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Modeling the effects of forest management on *in situ* and *ex situ* longleaf pine forest carbon stocks ☆

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ABSTRACT

Assessment of forest carbon storage dynamics requires a variety of techniques including simulation models. We developed a hybrid model to assess the effects of silvicultural management systems on carbon (C) budgets in longleaf pine (*Pinus palustris* Mill.) plantations in the southeastern U.S. To simulate *in situ* C pools, the model integrates a growth and yield model with species-specific allometric and biometric equations and explicitly accounts for the impacts of both thinning and prescribed fire. To estimate the *ex situ* C pool, the model used the outputs of merchantable products from the growth and yield model with current values of forest product conversion efficiencies and forest product decay rates. The model also accounts for C emissions due to transportation and silvicultural activities. Site productivity (site quality) was the major factor controlling stand C density followed by rotation length. Thinning reduced C sequestration, as the slow growth rate of longleaf pine reduced the potential of C sequestration in forest products. Prescribed burning reduced average C stock by about 16–19%, with the majority of the reduction in the forest floor. In a comparison of longleaf pine C dynamics with slash pine (*Pinus elliottii* Engelm.), both species reached a similar average C stock at age 75 years, but when averaged across the whole rotation, slash pine sequestered more C. Nevertheless, for medium quality sites, C sequestration was similar between thinned 75-year rotation longleaf pine and unthinned 25-year rotation slash pine. This longleaf pine plantation C sequestration model, based on empirical and biological relationships, provides an important new tool for developing testable research hypotheses, estimating C stocks for regional assessments or C credit verification, and for guiding future longleaf pine management.

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1. Introduction

Atmospheric carbon dioxide (CO_2) mitigation requires an approach that combines increasing terrestrial carbon (C) storage with CO_2 emission reductions (Sundquist et al., 2008). Forests and forest management play an important role in the mitigation of atmospheric CO_2 through the fixation of atmospheric CO_2 into plant tissue (Sedjo, 1989, 1997; Nabuurs, 2007). In the United States (U.S.), forests represent over 90% of the terrestrial C sink, which is equivalent to 12–16% of annual U.S. greenhouse gas (GHG) emissions (U.S. EPA, 2005). Southeastern U.S. forests contain 36% of the C sequestered in the contiguous U.S. (Turner et al., 1995), and these forests have the potential to sequester even more C via improved sustainable forest management (Johnsen et al., 2014).

Longleaf pine (*Pinus palustris* Mill.) was once a dominant forest type in the southeastern U.S., ranging from Virginia to Florida and Texas, but, due to logging and conversion to agriculture and other forest types, only about 1.2 million ha of longleaf pine forest remain (Frost, 2006). As part of the effort to restore longleaf pine ecosystems, longleaf pine is being planted in even-aged plantations. Currently there are approximately 0.4 million ha of longleaf pine plantations (Woudenberg et al., 2010). Longleaf pine is considered a slower growing species than loblolly (*Pinus taeda* L.) and slash (*Pinus elliottii* Engelm.) pines, the two other major commercial southern pines, but its relative longevity offers opportunities to sequester C in offset projects with longer contracts (Samuelson et al., 2014).

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Longleaf pine planted for ecosystem restoration is often established at lower tree densities than other southern pines, and this often results in a more abundant and diverse ground cover community that is typically managed with prescribed fire. Prescribed burning is an important management tool in longleaf forests, with recommended burning frequencies of at every two to four years (Chapman, 1932; Glitzenstein et al., 1995, 2003; Loudermilk et al., 2011). Prescribed burning is mainly used to control competing vegetation, favoring pine regeneration and increasing diversity and productivity of herbaceous plants (Haywood, 2007). Without frequent fire, longleaf forests typically succeed into hardwood dominated forests (Quarterman and Keever, 1962; Hartnett and Krofta, 1989; Mitchell et al., 2006). Thus, the role of frequent prescribed fire in carbon dynamics is important to assess. Fire volatilizes carbon, but may not represent a significant loss over a long rotation due to rapid recovery of biomass following fires.

The goal of this study was to develop a model that can be used to analyze the effects of silviculture on C budgets in longleaf pine plantations in the southeastern U.S. To simulate *in situ* C pools, we developed a hybrid model that integrates a growth and yield model for longleaf pine (Gonzalez-Benecke et al., 2012) with allometric and biometric equations determined for the species (Baldwin and Saucier, 1983; Gonzalez-Benecke et al., 2014; Samuelson et al., 2014). To estimate *ex situ* C pool dynamics, the model used the outputs of merchantable products from the growth and yield model and current values of forest product conversion efficiencies and forest product decay rates (Gonzalez-Benecke et al., 2010a, 2011). The model also simulated the C emissions of transportation and silvicultural activities of the various tested scenarios (Markewitz, 2006). Considering current and potential new management schemes, we used to the model to determine: (1) the degree to which site index and different management regimes, incorporating longer rotations and thinning, maximize accumulation of C *in situ* and *ex situ* pools; (2) how much prescribed burning reduces time-averaged C stocks; and (3) if C accumulation over longer rotations is comparable to slash pine, a more intensively managed southern pine species.

2. Materials and methods

All models used to estimate stand growth and biomass dynamics were based on longleaf pine datasets. Forest floor decay rate and *ex-situ* forest products functions were derived from slash pine publications. Emissions of transportation and silvicultural activities were assumed to be species independent, so we used the standards reported for loblolly pine.

2.1. Models

Growth and yield models were combined with allometric and biometric equations to estimate C fluxes and stocks. We used a longleaf pine growth and yield model reported by Gonzalez-Benecke et al. (2012). The model predicts stand growth in basal area (BA, $m^2\,ha^{-1}$), total volume (V, $m^3\,ha^{-1}$), dominant height (Hd, m), quadratic mean diameter (QMD, cm) and number of surviving trees (Nha, trees ha^{-1}), using as inputs site index (SI, m), and number of trees at planting (PD, trees ha^{-1}).The reference age for SI of longleaf pine was 50 years. The model can also simulate thinnings, where the user defines a thinning scheme that can be described by timing and intensity (by defining age and removal percentage), or by target BA (by defining target maximum BA that triggers the thinning and residual BA after thinning). From the original set of equations reported by Gonzalez-Benecke et al. (2012), the function to estimate survival was modified to include Reinecke's stand density index (SDI, trees ha^{-1}) as a covariate. The new model showed better fit and prediction accuracy than the model reported Gonzalez-Benecke et al. (2012), especially for mature and thinned stands. Table 1 presents a list of functions used for growth and yield modeling.

Using the data reported by Gonzalez-Benecke et al. (2012), we fit new models to estimate survival of planted longleaf pine trees. The dataset consisted of 267 plots regularly remeasured and maintained by the U.S. Forest Service's Laboratory at Pineville, LA. Each plot was measured for ~40 years at ~five-year intervals, averaging eight measurements per plot. Plantation ages ranged between 7 and 73 years; BA ranged between 6.6 and 55.9 $m^2\,ha^{-1}$; and SI ranged between 19.6 and 30.8 m (Gonzalez-Benecke et al., 2012). A negative-exponential survival model that includes Hdom and SDI was used to estimate survival using a modified version of the model proposed by Zhao et al. (2007) and Gonzalez-Benecke et al. (2012):

$$\mathrm{Nha}_2 = \mathrm{Nha}_1 \cdot e^{\left[\left(a_1 \frac{\mathrm{H}_{\mathrm{dom}_i}}{100} + a_2 \cdot \mathrm{SDIr}_i\right) \cdot (\mathrm{Age}_2^{a_3} - \mathrm{Age}_1^{a_4})\right]} + \varepsilon_1$$

where Nha_j is the number of trees ha^{-1} at age j (yr), Nha_i is the number of trees ha^{-1} at age i (yr) ($i < j$), $\mathrm{H}_{\mathrm{dom}_i}$ is the dominant height (m) at age i (yr), SDIr_i is the relative SDI at age i (yr), a_1 to a_4 are curve fit parameter estimates, SDIr is the SDI relative to a maximum observed of 1111 trees ha^{-1} (Gonzalez-Benecke et al., 2012) and ε_1 is the error term, with $\varepsilon_1 \sim N(0, \sigma_1^2)$.

At each age, allometric equations were used to estimate aboveground and belowground biomass. For belowground biomass we used the model reported by Samuelson et al. (2014). For aboveground biomass, we fitted new models to the data reported by Baldwin and Saucier (1983). We had access to the raw dataset that consisted of 111 trees sampled in 10 unthinned stands in Louisiana and Texas, with age ranging between 10 and 44 years, and dbh ranging between 2.8 and 52.3 cm (Baldwin and Saucier, 1983). The dataset included tree-level attributes, including dbh (cm), height (m) and dry weight (kg) of each tree aboveground tree component: living foliage, living branches, stemwood, stembark, stem outside bark (stem, the sum of stemwood and stembark), and the whole-tree aboveground biomass (TAGB, the sum of all components). The models selected to estimate aboveground biomass were:

$$\mathrm{TAGB, branch, stem, stemwood, stembark} = b_1 \cdot (\mathrm{dbh}^{b_2}) \cdot (\mathrm{Height}^{b_3}) + \varepsilon_2$$

$$\mathrm{Foliage} = b_1 \cdot (\mathrm{dbh}^{b_2}) \cdot (\mathrm{Height}^{b_3}) \cdot (\mathrm{Age}^{b_4}) + \varepsilon_2$$

where b_1 to b_4 are curve fit parameter estimates and ε_2 is the error term, with $\varepsilon_2 \sim N(0, \sigma_2^2)$. At each age, stand biomass was calculated by multiplying Nha, estimated by the growth and yield model, by the individual-tree biomass estimated with the fitted functions, using QMD as a surrogate of dbh and the mean height estimated using the model shown in Table 1 (reported by Gonzalez-Benecke et al., 2014).

At each age, mean yearly projected LAI of the longleaf pine overstory was estimated as the product between foliage biomass and the specific needle area (SNA, $m^2\,kg^{-1}$). Using data collected by Samuelson et al. (2012, 2014 and unpublished), Samuelson and Stokes (2012) and Gonzalez-Benecke et al. (2010b), the relationship between age and SNA was determined by fitting the following model:

$$\mathrm{SNA} = c_1 + c_2 \cdot e^{(-c_3 \cdot \mathrm{AGE})} + \varepsilon_3$$

where c_1 to c_3 are curve fit parameter and ε_3 is the error term, with $\varepsilon_3 \sim N(0, \sigma_3^2)$.

Annual needlefall (NF, Mg $ha^{-1}\,year^{-1}$) was assumed to correspond to half of foliage biomass of the previous year. The needlefall/litterfall ratio model reported by Gonzalez-Benecke et al.

Table 1
Equations used for growth and yield modeling and understory biomass determinations for longleaf pine stands in southeastern U.S.

Parameter	Equation	Refs.
H_{dom}	$= SI \cdot \left(\frac{1-e^{(-0.0369815 \cdot Age)}}{1-e^{(-0.0369815 \cdot 50)}}\right)^{1.2928702}$	a
BA	$= \exp(-4.6484039 + 0.4452486 \cdot \ln(Nha) + 1.6526307 \cdot \ln(H_{dom}))$	a
CI	$= 1 - \frac{BA_{at}}{BA_U}$	a
CI_2	$= CI_1 \times \exp\left(\left(\frac{-1.5476196}{AGE_j}\right) \cdot (AGE_j - AGE_i)\right)$	a
BA_{t_2}	$= BA_{U_2} \cdot (1 - CI_2)$	a
V_{IB}	$= \exp(3.0888853 - 0.1943861 \cdot \ln(Nha) + 1.2580580 \cdot \ln(BA) - 3.1281571 \cdot \ln(BA)/AGE - 0.098259 \cdot \ln(SI))$	a
$V_{d,t}$	$= V_{IB} \cdot \exp\left(-1.0537628\left(\frac{t}{QMD}\right)^{4.2527499} - 0.6545719 \cdot Nha^{-0.1365633\left(\frac{d}{QMD}\right)^{9.3108306}}\right)$	a
H	$=1.37 + \exp(0.05942 - 10.80378 \cdot dbh^{-1.1275} + AGE^{0.15053} + BA^{0.12124})$	b
GC_B	$= 5.9272 \cdot \exp^{(-0.04511 \cdot BA)}$	c
recGCB	$= \frac{1}{1+14.2946 \cdot \exp^{(-1.2124 \cdot TSF)}}$	c
LHp	$= 0.3416 \cdot (TSF^{-1.1361}) \cdot (BA^{-0.4461}) \cdot (AGE^{0.4316})$	c
LWp	$= \frac{1}{1+118.60 \cdot \exp^{(-2.4413 \cdot \ln(TSF)+-0.8725 \cdot \ln(BA))}}$	c

Notation: Hdom is dominant height (m); SI is site index (m); BA is stand basal area ($m^2\ ha^{-1}$); Nha is surviving trees per ha (ha^{-1}); CI is competition index at thinning Age; BA_{at} is basal area after thinning ($m^2\ ha^{-1}$); BA_U is basal area in the unthinned counterpart ($m^2\ ha^{-1}$); CI_2 is competition index at AGE 2; CI_1 is competition index at AGE 1; BA_{t2} is the basal area in the thinned stand at AGE 2 ($m^2\ ha^{-1}$); BA_{U2} is the basal area in the unthinned counterpart at AGE 2 ($m^2\ ha^{-1}$); V_{IB} is total inside bark stem volume ($m^3\ ha^{-1}$); $V_{d,t}$ is merchantable volume ($m^3\ ha^{-1}$) of trees with dbh $\geqslant$ d cm to a merchantable diameter *t* cm outside bark; QMD is quadratic mean diameter (cm); H is total height (m); GC_B is the biomass of the ground cover vegetation (Mg ha^{-1}); $recB_{GC\text{-}W}$ is the recovery rate after fire of woody dominated ground cover biomass (unitless); LHp is the ratio of living herbaceous to GC_B; LWp is the ratio of living woody to GC_B; TSF is the number of years after prescribed fire (years).
[a] Gonzalez-Benecke et al. (2012).
[b] Gonzalez-Benecke et al. (2014).
[c] Gonzalez-Benecke et al. (2015).

(2012) was used to estimate current year litterfall (LF, Mg ha^{-1} $year^{-1}$). A decay rate of 15 and 12%/year mass loss was assumed for foliage and coarse woody debris (CWD), respectively (Gholz et al., 1985, 1986; Radtke et al., 2009).

Standing dead trees estimated from mortality equations were incorporated into the dead component of total biomass. Similar to Gonzalez-Benecke et al. (2010a, 2011), we assumed that, due to the effects of resource competition on suppressed and weak trees, mortality occurs in diameter classes below the median and the diameter class of dying trees corresponds to percentile 25th (D_{25}, cm). A model similar to that reported by Pienaar et al. (1996) was fit to the data used to obtain the growth and yield model published by Gonzalez-Benecke et al. (2012) (Table 1). Biomass of dying trees was computed in the same way as standing biomass, but D_{25} at the previous year was used instead of QMD in order to estimate individual tree biomass.

The effect of thinning on C pools in forest floor and understory biomass was also incorporated into the model. At the time of thinning, reductions in longleaf pine foliage biomass were set to be proportional to reductions in BA due to thinning and therefore forest floor and understory biomass were affected due to their functional dependence on BA and foliage biomass. At thinning and final harvest (clear-cut), logging residues (root and crown biomass plus stem residues) from harvested tress were also included in the stock calculations and allocated to the dead biomass pool. We assumed that thinning was from below and the diameter class of thinned trees corresponded to the 35th percentile (D_{35}, cm). A decay rate of 15, 12 and 10%/year mass loss was assumed for foliage, CWD and lateral roots (Gholz et al., 1985, 1986; Radtke et al., 2009; Wang et al., 2012). For tap root decomposition we used the model reported by Anderson et al. (2014). Stem residues were obtained by assuming a harvest efficiency of 87% of V (Bentley and Johnson, 2004; Beltley and Harper, 2007).

Using the data reported by Gonzalez-Benecke et al. (2012), a modified version of the models proposed by Harrison and Borders (1996) was used to estimate D_{25} and D_{35} as follow:

$$D_{25}, D_{35} = d_1 \cdot Nha^{d_2} \cdot BA^{d_3} \cdot SI^{d_4} + \varepsilon_4$$

where d_1 to d_4 are curve fit parameter estimates and ε_4 is the error term, with $\varepsilon_4 \sim N(0, \sigma_4^2)$.

The dynamics of aboveground ground cover biomass, defined as the biomass of all live and dead plants <1 m in height, was determined using the models reported by Gonzalez-Benecke et al. (2015), that include functions to estimate total ground cover biomass, fractional recovery after fire and partitioning to living herbaceous, living woody and dead ground cover biomass. The effect of prescribed burning on biomass dynamics of ground cover, forest floor, CWD and standing dead trees was computed using the consumption standards reported by Reinhardt (2003), Ottmar et al. (2003) and Prichard et al. (2007). Table 2 presents a summary of consumption factors used.

Carbon mass (MgC ha^{-1}) was calculated using the C content reported by Samuelson et al. (2014) for longleaf pine and understory biomass components.

2.2. Model validation

There are few published reports of longleaf pine biomass accumulation. Model results were validated against published data of above ground biomass accumulation in live longleaf pine trees reported by Johnsen et al. (2014). The authors reported above ground biomass for a study installed in 1961 at the Harrison Experimental Forest in Saucier, Mississippi (Schmidtling, 1986). Initial parameters of the model, such as Nha and SI were set equal to those values reported in each plot used for validation. The study plots were measured at age 9, 12, 25, 39 and 46 years. The plots had SI ranging from 20.4 to 27.6 m. Validation of the growth and

Table 2
Fuel consumption factors.

Component	Consumption factor
Needles	0.950 (1)
Branches	0.784 (3)
CWD	0.200 (1)
Standing dead trees	0.040 (3)
Herbaceous ground cover	0.927 (2)
Woody ground cover	0.850 (1)
Harvest residues	0.800 (1)

Note: Sources: (1) Reinhardt (2003); (2) Ottmar et al. (2003); (3) Prichard et al. (2007).

yield model was carried out in Gonzalez-Benecke et al. (2012), and bias was shown to be less than 10% for Nha, Hdom, BA and V_{IB} estimations.

2.3. Ex situ wood products pools

Similar to Gonzalez-Benecke et al. (2010a, 2011), harvested roundwood (from thinnings or clear-cuts) was assigned to three main product classes depending on stem DBH and merchantable diameter; sawtimber (ST), chip-and-saw (CNS) and pulpwood (PW) using the model reported by Gonzalez-Benecke et al. (2012) (Table 1). Harvest efficiency of 87% of V was assumed (Bentley and Johnson, 2004; Beltley and Harper, 2007). Merchantable volume inside bark was calculated for each stand age and product volume was transformed to biomass (Mg ha^{-1}) by multiplying by an average whole-tree basic specific gravity (SG) of 0.585 ($n = 9$, SE = 0.012). This value of SG was obtained from trees sampled for biomass measurements, with dbh ranging between 8 and 49 cm (Samuelson et al., 2014). A C content of 50% was used to calculate C mass of each product type (Johnsen et al., 2014). Industrial conversion efficiencies of 65%, 65% and 58% were assigned to ST, CNS and PW, respectively (Gonzalez-Benecke et al., 2010a, 2011). All the product-types were divided into four life span categories according to the classification proposed by Liski et al. (2001) and Gundimeda (2001) and adapted to southern pine utilization patterns in the SE United States (Birdsey, 1996; Harmon et al., 1996; Row and Phelps, 1991, 1996; Skog and Nicholson, 1998). Table 3 presents a summary of wood products characteristics used to estimate *ex situ* C pool.

2.4. Carbon emissions of transportation and silvicultural activities

Carbon emitted by silvicultural activities was determined from Markewitz (2006) and Chapagain (2012). The C emission estimates include fuel and lubricant consumption of machinery, and emissions associated with prescribed burning and manufacture of fertilizer and herbicide. Similar to Gonzalez-Benecke et al. (2010a, 2011), C emitted in transportation of raw material from the forest to the mill was estimated according to White et al. (2005), assuming an average distance of 100 km from forest to mill, load per logging truck of 24 m^3 and fuel economy of diesel logging truck of 2.6 km l^{-1}. Details of C emissions are presented in Table 4.

2.5. Silvicultural management scenarios

To analyze the effect of silvicultural management and rotation length on C sequestration, C dynamics were simulated under four different scenarios for standard conditions of longleaf pine plantations. Initial parameters used were: SI = 23 m and Nha = 1500 trees ha^{-1}. First year survival of 75% was assumed. Clearcut harvest age was set at 75 years. We assumed prescribed burning each 3 years, starting at age 5 years, and burning residues after clearcut. Based on different management regimes reported for longleaf pine (Kush et al., 2006; Shaw and Long, 2007; Lauer and Kush, 2011), we defined the following three scenarios:

(i) U: No thinning.
(ii) T1: Thinning when the stand reaches a target BA of 26 m^2 ha^{-1} with a residual BA of 18 m^2 ha^{-1}.
(iii) T2: Thinning when the stand reaches a target SDI of 610 trees ha^{-1} with a residual SDI of 330 trees ha^{-1}. The SDI thresholds selected corresponds to 55% and 30% of maximum SDI of 1111 trees ha^{-1} reported by Gonzalez-Benecke et al. (2012).

Tree density and BA were highly dynamic (Fig. 1) over a 75 year simulation for the three scenarios selected under standard site quality and management conditions.

Table 4
Carbon emissions in silvicultural activities and product transportation to mill gate.

Activity	Description	C use (MgC ha^{-1})
Site preparation	Raking or spot piling + Weed control (application + product) + Bedding	0.357 (1)
Banded weed control	Banded Herbicide (backpack application + product)	0.091 (1)[a]
Initial fertilization (age 5)	120 kg ha^{-1} diamonium phosphate + 210 kg ha^{-1} urea	0.350 (1)
Prescribed burning	Manual burning by torch drip	0.017 (2)
Thinning	Commercial thinning	0.233 (2)
Final harvest	Clear cutting at rotation age	0.233 (2)
Transportation	Average for 24 m^3 load capacity	0.0026 (3)[b]

Note: Sources: (1) Makewitz (2006); (2) White et al. (2005); (3) Chapagain (2012).
[a] Carbon use in fertilization includes production, packing, transportation and application.
[b] Carbon use for transportation is expressed in MgC used per 24 m^3 transported.

2.6. Sensitivity analyses

A sensitivity analysis was conducted to determine the effects of changes in key parameters on total C balance. The effect of site quality was assessed by evaluating the model under contrasting SI of 16 and 30 m, which corresponds to the full range of site quality observed in longleaf pine plantations in the southeastern U.S. (Lauer and Kush, 2011; Gonzalez-Benecke et al., 2012). Initial stand density effect was evaluated by running the model with contrasting planting densities of 750 and 2250 trees ha^{-1}. Rotation length effects were assessed by evaluating the model under the thinned and unthinned scenarios for 50 and 100 years. Prescribed burning effects were evaluated by running the model under different burning regimes: frequencies of 0 (unburned), 1, 3 and 5 years. Average product life span was evaluated by changing the proportion of products in different life span classes. In the case of ST and CNS, the proportion of products in the long life classes (50 years) were changed by 25% (step up and down), distributing the residual proportion in equal parts to the rest of the life span classes. Sensitivity analyses to industrial conversion efficiencies were not considered

Table 3
Wood products characteristics.

Product	Product proportion by life span category (%)				Conversion efficiency (%)	Product class diameter (cm)	
	Long (50)	Medium-long (16)	Medium-short (4)	Short (1)		*d*	*t*
ST	50	25	0	25	65	30	20
CNS	25	25	0	50	65	20	15
PW	0	0	33	67	58	15	5

Note: ST: Sawtimber; CNS: Chip and Saw; PW: Pulpwood; *d*: minimum DBH; *t*: Merchantable diameter. Values in parenthesis indicate average life span for class (years).

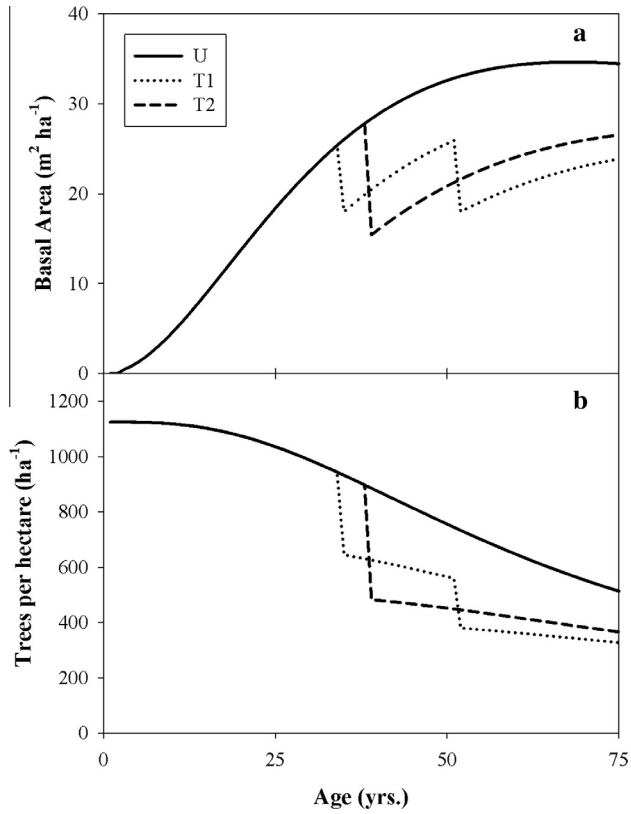

Fig. 1. Dynamics of basal area (a) and density (b) for the silvicultural management scenarios tested (U = unthinned; T1: thinning using target BA; T2: thinning using target SDI).

due to their low impact on *ex situ* C stocks (Gonzalez-Benecke et al., 2010a, 2011).

2.7. Comparison between longleaf and slash pine C stocks

We also compared estimates of longleaf pine C stocks with those of slash pine, an important commercial southern pine species, using a previously reported model for slash pine (Gonzalez-Benecke et al., 2010a) that was updated with relationships used to estimate LAI, litterfall and forest floor accumulation (Gonzalez-Benecke et al., 2011). Initial planting density was set equal for both species (i.e. 1500 trees ha^{-1}). In order to make appropriate comparisons of site productivity and taking in consideration that the reference age for SI was different for each species (50 years for longleaf and 25 years for slash pine), we defined comparable SI that represent similar site qualities. For longleaf pine stands, observed SI (base age 50 years) ranges between 16 and 29 m (Lauer and Kush, 2011; Gonzalez-Benecke et al., 2012). For slash pine, observed SI (base age 25 years) ranges between 15 and 28 m (Pienaar, 1996; Jokela et al., 2010). Therefore, we compared the species growing on sites with low, medium and high SI, corresponding to 16 and 15 m, 23 and 22 m, and 28 and 28 m, for longleaf and slash pine, respectively. We defined the categories of low, medium and high SI based on the observed range of SI for each species across the southeastern U.S. A similar SI does not mean both species are growing at the same geographic point but rather indicates a site with low, medium or high productivity within the species' range.

The comparative analysis was carried out for unthinned stands with rotation length of 75 years for both species (LL75, for longleaf pine; SL75, for slash pine), including alternative scenarios with rotation length of 25 years for slash pine (SL25) and thinning using a target BA of 26 m^2 ha^{-1} with a residual BA of 18 m^2 ha^{-1} and rotation length of 75 years for longleaf pine (LL75T). First year survival of 75% and 90% was assumed for longleaf and slash pine, respectively. For longleaf pine stands, prescribed burning every three years was included, beginning at age 5 years. For slash pine stands, no prescribed burning between planting and clearcut was assumed. We recognize that lack of prescribed fire in slash pine plantations over a 75 year period may increase the risk of wildfire, but the slash pine model does not to date include a prescribed fire option. For both species, we assumed burning of residues after clearcut harvest.

2.8. Model

Average C stock was defined as: Average C stock = Total C *in situ* (C stored in living longleaf pine trees + understory + forest floor + CWD + standing dead trees) + Total C *ex situ* (C stored in wood products ST + CNS + PW), averaged for all yearly values from the first ~300 years of management, stopping the simulation at the end of the rotation closest to the 300 year endpoint (not stopping the simulations midway into a rotation). For the scenarios with rotation length of 50, 75 and 100 years, the number of rotations simulated was 6, 4 and 3, respectively. This simulation length was chosen to be sufficiently long to approach steady state values for *ex situ* pools, while remaining within plausible bounds for consideration of future forest management scenarios. Reported values of the C emissions due to silvicultural activities, including transportation of supplies, was estimated as the mean value of the sum of all emissions during each rotation.

2.9. Statistical analysis

Three measures of accuracy were used to evaluate the "goodness of fit" between observed and predicted (simulated) values for each variable from the dataset obtained in the model validation: (i) Root mean square error (RMSE); (ii) Mean bias error (bias); and (iii) coefficient of determination (R^2). As non-linear model fitting was carried out, an empirical R^2 (Myers, 2000) was determined as:

$$R^2 = 1 - \frac{SSE/df_e}{SST/df_t} \tag{33}$$

where SSE and SST are the sum of squares of residuals and total, respectively, and df_e and df_t are the degrees of freedom of error and total, respectively.

3. Results

The model parameter estimates for the selected functions to project survival, and estimate D_{25}, D_{35}, aboveground biomass and SNA for longleaf pine trees growing in the southeastern U.S. are reported in Table 5. All parameter estimates were significant at $P < 0.05$.

The survival model was dependent on stand age, Hdom and SDI. The performance of the Nha model for the range of SI present on the dataset used for model fitting (i.e., between 20 and 30 m, see Gonzalez-Benecke et al., 2012; Table 1) and using a planting density of 1500 trees ha^{-1} showed little mortality and only small differences in survival at age 10 yrs. (between 1423 and 1417 trees ha^{-1}, for SI 20 and 29 m, respectively; data not shown). At age 70 yrs., however, the model estimated large differences in survival across SI's (between 707 and 506 trees ha^{-1}, for SI = 20 and 30 m, respectively; data not shown). For D_{25} and D_{35}, the parameter estimate for Nha had a negative value on the models, implying that trees growing in stands with the same productivity will have a smaller D_{25} and D_{35} if the stands have larger tree density.

Table 5
Parameter estimates and fit statistics of the selected functions to estimate survival, D_{25}, D_{35}, aboveground biomass and SNA for longleaf pine trees growing in southeastern U.S.

Trait	Model	Parameter	Parameter Estimate	SE	R^2	RMSE	CV %
N_j	$= N_i \cdot exp\left[\left(a_1 \cdot \frac{H_{dom_i}}{100} + a_2 \cdot SDIr_i\right) \cdot (AGE_j^{a_3} - AGE_i^{a_4})\right]$	a_1	0.00872	0.00352	0.997	45.12	6.7
		a_2	−0.01173	0.00463			
		a_3	1.25434	0.09715			
D_{25}	$= d_1 \cdot Nha^{d_2} \cdot BA^{d_3} \cdot SI^{d_4}$	d_1	94.5255	17.1452	0.987	2.18	12.4
		d_2	−0.6347	0.0075			
		d_3	0.5396	0.0117			
		d_4	0.00998	0.0024			
D_{35}	$= d_1 \cdot Nha^{d_2} \cdot BA^{d_3} \cdot SI^{d_4}$	d_1	67.7105	7.9660	0.995	1.58	8.1
		d_2	−0.582	0.00483			
		d_3	0.514	0.00755			
		d_4	0.260	0.0417			
TAGB	$= b_1 \cdot (dbh^{b_2}) \cdot (H^{b_3})$	b_1	0.0335	0.0094	0.994	40.43	11.0
		b_2	2.1535	0.0358			
		b_3	0.6903	0.0871			
Foliage	$= b_1 \cdot (dbh^{b_2}) \cdot (H^{b_3}) \cdot (AGE^{b_4})$	b_1	1.1846	0.6948	0.935	5.08	34.9
		b_2	2.3160	0.1313			
		b_3	−1.1735	0.2167			
		b_4	−0.4295	0.1381			
Branch	$= b_1 \cdot (dbh^{b_2}) \cdot (H^{b_3})$	b_1	0.00215	0.0023	0.946	24.61	41.3
		b_2	3.8375	0.1556			
		b_3	−0.9431	0.2982			
Stem	$= b_1 \cdot (dbh^{b_2}) \cdot (H^{b_3})$	b_1	0.0138	0.0034	0.996	27.99	8.9
		b_2	1.8044	0.0301			
		b_3	1.2912	0.0782			
Stemwood	$= b_1 \cdot (dbh^{b_2}) \cdot (H^{b_3})$	b_1	0.0099	0.0027	0.995	27.00	9.6
		b_2	1.8134	0.0327			
		b_3	1.3520	0.0846			
Stembark	$= b_1 \cdot (dbh^{b_2}) \cdot (H^{b_3})$	b_1	0.00932	0.0048	0.977	6.76	20.0
		b_2	1.7326	0.0663			
		b_3	0.7885	0.1706			
SNA	$= c_0 + c_1 \cdot e^{(-c_2 \cdot AGE)}$	c_0	2.8172	0.2437	0.411	0.50	14.5
		c_1	1.3218	0.2246			
		c_2	0.0366	0.0188			

Notation: N_j is surviving trees per ha at AGE j; N_i is surviving trees per ha at AGE i ($i < j$); AGE is stand age (years); $Hdom_i$ is dominant height at AGE i (m); $SDIr_i$ is the relative SDI at age i; Age is stand age (years); D_{25} is the 25th percentile of the diameter distribution (cm); Nha is surviving trees per ha (ha^{-1}); BA is stand basal area ($m^2\ ha^{-1}$); SI is site index (m); D_{35} is the 35th percentile of the diameter distribution (cm); TAGB is total above-ground biomass (kg $tree^{-1}$); dbh is stem diameter at breast height (cm); H is total height (m); Foliage is foliage biomass (kg $tree^{-1}$); Branch is branch biomass (kg $tree^{-1}$); Stem is stemwood + stembark biomass (kg $tree^{-1}$); Stemwood is stemwood biomass (kg $tree^{-1}$); Stembark is stembark biomass (kg $tree^{-1}$); SNA is projected specific needle area ($m^2\ kg^{-1}$).

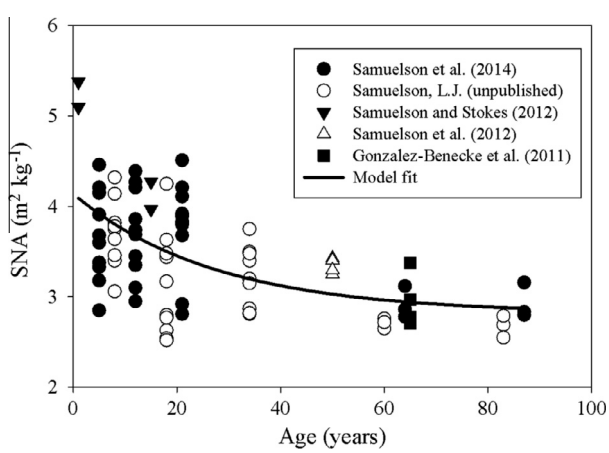

Fig. 2. Model fit to estimate specific needle area (SNA) from stand age.

The parameter estimate for age was significant only for foliage biomass. This age parameter had a negative value, implying that for the same size, older trees will have less foliage biomass. More data are needed to better evaluate the modeled trend.

Average SNA for seedlings (Fig. 2) was about 4.1 $m^2\ kg^{-1}$, and decreased to values of about 2.8 $m^2\ kg^{-1}$ as trees reached ages of 80–90 years. Stands 20 years old and younger had the largest variation in SNA.

Table 6
Summary of model evaluation statistics.

Variable	$\overline{P}$	$\overline{O}$	n	MAE	RMSE	Bias	R^2
BA	18.1	18.3	80	4.1 (22.5)	4.9 (27.1)	−0.11 (−0.6)	0.93
Nha	777.2	662.1	80	125.0 (18.9)	181.3 (27.4)	115.10 (17.4)	0.61
Hdom	15.3	15.7	80	1.1 (7.0)	1.3 (8.5)	−0.47 (−3.0)	0.99
QMD	16.5	19.1	80	2.7 (14.3)	3.3 (17.2)	−2.53 (−13.2)	0.96
AGB	107.5	94.3	80	25.2 (26.1)	35.2 (36.5)	10.89 (11.3)	0.97

Note: BA is basal area ($m^2\ ha^{-1}$); Nha is trees per hectare (ha^{-1}); Hdom is dominant height (m); QMD is quadratic mean diameter (cm); AGB is above-ground biomass (Mg ha^{-1}); $\overline{P}$ is the mean predicted value; $\overline{O}$ is the mean observed value; n is the number of observations; MAE is the mean absolute error; RMSE is the root of mean square error; bias is the bias estimator; R^2 is coefficient of determination. Values in parenthesis correspond to percentage to mean observed value.

3.1. Model validation

There was good agreement between observed and predicted values for plots used for validation of BA, Hdom, Nha, QMD and AGB. Estimated and observed values were highly correlated, with R^2 values greater than 0.61. Even though, bias was less than 13% for most of the variables tested, larger differences were observed for survival estimations (Table 6). This disagreement can be explained by increased mortality in three plots at age 12 years, where Nha was reduced from about 938 to 492 trees ha^{-1}. If those three plots were discarded, bias of Nha, QMD and AGB estimation

could be reduced to 10.6%, −11.0% and 9.2%, respectively. Another source of variation between observed and predicted AGB could be attributed to the functions used by Johnsen et al. (2014), who utilized a model that depended only on dbh, fitted from naturally-regenerated trees sampled in one site in Florida, with dbh ranging between 19 and 31 cm.

3.2. Silvicultural management effects on C sequestration

During the 300 year simulation period unthinned stands stored 26% more C than thinned stands harvested at age 75 years, and the two regimes that included thinning showed similar C sequestration. Average C stock, which corresponded to the average across the 300 year simulation period of total C *in situ* (living longleaf pine + understory + forest floor + CWD + standing dead trees + dead coarse roots) plus total C *ex situ* (C in wood products ST + CNS + PW), averaged 102, 80 and 82 MgC ha^{-1} for U, T1 and T2, respectively (Fig. 3). *In situ* C stock accounted for between 79% and 83% of the average C stock across silvicultural regimes. The relative impact on C sequestration for ST and CNS was similar, ranging between 8% and 10% of the average C stock. Due to frequent prescribed burning, the forest floor + understory components averaged ~2.5 MgC ha^{-1} (about 2% of gross C stock). Standing dead trees + CWD + dead coarse roots accounted for about 9–13% of the average C stock. The magnitude of emissions associated with silvicultural activities (including transportation) was between 2% and 4% of the average stock C stock.

At their respective rotation ages, *in situ* C stocks were 151, 105 and 115 MgC ha^{-1} for the U, T1 and T2 scenarios, respectively (Fig. 4). From that total, the C stock in living longleaf pine and the understory was 141, 95 and 106 MgC ha^{-1} for the same silvicultural regimes, respectively (data not shown). Total wood products C stock increased each rotation from 63, 48 and 51 MgC ha^{-1} during the first rotation, up to 73, 57 and 60 MgC ha^{-1} at the end of the rotation at 300 year endpoint, for the U, T1 and T2 scenarios, respectively. In general, after ~200 years, C flux in the wood products converged to stable values, reaching quasi-equilibrium minimum and maximum values (Fig. 4).

3.3. Prescribed burning effect on forest floor and ground cover C sequestration

Fig. 5 shows the dynamics of forest floor and ground cover C stock for longleaf pine stands growing under the U scenario with

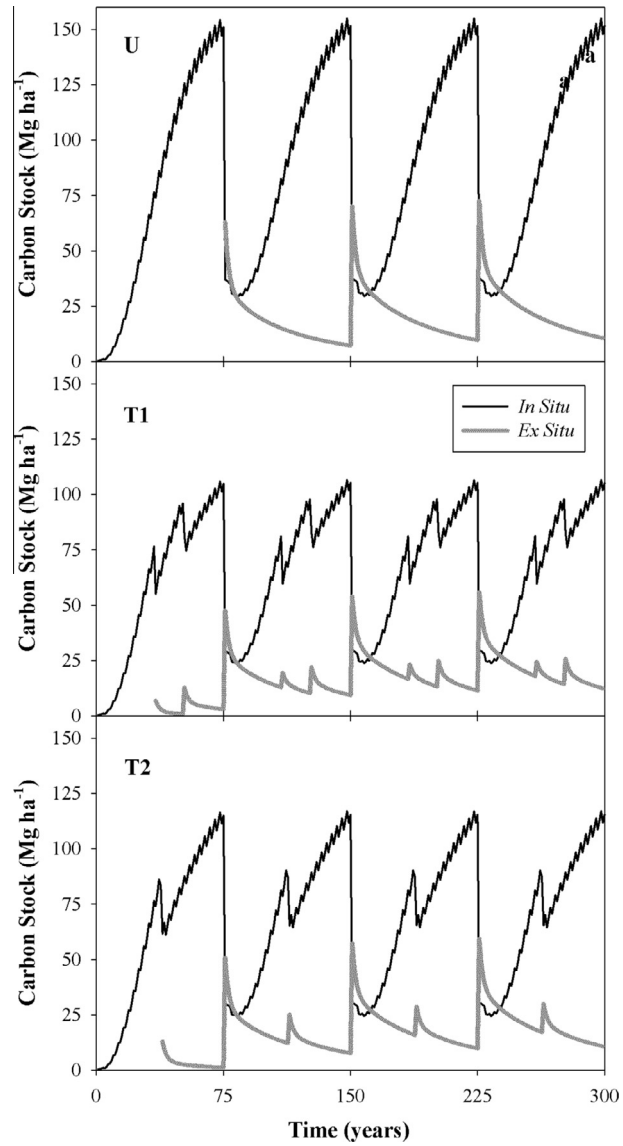

Fig. 4. Annual carbon stocks for longleaf pine plantations under different silvicultural scenarios for a 300-year simulation period (U: unthinned; T1: thinning using target BA; T2: thinning using target SDI).

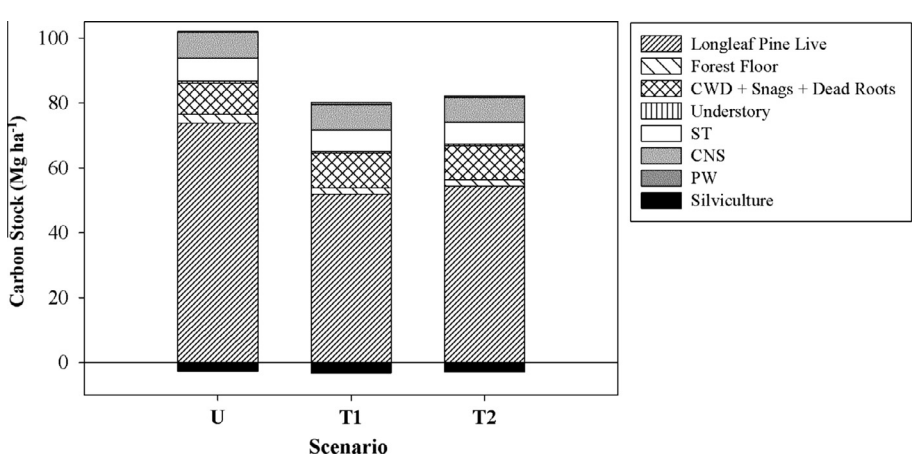

Fig. 3. Average carbon stocks for longleaf pine plantations for a 300-year simulation period under different silvicultural scenarios (U: unthinned; T1: thinning using target BA; T2: thinning using target SDI; CWD: coarse woody debris; ST: sawtimber; CNS: chip-and-saw; PW: pulpwood).

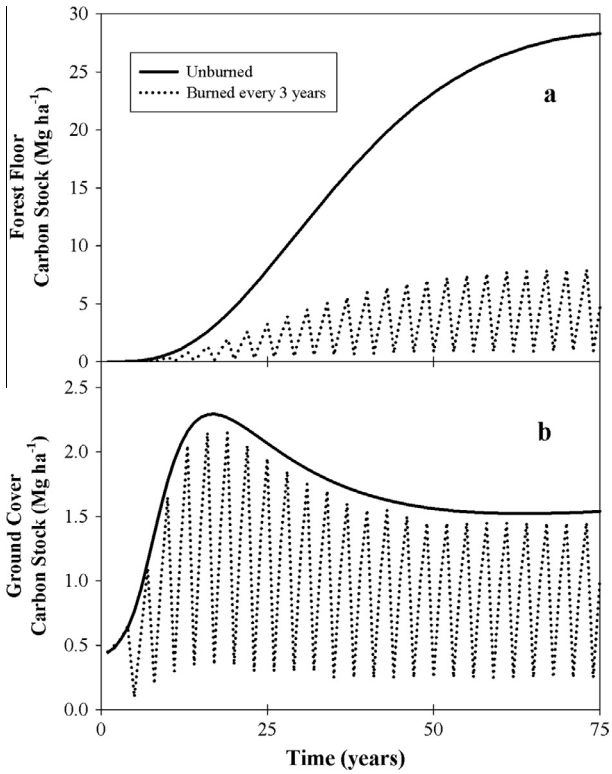

Fig. 5. Effect of prescribed burning on (a) forest floor and (b) ground cover C stock. Prescribed burning was initiated at age 5 years with a frequency of 3 years.

and without prescribed burning every 3 years. Prescribed burning had a large impact on forest floor C sequestration: at age 75 years, maximum C stock accumulation in the forest floor was 28 and 8 MgC ha^{-1}, for unburned and burned scenarios, respectively (Fig. 5a). When averaged across the rotation, C stock accumulation in the forest floor was 15 and 3 MgC ha^{-1} for the same scenarios, respectively. The impact of prescribed burning on ground cover C stock was smaller. At age 75 years the maximum C stock in ground cover was similar for the unburned and burned scenarios, between 1.5 and 1.4 MgC ha^{-1}, for the same scenarios, respectively, and averaged across the rotation was 1.7 and 1.0 MgC ha^{-1} for the same scenarios, respectively (Fig. 5b). It should be noted that the impacts of fire suppression would be a transition to a very different forest type.

3.4. Sensitivity analysis

Site quality reflected by SI was the major factor controlling C sequestration (Table 7). For example, on low productivity sites (e.g., SI = 16 m), average C stocks were about 54% lower than with the default site quality (SI = 23 m). In contrast, for high quality sites (e.g., SI = 30 m), C stocks across silvicultural regimes averaged about 74% greater than SI = 23 m (Table 7). When SI was set equal to 16 m, *ex situ* C stocks were reduced 12 MgC ha^{-1} for all management scenarios, and *in situ* C stocks were reduced 50, 29 and 31 MgC ha^{-1}, for the U, T1 and T2 scenarios, respectively. On the other hand, when SI was set equal to 30 m, *in situ* C stocks increased 75, 31 and 35 MgC ha^{-1}, and *ex situ* C stock augmented 33, 34 and 31 MgC ha^{-1}, for the U, T1 and T2 management regimes, respectively.

The effect of planting density on average C stocks was small for thinned scenarios (T1 and T2). For the unthinned scenario, reducing the initial planting density decreased average C stocks up to 17%, and increasing the planting density enhanced average C stocks by about 10%. The effect of planting density was largely reflected in *in situ* rather than *ex situ* C pools. By lowering planting density from 1500 trees ha^{-1} to 750 trees ha^{-1}, the average C stock decreased 17 and 3 MgC ha^{-1} for the U and T1 management systems, respectively (Table 7). This reduction was explained principally by a decrease in the *in situ* C stocks of 17 and 3.7 MgC ha^{-1} for the same silvicultural regimes. For the T2 scenario, there was an increase in average C stock of 2.9 MgC ha^{-1}, possibly explained by the absence of thinnings due to low SDI that never reached the threshold for thinning. The effects on *ex situ* C stocks were substantially smaller, producing positive and negative variations smaller than 1.2 MgC ha^{-1}, across all planting densities and management systems tested.

Rotation length had a larger impact than planting density on average C stock. Shortening the rotation length from 75 years to 50 years reduced the average C stock 30, 17 and 20 MgC ha^{-1} for the U, T1 and T2 management systems, respectively. When the rotation age was extended from 75 years to 100 years the magnitude of the effect was smaller: average C stocks increased 13, 10 and 11 MgC ha^{-1} for the same management systems, respectively.

Table 7
Sensitivity of average carbon stock for selected parameters under different silvicultural scenarios over a 300-year simulation period.

Parameter	Value	U		T1		T2	
		MgC ha^{-1}	Δ%	MgC ha^{-1}	Δ%	MgC ha^{-1}	Δ%
Average C stock (MgC ha^{-1})		102.0		80.0		82.2	
Site Index (m) (Default = 23)	16	39.7	−61%	39.7	−50%	39.7	−50%
	30	194.4	91%	130.1	63%	133.4	68%
Planting density (trees ha^{-1}) (Default = 1500)	750	85.1	−17%	77.5	−3%	85.1	7%
	2250	112.4	10%	79.8	0%	88.2	11%
Rotation length (years) (Default = 75)	50	72.0	−29%	63.3	−21%	62.4	−21%
	100	115.0	13%	89.9	12%	93.5	18%
Prescribed fire interval (years) (Default = 3)	0	117.1	15%	94.2	18%	95.7	21%
	1	98.4	−4%	76.0	−5%	78.0	−2%
	5	104.6	3%	82.8	4%	84.3	6%
ST percentage in long lifespan class (%) (Default = 50)	25	99.7	−2%	77.9	−3%	80.1	1%
	75	104.2	2%	82.0	3%	84.4	7%
CNS percentage in long lifespan class (%) (Default = 25)	0	97.8	−4%	75.8	−5%	78.3	−1%
	50	106.1	4%	84.1	5%	86.2	9%
PW percentage in medium-short lifespan class (%) (Default = 33)	0	101.8	0%	79.8	0%	82.0	4%
	67	102.1	0%	80.2	0%	82.5	4%

Note: Average carbon stock (MgC ha^{-1}) is the average of a ~300 year simulation period and Δ% is the percentage deviation from default parameter values used (site index = 23 m; planting density = 1500 trees ha^{-1}; rotation length = 75 years; Prescribed fire interval: 3 years; ST in long life class = 50%; CNS in long life class = 25%; PW in medium-short life class = 33%).

Similar to planting density, the effect of rotation length was largely reflected in *in situ* rather than *ex situ* C pools. By shortening rotation length to 50 years, *in situ* C stock decreased 27, 14 and 17 MgC ha^{-1} for the U, T1 and T2 management systems, respectively. Conversely, extending rotation length to 100 years, *in situ* C stock increased 15, 12 and 13 MgC ha^{-1} for the same management systems, respectively (Table 7).

If prescribed burning was implemented, changing the fire cycle interval between 1, 3 and 5 years produced little effect on C stock (Table 7). On average, across management systems tested, C sequestered in forest floor + CWD + understory was 9, 13 and 15 MgC ha^{-1} for burning cycle lengths of 1, 3 and 5 years, respectively. When prescribed burning was suppressed, C sequestered in forest floor + CWD + understory averaged 27 MgC ha^{-1}, across all management systems tested. Preliminary results from longleaf pine sites at Fort Benning, GA show that black C makes up less than 5% of soil C and considering the slow turnover of black C, the new inputs from decades of prescribed burning into the soil are small (Butnor et al., 2014). While not dismissing the contribution of char from forest floor burning, in longleaf pine systems the contribution of char is likely small relative to western pine ecosystems with longer fire return intervals and different climatic conditions (Deluca and Aplet, 2008).

Variations in average life span of wood products had little effect on average C stock, where paper products life span had the smaller effect on C storage (Table 7). Modifying average life span of ST by changing the product proportion in the long-lived class (half-life 50 years, Table 2), affected average C stocks by reductions of 2.3 to increments of 2.2 MgC ha^{-1}, across all management systems tested. The impact of the CNS half-life on average C stocks was more important than ST, affecting average C stocks by reductions of 4.2 to increments of 4.1 MgC ha^{-1}, across all management systems tested. The impact of the PW half-life on average C stocks was very small (less than 0.3 MgC ha^{-1}), across all management systems tested (Table 7).

3.5. Comparison of C sequestration between longleaf and slash pine stands

Under the default parameters used for simulations in unthinned stands harvested at age 75 years, average C stock of slash pine (SL75) stands was greater than of longleaf pine (LL75) stands. For scenarios of low, medium and high SI, average C stock of SL75 was 72, 138 and 207 MgC ha^{-1}, respectively. For LL75, average C stock was 41, 106 and 172 MgC ha^{-1}, for the same SI scenarios, respectively (Fig. 6). The peak current annual increment in average C stock of SL75 was 3.7, 7.1 and 10.5 MgC ha^{-1} year^{-1} at age 13, 11 and 10 years, for SI low, medium and high, respectively. On the other hand, LL75 peaked 1.4, 3.4 and 5.5 MgC ha^{-1} year^{-1} at age 36, 30 and 28 years, for the same SI's (data not shown; see arrows in Fig. 6). Current annual increment in average C stock of LL75 was larger than SL75 at about the same age when LL75 peaked (data not shown). When the species were compared using a rotation length of 25 years for slash pine (SL25), similar to operational rotations for industrial plantations in southeastern U.S (Gonzalez-Benecke et al., 2010a), average C stock of SL25 was lower than of

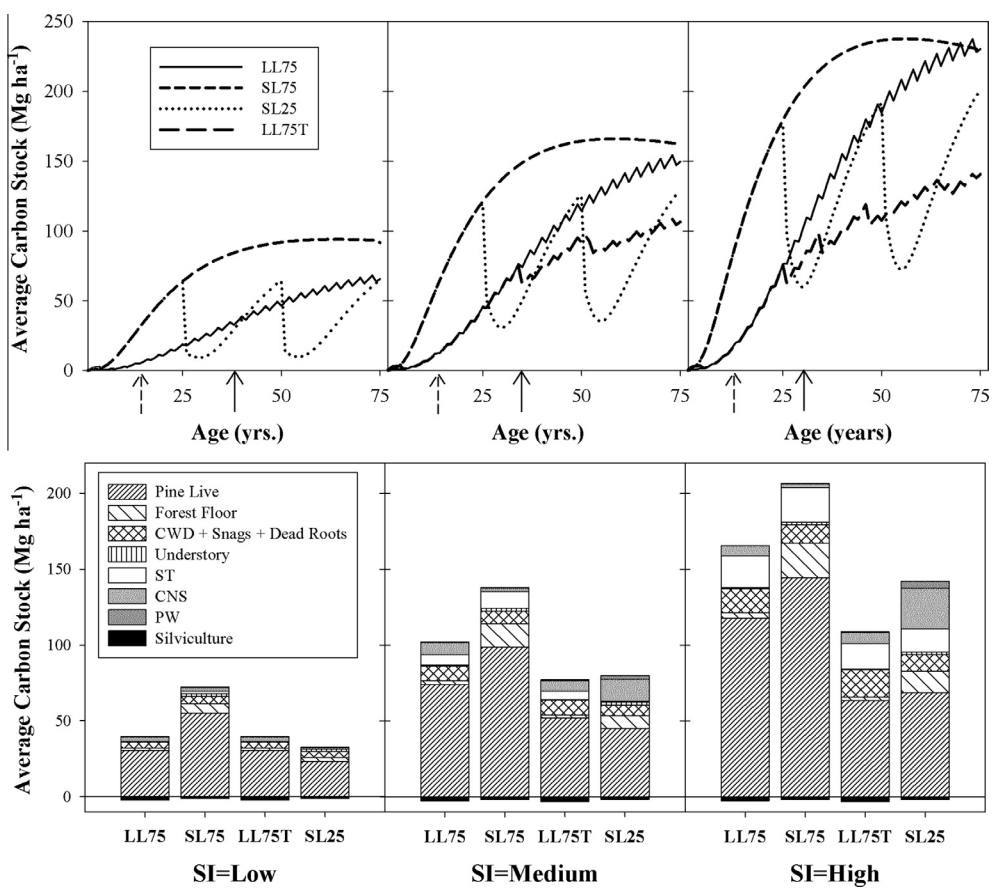

Fig. 6. Average C stock for unthinned 75 year rotation longleaf (LL75) and slash (SL75), thinned 75 year rotation longleaf (LL75T) and unthinned 25 year rotation slash (SL25) pine plantations growing under three different site qualities (site index low, medium and high). Upper panel shows the dynamics of average C stock for the first 75 years. Arrows indicate year when current annual increment in average C stock peaked for SL75 (dashed) and LL75 (solid). Lower panel shows average C stock for a 300-year simulation period (4 rotations of 75 years for LL75, SL75 and LL75T, and 12 rotations of 25 years for SL25) (CWD: coarse woody debris; ST: sawtimber; CNS: chip-and-saw; PW: pulpwood).

LL75, and was 33, 80 and 142 MgC ha^{-1} for SI of low, medium and high, respectively (Fig. 6). For thinned longleaf pine stands (LL75T) average C stock was 41, 77 and 109 MgC ha^{-1}, for scenarios of SI low, medium and high, respectively (Fig. 6). It is important to note that for the low SI scenario, LL75 and LL75T showed the same results as the stand never reached the target BA of 26 m^2 ha^{-1} that triggered thinning. For high quality sites, average C stock of SL25 (142 MgC ha^{-1}) was larger to that of thinned longleaf pine. Nevertheless, for sites of medium site quality, average C stock of SL25 (80 MgC ha^{-1}) was similar to that of LL75T (77 MgC ha^{-1}). These differences can be explained by analyzing the dynamics of average C stock showed in upper panel of Fig. 6. For the first 75 years (one rotation for SL75, LL75 and LL75T; 3 rotations for SL25), SL75 sequestered more C than LL75 for SI scenarios of low and medium, and more than LL75T for all SI scenarios. Only at the end of the rotation on high quality sites did LL75 attain a similar average C stock of the SL75. On the other hand, SL25 sequestered more C than LL75 only during first 25 years (ending age for first rotation for SL25), but after that time, LL75 sequestered more C than SL25. When compared SL25 with LL75T for medium SI, after 25 years (first rotation of SL25) there were periods of alternation that ultimately compensated for similar average C sequestration.

4. Discussion

Longleaf pine forests are characterized by longer tree longevity and longer rotations relative to other southern pines, and thus may offer opportunities for long-term C storage, but longleaf pine forests are typically of lower density with slower growth rates. Accurate determinations of C stocks and the understanding of factors controlling C dynamics are important for C offset projects and the development of sustainable management systems for longleaf pine. To validate the model we used data from a long-term experiment using plots with contrasting productivity, with SI covering the range observed for the species (see Table 1 in Gonzalez-Benecke et al., 2012). The good agreement between observed and predicted values supported the robustness of the model and its utility for assessing the effects of forest management activities on stand dynamics and C sequestration for planted longleaf pine in the southeastern U.S.

When compared with reported values of Johnsen et al. (2014), our estimates of BA and Hdom were highly correlated and closely estimated, but AGB estimates, even though they were highly correlated, had a larger bias, suggesting discrepancies between the allometric functions used. The authors reported ABG using a model that depended only on dbh, fitted from naturally-regenerated trees sampled in one site in Florida, with dbh ranging between 19 and 31 cm (Garbett, 1977). Even though our functions cover a wider range of age and tree size, further work is needed to validate the functions on other sites and expand the limits of applicability. Work is underway to create general biomass functions for the species. Our estimations are also within the range reported for the species with stands of similar structure. For thinned stands simulated (T1 and T2), at age 75 years total *in situ* C stock was about 100–110 MgC ha^{-1}. For a thinned 87 year-old naturally regenerated stand in Georgia (BA = 13.4 m^2 ha^{-1}; SI = 19 m), Samuelson et al. (2014) reported *in situ* C stock of 101 MgC ha^{-1}. For 50 year-old even-aged naturally regenerated stands thinned to BA ranging between 7 and 36 m^2 ha^{-1} (average SI = 21 m), Samuelson and Whitaker (2012) reported *in situ* C stock (not including ground cover and dead trees) of about 45–153 MgC ha^{-1}, respectively. For stands of the same age, SI and BA range, our model predicts *in situ* C stock (not including ground cover and dead trees) between 52 and 181 MgC ha^{-1} (data not shown).

Site quality was the major factor controlling C sequestration in longleaf pine stands, but the magnitude of the response interacted with rotation length and thinning regime. Similar responses have been reported elsewhere for other pine species (Balboa-Murrias et al., 2006; Gonzalez-Benecke et al., 2010a, 2011). When comparing sites with average productivity (e.g. SI = 23 m) and high productivity (e.g. SI = 30 m) under the U scenario, average C stock increased about 92 MgC ha^{-1}. Under thinned scenarios average C stock increased only 50 MgC ha^{-1}. The productivity of longleaf pine stands can be augmented by silvicultural management (including genetic improvement, seedling culture, site preparation and nutrient and competition management) (Haywood 2005, 2011, 2012; Johnsen et al., 2013; Jose et al., 2003; Loveless et al., 1989; Nelson et al., 1985; Ramsey et al., 2003). For example, at age 40 years, plots that received site preparation and fertilization at age 1 year accumulated about 50 MgC ha^{-1} more aboveground biomass than control plots (Johnsen et al., 2014). The amount of C sequestered in *ex situ* C pool was similar across management regimes for each site quality tested (about 3, 15 and 33 MgC ha^{-1} for SI = 16, 23 and 30 m, respectively). The development and application of techniques that increase productivity should increase C storage of future plantations, increasing not only *in situ* but also *ex situ* C, by extending the proportion of trees producing valuable product grades that have a longer life span.

Even though at rotation age unthinned and thinned stands reached C storage in forest products of about 100 and 70 MgC ha^{-1}, respectively (data not shown), the amount of *ex situ* C stored in long-lived products (i.e. sawtimber) was less than 45% and most of the C was sequestered in medium to short lived products. Nevertheless, the proportion of *ex situ* C stored in long-lived products increased as rotation length increased. For example, for average productivity sites (SI = 23 m), that proportion was 10% for stands harvested at age 50 yrs., and 65% for stands harvested at age 100 yrs (data not shown). On average, the *ex situ* C pool represented about 18% of average C sequestration. For slash pine, and loblolly pine stands, Gonzalez-Benecke et al. (2010a, 2011) reported that *ex situ* C pool accounted for 31% and 34% of average C sequestration, respectively. For longleaf pine forests, the *ex situ* C pool is not as important as for slash pine and loblolly pine, as the slower growth rate of longleaf pine reduces the potential of C sequestration in longer-lived forest products like sawtimber.

Prescribed burning reduced average C stock by about 16–19% and most of that reduction was observed in the forest floor. For unthinned and unburned stands, C sequestered in the forest floor was about 28 MgC ha^{-1} at age 75 years. This value is within the range of reported values for mature slash pine and loblolly pine stands (see Table A2 in Gonzalez-Benecke et al., 2012). Binkley et al. (1992) reported for a 30 year old mixed loblolly-longleaf stand with a BA of 32 m^2 ha^{-1}, forest floor biomass of about 38, 18 and 25 Mg ha^{-1} in stands unburned, burned every 2 years and burned every 4 years, respectively. We modified SI and planting density to get similar BA at the same age as Binkley et al. (1992), obtaining forest floor biomass of 37, 8 and 20 Mg ha^{-1} for the same burning scenarios, respectively (data not shown). Prescribed burning reduced C stored in the forest floor to average values of 0.2, 2.7 and 4.7 MgC ha^{-1} for burning frequencies of 1, 3 and 5 years, respectively. For 64 and 87 year-old stands, Samuelson et al. (2014) reported C stock in dead organic matter between 3 and 5 MgC ha^{-1} for stands burned every 2–3 years. Samuelson and Whitaker (2012) reported litter C stock of about 4.1–9.0 MgC ha^{-1}, respectively. For stands of the same structure our model predicts values between 2.6 and 9.4 MgC ha^{-1} (data not shown).

Our model predicts little effect of burning frequencies on C stored in ground cover. For unburned stands (thinned and unthinned), the mean C stock in ground cover was 1.8 MgC ha^{-1},

while on stands burned at frequencies of 1–5 years, the average C stock in ground cover was between 0.3 and 0.9 MgC ha^{-1}. These values are in agreement with reported data for ground cover C stock on longleaf pine stands. For example, for 64 and 87 year-old stands burned every 2–3 years, Samuelson et al. (2014) reported about 0.6 MgC ha^{-1} stored in ground cover. Brockway and Lewis (1997) reported, for a frequently burned 39 year-old stand, average C stock in herbaceous ground cover between 0.1 and 0.3 MgC ha^{-1}. Due to the low amount of ground cover biomass in longleaf stands, the benefit of prescribed burning on restoring or maintaining the diversity of herbaceous ground cover is not counteracted by the small reductions in C sequestration in ground cover.

The use of longer rotations has been suggested as one of the four major strategies to achieve increased C sequestration (Canadell and Raupach, 2008). On a regional basis, longer harvesting cycles maintains a higher mean C storage, even in a highly dynamic forest system (Cropper and Ewel, 1987). For longleaf pine, we estimated an average C stock increment of 13 and 10 MgC ha^{-1} when rotation length was increased from 75 to 100 years, and an average C stock reduction of 30 and 19 MgC ha^{-1} when rotation length was reduced from 75 to 50 years, on unthinned and thinned stands, respectively. A similar response was observed for other southern pine species (Gonzalez-Benecke et al., 2010a, 2011). The results of Liski et al. (2001) also support these results. They concluded that longer rotations increase C sequestration for *Pinus sylvestris* L. in Finland, with an approximate 12 MgC ha^{-1} increase in average C stock when rotation length was increased from 60 to 90 years.

The magnitude of the emissions associated with silvicultural management activities was low (between 2% and 4% of gross C stock), but since this emitted C comes from fossil fuels it should be noticed that after 25–50 rotations (between 1875 and 3750 yrs. in future), the decrease of fossil C pool resulting from silvicultural activities across all that time would be of the same magnitude of total C stocks, thus leading to a null average C stock. Although it is unlikely that site conditions and management plans can be projected so far into the future it is reasonable to conclude that longleaf pine plantations would more efficiently contribute to long-term C sequestration if the energy necessary for silvicultural practices were to come from renewable energy sources.

There is currently great interest in uneven aged silvicultural systems to manage older longleaf pine stands (Guldin, 2006; Mitchell et al., 2006; Brockway et al., 2014). The model developed in this study may have limited applications to stands that are managed with individual tree or group selection in order to restore or maintain an uneven aged structure. Models of these more complex longleaf stands should incorporate spatial relationships, including competition effects, and regeneration processes (e.g. Loudermilk et al., 2011). It is possible that management approaches, similar to the Stoddard-Neel approach (Jack, 2006), could result in greater stocks of stored carbon as well as better provision of wildlife habitat, plant diversity, and other ecosystem services, but this remains to be tested.

At age 75 years, unthinned slash pine and longleaf pine reached a similar average C stock on medium and high quality sites. Similar results have been reported when comparing productivity of longleaf pine and other southern pine species. For example, Schmidtling (1986) reported that at age 9 years growth of slash pine was greater than longleaf pine, but the two species were of similar size after age 25 years. Johnsen et al. (2014) reported similar biomass of loblolly and longleaf pine stands at age 40 years. Even though unthinned slash pine and longleaf pine reached similar average C stocks at age 75 years, on average, across all rotations, slash pine sequestered more C due to longer periods with greater growth. In contrast, when unthinned longleaf pine with 75 year rotation length was compared with three slash pine rotations of 25 years, longleaf pine sequestered more C. The periods of low C sequestration after slash pine's harvest, with even negative C fluxes for several years (Bracho et al., 2012), explains this last result. In contrast, for medium quality sites, C sequestration was similar between thinned 75-year rotation longleaf pine and unthinned 25-year rotation slash pine. Our results support the possible use of unthinned and long rotation longleaf pine stands for C offset projects when additionally is determined using slash pine with operational rotation length as the "business as usual" condition. Even though Remucal et al. (2013) concluded that low stand density longleaf pine stands managed primarily for ecological restoration may not be adequate for C offset projects, our results suggest that in medium quality sites, thinned longleaf pine can sequester similar amount of C than unthinned 25-year rotation slash pine.

5. Conclusion

We developed a model to account for C stock and fluxes in longleaf pine plantations ecosystems in the southeast U.S. The model performed accurately when tested against reported C measurements over a wide range of stand ages and site qualities. Using the model to evaluate the effects of silvicultural management systems on C sequestration over a 300 year simulation period, we conclude that: (i) site productivity was the major factor driving C sequestration in longleaf pine stands; (ii) increasing rotation length increased C storage; (iii) prescribed burning had a small effect on C sequestration; and (iv) for medium quality sites, C sequestration of thinned 75-year rotation longleaf pine stands was similar than unthinned 25-year rotation slash pine stands. This longleaf pine plantation C sequestration model is a useful tool for regional C stock assessments or for C credit verification.

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