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SHORT COMMUNICATION

Forest production dynamics along a wood density spectrum in eastern US forests

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Abstract

Key message **Emerging plant economics spectrum theories were confirmed across temperate forest systems of the eastern US where the use of a forest stand's mean wood density elucidated forest volume and biomass production dynamics integrating aspects of climate, tree mortality/growth, and rates of site occupancy.**

Abstract As a tree's functional trait of wood density has been used to refine models of tree competition, it may also aid in evaluating hypotheses of forest production such as declining growth and mortality across a spectrum of increasing wood density. The goal of this study was to examine trends in aboveground live tree production as related to mean wood density using a region-wide repeated forest inventory across eastern US forests. Using quantile regression, the 90th percentile of volume and biomass accretion was negatively related to the mean wood density of a stand's constituent tree species. This relationship was strongest on forest sites with the highest number of growing season degree days, as growing season length influences the rates of stand development. For these sites, variations in volume and biomass accretion were most pronounced in stands with low mean tree wood density, which also demonstrated the highest rates of site occupancy and mortality. This study confirmed aspects of the emerging theory of "fast–slow" plant economics spectrums across temperate forest ecosystems. Stands with relatively low wood density appear to occupy sites more rapidly leading to a concomitantly higher rate of tree mortality, but with less biomass accretion relative to volume due to allocating biomass or carbon to a greater tree volume. In contrast, stands with higher wood density exhibited slower site occupancy due to high wood density construction costs, but with increased biomass relative to volume accretion. These findings highlight the potential application of the plant economics spectrum theory in refining our understanding of general patterns of forest stand production, the role of plant traits in forest management, and knowledge gaps such a shifts in tree allometry during stand development.

Keywords Wood density · Forest productivity · Volume · Biomass · Tree · Relative density

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Introduction

Exploration of the relationship between plant traits and associated forest ecosystem processes (e.g., growth and survival) has emerged as a complementary body of knowledge to more traditional species-based examinations (Kattge et al. 2011). Research into the role of plant traits in functional ecology (e.g., Wright et al. 2004; Chave et al. 2009; Reich 2014) has identified trade-offs between functional and structural traits, such as wood density, which in turn may underlie numerous forest ecosystem processes such as interspecific C allocation patterns (i.e., tree growth dynamics; Santiago et al. 2004; Poorter et al. 2010; Wright et al. 2010; Hérault et al. 2011). Traits are often viewed along spectrums (e.g., range of leaf longevity) with identification of trade-offs in ecosystem processes such as fast C acquisition and decomposition for short leaf longevity compared to slower C acquisition and decomposition for long-lived leaves (Díaz et al. 2004; Wright et al. 2004; Reich 2014). Plant traits have been used to refine the understanding of ecosystem biomass production (Roscher et al. 2012), a key concern in forests given the focus on maintaining or increasing the land sink of carbon (C) (Pan et al. 2011) for the purpose of mitigating potential climate change (Ryan et al. 2010; McKinley et al. 2011). In addition, there is growing interest in managing forests as a biomass feedstock for wood energy (Malmsheimer et al. 2008). As forest management guidelines are largely based on a century of research focused on maximizing merchantable volume over time (e.g., Assmann 1970), there is an opportunity to refine our understanding of additional aspects of forest production (e.g., biomass or C) through trait-based investigations.

Wood density is a trait of forest trees that is central to numerous functional processes such as biomass or C accretion, water transport, and defense at scales ranging up to the community level (Santiago et al. 2004; King et al. 2006; Poorter et al. 2008, 2010; Wright et al. 2010; Kraft et al. 2010; Anten and Schieving 2010) and has been identified as the one tree trait that most strongly integrates a variety of wood properties (Chave et al. 2009). For example, tree growth has been found to be negatively correlated with wood density, while survival was found to be positively correlated (Santiago et al. 2004; King et al. 2006; Poorter et al. 2008; Reich 2014), which may all be partly explained by variations in wood density among individual tree species (Wright et al. 2010). In contrast, Baker et al. (2009) suggest that regional differences in biomass accretion in Amazonian forests are primarily driven by environmental gradients as opposed to plant trait attributes. Beyond elucidating production dynamics, wood density has also been used in forestry applications to predict interspecific differences in tree size–density relationships with obvious relationships between wood density and levels of species-specific stocking (Dean and Baldwin 1996; Woodall et al. 2005; Ducey and Knapp 2010). In addition, wood density has been identified as a significant variable in allometric tree biomass models (Ketterings et al. 2001; Baker et al. 2004; Ducey 2012). A large portion of the research conducted to date on the role of tree traits, including wood density, in forest ecosystem processes has been on tropical systems (e.g., King et al. 2006; Poorter et al. 2008; Baker et al. 2009; Wright et al. 2010), leaving key knowledge gaps for temperate and boreal forest systems (e.g., Thurner et al. 2014).

Given the results found in tropical ecosystems (King et al. 2006; Poorter et al. 2008; Wright et al. 2010), it can be hypothesized that differences in temperate forest production and site occupancy may be apparent across a spectrum of wood density given the role of wood density in individual tree allometry and resulting forest production. Additionally, it is our hypothesis that as a forest trees' wood density increases, the rates of accretion in components of production will decrease with a concomitant decrease in mortality consistent with recent theories forwarded by Reich (2014). Finally, we suggest that growing season length (i.e., indicator of rates of stand development) may be an important factor in explaining broad-scale patterns in these relationships given results observed in tropical systems. The evaluation of these hypotheses would inform the contemporary management of temperate forests where management objectives are moving beyond volume production to include biomass and C sequestration. Therefore, the goal of this study was to examine variation in the components of forest production (volume, biomass, mortality, and stand relative density) by a forest stand's mean wood density by classes of growing season degree days (GDD) in temperate forest ecosystems.

Methods

Field sample protocols

The field plot data used in this study came entirely from the national forest inventory program of the USA. The USDA Forest Service's Forest Inventory and Analysis (FIA) program is the primary source for information about the extent, condition, status, and trends of forest resources in the USA (Smith et al. 2009). FIA applies a nationally consistent sampling protocol using a systematic design covering all ownerships across the USA using a three-phase inventory (Bechtold and Patterson 2005). The FIA sampling design is based on a tessellation of the USA into hexagons, approximately 2,428 ha in size with at least one permanent plot (0.067 ha) established in each hexagon (i.e., national base sample intensity). In phase 1, the population of interest is stratified (e.g., forest canopy cover classes) and plots are assigned to strata to increase the precision of estimates. Remotely sensed data may also be used to determine if plot locations have forest cover; only forested land is included in the inventory, defined as areas at least 10 % stocked with tree species, at least 0.4 ha in size and 36.6 m wide (Bechtold and Patterson 2005). In phase 2, tree and site attributes are measured for plots established in the 2,428-ha hexagons. FIA inventory plots established in forested conditions consist of four 7.32-m fixed-radius subplots spaced 36.6 m apart in a triangular arrangement with one subplot in the center (USDA 2011; Woudenberg et al. 2010). All trees (live and standing dead) with a diameter at breast height of at least 12.7 cm are inventoried on forested subplots. Within each subplot, a 2.07-m fixed-radius microplot offset 3.66-m from the subplot center is established where only live trees with a d.b.h. between 2.5 and 12.7 cm are inventoried.

Data and analysis

Field data (USDA 2011) for this study were taken entirely from the FIA database (Woudenberg et al. 2010) sampled from 2002 to 2010 using the forest inventory in 37 eastern states for a total of 23,854 unique inventory plots and partial plots (i.e., split conditions such as forest/non-forest) (Fig. 1). States and regions of the USA have the opportunity to increase the sample intensity of both phase 2 plots, such that sample intensity may slightly vary by state. The associated field data are available for download at the following site: http://fiatools.fs.fed.us (FIA Datamart, USDA 2013).

This study employed a series of basic steps toward estimating volume and biomass associated with living trees based on national field inventories. First, the gross bole volume was calculated based on regional volume equations (Woodall et al. 2011). Second, sound bole volume was calculated based on regional volume equations along with merchantable stem deductions (through tree class code in FIADB) due to rough, rotten, and missing cull. Third, the sound bole volume was converted to bole biomass using species-specific wood density values (Miles and Smith 2009; Woudenberg et al. 2010). Fourth, total tree biomass was calculated using the component ratio method (CRM) (including bole and branches; Woodall et al. 2011). Briefly, the CRM facilitates calculation of tree component biomass (e.g., tops and limbs) as a proportion of the bole biomass based on component proportions from Jenkins et al. (2003). Mean wood density (unitless; SG_{m}) per plot was determined by averaging the specific gravity of all live trees on each plot based on specific gravity values within the tree species reference table of the national FIA database (Woudenberg et al. 2010). Although the term "wood density" is broadly used in the discussion of this study's results, the metric of specific gravity is deemed as interchangeable. Finally, to assess the role of growing season length (i.e., climatic attribute that indicates a site's potential rate of stand development), plots were assigned to classes based on quartiles of GDDs [high: 1st quartile (>3,076), moderate: 2nd and 3rd quartile (1,462–3,076), low: 4th quartile (<1,462)] (for detailed description of GDD calculation please refer to Rehfeldt 2006). To remove observations having relatively low signal to noise related to GDD as an explanatory variable, plots assigned to the moderate GDD class were excluded from analyses involving growing season length.

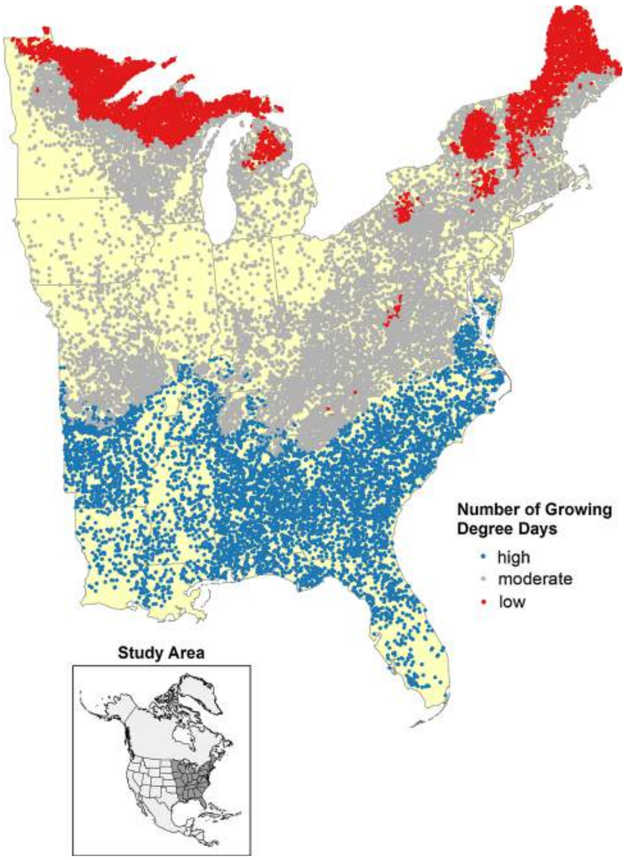

Fig. 1 Approximate study plot locations by categories of growing season degree days (Rehfeldt 2006) (high >3,076, moderate 1,462–3,607, low <1,462) in forests of the eastern USA

To frame this study's goals in the context of forest management, the stocking of live trees in each site was defined relative to an estimated maximum value. The current size/density status was calculated as the stand density index (SDI; Reineke 1933; Long 1985; Ducey and Larson 2003):

$$\mathrm{SDI} = \sum \mathrm{tph}_i (\mathrm{DBH}_i/25)^{1.6} \quad (1)$$

where DBH_i is the ith diameter of an individual tree (cm) and tph_i is the estimated number of trees per hectare that the ith tree represents in the forest inventory (Shaw 2000).

The potential maximum size/density relationship ($\mathrm{SDI}_{\max}$) was estimated from stand-level mean live tree wood density (Dean and Baldwin 1996; Woodall et al. 2005):

$$\mathrm{SDI}_{\max} = 3546.7 - 3927.3(\mathrm{SG}_{\mathrm{m}}) \tag{2}$$

where SG_{m} is the mean specific gravity (unitless) for all live trees in each plot at each time of measurement. The relative stand density (RSD) of each study plot was determined as current SDI (Eq. 1) divided by $\mathrm{SDI}_{\max}$ (Long 1985; Eq. 2). Changes in RSD over time were determined on an annual basis and serve as an indicator of a forest stand's location relative to the self-thinning line.

As a means to identify how differences in species associations (i.e., variation in wood density), site quality (e.g., Quesada et al. 2012), and natural disturbances might affect the distribution of volume and biomass accretion observations, selected percentiles (1, 10, 25, 50, 75, 90, and 99) were calculated by forest-type group, mean live tree specific gravity class (SG_{m}), site index class, and natural disturbance class. Forest-type group is based on FIA delineations of tree species associations (Woudenberg et al. 2010). Site index class was based on site index (m; base age 50 years) calculated at each plot using height and age information from cored trees and fitted to regional site index curves (Woudenberg et al. 2010; USDA 2011). Natural disturbance was the primary disturbance identified upon remeasurement that field crews deemed to have occurred over the course of the remeasurement period (USDA 2011).

To examine relationships between production rates and wood density, regression analysis was considered as an appropriate tool; however, traditional least-squares approaches were not seen as suitable given the numerous forest disturbances and management regimes across the eastern USA. In other words, this study's interest lies in quantifying the potential for tree growth and that in practice tree growth is reduced in most stands by disturbances and management activities. To avoid examining the mean stand condition across the eastern USA, quantile regression was employed to examine productivity measures at various quantiles of the data (Cade and Noon 2003). Upon examining the pattern (i.e., acceptable confidence intervals at the highest percentile) of the estimated slopes at various regression percentiles, the 90th percentile was selected to represent the various productivity measures:

$$y = b_0 + b_1\mathrm{SG}_{\mathrm{m}} \tag{3}$$

where SG_{m} is the mean specific gravity of all live trees in the plot at time 1 and b_0 and b_1 values are the intercept and slope coefficients, respectively, estimated from the 90th percentile using linear quantile regression. The dependent variables y were: (1) base 10 log of annual volume increment (m^3/ha/year), (2) base 10 log of annual biomass increment (Mg/ha/year), (3) difference in RSD over the remeasurement period (%/year), and (4) base 10 log of annual mortality expressed in volume (m^3/ha/year). Confidence intervals for the b_1 slope coefficient associated with the SG_{m} variable were examined to compare models fit at low versus high number of GDDs (plots with a "moderate" number of GDDs were excluded from the analysis [colored gray in Fig. 1]). Consideration was given to including GDD as a continuous variable in a multivariate quantile regression model. Unfortunately, the selection of optimal quantiles for achieving the study objectives was obfuscated in a multivariate model. Models were estimated using the quantreg package in R using a modified version of the Barrodale and Roberts algorithm with confidence limits estimated based on inversion of a rank test (Koenker 2013).

To facilitate interpretation of quantile regression results across the forests of the eastern USA, maps of interpolated forest tree specific gravity attributes (mean, standard deviation, and Shannon's diversity index of plot-level live tree specific gravity) and 90th percentile estimates of annual live tree volume and biomass accretion (Eq. 3) were created using inverse distance weighting (Johnston et al. 2001) in ARCGIS with a 1 km × 1 km non-forest mask applied (i.e., classified NLCD, Homer et al. 2007). While the mean values of SG may portray general differences in forest structure and composition, Shannon's diversity (H, Eq. 4) reflects the degree of heterogeneity in the distribution of SG across different tree species (Russell et al. 2014). Specific gravity classes were summed across classes of 0.05 units. Large values for H indicated a greater number of SG_{m} classes and were calculated using the formula from Staudhammer and LeMay (2001):

$$H_i = -\sum_{i=1}^{S} \frac{n_i}{N} \ln\left(\frac{n_i}{N}\right) \tag{4}$$

where S is the total number of classes in each plot, N is the total number trees in each plot, and n_i is the number of trees in each class i.

Results

The interpolated mean specific gravity of live trees in forests of the eastern USA (Fig. 2a) was highest (>0.52) in a band stretching from the central hardwoods (e.g.,

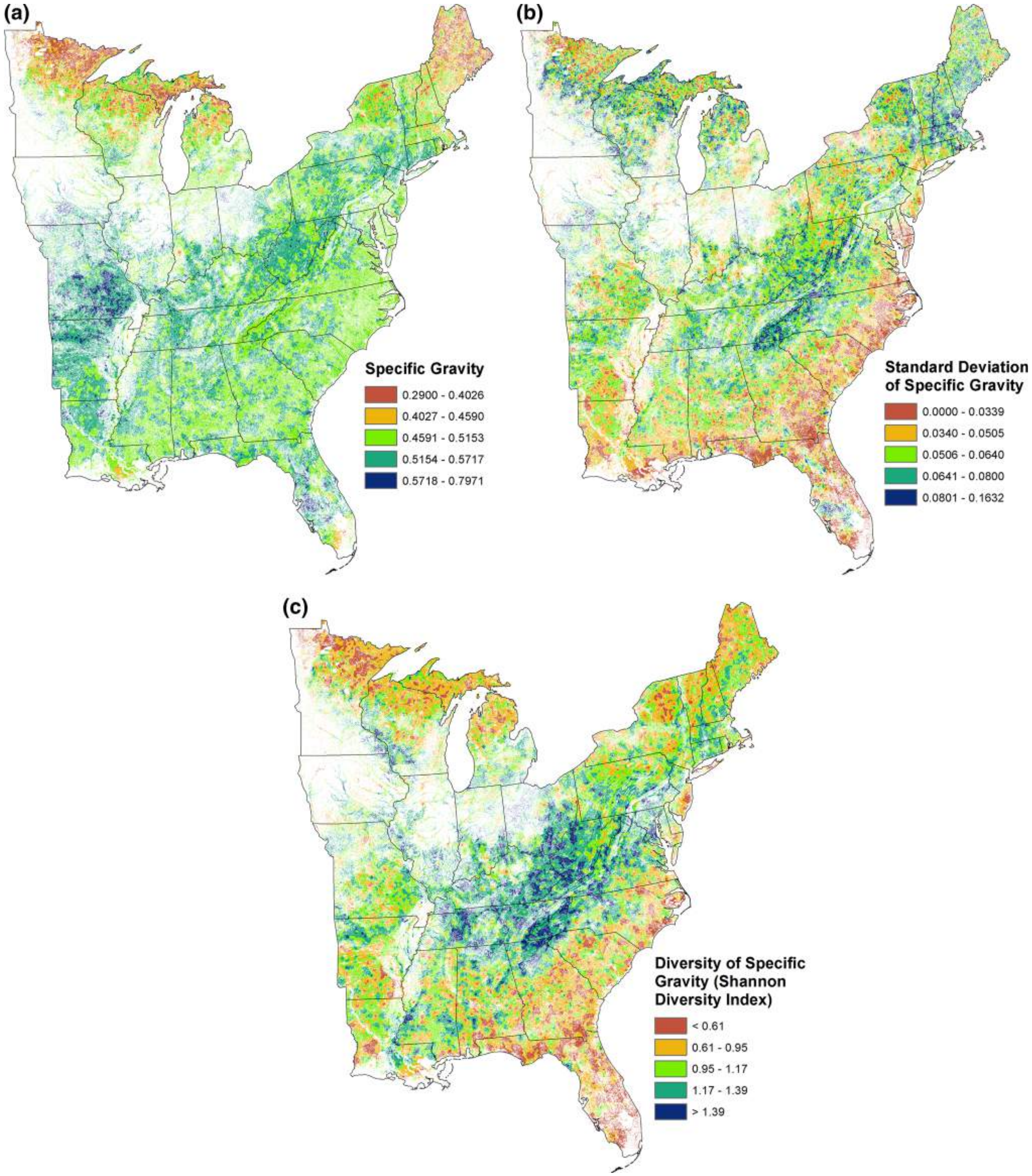

Fig. 2 Interpolated (inverse distance weighting) **a** mean, **b** standard deviation, and **c** Shannon's diversity index of specific gravity (unitless) for forests of the eastern USA

Missouri) to a portion of the Appalachian Mountains (West Virginia to New York). Mean specific gravity was lowest (<0.40) in portions of the upper Great Lakes and northern New England which suggests a general trend of decreasing specific gravity with increasing latitude. In contrast, the standard deviation associated with the mean specific gravities (Fig. 2b) was lowest (<0.03) in the coastal plain of the southeastern USA (Louisiana to Virginia) and

Table 1 Univariate statistics (P1: 1st percentile; P10: 10th percentile; Q1: 1st quartile; Q2: 2nd quartile; Q3: 3rd quartile; P90: 90th percentile; P99: 99th percentile) of volume accretion (m^3/ha/year) by specific gravity class, forest-type group, site index (m, base age 50 years), and natural disturbance category for all study observations (*n* number of observations)

Stand/site attribute	*n*	P1	P10	Q1	Q2	Q3	P90	P99
Specific gravity class								
<0.35	873	−7.86	−1.07	0.21	1.61	3.19	4.74	10.09
0.35–0.40	2,249	−7.14	−0.86	0.16	1.59	3.45	5.22	9.27
0.41–0.45	2,564	−11.30	−1.71	0.36	2.12	4.08	6.41	12.70
0.46–0.50	6,219	−12.13	−1.25	0.92	3.14	5.96	11.16	23.36
0.51–0.55	7,228	−10.57	−1.36	1.02	2.89	4.97	7.77	17.53
0.56–0.60	3,897	−10.80	−1.61	0.73	2.24	3.88	5.69	11.84
>0.60	661	−8.18	−1.35	0.39	1.66	2.98	4.40	9.13
Forest-type group								
White/red/jack pines	746	−11.25	−0.30	1.33	3.45	5.63	8.48	14.30
Spruce/fir	1,846	−7.86	−0.72	0.01	1.19	2.79	4.41	7.94
Southern pines	2,247	−6.82	0.72	3.16	6.96	12.63	18.18	27.34
Oak/pine	1,350	−8.78	−0.55	1.18	3.00	5.28	7.99	14.71
Oak/hickory	9,039	−10.73	−1.29	0.85	2.48	4.30	6.43	11.93
Oak/gum/cypress	1,219	−25.56	−4.09	0.09	3.02	6.19	9.28	21.04
Elm/ash cottonwood	1,214	−13.45	−2.12	0.29	2.07	4.14	7.07	14.73
Maple/beech/birch	3,844	−9.44	−1.91	0.56	2.35	3.79	5.17	8.28
Aspen/birch	1,947	−7.57	−1.74	0.06	1.55	3.30	5.04	8.39
Other	357	−22.44	−0.88	0.21	1.36	3.12	5.25	9.36
Site index class (m)								
<12.49	5,616	−12.06	−1.05	0.25	1.96	4.34	7.92	19.99
12.49–15.85	3,254	−8.27	−1.43	0.31	1.80	3.21	4.79	8.62
15.86–19.50	4,609	−9.57	−1.61	0.53	2.13	3.61	5.28	9.76
19.51–23.77	5,272	−9.55	−1.27	0.89	2.70	4.43	6.36	14.39
23.78–28.35	3,150	−11.60	−1.37	1.56	3.78	6.32	9.97	19.55
>28.35	1,782	−15.23	−1.25	2.29	5.27	9.40	15.50	26.10
Natural disturbance class								
Insects	284	−36.25	−7.98	−2.35	1.42	4.08	6.04	11.70
Disease	390	−17.55	−3.19	−0.56	1.76	3.54	6.29	19.33
Fire	356	−18.02	−2.23	0.49	2.55	5.33	9.85	20.52
Animal	488	−23.36	−1.97	0.47	1.82	3.24	5.25	10.15
Weather	776	−24.90	−7.47	−2.23	0.54	2.86	5.25	12.36
All observations	23,824	−10.68	−1.32	0.65	2.49	4.57	7.47	18.78

northern Minnesota. Standard deviations were highest in forests along the Appalachian Mountain chain, especially along the Tennessee and North Carolina border (i.e., Great Smoky Mountains). Somewhat related to patterns in standard deviation, the Shannon's diversity index of mean specific gravity was highest in the central hardwood and southern Appalachian Mountain region of the eastern USA (Fig. 2c). An important difference was identified in the upper Great Lakes where standard deviations were relatively high, but Shannon's diversity indices were low.

The percentile distribution of the volume and biomass accretion across all study plots was right skewed toward positive accretion (Tables 1, 2). For example, the 90th percentiles of volume accretion, regardless of classes of site index or forest type, were almost all >3.00 m^3/ha/year. In contrast, the majority of 10th percentiles of volume accretion across classes of stand/site attributes (e.g., site index and natural disturbance class) were between 0.00 and −1.00 m^3/ha/year. Trends in percentiles of volume and biomass accretion were most readily apparent across classes of site index and mean stand specific gravity. The only divergence in this trend was for the upper percentiles (90th and 99th) of volume and biomass accretion on the lowest quality sites which were located primarily in the southeastern USA where sites have high GDD. Stands that experienced natural disturbances such as insects or weather had the largest declines in annual accretion (1st and 10th percentiles). The trends in volume and biomass accretion among forest types were most strongly right skewed for southern pines, white/red/jack pines, and oak/gum/cypress

Table 2 Univariate statistics (P1: 1st percentile; P10: 10th percentile; Q1: 1st quartile; Q2: 2nd quartile; Q3: 3rd quartile; P90: 90th percentile; P99: 99th percentile) of biomass accretion (Mg/ha/year) by specific gravity class, forest-type group, site index (m, base age 50 years), and natural disturbance category for all study observations (*n* number of observations)

Stand/site attribute	*n*	P1	P10	Q1	Q2	Q3	P90	P99
Specific gravity class								
<0.35	873	−6.04	−0.79	0.39	1.37	2.36	3.55	6.83
0.35–0.40	2,249	−4.84	−0.82	0.25	1.33	2.54	3.77	6.40
0.41–0.45	2,564	−7.81	−1.25	0.35	1.69	3.05	4.42	8.20
0.46–0.50	6,219	−9.53	−1.15	0.75	2.52	4.67	7.71	14.81
0.51–0.55	7,228	−8.97	−1.27	0.77	2.44	4.08	6.04	12.23
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Weather	776	−18.54	−5.41	−1.85	0.45	2.19	3.77	8.26
All observations	23,824	−8.58	−1.18	0.52	2.07	3.70	5.71	12.51

(refer to Woudenberg et al. 2010 Appendix D for forest-type group descriptions). Based on these initial results of apparent trends in volume and biomass accretion among classes of site index and mean specific gravity with natural disturbances substantially reducing stand production, quantile regression was conducted among classes of GDD (associated with site production potential; i.e., site index) with specific gravity as an independent variable.

The 90th percentile annual change in live tree volume was negatively related to mean live tree specific gravity on high GDD sites with no relationship on low GDD sites (Fig. 3a). The slope coefficients for change in volume were $b_1 = -3.003$ (±0.15 SE) and $b_1 = -0.13$ (±0.18 SE), on high and low GDD sites, respectively. The estimated slope coefficient of volume accretion decreased as mean tree specific gravity increased from −1.15 (±0.34 SE) at the 10th percentile to −3.00 (±0.16 SE) at the 90th percentile on high GDD sites. At the 90th percentile the 95th percent confidence intervals of b_1 were [−3.32, −2.68] and [−0.29, 0.04] on high and low GDD sites, respectively.

The 90th percentile annual change in live tree biomass was negatively related to mean live tree specific gravity on high GDD sites with a weak positive relationship on low GDD sites (Fig. 3b). The slope coefficients for change in biomass were $b_1 = -2.01$ (±0.19 SE) and $b_1 = 0.35$ (±0.08 SE), on high and low GDD sites, respectively. The estimated slope coefficient of biomass accretion decreased as the mean tree specific gravity increased ranging from −1.43 (±0.36 SE) at the 10th percentile to −2.01 (±0.19 SE) at the 90th percentile on high GDD sites. At the 90th

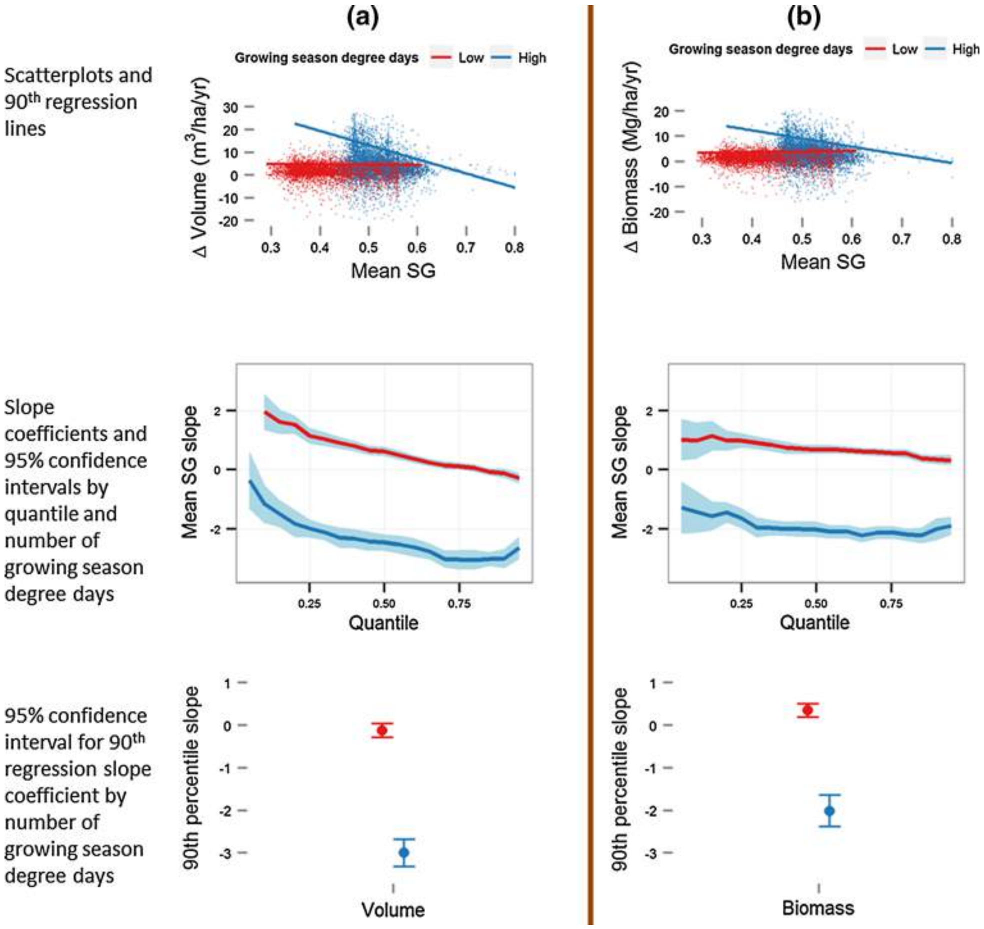


Fig. 3 Quantile regression results and fit statistics by classes of high and low number of growing season degree days for annual change in **a** volume (m^3/ha/year) and **b** biomass (Mg/ha/year) by a forest stand's mean specific gravity (SG) with 90th percentile regression lines (Eq. 3), slope coefficients and associated 95 % confidence intervals, and confidence intervals for the slope of the 90th percentile regression

percentile, the 95th percent confidence intervals of b_1 were [−2.38, −1.64] and [0.20, 0.50] on high and low GDD sites, respectively.

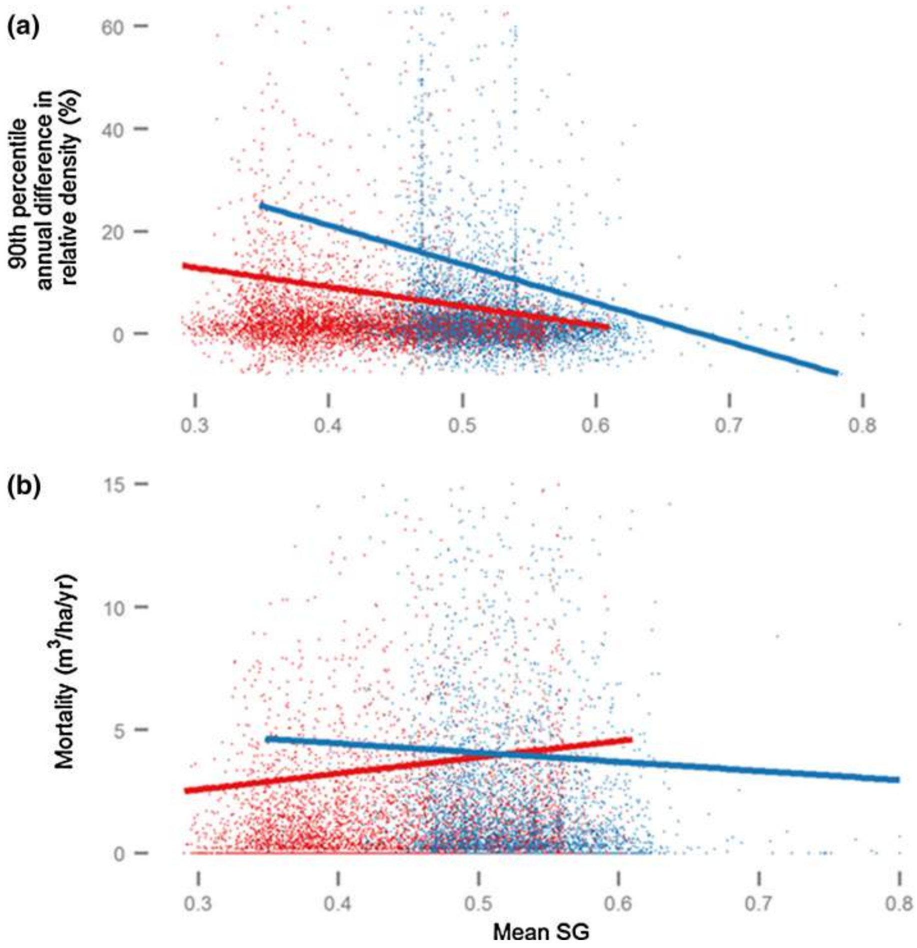
The 90th percentile annual difference in relative density (%) was negatively related to mean live tree specific gravity on high ($b_1 = -103.35$, ±8.76 SE) and low ($b_1 = -41.89$, ±2.86 SE) GDD sites (Fig. 4a). The change in relative density ranged from an estimated 27 % at 0.40 specific gravity to 6 % at 0.60 specific gravity for high GDD sites. On low GDD sites, the difference ranged from an estimated 10 % at 0.40 specific gravity to 1 % at 0.60 specific gravity. The 90th percentile average annual live tree mortality (m^3/ha/year) was negatively ($b_1 = -0.82$, ±0.34 SE) related to mean live tree specific gravity only on high GDD sites and weakly positively ($b_1 = 0.65$, ±0.14 SE) related on low GDD sites (Fig. 4b).

Using the parameter estimates from the 90th percentile models (Eq. 3), annual volume and biomass accretion by all classes of GDD were interpolated across forests of the eastern USA (Fig. 5a, b). There is obvious differentiation in annual volume and biomass accretion by classes of GDD. Beyond the influence of growing season length (i.e., GDD), there were slight differences in the estimated 90th percentile volume and biomass accretion that may be attributed to variation in tree species composition across the study region. There appears to be a greater disparity in volume growth, when compared with biomass growth, particularly in the Ozark Plateau of Missouri and coastal plain of the southeast.

Discussion

The spatial patterns in mean, standard deviation, and Shannon's diversity index of live tree specific gravities across forests of the eastern USA reflect the legacy of past land use, natural disturbances, and current management practices across this broad region. In particular, the low to moderate levels of mean wood density and associated low standard deviation and Shannon's diversity index in the coastal plains of the southeastern USA reflect the active management of large areas of plantation monocultures primarily composed of *Pinus taeda.* Similar trends in wood density in the upper Lake States highlight the dominance of *Populus tremuloides* over large areas: a result of the increased dominance of this species following logging and

Fig. 4 Quantile regression models by classes of high and low number of growing season degree days for **a** annual difference in relative density (%) and **b** tree mortality (m^3/ha/year)



associated fires in the early twentieth century and its maintenance via current coppice management practices. The management selection of these disturbance-adapted timber species has favored tree species that occupy sites at fast rates (as indicated by changes in RSD) in concert with relatively fast volume growth rates which aligns with emerging theories of "fast" plant economics (Reich 2014).

Do patterns of live tree specific gravities across forests of the eastern USA indicate patterns of live tree volume and biomass accretion? The true expression of the relationship between wood density traits of tree species and resulting volume and biomass production in temperate forests of the eastern USA may be obfuscated by the highly disturbed and stochastic nature of forests within this region. The median condition of forests across the eastern USA may be that of disturbance across spatial scales ranging from individual tree canopy gaps (Woodall et al. 2013) to widespread management activities (e.g., clear-cutting based silvicultural systems), especially within the "timber basket" of the southeastern USA (Smith et al. 2009; Hodges et al. 2012). An examination of the findings of this study supports such a view, especially for volume accretion. As quantile regression percentiles increase up to the 90th percentile, the corresponding estimated slope coefficients between volume and biomass accretion and live tree wood density decreased. The use of quantile regression in this ecological analysis (Cade and Noon 2003) allowed quantification of fundamental temperate forest stand dynamics beyond that of the mean condition. Although this study's identified relationships are most relevant to a stratum of stand conditions (i.e., the 90th percentile) considered to be least affected by recent management activities or disturbance, they provide a starting point for elucidating complex relationships between aspects of climate, tree functional traits, and forest production all within the context of the plant economics spectrum (Reich 2014).

Within this study's design, there was a negative relationship between a forest's mean live tree wood density and components of forest production on high GDD sites including live tree aboveground volume and biomass accretion and mortality. This relationship, which was detected across a large expanse of temperate forests, is consistent with findings in tropical regions where low wood density has been associated with relatively high growth rates and increased mortality (Baker et al. 2004; King et al. 2006; Chave et al. 2009; Kraft et al. 2010; Poorter et al.

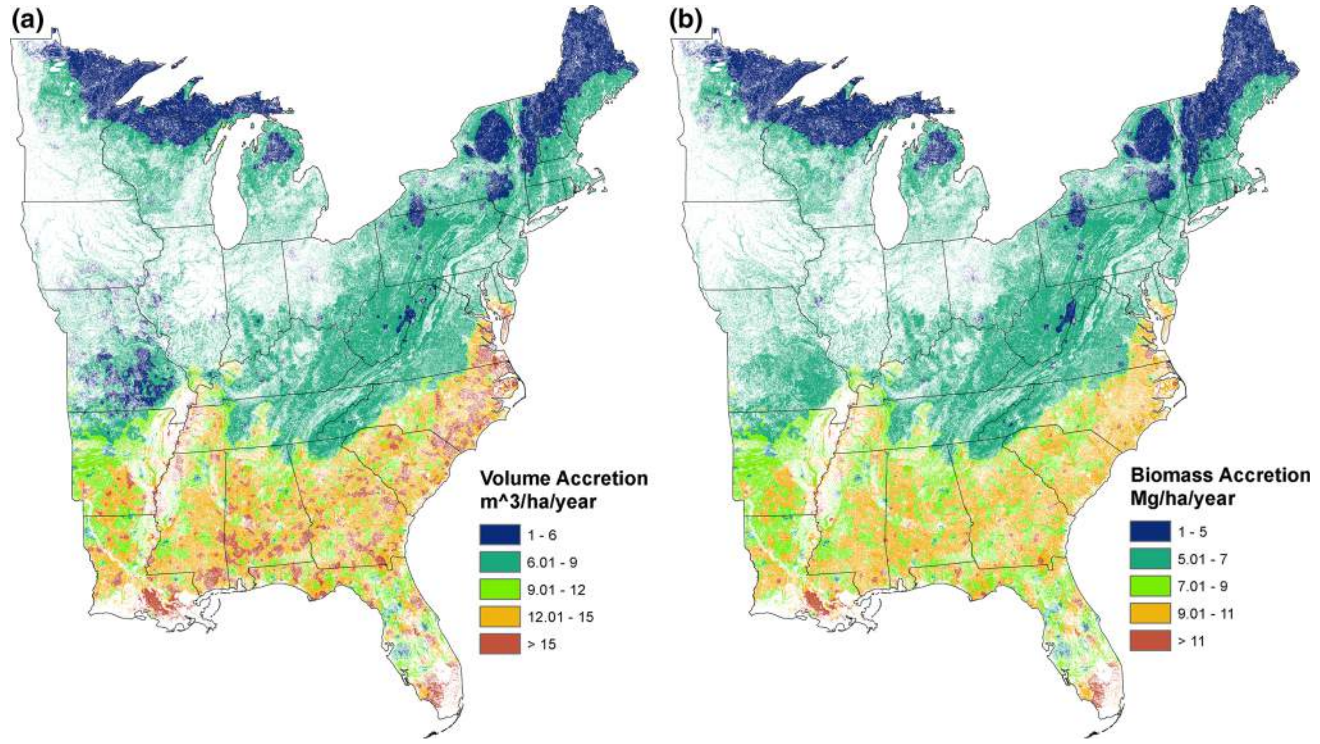


Fig. 5 Interpolated (inverse distance weighting) 90th percentile estimates (Eq. 3) of annual live tree **a** volume (m^3/year/ha) and **b** biomass (Mg/ha/year) accretion for forests of the eastern USA

2010; Wright et al. 2010). Across this study's spectrum of wood density tree species, there may be two contrasting strategies for occupying a forest site and strongly competing for resources to enhance survival and growth. On the one hand, trees may devote resources to growing bole volume at the fastest rate possible (i.e., producing wood of the lowest specific gravity compatible with maintaining their leaf area above that of competitors) (King et al. 2006; Poorter et al. 2008; Wright et al. 2010; Poorter et al. 2010; Reich 2014). As these trees with relatively low wood density may only mechanically support a correspondingly low amount of leaf area (Anten and Schieving 2010), many more stems can be grown per unit area relative to the carrying capacity of the site, which is defined by the maximum size–density relationship (Yoda et al. 1963). The ability of these tree species to more quickly occupy a site, as evidenced by increases in RSD observed in this study, results in rapid development toward the maximum size–density relationship and concomitant tree mortality. In addition to mortality from self-thinning processes, the relatively low construction costs of low wood density species contributes to low survival due to susceptibility to stem damage (Poorter et al. 2008). In contrast, high wood density trees may allocate more fixed C to structural development (i.e., denser wood per unit volume) which results in slower stand development (i.e., increased length of time to reach a point of self-thinning and resulting mortality), but with more resistance to stem damage (Poorter et al. 2008) and potentially greater shade tolerance (Wright et al. 2010).

Plant traits related to resource requirements, namely shade and drought tolerance, have long been used to guide forest management decisions; however, the broader suite of traits being considered in trait-based forest ecological studies (Wright et al. 2010; Russell et al. 2014) have had little transference to the forest management community. A key element to translating emerging results from this and other studies to forestry application is the use of common forest management metrics readily transferable to field-based application including RSD, differences between wood density of current versus desired species, and volume versus biomass yield differences. Potential application to management efforts could be enhanced through addressing a number of remaining knowledge gaps such as how variation in wood density among tree components (e.g., bole versus branch; Thurner et al. 2014), across spatial extents (i.e., regional genotypic variation), and through stand development (e.g., influence of wind in closed versus open canopy) affects forest production. Our study's use of a single mean wood density for a stand oversimplifies (Russell et al. 2014) these complex dynamics and we hypothesize that variations in forest production across a spectrum of wood density may be a combination of allometric change during tree growth and successional change as stands develop. This hypothesis can only be evaluated with additional information on wood density across tree components and through stand development.

Conclusions

This study contributes to a growing body of literature which indicates that wood density can elucidate broad-scale patterns in forest functions such as components of forest production, with this study serving as the first such evaluation across temperate forest ecosystems. It was found that the 90th percentile of volume and biomass accretion and mortality decreased along a range of increasing wood density across temperate forests of the eastern USA. Results of this study support emerging theories of the "fast–slow" plant economics spectrum across the temperate forest ecosystems of the eastern USA. Low wood density species may occupy high GDD sites more quickly due to allocating less biomass or C to stem development resulting in faster full site occupancy with concomitant increases in tree mortality (i.e., closer proximity to self-thinning line and susceptibility to stem damage). In contrast, high wood density tree species may occupy forest sites more slowly by allocating more biomass or C to units of volume but with the potential to more fully occupy sites with less mortality (i.e., higher maximum size–density relationships). These findings, in conjunction with future work, documenting dynamics such as changes in wood density due to allometric change, will enhance the ability to develop forest management strategies for achieving biomass- or C-related objectives.

Author contribution statement CWW, MBR, and SSS: developed research hypotheses; CWW, MBR, and BFW: conducted all analyses; All authors contributed to interpretation of results, writing, and edits.

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Conflict of interest The authors declare that they have no conflict of interest.

References

Anten NPR, Schieving F (2010) The role of wood mass density and mechanical constraints in the economy of tree architecture. Am Nat 175:250–260

Assmann E (1970) The principles of forest yield study: studies in the organic production, structure, increment, and yield of forest stands. Pergamon Press, New York

Baker TR, Phillips OL, Malhi Y et al (2004) Variation in wood density determines spatial patterns in Amazonian forest biomass. Glob Change Biol 10:545–562

Baker TR, Phillips OL, Laurance WF et al (2009) Do species traits determine patterns of wood production in Amazonian Forests? Biogeosciences 6:297–307

Bechtold WA, Patterson PL (eds) (2005) Forest Inventory and Analysis National Sample Design and Estimation Procedures. USDA For. Serv. Gen. Tech. Report. SRS-GTR-80

Cade BS, Noon BR (2003) A gentle introduction to quantile regression for ecologists. Front Ecol Environ 1:412–420

Chave JR, Coomes D, Jansen S, Lewis SL, Swenson NG, Zanne AE (2009) Towards a worldwide wood economics spectrum. Ecol Lett 12:351–366

Dean TJ, Baldwin VC (1996) The relationship between Reineke's stand-density index and physical stem mechanics. For Ecol Manage 8:25–34

Díaz S, Hodgson JG, Thompson K et al (2004) The plant traits that drive ecosystems: evidence from three continents. J Veg Sci 15:295–304

Ducey MJ (2012) Evergreenness and wood density predict height–diameter scaling in trees of the northeastern United States. For Ecol Manage 279:21–26

Ducey MJ, Knapp RA (2010) A stand density index for complex mixed species forests in the northeastern United States. For Ecol Manage 260:1613–1622

Ducey MJ, Larson BC (2003) Is there a correct stand density index? An alternate interpretation. West J Appl For 18:179–184

Hérault B, Bachelot B, Poorter L et al (2011) Functional traits shape ontogenetic growth trajectories of rain forest tree species. J Ecol 99:1431–1440

Hodges DG, Hartsell A, Brandeis C, Brandeis TJ, Bentley AJ (2012) Recession effects on the forests and forest products industries of the South. Forest Prod J 61:614–624

Homer C, Dewitz J, Fry J, Coan M, Hossain N, Larson C, Herold N, McKerrow A, VanDriel JN, Wickham J (2007) Completion of the 2001 national land cover database for the conterminous United States. Photogramm Eng Remote Sensing 73:337–341

Jenkins JC, Chojnacky DC, Heath LS, Birdsey RA (2003) National-scale biomass estimators for United States tree species. For Sci 49:12–35

Johnston K, Ver Hoef JM, Krivoruchko K, Lucas N (2001) Using ArcGIS geostatistical analyst. ESRI, Redlands

Kattge J, Diaz S, Lavorel S (2011) TRY—a global database of plant traits. Glob Change Biol 17:2905–2935

Ketterings QM, Coe R, van Noordwijk M, Ambagau Y, Palm CA (2001) Reducing uncertainty in the use of allometric biomass equations for predicting above-ground tree biomass in mixed secondary forests. For Ecol Manage 146:199–209

King DA, Davies SJ, Tan S, Noor NS (2006) The role of wood density and stem support costs in the growth and mortality of tropical trees. J Ecol 94:670–680

Koenker R (2013) Quantreg: Quantile regression. R package version 4.98. http://www.r-project.org.

Kraft NJB, Metz M, Condit RS, Chave J (2010) The relationship between wood density and mortality in a global tropical forest data set. New Phytol 188:1124–1136

Long JN (1985) A practical approach to density management. Forest Chron 61:23–27

Malmsheimer RW, Heffernan P, Brink S, Crandall D, Deneke F, Galik C, Gee E, Helms JA, McClure N, Mortimer M, Ruddell S, Smith M, Stewart J (2008) Forest management solutions for mitigating climate change in the United States. J For 106:115–171

McKinley DC, Ryan MG, Birdsey RA et al (2011) A synthesis of current knowledge on forests and carbon storage in the United States. Ecol Appl 21:1902–1924

Miles PD, Smith WB (2009) Specific gravity and other properties of wood and bark for 156 tree species found in North America. United States Department of Agriculture Forest Service, Northern Research Station, Newtown Square, p 35

Pan Y, Birdsey RA, Fang J (2011) A large and persistent carbon sink in the world’s forests. Science 333:988–993

Poorter L, Wright SJ, Paz H, Ackerly DD et al (2008) Are functional traits good predictors of demographic rates? Evidence from five neotropical forests. Ecology 89:1908–1920

Poorter L, McDonald I, Alarcon A et al (2010) The importance of wood traits and hydraulic conductance for the performance and life history strategies of 42 rainforest tree species. New Phytol 185:481–492

Quesada CA, Phillips OL, Schwarz M et al (2012) Basin-wide variations in Amazon forest structure and function are mediated by both soils and climate. Biogeosciences 9:2203–2246

Rehfeldt GE (2006) A spline model of climate for the western United States, USDA For. Serv. Gen. Tech. Rep. RMRS-165

Reich PB (2014) The world-wide ‘fast-slow’ plant economics spectrum: a traits manifesto. J Ecol 102:275–301

Reineke LH (1933) Perfecting a stand-density index for even-aged forests. J Agric Res 46:627–638

Roscher C, Schumacher J, Gubsch M, Lipowsky A, Weigelt A, Buchmann N, Schmid B, Schulze ED (2012) Using plant functional traits to explain diversity–productivity relationships. PLoS ONE 7:e36760

Russell MB, Woodall CW, D’Amato AW, Domke GM, Saatchi SS (2014) Beyond mean functional traits: influence of functional trait profiles on forest structure, production, and mortality across the eastern US. For Ecol Manage 328:1–9

Ryan MG, Harmon ME, Birdsey RA, Giardina CP, Heath LS, Houghton RA, Jackson RB, McKinley DC, Morrison JF, Murray BC, Pataki DE, Skog KE (2010) A synthesis of the science on forests and carbon for US forests. Issues Ecol 13:1–16

Santiago LS, Goldstein G, Meinzer FC, Fisher JB, Machado K, Woodruff D, Jones T (2004) Leaf photosynthetic traits scale with hydraulic conductivity and wood density in Panamanian forest canopy trees. Oecologia 140:543–550

Shaw JD (2000) Application of Stand Density Index to irregularly structured stands. West J Appl For 15:40–42

Smith WB, Miles PD, Perry CH, Pugh SA (2009) Forest resources of the United States, 2007. Gen. Tech. Rep. WO-78. U.S. Department of Agriculture, Forest Service, Washington Office, Washington DC

Staudhammer CL, LeMay VM (2001) Introduction and evaluation of possible indices of stand structural diversity. Can J For Res 31:1105–1115

Thurner M, Beer C, Santoro M et al (2014) Carbon stock and density of northern boreal and temperate forests. Glob Ecol Biogeogr 23:297–310

U.S. Department of Agriculture, Forest Service (2011) Forest inventory and analysis national core field guide, vol I. Field data collection procedures for phase 2 plots, version 5.1. U.S. Department of Agriculture, Forest Service, Washington, DC. http://www.fia.fs.fed.us/library

USDA (2013) FIA Datamart. http://www.fia.fs.fed.us/tools-data/

Woodall CW, Miles PD, Vissage JS (2005) Determining maximum stand density index in mixed species stands for strategic-scale stocking assessments. For Ecol Manage 216:367–377

Woodall CW, Heath LS, Domke GM, Nichols MC (2011) Methods and equations for estimating aboveground volume, biomass, and carbon for trees in the U.S. Forest Inventory, 2010. United States Department of Agriculture Forest Service, Northern Research Station, Newtown Square, p 30

Woodall CW, Zhu K, Westfall JA, Oswalt CM, D’Amato AW, Walters BF, Lintz HE (2013) Assessing the stability of tree ranges and influence of disturbance in eastern US forests. For Ecol Manage 291:172–180

Woudenberg SW, Conkling BL, O’Connell BM, LaPoint EB, Turner JA, Waddell KL (2010) The Forest Inventory and Analysis Database: Database Description and Users Manual Version 4.0 for Phase 2. United States Department of Agriculture Forest Service, Rocky Mountain Research Station, Fort Collins, p 336

Wright IJ, Reich PB, Westoby M et al (2004) The worldwide leaf economics spectrum. Nature 428:821–827

Wright SJ, Kitajima K, Kraft NJB, Reich PB et al (2010) Functional traits and the growth–mortality trade-off in tropical trees. Ecology 91:3664–3674

Yoda K, Kira T, Ogawa H, Hozumi K (1963) Intraspecific competition among higher plants. XI. Self-thinning in overcrowded pure stands under cultivated and natural conditions. J. Biol. Osaka City Univ 14:107–129