NRC Research Press

ARTICLE

Ecosystem carbon stocks in *Pinus palustris* forests

Lisa J. Samuelson, Tom A. Stokes, John R. Butnor, Kurt H. Johnsen, Carlos A. Gonzalez-Benecke, Pete Anderson, Jason Jackson, Lorenzo Ferrari, Tim A. Martin, and Wendell P. Cropper, Jr.

Abstract: Longleaf pine (*Pinus palustris* Mill.) restoration in the southeastern United States offers opportunities for carbon (C) sequestration. Ecosystem C stocks are not well understood in longleaf pine forests, which are typically of low density and maintained by prescribed fire. The objectives of this research were to develop allometric equations for above- and below-ground biomass and quantify ecosystem C stocks in five longleaf pine forests ranging in age from 5 to 87 years and in basal area from 0.4 to 22.6 $m^2 \cdot ha^{-1}$. Live aboveground C (woody plant + ground cover) and live root C (longleaf pine below stump + plot level coarse roots + plot level fine roots) ranged from 1.4 and 2.9 Mg $C \cdot ha^{-1}$, respectively, in the 5-year-old stand to 78.4 and 19.2 Mg $C \cdot ha^{-1}$, respectively, in the 87-year-old stand. Total ecosystem C (live plant + dead organic matter + mineral soil) values were 71.6, 110.1, 124.6, 141.4, and 185.4 Mg $C \cdot ha^{-1}$ in the 5-, 12-, 21-, 64-, and 87-year-old stands, respectively, and dominated by tree C and soil C. In the 5-year-old stand, ground cover C and residual taproot C were significant C stocks. This unique, in-depth assessment of above- and below-ground C across a series of longleaf pine stands will improve estimates of C in longleaf pine ecosystems and contribute to development of general biomass models that account for variation in climate, site, and management history in an important but understudied ecosystem.

Key words: longleaf pine, carbon sequestration, allometry, roots, ground-penetrating radar.

Résumé : La restauration du pin des marais (*Pinus palustris* Mill.) dans le sud-est des États-Unis offre une opportunité de stocker du carbone (C). Les stocks de C de l'écosystème ne sont pas bien connus dans les forêts de pin des marais qui ont typiquement une faible densité et se maintiennent grâce au brûlage dirigée. Les objectifs de ces travaux de recherche consistaient à élaborer des équations allométriques pour la biomasse aérienne et souterraine et à quantifier les stocks de C de l'écosystème dans cinq forêts de pin des marais dont l'âge allait de 5 à 87 ans et dont la surface terrière variait de 0,4 à 22,6 $m^2 \cdot ha^{-1}$. Le C aérien vert (plantes ligneuses + couverture végétale) et le C des racines vivantes (souches de pin des marais + grosses racines et racines fines présentes dans les placettes) variaient respectivement de 1,4 et 2,9 Mg $C \cdot ha^{-1}$ dans le peuplement âgé de 5 ans à 78,4 et 19,2 Mg $C \cdot ha^{-1}$ dans le peuplement âgé de 87 ans. Le C total de l'écosystème (plantes vivantes + matière organique morte + sol minéral) atteignait respectivement 71,6, 110,1, 124,6, 141,4 et 185,4 Mg $C \cdot ha^{-1}$ dans les peuplements âgés de 5, 12, 21, 64 et 87 ans et était dominé par le C des arbres et du sol. Dans le peuplement âgé de 5 ans, le C contenu dans la couverture végétale et les racines pivotantes résiduelles constituait un stock important de C. Cette évaluation unique et approfondie du C aérien et souterrain dans une série de peuplements de pin des marais améliorera les estimations du C dans les écosystèmes dominés par cette essence et contribuera au développement de modèles généraux de biomasse qui tiennent compte de la variation dans le climat, la station et l'historique d'aménagement dans un écosystème important mais peu étudié. [Traduit par la Rédaction]

Mots-clés : pin des marais, séquestration du carbone, allométrie, racines, géoradar.

Introduction

Forests serve as a means for mitigating climate change by acting as sinks for atmospheric CO_2 and storing carbon (C) in plant biomass, detritus, and forest soils. In the southeastern United States (US), forests contain 36% of the contiguous United States' sequestered C (Turner et al. 1995) and have the potential for greater sequestration with improved forest C management. Carbon accumulation in forest ecosystems is influenced by interactions among forest structure and development, site quality, and species composition, and thus there is a need for C assessment in a wide variety of ecosystems under different management scenarios (Birdsey et al. 2006). The weakest link in most tree growth models and subsequently C models is the estimation of tree biomass, which is the main input for estimation of C stocks (Vashum and Jayakumar 2012). Most assessments of forest carbon stocks rely on standard inventory data and general aboveground biomass equations from the published literature. Belowground biomass can be included and is most often calculated using generalized component ratio equations (Jenkins et al. 2004). These approaches are used because species- and site-specific allometric functions are usually not available, and though useful for making landscape-level estimates, general functions do not provide the accuracy needed to explicitly manage forests for C sequestration.

Longleaf pine (*Pinus palustris* Mill.) forests were once an important forest ecosystem in the southeastern US, and there is increased interest in the restoration of longleaf pine forests for not only traditional forest products, but also to provide a variety of ecosystem services and, more recently, as a species resistant to disturbances associated with climate change (Johnsen et al. 2009).

Received 29 October 2013. Accepted 24 January 2014.

L.J. Samuelson, T.A. Stokes, and L. Ferrari. School of Forestry and Wildlife Sciences, Auburn University, 3301 SFWS Building, Auburn, AL 36849, USA.
J.R. Butnor, K.H. Johnsen, P. Anderson, and J. Jackson. USDA Forest Service, Southern Research Station, 3041 Cornwallis Road, Research Triangle Park, NC 28809, USA.
C.A. Gonzalez-Benecke, T.A. Martin, and W.P. Cropper, Jr. School of Forest Resources and Conservation, University of Florida, P.O. Box 110410, Gainesville, FL 32611, USA.
Corresponding author: Lisa J. Samuelson (e-mail: samuelj@auburn.edu).

Can. J. For. Res. **44**: 476–486 (2014) dx.doi.org/10.1139/cjfr-2013-0446

Longleaf pine has been suggested as a species that can contribute to climate change mitigation because of long rotations and long-term C storage combined with greater resistance to insects, diseases, and wind damage, less energy inputs relative to the more intensively managed southern pines, and tolerance of drought (Johnsen et al. 2009). Longleaf pine has generally been considered a slower growing southern pine, but its longevity (up to 400 years) offers opportunities to sequester C, particularly in C offset projects with longer (100 year) contracts.

Longleaf pine plantations and naturally regenerated ("natural" pine sensu Smith et al. 2009) stands typically have lower tree densities than that of other southern pines with understory competition and ground cover diversity controlled by prescribed fire. Thus, assessments of C storage using allometic equations developed for other southern pines or for pine species in general may be inappropriate. For example, Remucal et al. (2013) applied a hypothetical offset project on a longleaf pine site in Georgia. The accounting approach used standardized biomass equations and look-up tables (Smith et al. 2006; Woodall et al. 2011). When compared with site-specific longleaf pine equations, the standardized equations underestimated aboveground C by 36% and significantly underestimated emissions reductions, making the project economically nonviable. The hypothetical project highlighted conflicts between ecological restoration and climate benefits from low-density semimature stands, typical of longleaf pine forests, and the need for better assessment of C stocks for effective C management in longleaf pine ecosystems.

The overall goal of this research was to improve our understanding of ecosystem C stocks in longleaf pine forests. Ecosystem C was defined as the summation of C in plants, detritus, and soil. Specific objectives were to (*i*) develop allometric equations for above- and below-ground biomass of longleaf pine trees and (*ii*) quantify C stocks in trees, ground cover vegetation, detritus, and soil in five longleaf pine stands ranging in age from 5 to 87 years. Belowground C was measured using a unique combination of below-stump excavations, soil cores, and ground-penetrating radar (GPR).

Methods and materials

Study area

The study was conducted at the Fort Benning military installation (32.38°N, 84.88°W), which occupies portions of Chattahoochee and Muscogee counties in Georgia and Russell County in Alabama. The installation covers 73 533 ha. Prior to becoming a military installation in 1918, land use was mainly farming and grazing with some remnant forest. Currently, 61 538 ha are forested, with approximately 9300 ha in managed pure longleaf pine and 9300 ha in managed mixed pine comprised of at least 25% longleaf pine. The terrain at Fort Benning ranges from predominately rolling to areas with flat ridges and gentle slopes, and elevations range from 58 to 225 m. The climate in the area is humid and mild. The 30-year (1982–2011) mean annual precipitation measured in Columbus, Georgia, is 1180 mm, and the 30-year mean annual temperature is 18.7 °C, with an average January temperature of 8.5 °C and an average July temperature of 28.1 °C (http://www7.ncdc.noaa.gov/).

Because the primary objective of the sampling was to obtain data from a wide range of tree sizes and not to develop relationships strictly with stand age, we chose to sample a larger number of ages rather than sampling in replicated stands from a smaller number of ages. Five longleaf pine stands on Fort Benning were selected and were 5, 12, 21, 64, and 87 years of age (Table 1). All stands were located in Georgia with the exception of the 64-year-old stand, which was located in Alabama. Stands were selected based on age and stand structure, similarities in soils, and the degree of access permitted by the military.

The 12-, 21-, and 87-year-old stands were located in the Southeastern Mixed Forest Province Southern Appalachian Piedmont Section Ecoregion characterized by deep, infertile, clayey soils that are highly eroded (Bailey 1995). The 5- and 64-year-old stands were located in the Southeastern Mixed Forest Province Coastal Plains Middle Section Ecoregion characterized by marine-deposited sediments ranging from sands and silt to chalk and clays. The soil series was a Nankin sandy clay loam (greater than 45% sand, less than 28% silt, and 20%–35% clay) for the 5- and 12-year-old stands, a Troup sandy loam (greater than 52% sand, 7%–20% clay, and the silt plus twice the clay fraction totals more than 30%) for the 21- and 87-year-old stands, and Troup Springhill Luverne sandy loam complex for the 64-year-old stand (Soil Survey Staff 1999).

The three youngest stands were planted, and the two oldest stands were naturally regenerated and had few other species at the time of sampling. The two youngest stands were planted with containerized seedlings and the 21-year-old stand was planted with bare root seedlings. No older planted stands were available for study. The 5- and 12-year-old stands were planted at a density of 1494 trees·ha^{-1} and the 21-year-old stand was planted at a density of 2235 trees·ha^{-1}. All planted longleaf pine in the 5-year-old stand was out of the grass stage. Prior to initiation of burn records in 1981, frequent fires were common as a result of live fire during military training. All stands were last burned in 2010 (Table 1). The only stand with a record of a thinning was the 64-year-old stand in which a thinning was conducted in 2004 or 2005, with no other details available. There was no record of thinning in the 87-year-old stand.

In February 2012, a 1 ha circular main plot (56.4 m radius) with four 0.04 ha circular subplots (11.3 m radius) was installed in each stand following the protocol of Law et al. (2008). In each stand, one subplot was positioned at the center of the main plot and three subplots were positioned 35 m from the center of the main plot at 0°, 120°, and 240° from north.

Forest inventories

Forest inventories were conducted in the four subplots in each stand in February 2012. Species, diameter at breast height (DBH) (groundline diameter (GLD) in the 5-year-old stand) to the nearest 0.1 cm, and total height to the nearest 0.1 m were recorded. In the 5- and 12-year-old stands, tree height was measured using a telescoping height pole. In the older stands, tree heights were measured using a laser hypsometer (TruPulse 200, Laser Technology, Inc., Centennial, Colorado). All dead stems (snags) were measured provided that the angle of the stem from true vertical was <45°.

In all stands, DBH, height of live trees and snags with DBH ≥ 10 cm, and GLD of all stumps were measured within the entire circular subplots (four per stand). DBH and height of all live trees and snags with DBH < 10 cm and height ≥2 m were measured within a 5 m radius of subplot center. In addition, to account for all planted trees in the three plantations, DBH or GLD (5-year-old stand) and height of all planted trees in the subplot were measured.

Understory was defined as all woody species ≥1 and <2 m in height. GLD and height of all understory woody plants were measured within five 1 m^2 circular sampling rings in each subplot located using the stratified random polar coordinates method described by Gaiser (1951).

Longleaf pine C stocks

Longleaf pine trees representing the range in DBH and height distribution in each stand were selected for felling (Table 1). Groundline diameter was used to select trees in the 5-year-old stand. In June 2012, 10 longleaf pine trees per stand were felled in the 5-, 12-, and 21-year-old stands and three longleaf pine trees per stand were felled in the 64- and 87-year-old stands, for a total of 36 trees. All trees were cut at ground level. Entire trees were sampled in the 5- and 12-year-old stands. Given the large range in

Table 1. Stand characteristics and range in diameter, height, and taproot depth of longleaf pine (*Pinus palustris*) trees selected for whole-tree harvests.

Stand age (years)	Planting density (trees·ha^{-1})	Burn history	Sample size	DBH (cm)	Height (m)	Taproot depth (m)
5	1494	2007, 2010	10	3.8–7.2	0.6–3.4	0.2–1.4
12	1494	2002, 2005, 2008, 2010	10	2.9–16.8	6.0–10.4	0.5–1.0
21	2235	1992, 1995, 1998, 2001, 2004*, 2005, 2006*, 2009, 2010*	10	3.2–16.2	4.5–14.4	0.9–1.8
64	Natural	1991, 1994*, 1999, 2002, 2003, 2008, 2010	3	22.8–36.9	16.1–23.5	1.1–1.5
87	Natural	1981, 1985*, 1990, 1992, 1994, 1998, 2001, 2004, 2006, 2008, 2010	3	34.3–48.6	27.3–29.9	1.6–3.1

Note: Groundline diameter (cm) was used for the 5-year-old stand. Burn records began in 1981, an asterisk (*) indicates wildfire. DBH, diameter at breast height.

tree size in the 21-year-old stand, the six smallest trees were sampled and the four larger trees were subsampled. In the 64- and 87-year-old stands, all trees were subsampled, with the exception of the largest tree in the 87-year-old stand for which all biomass was sampled due to difficulties in determining branch location after felling, which caused substantial breakage.

Biomass was separated into foliage, branches, and main stem and oven-dried at 70 °C until reaching a constant mass. To determine the dry mass of branches and foliage in subsampled trees, every branch from every whorl was cut adjacent to the stem and branch diameter was measured at the cut end in two directions using digital calipers. Green masses of entire branches were measured in the field using a digital scale (Intercomp CS200 Digital Hanging Scale, Intercomp Co, Inc., Medina, Minnesota). One branch was randomly selected from each whorl, separated into foliage and wood mass, and oven-dried. In 64- and 87-year-old trees, green masses of all branches were measured, but due to the large size of branches, dry mass was determined only on two branches randomly selected from each third of the canopy (six branches per tree). Stand-specific relationships between branch green mass, branch diameter, and oven-dried mass of foliage and woody tissues were developed by pooling all sample branches per stand. These relationships were then used to predict individual-tree foliage and branch dry mass from branch green mass.

In subsampled trees, the main stem was cut into 1.3 m sections, and the green mass of each section was measured in the field. A disc that included wood and bark was cut from the base of every other section and the green and dry masses were measured. Data were pooled by stand, and stem dry mass was predicted from green mass using relationships between green mass and the oven-dried mass of discs.

In July 2012, five of the 10 longleaf pine trees harvested from each of the 5-, 12-, and 21-year-old stands were randomly selected for below-stump excavations. Below-stump biomass was sampled in all three trees from the two older stands (six in total). The square area of the excavation pit ranged from the minimum set at 1 m^2 for the smallest tree to a set maximum of 4 m^2 for the largest tree. Pit size was limited to a maximum of 4 m^2 due to the time-demanding nature of manual root excavations in large tree pits. 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 calculated from the linear relationship between tree basal area and pit size developed using the minimum and maximum set pit size and the corresponding tree basal area. The goal of the calculation was to come up with a method to objectively vary pit size (and therefore effort) for different-sized trees and to keep pit size within the realm of field reality (e.g., no 10 cm diameter pits and no extremely large pits). Pits sizes ranged from 1.0 to 1.2 m^2 in the 5-year-old stand, 1.0 to 1.3 m^2 in the 12-year-old stand, 1.0 to 1.3 m^2 in the 21-year-old stand, 2.0 to 2.7 m^2 in the 64-year-old stand, and 2.6 to 4.0 m^2 in the 87-year-old stand.

All coarse roots ≥5 mm were manually extracted from the pit to a 1 m depth, and all lateral roots branching off the main taproot were cut at the pit wall. Soil to a 1 m depth was sieved using a 0.63 cm hardware cloth, and all roots ≥5 mm in diameter were collected. The pit was then excavated around the entire taproot, and the taproot was removed using a mini-excavator if needed. The length of all taproots was measured.

Table 2. Carbon concentrations (%) of plants in the ground cover layer (<1 m in height) by growth form and C concentrations in longleaf pine (*Pinus palustris*) tissues, litter, and duff in longleaf pine stands.

	Stand age (years)				
Component	5	12	21	64	87
Forbs	49.9±1.3	47.8±0.6	44.9±1.1	47.1±2.9	48.0±1.9
Graminoids	46.7±1.4	46.5±1.9	48.2±0.4	48.5±0.8	49.2±2.1
Legumes	47.2±1.1	45.7±4.0	48.2±2.1	51.5±1.6	47.1±2.3
Vines	50.0±0.6	49.1±1.0	49.9±1.3	48.1±1.0	49.8±0.7
LLP stem	51.6±0.4	51.6±0.1	51.0±0.4	51.2±0.2	53.9±0.5
LLP foliage	51.5±0.2	51.4±0.2	50.8±0.2	52.2±0.2	53.8±0.2
LLP coarse root	50.6±0.6	51.3±1.8	49.6±1.1	50.5±1.3	52.1±1.2
LLP fine root	40.3±4.1	44.7±1.0	43.4±1.3	43.4±2.7	37.5±1.9
Litter	48.3±0.5	50.5±1.1	50.6±0.2	51.2±0.5	51.4±0.3
Duff	43.9±1.9	41.3±7.0	49.0±2.9	21.7±7.5	54.8±1.3

Note: Values are means ± standard errors (SEs). For the ground cover, litter, and duff layers, SEs represent variation among subplots within a stand. For longleaf pine tissues, SEs represent variation among trees within a stand. LLP, longleaf pine.

Carbon concentrations were measured in two stem samples per harvested tree, one at DBH and the other at the base of the live crown, and in two composite samples of foliage per sample tree and averaged by stand (Table 2). In two stumps per stand, C concentration was measured in one random sample from the taproot, one from a large (50–100 mm) lateral root, and one from a small (10–50 mm) lateral root (Table 2). The mean of the small and large root sample was applied to all coarse roots (≥2 mm) extracted from the pits or detected by GPR. Carbon concentration was measured on a composite sample of fine roots (<2 mm) collected from each subplot, and each stand had a total of four samples. Branch C concentration was assumed to be the same as stem C concentration. All tissue samples were analyzed for total C using a using an NC soil analyzer (Flash EA 1112 series, Thermo Finnigan, Milan, Italy).

Other species C stocks

Across all stands, a total of eight species other than longleaf pine were recorded in the overstory. Allometric equations from the literature were used to predict aboveground biomass from DBH and included general oak and pine equations from Jenkins et al. (2004), a loblolly pine (*Pinus taeda* L.) equation from Naidu et al. (1998), and southern red oak (*Quercus falcata* Michx.), blackgum (*Nyssa sylvatica* Marsh.), and sweetgum (*Liquidambar styraciflua* L.) equations from Phillips (1981). Carbon concentrations in all tissues of species other than longleaf pine were assumed to be 50% (Woodbury 2007). Taproot mass of other pine species was predicted using the allometric equation that we developed for taproot biomass of longleaf pine because site characteristics such as depth to the clay layer may have more influence on taproot development than species. For example, Gibson et al. (1985) found no differences in below-stump biomass among longleaf pine, loblolly pine, and slash pine growing on the same site. We assumed that that GPR measurement of coarse roots captured all hardwood coarse root mass.

Understory and ground cover C stocks

For understory woody stems (between 1 and 2 m in height), allometric equations derived from the 5-year-old stand were used to predict aboveground biomass for longleaf pine between 1 and 2 m in height. If available, species-specific allometric relationships from Robertson and Ostertag (2009) were used to predict aboveground biomass of understory woody stems, otherwise a general equation was used (Robertson and Ostertag 2009).

Ground cover vegetation was defined as trees and shrubs <1 m in height, including longleaf grass stage seedlings (seven seedlings in the 64-year-old stand and two seedlings in the 87-year-old stand were found) and all herbaceous species. Within each 1 m^2 sample ring, all vascular plants were clipped at the root collar and bagged by category (shrubs and tree seedlings, vines, graminoids, legumes, forbs, and ferns) and placed in an oven at 70° for 72 h and weighed. Only plants rooted inside the sample ring were included. Carbon concentrations were measured in the nonwoody ground cover by category (vines, grass, legume, forbs) (Table 2). Two composite samples of each category were collected from each subplot and pooled by subplot. As ferns were found on only one subplot in the 64-year-old stand, the C concentration for ferns was assumed to be 50%.

Plot-level root C stocks

GPR was used to augment the below-stump root mass estimates by accounting for lateral root biomass between trees and outside the excavated pit area. At the center of each subplot, a square 100 m^2 GPR measurement plot was prepared by mowing and raking away all grass, woody brush, and accumulated litter. A series of 21 parallel transect lines 10 m long and 0.5 m apart were established on each subplot and scanned with a SIR-3000 radar unit (Geophysical Survey Systems Inc. (GSSI), Salem, New Hampshire) equipped with either a 900 or 1500 MHz antenna. Postcollection data processing was used to remove signal noise and determine the location and relative size of roots using RADAN 7 software (GSSI, Salem, New Hampshire). Image analysis was applied to summarize processed data and quantify root biomass at 65 locations along each transect (1365 total per subplot) using an approach described by Butnor et al. (2012*a*) with SigmaScan Pro Image Analysis software (Systat Software, Point Richmond, California). The relationship between GPR data and actual root mass was assessed at each stand using twenty-five 15 cm diameter validation root–soil cores, which were scanned with GPR prior to collection and then dry-sieved, washed, and oven-dried at 65 °C to a constant mass (Butnor et al. 2012*a*). In addition to GPR calibration, the subplot cores were used to determine fine root mass. Roots were hand-separated into categories of pine or non-pine, live or dead, and diameter class (<2 mm, 2–10 mm, >10 mm). Dead roots varied from being undetectable to marginally detectable, so GPR data were scaled using live root mass. To integrate GPR data with longleaf pine below-stump estimates derived from inventory data, it was assumed that GPR cannot detect fine roots (<2 mm diameter), taproots, or most decaying roots, and GPR has accounted for all lateral roots regardless of species (Butnor et al. 2012*a*). Because of the predominance of large overlapping roots in the excavation pits and potential underestimation by GPR of lateral roots in the pits, coarse root GPR C (taproot not included) was calculated using two different assumptions: (1) GPR captured all lateral root mass in the excavation pit area (coarse root GPR = GPR − predicted longleaf pine lateral roots in pits) or (2) GPR captured no lateral roots in the pits (coarse root GPR = GPR + predicted longleaf pine lateral roots in pits). The average of the two approaches was used in estimating ecosystem C.

Detritus C stocks

A total of 66, 14, 2, 12, and 14 stumps were tallied in the 5-, 12-, 21-, 64-, and 87-year-old stands, respectively. In the 5-year-old stand, the 66 stumps had an average top diameter of 31.7 cm. For these stumps, we assumed that the trees were cut in the year preceding planting. Initial taproot biomass was predicted from the groundline diameter relationship in Table 4, and residual taproot C after 5 years of decay was predicted using an exponential decay model and baseline decay rate of 0.15 (±25%) (Ludovici et al. 2002). The average C concentration measured for live taproots was used. The C in residual stumps in the other stands was not estimated or included in ecosystem C because time since cutting was unknown. Residual taproot C likely contributed additional dead organic matter C in the older stands, but the degree to which it contributed would depend on knowledge of decay duration, taproot size, resin content, and burning frequency.

A modified approach of the planar intersect technique described by Harmon and Sexton (1996) was used for sampling coarse woody debris (≥7.6 cm diameter, CWD) and fine woody debris (≥2.5 cm and <7.6 cm diameter, FWD). In May 2012, CWD was measured along four 56.4 m transects positioned 45°, 135°, 225°, and 315° from north in each subplot. The slope of each transect was recorded. Along the entire transect, CWD intersecting the transect plane to a height of 2 m was recorded. FWD was sampled along a subsection of each transect from 15 m to 37.6 m from plot center (22.6 m total). For each CWD intersection along the transect line, true diameter at the line intercept and one of five decay classes (Waddell 2002) were recorded. For FWD, the number of intersections was recorded.

The volume of logs per unit ground area for CWD from the line intercepts was calculated following Warren and Olsen (1964) and Van Wagner (1968). We assumed that all CWD was from longleaf pine trees. The volume of decaying CWD was converted to mass from the density of wood (0.5413 $g \cdot cm^{-3}$) reported for longleaf pine by Woodall and Monleon (2010) and applying a decay-class reduction factor (Waddell 2002). The volume of FWD per unit area from the line intercepts was calculated following Harmon and Sexton (1996) and the mass of FWD was calculated and corrected for slope following Parresol et al. (2006). Forest floor samples were collected from four 50 cm diameter PVC rings placed 2 m from subplot center at 0°, 90°, 180°, and 270° from north in each subplot in May 2012. All woody detritus ≥2.5 cm in diameter was discarded. Forest floor components were separated into: (1) duff, which consisted of the fermentation and humus layers combined and included the dark, partly decomposed organic material (unrecognizable plant forms) above the mineral soil, (2) litter on top of the duff and included recognizable plant parts such as leaves, flowers, and twigs <0.6 cm in diameter, (3) very fine woody debris ≥0.6 cm and <2.5 cm in diameter, and (4) cones. Samples were pooled by subplot and component and oven-dried. Very fine woody debris was added to the FWD category.

Carbon concentrations were measured in litter and duff samples. Duff C concentration was ash-corrected to remove the influence of any soil C in the sample. Because of low CWD and FWD in all stands and lack of range in decay classes, C concentration of CWD and FWD was assumed to be 50% (Prichard et al. 2000; Harmon et al. 2008).

Soil C

A 1.9 cm diameter push tube was used to collect samples at 2 m, 5 m, and 11 m from subplot center at 0°, 90°, 180°, and 270° from north (12 locations total per subplot) at 0.0–0.1 and 0.1–0.2 m depths (24 samples). A 10 cm diameter bucket auger was used to collect samples at 0.2–0.5 m and 0.5–1.0 m depths from two of the soil sampling locations (four samples). Within each subplot, the subsamples were combined by depth. Soil was air-dried for several weeks and passed through a 2 mm sieve to separate roots and rocks. Total soil C concentration was determined by dry combustion

Table 3. Structure of longleaf pine (*Pinus palustris*) stands.

Stand age (years)	Size class	Species	Basal area ($m^2 \cdot ha^{-1}$)	Density ($trees \cdot ha^{-1}$)	DBH (cm)	Height (m)
5	DBH ≥ 10 cm*	LLP	0.0	0.0	—	—
		Other	0.0	0.0	—	—
	DBH < 10 cm	LLP	0.4	150	3.7	2.4
		Other	0.04	64	2.6	2.7
	Understory†	LLP	—	625	—	<2
		Other	—	1000	—	<2
12	DBH ≥ 10 cm	LLP	3.4	300	12.3	9.1
		Other	4.4	219	15.6	10.5
	DBH < 10 cm	LLP	2.7	619	7.2	6.2
		Other	0.6	159	6.8	5.7
	Understory	LLP	—	0.0	—	<2
		Other	—	2500	—	<2
21	DBH ≥ 10 cm	LLP	18.6	1331	13.2	11.8
		Other	0.8	75	11.9	9.4
	DBH < 10 cm	LLP	2.3	481	7.6	8.7
		Other	0.6	95	9.3	8.0
	Understory	LLP	—	0.0	—	<2
		Other	—	500	—	<2
64	DBH ≥ 10 cm	LLP	7.5	94	30.2	19.1
		Other	2.4	37	26.7	16.8
	DBH < 10 cm	LLP	0.3	159	4.8	3.3
		Other	0.05	127	2.2	2.3
	Understory	LLP	—	0.0	—	<2
		Other	—	2000	—	<2
87	DBH ≥ 10 cm	LLP	13.4	87	43.7	29.0
		Other	0.0	0.0	—	—
	DBH < 10 cm	LLP	1.1	764	4.1	3.8
		Other	0.0	0.0	—	—
	Understory	LLP	—	500	—	<2
		Other	—	1500	—	<2

Note: Values are means of four subplots per stand. The two oldest stands were naturally regenerated and the others were planted. DBH, diameter at breast height; LLP, longleaf pine.

*The <10 cm DBH class included only stems ≥1 cm DBH and ≥2 m in height.

†Understory is all woody plants from ≥1 to <2 m in height. The 5-year-old stand understory also includes all planted longleaf <2 m in height.

with detection by thermal conductivity (Flash EA 1112 series CN analyzer, Thermo Finnigan Instruments, Milan, Italy). Soil bulk density was measured at the same depths at one of the soil sampling locations in a subplot, randomly selected, using a 5.7 cm diameter core (0200 Soil Core Sampler, Soil Moisture Equipment Corp., Goleta, California). Soil was oven-dried at 105 °C for 96 h and then passed through a no. 10 sieve, and roots and rocks were extracted and weighed separately. The effect of root volume on bulk density was negligible. Rock volume was determined by water displacement. Soil bulk density was then calculated by soil mass (minus rock and root mass) / soil volume (minus rock volume) (Law et al. 2008). Total percent C concentration was converted to content and scaled to $Mg \cdot ha^{-1}$ using stand-level soil bulk density means by depth.

Statistical analyses

Because the majority of longleaf pine in the 5-year-old stand had not reached DBH and only GLD was measured, allometric regressions were developed for the 5-year-old stand separately. The 5-year-old trees were in the process of bolting from the grass stage and had little if any branching. Branch biomass was therefore not predicted for the 5-year-old trees and any branch biomass was pooled into stem biomass. Data from all other stands were combined to develop regressions. Models were selected based on R^2 values and analysis of residuals. Three measures of accuracy were used to evaluate the goodness-of-fit between the observed and predicted values for the above- and below-ground allometric functions: (*i*) root mean squared error (RMSE); (*ii*) mean bias error (BIAS, the difference between mean observed and predicted values); and (*iii*) coefficient of determination (R^2). Because the chronosequences lacked true replication and stands varied in age, structure (basal area, density), and management history, differences between stands were not tested. Standard errors of the mean in tables and figures indicate variation among the four subplots within a stand.

Results

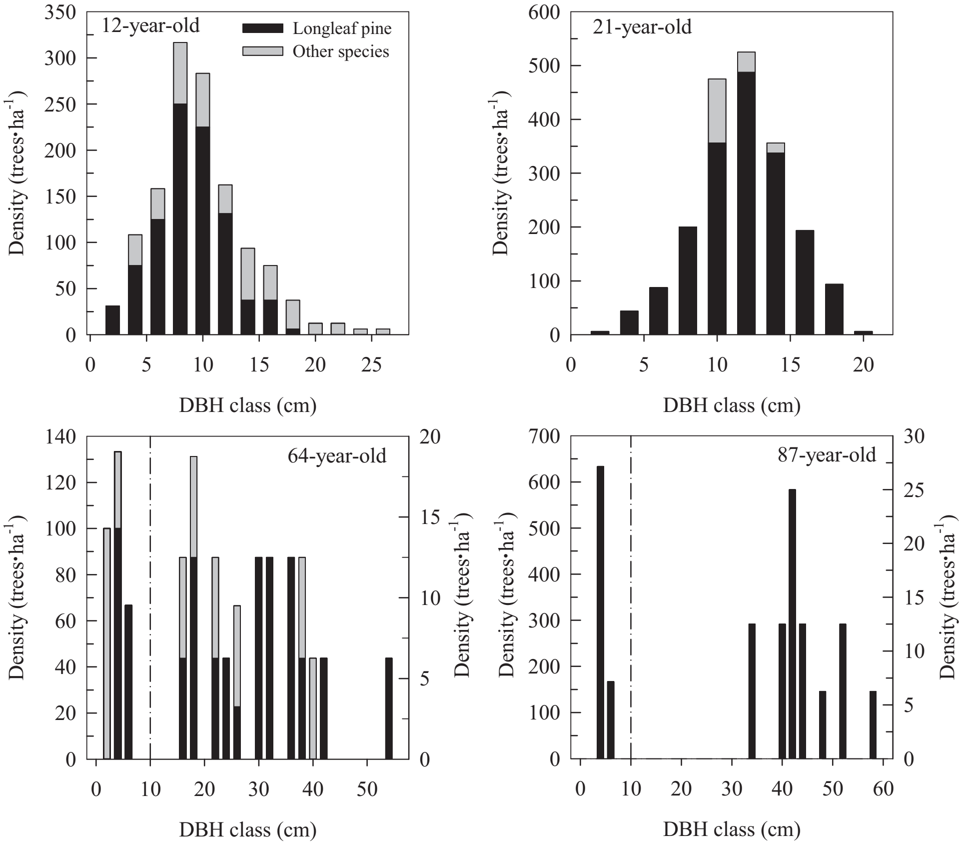
Stand structure

In the 5-year-old stand, the majority of longleaf pine trees ($625\ trees \cdot ha^{-1}$) were still in the understory layer (<2 m in height), and the understory layer in the 5-year-old stand was dominated by species other than longleaf pine (Table 3). In the 12-year-old stand, the majority (67%) of longleaf pine trees in the overstory layer was <10 cm DBH (Table 3; Fig. 1). The understory layer in all stands was dominated by species other than longleaf pine. In stands older than 5 years, the majority of basal area in the overstory was longleaf pine. In the two oldest stands, there were cohorts of smaller longleaf pine in the <10 cm DBH class. Compared with the younger stands, the two oldest stands were made up of fewer but larger trees up to 56 cm in DBH in the 64-year-old stand and 58 cm in the 87-year-old stand (Fig. 1; Table 3). Total basal area in longleaf pine was 6.1, 20.9, 7.8, and 14.5 $m^2 \cdot ha^{-1}$ in the 12-, 21-, 64-, and 87-year-old stands, respectively. The high basal area in the 21-year-old stand was due to the high planting density ($2235\ trees \cdot ha^{-1}$).

Allometric models

The best models tested were linear relationships between natural log transformed biomass and the product of natural log

Fig. 1. Density of trees by diameter class (DBH, diameter at breast height) for longleaf pine stands. For the 64- and 87-year-old stands, the right *y* axis applies to all classes greater than 10 cm DBH.



transformed diameter squared and height. Because the models were logarithmic regressions, a correction ratio (ratio of the sample mean to the predicted values) was applied to correct for proportional BIAS (Snowdon 1991). Nonlinear versions of the models were also evaluated but resulted in no improvement in model performance (data not shown). For the combined stands, regressions for all longleaf pine tree components were highly significant ($P < 0.001$), with R^2 ranging from 0.91 to 0.99 (Table 4). Allometric relationships for 5-year-old trees were significant but model R^2 values were lower, ranging from 0.84–0.96, most likely due to the smaller sample size and greater variability in tree size associated with bolting from the grass stage.

The model for aboveground biomass reported in this study produced BIAS and RMSE of 1.3% and 20.7 kg·tree^{-1}, respectively. When applied to our data, the longleaf pine allometric equations from Taras and Clark (1977) for natural uneven-aged sawtimber in Alabama, Baldwin and Saucier (1983) for unthinned plantations in Texas and Louisiana, Gibson et al. (1985) for 25-year-old plantations in Louisiana, and Mitchell et al. (1999) for uneven-aged stands in Georgia produced larger BIAS (18.8%, 25.4%, 28.9%, and 28.3%, respectively) and larger RMSE (108.9, 145.0, 165.7, and 120.8 kg·tree^{-1}, respectively). The equation of Mitchell et al. (1999) predicted negative aboveground biomass for trees with DBH of about 8 cm. The relationships between observed and predicted aboveground biomass using the five equations are shown in Fig. 2. The model for below-stump biomass reported in this study produced BIAS and RMSE of 9.5% and 30.3 kg·tree^{-1}, respectively. When applied to our data, the allometric equations from Gibson et al. (1985) produced smaller BIAS (–3.4%) but larger RMSE (35.2 kg·tree^{-1}) (Fig. 2).

Live plant C stocks

Carbon in longleaf pine trees was dominated by stem C followed by below-stump or branch C (Fig. 3). Foliage made up the least amount of within-tree C in all stands. Total live aboveground C ranged from 1.4 Mg C·ha^{-1} in the 5-year-old stand to 78.4 Mg C·ha^{-1} in the 87-year-old stand and in all stands except the youngest was dominated by woody plant C (Table 5). In the 5-year-old stand, the largest live aboveground C stock was ground cover C (Table 5; Fig. 3).

Longleaf pine live below-stump C varied from 0.2 Mg C·ha^{-1} in the youngest stand to 12.8 Mg C·ha^{-1} in the 21-year-old stand (Table 5). Plot-level measurements of lateral coarse root mass by GPR added from 2.2 to 7.1 Mg C·ha^{-1}, depending on the stand (Table 5). Carbon allocated to fine roots added from 0.6 to 1.4 Mg C·ha^{-1} to the total root C pool (Table 5). Pine fine root C was linearly related to pine basal area (Fig. 4). A nonlinear regression between all fine roots and total basal area provided the best fit for all fine roots combined.

A nonlinear relationship between live plant aboveground C and belowground C was observed (Fig. 5). In both functions, which included a minimum or maximum estimate of lateral coarse root C from GPR, proportionally less total root C was observed with higher aboveground C.

Detritus and soil C

A total of four snags ≥ 10 cm DBH were tallied: two longleaf pine in the 21-year-old stand, one non-pine in the 12-year-old stand, and one other pine in the 64-year-old stand. Only aboveground biomass of snags was predicted, and using allometric equations described previously and assuming no decay, snag C ranged from 0.1 to 0.7 Mg C·ha^{-1}. In the 5-year-old stand, residual taproot C was the

Table 4. Regression equations between dry weight biomass and tree size for longleaf pine (*Pinus palustris*) trees.

Stand age (years)	Dependent variable	n	β_0 (SE)	β_1 (SE)	CF	MSE	$P > F$	R^2
5	Foliage	10	−3.355±0.31	0.653±0.08	0.005	0.06	<0.001	0.89
	Branch	—	—	—	—	—	—	—
	Stem	10	−5.009±0.31	1.136±0.08	0.027	0.06	<0.001	0.96
	Total AG	10	−3.566±0.30	0.923±0.08	0.015	0.06	<0.001	0.94
	Below-stump*	5	−4.267±0.83	0.879±0.22	0.025	0.24	0.027	0.84
12–87 pooled	Foliage	26	−5.403±0.30	0.888±0.04	−0.085	0.27	<0.001	0.95
	Branch	26	−7.319±0.26	1.176±0.04	−0.054	0.21	<0.001	0.98
	Stem	26	−3.730±0.16	0.991±0.02	0.074	0.08	<0.001	0.99
	Total AG	26	−3.571±0.15	0.997±0.02	0.058	0.07	<0.001	0.99
	Below-stump	16	−3.730±0.47	0.837±0.06	0.200	0.36	<0.001	0.93
	Lateral roots†	16	−4.164±0.46	0.763±0.06	0.027	0.34	<0.001	0.93
	Taproot1	16	−4.706±0.38	0.911±0.05	0.001	0.23	<0.001	0.96
	Taproot2‡	16	−4.404±0.59	2.38±0.19	0.001	0.68	<0.001	0.91

Note: With the exception of Taproot2, the regressions were of the form $\ln(\text{biomass}) = \text{CF} + \beta_0 + \beta_1\ln(\text{DBH}^2 \times \text{H})$, where CF is a correction factor and β_0 and β_1 are estimated parameters. Groundline diameter (GLD) was used in regressions for the 5-year-old stand. Mass was measured in kilograms per tree; diameter at breast height (DBH) and GLD were measured in centimetres and height (H) was measured in metres. AG, aboveground biomass.

*Below-stump is taproot mass plus lateral coarse root (≥5 mm diameter) mass within the excavation pit area.

†Lateral roots are roots ≥5 mm in diameter in the excavation pit area and not including taproots.

‡Taproot regression of the form $\ln(\text{biomass}) = \text{CF} + \beta_0 + \beta_1\ln(\text{GLD})$.

highest dead organic matter stock at 4.9 Mg C·ha^{-1} (±25% boundary of 4.2 and 5.9 Mg C·ha^{-1}).

In stands older than 5 years, the second largest aboveground C stock after woody plant C was litter C, which ranged from 1.6 Mg C·ha^{-1} in the 12-year-old stand to 3.6 Mg C·ha^{-1} in the 21-year-old stand (Table 5; Fig. 3). The combined CWD and FWD pool contributed less than 1 Mg C·ha^{-1} in all stands, and duff contributed 0.1 to 1.1 Mg C·ha^{-1}. Total dead organic matter C ranged from 3.0 Mg C·ha^{-1} in the oldest stand to 6.2 Mg C·ha^{-1} in the 5-year-old stand. The range in soil C to a 1 m depth was from 52.9 Mg C·ha^{-1} in the 21-year-old stand to 85.9 Mg C·ha^{-1} in the 64-year-old stand (Table 5).

Ecosystem C stocks

The sum of all C stocks varied from 71.6 to 185.4 Mg C·ha^{-1} (Table 5). From 42% to 85% of ecosystem C was in soil C, depending mainly on the contribution of woody plant C. Live woody plant C exceeded soil C (1 m depth) in the 21- and 87-year-old stands.

Discussion

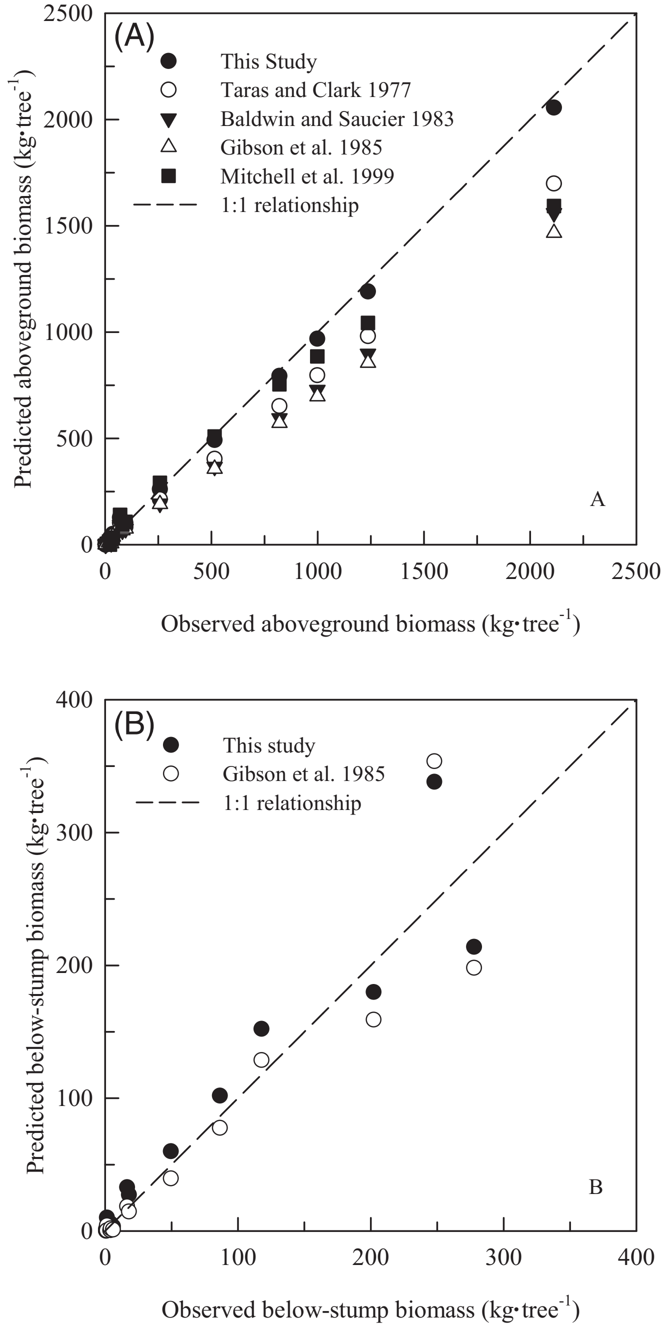
The inclusion of height in longleaf pine allometric equations has been shown to better predict biomass accumulation in longleaf pine than DBH alone (Taras and Clark 1977; Baldwin and Saucier 1983), and this was the case for longleaf pine in this study. The 12- and 64-year-old stands had similar basal area in longleaf pine but carbon stored in aboveground biomass of longleaf pine was 66% higher in the 64-year-old stand because of greater tree height. Chojnacky et al. (2014) recently updated generalized biomass equations for North American trees and used a modified equation similar to that of Taras and Clark (1977) for longleaf pine, which would underestimate biomass in our stands. Comparisons of our allometric models with other reported functions suggest that local models that take into account local site effects and management history may be needed in the absence of general models that account for differences in stand structural development, climate, and soils within the expansive range of longleaf pine.

Aboveground C stocks were dominated by live woody plant C in all stands except the youngest in which C in the ground cover layer and in residual taproots exceeded live woody plant C. Assessment of nonwoody C stocks indicated that litter C greatly exceeded all other nonwoody C pools in stands greater than 12 years of age and was highest in the 21-year-old stand, most likely because of the denser spacing and a high leaf area index. Litter and duff C pools are counted in some forest project protocols (www.climateactionreserve.org) and used in predicting first-order fire effects (Reinhardt 2003), and although relatively small C pools in regularly burned longleaf pine forests, litter and duff influence soil C flux (Samuelson and Whitaker 2012) and plant diversity in the ground cover layer (Hiers et al. 2007).

Live woody plant C in longleaf pine was within the range reported for other southern pines when comparisons were made with stands of similar structure. For example, 28.5 Mg C·ha^{-1} was reported for woody aboveground C in an even-aged, naturally regenerated 50-year-old longleaf pine stand in southern Alabama with 8 m^2·ha^{-1} basal area (Samuelson and Whitaker 2012), which is similar to the 64-year-old stand. In 18-year-old slash pine (*Pinus elliottii* Engelm.), basal area (21.0 m^2·ha^{-1}) and aboveground woody plant C (48 Mg C·ha^{-1}) (Gholz and Fisher 1982) were similar to those of the 21-year-old longleaf pine stand. Maximum aboveground C accumulation in longleaf pine trees was 78 Mg C·ha^{-1} in the 87-year-old stand. Lichstein et al. (2009) developed regional biomass chronosequences for many US tree species and projected average stem biomass accumulation of 63 Mg C·ha^{-1} in longleaf pine stands over 100 years. Similar biomass trajectories were projected for lodgepole pine (*Pinus contorta* Dougl. ex Loud var. *latifolia* Engelm.) and ponderosa pine (*Pinus ponderosa* Doug. ex Laws var. *scopulorum* Engelm.) (Lichstein et al. 2009), species that possess a life span similar to that of longleaf pine and are associated with frequent-fire environments.

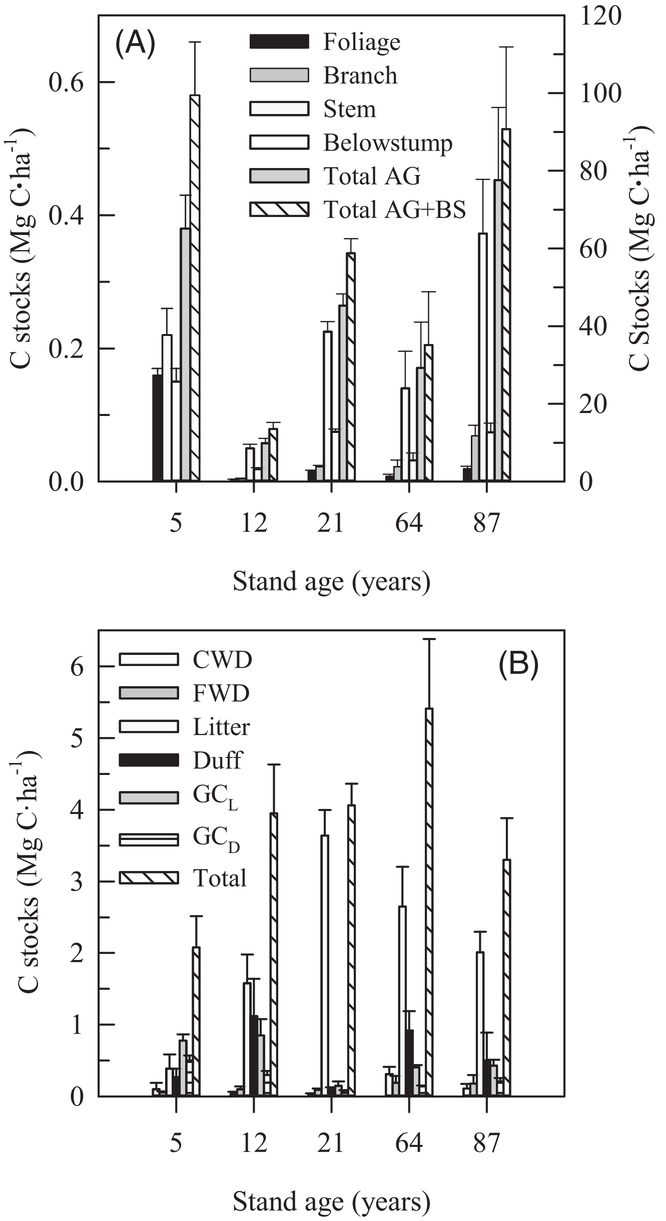
Lateral roots of longleaf pine are usually located in the upper 20 cm of soil, are commonly intermixed with roots of nearby trees, and can extend considerable distances from their source (Hodgkins and Nichols 1977). Hodgkins and Nichols (1977) found that longleaf pine lateral root length and spread was related to tree age and competitive position; lateral root spread averaged 5 m for dominant trees in a closed canopy, 7.4 m on edges, and 9.3 m for isolated trees aged 30–33 years in southwestern Alabama. In the present study, combining allometric equations to capture below-stump biomass with plot-level lateral coarse root biomass estimates with GPR provided a more comprehensive estimate of total belowground biomass. This was particularly relevant in accounting for root mass in the gaps in the 64-year-old stand with low basal area. Considering the tendency for longleaf pine roots to spread widely, it is likely that roots have entered from outside the measurement plots, as well as the reverse. Because the subplots were located on contiguous areas with the same stand history and density, the quantity of roots leaving and entering plots should be similar.

Fig. 2. Observed versus predicted aboveground (A) and belowground (B) biomass using equations from this study and from other longleaf pine studies. The broken line represents the 1:1 relationship.



Surface-based GPR excels in detecting lateral roots but is unable to delineate the mass of roots directly beneath a tree. In longleaf pine, taproots and vertical sinker roots adjacent to trees comprise much of the belowground biomass and were not detected by GPR. In older stands where large-diameter lateral roots overlap or are near the taproot, root mass may be underestimated. This left some uncertainty as to the area in which GPR was capable of detecting all lateral roots. Presenting the maximum (all lateral roots near tree detected) and minimum (no lateral roots near tree detected) ability of GPR to detect lateral root mass around trees in the pit areas constrains this uncertainty: at maximum aboveground C (100 Mg C·ha⁻¹), belowground C varied 20%.

Fig. 3. Carbon stocks in longleaf pine trees predicted using allometric equations developed from trees harvested from all stands (A) and C stocks in the forest floor and ground cover layer (B). For longleaf pine C stocks (A), the left *y* axis applies to the 5-year-old stand and the right *y* axis refers to all other stands. Values are means ± SEs. AG, aboveground; BS, below-stump; CWD, coarse woody debris; FWD, fine woody debris; GC_L, live ground cover; GC_D, dead ground cover.



Fine root C was a relatively small contribution to total root C, but high fine root turnover rates, estimated to range from one to three times standing biomass per year (West et al. 2004), make the fine root C pool a dynamic component in longleaf pine dominated ecosystems (Hendricks et al. 2006). Although total basal area was dominated by overstory longleaf pine, on all but the 21-year-old stand, non-pine fine roots (hardwoods, shrubs, herbaceous plants) comprised half or more of the fine root C pool. Pine fine root C ranged from 0.05 to 0.69 Mg C·ha⁻¹ across all sites and is in agreement with values of 0.20 to 0.65 Mg C·ha⁻¹ (calculated from standing biomass assuming 42% C content) reported by Carter et al. (2004) and Hendricks et al. (2006) for longleaf pine sites near

Table 5. Forest carbon stocks (Mg C·ha^{-1}) in longleaf pine (*Pinus palustris*) stands stands ranging in age from 5 to 87 years.

	Forest carbon stocks (Mg C·ha^{-1})				
	Age 5 years	Age 12 years	Age 21 years	Age 64 years	Age 87 years
Live aboveground					
LLP					
Overstory[*]	0.17±0.06	9.90±1.22	45.28±3.04	29.27±11.76	77.45±18.86
Understory[†]	0.21±0.02	0.0±0.0	0.0±0.0	0.0±0.0	0.18±0.18
Other woody species					
Overstory	0.01±0.01	8.00±5.51	3.90±1.80	5.42±2.26	0.0±0.0
Understory	0.23±0.17	0.33±0.13	0.005±0.005	0.58±0.35	0.36±0.21
Ground cover[‡]	0.78±0.04	0.85±0.23	0.15±0.06	0.41±0.03	0.43±0.08
Live aboveground total	1.41±0.09	19.08±4.57	49.33±4.71	35.68±10.79	78.42±18.78
Live belowground[§]					
LLP below-stump	0.15±0.02	3.25±0.36	12.83±0.76	5.45±1.94	12.66±2.43
Other pine taproot	0.0±0.0	1.30±0.93	0.37±0.07	1.12±0.52	0.0±0.0
Coarse roots (GPR)	2.22±0.19	5.89±0.43	3.94±0.47	7.14±0.51	5.62±0.48
Fine roots pine	0.05±0.01	0.44±0.08	0.69±0.07	0.44±0.11	0.46±0.07
Fine roots non-pine	0.52±0.06	0.91±0.16	0.42±0.06	0.73±0.11	0.46±0.06
Live belowground total	2.94±0.25	11.79±1.09	18.25±0.90	14.88±2.25	19.20±2.82
Dead organic matter					
Ground cover	0.60±0.07	0.30±0.06	0.07±0.02	0.14±0.01	0.21±0.05
Snags	0.0±0.0	0.06±0.05	0.27±0.18	0.73±0.73	0.0±0.0
CWD	0.11±0.09	0.04±0.02	0.03±0.01	0.31±0.10	0.11±0.06
FWD	0.06±0.01	0.10±0.04	0.09±0.02	0.19±0.10	0.18±0.12
Litter	0.39±0.19	1.58±0.40	3.64±0.36	2.65±0.55	2.01±0.29
Duff	0.27±0.12	1.12±0.52	0.10±0.03	0.93±0.27	0.50±0.39
Residual taproot[‖]	4.92±0.14	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0
Dead organic matter total	6.25±0.46	3.19±0.90	4.261±0.45	4.95±0.55	3.00±0.63
Soil (1 m depth)	61.01±5.16	75.99±9.13	52.86±5.30	85.91±8.30	84.82±4.09
Ecosystem total	71.61±5.25	110.06±15.45	124.65±10.36	141.42±5.63	185.44±19.26

Note: Values are means ± SEs. CWD, coarse woody debris; FWD, fine woody debris; GPR, ground-penetrating radar; LLP, longleaf pine.

[*] Overstory includes all trees ≥2 m in height.

[†] Understory includes all stems ≥1 and <2 m in height. The understory of the 5-year-old stand also includes all planted pine <2 m in height.

[‡] Ground cover is all plants <1 m in height.

[§] Below-stump is taproot plus lateral coarse roots (≥5 mm diameter) in the excavation pit area. Coarse roots (GPR) is lateral coarse roots (≥2 mm in diameter) (no taproot) measured by GPR and an average of values assuming GPR accounted for all or none of the lateral coarse roots in the excavation pit area. Fine roots are <2 mm in diameter.

[‖] Residual taproot in the 5-year-old stand was from the previous stand harvested before planting. Residual taproot C for old stumps was not determined in stands older than 5 years of age.

Newton, Georgia. Separating fine roots into pine and non-pine classes revealed a linear relationship between pine fine roots and pine basal area, but the nonlinear relationship between total fine root C and total basal area indicates full site occupancy of fine roots at approximately 8 m^2·ha^{-1} basal area. Samuelson and Whitaker (2012) report a similar range in total fine root C, from 0.8 to 1.4 Mg C·ha^{-1}, and no relationship between fine root mass and basal areas greater than 7 m^2·ha^{-1} in 50-year-old naturally regenerated longleaf pine stands.

In carbon accounting, belowground biomass is often predicted from a general root to shoot ratio such as 0.20 for softwood forests (Birdsey 1992; Brown et al. 1993). The belowground to aboveground C ratio was 0.20 or 0.25 in the 87-year-old stand, depending on how GPR lateral coarse root mass was calculated. Gholz and Fisher (1982) determined that the proportion of total coarse root mass to total aboveground wood mass generally decreased with increasing aboveground biomass in slash pine. For young loblolly pine plantations (7–18 years) with varying basal areas, total coarse root mass was 50% of stem mass (Albaugh et al. 2006). However, Van Lear and Kapeluck (1995) reported a coarse root to stem ratio of 0.30 for 48-year-old loblolly pine with average aboveground biomass of 144 Mg·ha^{-1}. In the 5-year-old stand, live root C exceeded live aboveground C, but in other stands, the relationship between belowground and aboveground C was not wholly dependent on stand age, as some subplots in older stands had low aboveground C. Given that tree age and size, stand density, soil conditions, and management influence root to shoot ratios (King et al. 2007; Litton et al. 2003), it is difficult to separate age differences from variation in stand structure and site conditions. Longleaf pine has been purported to invest proportionately more growth in belowground root mass than other southern conifers due to the presence of a grass stage and enhanced early taproot development. However, Gibson et al. (1985) found no differences in belowground biomass allocation between 25-year-old longleaf pine and loblolly pine and slash pine of the same age growing on the same sites.

Across all sites, soil C (measured to a depth of 1 m) averaged 72 Mg C·ha^{-1}, and soil C dropped precipitously with depth (data not shown) on all sites. Although stand age could not be compared statistically, soil C represented the greatest ecosystem C stock in the 5-, 12-, and 64-year-old stands and was almost equal to total plant C pools in the 87-year-old stand. The anomaly occurred in the 21-year-old stand where soil C represented 42% of the total ecosystem C. Thus, no general trend in increasing soil C with stand age was observed, and soil C was likely more related to land use history and soil type than stand age. Markewitz et al. (2002) reported no difference in soil C content on sandy soils up to 14 years after afforestation with longleaf pine on marginal agricultural lands on a 2- to 3-year fire interval, and on average, soil C to a 50 cm depth was 23 Mg C·ha^{-1} in plantations versus 42 Mg C·ha^{-1} in natural longleaf pine stands that were never tilled. Butnor et al. (2012*b*) reported 60 Mg C·ha^{-1} soil C (down to 30 cm) for coarse loamy soils in 50-year-old longleaf pine stands in Mississippi planted after clear-cutting a mature longleaf pine stand and

Fig. 4. Relationship between pine-only fine root C or total fine root (all species) C and pine or total basal area in longleaf pine stands. Open symbols represent pine fine roots and solid symbols represent fine roots of all species. The linear equation for pine fine root C was $y = 0.122 + 0.025x$, $R^2 = 0.63$, $P < 0.001$, where x is pine basal area. The nonlinear equation for all fine root C was $y = 1.16/[1 + e^{(-((x-0.62)/2.24))}]$, $R^2 = 0.50$, $P = 0.003$, where x is total basal area. Each point represents a subplot average.

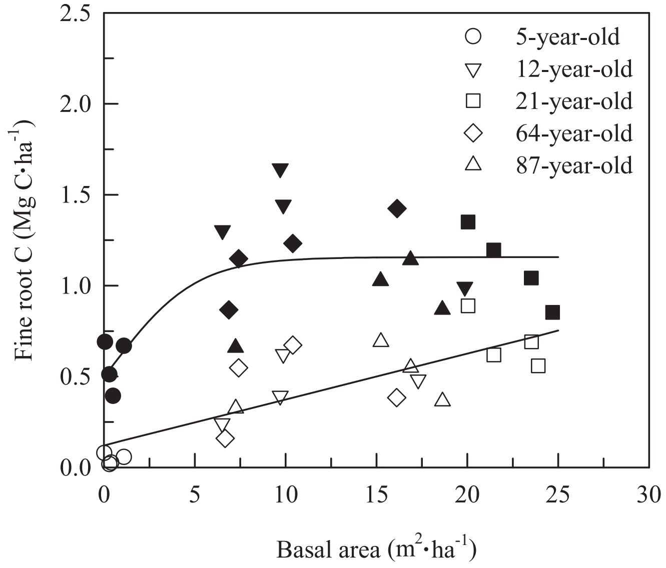
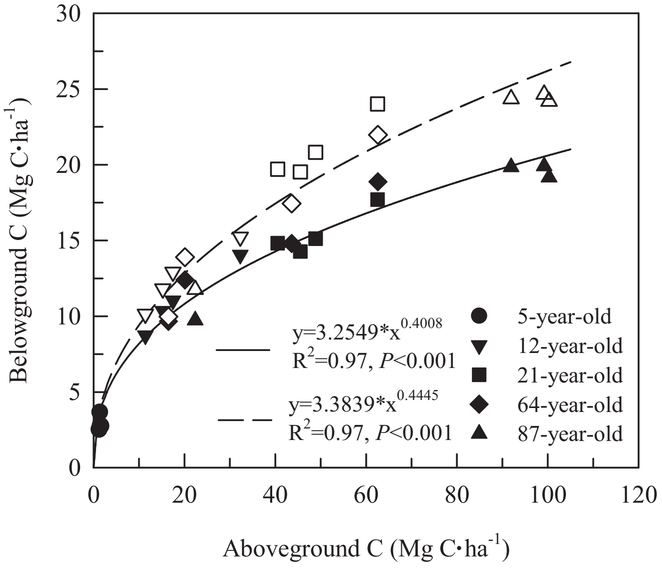


Fig. 5. Relationship between total live aboveground and belowground (below-stump + GPR lateral coarse roots + fine roots) C stocks in longleaf pine stands. The two lines indicate the maximum and minimum belowground C based on calculation of GPR lateral root C. GPR, ground-penetrating radar.



regularly burned. Mean soil C (to a 1 m depth) reported by Heath et al. (2001) was 166 Mg C·ha^{-1} for the longleaf pine – slash pine forest type group and 75 Mg C·ha^{-1} for the loblolly pine – shortleaf pine (*Pinus echinata* Mill.) forest type. Thus, soil C in longleaf pine stands in our study is comparable with other reports for southern pines.

In summary, ecosystem stocks excluding soil C ranged from 10.6 to 100.6 Mg C·ha^{-1} and including soil C ranged from 71.6 to 185.4 Mg C·ha^{-1}. Carbon accumulation in longleaf pine stands was similar to that in other *Pinus* ecosystems when comparisons were made with stands with similar structure. As observed for a lodgepole pine chronosequence in which average maximum total ecosystem C (150 Mg C·ha^{-1}) was attained at age 70 years, total ecosystem C was driven by live biomass C, related to stand basal area and density in addition to age, and soil C (Kashian et al. 2013). Although limited to one geographic area and pure, even-aged stands, the work reported here is the first comprehensive measurement of above- and below-ground C pools in longleaf pine forests across a range of stand ages and structures, site conditions, and management histories. The U.S. Department of Agriculture Forest Service Forest Inventory and Analysis (FIA) database indicates approximately 1 million ha in natural longleaf pine forest with the majority (88%) less than 80 years in age and 0.4 million ha in plantation longleaf pine with 77% in the age class of 0–20 years (Woudenberg et al. 2010). Therefore, this work is applicable to present-day and future longleaf pine forests.

Acknowledgements

This research was supported wholly (or in part) by the U. S. Department of Defense through the Strategic Environmental Research and Development Program (SERDP). The authors thank Jake Blackstock, Justin Rathel, Patrick Steele, Liz Jordon, Tyler Bowden, Brad Stone, Michael Gunter, and Adam Kelley for assistance in data collection and James Parker and Brian Waldrep from Fort Benning, Land Management Division, for their assistance. We appreciate the technical support provided by Joel Burley, Thomas Christensen, Robert Eaton, Shelly Hooke, and Karen Sarsony.

References

Albaugh, T.J., Allen, H.L., and Kress, L.W. 2006. Root and stem partitioning of *Pinus taeda*. Trees, **20**: 176–185. doi:10.1007/s00468-005-0024-4.

Bailey, R.G. 1995. Description of the ecoregions of the United States. 2nd ed. USDA For. Serv. Misc. Publ. No. 1391.

Baldwin, V.C., Jr., and Saucier, J.R. 1983. Aboveground weight and volume of unthinned, planted longleaf pine on West Gulf forest sites. USDA For. Serv. Res. Pap. SO-191.

Birdsey, R.A. 1992. Carbon storage and accumulation in United States forest ecosystems. USDA For. Serv. Gen. Tech. Rep. WO-59.

Birdsey, R., Pregitzer, K., and Lucier, A. 2006. Forest carbon management in the United States: 1600–2100. J. Environ. Qual. **35**: 1461–1469. doi:10.2134/jeq2005.0162.

Brown, S., Iverson., L.R., Prasda, A., and Liu, D. 1993. Geographical distributions of carbon in biomass and soils of tropical Asian forests. Geocarto Int. **8**: 45–59. doi:10.1080/10106049309354429.

Butnor, J.R., Barton, C., Day, F.P., Johnsen, K.H., Mucciardi, A.N., Schroeder, R., and Stover, D.B. 2012*a*. Using ground-penetrating radar to detect tree roots and estimate biomass. *In* Measuring roots. Chapter 12. *Edited by* S. Mancuso. Springer.

Butnor, J.R., Johnsen, K.H., Sanchez, F.G., and Nelson, C.D. 2012*b*. Impacts of pine species, cultivation, and fertilization on soil properties 50 years after planting. Can. J. For. Res. **42**(4): 675–685. doi:10.1139/x2012-024.

Carter, D.C., Hendricks, J.J., Mitchell, R.J., and Pecot, S.D. 2004. Fine root carbon allocation and fates in longleaf pine forests. For. Sci. **50**: 177–187.

Chojnacky, D.C., Heath, L.S., and Jenkins, J.C. 2014. Updated generalized biomass equations for North American tree species. Forestry, **87**: 129–151.

Gaiser, R.N. 1951. Random sampling within circular plots by means of polar coordinates. J. For. **49**: 916–917.

Gholz, H.L., and Fisher, R.F. 1982. Organic matter production and distribution in slash pine (*Pinus elliottii*) plantations. Ecology, **63**: 1827–1839. doi:10.2307/1940124.

Gibson, M.D., McMillin, C.W., and Shoulders, E. 1985. Above- and below-ground biomass of four species of southern pine growing on three sites in Louisiana. USDA, For. Serv. Final Report FS-SO-3201-59.

Harmon, M.E., and Sexton, J. 1996. Guidelines for measurements of woody detritus in forest ecosystems. Publication No. 20. U.S. LTER Network Office: University of Washington, Seattle, WA. 73 pp.

Harmon, M.E., Christopher, W., Fasth, B., and Sexton, J. 2008. Woody detritus density and density reduction factors for tree species in the United States: a synthesis. USDA For. Serv., Northern Research Station, Newtown Square PA. p. 84.

Heath, L.S., Birdsey, R.A., and Willimas, D.W. 2001. Methodology for estimating soil carbon for the carbon budget model of the United States, 2001. Environ. Pollut. **116**: 373–380.

Hendricks, J.J., Hendrick, R.L., Wilson, C.A., Mitchell, R.J., Pecot, S.D., and Guo, D. 2006. Assessing the patterns and controls of fine root dynamics: an empirical test and methodological review. J. Ecol. **94**: 40–57. doi:10.1111/j.1365-2745.2005.01067.x.

Hiers, J.K., O'Brien, J.J., Will, R.E., and Mitchell, R.J. 2007. Forest floor depth mediates understory vigor in xeric *Pinus palustris* ecosystems. Ecol. Appl. **17**: 806–814. doi:10.1890/06-1015.

Hodgkins, E.J., and Nichols, N.G. 1977. Extent of main lateral roots in longleaf pine as related to position and age of the trees. For. Sci. **23**(2): 161–166.

Jenkins, J.C., Chojnacky, D.C., Heath, L.S., and Birdsey, R.A. 2004. Comprehensive database of diameter-based biomass regressions for North American tree species. Gen. Tech. Rep. NE-319.

Johnsen, K.H., Butnor, J.R., Kush, J.K., Schmidtling, R.C., and Nelson, C.D. 2009. Longleaf pine displays less wind damage than loblolly pine. South. J. Appl. For. **33**: 178–181.

Kashian, D.M., Romme, W.H., Tinker, D.B., Turner, M.G., and Ryan, M.G. 2013. Postfire changes in forest carbon storage over a 300-year chronosequence of *Pinus contorta*-dominated forests. Ecol. Monogr. **83**: 49–66. doi:10.1890/11-1454.1.

King, J.S., Giardina, C.P., Pregitzer, K.S., and Friend, A.L. 2007. Biomass partitioning in red pine (*Pinus resinosa*) along a chronosequence in the Upper Peninsula of Michigan. Can. J. For. Res. **37**(1): 93–102. doi:10.1139/x06-217.

Law, B., Arkebauer, T., Campbell, J.L., Chen, J., Sun, O., Shwartz, M., van Ingen, C., and Verma, S. 2008. Terrestrial carbon observations: protocols for vegetation sampling and data submission. Terrestrial Carbon Observations (TCO) Panel of the Global Terrestrial Observing System (GTOS), FAO, Rome. Available from http://www.fao.org/gtos.

Lichstein, J.W., Wirth, C., Horn, H.S., and Pacala, S.W. 2009. Biomass chronosequences of United State forests: implications for carbon storage and forest management. Chapter 14. *In* Old-growth forests. *Edited by* Wirth et al. Ecological Studies, **207**: 301–341.

Litton, C.M., Ryan, M.G., Tinjer, D.B., and Knight, D.H. 2003. Belowground and aboveground biomass in young postfire lodgepole pine forests of contrasting tree density. Can J. For. Res. **33**(2): 351–363. doi:10.1139/x02-181.

Ludovici, K.H., Zarnoch, S.J., and Richter, D.D. 2002. Modeling in-situ pine root decomposition using data form a 60-year chronosequence. Can. J. For. Res. **32**(9): 1675–1684. doi:10.1139/x02-073.

Markewitz, D., Sartori, F., and Craft, C. 2002. Soil change and carbon storage in longleaf pine stands planted on marginal agricultural lands. Ecol. Appl. **12**: 1276–1285. doi:10.1890/1051-0761(2002)012[1276:SCACSI]2.0.CO;2.

Mitchell, R.J., Kirkman, L.K., Pecot, S.D., Wilson, C.A., Palik, B.J., and Boring, L.R. 1999. Patterns and controls of ecosystem function in longleaf pine – wiregrass savannas. I. Aboveground net primary productivity. Can. J. For. Res. **29**(6): 743–751. doi:10.1139/x99-051.

Naidu, S., DeLucia, E., and Thomas, R. 1998. Contrasting patterns of biomass allocation in dominant and suppressed loblolly pine. Can. J. For. Res. **28**(8): 1116–1124. doi:10.1139/x98-083.

Parresol, B.R., Shea, D., and Ottmar, R. 2006. Creating a fuels baseline and establishing fire frequency relationships to develop a landscape management strategy at the Savannah River site. *In* Fuels management: how to measure success. *Edited by* P.L. Andrews and B.W. Butler. USDA For. Serv., Rocky Mountain Research Station, Fort Collins, Colorado, Conference Proceedings RMRS-P-41.

Phillips, D.R. 1981. Predicted total-tree biomass of understory hardwoods. USDA For. Serv. Res. Pap. SE-223.

Prichard, S.J., Peterson, D.L., and Hammer, R.D. 2000. Carbon distribution in subalpine forests and meadows of the Olympic Mountains, Washington. Soil Sci. Soc. Am. J. **64**: 1834–1845. doi:10.2136/sssaj2000.6451834x.

Reinhardt, E.D. 2003. Using FOFEM 5.0 to estimate tree mortality, fuel consumption, smoke production and soil heating from wildland fire. *In* Proceedings of the 2nd International Wildland Fire Ecology and Fire Management Congress and 5th Symposium on Fire and Forest Meteorology. American Meteorological Society, Orlando, Florida. Page P5.2.

Remucal, J.M., McGee, J.D., Fehrenbacher, M.M., Best, C., and Mitchell, R.J. 2013. Application of the Climate Action Reserve's forest project protocol to a longleaf pine forest under restoration management. J. For. **111**: 59–66. doi:10.5849/jof.11-094.

Robertson, K.M., and Ostertag, T.E. 2009. Biomass equations for hardwood resprouts in fire-maintained pinelands in the southeastern United States. South. J. Appl. For. **33**: 121–238.

Samuelson, L.J., and Whitaker, W.B. 2012. Relationships between soil CO_2 efflux and forest structure in 50-year-old longleaf pine. For. Sci. **58**: 472–484. doi:10.5849/forsci.11-049.

Smith, J.E., Heath, L.S., and Birdsey, R.A. 2006. Methods for calculating forest ecosystem and harvested carbon with standard estimates for forest types of the United States. USDA For. Serv. Gen. Tech. Rep. NE-343.

Smith, W.B., Miles, P.D., Perry, C.H., and Pugh, S.A. 2009. Forest resources of the United States, 2007. USDA For. Serv. Gen. Tech. Rep. WO-78.

Snowdon, P. 1991. A ratio estimator for bias correction in logarithmic regressions. Can. J. For. Res. **21**(5): 720–724. doi:10.1139/x91-101.

Soil Survey Staff. 1999. Soil taxonomy: a basic system of soil classification for making and interpreting soil surveys. 2nd ed. USDA Soil Conservation Service, Washington, D.C.

Taras, M.A., and Clark, A., III. 1977. Aboveground biomass of longleaf pine in a natural sawtimber stand in southern Alabama. USDA For. Res. Pap. SE-162.

Turner, D.P., Koerper, G.J., Harmon, M.E., and Lee, J.J. 1995. A carbon budget for forests of the conterminous United States. Ecol. Appl. **5**: 421–436. doi:10.2307/1942033.

Van Lear, D.H., and Kapeluck, P.R. 1995. Above- and below-stump biomass and nutrient content of a mature loblolly plantation. Can. J. For. Res. **25**(2): 361–367. doi:10.1139/x95-040.

Van Wagner, C.E. 1968. The line intercept method in forest fuel sampling. For. Sci. **14**: 20–26.

Vashum, K.T., and Jayakumar, S. 2012. Methods to estimate above-ground biomass and carbon stock in natural forests — a review. J. Ecosyst. Ecogr. **2**: 4. doi:10.4172/2157-7625.1000116.

Waddell, K.L. 2002. Sampling coarse woody debris for multiple attributes in extensive resource inventories. Ecol. Indic. **1**: 139–153. doi:10.1016/S1470-160X(01)00012-7.

Warren, W.G., and Olsen, P.F. 1964. A line transect technique for assessing logging waste. For. Sci. **10**: 267–276.

West, J.B., Espeleta, J.F., and Donovan, L.A. 2004. Fine root production and turnover across a complex edaphic gradient of a *Pinus palustris* – *Aristida stricta* savanna ecosystem. For. Ecol. Manage. **189**: 397–406. doi:10.1016/j.foreco.2003.09.009.

Woodall, C.W., and Monleon, V.J. 2010. Estimating the quadratic mean diameters of fine woody debris in forests of the United States. For. Ecol. Manage. **260**: 1088–1093. doi:10.1016/j.foreco.2010.06.036.

Woodall, C.W., Heath, L.S., Domke, G.M., and Nichols, M.C. 2011. Methods and equations for estimating aboveground volume, biomass, and carbon for trees in the U.S. forest inventory, 2010. USDA For. Serv. Gen. Tech. Rep. NRS-88.

Woodbury, P.B. 2007. Carbon sequestration in the US forest sector from 1990 to 2010. For. Ecol. Manage. **241**: 14–27. doi:10.1016/j.foreco.2006.12.008.

Woudenberg, S.W, Conkling, B.L., O'Connell, B.M., LaPoint, E.B., Turner, J.A., and Waddell, K.L. 2010. The Forest Inventory and Analysis Database: database description and users manual version 4.0 for Phase 2. USDA For. Serv. Gen. Tech. Rep. RMRS-GTR-245.