

Biomass accumulation in trees and downed wood in northern hardwood forests: Repeated measures of a successional chronosequence in New Hampshire, USA

Joseph M. Nash ^{a,b}, Matthew A. Vadeboncoeur ^{b,c}, Gregory G. McGee ^{b,d}, Christopher W. Woodall ^{b,e}, and Ruth D. Yanai ^{b,a}

^aDepartment of Sustainable Resources Management, SUNY College of Environmental Science and Forestry, Syracuse, NY 13210, USA;

^bClare Conservation District, Harrison, MI 48625, USA; ^cEarth Systems Research Center, University of New Hampshire, Durham, NH 03824, USA; ^dDepartment of Environmental Biology, SUNY College of Environmental Science and Forestry, Syracuse, NY 13210, USA;

^eNorthern Research Station, USDA Forest Service, Durham, NH 03824, USA

Corresponding author: Ruth Yanai (email: rdyanai@esf.edu)

Abstract

Successional, second-growth forests dominate much of eastern North America; thus, patterns of biomass accumulation in standing trees and downed wood are of great interest for forest management and carbon accounting. The timing and magnitude of biomass accumulation in later stages of forest development are not fully understood. We applied a “chronosequence with resampling” approach to characterize live and dead biomass accumulation in 16 northern hardwood stands in the White Mountains of New Hampshire. Live aboveground biomass increased rapidly and leveled off at about 350 Mg/ha by 145 years. Downed wood biomass fluctuated between 10 and 35 Mg/ha depending on disturbances. The species composition of downed wood varied predictably with overstory succession, and total mass of downed wood increased with stand age and the concomitant production of larger material. Fine woody debris peaked at 30–50 years during the self-thinning of early successional species, notably pin cherry. Our data support a model of northern hardwood forest development wherein live tree biomass accumulates asymptotically and begins to level off at ~140–150 years. Still, 145-year-old second-growth stands differed from old-growth forests in their live ($p = 0.09$) and downed tree diameter distributions ($p = 0.06$). These patterns of forest biomass accumulation would be difficult to detect without a time series of repeated measurements of stands of different ages.

Key words: carbon cycling, diameter distribution, forest stand development, old-growth forest, woody debris

Introduction

Forest biomass is an important carbon stock, and forest growth currently offsets more than 10% of annual US greenhouse gas emissions (Domke et al. 2022). Predicting carbon accumulation in aging forests is important in eastern North America where much of the landscape consists of maturing second-growth forests that established following large-scale clearing of primary forests in the 18th and 19th centuries (Considine 1984; Nyland et al. 1986; Irland 1999; Bellemere et al. 2002). Thus, the development of successional forests in the northern hardwoods type of eastern North America (Dyer 2006) is of concern for both forest management and carbon accounting (Birdsey et al. 2023), especially as climate change may exacerbate future disturbances including mortality from insects and disease. Management decisions may need to consider carbon sequestration goals and maintenance of a variety of ecosystem services including critical structural habitat features, biodiversity, nutrient retention, and recreational opportunities that develop in older forests (Michel and Winter 2009; Puhlick et al. 2020; Larrieu et al. 2022).

Forest biomass accumulation is driven by tree growth and mortality while exhibiting a high degree of spatial and temporal variation. Standing and downed trees are two major carbon stocks in forests. Standing tree biomass accumulates as a function of tree growth and mortality, while downed woody debris (DWD) accumulation is driven by inputs from overstory trees and outputs via decomposition and combustion during stand development. In theory, as forests age, biomass pools should reach a dynamic steady-state where inputs and outputs are roughly balanced (Bormann and Likens 1979; Oliver and Larson 1996), but in northern hardwoods, the accumulation of tree biomass following stand-replacing disturbances such as clearcutting or blowdowns is difficult to predict. A variety of simulation models have been used to characterize forest biomass dynamics, but empirical data are critical for evaluating them. One such model, developed at Hubbard Brook, NH, USA, described live aboveground biomass in northern hardwood forests increasing for about 100 years following disturbance and then decreasing slightly as even-aged stands transition to uneven-aged structures

characterized by regeneration within small canopy gaps formed by the death of single or multiple trees (Bormann and Likens 1979). Observational studies have reported a wide range of biomass accumulation trajectories at different sites. Aboveground live biomass at the Hubbard Brook Experimental Forest peaked and declined earlier than expected, at about 80 years (Battles et al. 2014). In a meta-analysis of data from sites across the northeastern United States, aboveground live biomass was observed to accumulate for over 200 years before reaching an asymptote (Keeton et al. 2011). Importantly, observations are sparse for forests within the transition period (100–200 years after harvest) proposed by Bormann and Likens (1979). Since this is the developmental stage that many successional northeastern forests are currently approaching, a comprehensive understanding of carbon dynamics in these forests is needed for scientifically informed forest management strategies.

With time and development, successional forests may eventually resemble old growth in structure and function. One of the defining features of old-growth forests is the presence of large standing and downed trees. Old-growth stands differed from maturing (~100 years old, post-fire) stands in the Adirondacks by having six times more live trees >50 cm diameter at breast height (dbh), with ~85% of large-diameter trees in the maturing stands being residual stems that survived the stand-replacing fires (McGee et al. 1999). Old-growth stands may also have about twice as much DWD exhibiting signs of advanced decomposition and 10 times more in logs ≥50 cm compared to maturing stands (McGee et al. 1999). While there are general time frames proposed for aging forests to resemble old growth, additional data from a range of site ages would allow for a more accurate estimate of how many years are needed for the diameter distribution of stems, and therefore the structural complexity of maturing forests, to resemble old growth.

DWD is an integral component of forest ecosystem processes including carbon and nutrient cycling (Lasota et al. 2018; Harmon et al. 2020). Finer downed material (fine woody debris) is less often studied but represents an appreciable stock of carbon in forests (Mattson et al. 1987) that is easily influenced by insect and disease outbreaks (Orwig and Foster 1998). DWD provides habitat for bryophytes (Anderson and Hytteborn 1991), insects (Grove 2002), small mammals (Ucitel et al. 2003), amphibians (DeGraaf and Yamasaki 2001) and fungi (Nordén et al. 2004; Brazee et al. 2014) and provides germination sites for many vascular plants (McGee and Birmingham 1997; McGee 2001). The size distribution of woody debris is relevant for fire ecology as it determines fuel loads, fuel drying rates, and the severity of fires (Shang et al. 2004; Peterson et al. 2015). Decomposition rates vary with the size and species of woody debris (Scheu and Schauermaun 1994) as well as climate (Berbeco et al. 2012) and microbial communities (Eriksson et al. 1990). Physical and chemical properties of soil are altered by decomposing woody debris and the subsequent additions of organic matter, which improve water retention and promote microbial activity (Stutz et al. 2017; Piaszczyk et al. 2019).

Inputs of DWD are related to the frequency and severity of disturbance and subsequent stand development (Gore and

Patterson 1985; Harmon et al. 1986; Publick et al. 2016). DWD in a mature forest consists of large logs and branches that have fallen to the forest floor. A stand-replacing disturbance such as a clearcut, blowdown, or fire generally augments DWD pools, depending on the nature of the disturbance. Both the remnant DWD and that generated by disturbance are gradually lost to fragmentation and decomposition, but new DWD is added as small stems and branches, particularly during stem exclusion (peaking 20–30 years after stand initiation) when the mortality of suppressed individuals is greatest (Franklin et al. 1987). The balance of additions and removals is reflected in the ratio of downed tree biomass to standing live tree biomass, which has a secondary peak during self-thinning, but is highest following a stand-replacing disturbance (Harmon 2001). As forests mature, the major cause of mortality shifts from density-dependent factors leading to self-thinning to the natural senescence of individual trees, stochastic disturbances such as windthrow, and mortality induced by native or introduced pests or disease. This change is reflected in a shift from twigs and small DWD to larger stems and from shade-intolerant to tolerant species in DWD assemblages (Allison et al. 2003; Vanderwel et al. 2008). Disturbances from invasive pests and diseases cause mortality for some species more than others. Mortality from beech bark disease, for example, has resulted in greater DWD compared to standing biomass (McGee 2000) and an increased presence of American beech (*Fagus grandifolia* Ehrh.) wood in DWD compared to sugar maple (*Acer saccharum* Marsh.). The ratio of DWD volume to live basal area (m³:m²/ha) of sugar maple ranged from 0.00 to 0.45 in maturing stands to 0.05 to 1.04 in old-growth stands, while the ratios for beech ranged from 0.05 to 0.99 in maturing stands and 0.05 to 2.72 in old-growth stands (McGee 2000). Throughout stand development, the pool of DWD is determined by the frequency and intensity of disturbances that create new DWD, combined with the rate of decomposition, which varies with species, climate, microbial communities, and the size of the woody material (Liu et al. 2013; Kahl et al. 2017; Eriksson et al. 1990).

Forest development takes place over long periods of time and as a result is difficult to study directly. Forest surveys date from the late Middle Ages in Europe (Gschwantner et al. 2022), but the US national forest inventory was established only 100 years ago and has used repeated measures of permanent plots only since 2000 (Domke et al. 2022). An alternative approach is to substitute space for time by studying stands of different ages that have developed under similar climatic and edaphic conditions and interpreting them as a chronosequence. This approach, while efficient and powerful, is potentially problematic because it assumes that historic stand-setting disturbances are similar to recent disturbances, which is not always justified (Johnson and Miyanishi 2008). Rather, methods used to conduct forest management and the conditions under which stand-replacing natural disturbances occur are not static but change with technological advances, environmental regulations, market influences, and environmental drivers. The effects of these changes could be incorrectly interpreted as a response to time since treatment. Repeated sampling can help overcome this limitation by tracking the progression of stands within the

chronosequence, and thereby confirm or reject the patterns suggested by the space-for-time substitution (Yanai et al. 2000).

Objectives

We studied a chronosequence of northern hardwood stands ranging in age from 4 to 118 years since clearcutting at the time of their first measurement in 1994. Remeasurement at three intervals of 8–10 years allowed us to describe the progression of standing and downed woody biomass during stand development with better controls for interannual variation and peculiarities of stand history than a single measurement could provide. We also quantified the species composition of standing trees and both species and stage of decay for downed wood to relate patterns of DWD and live trees to stand development. We addressed whether coarse (≥ 7.6 cm diameter) woody debris may reach steady state conditions on time scales different from fine (3.0–7.6 cm) woody debris and twigs (< 3.0 cm) due to a shift during overstory succession to larger trees and shade-tolerant species. Comparing these characteristics allowed us to determine the patterns of biomass accumulation as stands approached steady state conditions and to test whether the oldest successional northern hardwood stands in our chronosequence at 145 years resembled true old growth in stem sizes and biomass.

Methods

Site description

This study was conducted in the White Mountain National Forest (WMNF) of New Hampshire (44° N, -71° W) (Nash 2022). The regional climate is cool-temperate humid continental, with a mean temperature range of -9° C in January to 18° C in July (Campbell et al. 2007). Average annual precipitation is ~ 140 cm, about 25% of which falls as snow (Campbell et al. 2007). Soils of the study sites were moderately drained to well-drained Spodosols and Inceptisols with a mor-type forest floor and granitic glacial till parent material (Federer 1984; Hoover et al. 2012).

The chronosequence consisted of 16 northern hardwood stands. Six stands were located in Bartlett Experimental Forest, one in Hubbard Brook Experimental Forest, and seven in the surrounding WMNF for a total of 14 successional stands. This chronosequence has a long history that began with efforts to characterize forest floor dynamics following clearcutting (Hart 1961; Federer 1982; Federer 1984; Yanai et al. 1999; Yanai et al. 2000; Yanai et al. 2003) and to quantify patterns in leaf litter biomass and nutrient content (Yanai et al. 2012) and soil carbon and nutrient stocks (Vadeboncoeur et al. 2012; Vadeboncoeur et al. 2014). The two old-growth stands were The Bowl Research Natural Area (RNA) in Grafton County, NH, and Mountain Pond, a proposed RNA in Chatham, Carroll County, NH (Fig. 1).

The successional stands were all heavily cut in the late 19th century, and some were cut again in the 20th century (Table 1). The two old-growth stands show no evidence of past harvesting, and both support an overstory of mature

American beech, yellow birch (*Betula alleghaniensis* Britt.), and sugar maple (Hoover et al. 2012). Hereafter stands will be referenced with the name and year cut, for example, CC2-1989. The date of the initiation of each successional stand was determined from the United States Forest Service (USFS) timber sale records.

Live and standing dead tree inventory

Live and standing dead trees were inventoried in the successional stands in 1994, 2004, 2012, and 2021. The 1994 inventories were conducted in all of the successional stands, with the exception of CC2-1989. Stand CC2-1989 was first inventoried in 2004. Hence, four inventories were conducted in all 14 of the successional stands except for CC2-1989 which had three inventories. In 2021, The Bowl and Mountain Pond were also sampled.

Five belt transects were used for tree inventory in all 16 stands. In the 14 successional stands, tree inventories were conducted along five transects that were previously used for a study of litterfall mass (Yanai et al. 2012). In most of the stands, the transects were 50 m long. Two of the stands (H1-1939 and CC2-1989) were smaller, requiring transects 30 m long to fit within the area with a uniform disturbance history. In the two old-growth stands, the transects were 70.7 m long to accommodate higher spatial variation in these stands. We identified and measured all live and standing dead trees ≥ 10.0 cm dbh within 5.0 m of either side of the transect, except in the two smaller stands, where the tree inventory was conducted within 2.5 m of the transects. Standing trees were included in the inventory if they were leaning at an angle $< 45^\circ$ from vertical. Standing tree biomass was calculated from the dbh of both live and dead trees using species-specific allometric equations developed at Hubbard Brook by Whittaker et al. (1974) with modifications by Siccama et al. (1994) for sugar maple, striped maple (*Acer pensylvanicum* L.), yellow birch, American beech, and red spruce (*Picea rubens* Sarg.). These equations described most of the species we encountered, and the remaining species were estimated using substitutions common to biomass calculations at Hubbard Brook (Whittaker et al. 1974).

DWD inventory

For the purpose of this study, DWD was separated into twigs, fine woody debris (FWD), and coarse woody debris (CWD). We defined twigs as FWD < 3.0 cm diameter, not including any portion buried by leaf litter. Buried twigs and wood have been reported for six of these stands using quantitative soil pits (Vadeboncoeur et al. 2012); traditional soil sampling excludes buried wood that does not pass a 2 mm sieve (Yanai et al. 2003). Fine woody debris was DWD ≥ 3.0 cm but < 7.6 cm in diameter, and CWD was DWD ≥ 7.6 cm in diameter and at least 1 m in length. FWD and CWD were sampled in the successional stands in 2004, and twigs were sampled in 2006. Twigs, FWD, and CWD were resampled in 2020 using the same methods employed in 2004 and 2006. The stand H1-1939 was sampled in 2004 and 2006 but was not resampled in 2020 due to recent installation of a fence that produced DWD not representative of an even-aged stand

Fig. 1. Stands included in this chronosequence study. White Mountain National Forest, NH, USA. The figure was created using ArcGISPro version 2.4.0 and assembled from the following data sources: United States Forest Service Open Data (United States Forest Service 2023. “USA Proclaimed Forests”) accessed online at <https://data.fs.usda.gov/geodata/edw/datasets.php?xmlKeywo rd=Original+Proclaimed+National+Forests>. Base map from USGS The National Map, courtesy of ESRI. Sources: Airbus, CGIAR, DS, ESRI, FAO, FEMA, Garmin, Geodatastyrelsen, Geoland, GSA, HERE, Intermap, NASA, NCEAS, NGA, NLS, NMA, NOAA, N Robinson, OS, Rijkswaterstaat, USGS, and the GIS User community.

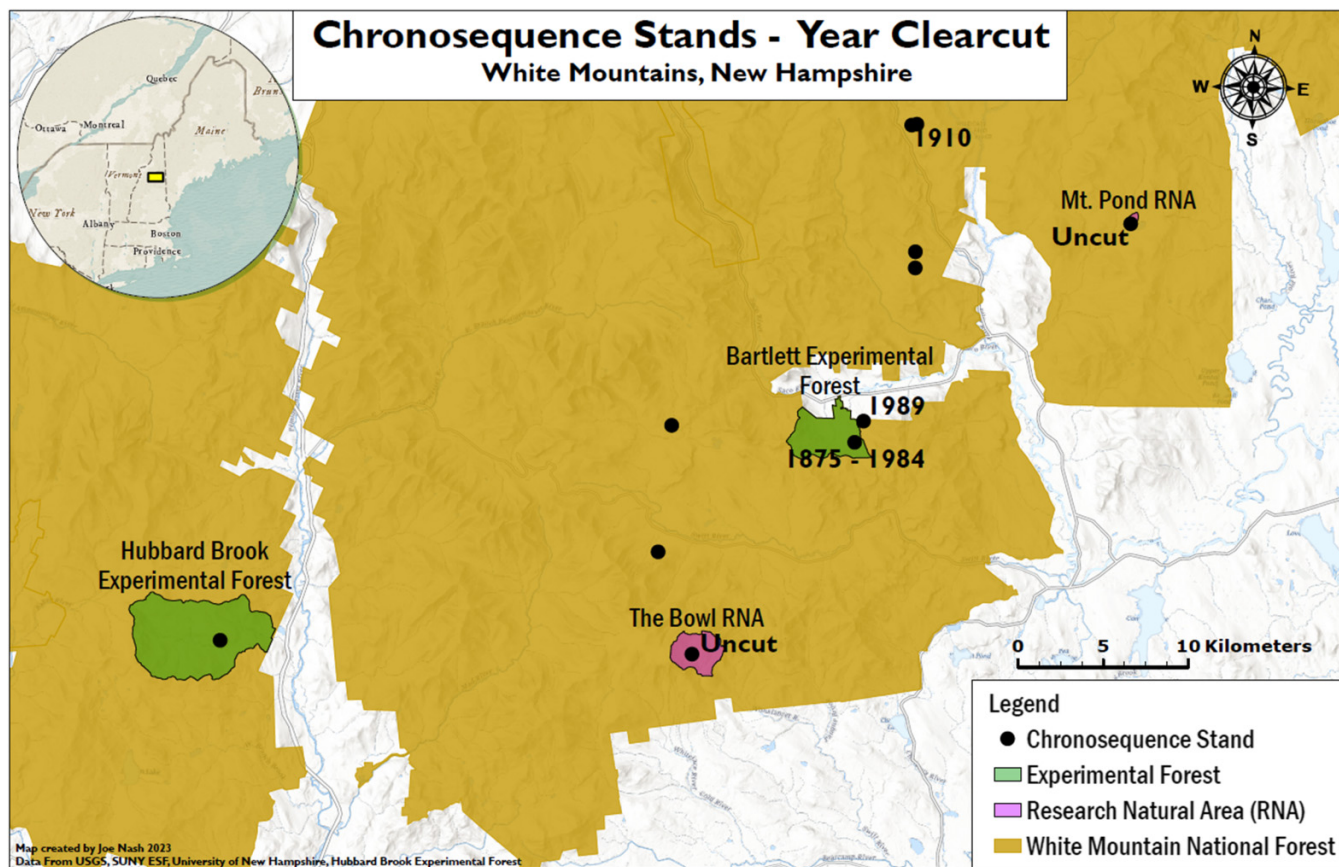


Table 1. Characteristics of 16 stands in the White Mountain National Forest, NH.

Stand	Latitude	Longitude	Stand history	Treatment year	Aspect	Slope (%)	Elevation (m)
CC2	44.067	-71.267	Clearcut	1989	SSW	21	330
H6	44.050	-71.283	Clearcut	1983–1984	Flat to NW	6	330
M6	44.000	-71.417	Clearcut	1979–1980	Flat	2	540
M5	44.217	-71.233	Clearcut, followed by timber stand improvement thinning	1976–1977	Flat	3	630
101	43.933	-71.733	Clearcut	1970	Flat	5	520
H5	44.050	-71.283	Clearcut strips, scarified	1967	NNE	18	360
T20	44.067	-71.417	Heavily cut, with some cull trees girdled	1958	NNE	18	540
M4	44.150	-71.233	Clearcut	1949–1950	NNE	12	460
T30	44.150	-71.233	Intensity of cut unknown	1948	SSW	26	550
H1	44.050	-71.283	Clearcut after 1938 hurricane, removing all stems >5 cm diam	1939	NNE	9	320
H4	44.050	-71.283	Clearcut. Thinning in 1959—45% of basal area removed	1933–1935	SSW	28	350
M3	44.217	-71.250	Presumed clearcut	1910	WNW	19	580
H2	44.050	-71.283	Clearcut, used as pasture. Thinned in 1936—20–30% removed	~1875	ESE	14	320
H3	44.050	-71.283	Clearcut, used as pasture	~1875	NNE	13	320
The Bowl	43.938	-71.392	Uncut	—	ESE	10	610
Mt. Pond	44.172	-71.079	Uncut	—	Flat to SE	7	518

last managed in 1939. Fine and coarse woody debris were inventoried at the old-growth stands in 2021. Twig sampling was prohibited in the two old-growth stands because the sampling methods are destructive.

FWD and CWD survey and sampling

Fine and coarse woody debris were surveyed with the line-intercept sampling method used by the USFS for Forest Inventory and Analysis (FIA) (Van Wagner 1968; U.S. Forest Service 2019). In each stand, we established three permanent clusters, each composed of three 25 m transects separated by 120° diverging from a randomly placed center point, monumented with a 1 m tall fiberglass post. The clusters were randomly oriented in the stands, with the constraint that they do not overlap. In two stands, alternative transect layouts were used for line-intercept sampling due to stand size limitations (CC2-1989) or to avoid a skid trail (T20-1958) (Nash et al. 2023).

Exact clusters and azimuths were re-surveyed in 2020 whenever possible. If a center monument could not be re-located, its location was approximated based on hand-drawn maps created in 2004. Four clusters, rather than the usual three, were used in the two old-growth stands because they were expected to be more heterogeneous.

From the center point outward, we recorded FWD from 5 to 10 m and CWD from 5 to 25 m. Thus total transect lengths were 45 m for FWD and 180 m for CWD in every stand where standard clusters were used.

We followed the USFS FIA protocol and included FWD or CWD in sampling if it was the target size at the point of intersection with the transect, at least 1 m long and at least partially above the soil surface (U.S. Forest Service 2005; Woodall and Monleon 2008). We also included debris if it was above the soil surface but leaning at an angle of <45° from the ground (U.S. Forest Service 2005; Woodall and Monleon 2008). To be counted, debris had to intersect the transect through the central axis of the piece. If a piece of debris was fractured and would pull apart easily at the intersection with the transect, we counted it as two pieces, if not, we counted it as one (U.S. Forest Service 2005). We included debris if it retained enough structure to differentiate the sample from surrounding forest soil. We did not include heavily decomposed debris that had lost all original shape and form such that it could not be picked up without crumbling into pieces <3.0 cm.

We identified the species when possible, and decay class (1: least decayed, 5: most decayed) of all debris intersected on the transects (U.S. Forest Service 2005). If debris was unidentifiable to species due to advanced stages of decomposition, we identified debris to genus or at least a classification of gymnosperm or angiosperm. We recorded the length of each piece, the diameter at intersection, and the small-end and large-end diameters. We took all diameter measurements perpendicular to the length of the wood sample. The volume of each piece of wood was calculated using the small- and large-end diameters as:

$$X_i = \frac{\frac{\pi}{8} (D_{Si}^2 + D_{Li}^2) l_i}{10\,000}$$

where X_i is the volume (m^3/ha) of the i th piece of woody debris, D_{Si} is the small-end diameter (cm), D_{Li} is the large-end diameter (cm), and l_i is the debris length (m). The term 10 000 accounts for the use of centimeters for diameter and meters for length. Only one diameter (diameter at intersection, D_i) was recorded for each piece of FWD, so the volume of a single piece of FWD was calculated as:

$$X_i = \frac{\frac{\pi}{8} D_i^2 l_i}{10\,000}$$

The volume of wood per unit area was calculated as:

$$\text{Volume} \left(\frac{\text{m}^3}{\text{ha}} \right) = \left(\frac{\pi}{2L} \sum \frac{X_i}{l_i} \right) \times 10\,000$$

where X_i is the volume (m^3/ha) of the i th piece of woody debris, L is the transect length (m), and l_i is the debris length (m) (Woodall and Monleon 2008).

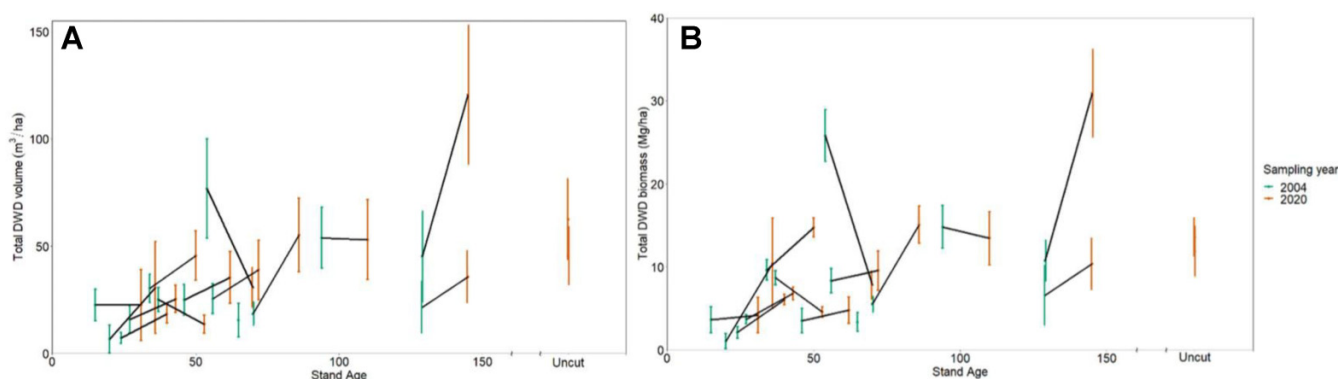
Wood density measurements

CWD density was measured in 2004 by collecting samples from the first piece of CWD of each species and decay class combination encountered along each transect (Acker 2006; Nash et al. 2023). Samples were collected by cutting a disc ~5–10 cm thick with a bow saw or chainsaw. Each CWD sample was vacuum-sealed and frozen. Volume was measured by water displacement with a correction of 30 mL to account for the volume of the vacuum bag, based on tests of the volume of sealed and unsealed objects. The wood samples were subsequently dried at 60 °C to constant mass and weighed. The fresh volume and dry mass were used to calculate wood density. Samples were ground and analyzed for chemical composition (not reported here). The volume and dry mass were used to calculate wood density. The average density of wood by species and decay class was used in calculation (Table A1). For the eight combinations of species and decay class that were not found during 2004 inventories, we used densities from a national database (Harmon et al. 2008; Table A1). A comparison of 23 densities reported by both Harmon et al. (2008) and this study showed no bias in a paired t -test ($p = 0.46$).

Twig sampling

We sampled twigs from five 4 m^2 subplots per site. We rejected subplots if they occurred on ephemeral or perennial streams, which can redistribute these size classes of dead wood. We randomly placed each plot based on a stratified design utilizing permanently marked inventory transects (Yanai et al. 2000; Yanai et al. 2012). The twig sample subplots were independently located in 2006 and 2020. In each subplot, we collected every part of twigs and branches 16–30 mm in diameter. We cut twigs with pruning shears where the diameter was >30 mm or where the debris crossed the subplot boundary. We collected twigs <16 mm in 0.5 m^2 nested subplots in the same manner. We also collected dead branches not attached to trees suspended up to 2.5 m above the ground. We did not collect dead branches attached to living or dead trees, unless the tree was dead and leaning at an angle of <45° from

Fig. 2. Total volume (A) and biomass (B) of downed woody debris (DWD) at the 16 stands included in this study, sampled in 2004 and 2020. Points represent estimates of stand volume or biomass, and error bars are ± 1 standard error. The lines connecting two points illustrate the change in stand observations from 2004 and 2020.



the forest floor. We also did not include twigs that were covered by leaf litter. Twigs were separated into size classes ≤ 7.5 , 7.5–16, and 16–30 mm and then oven dried at 60 °C to constant mass.

Statistical analysis

To test whether the biomass of downed wood changed with stand age, we used analysis of variance with stand age and sampling year as predictor variables. Stand was a random effect in the model. Anderson-Darling tests were used to test whether the size distribution of live and downed stems in the oldest successional stands differed from the stem distributions in the true old-growth stands. Statistical analyses were performed in R (R Core Team 2020) with the packages knitr (Yihui 2022), dplyr (Wickham et al. 2022), ggplot2 (Wickham 2016), nlme (Pinheiro et al. 2022), tidyr (Wickham and Girlich 2022), vegan (Oksanen et al. 2022), lmerTest (Kuznetsova et al. 2017), and nortest (Gross and Ligges 2015).

Results

Standing biomass

Standing biomass increased rapidly up to about 60 years (Fig. 2A). Variation among stands in these aggrading forests was high, with a standard deviation of 48 Mg/ha in stands 20–40 years old and 46 Mg/ha in stands 40–60 years old. Stands over 85 years old did not aggrade substantially over our 20 years of observation. Live tree biomass in this chronosequence appeared to reach a maximum of ~ 350 Mg/ha at ~ 100 –145 years (Fig. 2A). Of the two old-growth stands, the Bowl and Mountain Pond, which were sampled only once, one was similar in standing live biomass to our oldest successional stands (145 years old), but the other had significantly higher standing live and dead biomass.

The old-growth stands had greater standing dead biomass than the successional stands (Fig. 2B) consistent with the larger trees that were present at these stands compared to the successional stands. Three values at M3-1910 were outliers among the standing dead biomass observations at these stands (Fig. 2B). In that stand, standing dead biomass peaked in 2004 at 100 Mg/ha and declined to 91 Mg/ha in 2012 and

55 Mg/ha in 2021. The biomass at this stand was dominated by American beech trees > 30 cm, which likely died of beech bark disease. Forty-three percent of the standing dead basal area at M3-1910 in 2021 was accounted for by American beech (2.5 of the total 5.8 m²/ha). Standing dead red maple trees > 30 cm also contributed to the high standing dead biomass at this stand. Variation in standing dead biomass was high across stands, but lower than variations in standing live trees. The standard deviation of stands 0–20 years old was 17 Mg/ha but was 37 Mg/ha among stands 80–100 years old.

Downed wood

The biomass of DWD increased asymptotically with age across the chronosequence to an average 11.8 ± 1.3 Mg/ha in the oldest successional stands and 12.7 ± 0.8 Mg/ha in the old-growth stands. While the young (< 50 years old) stands all increased in total DWD biomass from 2004 to 2020, the older stands were more variable with some increasing and some decreasing as a result of disturbance history. Specifically, in M4, high DWD in 2004 was attributed to a recent windthrow event, which was no longer evident as an outlier in DWD biomass by 2020. In H3, DWD was very high in 2020, and again this was associated with a windthrow event that occurred sometime after 2004. Variation in DWD biomass was high across stands, particularly in stands 40–60 years old with a standard deviation of 7.8 Mg/ha and in stands 100–150 years old with a standard deviation of 9.5 Mg/ha. Stands 80–100 years old did not change substantially in DWD biomass during the 16-year sampling interval (standard deviation = 0.2 Mg/ha). Resampling the chronosequence revealed a decrease in CWD biomass from 25.0 to 7.2 Mg/ha in a 70-year-old stand and an increase from 10.6 to 30.1 Mg/ha in a 145-year-old stand, due to infrequent disturbances (Fig. 3). The average biomass of downed wood in our maturing (80–145 years old) stands was 14.5 ± 2.9 Mg/ha when including the blowdown in H3-1875 and 11.8 ± 1.3 Mg/ha excluding this observation. The total biomass of coarse and fine woody debris in the oldest successional stands was not statistically distinguishable from the true old-growth stands (Fig. 3) ($p = 0.58$).

Twig mass peaked at 5.2 Mg/ha at 36 years during stem exclusion and then declined to relatively stable levels of

Fig. 3. Live (A) and dead (B) overstory (>10 cm diameter at breast height [dbh]) tree aboveground biomass at the 16 stands included in this study, sampled in 1994, 2004, 2012, and 2021. Points represent estimates of stand biomass, and error bars are ± 1 standard error. The lines connecting two points illustrate the change in stand observations from 2004 to 2020.

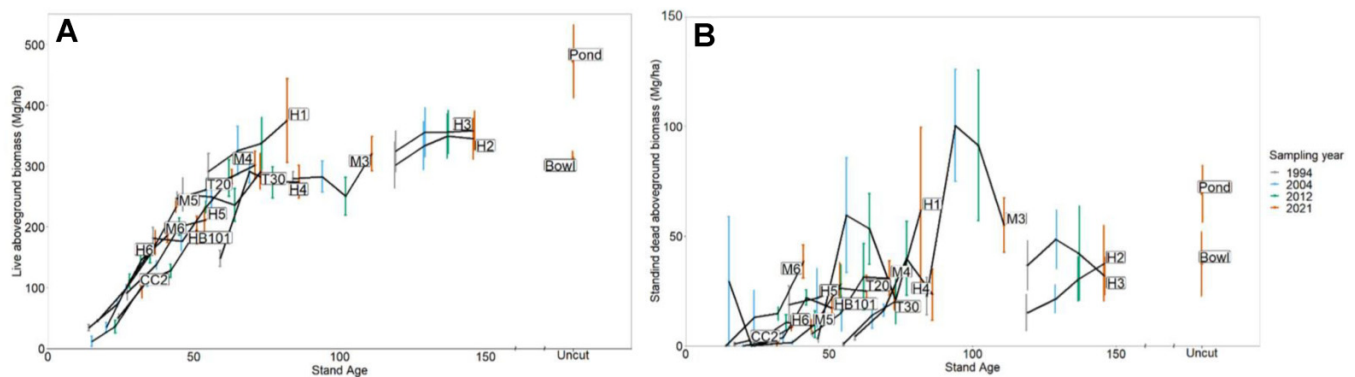
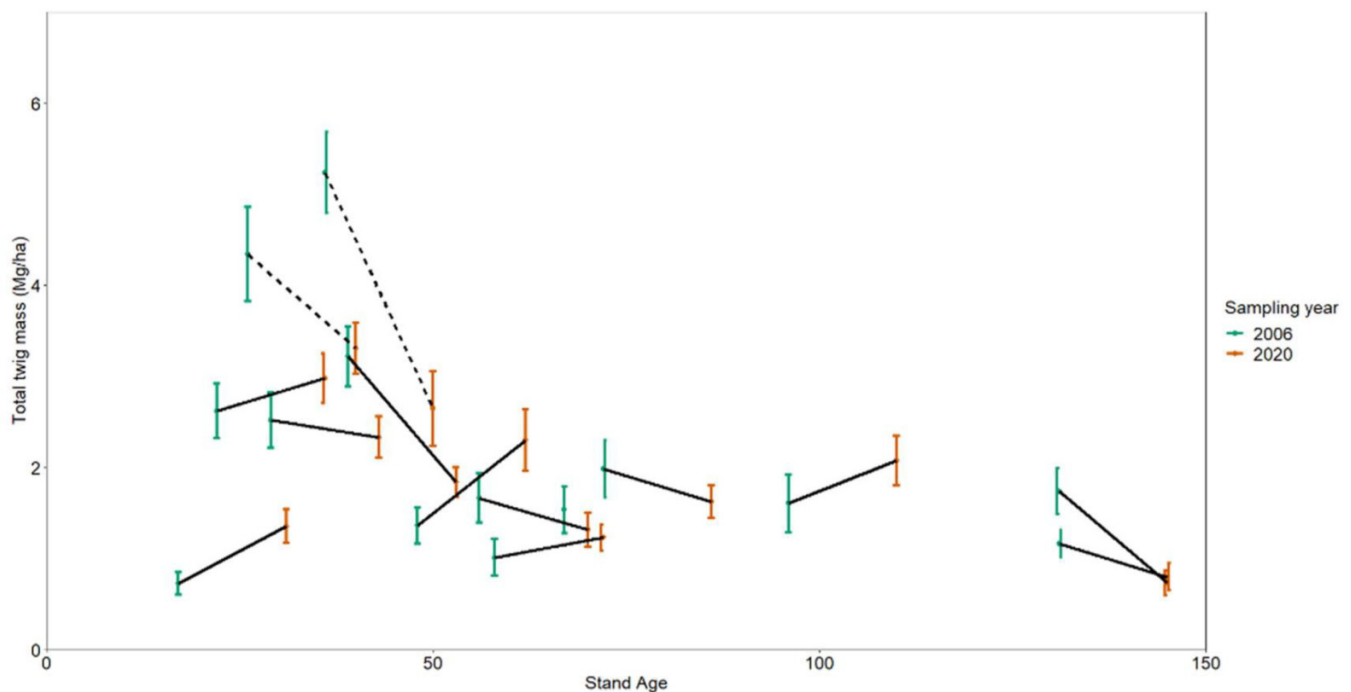


Fig. 4. Total twig (downed woody debris <3.0 cm) biomass at the 16 stands included in this study, sampled in 2006 and 2020. Stands with >20% basal area occupied by pin cherry (*Prunus pensylvanica* L.f.) are shown in dashed lines. Points represent estimates of stand biomass, and error bars are ± 1 standard error. The lines connecting two points illustrate the change in stand observations from 2004 to 2020.



1.0–2.6 Mg/ha beginning at about 50 years (Fig. 4). The oldest successional stands (145 years old) had twig mass similar to the youngest stands. The young stands that were dominated by pin cherry (M6-1978 and HB101-1970) had about twice as much total twig biomass than stands of similar ages dominated by beech and birch.

Ratio of downed to live biomass

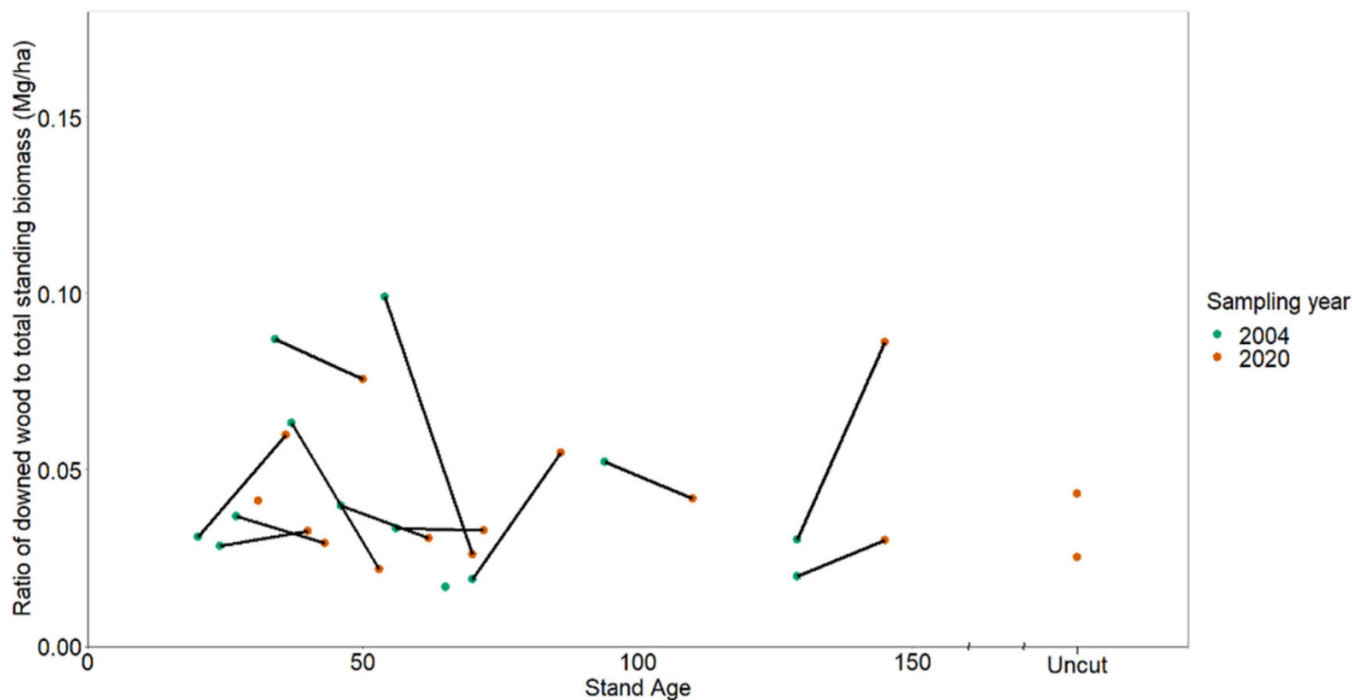
The ratio of DWD biomass to live tree biomass was about 0.05 in most stands. It was greatest at 0.8 in the youngest stand (CC2-1989) due to residual debris from the previous overstory and the small biomass of standing trees. The

next highest ratios were found in young stands during self-thinning, with ratios >0.10. A ratio >0.10 was also found after a blowdown in H3-1875 that occurred sometime between 2004 and 2020 (Fig. 5).

Diameters of downed wood and live trees

We found that the old-growth stands had larger stems than the successional stands, and this was true for both live trees and CWD (Fig. 6). The distribution of live tree diameters consisted of slightly larger stems in the old growth compared to 145-year-old successional stands ($p = 0.09$ for Anderson-Darling test of live tree diameter distributions). The Bowl had

Fig. 5. The mass ratio of downed woody debris (DWD) to standing tree biomass at each site sampled in 2004 and 2020. The lines connecting two points illustrate the change in stand observations from 2004 and 2020.



28 and Mountain Pond 40 live trees/ha >50 cm dbh, while H2-1875 and H3-1875 had 16 and 32 trees/ha, respectively, of this size. The distribution of CWD diameters was more variable, and not as clearly influenced by stand age as the live tree diameters (Fig. 6). We sampled 10 pieces of CWD/ha with large-end diameters >40 cm in the two old-growth stands, while in one of the oldest successional stands, we sampled 12 pieces/ha, and in the other, we sampled 0 pieces/ha. The distribution of CWD large-end diameters consisted of larger stems in the old-growth compared to 145-year-old successional stands ($p = 0.06$ for Anderson-Darling test of CWD large-end diameter distributions).

Species and decay class composition

Live tree species composition varied with stand age. Pin cherry and birch dominated the basal area of stands <50 years old, while stands >50 years old were dominated by shade-tolerant and mid-tolerant species such as sugar maple, beech, and ash. Stand age did not, however, explain all of the variation in species dominance of live trees. Stands H2 and H3 were both harvested in ~1875, but H2 was dominated by sugar maple, while H3 was dominated by red maple (*Acer rubrum* L.) (Fig. A1). Pin cherry was a greater component of the basal area in H6-1983 and HB101-1970 in the first three inventories compared to H5-1967 and CC2-1989 at similar ages (ranging from 15 to 28 years since clearcutting).

The contribution of certain species and decay classes to the total biomass of downed wood in these stands was distinct at three stages of overstory succession: from establishment to the start of stem-exclusion at about 35 years, from about

35–55 years when there is an influx of early successional species, and from after about 55 years until the stand reaches old-growth status, which according to our results could take longer than 145 years.

Total CWD biomass was the lowest in the youngest stands and increased with stand age (Fig. 7). The composition of CWD shifted from a dominance of large conifers that were highly decayed in young stands (as in CC2-1989, 31 years old) to a dominance of not well decayed, early successional species, especially pin cherry, from ages ~35–50 years. After 50 years, woody debris included a diverse mix of species and decay classes. The true old-growth stands had a greater contribution of yellow birch and highly decayed debris than the stands aged 60–145 years (Fig. 7).

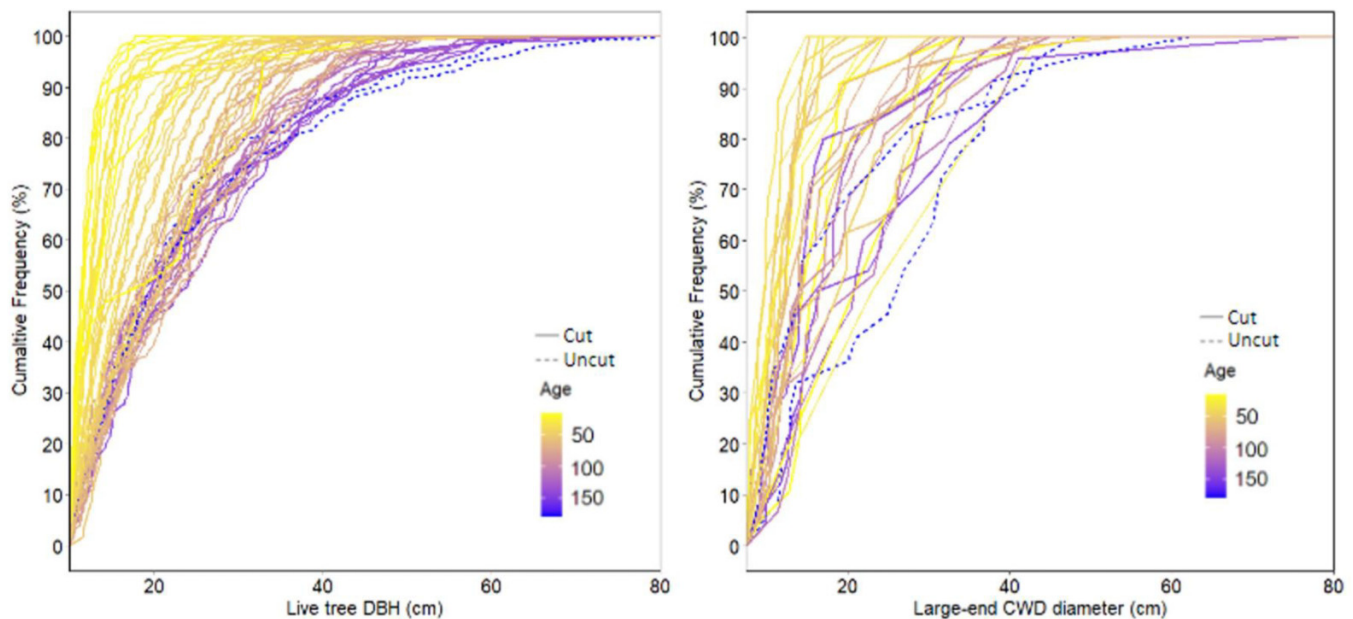
Discussion

Standing tree biomass

In these northern hardwood forests, young successional stands were distinctly different in live, standing dead, and downed biomass pools from old successional stands. The old-growth stands had more live and standing dead biomass than the two oldest (145 years old) successional stands, adding to the growing evidence that northern hardwood forests may accumulate live aboveground biomass for 400 years or more following stand-replacing disturbance (McGarvey et al. 2015; Urbano and Keeton 2017).

We observed greater biomass in the successional stands than others have reported. Our results suggest that live

Fig. 6. Cumulative frequency of live tree diameter at breast height (dbh) (left) and large-end coarse woody debris (CWD) diameters (right) for the 16 stands included in this study at each sampling period; 1994, 2004, 2012, and 2021 for live trees and 2004 and 2020 for coarse woody debris.



aboveground biomass in northern hardwood forests has the potential to reach 300 Mg/ha in 145 years (Fig. 2), which is at the high end of the range calculated from USFS FIA data in New Hampshire of 36–344 Mg/ha (Brown et al. 1999). Live aboveground biomass in the area west of the reference watershed (W6) at Hubbard Brook attained 260 Mg/ha after 100 years (Siccama et al. 2007), which is consistent with our chronosequence. Similarly, the average aboveground live tree biomass in 80- to 120-year-old second-growth northern hardwood stands at Harvard Forest, MA, were estimated at 239 ± 75 Mg/ha. However, aboveground biomass in W6 peaked at only 190 Mg/ha after about 100 years (Battles et al. 2014). Another study estimated live aboveground biomass in old-growth northern hardwood stands in northern New England at 232 Mg/ha in Vermont, New Hampshire, and Maine (Hoover et al. 2012). In a meta-analysis of sites across the northeastern United States, live aboveground biomass did not reach 300 Mg/ha even after 300 years of stand development (Keeton et al. 2011).

A major difference between our study and those previously published is the rate of biomass accumulation in the early stages of succession (up to 70 years). We observed steeper biomass accumulation curves in stands 50–70 years old than reported by Battles et al. (2014) and Siccama et al. (2007) at Hubbard Brook. Our observations were more similar to a model of sugar maple forests of Northern Wisconsin, USA, where live tree biomass increased rapidly to about 200 Mg/ha in only 50 years with slight increases thereafter (Scheller and Mladenoff 2004). Changing environmental conditions conducive to tree growth such as a warming climate, increased atmospheric CO₂, and the thinning of a canopy due to pests and disease (McDowell et al. 2020; Wang et al. 2016) may

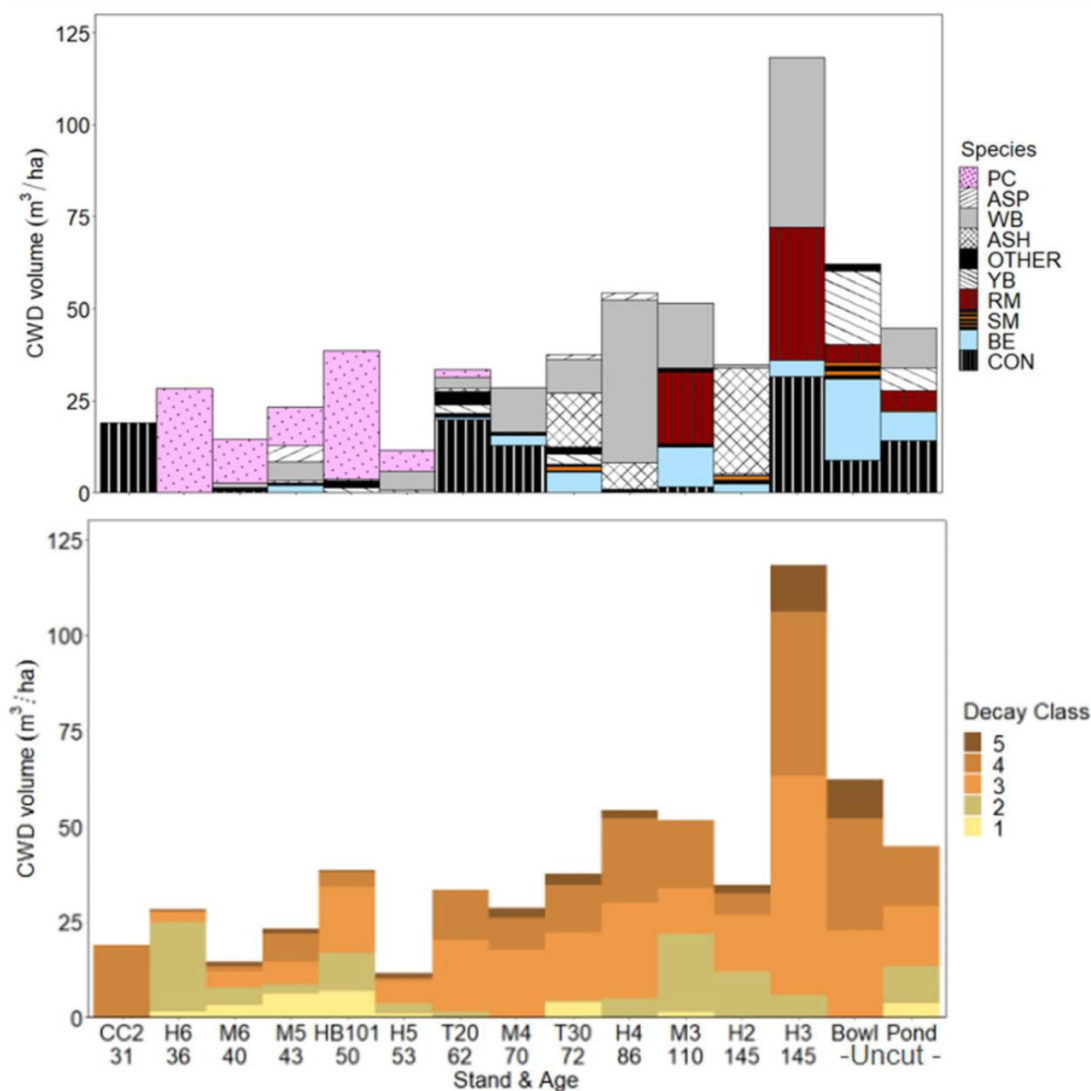
have increased the rates of aboveground biomass accumulation over the time period of this study (1994–2021), but this change would be undetectable with our dataset. Our observations of steep biomass accumulation curves are more likely a result of the variability across the study sites. These observations add to the growing literature of different pathways that any particular stand may take in accumulating standing biomass.

Downed wood

Although live standing biomass was higher in our old-growth stands than 145-year-old stands, the biomass of downed wood was similar between these age classes. Large downed wood produced from disturbances that killed large trees such as windthrow and beech bark disease greatly influenced the biomass of downed wood in the old successional and old-growth stands. The stability of downed wood after 100 years in this study suggests that the influx of downed trees is roughly balanced with the decomposition of downed wood (Yamasaki and Leak 2006).

Our estimates of downed wood biomass across all ages (9.4 ± 1.2 Mg/ha) were higher than the average for FIA data in New Hampshire of 6.9 Mg/ha (Chojnacky et al. 2004). Our average in mature stands (70–145 years old) (12.5 ± 2.3 Mg/ha) is lower than reported estimates from Maine (24.2 ± 6.0 Mg/ha) and New York (29.9 ± 8.5 Mg/ha) (Keeton et al. 2011), but within the range of 17 ± 16 Mg/ha reported for 80- to 120-year-old northern hardwood stands at Harvard Forest (Finzi et al. 2020). In the old-growth stands, our estimates of the biomass of downed wood were similar to the average observed biomass of 12 ± 2.5 Mg/ha across three old-growth

Fig. 7. Species (top) and decay classes (bottom) of coarse woody debris (CWD) volume in the 16 stands included in this study in 2020. PC, pin cherry; ASP, aspen; WB, white birch; ASH, ash; OTHER, mountain maple; striped maple, ironwood; YB, yellow birch; RM, red maple; SM, sugar maple; BE, American beech; CON, conifers.



hardwood stands in Maine, Vermont, and New Hampshire (Hoover et al. 2012).

The proportion of downed wood biomass to live tree biomass is used to indicate the relationship of standing to downed trees and carbon storage potential. We observed ratios that ranged from 0.03 to 0.11, which is at the low end of the range reported for U.S forests of 0.05-0.30 (Harmon 2001) but similar to the value of 0.08 reported for forests of New Hampshire (Woodall et al. 2013).

Old-growth characteristics

Large standing trees and CWD are often used as an indicator of old-growth status. Authors have used 40 or 50 cm diameter as a threshold to define large standing trees in the northeastern United States (Hura and Crow 2004). Our old-growth stands had about twice as many standing trees >50 cm as the oldest chronosequence stands—particularly more standing dead trees >50 cm. Based on these results,

145 years are not sufficient for a northern hardwood forest regenerating after clearcutting to reach the distribution of large stems resembling true old-growth forests. Achieving old-growth characteristics will require not only managing for DWD but also leaving trees to grow past financial maturity. Assessing progress toward achieving old-growth characteristics should include attention to the number and size of large living and standing dead trees.

Repeated measures of a chronosequence

We measured live trees in this chronosequence four times and measured twigs, FWD, and CWD twice. Variability in live biomass and woody debris from stand to stand was high (Fig. 2). Across stands classified as northern hardwoods, site differences in soil hydrology and nutrient availability, microclimate, disturbance history, seedling herbivory, pests, pathogens, and other selective pressures can exert strong influences on species composition, growth rates, and tree

longevity, and therefore on live biomass and the production of standing dead and downed wood pools (Leak 2006, Leak and Yamasaki 2010; Vadeboncoeur et al. 2012; Puhlick et al. 2022). Even in the absence of stochastic events such as blowdowns, this variation means that characterizing the development of these pools is better accomplished by remeasurement over time than by comparing sites of different ages. For example, of the young stands in the chronosequence, M6-1978 and HB101-1970 had greater twig mass (Fig. 4) as a result of self-thinning from pin cherry, which occupied a larger percentage of basal area in these stands (see Appendix A). Repeated measures of a chronosequence improve interpretation because of the variation from stand to stand due to spatial rather than temporal variation (Johnson and Miyanishi 2008).

Without repeated measures, the interpretation of chronosequence results can be further confounded by historical changes in treatments or environmental characteristics. Forest management practices evolve over time; the oldest stands in our chronosequence were logged with horses. The change to tractor logging and then to rubber tired skidders had profound effects on forest floor disturbance (Yanai et al. 2000). The change from horse to tractor logging likely reduced the amount of CWD left on site following harvests, but the evidence of this difference is likely long gone.

Finally, the repeated measurements revealed outliers in the data produced from stochastic events. The outliers in DWD biomass at M4 in 2004 and H3 in 2020 resulted from windthrow of large trees that produced large amounts of DWD. If we had sampled DWD only in 2004, we might have concluded that downed biomass peaked at ~60 years, while the 2020 inventory, taken alone, would have suggested that downed biomass peaked at 145 years. The use of repeated measurements of a chronosequence is especially valuable for processes such as forest dynamics that involve stochastic events and change in drivers over time.

Acknowledgements

Tony Federer established the original 13 stands in the chronosequence in 1979–1980 and helped to relocate them in 1994–1995, at which time Mary Arthur initiated long-term vegetation monitoring. Marty Acker led field measurements in 2002–2004, adding two younger stands, and Adam Wild led field measurements in 2012. Many summer interns, most recently April Zee and Erin Cornell, were essential to field measurements. Chris Costello and the USFS provided logistical support and assistance with study site locations. We are grateful for the cooperation and support of the White Mountain National Forest and the Hubbard Brook and Bartlett Experimental Forests. This study is a contribution to the Hubbard Brook Ecosystem study.

Article information

History dates

Received: 21 March 2023

Accepted: 11 October 2023

Accepted manuscript online: 26 October 2023

Version of record online: 1 December 2023

Copyright

© 2023 Authors Nash, Vadeboncoeur, McGee, and Yanai. Permission for reuse (free in most cases) can be obtained from copyright.com.

Data availability

The data are available in the Environmental Data Initiative repository: Nash, J.M., M.A. Vadeboncoeur, A.D. Wild, A. Zee, E.A. Cornell, M.A. Arthur, and R.D. Yanai. 2023. Biomass accumulation in trees and downed wood at Bartlett Experimental Forest, Hubbard Brook Experimental Forest, the Bowl Natural Research Area, and the White Mountain National Forest, NH, USA ver 1. <https://doi.org/10.6073/pasta/bd190341e6c15c02815966083f75ffbb>.

Author information

Author ORCIDs

Joseph M. Nash <https://orcid.org/0000-0001-7695-1441>

Matthew A. Vadeboncoeur <https://orcid.org/0000-0002-8269-0708>

Gregory G. McGee <https://orcid.org/0000-0001-7437-8100>

Christopher W. Woodall <https://orcid.org/0000-0001-8076-6214>

Ruth D. Yanai <https://orcid.org/0000-0001-6987-2489>

Author contributions

Conceptualization: JMN, MAV, RDY

Data curation: JMN, MAV

Formal analysis: JMN, MAV

Funding acquisition: RDY

Investigation: JMN, MAV, RDY

Methodology: JMN, MAV, GGM, CWW, RDY

Project administration: RDY

Visualization: JMN, MAV

Writing – original draft: JMN

Writing – review & editing: JMN, MAV, GGM, CWW, RDY

Competing interests

The authors declare that they have no competing interests.

Funding

This research was funded by USDA NRICGP 93-37101-8582, NSF DEB- 0235650 and DEB-949324, LTER DEB-0423259 and DEB-1114804, and USDA NIFA 2019-67019-29464.

References

- Acker, M. 2006. Base cation concentration and content in litterfall and woody debris across a northern hardwood forest chronosequence. Ph.D. dissertation, University of Kentucky, Lexington, KY.
- Adams, M.B., and Owens, D.R. 2001. Specific gravity of coarse woody debris for some central Appalachian hardwood forest species. Vol. 716. US Department of Agriculture, Forest Service, Northeastern Research Station, Newton Square, PA.
- Allison, R.D., Art, H.W., Cunningham, F.E., and Teed, R. 2003. Forty-two years of succession following strip clearcutting in a northern

- hardwoods forest in northwestern Massachusetts. *For. Ecol. Manag.* **182**: 285–301. doi:[10.1016/S0378-1127\(03\)00066-5](https://doi.org/10.1016/S0378-1127(03)00066-5).
- Andersson, L.I., and Hytteborn, H. 1991. Bryophytes and decaying wood—a comparison between managed and natural forest. *Hol. Ecol.* **14**: 121–130.
- Arthur, M.A., Tritton, L.M., and Fahey, T.J. 1993. Dead bole mass and nutrients remaining 23 years after clear-felling of a northern hardwood forest. *Can J For Res.* **23** (7): 1298–1305. doi:[10.1139/x93-166](https://doi.org/10.1139/x93-166).
- Battles, J.J., Fahey, J., Driscoll, C.T., Blum, J.D., and Johnson, C.E. 2014. Restoring soil calcium reverses forest decline. *Environ. Sci. Technol. Lett.* **1**(1): 15–19. doi:[10.1021/ez400033d](https://doi.org/10.1021/ez400033d).
- Bellemare, J., Motzkin, G., and Foster, D.R. 2002. Legacies of the agricultural past in the forested present: an assessment of historical land-use effects on rich mesic forests. *J. Biol.* **29**(10–1): 1401–1420.
- Berbeco, M.R., Melillo, J.M., and Orians, C.M. 2012. Soil warming accelerates decomposition of fine woody debris. *Plant and soil*, **356**: 405–417. doi:[10.1007/s11104-012-1130-x](https://doi.org/10.1007/s11104-012-1130-x).
- Birdsey, R.A., DellaSala, D.A., Walker, W.S., Gorelik, S.R., Rose, G., and Ramírez, C.E. 2023. Assessing carbon stocks and accumulation potential of mature forests and larger trees in US federal lands. *Front. For. Glob. Change* **5**: 277.
- Bormann, F.H., and Likens, G.E. 1979. Catastrophic disturbance and the steady state in northern hardwood forests: a new look at the role of disturbance in the development of forest ecosystems suggests important implications for land-use policies. *Am. Sci.* **67**(6): 660–669.
- Brazee, N.J., Lindner, D.L., D'Amato, A.W., Fraver, S., Forrester, J.A., and Mladenoff, D.J. 2014. Disturbance and diversity of wood-inhabiting fungi: effects of canopy gaps and downed woody debris. *Biodivers. Conserv.* **23**: 2155–2175. doi:[10.1007/s10531-014-0710-x](https://doi.org/10.1007/s10531-014-0710-x).
- Brown, S.L., Schroeder, P., and Kern, J.S. 1999. Spatial distribution of biomass in forests of the eastern USA. *For. Ecol. Manag.* **123**(1): 81–90. doi:[10.1016/S0378-1127\(99\)00017-1](https://doi.org/10.1016/S0378-1127(99)00017-1).
- Campbell, J.L., Driscoll, C.T., Eager, C., Likens, G.E., Siccama, T.G., Johnson, C.E., et al. 2007. Long-term trends from ecosystem research at the Hubbard Brook Experimental Forest. Technical Report NRS-17. United States Department of Agriculture Forest Service Northern Research Station, Newtown Square, PA.
- Chojnacki, D.C., Mickler, R.A., Heath, L.S., and Woodall, C.W. 2004. Estimates of down woody materials in eastern US forests. *Environ. Manag.* **33**: S44–S55.
- Considine, T.J. 1984. An analysis of New York's timber resources (Vol. 20). US Department of Agriculture, Forest Service, Northeastern Forest Experiment Station, Upper Darby, PA.
- DeGraaf, R.M., and Yamasaki, M. 2001. New England wildlife: habitat, natural history, and distribution. University Press of New England, Lebanon, NH.
- Domke, G.M., Walters, B.F., and Smith, J.E. 2022. Carbon stocks and stock changes in U.S. forests. In: W.L. Hanson, S.J. Del Grosso and L. Gallagher(eds.). *U.S. Agriculture and Forestry Greenhouse Gas Inventory: 1990–2018*. Technical Bulletin No. 1957. United States Department of Agriculture, Office of the Chief Economist, Washington, DC. pp. 160–175.
- Dyer, J.M. 2006. Revisiting the deciduous forests of eastern North America. *BioScience*, **56**(4): 341–352. doi:[10.1641/0006-3568\(2006\)56\[341:RTDFOE\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2006)56[341:RTDFOE]2.0.CO;2).
- Eriksson, K.E.L., Blanchette, R.A., and Ander, P. 1990. Morphological aspects of wood degradation by fungi and bacteria. Microbial and enzymatic degradation of wood and wood components, 1–87.
- Federer, C.A. 1982. Subjectivity in the separation of organic horizons of the forest floor. *Soil Sci. Soc. Am. J.* **46**(5): 1090–1093. doi:[10.2136/sssaj1982.03615995004600050041x](https://doi.org/10.2136/sssaj1982.03615995004600050041x).
- Federer, C.A. 1984. Organic matter and nitrogen content of the forest floor in even-aged northern hardwoods. *Can. J. For. Res.* **14**: 763–767. doi:[10.1139/x84-136](https://doi.org/10.1139/x84-136).
- Finzi, A.C., Giasson, M.A., Barker Plotkin, A.A., Aber, J.D., Boose, E.R., Davidson, E.A., et al. 2020. Carbon budget of the Harvard Forest Long-Term Ecological Research site: pattern, process, and response to global change. *Ecol. Monogr.* **90**(4): e01423. doi:[10.1002/ecm.1423](https://doi.org/10.1002/ecm.1423).
- Franklin, J.F., Shugart, H.H., and Harmon, M.E. 1987. Tree death as an ecological process. *BioScience* **37**(8): 550–556. doi:[10.2307/1310665](https://doi.org/10.2307/1310665).
- Gore, J.A., and Patterson, W.A., III. 1985. Mass of downed wood in northern hardwood forests in New Hampshire: potential effects of forest management. *Can. J. For. Res.* **16**: 335–339. doi:[10.1139/x86-057](https://doi.org/10.1139/x86-057).
- Gross, J., and Ligges, U. 2015. nortest: tests for normality. R package version 1.0-4. <https://CRAN.R-project.org/package=nortest>.
- Grove, S.J. 2002. Saproxylic insect ecology and sustainable management of forests. *Annu. Rev. Ecol. Syst.* **33**: 1–23. doi:[10.1146/annurev.ecolsys.33.010802.150507](https://doi.org/10.1146/annurev.ecolsys.33.010802.150507).
- Gschwantner, T., Alberdi, I., Bauwens, S., Bender, S., Borota, D., and Bosela, M., 2022. Growing stock monitoring by European National Forest Inventories: historical origins, current methods and harmonisation. *For. Ecol. Manag.* **505**: 119868. doi:[10.1016/j.foreco.2021.119868](https://doi.org/10.1016/j.foreco.2021.119868).
- Harmon, M.E. 2001. Moving towards a new paradigm for woody detritus management. *Ecol. Bull.* **49**: 269–278.
- Harmon, M.E., Fasth, B.G., Yatskov, M., Kastendick, D., Rock, J., and Woodall, C.W. 2020. Release of coarse woody detritus-related carbon: a synthesis across forest biomes. *Carbon Balance Manag.* **15**: 1–21. doi:[10.1186/s13021-019-0136-6](https://doi.org/10.1186/s13021-019-0136-6). PMID: 31940113.
- Harmon, M.E., Franklin, J.F., Swanson, F.J., Sollins, P., Gregory, V., Latting, J.D., et al. 1986. Ecology of coarse woody debris in temperate ecosystems. *Adv. Ecol. Res.* **15**: 133–302. doi:[10.1016/S0065-2504\(08\)60121-X](https://doi.org/10.1016/S0065-2504(08)60121-X).
- Harmon, M.E., Woodall, C.W., Fasth, B., and Sexton, J. 2008. Woody detritus density and density reduction factors for tree species in the United States: a synthesis. Gen. Tech. Rep. NRS-29. U.S. Department of Agriculture, Forest Service, Northern Research Station, Newtown Square, PA.
- Hart, G. 1961. Humus depths under cut and uncut northern hardwood forests. Forest Research Note NE-113. US Department of Agriculture, Forest Service, Northeastern Forest Experiment Station, Upper Darby, PA.
- Hoover, C.M., Leak, W.B., and Keel, B.G. 2012. Benchmark carbon stocks from old-growth forests in northern New England, U.S.A. *For. Ecol. Manag.* **266**: 108–114.
- Hura, C.E., and Crow, T.R. 2004. Woody debris as a component of ecological diversity in thinned and unthinned northern hardwood forests. *Nat. Areas J.* **24**: 57–64.
- Irland, L.C. 1999. Northeast's changing forests. Harvard University Press for Harvard Forest, United Kingdom.
- Johnson, E.A., and Miyanishi, K. 2008. Testing the assumptions of chronosequences in succession. *Ecol. Lett.* **11**(5): 419–431. doi:[10.1111/j.1461-0248.2008.01173.x](https://doi.org/10.1111/j.1461-0248.2008.01173.x). PMID: 18341585.
- Kahl, T., Arnstadt, T., Baber, K., Bässler, C., Bauhus, J., Borken, W. et al. 2017. Wood decay rates of 13 temperate tree species in relation to wood properties, enzyme activities and organismic diversities. *Forest Ecol. Manag.* **391**: 86–95. doi:[10.1016/j.foreco.2017.02.012](https://doi.org/10.1016/j.foreco.2017.02.012).
- Keeton, W.S., Whitman, A.A., McGee, G.C., and Goodale, C.L. 2011. Late-successional biomass development in northern hardwood - conifer forests of the northeastern United States. *For. Sci.* **57**(6): 489–505.
- Kuznetsova, A., Brockhoff, P.B., and Christensen, R.H.B. 2017. lmerTest Package: tests in linear mixed effects models. *J. Stat. Softw.* **82**(13): 1–26. doi:[10.18637/jss.v082.i13](https://doi.org/10.18637/jss.v082.i13).
- Larrieu, L., Courbaud, B., Drénou, C., Goulard, M., Büttler, R., Kozák, D., et al. 2022. Perspectives: key factors determining the presence of tree-related microhabitats: a synthesis of potential factors at site, stand and tree scales, with perspectives for further research. *For. Ecol. Manag.* **515**: 120235. doi:[10.1016/j.foreco.2022.120235](https://doi.org/10.1016/j.foreco.2022.120235).
- Lasota, J., Błońska, E., Piaszczyk, W., and Weicheć, M. 2018. How the deadwood of different species in various stages of decomposition affected nutrient dynamics. *J. Soils Sediments* **18**: 2759–2769. doi:[10.1007/s11368-017-1858-2](https://doi.org/10.1007/s11368-017-1858-2).
- Leak, W.B. 2006. Fifty-year impacts of the beech bark disease in the Bartlett Experimental Forest, New Hampshire. *North J Appl For.* **23**(2): 141–143.
- Leak, W.B., and Yamasaki, M. 2010. Seventy-year record of changes in the composition of overstory species by elevation on the Bartlett Experimental Forest. USDA Forest Service, Northeastern Forest Experiment Station, Newton Square, PA.
- Liu, W., Schaefer, D., Qiao, L., and Liu, X. 2013. What controls the variability of wood-decay rates?. *Forest Ecol. Manag.* **310**: 623–631. doi:[10.1016/j.foreco.2013.09.013](https://doi.org/10.1016/j.foreco.2013.09.013).

- Mattson, K.G., Swank, W.T., and Waide, J.B. 1987. Decomposition of woody debris in a regenerating, clear-cut forest in the southern Appalachians. *Can. J. For. Res.* **17**(7): 712–721. doi:10.1139/x87-114.
- McDowell, N.G., Allen, C.D., Anderson-Teixeira, K., Aukema, B.H., Bond-Lamberty, B., Chini, L., et al. 2020. Pervasive shifts in forest dynamics in a changing world. *Science* **368**: 964: 1–10.
- McGarvey, J.C., Thompson, J.R., Epstein, H.E., and Shugart, H.H., Jr. 2015. Carbon storage in old-growth forests of the mid-atlantic: toward better understanding the eastern forest carbon sink. *Ecology* **96**(2): 311–317. doi:10.1890/14-1154.1. PMID: 26240851.
- McGee, G.G. 2000. The contribution of beech bark disease-induced mortality to coarse woody debris loads in northern hardwood stands of Adirondack Park, New York, USA. *Can. J. For. Res.* **30**(9): 1453–1462. doi:10.1139/x00-053.
- McGee, G.G. 2001. The influence of decaying logs on understory vascular plant communities in Adirondack northern hardwood forests. *J. Torrey Bot. Soc.* **128**: 370–380. doi:10.2307/3088669.
- McGee, G.G., and Birmingham, J.P. 1997. Decaying logs as germination sites in northern hardwood forests. *North. J. Appl. For.* **14**(4): 178–182. doi:10.1093/njaf/14.4.178.
- McGee, G.G., Leopold, D.J., and Nyland, R.D. 1999. Structural characteristics of old-growth, maturing, and partially cut northern hardwood forests. *Ecol. Appl.* **9**(4): 1316–1329. doi:10.1890/1051-0761(1999)009%5b1316:SCOOGM%5d2.0.CO;2.
- Michel, A.K., and Winter, S. 2009. Tree microhabitat structures as indicators of biodiversity in Douglas-fir forests of different stand ages and management histories in the Pacific Northwest, U.S.A. *For. Ecol. Manag.* **257**: 1453–1464. doi:10.1016/j.foreco.2008.11.027.
- Nash, J. 2022. Downed woody debris, forest development, and tree biomass in the white mountains of New Hampshire. Thesis Dissertation, State University of New York College of Environmental Science and Forestry, Syracuse, NY.
- Nash, J.M., Vadeboncoeur, M.A., Wild, A.D., Zee, A., Cornell, E.A., Arthur, M.A., and Yanai, R.D. 2023. Biomass accumulation in trees and downed wood at Bartlett Experimental Forest, Hubbard Brook Experimental Forest, the Bowl Natural Research Area, and the White Mountain National Forest, NH, USA ver 1. Environmental Data Initiative. doi:10.6073/pasta/bd190341e6c15c02815966083f75ffbb [accessed 14 August 2023].
- Nordén, B., Ryberg, M., Götmark, F., and Olausson, B. 2004. Relative importance of coarse and fine woody debris for the diversity of wood-inhabiting fungi in temperate broadleaf forests. *Biol. Conserv.* **117**: 1–10. doi:10.1016/S0006-3207(03)00235-0.
- Nyland, R.D., Zipperer, W.C., and Hill, D.B. 1986. The development of forest islands in exurban central New York State. *Landsc. Urban Plan.* **13**: 111–123. doi:10.1016/0169-2046(86)90016-2.
- Oksanen, J., Simpson, G., Blanchet, F., Kindt, R., Legendre, P., Minchin, P., et al. 2022. vegan: community ecology package. R package version 2.6-4. <https://CRAN.R-project.org/package=vegan>.
- Oliver, C.D., and Larson, B.C. 1996. *Forest stand dynamics*. Wiley Publishing, New York.
- Orwig, D.A., and Foster, D.R. 1998. Forest response to the introduced hemlock woolly adelgid in southern New England, USA. *J. Torrey Bot. Soc.* **125**(1): 60–73. doi:10.2307/2997232.
- Peterson, D.W., Dodson, E.K., and Harrod, R.J. 2015. Post-fire logging reduces surface woody fuels up to four decades following wildfire. *For. Ecol. Manag.* **338**: 84–91. doi:10.1016/j.foreco.2014.11.016.
- Piaszczyk, W., Lasota, J., and Blonska, E. 2019. Effect of organic matter released from deadwood at different decomposition stages on physical properties of forest soil. *Forests* **11**(24): 1–13.
- Pinheiro, J., and Bates, D., R Core Team. 2022. nlme: linear and nonlinear mixed effects models. R package version 3.1-157. <https://CRAN.R-project.org/package=nlme>.
- Puhlick, J.J., Weiskittel, A.R., Fernandez, I.J., Solarik, K.A., and Sleep, D.J. 2022. Evaluation of projected carbon accumulation after implementing different forest management treatments in mixed-species stands in northern Maine. *Carbon Manag.* **13**(1): 190–204. doi:10.1080/17583004.2022.2063761.
- Puhlick, J.J., Weiskittel, A.R., Fraver, S., Russell, M.B., and Kenefic, L.S. 2016. Assessing the role of natural disturbance and forest management on dead wood dynamics in mixed-species stands of central Maine, USA. *Can. J. For. Res.* **46**(9): 1092–1102. doi:10.1139/cjfr-2016-0177.
- Puhlick, J.J., Weiskittel, A.R., Kenefic, L.S., Woodall, C.W., and Fernandez, I.J. 2020. Strategies for enhancing long-term carbon sequestration in mixed-species, naturally regenerated northern temperate forests. *Carbon Manag.* **11**: 381–397.
- R Core Team. 2020. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/> [accessed 14 Sep 2021].
- Scheller, R.M., and Mladenoff, D.J. 2004. A forest growth and biomass module for a landscape simulation model, LANDIS: design, validation, and application. *Ecol. Modell.* **180**(1): 211–229. doi:10.1016/j.ecolmodel.2004.01.022.
- Scheu, S., and Schauermaun, J. 1994. Decomposition of roots and twigs: effects of wood type (beech and ash), diameter, site of exposure and macrofauna exclusion. *Plant Soil* **163**: 13–24. doi:10.1007/BF00033936.
- Shang, B.Z., He, H.S., Crow, T.R., and Shifley, S.R. 2004. Field load reductions and fire risk in central hardwood forests of the United States: a spatial simulation study. *Ecol. Modell.* **180**: 89–102. doi:10.1016/j.ecolmodel.2004.01.020.
- Siccama, T.G., Fahey, T.J., Johnson, C.E., Sherry, T.W., Denny, E.G., Girdler, E.B., et al. 2007. Population and biomass dynamics of trees in a northern hardwood forest at Hubbard Brook. *Can. J. For. Res.* **37**: 737–749. doi:10.1139/X06-261.
- Siccama, T.G., Hamburg, S.P., Arthur, M.A., Yanai, R.D., Bormann, F.H., and Likens, G.E. 1994. Corrections to allometric equations and plant tissue chemistry for Hubbard Brook experimental forest. *Ecology* **75**: 246–248. doi:10.2307/1939398.
- Stutz, K.P., Dann, D., Wambsganss, J., Scherer-Lorenzen, M., and Lang, F. 2017. Phenolic matter from deadwood can impact forest soil properties. *Geoderma* **288**: 204–212. doi:10.1016/j.geoderma.2016.11.014.
- U.S. Forest Service. 2005. Phase 3 field guide—downed woody materials. U.S. Department of Agriculture, Forest Service, North Central Research Station, St. Paul, MN.
- U.S. Forest Service. 2019. National core field guide. U.S. Department of Agriculture, Forest Service, Washington, D.C.
- Ucitel, D., Christian, D.P., and Graham, J.M. 2003. Vole use of coarse woody debris and implications for habitat and fuel management. *J. Wildl. Manag.* **67**: 65–72. doi:10.2307/3803062.
- Urbano, A.R., and Keeton, W.S. 2017. Carbon dynamics and structural development in recovering secondary forests of the northeastern U.S. *For. Ecol. Manag.* **392**: 21–35. doi:10.1016/j.foreco.2017.02.037.
- Vadeboncoeur, M.A., Hamburg, S.P., Blum, J.D., Pennino, M.J., and Yanai, R.D. 2012. The quantitative soil pit method for measuring below-ground carbon and nitrogen stocks. *Soil Sci. Soc. Am. J.* **76**: 2241–2255. doi:10.2136/sssaj2012.0111.
- Vadeboncoeur, M.A., Hamburg, S.P., Yanai, R.D., and Blum, J.D. 2014. Rates of sustainable forest harvest depend on rotation length and weathering of soil minerals. *For. Ecol. Manag.* **318**: 194–205. doi:10.1016/j.foreco.2014.01.012.
- Van Wagner, E. 1968. The line intersect method in forest fuel sampling. *For. Sci.* **14**: 20–27.
- Vanderwel, M.C., Thorpe, H.C., Shuter, J.L., Caspersen, J.P., and Thomas, S.C. 2008. Contrasting downed woody debris dynamics in managed and unmanaged northern hardwood stands. *Can. J. For. Res.* **38**: 2850–2861. doi:10.1139/X08-130.
- Wang, W.J., He, H.S., Thompson, F.R., III, Fraser, J.S., and Diak, W.D. 2016. Changes in forest biomass and tree species distribution under climate change in the eastern United States. *Landsc. Ecol.* **32**: 1399–1413. doi:10.1007/s10980-016-0429-z.
- Whittaker, R.H., Likens, G.E., Bormann, F.H., and Siccama, T.G. 1974. The Hubbard Brook ecosystem study: forest biomass and production. *Ecol. Monogr.* **44**(2): 233–254. doi:10.2307/1942313.
- Wickham, H. 2016. *ggplot2: elegant graphics for data analysis*. Springer-Verlag, New York.
- Wickham, H., and Girlich, M. 2022. tidy: tidy messy data. R package version 1.2.1. <https://CRAN.R-project.org/package=tidy>.
- Wickham, H., François, R., Henry, L., and Müller, K. 2022. dplyr: a grammar of data manipulation. R package version 1.0.10. <https://CRAN.R-project.org/package=dplyr>.
- Woodall, C.W., and Monleon, V.J. 2008. Sampling protocol, estimation, and analysis procedures for the down woody materials

- indicator of the FIA program. U.S. Department of Agriculture, Forest Service. North Central Research Station, Newton Square, PA.
- Woodall, C.W., Walters, B.F., Oswalt, S.N., Domke, G.M., Toney, C., and Gray, A.N. 2013. Biomass and carbon attributes of downed woody materials in forests of the United States. *For. Ecol. Manag.* **305**: 48–59. doi:[10.1016/j.foreco.2013.05.030](https://doi.org/10.1016/j.foreco.2013.05.030).
- Yamasaki, M., and Leak, W.B. 2006. Snag longevity in managed northern hardwoods. *North. J. Appl. For.* **23**(3): 215–217. doi:[10.1093/njaf/23.3.215](https://doi.org/10.1093/njaf/23.3.215).
- Yanai, R.D., Arthur, M.A., Acker, M., Levine, C.R., and Park, B.B. 2012. Variation in mass and nutrient concentration of leaf litter across years and sites in a northern hardwood forest. *Can. J. For. Res.* **42**: 1597–1610. doi:[10.1139/x2012-084](https://doi.org/10.1139/x2012-084).
- Yanai, R.D., Arthur, M.A., Siccama, T.G., and Federer, C.A. 2000. Challenges of measuring forest floor organic matter dynamics: repeated measures from a chronosequence. *For. Ecol. Manag.* **138**: 273–283. doi:[10.1016/S0378-1127\(00\)00402-3](https://doi.org/10.1016/S0378-1127(00)00402-3).
- Yanai, R.D., Currie, W.S., and Goodale, C.L. 2003. Soil carbon dynamics after forest harvest: an ecosystem paradigm reconsidered. *Ecosystems* **6**(2): 197–212. doi:[10.1007/s10021-002-0206-5](https://doi.org/10.1007/s10021-002-0206-5).
- Yanai, R.D., Siccama, T.G., Arthur, M.A., Federer, C.A., and Friedland, A.J. 1999. Accumulation and depletion of base cations in forest floors in the northeastern United States. *Ecology* **80**(8): 2774–2787. doi:[10.1890/0012-9658\(1999\)080%5b2774:AAD0BC%5d2.0.CO;2](https://doi.org/10.1890/0012-9658(1999)080%5b2774:AAD0BC%5d2.0.CO;2).
- Yihui, X. 2022. knitr: a general-purpose package for dynamic report generation in R. R package version 1. <https://www.r-project.org/nosvn/pandoc/knitr.html>.

Appendix A

Table A1. Density for each species and decay class used for downed wood biomass calculations, with values from [Harmon et al. \(2008\)](#) indicated in italics. ASH, white ash (*Fraxinus americana* L.); ASP, aspen (*Populus* spp.); BASS, American baswood (*Tilia Americana* L.); BE, American beech (*Fagus grandifolia* Ehrh.); FIR, Balsam fir (*Abies balsamea* L. (Mill.)); HEM, hemlock (*Tsuga canadensis* L.); OV, ironwood (*Ostrya virginiana* Mill.); PC, pin cherry (*Prunus pensylvanica* L.f.); RM, red maple (*Acer rubrum* L.); SM, sugar maple (*Acer saccharum* Marshall.); SP, red spruce (*Picea rubens* Sarg.); STM, striped maple (*Acer pensylvanicum* L.); UNK, unknown species (unidentifiable); WB, white birch (*Betula papyrifera* Marshall); YB, yellow Birch (*Betula alleghaniensis* Britt.). An estimate of 0.14 g/cm³ was used for decay classes 4 and 5 based on results by [Arthur et al. \(1993\)](#) and [Adams and Owens \(2001\)](#).

Species	Decay class		
	1	2	3
ASH	NA	0.41	0.26
ASP	0.34	0.34	0.23
BASS	NA	0.33	NA
BE	0.57	0.32	0.34
FIR	NA	0.29	NA
HEM	0.46	0.27	0.29
OV	NA	0.42	0.37
PC	0.43	0.34	0.32
RM	0.54	0.26	0.36
SM	0.38	0.35	0.36
SP	0.33	0.25	0.26
STM	0.54	0.39	0.33
UNK	NA	0.29	0.22
WB	0.32	0.49	0.36
YB	0.58	0.31	0.34

Fig. A1. Basal area of each species >10 cm in the live tree inventories (1994, 2004, 2012, and 2021) of the 16 stands included in this study. PC, pin cherry (*Prunus pensylvanica* L.f.); ASP, aspen (*Populus* spp.); WB, white birch (*Betula papyrifera* Marshall); ASH, white ash (*Fraxinus americana* L.); OTHER, mountain maple (*Acer spicatum* Lam.); striped maple (*Acer pensylvanicum* L.); ironwood (*Ostrya virginiana* Mill.); YB, yellow Birch (*Betula alleghaniensis* Britt.); RM, red maple (*Acer rubrum* L.); SM, sugar maple (*Acer saccharum* Marshall.); BE, American beech (*Fagus grandifolia* Ehrh.); CON, conifers.

