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

Joseph M. Nash, Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Visualization, Writing – original draft, Writing – review & editing[a,b], Matthew A. Vadeboncoeur, Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Visualization, Writing – review & editing[c], Gregory G. McGee, Methodology, Writing – review & editing[d], Christopher W. Woodall, Methodology, Writing – review & editing[e] and Ruth D. Yanai, Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Writing – review & editing[a,*]

[a]Department of Sustainable Resources Management, SUNY College of Environmental Science and Forestry, Syracuse, NY 13210, USA Q3 [Copyeditor to Author] AU: Please check that author names and their corresponding affiliations are presented and spelled correctly. [Reply by Author] All are correct. Edit Reply

[b]Clare Conservation District, Harrison, MI 48625, USA

[c]Earth Systems Research Center, University of New Hampshire, Durham, NH 03824, USA

[d]Department of Environmental Biology, SUNY College of Environmental Science and Forestry, Syracuse, NY 13210, USA

[e]Northern Research Station, USDA Forest Service, Durham, NH 03824, USA

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

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Q1: AUTHOR: Please check that all author names are spelled correctly, and that the details of the affiliation(s) and author contributions are complete and associated with the correct author. Please provide ORCID numbers if available.
Reply: All author names and affiliations are correct. ORCID numbers are as follows: Joseph M. Nash: 0000-0001-7695-1441 Matthew A.Vadeboncoeur: 0000-0002-8269-0708 Gregory G.McGee: 0000-0001-7437-8100 Christopher W.Woodall: 0000-0001-8076-6214 Ruth D. Yanai:

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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) ▼ **Q4 [Copyeditor to Author]** The reference 'Dyer 2006' is cited in the text but is not listed in the references list. Please either delete the in-text citation or provide full reference details following journal style. **[Reply by Author]** Dyer, J. M. 2006. Revisiting the deciduous forests of eastern North America. BioScience, 56(4), 341-352. **Edit Reply** 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 ▶ **Q5** **Edit Reply**; 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) ▶ **Q6** **Edit Reply**, 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). ▼ **Q7 [Copy Editor Aptara to Author]** Please check the term "Northeast" for correctness in the sentence "In a meta-analysis of data from sites across ..." **[Reply by Author]** Changed to "northeastern United States". **Edit Reply** 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. ▼ **Q8 [Copy Editor Aptara to Author]** Please check the text "and therefore the structural complexity of maturing forests to resemble old growth" for its intended meaning in the sentence and amend if necessary. **[Reply by Author]** Comma added after "maturing forests" **Edit Reply**

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

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Reply: Dyer, J. M. 2006. Revisiting the deciduous forests of eastern North America. BioScience, 56(4), 341-352.

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Inputs of DWD are related to the frequency and severity of disturbance and … 986; Puhlick et al. 2016). DWD in a mature forest consists of large logs and branches that have fallen to the forest floor. A stand-re… pending on the nature of the disturbance. Both the remnant DWD and that generated by disturbance are gradually lost to fragmentati… g stem exclusion (peaking 20–30 years after stand initiation) when the mortality of suppressed individuals is greatest (Franklin et … omass to standing live tree biomass, which has a secondary peak during self-thinning, but is highest following a stand-replacing d… y-dependent factors leading to self-thinning to the natural senescence of individual trees, stochastic disturbances such as windthrow, … ift from twigs and small DWD to larger stems and from shade-intolerant to tolerant species in DWD assemblages (Allison et al. 200… me 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 (m^3:m^2/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). ▼ Q12 [Copy Editor Aptara to Author] Please check the unit "m3:m2/ha" for correctness. [Reply by Author] Does it help to change to "ratio of DWD volume to live basal area"? It's a ratio, hence the colon. Edit Reply 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 ▶ Q13 Edit Reply; Kahl et al. 2017; Eriksson et al. 1990) ▶ Q14 Edit Reply.

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).

+No. 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

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Introduction

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

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

e that they have no competing interests.