chestnut-dominated stands. It was assumed that no wood was harvested; therefore, the production of CWD was equal to the turnover from live biomass. Each simulation describes biomass in two live, aboveground biomass pools (for boles and crowns) and in one decomposition pool (all in kg C ha^{-1}). CWD is the sum of CWD production from the two decomposition pools according to the following equation:

$$(1) \quad \frac{\delta \text{CWD}}{\delta t} = \text{TO}_{\text{snags}} + \text{TO}_{\text{boles}} - \text{Rh}$$

where TO is the turnover and Rh is decomposition. We used growth data from [Jacobs et al. \(2009\)](#) for Wisconsin (simulation 1) and [Reynolds and Burke \(2011\)](#) for Virginia (simulation 2) to fit a diameter at breast height (dbh; 1.3 m) model that expresses the annual increment of dbh as it depends on dbh (Table 2). The behavior of this model is a steep increase of diameter early in the life of a tree, followed by a gradual incremental decline as the tree ages. Preliminary simulations indicated that the sensitivity of predicted CWD pools to initial dbh (dbh_i) was minimal, provided that $\text{dbh}_i < 10 \text{ cm}$. For simplicity, dbh_i remained constant ($\text{dbh}_i = 1 \text{ cm}$) in all simulations. Aboveground biomass and the root to shoot ratio are derived from dbh according to allocation coefficients for hardwood tree species with growth forms comparable with those of chestnut (see table 2: allocation coefficients derived from hard maple–oak–hickory–beech in [Zhou and Hemstrom 2009](#)). We assumed identical allocation coefficients for Virginia and Wisconsin.

Turnover is expressed according to a simplification of the self-thinning model by [Franklin et al. \(2009\)](#) that can be derived when it is assumed that all the trees are of equal size (Table 2). The calculation of turnover uses a parameter ε that is species specific and depends on factors such as root dynamics and crown width that determine stem-density dynamics in the course of the maturation of a tree stand. [Franklin et al. \(2009\)](#) proposed an ε that ranged from 1.7 to 2.2 for different tree species. We used $\varphi(\varepsilon) \sim U[1.7, 2.2]$ and fitted the ε to typical stem densities for European beech (*Fagus sylvatica* L.) reported in a silviculture manual ([Jansen et al. 1996](#)). We selected European beech because it is in the same family as the American chestnut and shares a similar crown width, stature, and ecological niche and a somewhat comparable shade tolerance. Stem density is used to implement turnover via ANPP, which can be derived from biomass increments in stems and branches. The number of trees is decreased and the stem and boles litter pools are increased with the stem and (or) bole mass of the dead tree when the amount of dead biomass exceeds the simulated biomass of a tree.

Rh was calculated with the decomposition model that best described measured mass reductions from all the decomposition samples according to the AIC_w . The decomposition parameters were random draws from parameter combinations generated in MCMC-MH applied to wood samples from either Wisconsin or Virginia that met the acceptance criterion in MCMC-MH. The simulation length of each of the simulations was set at 350 years, which is equal to the approximate longevity of chestnut ([Loehle 1987](#)).

We evaluated whether the model was projecting plausible biomass dynamics by comparing the range of modeled biomass with that of measured hardwood systems from the same region based on Forest Inventory and Analysis (FIA) data (see table 10 in [Smith et al. 2006](#)). Simulated DW at the Wisconsin sites was compared with measurements that were selected from entries of the Northern Lake States. Simulated biomass at the Virginia sites were compared with FIA measurements from the southeastern U.S. Simulated CWD

pools were compared with measurements for all hardwood forest types reported in (raw) FIA data. There were more CWD measurements available from the FIA dataset for the Wisconsin area than for the southeastern U.S. Therefore, we used a narrower selection criterion for biomass measurements in Wisconsin than in Virginia. In Wisconsin, we used FIA biomass measurements from counties with a seat within 100 km of West Salem. FIA data for nearby locations in Virginia were scarce, so we were forced to include data from the entire state for Virginia.

We evaluated the contribution of the different sources of uncertainty (growth, demography, decomposition) to overall uncertainty. Overall uncertainties (of the combined growth, demography, and decomposition simulations) were determined by allowing all the simulation parameters to vary in the MCMC-MH procedure. In subsequent runs, the uncertainty from one of the three sources was excluded by fixing the values of parameters used to calculate growth, demography, or decomposition in values that were associated with L_m . For example, a , b , f_{labile} , m_{sat} , Q_{10} , and T_{opt} were fixed to exclude decomposition, or α and β were fixed to exclude growth, or N_i and ε were fixed to exclude uncertainties in stem density.

The variability of model output associated with the two remaining sources of uncertainty was compared with the total spread in the outputs of CWD. For example, when the uncertainty ranges that are found when a particular group of parameters (decomposition, growth, demographics) are fixed are considerably smaller than when all uncertainty is taken into account, then this can be interpreted as an indication that much of the overall uncertainty is related to the parameters that are fixed. Hence, when a strong convergence of the maximum and minimum curves occurs with fixing a particular set of parameters, this indicates that much of the overall uncertainty was associated with this mechanism. Additionally, we can derive whether there is a threat of model bias related to uncertainty in particular sets of parameters. For example, when fixing a set of parameters (associated with growth, decomposition, demographics) leads to generally higher CWD, this can be understood as an indication that uncertainty in growth, decomposition, and demographics tends to lead to an overestimation of predicted CWD pools in forest C modeling.

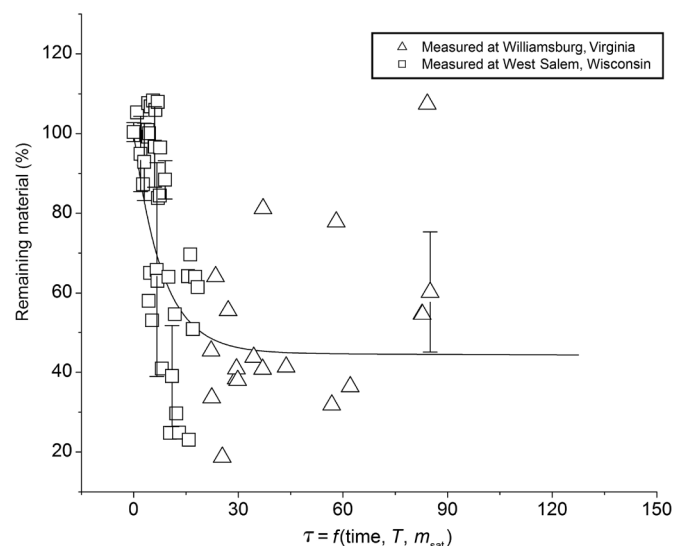
Results

Decomposition samples and simulation

Sixty-seven wood samples were taken in West Salem and 39 in Williamsburg, for a total of 106 samples. There was a strong representation of 11- and 85-year-old samples, which is due to the sampling of the fence posts. The mean diameter of the samples was $11.2 \pm 0.7 \text{ cm}$, the minimum was 4.7 cm, and the maximum was 37.7 cm. The mean volume of samples was $756.6 \pm 95.0 \text{ cm}^3$, and the mean estimated mass loss fraction was 0.38 ± 0.12 per year. In 16 of 106, the Y_t exceeded Y_0 because of uncertainties in V_0 . Tukey's HSD test indicated that there were highly significant differences in the annual mean decomposition rates between the Wisconsin samples that decomposed in contact with the soil and the Wisconsin or Virginia samples that did not decompose in contact with the soil ($p < e^{-7}$). However, there was no significant difference between samples that decomposed without soil contact in either Wisconsin or Virginia ($p = 0.87$). The best decomposition model was a two-component exponential decomposition model (TwoCompExp), which took the temperature and sample moisture content into account (Fig. 2; Table 3, row 2, column 2; note that a good model performance is associated with high R^2 , low AIC, and high AIC_w).

The expressions for the driving variables τ for the high-ranked decomposition simulation models were heterogeneous. Surprisingly, the simplest form of τ , which did not account for any climatic conditions, occurred two times in the top five ranked models (Table 3, case 3; Table 3, case 5). This indicates that the

Fig. 2. Optimum decomposition (remaining material (%)) model fit with a two-component exponential model ($\tau = f(\text{time}, T, m_{\text{sat}})$) that accounts for sample moisture content (m_{sat}) and air temperature (T).



Akaike penalty for additional parameters is high even when $n = 106$, which is a relatively high number of samples for decomposition studies. Similarly, models that take both temperature and precipitation deficit (pdef) into account tended to perform worse than models that accounted for only temperature or moisture (Table 3; note that $\lambda_{m,pdef}$ -dependent drivers are absent in the best performing versions of TwoCompExp or FangAndLI). Estimated labile fractions, f_{labile} , were consistent among the expressions of TwoCompExp that accounted for climate (ranging from 0.44 to 0.49); however, $f_{\text{labile}} = 0.26$ when the driving variable did not correct for climate. The estimates of the temperature response parameter Q_{10} ranged from 2.1 to 2.4, and the estimates for the optimum decomposition temperature, T_{opt} , ranged from 20.6 to 25.5 °C.

Decomposition rates were considerably higher in Wisconsin than in Virginia. Annual decomposition rates, estimated with a single-component exponential model (i.e., the parameter b in exponential, Tables 2 and 3), were an order of magnitude higher in Wisconsin than in Virginia. For our Wisconsin decomposition samples, we found decomposition rates of $4.3 \pm 0.3\%$ per year. In contrast, we found decomposition rates of $0.8 \pm 0.1\%$ per year for the wood samples from Virginia. However, there were similarly large differences within Wisconsin decomposition samples. Downed dead wood decomposed at a rate of $8.1 \pm 1.9\%$ per year in Wisconsin locations. Standing dead wood samples decomposed slower in Wisconsin than in Virginia, with a rate of $0.7 \pm 0.0\%$ per year. Confidence intervals of the decomposition rate measurements from standing wood in Wisconsin overlap with the decomposition rate estimates of standing wood in Virginia, which confirms the results of the Tukey's HSD test.

Stand-level stem growth and CWD

Growth rates of chestnut trees that were documented in West Salem by Jacobs et al. (2009) are considerably higher than growth rates documented in JNF by Reynolds and Burke (2011). Growth rates measured in JNF ranged from 0.63 ± 0.14 cm annual dbh increment in the first 10 years of a life span to 0.60 ± 0.22 in the last 10 years of the life span of the tree. Jacobs et al. (2009) measured much faster increments in tree dbh in the Wisconsin sites, which ranged from 1.6 ± 0.05 to 1.8 ± 0.07 cm per year.

The curves fitted through measurements of dbh from the two locations captured the observed differences in growth rates in Wisconsin well ($R^2 = 0.68$) but did not capture the growth rates in

Virginia forests ($R^2 = 0.01$). The maximum optimum in simulated annual dbh increment occurred early in the life of chestnut trees, at 8 years old in Wisconsin, and at 9 years old in Virginia, with growth rates then declining in both locations. Simulated stand-level aboveground biomass reached a maximum around 200 years in both sites (Fig. 3; Table 4). In Wisconsin, this maximum exceeded the maximum in Virginia by $\sim 100\%$ (Table 4). Wisconsin biomass predictions of 524 ± 58 Mg DW·ha⁻¹ were high compared with the 99% upper percentiles in FIA data (Smith et al. 2006) in the Northern Lake States: aspen–birch forest (340 Mg DW·ha⁻¹), elm–ash–cottonwood (600 Mg DW·ha⁻¹), and maple–beech–birch (460 Mg C·ha⁻¹). In Virginia, the maximum biomass prediction of 362 ± 51 Mg DW·ha⁻¹ was somewhat lower than the 99% upper percentiles in FIA data (Smith et al. 2006) in southeastern hardwoods: oak–gum–cypress (527 Mg DW·ha⁻¹) and oak–hickory (584 Mg DW·ha⁻¹). In Wisconsin, forecasts of CWD pools reached a maximum of 91 ± 51 Mg DW·ha⁻¹ after 261 years. This is much lower than in Virginia, where CWD pools were still increasing at the end of the simulation of 350 years. CWD pools in nearby Wisconsin FIA plots ranged from ~ 22 Mg DW·ha⁻¹ ($n = 1$) for red maple–oak, to 365 ± 136 Mg DW·ha⁻¹ for lowland red maple ($n = 16$). Note that because $n = 1$ for red maple–oak and because the highest volume of CWD was measured in red maple dominated forest types, measured CWD in red maple–oak could have been an anomaly. If the red maple–oak measured CWD is ignored, the lowest CWD in Wisconsin was measured in paper birch: 17.2 ± 8.8 Mg DW·ha⁻¹ ($n = 12$). CWD pools in Virginia ranged from 311 ± 118 Mg DW·ha⁻¹ ($n = 10$) to 444 ± 107 Mg DW·ha⁻¹ ($n = 16$).

There was a considerable convergence of uncertainty ranges in the simulations of Wisconsin when decomposition parameters remained constant (Fig. 3). This contrasted strongly with the simulation of Virginia, where uncertainty ranges in predictions barely converged (Fig. 3). The uncertainty ranges in CWD predictions with fixed decomposition parameters are in the lower ranges of the overall prediction ranges in the Wisconsin simulations but are higher than overall uncertainty ranges in the Virginia simulations. The sensitivity to uncertainties in growth parameters was more consistent among the two simulations (Fig. 3). There was little or no convergence of uncertainty ranges in either simulation when growth parameters were fixed. In both simulations, uncertainty ranges were in the upper ranges of overall uncertainty. There was no convergence of uncertainty ranges in either simulation when demographic parameters were fixed. In both simulations, uncertainty ranges associated with fixed demographics parameters exceeded ranges of overall uncertainty.

Discussion

Observed variability in American chestnut decay rates

Multiple sources indicate that chestnut wood is highly resistant to decomposition (Brown and Panshin 1940; Mattson et al. 1987; Moss 1973; Forest Products Laboratory 1999; Smith 2000; Youngs 2000). These claims should be interpreted with caution, primarily because Brown and Panshin (1940), Moss (1973), and the Forest Products Laboratory (1999) evaluate the longevity of chestnut wood from a silvicultural rather than ecological perspective. Smith (2000) and Youngs (2000) refer to Brown and Panshin (1940) and Moss (1973) but do not add any new knowledge about decomposability. In fact, the only published estimate of chestnut decomposition in a (semi-) natural environment was derived from a single log (Mattson et al. 1987).

Our study provides a greater range of site conditions, and we measured decomposition rates from a substantially larger dataset ($n = 106$). We recognize the limitations of our dataset (see caveats below) but believe that they allow a useful first approximation of chestnut decomposition rates. Our estimate of $4.3 \pm 0.3\%$ per year ($n = 106$) is slightly higher than the 4.1% per year ($n = 1$) estimate of Mattson et al. (1987), which ranks decomposability of chestnut

Table 3. Performance of candidate decomposition models used to evaluate changes in Y in decomposition data from Williamsburg and from West Salem.

Model	CurveShape	Driving variable	m_{sat}	f_{labile}	a	b	Q_{10}	T_{opt}	R^2	AIC _w
1	TwoCompExp	Time and $\lambda_{m,\text{msat}}$ dependent	0.10	0.45	0.001	0.121	—	—	0.37	0.145
2	TwoCompExp	Time and λ_t dependent	—	0.49	0.511	0.000	—	—	0.30	0.123
3	TwoCompExp	Time dependent	—	0.43	0.127	0.001	—	—	0.29	0.099
4	TwoCompExp	Time, λ_t , and $\lambda_{m,\text{pdef}}$ dependent	—	0.51	0.601	0.000	1.6	24.6	0.41	0.093
5	FangAndLI	Time dependent	—	—	0.031	0.144	—	—	0.23	0.088
6	FangAndLI	Time and λ_t dependent	—	—	0.076	0.000	—	—	0.22	0.077
7	ChaRi	Time dependent	—	—	0.001	0.262	—	—	0.22	0.073
8	ChaRi	Time and λ_t dependent	—	—	0.000	0.179	—	—	0.20	0.051
9	FangAndLI	Time and $\lambda_{m,\text{pdef}}$ dependent	0.05	—	0.021	0.285	—	—	0.25	0.044
10	Rational	Time and $\lambda_{m,\text{pdef}}$ dependent	0.04	—	—	0.033	—	—	0.23	0.043
11	ChaRi	Time and $\lambda_{m,\text{pdef}}$ dependent	0.07	—	0.004	0.389	—	—	0.24	0.041
12	TwoCompExp	Time and $\lambda_{m,\text{pdef}}$ dependent	0.07	0.50	0.111	0.000	—	—	0.30	0.039
13	FangAndLI	Time and $\lambda_{m,\text{msat}}$ dependent	0.02	—	0.043	0.100	—	—	0.21	0.019
14	ChaRi	Time and $\lambda_{m,\text{msat}}$ dependent	0.12	—	0.001	0.249	—	—	0.19	0.012
15	FangAndLI	Time, λ_t , and $\lambda_{m,\text{pdef}}$ dependent	—	—	0.086	0.000	1.5	22.4	0.23	0.010
16	Weibull	Time and λ_t dependent	—	—	1.000	0.090	—	—	0.18	0.008
17	Rational	Time and $\lambda_{m,\text{msat}}$ dependent	0.13	—	—	0.049	—	—	0.21	0.006
18	Exponential	Time and $\lambda_{m,\text{pdef}}$ dependent	0.22	—	—	0.020	—	—	0.20	0.005
19	ChaRi	Time, λ_t , and $\lambda_{m,\text{pdef}}$ dependent	—	—	0.001	0.180	2.2	24.0	0.19	0.004
20	FangAndLI	Time, λ_t , and $\lambda_{m,\text{psat}}$ dependent	0.01	—	0.083	0.000	1.6	22.9	0.24	0.004
21	TwoCompExp	Time, λ_t , and $\lambda_{m,\text{psat}}$ dependent	0.20	0.49	0.539	0.000	1.6	24.9	0.30	0.004
22	Rational	Time dependent	—	—	—	0.020	—	—	0.19	0.003
23	ChaRi	Time, λ_t , and $\lambda_{m,\text{psat}}$ dependent	0.09	—	0.002	0.230	2.2	23.2	0.21	0.002
24	Weibull	Time dependent	—	—	1.000	0.035	—	—	0.09	0.002
25	Weibull	Time and $\lambda_{m,\text{msat}}$ dependent	0.05	—	1.000	0.041	—	—	0.09	0.001
26	Weibull	Time and $\lambda_{m,\text{pdef}}$ dependent	0.11	—	1.000	0.035	—	—	0.08	0.001
27	Weibull	Time, λ_t , and $\lambda_{m,\text{pdef}}$ dependent	—	—	1.000	0.136	1.9	22.7	0.21	0.001
28	Exponential	Time dependent	—	—	—	0.010	—	—	0.16	0.000
29	Exponential	Time and $\lambda_{m,\text{msat}}$ dependent	0.23	—	—	0.035	—	—	0.16	0.000
30	Exponential	Time and λ_t dependent	—	—	—	0.016	—	—	0.14	0.000
31	Exponential	Time, λ_t , and $\lambda_{m,\text{pdef}}$ dependent	—	—	—	0.140	2.2	24.7	0.19	0.000
32	Exponential	Time, λ_t , and $\lambda_{m,\text{psat}}$ dependent	0.15	—	—	0.035	2.2	24.5	0.15	0.000
33	Rational	Time and λ_t dependent	—	—	—	0.029	—	—	0.14	0.000
34	Rational	Time, λ_t , and $\lambda_{m,\text{pdef}}$ dependent	—	—	—	0.173	2.1	23.6	0.20	0.000
35	Rational	Time, λ_t , and $\lambda_{m,\text{psat}}$ dependent	0.04	—	—	0.073	2.0	22.7	0.17	0.000
36	Weibull	Time, λ_t , and $\lambda_{m,\text{psat}}$ dependent	0.05	—	1.000	0.111	1.6	21.3	0.19	0.000

Note: All the curves were tested using time as a driving variable (τ) or using an “equivalent temperature and water saturated time” that depends on temperature and either a site-specific precipitation deficit (P/PET) or the moisture content of the sample (m) relative to a saturation point (m_{sat}), where $\tau_{\text{ms}} = \tau_t \cdot m/m_{\text{sat}}$ · time when $m < m_{\text{sat}}$ or $\tau_{\text{ms}} = 1$ when $m \geq m_{\text{sat}}$. a and b are shape parameters, and f_{labile} is a fraction of labile components in the wood.

wood between scarlet oak (*Quercus coccinea* Münchh.; $5.0\% \pm 0.6\%$ per year, $n = 13$) and eastern hemlock (*Tsuga canadensis* (L.) Carrière; $2.4\% \pm 0.3\%$ per year, $n = 2$) or black locust (*Robinia pseudoacacia* L.; $1.5\% \pm 0.5\%$ per year, $n = 6$) (Mattson et al. 1987). We found dramatic differences between decomposition rates in Wisconsin plantations ($4.3\% \pm 0.3\%$ per year) and Virginia forests ($0.8\% \pm 0.1\%$ per year), as well as between samples that did not touch the ground ($0.7\% \pm 0.0\%$ per year) and samples that did touch the ground ($8.1\% \pm 1.9\%$ per year). The mixing of standing and downed dead wood in our dataset may have caused much of the difference in decomposition rates between Virginia and Wisconsin. Wisconsin samples decomposed approximately five times faster than Virginia samples, but we did not have samples of downed dead wood from Virginia. Decomposition rates in standing dead wood (including fence posts) were nearly identical.

Because we had no downed dead wood from the Virginia sites at our disposal, it would be premature to conclude that chestnut wood decomposes faster in our Wisconsin sites than in Virginia. However, we believe that there are strong indications that chestnut decomposition in the Wisconsin plantation was exceptionally high. For example, our reduction rate of approximately 8% per year contrasts with Smith (2000) and Moss (1973) who anecdotally suggest that untreated chestnut beams used as railroad ties “would last for decades on the ground without treatment.” Furthermore, the estimated decomposition rate of downed chestnut wood by Mattson et al. (1987) from the southern Appalachians lies

well outside our confidence interval for the chestnut decomposition rate of downed dead wood in Wisconsin. In fact, a rate of decomposition of $8.1\% \pm 1.9\%$ per year puts the chestnut decomposition rate among the most rapid half of tree species discussed in Mattson et al. (1987). This is remarkable because the Wisconsin locations are both colder and drier than either Williamsburg in Virginia or the southern Appalachians where Mattson et al. (1987) studied decomposition, and all of these three locations lie in temperature-limited biomes (Way and Oren 2010).

We speculate that the growth rates of the donating trees may be responsible for the faster decomposition rates in Wisconsin. Wood from slower growing trees with generally higher wood density tends to decompose less rapidly than the low-density wood from the faster growing trees (Cornelissen et al. 2012). There are several indications that the chestnuts in Wisconsin were growing exceptionally fast. For example, Jacobs et al. (2009) measured growth rates of chestnut in Wisconsin that were two to three times as fast as those measured by Reynolds and Burke (2011) in Virginia. This may be related to differences in the light regime — evidence from tree rings and other eco-physiological studies suggests that the chestnut exhibits strong positive growth responses based on the light environment (McEwan et al. 2006; Jacobs 2007; Joesting et al. 2007). The chestnuts in Wisconsin were plantation grown with no overstory and would have received much more radiation than the chestnuts in JNF that grew in a natural forest. Additionally, the loamy southern Wisconsin soils are generally

Fig. 3. Modeled quantitative CWD ($\text{Mg C}\cdot\text{ha}^{-1}$) dynamics in two chestnut monocultures and uncertainty analysis in CWD predictions according to source. Shown are simulations based on data from Wisconsin plantations and the Virginia forest site. Each scenario represents a Markov Chain application in which the parameters associated with growth, demographics, and decomposition are fixed (i.e., uncertainty in representations of growth, demographics, and decomposition are excluded from the combined model uncertainty). Each scenario is shown in threefold such that the center line represents the optimal model performance, the upper line represents +1 SD and the lower line represents -1 SD. Simulated dynamics of CWD are compared with CWD measured in FIA inventories in nearby locations in other forest types (<100 mile radius in Wisconsin; all of Virginia, $\pm\text{SE}$).

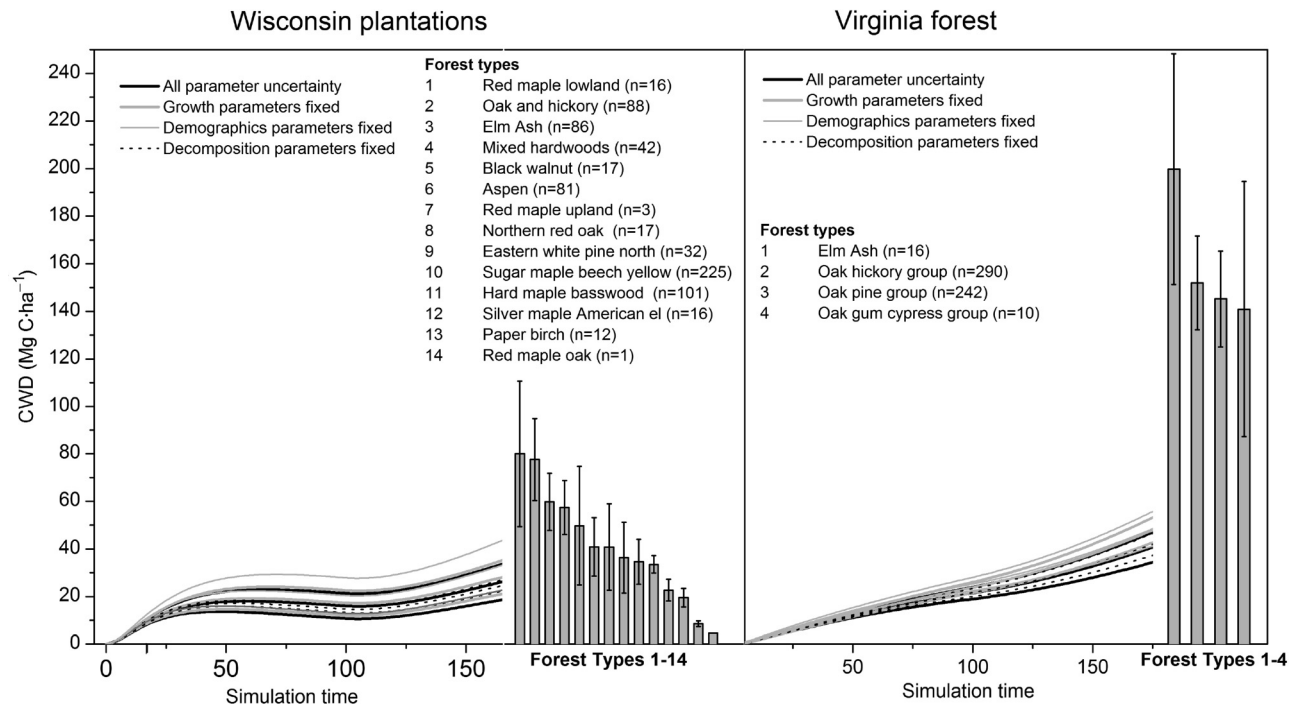


Table 4. Maxima in simulations of CWD using three different decomposition models ($\pm\text{SD}$).

	Virginia	Wisconsin
Maximum biomass, $\text{Mg DW}\cdot\text{ha}^{-1}$	385 ± 51 (174 years)	542 ± 58 (163 years*)
Maximum CWD, $\text{Mg C}\cdot\text{ha}^{-1}$	98 ± 23 (350 years)	41 ± 23 (261 years)

*The time at which the maxima occurred.

more fertile than southern Appalachian soils. It is likely that the site fertility enhances decomposition processes because high nitrogen concentrations in bacterial tissues require decomposer communities to extract soil nitrogen to build body mass when their food source is low in nitrogen (Norris et al. 2013). Tree growth and decomposition rates of wood are likely to respond to similar site conditions such as nitrogen, water availability, and temperature. Therefore, there is a relationship between growth and decomposition rates through the density of the wood, and they are positively correlated because they are driven by common factors such as soil nutrients, water availability, and temperature (Weedon et al. 2009). Because growth and decomposition rates are correlated, it is not straightforward to predict how CWD pools depend on either factor when viewed in isolation. Chestnut remains extirpated; therefore, it will be impossible to compare how CWD in chestnut sites respond to site fertility for at least three decades. However, the consistency between simulated CWD in Wisconsin and Virginia and corresponding measurements of CWD in other forest types in these two locations is interesting and warrants further exploration (Fig. 3). Results of our sensitivity analysis that focused on the importance of the different processes (growth demographics and decomposition) indicate that not only the size of predicted CWD

pools but also the importance of the three processes (growth, turnover, and decomposition) depend on tree growth. For example, the uncertainty ranges in predicted CWD sizes decreased substantially more in the Wisconsin simulations than in the Virginia simulation (Fig. 3), where decomposition parameters remained constant. Simulated growth rates in the Wisconsin plantations were substantially higher than in the Virginia site. We hypothesize that the sensitivity of CWD pools to decomposition rates is much higher in a fast-growing stand such as the Wisconsin plantations than in a slow-growing stand such as the Virginia site. Therefore, when simulating CWD accumulation as a function of growth and decomposition, it will be more important to obtain accurate estimates of decomposition rates in fertile sites; whereas in slower growing sites, published estimates may be sufficient to predict CWD accumulation. The magnitude of uncertainty in CWD predictions differs not only with site fertility but also with the direction of potential error. Fixed decomposition parameters were generally associated with lower CWD estimates in Wisconsin, whereas the reverse held true for the Virginia predictions of CWD (Fig. 3). This indicates that simulated CWD pools are prone to overestimation due to uncertainties in decomposition rates in fertile locations but underestimation in nutrient poor locations.

Assumptions and caveats

1. The most important caveat is that the ratio of downed versus standing debris in our samples is not necessarily representative of a forest ecosystem. This is a problem because we found that the decomposition rate of downed dead wood is almost an order of magnitude faster than that of standing dead wood. Little is known about factors such as snag fall or branches that break during senescence, but the proportion of biomass that reaches the ground has important consequences for carbon

sequestration. A related caveat is our reliance on fence posts for decomposition samples. We relied on fence posts because the dates when the fences were constructed were documented, whereas we typically do not know when individual trees in a stand died. However, we believe that this is not a major issue because there was no significant difference in the decomposition rates of standing dead wood and the aboveground parts of fence posts (ANOVA, $p < 0.001$), which suggests that the decomposition of aboveground fence posts is a good representation of decomposition of standing dead wood. Similarly, we did not find a significant difference in the decomposition of downed dead wood and belowground or surface fence posts (ANOVA, $p < 0.001$), which indicates that decomposition in surface or belowground fence posts is a good representation of downed dead wood.

2. Both the documented growth rates and the decomposition samples were taken from young trees. Our samples were from trees that had been dead for less than 18 years and originated from young (<19 years old) trees and (or) smaller sized wood. The Virginia samples were all 85 years old, whereas the growth measurements originated from trees that were <58 years old. We are unaware of the existence of more appropriate chestnut stands for study (i.e., old chestnut trees that died at a time that is well documented). As far as the growth of chestnut is concerned, it should be possible to retrieve better estimates of historic growth rates of chestnuts from the tree rings of blight-killed chestnut trees in the Appalachians, but to our knowledge, there are no such datasets currently available. The consequences of our reliance on young trees for both growth and decomposition estimates on predictions of carbon dynamics is highly uncertain. Typically, older trees grow more slowly and produce more dense wood that decomposes less rapidly, which suggests that the two inaccuracies may cancel each other out to some extent. However, it is possible to evaluate the usefulness of the simulation results in different temporal ranges. The purpose of this research is to analyze the sensitivity of the accumulation of biomass and CWD pools to growth, decomposition, and demographics and to derive quantitative first approximation estimates of pool sizes. We believe that our quantitative pool size estimates should be considered valid for only slightly more than the age range found in our samples (i.e., approximately 0–20 years for Wisconsin and 0–60 years for Virginia). The temporal range of usefulness of the simulation results for an analysis of the sensitivity of the accumulation of CWD to growth, demographics, and decomposition is wider, primarily because the onset of slower growth was predicted to occur at the young age of 8 years in Wisconsin and 9 years in Virginia. It is very likely that the simulations accurately predict the timing when biomass reaches a maximum and, because CWD strongly depends on productivity, the accumulation of CWD. Maximum biomass was predicted at the age of 174 years in Virginia and 163 years in Wisconsin.
3. We were forced to assume that no considerable loss of volume had occurred in the decomposition samples that appeared intact because we had no measurements of the initial diameters or volumes of the wood. This was a considerable problem when we were dealing with highly decomposed CWD. In such cases, original volumes were not easy to estimate and our calculations probably underestimated the V_0 of the sample. However, we discarded highly decomposed samples that we believed precluded an accurate estimate of V_0 .
4. We assumed that our estimates of growth and decomposition rates could be pooled by state, resulting in just one simulation for each state. Because we found that the fertility and growth rates explain many of the differences between decomposition rates, this assumption is more justified if the wood in the College Woods grew at a similar rate as the trees in JNF or if the wood in West Salem grew at a similar rate as the trees in

other Wisconsin plantations. We evaluated these assumptions by comparing reported tree ring thickness with measurements of the mean thickness of the oldest five tree rings in our decomposition samples. This was done with selected samples that were taken at 20 cm above the ground to allow for a comparison with basal increments as reported by [Jacobs et al. \(2009\)](#). The Virginia samples were all taken from fences; therefore, it was unclear from what part of the original tree stems the wood originated. In spite of this uncertainty, we gained additional estimates of the historical growth rates by measuring growth ring thickness of Virginia fence posts. The mean thickness of the inner growth rings of samples from Williamsburg was 0.4–0.5 cm. The mean thickness of the inner growth rings in wood samples from Wisconsin was 1.7 ± 0.2 cm. This indicates that the growth rates in JNF ([Reynolds and Burke 2011](#)) were comparable with the growth rates of the donated tree samples from Williamsburg, thus allowing for the pooling of JNF and Williamsburg data. Similarly, growth rates in the different Wisconsin plantations were comparable with growth rates in West Salem based on a comparison of documented tree growth with measured tree ring thickness from the wood samples ([Jacobs et al. 2009](#); [Reynolds and Burke 2011](#)).

5. Our simulations represented a monoculture of single-aged chestnut stands. Other than in plantation settings, however, chestnuts are likely to occur in stands of mixed age and species composition. It is unlikely that chestnuts ever completely dominated forests in the Appalachians, historically occupying only up to 45%–50% of the canopy even prior to the blight ([Keefer 1953](#)). Similarly, the measurements of growth in our study are based on relatively young trees; the contribution of older trees is slightly better for the Virginia data (maximum 58 years old) than for the Wisconsin data (maximum 17 years old).
6. In Wisconsin, we used FIA biomass measurements from counties with a seat within a radius of 100 km from West Salem, and we used the entire state for Virginia. It is unclear if more CWD measurements from closer Virginia locations would have changed our conclusions. In particular, oak species were more abundant in CWD measurements from Virginia. We speculated that CWD may be higher in the Virginia locations due to lower fertility in the sandy Appalachian soils. Due to the strong representation of oaks in the Virginia FIA measurements, there is still a potentially important role for species-specific decomposition traits.

Conclusions

Our results are only somewhat consistent with anecdotal evidence suggesting that chestnut wood is moderately resistant to decomposition, which would increase chestnut C sequestration potential, particularly in nonharvested forests. We found that the decomposition of chestnut wood is highly dependent on whether the wood is downed or standing, with decomposition rates approximately an order of magnitude higher for downed dead wood. Several researchers have found similar results ([Harmon et al. 1986](#)). This issue remains important for projections of long-term CWD pools for chestnut because the dead tree fall rate cannot be estimated with any certainty. Furthermore, our comparison across study sites and other available literature appears to indicate that decomposition rates of chestnut wood depend strongly on growth rates, suggesting a need for a more holistic approach that compares growth and decomposition responses to site qualities rather than growth or decomposition in isolation. Our simulations indicate that chestnut produces larger CWD pools in nutrient-poor locations than in nutrient-rich locations. These results agreed with FIA data indicating that CWD pools in other forest types tend to be higher in Virginia than in Wisconsin. Compared with other

forest types, we predicted CWD pool sizes that are moderate to high in Wisconsin but on the low side in Virginia. However, due to the uncertainties that are inherent when simulating biomass dynamics of a species that currently is as rare as chestnut, a straightforward and quantitative comparison of our simulation results with measured CWD is difficult. In spite of these uncertainties, we were able to derive several important indications with respect to predictions of carbon sequestration potentials in chestnut

- We produced better estimates of chestnut wood decay rates and variability than previously available.
- We found a considerable difference between decomposition rates of standing and downed dead wood. Although it is well known that downed dead wood decomposes much faster than standing dead wood, there are few or no studies that quantified this rate difference for American chestnut.
- Simulations of CWD accumulation suggested that decomposition rates have a stronger effect than growth rates on long-term CWD in a nondisturbed site.
- There were indications that the uncertainty in predictions of CWD pools by forest carbon models is larger in fast-growing ecosystems, and the potential to overestimate carbon due to unknown decomposition rates is larger in infertile ecosystems.

We expect that these findings bear relevance for forest carbon simulations not only of chestnut trees, but also of other species.

Acknowledgements

Funding support was provided by Purdue University, USDA Forest Service, and USDA National Institute of Food and Agriculture Grant No.105321. We thank Shawn Fraver for help with model selection and a rich input of ideas and Bill Mattson for information on wood decomposer communities. We also thank the Associate Editor and anonymous reviewers who helped improve the manuscript.

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