



Allometric equations quantify accelerated growth and carbon fixation in trees of northeastern north America



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ABSTRACT

A tree's basal area (BA) and wood volume scale exponentially with tree diameter in species-specific patterns. Recent observed increases in tree growth suggest these allometric relationships are shifting in response to climate change, rising CO₂ levels, and/or changes in forest management. We analyzed 9,214 cores from nine conifer and 11 broadleaf species grown in managed mixed-species stands in the upper Midwest to quantify how well diameter (diameter at breast height (DBH)) serves to predict BA growth and above-ground wood and carbon (C). These samples include many large trees. We fit mixed models to predict BA growth and above-ground biomass/C from diameter, tree height, and the BA of nearby trees while controlling for site effects. Models account for 55%–83% of the variance in log(recent growth), improving predictions over earlier models. Growth-diameter scaling exponents covary with certain leaf and stem (but not wood) functional traits, reflecting growth strategies. LogBA increment scales linearly with log(diameter) as trees grow bigger in 16/20 species and growth actually accelerates in *Quercus rubra* L. Three other species plateau in growth. Growth only decelerates in red pine, *Pinus resinosa* Ait. Growth in whole-tree, above-ground biomass, and C accelerate even more strongly with diameter (mean exponent: 2.08 vs. 1.30 for BA growth). Sustained BA growth and accelerating wood/C growth contradict the common assumption that tree growth declines in bigger trees. Yield tables and silvicultural guidelines should be updated to reflect these current relationships. Such revisions will favor delaying harvests in many managed stands to increase wood production and enhance ecosystem values including C fixation and storage. Further research may resolve the relative roles of thinning, climatic conditions, nitrogen inputs, and rising CO₂ levels on changing patterns of tree growth.

1. Introduction

Temperate forests support a remarkable diversity of plant, animal, fungal, and microbial species while generating valued forest products and sustaining hydrologic and biogeochemical processes with immense biotic and economic value. These benefits include moderating runoff and local temperatures, absorbing nutrients, recharging aquifers, supporting biodiversity, and absorbing and storing huge quantities of carbon (Alverson et al., 1994). Maintaining forest carbon sinks is vital for meeting the 2015 Paris Climate Accord targets (IPCC, 2018; Fargione et al., 2018; Moomaw et al., 2019). Forest carbon sinks removed ~30% of global fossil fuel emissions annually between 2009 and 2018 (Friedlingstein et al., 2020) with ~44% coming from temperate forests.

Temperate forests are the strongest land sinks in the USA, offsetting about 14% of our CO₂ emissions (U.S. EPA, 2020) with forests in the lower 48 absorbing an estimated 206 Tg C·year⁻¹ between 1950 and 2010 mostly as living biomass (87%, 180 Tg C·year⁻¹; Zhang et al., 2012). In contrast, forest harvests release greenhouse gases, greatly reducing forest C capture and storage. These emissions take many decades to recapture via growth, incurring annualized carbon costs estimated at 3.5–4.2 Gt CO₂e·year⁻¹ globally (Peng et al., 2023). Enhancing atmospheric CO₂ removal via forests is thus thought to be the most efficient and significant terrestrial natural climate solution (Griscom et al., 2017).

Individual tree growth reflects species' traits and growth patterns interacting with environmental conditions, competitors, mutualists,

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pathogens, and herbivores. Ecologists and dendrochronologists use annular growth rings to quantify tree growth trajectories and to infer how ecological conditions and interactions in the past have changed growth (Smith, 2008). Growth in many temperate tree species has increased markedly in recent decades (De Vries et al., 2009; Cole et al., 2010; McMahon et al., 2010; Pretzsch et al., 2014; Schulte-Uebbing and de Vries, 2018; Etzold et al., 2020; Davis et al., 2022; Hogan et al., 2024). These increases likely reflect shifts in climate (e.g., longer growing seasons or increased precipitation), increasing CO₂ levels, and/or aerial N fertilization.

Foresters commonly assert that diameter and wood growth decline in larger trees and “overmature” stands leading them to schedule harvests at “the culmination of mean annual increment” which can be as short as 25–30 years for aspen in northeastern North America but rarely exceeds 70–90 years even for long-lived species (Alverson et al., 1994). As forest managers often use yield tables and allometric tree models from 30 to 50+ years ago, we should ask whether these are still accurate or might rather mislead us by underestimating tree and stand growth and thus the wood and C accrued by bigger trees and older forest stands. Trouillier et al. (2019) reviewed equations for diameter growth and found that in 35 of 41 temperate tree species, biomass growth continues to increase with diameter through the largest sizes. Stephenson et al. (2014) found the most biomass growth in the biggest stems for all but 3% of 403 species. Large open-grown trees support, on average, 83% more wood volume than expected based on allometric equations from forest trees

(Moeys et al., 2025). Lutz et al. (2018) found that the largest 1% of trees account for half the aboveground biomass globally and ~30% within USA forests. In the Pacific NW, trees >53 cm in diameter account for 33%–46% of total above-ground carbon while representing 2%–3.7% of all tree stems (Mildrexler et al., 2020).

How forest management affects forest C stocks and dynamics is challenging to assess and model (Clark et al., 2001; Jenkins et al., 2003; IPCC, 2003). Forest C stocks are often estimated using remotely sensed data and statistical inference (Weiskittel et al., 2015; Huang et al., 2019). Such estimates improve when calibrated against ground-truth data on forest biomass volumes and rates of tree growth, quantified using tree ring data (Dye et al., 2016; Evans et al., 2017, 2022). Accurate models of tree growth for many species growing under varied circumstances and management regimes help us understand how the growth and survival of individual trees combine to affect standing volume, forest biomass, and carbon sequestration from local to global scales (Kearsley et al., 2013; Ni et al., 2014; Xu et al., 2019). Allometric models for large trees are particularly important given their importance for wood and carbon dynamics, but we often lack data from big trees (Muller-Landau et al., 2014; Zhang et al., 2020). Measurements of tree and stand growth may also derive from monocultures that may not accurately capture growth dynamics in mixed-species stands (Berkhout and Tham, 1992; Zhao et al., 2004; Pretzsch et al., 2015). Forest models like the U.S. Forest Service's forest vegetation simulator are based on Forest Inventory and Analysis (FIA) data from randomly selected and



Fig. 1. Locations of BPCL lands relative to other public lands in the region.

thus heterogeneous stands. Given that many stands are monocultures or managed intensely using short rotations, these data may not be reliable for predicting the growth of big trees in mature, mixed-species stands.

To address needs for updated data and models of tree growth and biomass/C dynamics in managed temperate forests, we describe and compare patterns of tree growth and allometry in nine conifer and 11 deciduous species growing in mixed-species, multi-aged stands in the upper Midwest, USA (Fig. 1 and Table 1). We analyze data for >9,000 trees growing in managed stands across a range of soils, site productivities, structural characteristics, and age distributions. We sought to 1) characterize the distributions of tree diameters and growth rates (annual increments in tree basal area) in these 20 species; 2) explore relationships between tree diameter and growth rates in each species and compare how these vary; 3) statistically model BA growth as a function of tree diameter, height, and competition from other trees, taking into account stand-to-stand variation in overall growing conditions; 4) compare these models to growth equations used previously and recent models of whole-tree biomass and carbon; and 5) compare patterns of growth and biomass/carbon allocation within and among species to assess possible trade-offs among species with different life histories and ecologies.

2. Field methods

2.1. Study area

The study area covers 14,000 ha of upland forests in the Laurentian mixed forest region occupying ~20,000 km² in northern Wisconsin, USA, and extending ~200 km east to west (88°20' to 90°40' W) and 100 km north to south (46°15' to 45°20' N, Fig. 1). These humid-continental, mixed upland forest habitats vary in site conditions with soils ranging from coarse outwash sands to deep, fine textured, aeolian derived silt loams on drumlins. Forests at these sites originated primarily via natural regeneration except for red pines (*Pinus resinosa*) which were largely planted in the 1930s–1950s. Natural disturbances once dominated this landscape (e.g., wind/ice storms and fires on drier sandy sites). Fire scars are still present on larger pine trees (*Pinus* sp.) despite being suppressed since the 1930s. Since then, disturbances have been mostly windthrow and insect defoliations.

2.2. Land ownership and forest management

The trees we cored and analyzed grew on timberlands managed by the Wisconsin Board of Commissioners of Public Lands (BCPL) within lands ceded to the United States by Ojibwe Tribes via treaties in the 1840s and 1850s. Most public and private forestlands here experienced extensive logging and multiple fires in the late 19th/early 20th century when Europeans settled the region. The BCPL forestlands, however, experienced less intensive logging and thus retained more structural diversity, disturbance-sensitive species, and mature trees (some to 90+ cm in diameter). Since 1943, BCPL forests have been actively managed using selection-cut treatments to sustain uneven-aged forests for forest types appropriate to soils and the region.

The data reflect a broad range of species, tree sizes, and growth rates derived from forest stands that cover the full range of growing conditions in the study area. These stands were usually managed using thinning to release faster-growing trees via single tree and small-group selection harvests with residual stocking levels of 16–20 m²·ha⁻¹. Such management resembles practices followed on larger Indian reservations in Wisconsin (Waller and Reo, 2018) and carefully managed forests in the USA, Europe, and Asia (Morales-Hidalgo et al., 2015; Sabatini et al., 2020). Removing slow-growing suppressed trees reduced the chance of underestimating growth in larger trees.

2.3. Study species and tree growth

We analyzed growth in 20 tree species capable of growing into forest canopies (Table 1) excluding understory species (e.g., ironwood (*Ostrya virginiana*) and pin cherry (*Prunus pensylvanica*)), species not native to the region (black locust, *Robinia pseudoacacia*), and those with <75 trees (*Fraxinus americana* and *Quercus alba*). These 20 species vary in shade tolerance, lifespan, and maximum size and represent the species commonly found in the Laurentian mixed forest (Ecological Province 212, Avers and McNab, 1994; McNab et al., 2007).

Between 2005 and 2018, the BCPL's continuous forest inventory team extracted increment cores from the first and third tree sampled within each forest inventory plot (generally >10 cm DBH). Such samples ensure that trees were sampled in proportion to their abundance while avoiding sampling adjacent trees whose growth might be correlated.

Table 1
Tree species functional characteristics.

Species	Conifer/ deciduous	Wood density (g·cc ⁻¹)	Leaf dry matter content	Leaf thickness (mm)	Leaf N (%)	SLA (cm ² ·g ⁻¹)	log ₁₀ (seed mass (mg))
<i>Abies balsamea</i> L.	C	0.33	402.1	0.4389	1.477	9.164	0.882
<i>Larix laricina</i> (Du Roi) K. Koch	C	0.49	432.1	0.2579	1.408	–	0.1728
<i>Picea glauca</i> (Moench) Voss	C	0.33	379.5	0.775	1.173	–	0.2169
<i>Picea mariana</i> (Mill.) B.S.P.	C	0.38	521.8	0.6738	0.9065	–	-0.1175
<i>Pinus banksiana</i> Lamb.	C	0.4	433.9	0.5804	1.5089	5.226	0.6041
<i>Pinus resinosa</i> Ait	C	0.41	410.9	0.5944	1.21	5.175	0.7758
<i>Pinus strobus</i>	C	0.34	441.6	0.498	1.3679	10.291	1.1754
<i>Thuja occidentalis</i> L.	C	0.29	437.1	0.5955	1.2652	7.343	0.021
<i>Tsuga canadensis</i> L.	C	0.38	396.4	0.3247	1.3543	12.12	0.1234
<i>Acer rubrum</i> L.	D	0.49	388.6	0.1282	1.9066	27.252	0.9688
<i>Acer saccharum</i> Marshall	D	0.44	332	0.1184	2.0474	40.759	1.8689
<i>Betula alleghaniensis</i> Britton	D	0.55	268.4	0.1684	2.4549	39.202	-0.0975
<i>Betula papyrifera</i> Marshall	D	0.48	356.7	0.1713	2.4144	24.849	-0.6645
<i>Fraxinus nigra</i> Marshall	D	0.45	232.8	0.155	2.4468	40.007	1.4996
<i>Populus grandidentata</i> Michx.	D	0.36	369.1	0.1495	3.3983	22.451	-0.8861
<i>Populus tremuloides</i> Michx.	D	0.35	352.1	0.172	2.2453	27.646	-0.9208
<i>Prunus serotina</i> Ehrh.	D	0.47	319.6	0.1686	2.7776	28.653	1.9645
<i>Quercus ellipsoidalis</i> E.J.Hill	D	0.58	397	0.2048	2.9637	18.537	3.1925
<i>Quercus rubra</i> L.	D	0.56	387.6	0.1405	2.3044	25.338	3.2144
<i>Tilia americana</i> L.	D	0.32	263.4	0.1423	3.1765	50.605	1.8305

Note: C: conifer; D: deciduous.

Teams measured DBH to the nearest 2.6 mm using a tape and estimated tree height to the nearest foot (31 cm) using a clinometer, visually categorizing the crown into five classes: (1) suppressed (no exposed crown), (2) intermediate, (3) co-dominant, (4) dominant, and (5) super-canopy (emergent above the surrounding canopy).

2.4. Core extraction and tree ring counting

Field inventory staff extracted cores from the main bole under a point of average crown width. Cores were drilled inward to a depth of 5–6 cm which reflects growth from roughly 1985 to 2018. No attempt was made to drill to the pith of the tree. Cores were mounted in wooden core holders, sanded using 400 grit sandpaper, and stained with water or an iodine-water mixture to provide contrast for counting annual rings. A dissecting microscope ($10\times$) allowed us to count the number of rings spanning the outermost 2.54 cm of growth (excluding the bark). Cores missing bark were discarded. Partial rings were rounded to the nearest integer. Most cores had 10–20 rings in this annulus (annual ring width 1.3–2.5 mm), implying an accuracy within 5%–10%. We estimate DBH at the beginning of the growth period as the final DBH (measured when the core was collected) minus 5.08 cm. We estimate basal area increases from differences in cross-sectional area, assuming successive tree disks to be circles of area πr^2 . Averaging growth estimates over the previous 10–20 years reduces the noise inherent in shorter-term (e.g., annual) measurements (Alexander et al., 2018).

3. Analyses

Foresters use DBH to predict tree growth (annual increments in basal area, or BA) and biomass/carbon dynamics (Vanclay, 1995). Models to predict tree growth are mostly based on allometric equations relating increases in BA, wood, and C to DBH (Guo et al., 2010; Domke et al., 2012; Liu et al., 2019; Westfall et al., 2024). Their functional forms vary, applying various terms and coefficients to model trees of different sizes and species (Peichl and Arain, 2007; Zhou et al., 2021). We build on existing studies in our region like Jenkins et al. (2003), who strove to model the allometry of tree growth and biomass to improve estimates of forest carbon stocks and dynamics. Westfall et al. (2024) extended their approach, modeling tree volume, biomass, and carbon using more restricted equations and more extensive, accurate, and regionally segregated data. They also used improved estimates of biomass and C in upper limbs and species-specific carbon fractions (rather than 0.5). Their updated national-scale volume and biomass (NSVB) methods supersede older component ratio models. Still, they reiterated Frank et al.'s (2019) concerns about lacking data on bigger trees for many species. We address these gaps here and extend our results by using Westfall et al.'s (2024) equations to predict whole-tree biomass and C.

Our data for 9,453 trees included plot and stand ID, geographic location, estimated total plot basal area (BA per acre or ha), species, initial DBH, height, crown class, and counts of growth rings in the outer 2.56 cm of wood. Sample sizes exceeded 400 for six long-lived species and varied from 76/77 trees for *Larix laricina*/*Prunus serotina* to 2,310 trees for *Acer saccharum* with a mean (median) sample size of 483.1 (298). Such samples lend statistical accuracy to our models and power for testing the effects of individual predictor variables.

Both simple power-law expressions and more complex models are used to predict tree growth (Muller-Landau et al., 2006; Schafer and Mack, 2014; Poorter et al., 2015; Picard et al., 2015; Zhou et al., 2021). These equations vary in which data they use and to what extent they address how tree growth varies among stands growing under different conditions (Poorter et al., 2003; Zhao et al., 2013; Wang et al., 2017; Soh et al., 2019; Subedi et al., 2019; Looney et al., 2021). Such differences include age structures, management histories (Nyland et al., 2021), species functional groups (Osunkoya et al., 2007; Russo et al., 2007; Sterck and Bongers, 1998; Olson et al., 2021), and site conditions (Hulshof et al., 2015; Lines et al., 2012; Zhang et al., 2020).

We first analyzed distributions and bivariate relationships among the predictor and response variables. Distributions of DBH were close to log-normal in most species but closer to normal in a few long-lived tree species (*Betula alleghaniensis*, *Pinus strobus*, *Quercus rubra*, and *Tsuga canadensis*). Growth in BA and whole-tree biomass and C were always log-normal. Relationships between DBH and growth were decidedly non-linear and heteroscedastic. In contrast, log(BA growth) vs. logDBH relationships were mostly linear and homoscedastic. Basal area increments capture growth patterns in relation to tree size and age better than simple tree-ring widths (Biondi and Qeadan, 2008). Simple multivariate models using log-transformed DBH, species, and their interaction to predict logBA increment showed more uniformly distributed residuals, greater effects for diameter and species, less interaction between these variables (higher additivity), and greater explanatory power (R^2 values) than parallel models using untransformed variables. We thus use log-transformed DBH and growth values. Because plot BA (ha) and tree height were close to normally distributed with biplots against log(growth) showing mostly linear effects and uniform residuals, we did not transform these variables.

We modeled tree growth using a simple and consistent set of predictors in line with previous studies. We first modeled growth (mean annual basal area increment in the outmost annulus) across all trees as a function of species, diameter (DBH at the start of the growth period), height, crown class, and competition (plot basal area minus focal tree BA). Using both diameter and height improves tree growth predictions despite their collinearity (e.g., Picard et al., 2015) as does including plot BA to control for competition (e.g., Forrester, 2021). We then built separate models for each species to improve accuracy by accounting for how the predictors affect growth differently in different species. Species-specific models included site (stand ID) as a random factor to adjust the models for different local growing conditions (Jenkins et al., 2003). Stand ID exerted significant effects in most species, improving estimates how other predictors affected growth. Our initial species-specific mixed models had one random and five fixed factors:

$$\log(\text{BA increment}) \sim \text{intercept} + \text{stand ID (random)} + b1 \times \log(\text{DBH}) + b2 \times (\log(\text{DBH}))^2$$

$$+ c \times \text{height} + d \times \text{competing plot BA (ha)} + e \times \text{crown class} + \text{error} \quad (1)$$

Crown class only affected BA growth in seven species with a small mean effect ($F = 2.33$ vs. 8.7 to 277 for other variables). We decided to drop crown class from further modeling given these small effects, how the categories involve subjective judgments, and that we sought general models that could be applied by others in situations lacking crown class data.

LogDBH was invariably the most important predictor. Stand ID lacked significance in three of 20 species, but was included in all models for consistency and to improve estimates of other variables. Finally, to obtain species models that are simpler to implement and interpret, we used backward elimination to sequentially remove non-significant fixed-effect variables. The resulting models include the quadratic logDBH term in 15 species, tree height in 13 species, and competing plot BA in seven species.

3.1. Relating diameter and growth to whole-tree biomass and carbon

We estimated whole-tree above-ground biomass and carbon for all but two species (*Fraxinus nigra* and *Quercus ellipsoidalis*) using equations from Westfall et al. (2024) specific to our region (210 Warm Continental Division, Fig. 1a). These equations parallel our allometric models which fitted exponents to relate $\log_{10}(\text{BA growth})$ to $\log_{10}(\text{diameter})$ and other variables. In 13 species, Westfall et al. (2024) applied their "model 1", fitting three parameters to the classic Schumacher and Hall (1933) allometric equation (Eq. 2):

$$\text{Biomass} \sim a \times (\text{DBH})^b \times (\text{height})^c + \text{error} \quad (2)$$

(DBH in inches and height in feet). They chose this form as it generates parsimonious models with consistent performance across many data sources. In four other species (*Abies balsamea*, *Pinus resinosa*, *Thuja occidentalis*, and *Tsuga canadensis*), they applied a “Segmented model 2” using two distinct forms of the equation (with unique b coefficients) for trees above and below a threshold diameter (9 inches). Finally, Westfall et al. (2024) applied a modified “Wiley 4” model to *Acer rubrum* to fit two b parameters plus an additional exponential term.

3.2. Trade-offs between components of growth in relation to functional traits

We compared among-species variation in diameter-BA growth exponents (Eq. 1) to a few functional traits linked to tree growth under various conditions (Table 1). We analyzed the effects of taxonomy (coniferous vs. deciduous), wood density (reflecting investment in strong wood tissue), leaf dry matter content (g dry mass·g fresh mass⁻¹), a predictor of net primary productivity (Smart et al., 2017), leaf thickness (thinner leaves are generally better adapted to shady conditions), leaf nitrogen (% of leaf dry weight, reflecting concentrations of photosynthetic enzymes), specific leaf area (SLA; mm²·mg dry leaf⁻¹), correlated with relative growth rate in spruce seedlings (Miyazawa and Lechowicz, 2004)), and seed mass (reflecting reproductive characteristics and negatively related to seedling relative growth rate (Westoby et al., 2002)). Most functional trait data reflect measurements in Wisconsin trees (Waller et al., 2021) except that values for wood density in *Quercus ellipsoidalis* come from Ter-Mikaelian et al. (2008); seed mass data in *Abies balsamea*, *Populus grandidentata* and *tremuloides*, and *Quercus ellipsoidalis* from the seed information database (<https://ser-sid.org/>); and leaf nitrogen data in *Picea* and *Larix* from the TRY database (Kattge et al., 2020). Because our focus in these comparisons was to explore relationships rather than test hypotheses, we used simple biplots and linear regressions and did not correct for multiple comparisons.

All analyses used JMP, version 17 (SAS Institute Inc., USA, 1989–2023).

4. Results

4.1. Species vary in growth

Tree diameters and growth vary considerably within species but also substantially among species which account for 32.2% and 16.8% of the total variation, respectively (Fig. 2). Early successional taxa (*Abies balsamea*, *Betula papyrifera*, *Populus*, and *Prunus*) and bog-inhabiting taxa (*Picea mariana* and *Larix*) had smaller diameters than other species so several of these taxa also had smaller BA increments (*Picea mariana*, *Larix laricina*, *Abies balsamea*, *Thuja occidentalis*, and *Betula papyrifera*). *Pinus strobus*, *Tsuga canadensis*, and *Tilia americana* included most of the largest individuals. The fastest growth rates occurred in *Pinus resinosa* and *Quercus rubra*. The multi-species model that included species interactions with other variables confirmed that diameter predicts growth far better than other variables (including species). This combined model accounts for two-thirds (66.1%) of the total variation in growth across all trees despite omitting site effects (that account for, on average, 30% of the variation in the individual species models).

4.2. Species-specific allometric equations

Diameter strongly and positively affected BA growth with far stronger effects than the other variables across all species (Table 2). Nevertheless, growth still varied considerably among trees with similar diameters likely reflecting variation in local growth conditions and genetic differences. The mean F -value for $\log_{10}\text{DBH}$ was 278, reflecting the remarkable power of this predictor relative to height, competing stand BA, and $\log_{10}\text{DBH}^2$ (mean $F = 12.8$, 9.8, and 8.7, respectively). In all 13 species where competing biomass affected growth, this index reduced

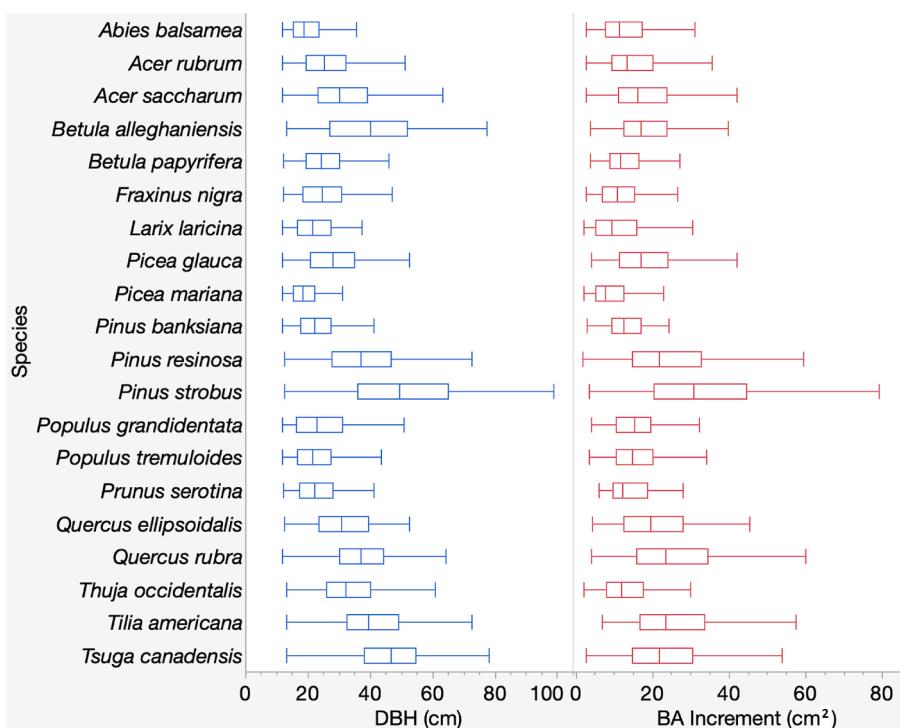


Fig. 2. Variation in tree diameter (DBH) and growth (mean annual BA increase over recent years (cm²)) within and among species. Box plots show range, means, and 25th and 75th percentiles. Species account for 32.2% of the variation in diameter (one-way ANOVA, $F = 235$, $p < 0.0001$) and 16.8% of the variation in $\log(\text{BA growth})$ ($F = 99.9$, $p < 0.0001$).

Table 2

Allometric equations describing tree growth (log of mean annual increment in basal area) for 9 conifer (top) and 11 deciduous (bottom) north temperate tree species. Mixed models were fit to each species using four fixed effects (to the right of the intercept column) and stand ID as a random effect, sequentially eliminating non-significant fixed-effect predictors. Columns show the intercepts and coefficients for all fixed effect predictor variables that were statistically significant for that species and associated overall statistics. Stand ID was not significant in three cases.

Species	N	R ²	Adj-R ²	Intercept	logDBH	log(DBH ²)	Height	Stand BA	Stand ID % Var	Root mean square error
<i>Abies balsamea</i>	422	0.75	0.749	-0.5623	1.4679	-	-0.01453	-0.00527	38.13	0.1371
<i>Larix laricina</i>	76	0.787	0.784	-1.148	1.59545	-	-	-	57.21	0.1648
<i>Picea glauca</i>	224	0.626	0.621	-0.5561	1.46155	-	-0.01662	-0.00308	23.65	0.1547
<i>Picea mariana</i>	103	0.827	0.823	-0.6827	1.50515	-	-0.02522	-	57.97	0.1291
<i>Pinus banksiana</i>	158	0.655	0.651	-0.3648	1.29763	-	-0.02162	-	51.99	0.1241
<i>Pinus resinosa</i>	701	0.736	0.735	-0.2032	1.37974	-2.18885	-0.02359	-0.00351	35.3	0.1457
<i>Pinus strobus</i>	390	0.757	0.755	-0.4735	1.30557	-	-0.00571	-0.00284	34.66	0.143
<i>Thuja occidentalis</i>	204	0.738	0.724	-0.8068	1.30571	-1.0338	-	-0.0026	19.63	0.1333
<i>Tsuga canadensis</i>	838	0.549	0.548	-0.8479	1.35431	-	-	-0.002	13.63	0.1726
<i>Acer rubrum</i>	991	0.749	0.748	-0.4806	1.18569	-	-	-0.00185	24.97	0.1245
<i>Acer saccharum</i>	2310	0.778	0.773	-0.4374	1.14545	-0.5319	-	-0.0015	26.77	0.1149
<i>Betula alleghaniensis</i>	455	0.616	0.614	0.0181	0.83303	-0.44772	-	-0.00289	10.67	0.1425
<i>Betula papyrifera</i>	298	0.66	0.658	-0.3655	1.07896	-	-	-0.00176	26.62	0.1275
<i>Fraxinus nigra</i>	164	0.67	0.666	-0.6892	1.34832	-	-	-0.0057	7.12	0.1619
<i>Populus grandidentata</i>	130	0.716	0.711	-0.2825	1.21319	-	-0.01029	-	25.53	0.1284
<i>Populus tremuloides</i>	996	0.71	0.71	-0.2639	1.08478	-	-	-0.00115	36.43	0.1136
<i>Prunus serotina</i>	77	0.832	0.827	-0.0064	0.88065	-	-	-0.00314	52.05	0.0906
<i>Quercus ellipsoidalis</i>	93	0.668	0.664	-0.4952	1.2063	-	-	-	16.32	0.1522
<i>Quercus rubra</i>	329	0.638	0.635	-0.8887	1.44403	0.84259	-	-	21.2	0.1594
<i>Tilia americana</i>	255	0.723	0.722	-0.4489	1.14688	-	-	-	20.59	0.1206
Mean	460.7	0.709	0.706	-0.4993	1.262	-0.6719	-0.0168	-0.0029	30.2	0.1378

growth, as expected (Table 2). Seven species also showed significant declines in growth with height. Site differences (Stand ID, the random effect) accounted for 30.2% of the variation in growth within species on average (range: 7.1% in *Fraxinus nigra* to 57.2% in *Picea mariana*).

The one to four predictor variables account for much of the variation in growth in most species (mean: 71%, Table 2). Growth is most predictable in *Prunus serotina* ($R^2 = 82.7\%$) and *Picea mariana* ($R^2 = 82.3\%$) perhaps reflecting strong site effects (accounting for 52%–58% of the variation). Growth was least predictable in *Tsuga canadensis* ($R^2 = 54.8\%$) and *Betula alleghaniensis* ($R^2 = 61.4\%$). This may reflect how growth is affected by many unmeasured local differences in growing conditions over the long lives of these late-successional species. These coefficients of determination are high relative to other published models. The power of these models is also reflected in their low root mean square error ranging from 0.091 to 0.114 in two early successional species (*Prunus serotina* and *Populus tremuloides*) to 0.162 and 0.173 in *Fraxinus nigra* and *Tsuga canadensis*. The average mean square error (0.138) implies that these equations typically predict log(BA increments) to within $\pm 37.4\%$ despite those values ranging over 1–1.5 orders of magnitude.

In 16 of the 20 species, strong growth continued through the full range of diameters measured. In fact, BA growth actually accelerated as

diameter increased in red oak (*Quercus rubra* (Fig. 3a)) through very large diameters (75–80 cm DBH; positive quadratic term in Table 2). This surprised us given that the exponent relating growth to diameter is already high (1.44). The allometric parameter (exponent of diameter related to BA growth) ranged from 0.833 in long-lived *Betula alleghaniensis* to 1.59 in the deciduous bog-dwelling conifer, *Larix laricina* (mean: 1.26, Table 2). This exponent always exceeded one except in *B. alleghaniensis* and *Prunus serotina*, indicating that BA growth increases at rates faster than diameter increases in most species. These linear increases on the log scale translate into exponential increases for untransformed growth (BA increment). Exponents are particularly high in three conifers: *Abies balsamea* (1.468), *Picea mariana* (1.505), and *Larix laricina* (1.595), where BA increments rise far faster than initial increases in diameter.

Only four species (*Acer saccharum*, *Betula alleghaniensis*, *Thuja occidentalis*, and *Pinus resinosa*) showed reduced increases in basal area growth as trees grew bigger (a significant negative DBH² coefficient, Table 2). This was most pronounced in red pine (*P. resinosa*), which had a quadratic term coefficient of -2.19, twice as large as the other three species (Fig. 3b). Despite decelerating growth increases in red pine, the data points show that BA growth mostly levels off rather than declining in the largest trees measured (~66 cm DBH).

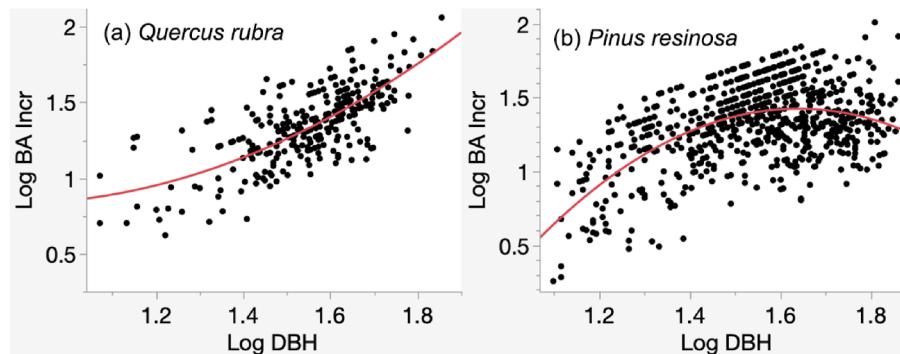


Fig. 3. How tree diameter affects growth. Effects of tree diameter (DBH) on growth (annual BA increment) in (a) red oak (*Quercus rubra*) and (b) red pine (*Pinus resinosa*). Note the acceleration in growth in larger red oaks ($N = 329$, $t = 3.14$ for $\log(\text{DBH}^2)$, $p = 0.002$) and the contrasting rapid rise then leveling off in growth in larger red pines ($N = 735$, quadratic $t = -11.1$, $p < 0.0001$).

4.3. Coniferous vs. deciduous growth, trade-offs, and functional trait effects

Conifers in our region dominate nutrient-poor sites including histosols (*Thuja*), nutrient-poor bogs and swamps (*Larix*), and sandy soils where fires recur (*Pinus*). The nine conifers have lower wood density (0.372 vs. 0.459, $p = 0.02$) and the evergreen needle leaves they support make efficient use of resources being thicker with higher dry matter content and less N (1.30% vs. 2.46%, all $p < 0.001$, t -tests). These traits allow these conifers to grow relatively quickly: their growth exponents (b) relating BA growth to DBH are higher than the 11 broadleaved species occurring commonly on sites with richer soils (1.408 vs. 1.142, $p < 0.001$). Initial growth rates (intercept values), however, varied little between the two groups ($F = 3.59$, $p = 0.07$, $R^2 = 16.7\%$). Growth in *Pinus resinosa* and *Thuja occidentalis* plateaued with negative quadratic effects for $\log_{10}\text{DBH}$.

Among species, there was a pronounced trade-off between early growth (intercept of the logBA vs. logDBH relationship) and b , the growth exponent relating growth to diameter ($r = -0.80$, $p < 0.0001$, Fig. 4a). This likely reflects how traits adapting a tree to rapid initial growth in pioneer species contribute less to or interfere with, later growth (Horn, 1971).

Exponents relating BA growth to diameter declined in species with faster initial growth (intercept of the log(BA growth) vs. logDBH line), more leaf N, and higher specific leaf area (Fig. 4). In contrast, growth scales faster with diameter in species with more leaf and stem dry matter (Fig. 4c) and thicker leaves (Fig. 4d). Initial tree growth (intercepts) is slightly higher in species with more leaf nitrogen ($r = 0.42$, $p = 0.07$). The fact that initial and later growth (in larger trees) vary in opposite directions with leaf nitrogen suggests that species with high leaf N grow quickly when young and then slow down and die soon. These relationships may reflect the leaf economic spectrum (i.e., relationships between size and competition for light, Maynard et al., 2022). We found no relationship between DBH-growth exponents and two wood traits (density and stem lignin, $r = 0.26$ and 0.33, $p = 0.27$ and 0.35, respectively).

4.4. Allometry of whole-tree biomass and carbon

While growth rates always scale as some power of diameter, biomass and carbon (essentially the same variable) scale at rates much higher than increases in BA growth (b and b_1 in Table 3, Fig. 5). This dramatic difference (mean exponent of 2.08 for biomass vs. 1.30 for BA growth) is expected given that two-dimensional bole growth necessarily scales as a

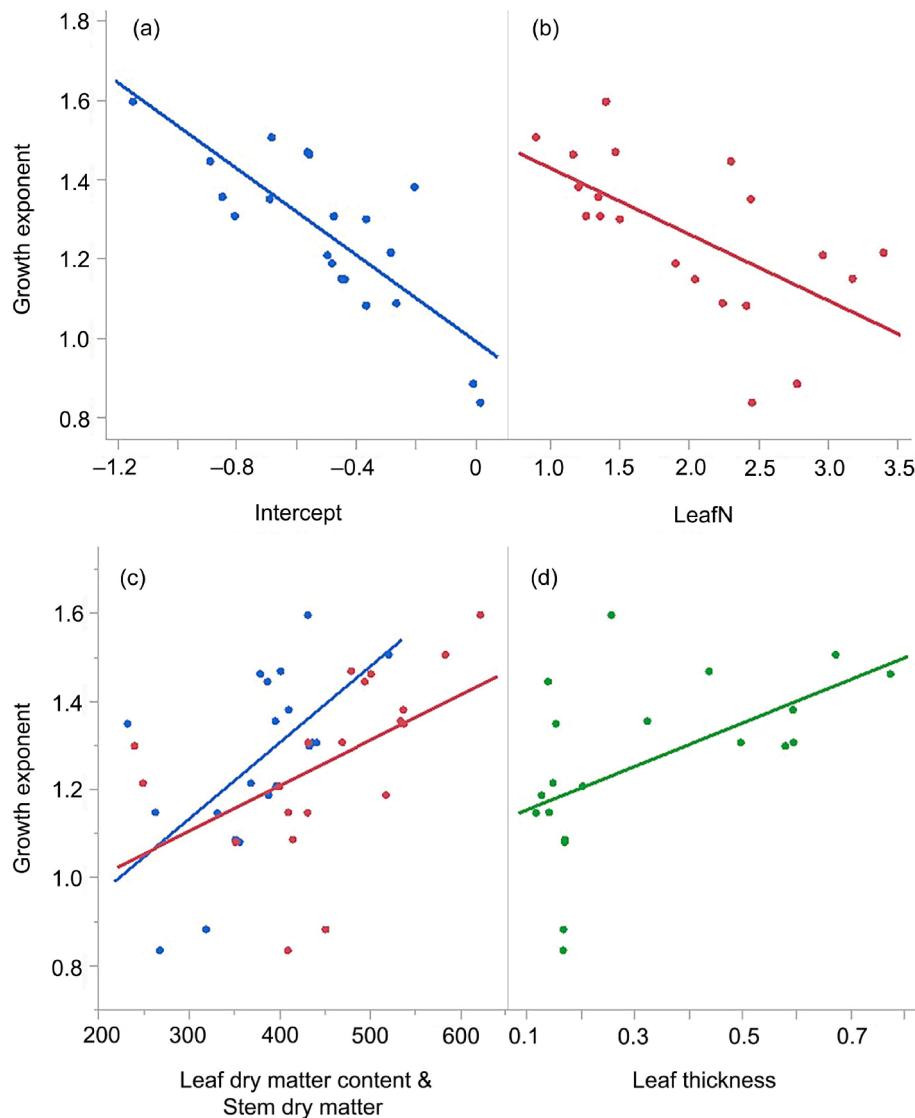


Fig. 4. Effects of functional traits on tree growth. Variation in the growth exponent among species reflects variation in several functional traits. Traits: (a) initial growth (intercept of log(growth) vs. logDBH line), (b) leaf nitrogen (%), (c) leaf and stem dry matter content, and (d) leaf thickness (mm).

Table 3

Allometric equation coefficients from Westfall et al. (2024) for predicting above-ground whole-tree biomass and carbon based on measures of diameter and height for 18 of the 20 species featured in this study (Westfall et al. (2024) omit models for *Fraxinus nigra* or *Quercus ellipsoidalis*). Coefficients *b* and *b1* represent exponents relating biomass to diameter in trees either of all sizes (Model 1) or trees >23 cm DBH (Model 2 (Section 2)). Last column shows the variable carbon fractions of dry biomass measured in each species.

Species	Westfall Model	Fitted parameters a	b	b1	c	C (%)
<i>Acer saccharum</i>	1	0.19749	1.93181	—	0.92308	48.55
<i>Betula alleghaniensis</i>	1	0.0652	1.90493	—	1.18684	48.78
<i>Betula papyrifera</i>	1	0.92184	2.20809	—	0.3652	51.91
<i>Larix laricina</i>	1	0.66412	2.01038	—	0.5092	47.59
<i>Picea glauca</i>	1	0.03924	2.22601	—	1.14434	51.16
<i>Picea mariana</i>	1	0.31362	2.12237	—	0.62071	47.97
<i>Pinus banksiana</i>	1	0.49564	2.10901	—	0.50848	47.9
<i>Pinus strobus</i>	1	0.27234	1.97876	—	0.70625	50.71
<i>Populus grandidentata</i>	1	0.44637	2.30751	—	0.44076	48.04
<i>Populus tremuloides</i>	1	0.21958	2.15217	—	0.7025	47.92
<i>Prunus serotina</i>	1	0.09232	1.81913	—	1.13745	47.66
<i>Quercus ellipsoidalis</i>	—	—	—	—	—	47.24
<i>Quercus rubra</i>	1	0.80692	2.08613	—	0.50113	47.83
<i>Tilia americana</i>	1	0.35929	2.04307	—	0.61064	48.21
Means for 13 species in Model 1	—	0.37646	2.06918	—	25.5855	48.68
<i>Abies balsamea</i>	2	0.32893	0.32893	2.06831	2.17371	50.55
<i>Pinus resinosa</i>	2	0.16347	0.16347	2.03362	2.14015	53.28
<i>Thuja occidentalis</i>	2	0.39329	0.39329	1.92034	2.03034	50.07
<i>Tsuga canadensis</i>	2	0.42833	0.42833	1.85929	2.07595	47.97
Means for 4 species in Model 2	—	0.3285	0.3285	1.97039	2.10504	50.46896
<i>Acer rubrum</i>	4	0.18142	1.7105	0.0251	0.95396	48.57

lower power than 3D whole-tree mass. This explains why whole tree biomass and C growth reach such high levels in big trees. The equations of Westfall and Nelson (2023) that we use to predict whole-tree C in 18 of our 20 species are based on extensive data specific to our ecoregion. As for BA growth, DBH is mainly used to predict whole-tree biomass and carbon. Interestingly, species vary less in biomass/carbon at any given diameter than BA growth (Fig. 5). This suggests that the diameter–total tree biomass relationship is more constrained than the diameter–bole growth relationship. This variability in BA growth among species supports the idea that species pursue different design and growth strategies (Horn, 1971) as evidenced by a non-significant correlation between the exponents relating diameter to BA growth and biomass/carbon ($r = 0.28, p = 0.25$).

5. Discussion

5.1. The importance of tree allometry

Understanding the allometry of how trees grow allows commercial foresters to predict when to harvest trees and when and whether to thin maturing stands to enhance growth and maximize pulpwood or sawtimber production. These predictions are the basis for the yield tables developed in the mid-twentieth century. Recent evidence suggests these tools now underestimate actual growth, reflecting bias in the stands and tree sizes used to fit these models and actual recent increases in growth in many temperate tree species in response to changes in climate and fertilization effects from increased CO₂ and nitrogen deposition (Section 1). If so, updating the allometric equations used to predict tree growth would improve our ability to predict wood production and understand how whole tree growth affects tree- and stand-level carbon dynamics.

The models we developed should help foresters accurately predict the potential of these 20 tree species to add wood as they increase in diameter while also increasing how accurately we can predict C uptake and storage. Maturing forests have increased C stocks in northern Wisconsin forests by $\sim 1 \text{ Tg}\cdot\text{year}^{-1}$ ($0.22 \text{ Mg}\cdot\text{ha}^{-1}$) in recent years, mostly as live biomass (Birdsey et al., 2014). Using updated carbon accumulation curves based on recent inventories and actual growth, Birdsey et al. (2023) predicted that avoiding harvests in eastern US forests would likely double total forest biomass stocks by 2100.

5.2. Factors affecting tree growth

How growth depends on diameter and other variables differs among species. Across all trees, species accounts for 1/3 of the variation in diameter and 1/6 of the variation in recent BA growth. Within species, diameter dominates predictions for BA growth and whole-tree biomass and carbon. These variables all increase in tandem with diameter reflecting fundamental mechanical constraints on tree allometry (McMahon and Kronauer, 1976; Niklas, 1992). We also examined the effects of estimated height, plot basal area ($\text{m}^2\cdot\text{ha}^{-1}$, reflecting competition), and Stand ID (accounting for local conditions). When variables lacked significance, they were dropped from that species' model, simplifying the equation. Including stand increased power, improving our ability to accurately estimate the effects of the other variables. The stand random variable accounted for between 7.1% of the variance in $\log_{10}(\text{BA increment})$ (*Fraxinus nigra*) and 57.2% (*Picea mariana*; mean: 30%).

Tree height and local competing BA had smaller effects on BA growth but these were always negative, reducing growth when significant (in seven species each). Tree growth is expected to decline in taller trees given the higher structural and physiological costs associated with constructing and maintaining a tall crown (Woodruff et al., 2004). Stomatal conductance, photosynthesis, leaf-specific hydraulic conductance, and upper crown turgor pressure all decline in taller trees eventually limiting height (Ryan et al., 2006). Height might have exerted stronger effects were it not highly correlated with diameter (mean $r = 0.71$). Local competition consistently reduced BA growth and was significant in 13/20 species. Species lacking this effect include those limited by abiotic stress (e.g., *Larix laricina* and *Picea mariana*), fast-growing competitive species (*Quercus rubra* and *Tilia americana*), and species with small sample sizes (*L. laricina* and *Q. ellipsoidalis*). The fact that most stands were thinned may have reduced effect sizes for both height and competing BA.

After accounting for the significant predictors, fitted models still sustained residual variation in BA growth. This residual variation means we are still underestimating rates of growth and biomass/C accumulation in some situations. It presumably reflects local variation in growing conditions, size asymmetries between adjacent trees, and perhaps genetic variation.

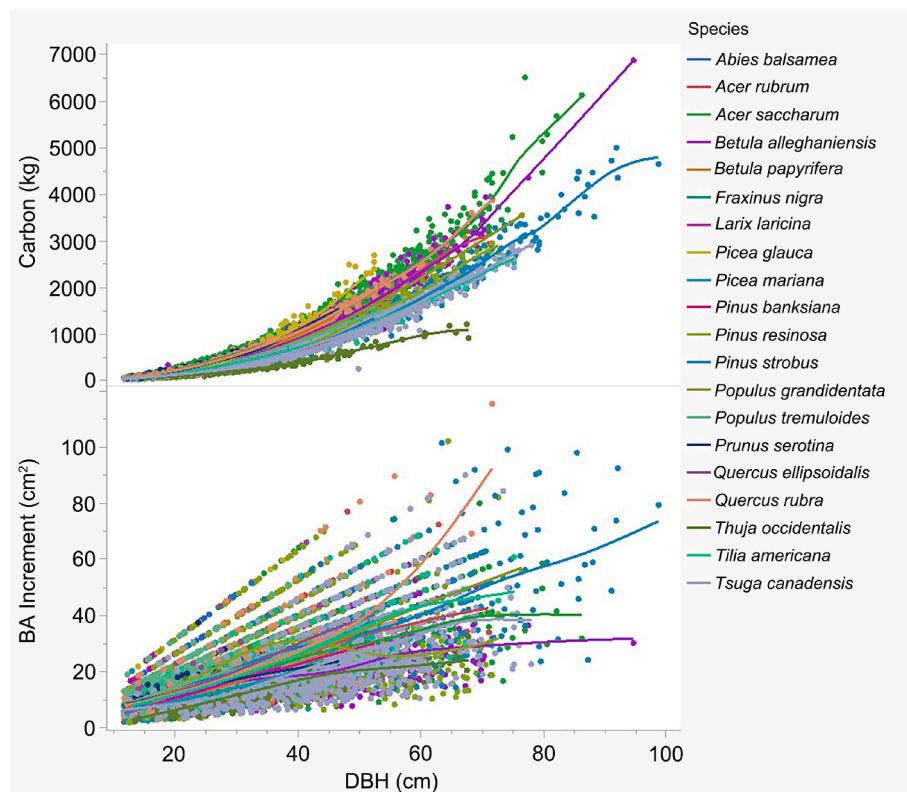


Fig. 5. Total above-ground tree carbon (kg) and tree growth (mean recent annual increase in BA (cm^2)) both scale allometrically with tree diameter. Whole-tree carbon, however, scales at a higher rate (exponent) and displays less variation.

5.3. Allometric models compared

Models of tree growth and forest carbon continue to evolve. Ours sought to improve estimates of tree growth and biomass/carbon assimilation by using large sample sizes to fit a simple allometric model and a consistent set of predictor variables. Our samples included more big trees than commonly used and many trees from thinned stands. Applying consistent statistical models to all species avoided making a priori assumptions about how species grow and facilitated comparisons among species and studies. Our models had high predictive power, accounting for 55%–83% (mean: 71%) of the total variation in recent $\log_{10}(\text{BA growth})$ across 20 species in our region. The average root mean error of our models was 0.138 implying that these estimates of growth are, on average, accurate to within 37% (relative to 30+ fold variation overall). We are not aware of more accurate equations to predict growth in these species.

Jenkins et al. (2003) estimated growth and biomass accumulation using allometric equations like ours. Domke et al. (2012) changed course by instead using “component ratio” methods that estimate tree component volumes, particularly for boles (commercial wood; MacFarlane, 2015). They claimed theirs to be “improved” by including tree height as a predictor. This seems unlikely given how little tree height affected growth in our analyses. Curiously, their models dropped estimated national tree carbon stocks by ~16%. Westfall et al. (2024) later used simpler allometric models based on extensive, regionally segregated data and species-specific carbon fractions. They obtained improved estimates of biomass and carbon (especially in upper limbs) but reiterated Frank et al.’s (2019) concern about lacking full species coverage and data on bigger trees. We sought to fill these gaps here. Westfall et al.’s (2024) models increased estimates of forest biomass and carbon by 20% to over 30% over Domke et al.’s (2012) estimates in Midwestern forests (see their Fig. 3a). These dramatic swings in estimated forest biomass and C reinforce the need for accurate models of

tree growth and biomass accumulation, especially given high skepticism about C markets (Popkin, 2019).

Previous studies like Choi et al. (2001) and Canham et al. (2018) used data from the USDA-Forest Service FIA program based on an array of random locations. This program generates many data but many to most derive from managed stands with smaller trees (Zhao et al., 2021). For example, Canham et al. (2018) found mean diameters of 20.9, 22.4, 22.0, and 22.0 cm for *Acer rubrum*, *A. saccharum*, *Betula alleghaniensis*, and *Quercus rubra*, respectively, in New England, PA, OH, and WV forests. Our corresponding mean diameters were 27.0, 32.5, 39.7, and 37.4 cm (86% higher), confirming that big trees are scarce in FIA samples. Nevertheless, our models are reassuringly similar for the 14 species they share (Appendix S2). Choi et al. (2001) analyzed $\log(\text{BA growth})$ in species that dominate many stands in northern Wisconsin. Their predictors included $\log(\text{DBH})$, indexes of competition based on nearby trees, and stocking densities. They report equations with high R^2 values showing strong effects of DBH as we found. Nevertheless, our equations have higher explanatory power with R^2 values for *Acer rubrum*, *A. saccharum*, *Betula alleghaniensis*, and *Quercus rubra* of 0.75, 0.78, 0.62, and 0.6, respectively, compared to theirs of 0.23, 0.17, 0.19, and 0.31 (Table S1). That our models have higher precision may reflect the narrower geographic range of our data, consistent management on most BCPL forestlands, and/or using stand as a random effect. Stand effects reflect differences in local growing conditions (soil texture, chemistry, slope, etc.) and/or genetic effects like those observed in red oak (Gómez Quijano et al., 2024).

5.4. Diameter–growth allometry

All 20 species display continuous growth in BA, biomass, and carbon accumulation through the largest diameters measured. In 16 species, growth continued to increase through large diameters (55–90 cm). Trees >45 cm DBH are commonly assumed to lose efficiency prompting

recommendations to harvest trees at 30–50 cm in our region. Although growth eventually slowed, our extensive samples failed to reach that limit in all species except red pine. *Pinus strobus* and *Acer saccharum* regularly grow up to 1.68 and 1 m DBH, respectively, though such trees are now rare in Wisconsin.

The scaling exponent relating annual growth to initial increases as diameter ranged from 0.83 in long-lived *Betula alleghaniensis* to 1.59 in the deciduous bog-dwelling conifer, *Larix laricina* (Table 2). Scaling exponents (*b*) exceed 1.0 in 18 of the 20 species (mean: 1.26). Long-lived *Pinus strobus*, *Quercus rubra*, and *Tilia americana* show no reduction in growth through the largest DBH measured (80–90 cm). These fast-growing, mid-successional species can expand their crowns laterally to fill gaps. *Quercus rubra* expressed both a high initial exponent (1.44) plus the remarkable ability to accelerate its growth through large diameters (Fig. 3a). Managers intent on maximizing returns in terms of wood or carbon sequestration/storage should delay harvests to encourage continued growth in this species.

In four species (*Acer saccharum*, *Betula alleghaniensis*, *Pinus resinosa*, and *Thuja occidentalis*), growth plateaus in very big trees. Only red pine (*P. resinosa*), however, shows enough reduction in growth to justify early harvests (Fig. 3b). In *A. saccharum* and *Betula*, only large trees >63 cm DBH plateaued in BA growth, a threshold reached at ~50 cm in *Thuja* (Fig. S1). *Acer saccharum* and *Thuja* attain lifespans of 300–400+ years (Fowels, 1965; Lorimer et al., 2001; Larson and Kelly, 2011). Growth exponents (*b*) in *Betula alleghaniensis* and *Prunus serotina* are <1.0, meaning log(BA growth) increases less than fully proportionally as log(DBH) increases. Both *Pinus resinosa* and *T. occidentalis* occur on nutrient-poor soils where they grow quickly initially but then more slowly as their small crowns reduce ratios of leaf area to branch and bole wood.

We estimated whole-tree biomass and carbon using Westfall et al.'s (2024) allometric models available for 18 of our 20 species in our region. Biomass and carbon scale as higher powers of diameter with means of 2.08 for *b* or *b1* in Westfall et al.'s (2024) models 1 and 2 (Table 3) compared to 1.30 for BA growth (Table 2). Trees of any given diameter appear to vary less in biomass than BA growth (Fig. 4), perhaps reflecting biomechanical constraints.

5.5. Effects of thinning

The BCPL stands used thinnings to remove slow-growing trees encouraging growth in the remaining trees. Thinning enhances light and soil resources for remaining trees, advancing mature forest structures and generating valuable large-diameter trees (Scharenbroch and Bockheim, 2007). Such strategic thinning contrasts with “high-grading” which removes larger, more valuable trees, greatly delaying mature forest structure (Mao et al., 2020; Nyland et al., 2021). Such management slows or prevents trees from achieving the increases in growth and biomass accumulation documented here. Because such practices are common on private lands, estimates of tree and stand growth based on random stand selection (like the FIA data) may be biased downward. Such “stump bias” may help account for why previous estimates of growth allometry often show early plateaus in growth. The equations presented here suggest that proper thinning accelerates growth and enhances stand biomass.

5.6. Why bigger trees grow faster

In 19 of the 20 species analyzed, bigger trees grew faster. This reflects the asymmetry of plant competition. Taller trees overtop competitors, allowing them to acquire more light (Weiner, 1990; Sheil et al., 2006; DeMalach et al., 2016; Forrester, 2019). Taller trees use the resulting photosynthate to either grow even taller or to acquire more water and nutrients via bigger root systems or increasing support for fungal and bacterial symbionts to increase water and nutrient acquisition (Kerhoulas et al., 2013). More sunlit trees can also fill gaps faster via

lateral branch growth and exploit more of their aerial and subterranean environment. Larger crowns and root systems are also able to obtain resources more consistently, increasing tree resilience and survival (Hu et al., 2024). Large mature trees also support large bark surfaces supporting N-fixing lichens like *Pulmonaria*, increasing supplies of that nutrient (Millbank, 1978; Becker, 1980). These advantages accelerate growth, allowing dominant trees to accumulate even higher biomass (Stephenson et al., 2014; Lutz et al., 2018; Mildrexler et al., 2020). These trees gain further growth advantages with increases in atmospheric CO₂ and N-deposition (De Vries et al., 2009; Cole et al., 2010; McMahon et al., 2010; Pretzsch et al., 2014; Schulte-Uebbing and de Vries, 2018; Etzold et al., 2020; Davis et al., 2022; Hogan et al., 2024).

5.7. Management implications

Conventional forest management in northeastern North America emphasizes either even-aged management based on short- to medium-term rotations (e.g., for aspen and red pine) or selectively harvesting trees once they reach a merchantable size (common for multi-aged and all-aged stands of northern hardwoods). In the latter, decisions to harvest particular trees within complex forests based upon tree characteristics our updated allometric equations are particularly useful. Harvest ages in our region range from 25–35 years in *Populus tremuloides* to perhaps 80–100 years in slower-growing conifers and hardwoods. Our analyses led us to suggest that both traditional guidelines may reflect the use of biased or obsolete data from smaller trees yet to reach their growth potential, or from “high-graded” stands, or from stands sampled decades ago when many temperate trees grew more slowly. Under such cases, management prescriptions should be reconsidered to utilize more recent and accurate data. Updated models will likely reveal that many trees being considered for harvest have high potential to enhance their BA growth, produce more wood, and fix and store more carbon. Such reconsideration is especially appropriate for state and national forests in the eastern U.S. where rates of harvesting have tended to increase in recent years despite broadening public support for enhancing biodiversity, recreational opportunities in older forests, and forest C uptake. Delaying harvests of healthy large trees in these forests would likely enhance wood production and undoubtedly carbon sequestration and storage.

For even-aged management based on stand-level metrics, do the increases in growth observed in 15 of 20 tree species simply act to increase mortality and reduce stand density, yielding no net increase in wood production per unit area, or will higher tree growth generate increased wood harvests? Because we lack measures of stand-level BA and biomass/carbon on the BPCL lands, we cannot answer this question directly. However, a recent study suggests that stands with bigger trees also support more BA, biomass, and carbon. Working in unmanaged Swiss forests, Marqués et al. (2023) found that increases in stand density and biomass parallel increases in growth and biomass in big trees within those stands. That is, bigger trees tend to occur within stands that sequester and store more biomass. This result reinforces our recommendation that foresters revisit models of tree growth and stand yield based on older data and smaller trees.

Knowing just how dominance effects vary across site conditions and among thinning treatments might allow foresters to tailor their management to the particular species growing at specific sites. Such fine-scale management would mimic how farmers now practice “precision agriculture.” Foresters overseeing large acreages could measure growth by coring many trees and working with researchers to build models linking growth to local conditions. Such models could compare expected outcomes under a range of management scenarios to assess the effects of thinning or delayed harvests under current conditions. One might also compare our models, based on selectively thinned stands, to models based on data from trees being managed using other methods, allowing foresters to disentangle the effects of management from CO₂ and N fertilization effects. Foresters could also explore how replacing slower-

growing species like red maple and balsam fir with fast-growing, long-lived species like red oak, basswood, and white pine might enhance wood production and C sequestration and storage.

Beyond enhancing tree growth and wood production, allowing more trees to mature to large diameters enhances ecological values. These include old-growth structures key for many species (Tyrrell and Crow, 1994; Choi et al., 2007); reducing hot, dry conditions within forests (De Frenne et al., 2013); and reducing flood and fire events, promoting mast crops of nuts like acorns, a key wildlife food, and enhancing carbon fixation and storage (Bull et al., 1997; Brooks et al., 2002; Brown et al., 2004; Luyssaert et al., 2008; Beiler et al., 2015; Lindenmayer and Laurance, 2017). Given these key roles and increasing concerns with carbon emissions, forest managers should seek to enhance near-term forest carbon fixation and storage by favoring growth in larger trees while postponing timber harvests (Lewis et al., 2019; DellaSala et al., 2022; Mildrexler et al., 2023). Such “proforestation” generates valuable forest products that can replace carbon-intensive materials like plastic or concrete (Griscom et al., 2017; Moomaw et al., 2019). Tribal forests in northern Wisconsin confirm that such management enhances many ecological values (Waller and Reo, 2018).

It is sometimes argued that C releases associated with logging are counterbalanced by carbon sequestration during subsequent growth. Such arguments ignore the time costs of C release and uptake (Peng et al., 2023). It takes decades for forests to “break even” after harvest on net C exchange and more decades before forests regain their capacity to fix so much C. The balance sheet for short-rotation pulp harvests is worse as growth stops sooner and the resulting products are short-lived. Including the “time-costs” of carbon suggests that forest harvests between 2010 and 2050 will incur carbon costs of 3.5–4.2 Gt CO₂e·year⁻¹, approaching all the emissions from expanding agricultural land use. Such analyses reinforce our conclusions.

6. Conclusions

Extensive data on 20 tree species from managed forests in northern Wisconsin yield newer and more accurate models of how basal area growth and above-ground biomass and carbon scale with tree diameter. Surprisingly, trees of most species sustain high growth through the highest diameters measured even accelerating in red oak. Only red pine, commonly grown in plantations, shows strongly curtailed growth, justifying recurrent harvests. These findings suggest that applying selective thinning to more stands and extending rotation ages in northeastern North America beyond those conventionally applied to favor older forests with more large trees could substantially expand sawtimber yields while reducing C emissions, increasing C storage, and enhancing other forest values (Mo et al., 2023).

CRediT authorship contribution statement

John Schwarzmüller: Writing – review & editing, Writing – original draft, Project administration, Methodology, Funding acquisition, Data curation, Conceptualization. **Donald M. Waller:** Writing – original draft, Software, Investigation, Formal analysis, Conceptualization.

Data availability

The data that support the findings of this study are openly available in Dryad at <https://doi.org/10.5061/dryad.t4b8gtjbm>.

Declaration of competing interest statement

The authors declare that they have no competing interests or conflicts of interest.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.fecs.2025.100347>.

References

- Alexander, M.R., Rollinson, C.R., Babst, F., Trouet, V., Moore, D.J.P., 2018. Relative influences of multiple sources of uncertainty on cumulative and incremental tree-ring-derived aboveground biomass estimates. *Trees (Berl.)* 32, 265–276. <https://doi.org/10.1007/s00468-017-1629-0>.
- Alverson, W.S., Kuhlmann, W., Waller, D.M., 1994. *Wild Forests: Conservation Biology and Public Policy*. Island Press, Washington, DC.
- Avers, P.E., McNab, H.W., 1994. *Ecological Subregions of the United States*. US Forest Service.
- Becker, V.E., 1980. Nitrogen fixing lichens in forests of the southern appalachian mountains of North Carolina. *Bryologist* 29–39. <https://doi.org/10.2307/32422391>.
- Beiler, K.J., Simard, S.W., Durall, D.M., 2015. Topology of tree–mycorrhizal fungus interaction networks in xeric and mesic Douglas-fir forests. *J. Ecol.* 103, 616–628. <https://doi.org/10.1111/1365-2745.12387>.
- Biondi, F., Qeadan, F., 2008. A theory-driven approach to tree-ring standardization: defining the biological trend from expected basal area increment. *Tree-Ring Res.* 64 (1), 81–96. <https://doi.org/10.3959/2008-6>.
- Birdsey, R., Pan, Y., Janowiak, M., Stewart, S., Hines, S., Parker, L., Gower, S., Lichstein, J., McCullough, K., Zhang, F., Chen, J., Mladenoff, D., Wayson, C., Swanston, C., 2014. Past and prospective carbon stocks in forests of northern Wisconsin: a report from the chequamegon-nicolet national forest climate change response framework. U.S. Department of Agriculture, Forest Service, Northern Research Station, Gen. Tech. Rep. 57. NRS-127.
- Birdsey, R., Castanho, A., Houghton, R., Savage, K., 2023. Middle-aged forests in the Eastern U.S. have significant climate mitigation potential. *For. Ecol. Manag.* 548, 121373. <https://doi.org/10.1016/j.foreco.2023.121373>.
- Brooks, T.M., Mittermeier, R.A., Mittermeier, C.G., Da Fonseca, G.A., Rylands, A.B., Konstant, W.R., Flick, P., Pilgrim, J., Oldfield, S., Magin, G., Hilton-Taylor, C., 2002. Habitat loss and extinction in the hotspots of biodiversity. *Conserv. Biol.* 16, 909–923. <https://doi.org/10.1046/j.1523-1739.2002.00530>.
- Brown, R.T., Agee, J.K., Franklin, J.F., 2004. Forest restoration and fire: principles in the context of place. *Conserv. Biol.* 18, 903–912. https://doi.org/10.1111/j.1523-1739.2004.521_1.x.
- Bull, E.L., Parks, C.G., Torgersen, T.R., 1997. Trees and logs important to wildlife in the interior Columbia River basin. *Gen. Tech. Rep. PNW-GTR-391*. Portland, OR US Department of Agriculture, Forest Service, Pacific Northwest Research Station 55. <https://doi.org/10.2737/PNW-GTR-391>.
- Burkhardt, H.E., Tham, A., 1992. Predictions from growth and yield models of the performance of mixed-species stands. In: Cannell, M.G.R., Malcolm, D.C., Robertson, P.A. (Eds.), *The Ecology of Mixed-Species Stands of Trees*, Special Publications Series of the British Ecological Society, vol. 11. British Ecological Society, Oxford, U.K.
- Canham, C.D., Murphy, L., Riemann, R., McCullough, R., Burrill, E., 2018. Local differentiation in tree growth responses to climate. *Ecosphere* 9. <https://doi.org/10.1002/ecs2.2368>.
- Choi, J., Lorimer, C.G., Vanderwerker, J., Cole, W.G., Martin, G.L., 2001. A crown model for simulating long-term stand and gap dynamics in northern hardwood forests. *For. Ecol. Manag.* 152, 235–258. [https://doi.org/10.1016/S0378-1127\(00\)00606-X](https://doi.org/10.1016/S0378-1127(00)00606-X).
- Choi, J., Lorimer, C.G., Vanderwerker, J.M., 2007. A simulation of the development and restoration of old-growth structural features in northern hardwoods. *For. Ecol. Manag.* 249, 204–220. <https://doi.org/10.1016/j.foreco.2007.05.008>.
- Clark, D.A., Brown, S., Kicklighter, D.W., Chambers, J.Q., Thomlinson, J.R., Ni, J., 2001. Measuring net primary production in forests: concepts and field methods. *Ecol. Appl.* 11, 356–370. [https://doi.org/10.1890/1051-0761\(2001\)011\[0356:MNPPF\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2001)011[0356:MNPPF]2.0.CO;2).
- Cole, C.T., Anderson, J.E., Lindroth, R.L., Waller, D.M., 2010. Rising concentrations of atmospheric CO₂ have increased growth in natural stands of quaking aspen (*Populus tremuloides*). *Glob. Change Biol.* 16, 2186–2197. <https://doi.org/10.1111/j.1365-2486.2009.02103.x>.
- Davis, E.C., Sohngen, B., Lewis, D.J., 2022. The effect of carbon fertilization on naturally regenerated and planted US forests. *Nat. Commun.* 13, 1–11. <https://doi.org/10.1038/s41467-022-33196-x>.

- De Frenne, P., Rodríguez-Sánchez, F., Coomes, D.A., Baeten, L., Verstraeten, G., Vellen, M., Bernhardt-Römermann, M., Brown, C.D., Brunet, J., Cornelis, J., Decocq, G.M., Dierschke, H., Eriksson, O., Gilliam, F.S., Hédl, R., Heinken, T., Hermy, M., Hommel, P., Jenkins, M.A., Kelly, D.L., Kirby, K.J., Mitchell, F.J.G., Naaf, T., Newman, M., Peterken, G., Petřík, P., Schultz, J., Sonnier, G., Van Calster, H., Waller, D.M., Walther, G.-R., White, P.S., Woods, K.D., Wulf, M., Graae, B.J., Verheyen, K., 2013. Microclimate moderates plant responses to macroclimate warming. *Proc. Natl. Acad. Sci. USA.* 110, 18561–18565. <https://doi.org/10.1073/pnas.1311190110>.
- De Vries, W., Solberg, S., Dobbertin, M., Sterba, H., Laubhann, D., Van Oijen, M., Evans, C., Gundersen, P., Kros, J., Wamelink, G.W.W., Reinds, G.J., 2009. The impact of nitrogen deposition on carbon sequestration by European forests and heathlands. *For. Ecol. Manag.* 258, 1814–1823. <https://doi.org/10.1016/j.foreco.2009.02.034>.
- Dellasala, D.A., Mackey, B., Norman, P., Campbell, C., Comer, P.J., Kormos, C.F., Keith, H., Rogers, B., 2022. Mature and old-growth forests contribute to large-scale conservation targets in the conterminous United States. *Front. For. Glob. Change* 5, 979528. <https://doi.org/10.3389/ffgc.2022.979528>.
- DeMalach, N., Zaady, E., Weiner, J., Kadmon, R., 2016. Size asymmetry of resource competition and the structure of plant communities. *J. Ecol.* 104, 899–910.
- Domke, G.M., Woodall, C.W., Smith, J.E., Westfall, J.A., McRoberts, R.E., 2012. Consequences of alternative tree-level biomass estimation procedures on U.S. forest carbon stock estimates. *For. Ecol. Manag.* 270, 108–116. <https://doi.org/10.1016/j.foreco.2012.01.022>.
- Dye, A., Barker Plotkin, A., Bishop, D., Pederson, N., Poulter, B., Hessl, A., 2016. Comparing tree-ring and permanent plot estimates of aboveground net primary production in three eastern U.S. forests. *Ecosphere* 7. <https://doi.org/10.1002/ecs2.1454>.
- Etzold, S., Ferretti, M., Reinds, G.J., Solberg, S., Gessler, A., Waldner, P., Schaub, M., Simpson, D., Benham, S., Hansen, K., Ingerslev, M., Jonard, M., Karlsson, P.E., Lindroos, A.J., Marchetto, A., Manning, M., Meesenburg, H., Merilä, P., Nöjd, P., Rautio, P., Sanders, T.G.M., Seidling, W., Skudník, M., Thimonier, A., Verstraeten, A., Vesterdal, L., Vejpustková, M., de Vries, W., 2020. Nitrogen deposition is the most important environmental driver of growth of pure, even-aged and managed European forests. *For. Ecol. Manag.* 458, 117762. <https://doi.org/10.1016/j.foreco.2019.117762>.
- Evans, M.E.K., Falk, D.A., Arizpe, A., Swetnam, T.L., Babst, F., Holsinger, K.E., 2017. Fusing tree-ring and forest inventory data to infer influences on tree growth. *Ecosphere* 8. <https://doi.org/10.1002/ecs2.1889>.
- Evans, M.E.K., Justin Derose, R., Klesse, S., Girardin, M.P., Heilman, K.A., Ross Alexander, M., Arsenault, A., Babst, F., Bouchard, M., Cahoon, S.M.P., Campbell, E.M., Dietze, M., Duchesne, L., Frank, D.C., Giebink, C.L., Gómez-Guerrero, A., García, G.G., Hogg, E.H., Metsaranta, J., Ols, C., Rayback, S.A., Reid, A., Ricker, M., Schaberg, P.G., Shaw, J.D., Sullivan, P.F., Gaytán, S.A.V., 2022. Adding tree rings to north America's national forest inventories: an essential tool to guide drawdown of atmospheric CO₂. *Bioscience* 72, 233–246. <https://doi.org/10.1093/biosci/biab119>.
- Fargione, J.E., Bassett, S., Boucher, T., Bridgman, S.D., Conant, R.T., Cook-Patton, S.C., Ellis, P.W., Faleucci, A., Fourqurean, J.W., Gopalakrishna, T., Gu, H., 2018. Natural climate solutions for the United States. *Sci. Adv.* 4, eaat1869. <https://doi.org/10.1126/sciadv.aat1869>.
- Forrester, D.I., 2019. Linking forest growth with stand structure: tree size inequality, tree growth or resource partitioning and the asymmetry of competition. *For. Ecol. Manag.* 447, 139–157. <https://doi.org/10.1016/j.foreco.2019.05.053>.
- Forrester, D.I., 2021. Does individual-tree biomass growth increase continuously with tree size? *For. Ecol. Manag.* 481, 118717. <https://doi.org/10.1016/j.foreco.2020.118717>.
- Fowels, H.A., 1965. *Silvics of Forest Trees of the United States Agriculture Handbook*. US Department of Agriculture Forest Service, Washington, DC.
- Frank, J., Weiskittel, A., Walker, D., Westfall, J.A., Radtke, P.J., Affleck, D.L.R., Coulston, J., MacFarlane, D.W., 2019. Gaps in available data for modeling tree biomass in the United States. *Gen. Tech. Rep. NRS-184*. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northern Research Station 57. <https://doi.org/10.2737/NRS-GTR-184>.
- Friedlingstein, P., O'sullivan, M., Jones, M.W., Andrew, R.M., Hauck, J., Olsen, A., Peters, G.P., Peters, W., Pongratz, J., Sitch, S., Le Quéré, C., 2020. Global carbon budget 2020. *Earth Syst. Sci. Data, Papers Open Discuss.* 1–3. <https://doi.org/10.5194/essd-12-3269-2020>.
- Gómez Quijano, M.J., Gross, B.L., Etterson, J.R., 2024. Genetic differentiation across a steep and narrow environmental gradient: quantitative genetic and genomic insights into Lake Superior populations of *Quercus rubra*. *Mol. Ecol.* 33:e17483. <https://doi.org/10.1111/mec.17483>.
- Griscom, B.W., Adams, J., Ellis, P.W., Houghton, R.A., Lomax, G., Miteva, D.A., Schlesinger, W.H., Shoch, D., Siikamäki, J.V., Smith, P., Woodbury, P., Zganjar, C., Blackman, A., Campari, J., Conant, R.T., Delgado, C., Elias, P., Gopalakrishna, T., Hamsik, M.R., Herrero, M., Kiesecker, J., Landis, E., Laestadius, L., Leavitt, S.M., Minnemeyer, S., Polasky, S., Potapov, P., Putz, F.E., Sanderman, J., Silvius, M., Wollenberg, E., Fargione, J., 2017. Natural climate solutions. *Proc. Natl. Acad. Sci. USA* 114, 11645–11650. <https://doi.org/10.1073/pnas.1710465114>.
- Guo, Z., Fang, J., Pan, Y., Birdsey, R., 2010. Inventory-based estimates of forest biomass carbon stocks in China: a comparison of three methods. *For. Ecol. Manag.* 259, 1225–1231. <https://doi.org/10.1016/j.foreco.2009.09.047>.
- Hogan, J.A., Domke, G.M., Zhu, K., Johnson, D.J., Lichstein, J.W., 2024. Climate change determines the sign of productivity trends in US forests. *Proc. Natl. Acad. Sci. USA* 121, e231132121. <https://doi.org/10.1073/pnas.231132121>.
- Horn, H.S., 1971. *The Adaptive Geometry of Trees*. Princeton University Press, Princeton.
- Hu, M., Shi, H., He, R., Wen, B., Liu, H., Zhang, K., Shu, X., Dang, H., Zhang, Q., 2024. Disparities in tree mortality among plant functional types (PFTs) in a temperate forest: insights into size-dependent and PFT-specific patterns. *For. Ecosyst.* 11, 100208. <https://doi.org/10.1016/j.fecs.2024.100208>.
- Huang, J., Liu, C., Chen, S., Huang, X., Hao, Y., 2019. The convergence characteristics of China's carbon intensity: evidence from a dynamic spatial panel approach. *Sci. Total Environ.* 668, 685–695. <https://doi.org/10.1016/j.scitotenv.2019.02.413>.
- Hulshof, C.M., Swenson, N.G., Weiser, M.D., 2015. Tree height-diameter allometry across the United States. *Ecol. Evol.* 5, 1193–1204. <https://doi.org/10.1002/ee.31328>.
- IPCC (International Panel on Climate Change), 2018. Global warming of 1.5 °C. <https://www.ipcc.ch/sr15/>. (Accessed 5 February 2025).
- Jenkins, J.C., Chojnacky, D.C., Heath, L.S., Birdsey, R.A., 2003. National-scale biomass estimators for United States tree species. *For. Sci.* 49, 12–35.
- Kattge, J., Boenisch, G., Diaz, S., Lavorel, S., Prentice, I.C., Leadley, P., et al., 2020. TRY plant trait database - enhanced coverage and open access. *Glob. Change Biol.* 26, 119–118. <https://doi.org/10.1111/gcb.14904>.
- Kearsley, E., De Haulleville, T., Hufkens, K., Kidimbu, A., Toirambe, B., Baert, G., Huygens, D., Kebede, Y., Defourny, P., Bogaert, J., Beeckman, H., 2013. Conventional tree height-diameter relationships significantly overestimate aboveground carbon stocks in the Central Congo Basin. *Nat. Commun.* 4, 2269. <https://doi.org/10.1038/ncomms3269>.
- Kerhouas, L.P., Kolb, T.E., Koch, G.W., 2013. Tree size, stand density, and the source of water used across seasons by ponderosa pine in northern Arizona. *For. Ecol. Manag.* 289, 425–433. <https://doi.org/10.1016/j.foreco.2012.10.036>.
- Larson, D.W., Kelly, P.E., 2011. The extent of old-growth *Thuja occidentalis* on cliffs of the Niagara Escarpment. *Can. J. Bot.* 69, 1628–1636. <https://doi.org/10.1139/b91-206>.
- Lewis, S.L., Wheeler, C.E., Mitchard, E.T., Koch, A., 2019. Restoring natural forests is the best way to remove atmospheric carbon. *Nature* 568, 25–28. <https://doi.org/10.1038/d41586-019-01026-8>.
- Lindenmayer, D.B., Laurance, W.F., 2017. The ecology, distribution, conservation and management of large old trees. *Biol. Rev. (Camb.)* 92, 1434–1458. <https://doi.org/10.1111/brv.12290>.
- Lines, E.R., Zavala, M.A., Purves, D.W., Coomes, D.A., 2012. Predictable changes in aboveground allometry of trees along gradients of temperature, aridity and competition. *Global Ecol. Biogeogr.* 21, 1017–1028. <https://doi.org/10.1111/j.1466-8238.2011.00746>.
- Liu, C., Liu, Y., Lu, Y., Liao, Y., Nie, J., Yuan, X., Chen, F., 2019. Use of a leaf chlorophyll content index to improve the prediction of above-ground biomass and productivity. *PeerJ* 6, e6240. <https://doi.org/10.7717/peerj.6240>.
- Looney, C.E., D'Amato, A.W., Jovan, S., 2021. Investigating linkages between the size-growth relationship and drought, nitrogen deposition, and structural complexity in western US Forests. *For. Ecol. Manag.* 497, 119494. <https://doi.org/10.1016/j.foreco.2021.119494>.
- Lorimer, C.G., Dahir, S.E., Nordheim, E.V., 2001. Tree mortality rates and longevity in mature and old-growth hemlock-hardwood forests. *J. Ecol.* 89, 960–971. <https://doi.org/10.1111/j.1365-2745.2001.00619.x>.
- Lutz, J.A., Furniss, T.J., Johnson, D.J., Davies, S.J., Allen, D., Alonso, A., Anderson-Teixeira, K.J., Becker, K.M.L., Andrade, A., Baltzer, J., Blomdahl, E.M., Bourg, N.A., Bunyavejchewin, S., Burslem, D.F.R.P., Cansler, C.A., Fischer, G.A., Fletcher, C., Freund, J.A., Giardina, C., Germain, S.J., 2018. Global importance of large-diameter trees. *Global Ecol. Biogeogr.* 27, 849–864. <https://doi.org/10.1111/geb.12747>.
- Luysaart, S., Schulze, E.D., Börner, A., Knöhl, A., Hessenmöller, D., Law, B.E., Caias, P., Grace, J., 2008. Old-growth forests as global carbon sinks. *Nature* 455, 213–215. <https://doi.org/10.1038/nature07276>.
- MacFarlane, D.W., 2015. A generalized tree component biomass model derived from principles of variable allometry. *For. Ecol. Manag.* 354, 43–55. <https://doi.org/10.1016/j.foreco.2015.06.038>.
- Mao, L., Swenson, N.G., Sui, X., Zhang, J., Chen, S., Li, J., Peng, P., Zhou, G., Zhang, X., 2020. The geographic and climatic distribution of plant height diversity for 19,000 angiosperms in China. *Biodivers. Conserv.* 29, 487–502. <https://doi.org/10.1007/s10531-019-01895-5>.
- Marquéz, L., Weng, E., Bugmann, H., Forrester, D.I., Rohner, B., Hobart, M.L., Trotsiuk, V., Stocker, B.D., 2023. Tree growth enhancement drives a persistent biomass gain in unmanaged temperate forests. *AGU Adv* 4, e2022AV000859.
- Maynard, D.S., Bialic-Murphy, L., Zohner, C.M., Averill, C., van den Hoogen, J., Ma, H., Mo, L., Smith, G.R., Acosta, A.T.R., Aubin, I., Berenguer, E., Bonnman, C.C.F., Catford, J.A., Cerabolini, B.E.L., Dias, A.S., González-Melo, A., Hietz, P., Lusk, C.H., Mori, A.S., Niinemets, Ü., Pillar, V.D., Pinho, B.X., Rosell, J.A., Schurr, F.M., Sheremetev, S.N., da Silva, A.C., Sosinski, Ě., van Bodegom, P.M., Weiher, E., Bönisch, G., Kattge, J., Crowther, T.W., 2022. Global relationships in tree functional traits. *Nat. Commun.* 13, 3185. <https://doi.org/10.1038/s41467-022-30888-2>.
- McMahon, T.A., Kronauer, R.E., 1976. Tree structures: deducing the principle of mechanical design. *J. Theor. Biol.* 59, 443–466. [https://doi.org/10.1016/0022-5193\(76\)90182-X](https://doi.org/10.1016/0022-5193(76)90182-X).
- McMahon, S.M., Parker, G.G., Miller, D.R., 2010. Evidence for a recent increase in forest growth. *Proc. Natl. Acad. Sci.* 107, 3611–3615. <https://doi.org/10.1073/pnas.0912376107>.
- McNab, W.H., Cleland, D.T., Freeouf, J.A., Nowacki, G.J., Carpenter, C.A., 2007. Description of ecological subregions: sections of the conterminous United States. General Technical Report WO-76B 76, 1–82. <https://doi.org/10.2737/WO-GTR-76B>.
- Mildrexler, D.J., Berner, L.T., Law, B.E., Birdsey, R.A., Moomaw, W.R., 2020. Large trees dominate carbon storage in forests East of the Cascade crest in the United States Pacific Northwest. *Front. For. Glob. Change.* 3, 1–15. <https://doi.org/10.3389/ffgc.2020.594274>.

- Mildrexler, D.J., Berner, L.T., Law, B.E., Birdsey, R.A., Moomaw, W.R., 2023. Protect large trees for climate mitigation, biodiversity, and forest resilience. *Conserv. Sci. Pract* 1–10. <https://doi.org/10.1111/csp.12944>.
- Millbank, J.W., 1978. The contribution of nitrogen fixing lichens to the nitrogen status of their environment. *Ecol. Bull.* 260–265.
- Miyazawa, K., Lechowicz, M.J., 2004. Comparative seedling ecology of eight North American spruce (*Picea*) species in relation to their geographic ranges. *Ann. Bot.* 94, 635–644. <https://doi.org/10.1093/aob/mch184>.
- Mo, L., Zohner, C.M., Reich, P.B., Liang, J., De Miguel, S., Nabuurs, G.J., Renner, S.S., van den Hoogen, J., Araza, A., Herold, M., Mirzagholi, L., 2023. Integrated global assessment of the natural forest carbon potential. *Nature* 624, 92–101. <https://doi.org/10.1038/s41586-023-0203>.
- Moeyns, K., Van den Bossche, A., Verhelst, T., De Frenne, P., Thomaes, A., Brunet, J., Cousins, S.A.O., De Pauw, K., Diekmann, M., Graae, B.J., Hagenblad, J., Per-Ola, H., Heinken, T., Huang, S., Lenoir, J., Lindgren, J., Mazalla, L., Naaf, T., Orczewska, A., Paulissen, J., Plue, J., Spicher, F., Vannestre, T., Verschuren, L., Visakorpi, K., Wulf, M., Calders, Van Meerbeek, K., 2025. Allometric equations underestimate woody volumes of large solitary trees outside forests. *Urban For. Urban Green.* <https://doi.org/10.1016/j.ufug.2025.128839>.
- Moomaw, W.R., Masina, S.A., Faison, E.K., 2019. Intact forests in the United States: proforestation mitigates climate change and serves the greatest good. *Front. For. Glob. Change* 2, 1–10. <https://doi.org/10.3389/ffgc.2019.00027>.
- Morales-Hidalgo, D., Oswalt, S.N., Somanathan, E., 2015. Status and trends in global primary forest, protected areas, and areas designated for conservation of biodiversity from the Global Forest Resources Assessment 2015. *For. Ecol. Manag.* 352, 68–77. <https://doi.org/10.1016/j.foreco.2015.06.011>.
- Muller-Landau, H.C., Detto, M., Chisholm, R.A., Hubbell, S.P., Condit, R., 2014. Detecting and projecting changes in forest biomass from plot data. *For. Glob. Change*, 17, 381–416.
- Muller-Landau, H.C., Condit, R.S., Chave, J., Thomas, S.C., Bohlman, S.A., Bunyavejchewin, S., Davies, S., Foster, R., Gunatilleke, S., Gunatilleke, N., Harms, K.E., 2006. Testing metabolic ecology theory for allometric scaling of tree size, growth and mortality in tropical forests. *Ecol. Lett.* 9, 575–588. <https://doi.org/10.1111/j.1461-0248.2006.00904.x>.
- Ni, J., Cao, X., Jeltsch, F., Herzschuh, U., 2014. Biome distribution over the last 22,000 yr in China. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 409, 33–47. <https://doi.org/10.1016/j.palaeo.2014.04.023>.
- Niklas, K.J., 1992. *Plant Biomechanics: an Engineering Approach to Plant Form and Function*. University of Chicago Press, Chicago, IL.
- Nyland, R.D., Bevilacqua, E., Ruff, D.A., Kiernan, D.H., 2021. Sugar maple, red maple, and yellow birch growth and mortality in even-aged Adirondack northern hardwoods. *For. Sci.* 67, 83–92. <https://doi.org/10.1093/forsci/fxaa033>.
- Olson, M.E., Anfodillo, T., Gleason, S.M., McCulloh, K.A., 2021. Tip-to-base xylem conduit widening as an adaptation: causes, consequences, and empirical priorities. *New Phytol.* 1, 1877–1893. <https://doi.org/10.1111/nph.16961>.
- Osunkoya, O.O., Omar-Ali, K., Amit, N., Dayan, J., Daud, D.S., Sheng, T.K., 2007. Comparative height–crown allometry and mechanical design in 22 tree species of Kuala Belalong rainforest, Brunei, Borneo. *Am. J. Bot.* 94, 1951–1962. <https://doi.org/10.3732/ajb.94.12.1951>.
- Peichel, M., Arain, M.A., 2007. Allometry and partitioning of above-and belowground tree biomass in an age-sequence of white pine forests. *For. Ecol. Manag.* 253, 68–80. <https://doi.org/10.1016/j.foreco.2007.07.003>.
- Peng, L., Searchinger, T.D., Zontes, J., Waite, R., 2023. The carbon costs of global wood harvests. *Nature* 620, 110–115. <https://doi.org/10.1038/s41586-023-06187-1>.
- Picard, N., Rutishauser, E., Ploton, P., et al., 2015. Should tree biomass allometry be restricted to power models? *For. Ecol. Manag.* 353, 156–163. <https://doi.org/10.1016/j.foreco.2015.05.035>.
- Poorter, L., Bongers, F., Sterck, F.J., Wöll, H., 2003. Architecture of 53 rain forest tree species differing in adult stature and shade tolerance. *Ecology* 84, 602–608. [https://doi.org/10.1890/0012-9658\(2003\)084\[0602:AORFTSJ\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2003)084[0602:AORFTSJ]2.0.CO;2).
- Poorter, H., Jagodzinski, A.M., Ruiz-Peinado, R., Kuyah, S., Luo, Y., Oleksyn, J., Usołtsev, V.A., Buckley, T.N., Reich, P.B., Sack, L., 2015. How does biomass distribution change with size and differ among species? An analysis for 1200 plant species from five continents. *New Phytol.* 208, 736–749. <https://doi.org/10.1111/nph.13575>.
- Popkin, G., 2019. The Forest Question: how much can forests fight climate change? *Nature* 565, 280–282. <https://doi.org/10.1038/d41586-019-00122-z>.
- Pretzsch, H., Biber, P., Schütze, G., Uhl, E., Rötzer, T., 2014. Forest stand growth dynamics in Central Europe have accelerated since 1870. *Nat. Commun.* 5, 1–10. <https://doi.org/10.1038/ncomms5967>.
- Pretzsch, H., Forrester, D.I., Rötzer, T., 2015. Representation of species mixing in forest growth models. A review and perspective. *Ecol. Model.* 313, 276–292. <https://doi.org/10.1016/j.ecolmodel.2015.06.044>.
- Russo, S.E., Wiser, S.K., Coomes, D.A., 2007. Growth-size scaling relationships of woody plant species differ from predictions of the Metabolic Ecology Model. *Ecol. Lett.* 10, 889–901. <https://doi.org/10.1111/j.1461-0248.2007.01079.x>.
- Ryan, M.G., Phillips, N., Bond, B.J., 2006. The hydraulic limitation hypothesis revisited. *Plant Cell Environ.* 29, 367–381. <https://doi.org/10.1111/j.1365-3040.2005.01478.x>.
- Sabatini, F.M., Keeton, W.S., Lindner, M., Svoboda, M., Verkerk, P.J., Bauhus, J., Bruehlheide, H., Burrascano, S., Debaive, N., Duarte, I., Garbarino, M., 2020. Protection gaps and restoration opportunities for primary forests in Europe. *Divers. Distrib.* 26, 1646–1662. <https://doi.org/10.1111/ddi.13158>.
- Schafer, J.L., Mack, M.C., 2014. Growth, biomass, and allometry of resprouting shrubs after fire in scrubby flatwoods. *Am. Midl. Nat.* 172, 266–284. <https://doi.org/10.1674/0003-0031-172.2.266>.
- Scharenbroch, B.C., Bockheim, J.G., 2007. Impacts of forest gaps on soil properties and processes in old growth northern hardwood-hemlock forests. *Plant Soil* 294, 219–233. <https://doi.org/10.1007/s11104-007-9248-y>.
- Schulte-Uebbing, L., de Vries, W., 2018. Global-scale impacts of nitrogen deposition on tree carbon sequestration in tropical, temperate, and boreal forests: a meta-analysis. *Glob. Change Biol.* 24, e416–e431. <https://doi.org/10.1111/gcb.13862>.
- Schumacher, F.X., Hall, S.H., 1933. Logarithmic expression of timber-tree volume. *J. Agric. Res.* 47, 719–734.
- Sheil, D., Salim, A., Chave, J.R., Vanclay, J., Hawthorne, W.D., 2006. Illumination-size relationships of 109 coexisting tropical forest tree species. *J. Ecol.* 94, 494–507.
- Smart, S.M., Glanville, H.C., Blanes, M.d.C., Mercado, L.M., Emmett, B.A., Jones, D.L., Cosby, B.J., Marrs, R.H., Butler, A., Marshall, M.R., Reinsch, S., Herrero-Jáuregui, C., Hodgson, J.G., 2017. Leaf dry matter content is better at predicting above-ground net primary production than specific leaf area. *Funct. Ecol.* 31, 1336–1344. <https://doi.org/10.1111/1365-2435.12832>.
- Smith, K.T., 2008. An organismal view of dendrochronology. *Dendrochronologia* (Verona) 26, 185–193. <https://doi.org/10.1016/j.dendro.2008.06.002>.
- Soh, W.K., Yiotis, C., Murray, M., Parnell, A., Wright, I.J., Spicer, R.A., Lawson, T., Caballero, R., McElwain, J.C., 2019. Rising CO₂ drives divergence in water use efficiency of evergreen and deciduous plants. *Sci. Adv.* 5, eaax7906. <https://doi.org/10.1126/sciadv.aax7906>.
- Stephenson, N.L., Das, A.J., Condit, R., Russo, S.E., Baker, P.J., Beckman, N.G., Coomes, D.A., Lines, E.R., Morris, W.K., Rüger, N., Álvarez, E., 2014. Rate of tree carbon accumulation increases continuously with tree size. *Nature* 507, 90–93. <https://doi.org/10.1038/nature12914>.
- Sterck, F.J., Bongers, F., 1998. Ontogenetic changes in size, allometry, and mechanical design of tropical rain forest trees. *Am. J. Bot.* 85, 266–272. <https://doi.org/10.2307/2446315>.
- Subedi, S.C., Ross, M.S., Sah, J.P., Redwine, J., Baraloto, C., 2019. Trait-based community assembly pattern along a forest succession gradient in a seasonally dry tropical forest. *Ecosphere* 10, e02719. <https://doi.org/10.1002/ecs2.2719>.
- Ter-Mikaelian, M.T., Colombo, S.J., Chen, J., 2008. Amount of downed woody debris and its prediction using stand characteristics in boreal and mixedwood forests of Ontario, Canada. *Can. J. For. Res.* 38, 2189–2197. <https://doi.org/10.1139/X08-067>.
- Trouillier, M., van der Maaten-Theunissen, M., Scharnweber, T., Wirth, D., Burger, A., Schnittler, M., Wilming, M., 2019. Size matters—a comparison of three methods to assess age- and size-dependent climate sensitivity of trees. *Trees (Berl.)* 33 (1), 183–192.
- Tyrrell, L.E., Crow, T.R., 1994. Structural characteristics of old-growth hemlock-hardwood forests in relation to age. *Ecology* 75, 370–386. <https://doi.org/10.2307/1939541>.
- U.S. EPA, 2020. Inventory of U.S. Greenhouse gas emissions and sinks. <https://www.epa.gov/ghgemissions/inventory-us-greenhouse-gas-emissions-and-sinks>. (Accessed 5 February 2025).
- Vanclay, J.K., 1995. Synthesis: growth models for tropical forests: a synthesis of models and methods. *For. Sci.* 41, 7–42. <https://doi.org/10.1093/forestscience/41.1.7>.
- Waller, D.M., Reo, N.J., 2018. First stewards: ecological outcomes of forest and wildlife stewardship by indigenous peoples of Wisconsin, USA. *Ecol. Soc.* 23, 45. <https://doi.org/10.5751/ES-09865-230145>.
- Waller, D.M., Bai, C., Li, D., Paulson, A., Richards, J., Rogers, D., Sonnier, G., Toczyldowski, R., 2021. Functional trait data for vascular plant species from eastern North America. *Ecology*. <https://doi.org/10.17605/OSF.IO/72BN5>.
- Wang, X., Yu, D., Wang, S., Lewis, B.J., Zhou, W., Zhou, L., Dai, L., Lei, J.P., Li, M.H., 2017. Tree height-diameter relationships in the alpine treeline ecotone compared with those in closed forests on Changbai Mountain, northeastern China. *Forests* 8, 132. <https://doi.org/10.3390/f8040132>.
- Weiner, J., 1990. Asymmetric competition in plant populations. *Trends Ecol. Evol.* 5, 360–364. [https://doi.org/10.1016/0169-5347\(90\)90095-U](https://doi.org/10.1016/0169-5347(90)90095-U).
- Weiskittel, A.R., MacFarlane, D.W., Radtke, P.J., Affleck, D.L., Temesgen, H., Woodall, C.W., Westfall, J.A., Coulston, J.W., 2015. A call to improve methods for estimating tree biomass for regional and national assessments. *J. For.* 113, 414–424. <https://doi.org/10.5849/jof.14-091>.
- Westfall, J.A., Nelson, M.D., 2023. Addressing nonresponse bias in forest inventory change estimation using response homogeneity classifications. *For. Ecosyst.* 10, 100099. <https://doi.org/10.1016/j.fecs.2023.100099>.
- Westfall, J.A., Coulston, J.W., Gray, A.N., Shaw, J.D., Radtke, P.J., Walker, D.M., Weiskittel, A.R., MacFarlane, D.W., Affleck, D.L.R., Zhao, D., Temesgen, H., Poudeville, K.P., Frank, J.M., Prisley, S.P., Wang, Y., Sánchez Meador, A.J., Auty, D., Domke, G.M., 2024. A National-Scale Tree Volume, Biomass, and Carbon Modeling System for the United States. *Gen. Tech. Rep. WO-104. U.S. Department of Agriculture, Forest Service, Washington, DC*, p. 60. <https://doi.org/10.2737/WO-GTR-104>.
- Westoby, M., Falster, D.S., Moles, A.T., Veski, P.A., Wright, I.J., 2002. Plant ecological strategies: some leading dimensions of variation between species. *Ann. Rev. Ecol. Syst.* 33, 125–159. <https://doi.org/10.1146/annurev.ecolsys.33.010802.150452>.
- Woodruff, D.R., Bond, B.J., Meinzer, F.C., 2004. Does turgor limit growth in tall trees? *Plant Cell Environ.* 27, 229–236. <https://doi.org/10.1111/j.1365-3040.2003.01141.x>.
- Xu, Z., Fan, W., Wei, H., Zhang, P., Ren, J., Gao, Z., Ulgiati, S., Kong, W., Dong, X., 2019. Evaluation and simulation of the impact of land use change on ecosystem services based on a carbon flow model: a case study of the Manas River Basin of Xinjiang, China. *Sci. Total Environ.* 652, 117–133. <https://doi.org/10.1016/j.scitotenv.2018.10.206>.
- Zhang, F., Chen, J.M., Pan, Y., Birdsey, R.A., Shen, S., Ju, W., He, L., 2012. Attributing carbon changes in conterminous U.S. forests to disturbance and non-disturbance

- factors from 1901 to 2010. *J. Geophys. Res. Biogeosci.* 117, 1–18. <https://doi.org/10.1029/2011JG001930>.
- Zhang, W.P., Zhao, L., Larjavaara, M., Morris, E.C., Sterck, F.J., Wang, G.X., 2020. Height-diameter allometric relationships for seedlings and trees across China. *Acta Oecol.* 108, 103621. <https://doi.org/10.1016/j.actao.2020.103621>.
- Zhao, D., Borders, B., Wilson, M., 2004. Individual-tree diameter growth and mortality models for bottomland mixed-species hardwood stands in the lower Mississippi alluvial valley. *For. Ecol. Manag.* 199, 307–322. <https://doi.org/10.1016/j.foreco.2004.05.043>.
- Zhao, M., Xiang, W., Tian, D., Deng, X., Huang, Z., Zhou, X., Peng, C., 2013. Effects of increased nitrogen deposition and rotation length on long-term productivity of *Cunninghamia lanceolata* plantation in southern China. *PLoS One* 8, e55376. <https://doi.org/10.1371/journal.pone.0055376>.
- Zhao, M., Tian, S., Zhu, Y., Li, Z., Zeng, S., Liu, S., 2021. Allometric relationships, functional differentiations, and scaling of growth rates across 151 tree species in China. *Ecosphere* 12, e03522. <https://doi.org/10.1002/ecs2.3522>.
- Zhou, X., Yang, M., Liu, Z., Li, P., Xie, B., Peng, C., 2021. Dynamic allometric scaling of tree biomass and size. *Nat. Plants* 7, 42–49. <https://doi.org/10.1038/s41477-020-00815-8>.