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Ecosystem carbon density and allocation across a chronosequence of longleaf pine forests

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Abstract. Forests can partially offset greenhouse gas emissions and contribute to climate change mitigation, mainly through increases in live biomass. We quantified carbon (C) density in 20 managed longleaf pine (*Pinus palustris* Mill.) forests ranging in age from 5 to 118 years located across the southeastern United States and estimated above- and belowground C trajectories. Ecosystem C stock (all pools including soil C) and aboveground live tree C increased nonlinearly with stand age and the modeled asymptotic maxima were 168 Mg C/ha and 80 Mg C/ha, respectively. Accumulation of ecosystem C with stand age was driven mainly by increases in aboveground live tree C, which ranged from <1 Mg C/ha to 74 Mg C/ha and comprised <1% to 39% of ecosystem C. Live root C (sum of below-stump C, ground penetrating radar measurement of lateral root C, and live fine root C) increased with stand age and represented 4–22% of ecosystem C. Soil C was related to site index, but not to stand age, and made up 39–92% of ecosystem C. Live understory C, forest floor C, downed dead wood C, and standing dead wood C were small fractions of ecosystem C in these frequently burned stands. Stand age and site index accounted for 76% of the variation in ecosystem C among stands. The mean root-to-shoot ratio calculated as the average across all stands (excluding the grass-stage stand) was 0.54 (standard deviation of 0.19) and higher than reports for other conifers. Long-term accumulation of live tree C, combined with the larger role of belowground accumulation of lateral root C than in other forest types, indicates a role of longleaf pine forests in providing disturbance-resistant C storage that can balance the more rapid C accumulation and C removal associated with more intensively managed forests. Although other managed southern pine systems sequester more C over the short-term, we suggest that longleaf pine forests can play a meaningful role in regional forest C management.

Key words: carbon dynamics; carbon storage; chronosequence; forest structure; longleaf pine; Pinus palustris; *root-to-shoot ratio; stand age.*

Introduction

Forests can partially offset greenhouse gas emissions and contribute to climate change mitigation, mainly through increases in live biomass both above- and belowground (Heath et al. 2011). The total carbon (C) stock, not including soil, in temperate forests in the conterminous United States was estimated as 43×10^9 Mg C in 2007 (Pan et al. 2011), and forests sequestered an estimated 790×10^6 Mg of CO_2 equivalent on 253×10^6 ha of forestland in 2008 (Heath et al. 2011). More recent analysis of forest C stocks and stock change from 1990 to 2016 indicated that forest growth and expansion offset 15% of the annual C emission from combustion of fossil fuels in the United States (Woodall et al. 2015*a*). Accurate estimates of total ecosystem C stocks are critical, because changes in C stocks may influence the balance between terrestrial and atmospheric C (Keith et al. 2010). Furthermore, total ecosystem C stocks can be used as a C carrying capacity baseline to evaluate the impact of changes in land use, forest management, and forest health on C storage and climate change mitigation (Keith et al. 2010). Forest biomass chronosequences have been used to define C storage potential of forests in the United States, with the majority constructed using data from the Forest Inventory and Analyses National Program (FIA) and genus-level allometric equations from the literature (Lichstein et al. 2009, McKinley et al. 2011, Chojnacky et al. 2014), and fewer based on actual sampling of tree biomass and C concentrations (King et al. 2007, Kashian et al. 2013). However, the paucity of biomass

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chronosequences is a major source of inconsistencies among national estimates of C stocks (Williams et al. 2012). Keith et al. (2014) identify the need for chronosequences of known age and the assumption of space-for-time substitution to calibrate growth functions for prediction of C stocks at the site and landscape scales. Furthermore, lack of empirical information on belowground tree biomass has hampered accurate estimations of forest C stocks and subsequent understanding of forest C dynamics (McKinley et al. 2011, Russell et al. 2015).

Longleaf pine forests (*Pinus palustris* Mill.), valued for high quality timber and nontimber benefits (Alavalapati et al. 2002), were once a dominant forest type in the Coastal Plain of the southeastern United States, and their restoration may serve as a pathway to increase the resilience of forests to changing climate, because of resistance to disturbance, disease, and insects (Johnsen et al. 2009, Churchhill et al. 2013). Longleaf pine is sensitive to competition, and frequent fire is necessary to reduce hardwood encroachment as well as expose mineral soil to facilitate natural regeneration (Mitchell et al. 2006). Frequent prescribed fire, combined with low stand density, also supports high native plant biodiversity in the ground cover layer of longleaf pine ecosystems (Mitchell et al. 2006). While higher quality sites have the greatest forest C carrying capacity, less productive sites (which in the southeastern United States are often planted with longleaf pine) may also be suitable for greenhouse gas mitigation projects (Hoover and Smith 2012). Reductions in terrestrial C stocks as a result of conversion of forest land to other uses, such as agriculture and urbanization, have increased the importance of climate change mitigation by forest lands with typically lower C stocks (Birdsey and Pan 2015). Although longleaf pine forests are low-density forests, managed longleaf pine forests can sequester comparable C over longer rotations relative to other plantation species in the southeastern United States. For example, Gonzalez-Benecke et al. (2015*a*), using a growth-and-yield-based C model that simulated *in situ* and *ex situ* C pools and accounted for C emissions from transportation and silvicultural activities, reported higher average C stock over a 300-yr simulation period for longleaf pine plantations on a 75-yr rotation length compared to *Pinus elliotii* var. *elliottii* plantations on a 25-yr rotation, a length typical for industrial plantations in the southeastern United States. In addition, natural longleaf pine forests commonly experience only small-scale disturbances that are mimicked by uneven-aged management (Brockway et al. 2014), which can extend C storage by limiting harvest removals (Ryan et al. 2010). Longleaf pine ecosystems may be well suited for applied long-term forest C management because of greater tree longevity and longer rotations relative to other southern pines, and when biodiversity (Martin et al. 2015) and resilience to wildfire (and other disturbances) are important forest management goals (Schwenk et al. 2012). However, unlike other pines, less is known about the potential role of longleaf pine restoration across the landscape in offsetting greenhouse gas emissions (Susaeta et al. 2014). This knowledge gap is particularly relevant given the recent emphasis on longleaf pine restoration by federal and state private landowner incentive programs (as an example, the USDA Natural Resources Conservation Service Longleaf Pine Initiative).

In previous work, we quantified ecosystem C stocks in five different-aged longleaf pine stands in Georgia (Samuelson et al. 2014). Here, we combine those data with similar C data collected in 15 additional longleaf pine stands positioned across the native range of longleaf pine in Louisiana, North Carolina, and Florida to construct a C chronosequence spanning from 5 yr of age to a mean canopy age of 118 yr. Stands selected for sampling represented the current condition of the longleaf pine resource (Oswalt et al. 2012). We sampled aboveground and belowground biomass to develop robust allometric equations for longleaf pine and quantified C density in live tree biomass, live understory biomass, standing dead trees, downed dead wood, the forest floor, and soil to a 1 m depth. Our specific objectives were to (1) quantify C density in longleaf pine forests representing ranges in age, forest structure, management and site quality; (2) estimate above- and belowground C accumulation trajectories for longleaf pine over time; and (3) determine if age, forest structure, and site index could be used as explanatory variables for ecosystem C (sum of all C pools including soil C). Examples of old-growth forests are rare in the eastern United States (Lichstein et al. 2009). Mitchell et al. (2009) suggested that old-growth characteristics of old longleaf pine forests, such as trees >50 cm dbh (diameter at 1.37 m), large standing and downed dead wood pools and patches of varying age classes, begin to develop at 115–120 yr of age. Because our chronosequence spanned the seedling grass stage to a mean canopy age of 118 yr and many older stands consisted of trees ≥50 cm dbh, we hypothesized that live biomass C density would increase with age following a saturation function (e.g. Michaelis-Menton equation), as reported for chronosequences of temperate (Pregitzer and Euskirchen 2004) and *Pinus*-dominated forests (Kashian et al. 2013). Due to the long residence time of mineral soil C and variability in soil C stabilization mechanisms across the landscape (Pregitzer and Euskirchen 2004), we also hypothesized that soil C content would not accrue with age. Foresters and forest landowners manage forests for a diverse array of societal and direct economic benefits including wood production, maintenance of biodiversity, and C sequestration. There are generally trade-offs among these benefits; therefore, our overall goal was to define long-term C sequestration potential in managed longleaf pine forests.

METHODS

Study sites

A total of 20 stands ranging in age from 5 to 118-yr-old were sampled across the range of longleaf pine in Georgia

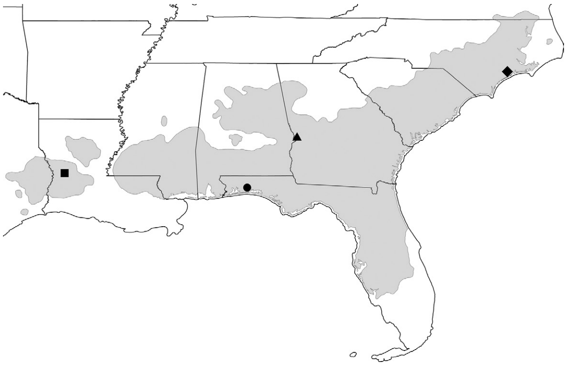

FIG. 1. Location of sampling sites within the historic range of longleaf pine (range map from U.S. Geological Survey [1999]). Symbols denote Camp Lejeune, North Carolina (diamond), Fort Benning, Georgia (triangle), Eglin Air Force Base, Florida (circle), and Kisatchie National Forest, Louisiana (square). Stands were 15, 25, 65, and 79 yr of age in North Carolina; 5, 12, 21, 64, and 87 yr of age in Georgia; 9, 19, 43, 50, 85, and 118 yr of age in Florida; and 8, 18, 34, 60, and 83 yr of age in Louisiana.

(Fort Benning at the Georgia–Alabama border, the 64-yr-old stand was located in Alabama and the other four stands were in Georgia), Louisiana (Kisatchie National Forest), North Carolina (Camp Lejeune), and Florida (Eglin Air Force Base; Fig. 1; Appendix S1: Table S1). Stands were managed for both timber production and biodiversity benefits. The 30-yr (1982–2011) average annual precipitation, average annual temperature, and average maximum and minimum temperatures for each site were 1,180 mm, 18.7°C, 24.6°C, and 12.8°C, respectively, for Columbus, Georgia (station COOP_092166); 1,447 mm, 18.9°C, 25.3°C, and 12.4°C, respectively, for Leesville, Louisiana (station GHCND: USC00165266); 1,356 mm, 17.4°C, 23.3°C, and 11.5°C, respectively, for Jacksonville, North Carolina (station GHCND:USW00093727); and 1,486 mm, 19.4°C, 26.2°C, and 12.6°C, respectively, for Crestview, Florida (station GHCND:USW00013884; data *available online*).[8]

All Louisiana stands were planted, but the planting density of the two oldest stands was unknown (Appendix S1: Table S1). For all other sites, stands less than 60 yr of age were plantations, planted at a known density, and older stands were established from natural regeneration and their initial density was unknown. For natural stands, stand age was based on the mean age of canopy trees and inventory records. All natural stands were dominated by one age class in the canopy, with the exception of the 118-yr-old stand in Florida in which two cohorts were dominant, one approximately 160 yr of age and a second approximately 75 yr old. Forest management records indicate one thinning in the 83-yr-old stand in Louisiana and one thinning in the 65-yr-old stand in North Carolina, both 5–7 yr before sampling. Approximately 5 m^2/ha of basal area was removed from the 83-yr-old stand and 1 m^2/ha was removed from the 65-yr-old stand. Otherwise, there were no records of forest management activities besides prescribed fire. Stands were burned regularly and the majority of stands were burned 1–3 yr prior to sampling, the exception being the 50-yr-old stand, which was burned five years before sampling and the 25-yr-old stand, which was burned four years before sampling (Appendix S1: Table S1).

Georgia stands (5, 12, 21, 64, and 87 yr of age) were sampled in 2012 (Samuelson et al. 2014). Louisiana stands (8, 18, 34, 60, and 83 yr of age) were sampled in 2013; North Carolina stands (15, 25, 65, and 79 yr of age) were sampled in 2014; and Florida stands (9, 19, 43, 50, 85, and 118 yr of age) were sampled in 2015. Sampling was conducted from May through October of each sample year with the exception of Florida stands, which were sampled from February through June. At sampling, stands varied in density and tree size distributions (Fig. 2). With the exception of the 65-yr-old stand, stands older than 59 yr contained some trees with dbh ≥ 50 cm (Fig. 2). For the majority of stands (14), longleaf pine comprised >90% of the total basal area and, for the remaining stands, longleaf pine was 56–82% of total basal area (Appendix S1: Table S2).

Forest inventories

In all stands, a 1-ha circular main plot and four 400-m^2 circular subplots within the main plot were located as described in Samuelson et al. (2014). Forest inventories were conducted in January or February of the designated sampling year as described by Samuelson et al. (2014). In order to provide an old-growth reference, height and dbh of trees in a longleaf pine forest representative of old-growth known as the Wade Tract (30.758° N, 84.001° W) located near Thomasville, Georgia were measured in October 2014. The Wade Tract was previously described (Platt et al. 1988, West et al. 1993, Noel et al. 1998) and contains many large trees 100–400 years of age. Plots were located in an area roughly 7 ha in size within the south-central portion of the 84-ha tract. Nine variable radius plots were sampled using a 10 basal area factor prism. All trees within each plot were longleaf pine. Plot centers were established by selecting a large presumably old-growth tree based on dbh and age relationships reported in Platt et al. (1988) and West et al. (1993). Plot center trees ranged in dbh from 46 to 70 cm with the majority > 60 cm dbh, suggesting an age range of 100–396 yr at sampling, and a median age of 248 yr (West et al. 1993). Plot basal area and density ranged from 9 to 25 m^2/ha and 38 to 395 trees/ha, respectively, and the corresponding means were 16 m^2/ha and 102 trees/ha, respectively.

Longleaf pine biomass

A total of 117 longleaf pine trees in stands older than five years of age, representing the range in dbh and height,

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[8] http://www.ncdc.noaa.gov

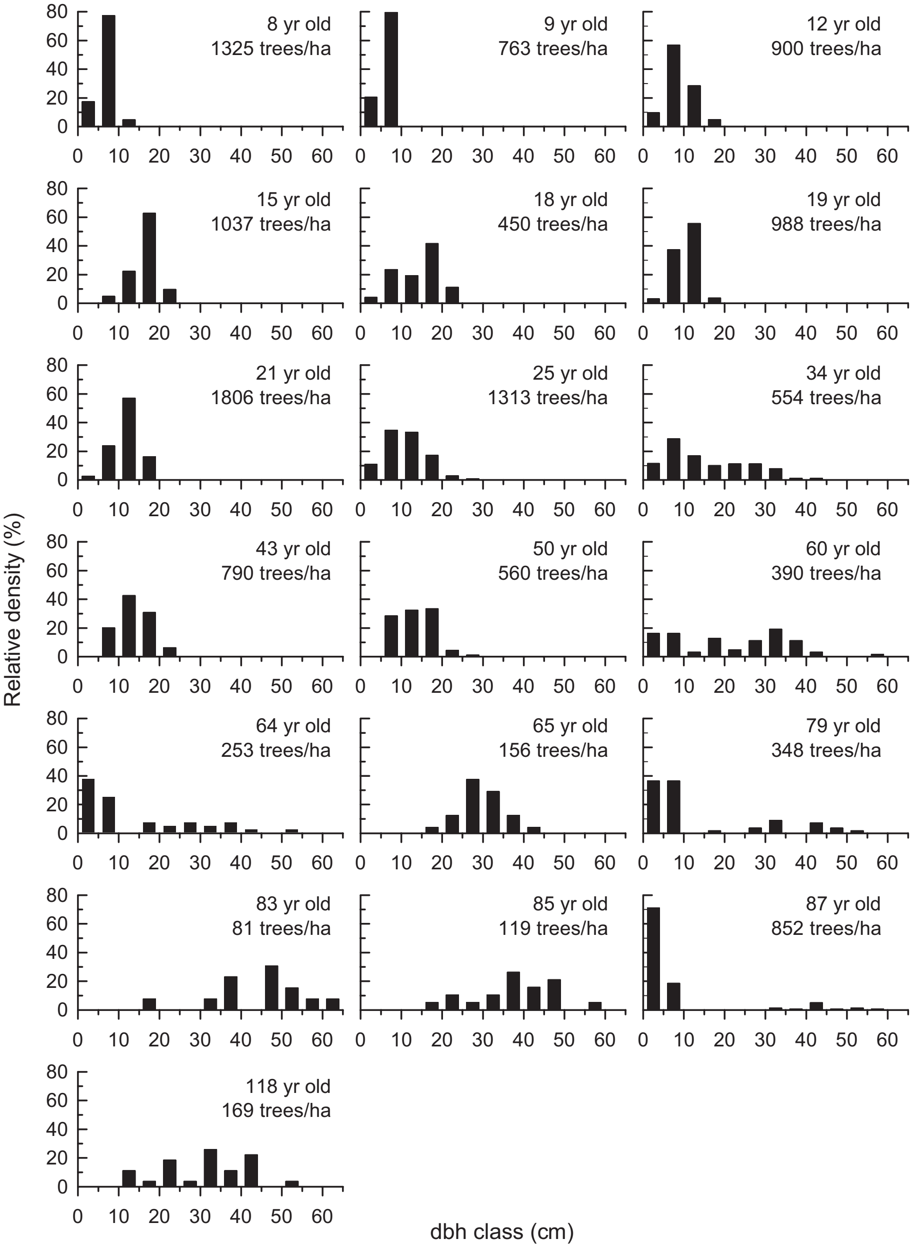

FIG. 2. Relative density (percentage of total density) by dbh class of longleaf pine stands. Age and total density at sampling are indicated for each stand.

were selected for biomass sampling (Appendix S1: Table S3). In addition to subsampling within the defined stands, two older isolated trees (188 yr of age) in a tract with scattered old trees were harvested in Florida, for a total of 119 trees. The majority of planted pine in the 5-yr-old stand was in the grass stage (an extended seedling stage in which shoot elongation is inhibited) and allometric equations from Samuelson et al. (2014) based on ground-line diameter were used to predict aboveground and below-stump biomass. Tree biomass data collected in Georgia stands older than five years were combined with biomass data from the other sites to develop new allometric equations and estimate biomass.

For trees <18 cm dbh, the aboveground biomass of the entire tree was collected and separated into foliage, branch, and main stem components and oven-dried at 70°C for foliage and 105°C for woody tissues until reaching a constant mass. Trees larger than approximately 18 cm dbh (crown development greatly increased at a mean dbh of 18 cm and trees required substantially more time to sample) were subsampled following procedures described by Samuelson et al. (2014).

For below-stump sampling, depending on the site and tree size, all or a subset of harvested trees was randomly selected for excavations. Across all stands older than five years of age, a total of 82 trees were excavated (Appendix S1: Table S2). The square area of the excavation pit ranged from the minimum set at 1 m^2 for the smallest diameter trees, a standard size for sampling *Pinus* plantations in the southern United States (Butnor et al. 2016), to a maximum of 4 m^2 for the largest diameter trees. Pit size was limited to a maximum of 4 m^2 due to the time demanding nature of manual excavations. The area of the stump was excluded from the pit area and length and width of the pit was measured beginning at the stump edges. Pit size for remaining trees was scaled with tree dbh approximated by pit area (m^2) = $0.8322 \times e^{0.0301 \times \mathrm{dbh}}$ (Butnor et al. 2016; Appendix S1: Table S2). Excavation methodologies were detailed in Samuelson et al. (2014).

Longleaf pine allometric model development

For each biomass component (foliage, live branch, stem, tap root and lateral root mass in pits), model performance and fit were tested on three forms of allometric equations:

$$W = \beta_o dbh^{\beta 1}$$

$$W = \beta_o dbh^2 height^{\beta 1}$$

$$W = \beta_o dbh^{\beta 1} height^{\beta 2}$$

(where W is biomass per tree and height is total tree height) using nonlinear regression techniques (MODEL procedure in SAS version 9.3; SAS Institute, Cary, North Carolina, USA). Models were selected based on analyses of residuals and goodness-of-fit parameters including P values, pseudo-R^2 ($1 - SS_{\mathrm{error}}/SS_{\mathrm{corrected\ total}}$) and root mean square error (RMSE). Allometric models were used to predict the aboveground and below-stump biomass of all longleaf pine trees ≥1 cm dbh and ≥2 m height tallied in the forest inventories.

Other tree species biomass

Allometric equations from the literature were used to predict aboveground biomass from dbh for species other than longleaf pine (Jenkins et al. 2003). Below-stump biomass of other pine species was predicted using the allometric equation developed in this work, because site may have more influence on tap root development than species (Gibson et al. 1986). We assumed that the ground-penetrating radar (GPR) measurement of coarse roots (described in *Plot-level root biomass*) captured all hardwood coarse root biomass.

Live understory biomass

The live understory was measured in Georgia, Louisiana, and North Carolina stands. Live understory was considered the sum of woody stems ≥1 m and <2 m height, and ground cover vegetation (all vegetation < 1 m in height). Procedures for sampling woody stems ≥1 m and <2 m height and ground cover vegetation followed those described in Samuelson et al. (2014), and ground cover values were previously reported by Gonzalez-Benecke et al. (2015*b*). Allometric equations published for the 5-yr-old longleaf pine stand (Samuelson et al. 2014) were used to predict aboveground biomass for longleaf pine; otherwise, species-specific or general allometric equations were used to predict aboveground biomass of understory woody stems from ground-line diameter (Robertson and Ostertag 2009). We assumed that GPR measurements accounted for coarse root mass of the understory.

Live understory C for Florida stands was predicted from the nonlinear relationship between live understory C and total basal area (m^2/ha) developed using data from the other sites. The high value (5 Mg/C ha) in the 60-yr-old stand in Louisiana was due to dense patches of longleaf pine seedling regeneration recorded on two of the subplots. The relationship between live understory C and basal area was significant only when the high value for understory C from the 60-yr-old stand in Louisiana was not included in the regression, as this stand also had high basal area. Live understory C (Mg C/ha) was significantly and negatively related to basal area ($y = 2.0911 \times e^{-0.0560 \mathrm{basalarea}}$, $R^2 = 0.40$, $P < 0.001$). For calculation of the root-to-shoot ratio (R:S) that included all aboveground biomass, a similar function was used to predict live understory mass (Mg/ha) for Florida stands ($y = 4.158 \times e^{-0.0616 \mathrm{basalarea}}$, $R^2 = 0.48$, $P < 0.001$).

Plot-level root biomass

Fine root biomass from manual coring and plot-level coarse root biomass estimated by GPR were measured at all sites except Florida. GPR cannot readily detect dead roots, fine roots, or separate roots by species; hence GPR-estimated root mass includes live coarse root biomass regardless of species (Butnor et al. 2003, 2012*a*). A 100-m^2 measurement plot was located at the center of each subplot. Plots were prepared by cutting woody brush and herbaceous cover to the ground level and removing surface debris. Ground-penetrating radar data were collected with a SIR-3000 radar unit (Geophysical Survey Systems [GSSI], Nashua, New Hampshire, USA) connected to 1,500 MHz antenna along 21 10-m transects spaced 50 cm apart in each plot. Post-collection data processing and root mass quantification were previously described by Samuelson et al. (2014). GPR reliably detects belowground lateral roots under suitable soil conditions, but the area directly beneath trees where tap roots and large overlapping lateral roots reside is largely underestimated by GPR (Butnor et al. 2016). There is overlap between below-stump biomass modeled with allometric equations and coarse root mass estimated with GPR. Butnor et al. (2016) determined that GPR detected

100% of below-stump biomass of longleaf pine trees <3.5 cm dbh, therefore the amount of root mass estimated by allometric modeling of below-stump mass of trees ≥3.5 cm dbh was deducted from the GPR estimates to eliminate double counting of mass between methods. The GPR data previously used for Georgia stands (Samuelson et al. 2014) were reprocessed using the current protocol. Live fine root (<2 mm diameter) sampling was described in Samuelson et al. (2014).

Total live root mass C was considered the sum of below-stump C of pines ≥3.5 cm dbh, GPR detected lateral root C and fine root C. For smaller pines (<3.5 cm dbh), GPR was assumed to account for below-stump C. The sum of fine root C and GPR lateral root C (Mg C/ha) was predicted for Florida stands from below-stump C of trees ≥3.5 cm dbh (Mg C/ha) and site index (SI, base age 50 yr in meters) using a regression function developed from the other 14 stands ($y = 13.911 + 0.364$ below-stump C − 0.510SI; $R^2 = 0.61$; $P = 0.002$). A similar function was used to predict total live root mass (Mg/ha) of Florida stands for calculation of $R{:}S$ ($y = 28.185 + 0.364$ below-stump mass − 1.032SI; $R^2 = 61$; $P = 0.002$).

Detritus

Coarse woody debris (≥7.6 cm diameter) and fine woody debris (≥2.5 cm and <7.6 cm diameter) were sampled following a modified approach of the planar intersect technique (Harmon and Sexton 1996) and sampling procedures described by Samuelson et al. (2014). The forest floor was considered the sum of three categories: (1) duff (dark, partly decomposed, organic material) above the mineral soil, (2) litter on top of duff, including recognizable plant parts such as leaves, flowers, and twigs <0.6 cm in diameter, and (3) very fine woody debris (≥0.6 cm and <2.5 cm in diameter; Smith et al. 2013).

Carbon in decaying stumps was not included, because the year of mortality was unknown and lack of information on stump decay rates across sites. Therefore, only coarse woody debris was considered in the downed dead wood pool. To estimate aboveground C in the standing dead wood pool (trees with dbh ≥ 1 cm and height ≥ 2 m), the amount of aboveground biomass was estimated as previously described. The same decay-class reduction factors used for coarse woody debris were used for estimating the decay class of standing dead trees. In addition, the degree of retention of branches and twigs was also considered in determining the decay factor. No standing dead trees exhibited broken tops and all standing dead trees fell into decay class 1 (no change in mass). Based on the range of 3–12% in the ratio of foliage to total aboveground mass for hardwoods and 10–30% range for softwoods (Jenkins et al. 2003), 8% of aboveground biomass was subtracted from hardwood biomass and 20% subtracted from pine biomass to account for foliage loss in standing dead trees. We recognize that, in some cases, branch biomass in standing dead trees may be overestimated. Belowground C of standing dead trees was not estimated, since the number and sizes of dead trees were small, the exception being the 118-yr-old stand in which three dead longleaf pine trees (20–32 cm dbh) and one dead oak tree (27 cm dbh) were tallied on one subplot.

Carbon concentration

Carbon concentrations were measured in Georgia, North Carolina, and Louisiana stands, and sampling protocols for plant tissues and litter and duff pools were described by Samuelson et al. (2014). The C concentrations of live trees and live woody stems ≥1 m and <2 m height of species other than longleaf pine was assumed to be 50% (Woodbury 2007). To calculate ground cover C, ground cover was separated into graminoid, woody, and "other" classes for C concentration measurements. Because of low coarse, fine, and very fine woody debris in all stands and the lack of range in decay classes, C concentration of all woody debris classes was assumed to be 50% (Prichard et al. 2000, Harmon et al. 2008).

Soil C and soil texture

Soil samples were collected at four depths (0.0–0.1 m, 0.1–0.2 m, 0.2–0.5 m, 0.5–1.0 m) as previously described (Samuelson et al. 2014), with the modification that only four soil cores per subplot rather than 12 were collected for the two shallowest depths in Florida stands. Soil bulk density and soil C (Mg C/ha) to a 1 m depth were determined as described by Samuelson et al. (2014). Total C concentration of soil was determined by dry combustion with detection by thermal conductivity (Flash EA 1112 series CN analyzer; Thermo Finnigan Instruments, Milan, Italy). The soils across the region have negligible inorganic C contents (Soil Survey Staff 2000), therefore soil organic content was presumed to be equal to total C concentration. Average texture to a 1 m depth was determined by averaging the results of particle size analysis using the hydrometer method (Bouyoucos 1962) of soil from the four depth intervals weighted by depth length.

Statistical analysis

The stand was the sample unit and values for each subplot were averaged by stand. All analyses were performed using SAS version 9.3 (SAS Institute). Linear ($y = \beta_1 x$), power ($y = \beta_1 x^{\beta 2}$), saturation ($y = \beta_1 x/[\beta_2 + x]$), Chapman-Richards ($y = \beta_1[1 - e^{-\beta 2x}]$), and negative exponential ($y = \beta_1 e^{-\beta 2x}$) functions were tested to determine relationships between C density and stand age. The best models were selected based on plots of residuals, R^2 or pseudo-R^2, RMSE and P values. Live tree C from the Wade Tract was not included in model fitting. Site index, stand age, and forest structure variables were also investigated as explanatory variables for ecosystem C using stepwise multiple linear regression with a threshold significance of 0.15 for variable selection and retention (Neeter

TABLE 1. Regression models for longleaf pine tree biomass.

Biomass component and variable	Coefficient	Estimate	SE	P	CF	R^2
Stem	β_0	0.021	0.002	<0.001	1.02	0.98
dbh	β_1	2.139	0.072	<0.001		
Height	β_2	0.844	0.094	<0.001		
Foliage	β_0	0.018	0.003	<0.001	1.12	0.81
dbh	β_1	2.056	0.053	<0.001		
Live branch	β_0	0.001	<0.001	<0.001	1.09	0.76
dbh	β_1	3.216	0.049	<0.001		
Lateral root	β_0	0.009	0.002	<0.001	1.21	0.62
dbh	β_1	2.310	0.088	<0.001		
Tap root	β_0	0.007	0.001	<0.001	1.05	0.88
dbh	β_1	2.729	0.045	<0.001		

Notes: Stem includes bark and lateral root mass is from excavation pits. The component models were biomass (as kg/tree) = $\beta_0 \text{dbh}^{\beta_1} \text{height}^{\beta_2} \text{CF}$ or $\beta_0 \text{dbh}^{\beta_1} \text{CF}$ where dbh is diameter at 1.37 m in centimeters, height is total height in meters, and CF is the correction factor for systematic bias introduced by anti-log transformation.

et al. 1996). Data were held back from one stand randomly selected from each site (12-yr-old stand in Georgia, 60-yr-old stand in Louisiana, 25-yr-old stand in North Carolina, and 85-yr-old stand in Florida) to develop the model and the model was then evaluated on the remaining four stands. The variance inflation factor (VIF) was monitored to detect multicollinearity between predicting variables, and variables with VIF > 5 were discarded, as suggested by Neeter et al. (1996). Student's t tests were used to determine if the intercept and slope of the relationship between predicted and observed ecosystem C were significantly different from 0 and 1, respectively. Relationships between tap root depth and tree dbh, height, age, and percent sand, silt, or clay to a 1 m depth were examined using linear and nonlinear regression.

RESULTS

Longleaf pine allometric models

The best models for all biomass components were based on a multiplicative error structure (i.e., $\ln W = \ln\beta_o + \beta_1 \ln\text{dbh} + \varepsilon$ or $\ln W = \ln\beta_o + \beta_1 \ln\text{dbh} + \beta_2 \ln\text{height} + \varepsilon$) to stabilize heteroscedastic variance (Mascaro et al. 2011, Dong et al. 2015). Equations for all components except stem included only dbh and, for stem mass, included dbh and height (Table 1). A correction factor ($\text{CF} = e^{(\text{MSE}/2)}$, where MSE is the mean square error of the regression) for systematic bias introduced by anti-log transformation (Baskerville 1972) was applied to each component model. Scatter plots of residuals showed no evidence of bias for any of the final models. The spatial heterogeneity of secondary woody roots led to higher uncertainty in lateral root mass than for other component predictions.

Carbon concentration

Ranges in C concentrations of plant tissues and litter and duff pools across stands within a site were similar, and no significant effects of stand age on C concentrations were observed (data not shown). Therefore, values were averaged across all stands (Table 2) and the means used in calculating C density.

Carbon density

The relationship between ecosystem C (sum of all pools including soil C) and stand age was best modeled with a saturation function (Fig. 3a, Table 3). The predicted asymptotic maximum of the nonlinear model for ecosystem C was 168 ± 17 Mg C/ha (mean ± SE). The relationship between live tree C (aboveground C of trees ≥1 cm dbh and ≥2 m height) and stand age was also best modeled with a saturation function with a predicted asymptotic maximum of 80 ± 22 Mg C/ha (Fig. 3b, Table 3). Live tree C of the 248-yr-old stand (Wade Tract) was not included in model fitting. The modeled and biometric estimations of live tree C for the Wade Tract were 69 Mg C/ha and 72 Mg C/ha, respectively. Live tree C represented <10% of ecosystem C in stands less than 12 years of age and as much as 39% of ecosystem C in older stands (ages 60, 85, and 87 yr).

The relationship between live root C, based on either below-stump C (pines ≥1.0 cm dbh and ≥2 m height) or total live root C (below-stump C of pines ≥3.5 cm dbh + ground penetrating radar detection of lateral root C + fine root C), and stand age was best modeled with a power function (Fig. 3c, Table 3). Mean total live root C was approximately double mean below-stump C, mainly due to the addition of lateral root C detected by GPR rather than the addition of fine root C, which contributed from <1 Mg C/ha to 2 Mg C/ha (data not shown). Total live root C ranged from 3 Mg C/ha to 25 Mg C/ha and represented 4–22% of ecosystem C.

Other plant C pools represented a smaller proportion of ecosystem C. Live understory C ranged from <1 Mg C/ha to 5 Mg C/ha and was unrelated to stand age and represented at most 3% of ecosystem C (Fig. 4). Forest floor C ranged from <1 Mg C/ha to 6 Mg C/ha and was best modeled with a Chapman-Richards function (Fig. 5a, Table 3). Maximum downed dead wood C was <1 Mg C/ha

Table 2. Carbon concentrations in longleaf pine forests.

Component	Carbon concentration (%)
Longleaf pine	
Foliage	51.27 (0.25)
Stem wood	51.97 (0.31)
Coarse root	51.12 (0.24)
Fine root	43.59 (0.87)
Forest floor	
Litter	50.54 (0.41)
Duff	41.52 (2.14)
Groundcover	
Graminoid	47.38 (0.62)
Woody	50.36 (0.60)
Other	46.93 (0.52)

Note: Standard errors are indicated in parentheses.

and unrelated to stand age or stand structure (Fig. 5b). With the exception of the 118-yr-old stand, standing dead wood C was less than 2 Mg C/ha (Fig. 5c). Standing dead wood C was unrelated to stand age or structure. The total of forest floor C and standing and downed dead wood C composed from 1% to 7% of ecosystem C.

Soil C was generally lower in Florida stands (32–58 Mg C/ha) and highest in Louisiana stands (79–98 Mg C/ha) and unrelated to stand age (Fig. 6a). Soil C comprised 39% of ecosystem C in the oldest stand and 92% of ecosystem C in the youngest stand. No significant relationships between soil C and stand structure were observed, but soil C was significantly related to SI (soil C = 22.424 + 2.575SI, $R^2 = 0.25$, $P = 0.026$).

The predictive model for ecosystem C included stand age, SI, total basal area, and density (Table 3). Stand age and SI explained 39% and 37%, respectively, of the variation in ecosystem C, with basal area and density accounting for the remaining 12%. The intercept and slope of the relationship between observed and predicted ecosystem C for the four stands not used in model fitting were not significantly different from 0 and 1, respectively (Fig. 6b).

Rooting depth and root:shoot ratio

Maximum tap root depth was 4 m and recorded in the 118-yr-old stand in Florida (Fig. 7b). Tap root depth increased nonlinearly with increasing dbh, average percent sand in soil to a 1 m depth and tree age, with 47% of the variation in tap root depth explained by dbh alone in the model and 76% explained with all three variables in the model (Table 3). The 5-yr-old stand was not included in model fitting of tap root depth because most trees had not reached 1.37 m height. Average percent sand in soil was 61%, 71%, 92%, and 93% at the Louisiana, Georgia, North Carolina, and Florida sites, respectively (Appendix S1: Table S1).

The *R:S*, calculated as the ratio of total live root mass (below-stump mass of pines ≥3.5 cm dbh + GPR detection of lateral root mass + fine root mass) to total live aboveground mass (all trees + understory) or as the ratio of live below-stump mass to live aboveground mass of only longleaf pine trees (≥1.0 cm dbh and ≥2 m height), declined nonlinearly with stand age and was best modeled with a power function (Fig. 7a). To compare to other reports in the literature, an overall *R:S* mean was

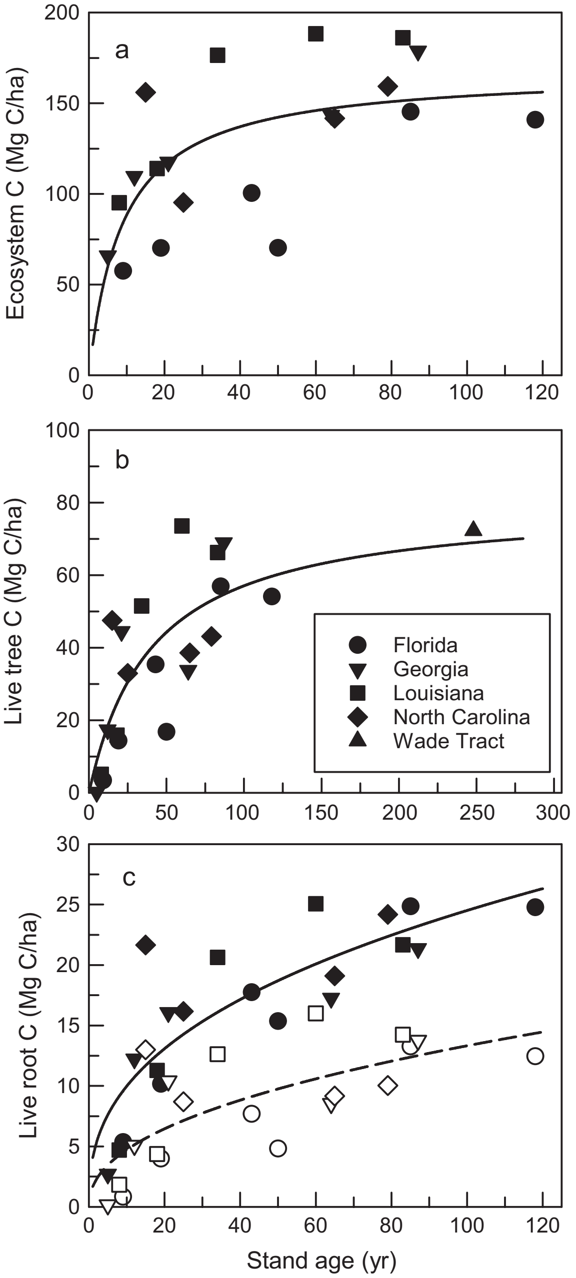

Fig. 3. (a) Ecosystem C (sum of all pools including soil C), (b) live tree C (aboveground C of trees ≥1 cm dbh and ≥2 m height), and (c) live root C vs. stand age in longleaf pine forests. In panel a, live tree C of the old-growth Wade Tract was not used in model fitting. In panel c, the solid line indicates total live root C (below-stump C of pines ≥3.5 cm dbh + ground-penetrating radar detection of lateral root C + fine root C), and the dashed line indicates below-stump C (pines ≥1.0 cm dbh and ≥2 m height).

TABLE 3. Regression models for longleaf pine forests.

Dependent variable	Model form	β_1	β_2	β_3	β_4	β_5	Model *P*	R^2
Ecosystem C (Mg C/ha)	S	167.779 (17.246)	8.944 (4.048)				<0.001	0.40
Ecosystem C (Mg C/ha)	L	−23.128 (29.851)	5.522 (1.305)	0.740 (0.211)	3.008 (0.777)	−0.023 (0.010)	<0.001	0.88
Live tree C (Mg C/ha)	S	80.284 (21.500)	40.616 (25.323)				<0.001	0.56
Below-stump C (Mg C/ha)	PWR	1.677 (0.857)	0.450 (0.125)				<0.001	0.50
Total live root C (Mg C/ha)	PWR	4.068 (1.156)	0.390 (0.070)				<0.001	0.69
Forest floor C (Mg C/ha)	CR	4.465 (0.376)	0.0778 (0.025)				<0.001	0.42
Tap root depth (m)	PWR	0.002 (0.002)	0.324 (0.080)	1.098 (0.164)	0.229 (0.062)		<0.001	0.76
Root:shoot								
Below-stump	PWR	1.326 (0.319)	−0.467 (0.085)				<0.001	0.55
Total live root	PWR	3.175 (0.862)	−0.517 (0.099)				<0.001	0.54

Notes: Standard errors are indicated in parentheses. Abbreviations are S, saturation function $y = \beta_1\mathrm{age}/(\beta_2 + \mathrm{age})$; L, linear function $y = \beta_1 + \beta_2\mathrm{site\ index} + \beta_3\mathrm{age} + \beta_4\mathrm{basal\ area} + \beta_5\mathrm{density}$; PWR, power function $y = \beta_1\mathrm{age}^{\beta 2}$; CR, Chapman Richards function $y = \beta_1(1{-}\exp^{\beta 2\mathrm{age}})$. The model for tap root depth was $y = \beta_1\mathrm{dbh}^{\beta 2}\mathrm{sand}^{\ \beta 3}\mathrm{age}^{\beta 4}$. Units are age, yr; site index, m; basal area, m^2/ha; density, number/ha; sand, %.

calculated with the grass-stage stand (5-yr-old stand) excluded from the average, because of its very high *R:S* and the lack of a grass stage in most other tree species. Mean *R:S* across all other stands based on the ratio of total live root mass to total live aboveground mass was 0.54 (standard deviation of 0.19) and, when based on the ratio of below-stump mass to aboveground mass of longleaf pine, was 0.26 (standard deviation of 0.04).

DISCUSSION

Status of the longleaf pine resource

Utilizing a chronosequence assumes that variation among stands is due only to age (Jenny 1941), but for longleaf pine ecosystems meeting this assumption was difficult to impossible, as longleaf forests are now restricted to about 3% of their historical distribution and dominated by second growth and plantation stands (Oswalt et al. 2012). However, replicating the chronosequence across the landscape as we did strengthens the inference space, if stands and sites are representative of the landscape (Kashian et al. 2013). Oswalt et al. (2012), in an assessment of the current status of longleaf pine forests sampled by the FIA program, reported that, as of 2010, 58% of the longleaf pine forest type consisted of stands ≤50 yr of age and only 7% of the longleaf acreage was older than 80 yr. Thirteen percent of natural stands were ≤25 yr of age, whereas 84% of planted stands were ≤25 yr of age (Oswalt et al. 2012). In the East Coastal Plain and Piedmont, longleaf pine forests exhibit a bimodal age class structure with peaks in the 61–70-yr age class and 0–10-yr age class. Thus, our selection of stands represented the current status of longleaf pine forests.

C density and ecosystem C

Mean live tree C of longleaf pine was 36 Mg C/ha and similar to the regional mean live tree C of 31 Mg C/ha estimated for the longleaf/slash pine (*Pinus elliottii* var. *elliottii*) forest type (Smith et al. 2013). However, regional mean C density for standing and downed dead wood, and forest floor pools in the longleaf/slash pine forest type estimated by Smith et al. (2013) were higher than observed in this study. Higher C density in detritus reported by Smith et al. (2013) could be a result of combining longleaf pine and slash pine into one forest type, variation in prescribed burning across the region, and the substantial

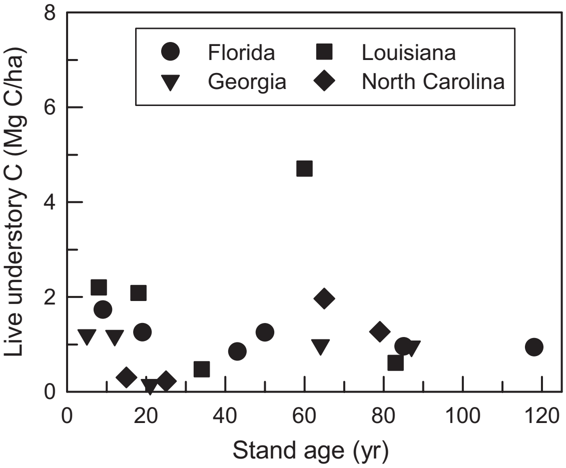

FIG. 4. Live understory C (aboveground C of woody plants ≥1 m and <2 m height + ground cover C) vs. stand age in longleaf pine forests.

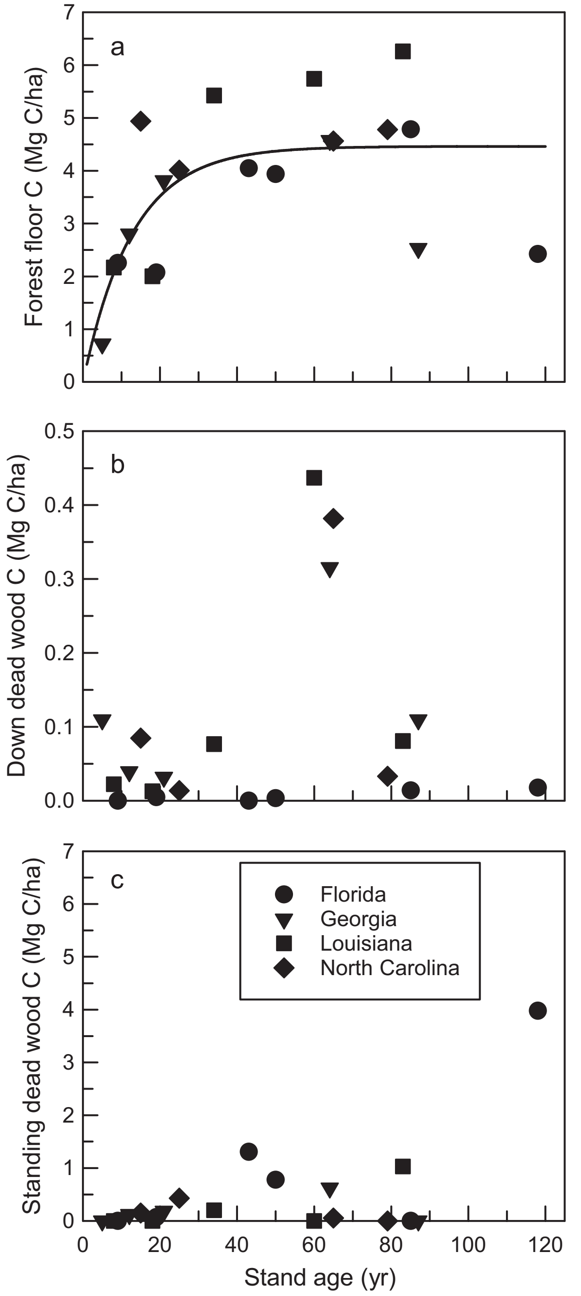

FIG. 5. (a) Forest floor C, (b) downed dead wood C, and (c) standing dead wood C vs. stand age in longleaf pine forests.

uncertainty associated with modeling dead wood C and forest floor C at large scales (Coulston et al. 2015). The absence of age-related changes in downed dead wood and standing dead wood, attributes suggested as characterizing old-growth longleaf pine forests (Mitchell et al. 2009), is likely explained by several factors including the lack of legacy wood from previous stands (McGarvey et al. 2015), the stochastic nature of the dead wood C stock (Woodall et al. 2015*b*), and the combustion of dead wood from prescribed burning.

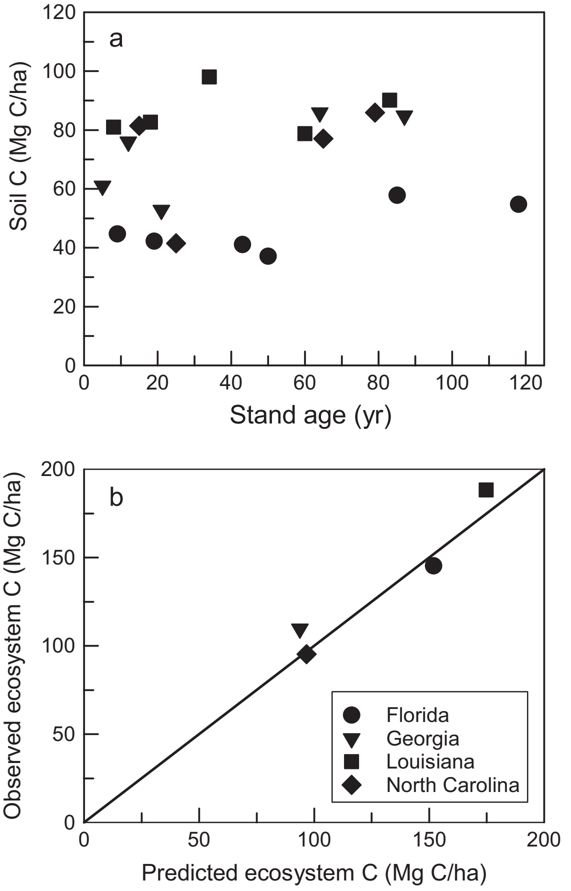

FIG. 6. (a) Soil C vs. stand age and (b) predicted vs. observed ecosystem C in longleaf pine forests. The line in panel b represents the 1:1 relationship.

Carbon in living biomass of temperate forests increases hyperbolically with age and older age classes (up to 200 yr) contain 2–10 times as much living biomass C as the youngest age class (Pregitzer and Euskirchen 2004). Increases in longleaf pine ecosystem C with age were driven by increases in live tree C, predominantly aboveground, rather than age-related changes in soil C. Similarly, the majority of ecosystem C accumulation in *Pinus contorta*-dominated forests over 270 yr was driven by accrual in live vegetation (Kashian et al. 2013), and C accumulation over 250 yr in a sub-boreal *Picea* forest was also driven by gains in aboveground large tree C (Bois et al. 2009). Ecosystem C accumulation over 300 yr in *Pinus resinosa* forests was also mainly in response to age-related increases in aboveground live tree C (Powers et al. 2012). In most forest types in the United States, aboveground biomass stabilizes or even increases in late succession (Lichstein et al. 2009). In longleaf pine, predicted live tree C at 100 yr was 57 Mg C/ha and 71% of the modeled maximum, indicating that longleaf pine stands may continue to accumulate C during as well as beyond the first century. A comparable 100 yr trajectory in live tree C of longleaf pine forests (50–63 Mg C/ha, assuming

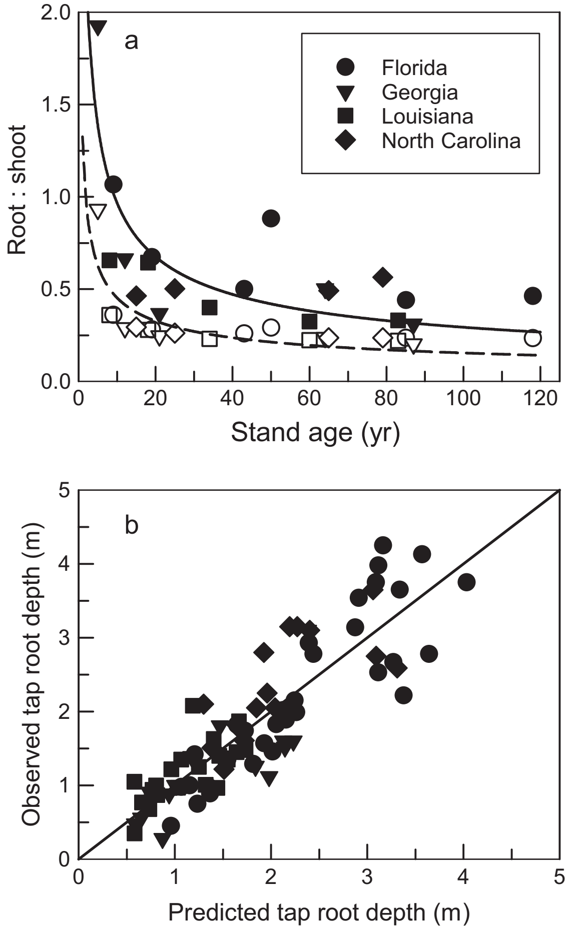

FIG. 7. (a) Relationship between the root-to-shoot ratio and stand age and (b) predicted vs. observed tap root depth in longleaf pine forests. In panel a, the solid line is the ratio of total live root mass (below-stump mass of pines ≥3.5 cm dbh + ground-penetrating radar detection of lateral root mass + fine root mass) to live aboveground mass (all trees + understory), and the dashed line is the ratio of live below-stump mass to aboveground mass of only longleaf pine (≥1.0 cm dbh and ≥2 m height). The line in panel b represents the 1:1 relationship.

a 2:1 biomass to C ratio) was estimated by Lichstein et al. (2009) using inventory data from the FIA database and general allometric equations (Jenkins et al. 2003). The Wade Tract is recognized as one of the few remaining remnant old-growth tracts of longleaf pine and provides an opportunity for comparison of modeled maximum C accumulation based on secondary growth and plantations to a forest structure that is the goal of current restoration efforts (Gilliam et al. 2006). The modeled and biometric estimations of live tree C for the Wade tract were surprisingly similar (69 vs. 72 Mg C/ha, respectively), given model extrapolation out from 118 yr of age. As observed for standing volume in other remnant old-growth pine ecosystems in the southern United States (Bragg 2002), the exceptional size of individuals at the Wade Tract did not translate into exceptionally high C density due to the openness of stands and spatial heterogeneity of stocking.

The quantity of soil C in managed pine forests in the southeastern United States is varied and dependent on soil mineralogy and land use history. Highly productive sites can retain large quantities of soil C as well as support stands with higher productivity, and soil C and consequently ecosystem C were related to SI in this study. *Pinus taeda* planted on former agricultural land in southwest Georgia contained 268 Mg C/ha in the upper 0.3 m of soil (Johnsen et al. 2013) and a *Pinus taeda* plantation in the coastal plain of South Carolina contained 171 Mg C/ha in the upper 0.6 m (Maier et al. 2012). Thus, soil C in the present study (32–98 Mg C/ha) was lower than values reported for highly productive sites. However, soil C was in the range reported for pine plantations on eroded soils where marginal farmland was converted to pine plantations (Garten 2002, Markewitz et al. 2002, Sartori et al. 2007, Butnor et al. 2012*b*). While prescribed burning periodically reduces the forest floor and C in surface soils, it has little effect on mineral soil C (Binkley et al. 1992, Lavoie et al. 2010). Soil C was unrelated to stand age in longleaf pine, which was expected, since the long-term rate of soil C accumulation is slow and changes in the terrestrial C sink are driven mainly by changes in vegetation biomass (Schlesinger 1990). Conversion from agricultural land to forest may lead to increased soil C, though the process is gradual and much of the accumulated C is in the near surface (Nave et al. 2013). In a meta-analysis of 39 studies in the United States, Nave et al. (2013) found that afforestation of agricultural land resulted in small reductions in soil C for the first 15 years followed by gradual increases in soil C compared to the nonafforested baseline over time.

Rooting depth and extent

Rooting depth is important to understanding plant productivity and biosphere–atmosphere interactions (Jackson et al. 1999). Reports of maximum rooting depth for mature pines in the southeastern United States include 5 m for longleaf pine, 3–5 m for *Pinus elliottii* var. *elliottii*, 3 m for *Pinus echinata*, 4 m for *Pinus clausa*, and 4–6 m for *Pinus taeda* (Stone and Kalisz 1991, Canadell et al. 1996). Gibson et al. (1986) reported maximum tap root depths of 2–3 m for 26-yr-old *Pinus taeda*, *Pinus echinata*, *Pinus elliottii* var. *elliottii*, and longleaf pine trees on the same dry site. Tap root depths of longleaf pine were therefore within the range of other pine species in the region. The deepest (4 m) rooting depth was observed in the 118-yr-old stand on the deep sandy soils of coastal Florida. Tap root depth was related to percent sand in soil, most likely because of the deep infiltration depths typical of coastal soils (Schenk and Jackson 2002). Tap root depths in the 5-yr-old grass-stage stand were variable (≤1 m), but the majority were deeper than depths reported for planted 6-yr-old *Pinus taeda* and 5-yr-old *Pinus echinata* (Harrington et al. 1989), presumably an outcome of preferential allocation of carbohydrates to root growth and storage in pines with a grass stage (Keely and Zedler 1998).

A power function rather than a saturation model best fit root C, which may be explained by sampling limitations (i.e., limiting the maximum pit size to 4 m^2) as well as the potential for continued lateral root extension in large, old, longleaf pine trees. The contribution of lateral coarse roots outside the excavation pits in longleaf pine forests was considerable. The percentage of land area covered by modeled below-stump C was at most 21% in the dense 21-yr-old stand and otherwise ranged from 3% to 15%. Coarse roots detected by GPR outside of the excavation pits accounted for 95% of the plot area in stands older than 30 years of age and 88% of the plot area in the younger stands. Extensive lateral root spread has been reported for longleaf pine. Heyward (1933) excavated a lateral root of a mature longleaf pine and traced its linear extension to 15 m from the tap root, with branching that increased its extension to 22 m. Hough et al. (1965) reported a lateral root spread of 17 m in mature longleaf pine. Linear lateral root spread was 8 m in longleaf pine trees 30–33 yr of age and 9 m in trees 115–125 yr of age (Hodgkins and Nichols 1977). In their review on the maximum extent of tree roots, Stone and Kalisz (1991) concluded that many tree species are capable of producing far-reaching lateral roots in the absence of restrictive soil. While excavation pits offer the advantage of direct quantification of roots concentrated around the stem, where the majority of coarse root biomass may be concentrated (Addo-Danso et al. 2016), pit excavations by themselves can underestimate root C in species with far-reaching lateral roots such as longleaf pine.

Root:shoot ratio

Root C increased with stand age whereas *R*:*S* decreased with stand age, as reported for a wide variety of forests (Mokany et al. 2006). Thus, root C carrying capacity appears to be lower than aboveground C carrying capacity. When based on only below-stump and aboveground mass of longleaf pine, average *R*:*S* across all stands (excluding the grass stage with high *R*:*S*) was 0.26 (standard deviation of 0.04) and comparable to the average 0.26 for gymnosperms (Cairns et al. 1997), 0.18 for temperate coniferous forests (Jackson et al. 1996), and 0.21 for the longleaf/slash pine forest type group (Smith et al. 2013). However, inclusion of all live root mass and live aboveground biomass increased mean *R*:*S* (excluding the grass-stage stand) to 0.54 (standard deviation of 0.19). There have been other reports of high *R*:*S* in conifers. For example, Litton et al. (2003) observed a range in *R*:*S* from 0.21 to 0.68 in 13-yr-old *Pinus contorta* var. *latifolia* forests varying in density. Mokany et al. (2006) reported a maximum *R*:*S* of 0.50 for temperate conifer forests/plantations with a similar range in shoot mass (50–150 Mg/ha).

Conventional wisdom assumes that longleaf pine allocates more biomass to roots than other southern pines, presumably as an adaptation to soil water limitation (Hodgkins and Nichols 1977). With the exception of the grass-stage stand, our data from pit excavations alone do not support this assumption. For example, *R*:*S* of other species based on pit excavations was 0.31–0.35 in a 6-yr-old *Pinus taeda* plantation (Samuelson et al. 2004), 0.20 for 22-yr-old *Pinus elliottii* var. *elliottii* trees (Howard 1973), and 0.26 for a 23-yr-old *Pinus taeda* plantation (Miller et al. 2006). Gonzalez-Benecke et al. (2016) reported an asymptotic minimum of 0.23 (below-stump to woody shoot ratio) for *Pinus taeda* trees ranging in age from 2 to 27 years. However, Van Lear and Kapeluck (1995) excavated the entire coarse root systems of three 48-yr-old *Pinus taeda* trees and determined a mean *R*:*S* of 0.25. In longleaf pine stands with trees of similar dbh to those studied by Van Lear and Kapeluck (1995; stands greater than 50 years of age), mean *R*:*S* based on all live roots was 0.43 (standard deviation of 0.10), thus suggesting greater allocation to coarse roots in longleaf pine than in *Pinus taeda*, but considerable variation existed among stands. Lacking species comparisons on the same sites among stands of similar forest structure, it remains unclear if high *R*:*S* values were a result of more intensive sampling, the more open nature of longleaf pine stands that may facilitate greater lateral root spread (Hodgkins and Nichols 1977), or proportionally greater allocation to far-reaching lateral roots in longleaf pine relative to other southern pines. In any case, this work supports the hypothesis of Robinson (2007) of a larger-than-suspected root C pool that may be ecosystem, and perhaps site, specific.

Conclusions

Restoration of longleaf pine forests could assist in reducing the effects of increasing forest disturbance (Overpeck et al. 1990, Seidl et al. 2011) on C storage and sequestration, because of resistance of longleaf pine forests to damage from insects, disease, hurricanes, and wildfire, when burned regularly (Johnsen et al. 2009, Mitchell et al. 2014). Longer rotations and less C removal from intermediate harvests, typical of longleaf pine management, would also increase forest C storage potential (Cropper and Ewel 1987, Ryan et al. 2010). In longleaf pine forests managed for long rotations with frequent prescribed fire, ecosystem C is dominated by age-related biomass accumulation in overstory trees and variation in soil C related to site index. The understory plant community, while important for compositional and functional diversity (Mitchell et al. 2006), represents a small fraction of ecosystem C, and along with the forest floor and dead wood pools, is moderated and reduced by frequent prescribed fire. Live tree C, however, continues accumulating into the second century, with belowground accumulation of root C, owing to high biomass in lateral coarse roots, apparently playing a larger role than in many other forest types.

Forest management cannot simultaneously optimize for biomass standing crop, C storage rate, habitat quality, and timber revenue. As an example, thinning and prescribed burning to improve habitat for Red-cockaded

Woodpecker (*Picoides borealis*) in longleaf pine forests may reduce ecosystem C; therefore, co-benefits from a variety of ecosystem services should be evaluated (Martin et al. 2015). In an application of the climate action reserve (CAR) forest project protocol to a hypothetical longleaf pine forest under restoration management, Remucal et al. (2013) recommended higher density stands and reduced harvesting to generate net emissions reductions credit under the CAR protocol, but recognized the potential conflict of managing for both climate benefits and ecological restoration. Although other managed southern pine systems sequester more C over the short term (Johnsen et al. 2014, Gonzalez-Benecke et al. 2015*a*), we suggest that longleaf forests can play a meaningful role in regional forest C management. Although it might appear that a management scheme based on long rotations would never be chosen over plantation management, careful evaluation of long-term longleaf pine C storage patterns contradicts this idea. Over time, more rapid C accumulation associated with intensively managed southern pine forests can be balanced by the sustainable, disturbance-resistant C storage potential of longleaf pine forests. We conclude, therefore, that a portfolio of diverse longleaf pine forest types and stand management regimes can contribute to societal climate mitigation objectives, in addition to the myriad of other benefits derived from these forests.

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Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.1439/full

Data Availability

Data associated with this paper have been deposited in the Dryad digital repository: http://dx.doi.org/10.5061/dryad.760b3