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Understory plant biomass dynamics of prescribed burned *Pinus palustris* stands

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abstract

Longleaf pine (*Pinus palustris* Mill.) forests are characterized by unusually high understory plant species diversity, but models describing understory ground cover biomass, and hence fuel load dynamics, are scarce for this fire-dependent ecosystem. Only coarse scale estimates, being restricted on accuracy and geographical extrapolation, are available. We analyzed the dynamics of ground cover biomass under different prescribed burning regimes in longleaf pine stands in the southeastern United States. We developed a set of functions to simulate ground cover biomass dynamics in stands of varying age, basal area and fire management history. The subsequent models allow for estimation of ground cover biomass for unburned stands and living woody and herbaceous ground cover biomass for burned stands. Woody ground cover was highly reduced as fire frequency increased, and also affected by stand basal area when time since last burning was longer than two years. Herbaceous ground cover was affected little by burning frequency but was reduced as basal area increased. This novel model system is a useful tool that can be incorporated into fire management and carbon balance models.

1. Introduction

Longleaf pine (*Pinus palustris* Mill.) forests harbor a diverse community of plant species in the ground cover layer, with as many as 40 species per square meter (Peet and Allard, 1993). High plant diversity of the ground cover layer is maintained by frequent fire and an open discontinuous tree canopy (Glitzenstein et al., 1995). Prescribed burning is an important management tool in longleaf forests, with recommended burning frequencies of at least once per 10 years but ideally, in many cases, every two to four years (Chapman, 1932; Glitzenstein et al., 2003; Loudermilk et al., 2011). The benefits of periodic prescribed fire in longleaf pine ecosystems include not only restoration of diverse native plant communities, but also seedbed preparation for longleaf seed germination and control of fuel quantity and quality, which affects fire intensity (Brockway et al., 2006; Harrington, 2011) and thus plant community structure (Hiers et al., 2007). Without frequent fire, longleaf ecosystems become susceptible to woody plant encroachment and may transition to hardwood dominated forests (Quarterman and Keever, 1962; Hartnett and Krofta, 1989).

Ground cover biomass has been shown to be linearly related to ground cover species richness and proportional to stand productivity in longleaf pine-wiregrass systems (Kirkman et al., 2001). Similarly, Brockway and Lewis (1997) demonstrated that recurrent fire over four decades increased ground cover diversity and the standing biomass of grasses and all forbs relative to less frequent burn intervals in a flatwoods longleaf pine-wiregrass ecosystem (Brockway and Lewis, 1997). In addition, the contribution of the ground cover layer to annual net primary productivity may be significant (Mitchell et al., 1999) and important in assessment of carbon stocks in low density stands (Samuelson et al., 2014). While fire volatilizes carbon, the immediate loss of plant carbon may not constitute a long-term loss in carbon stocks because of understory growth following fire.

Relationships between the forest understory and overstory offer a useful framework to understand the impact of forest management on species and community distribution and productivity. Management activities such as thinning and prescribed burning will alter those relationships. For example, thinning will reduce the number of trees and hence the basal area and leaf area index of the overstory, thereby altering the environment for ground cover species, and fire will directly affect the composition and biomass of the ground cover layer. Longleaf pine has wide ecological

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amplitude (Fig. 1) and ground cover biomass across the species range varies not only with fire interval and stand structure but also soils, climate, management history and native vegetation (Hiers et al., 2003; Scott and Burgan, 2005). However, models for prediction of ground cover biomass, and hence fuel load, are scarce and only provide coarse scale estimates (Scott and Burgan, 2005; Ottmar et al., 2009) or are restricted on accuracy and geographical extrapolation (Parresol et al., 2012).

In this study we analyzed the dynamics of ground cover understory biomass of longleaf pine stands with varying stand structure and fire management history in stands located in Georgia, Louisiana and North Carolina (Fig. 1). The objectives of the study were: (1) develop models to estimate ground cover biomass for unburned and burned longleaf pine stands, (2) develop models to estimate ground cover biomass partitioning into woody and herbaceous plants, and (3) assess the impact of stand density and prescribed fire frequency on ground cover biomass dynamics.

2. Materials and methods

2.1. Ground cover biomass for unburned stands

Ground cover biomass (GC_B) in all cases is defined as all live and dead plants <1 m in height. Because the majority of reports in the literature are for burned longleaf pine stands, we included data from two other southern pine species, loblolly pine (*Pinus taeda* L.), and slash pine (*Pinus elliottii* Engelm.), in modeling the dynamics of GC_B under unburned conditions (Bracho et al., 2012; Clark et al., 2004; Gholz and Fisher, 1982; Haywood and Grelen, 2000; Kush et al., 1999; Neary et al., 1990; Subedi et al., 2014; Vogel et al., 2011). In all reports in Table A1, GC_B was measured using clip plots (0.2–4.0 m^2) located randomly within a stand. The number of clip plots ranged between 4 and 20 for each site. Table A1 summarizes stand characteristics used for model fitting (all data from literature).

For the stands without periodic prescribed burning, GC_B was correlated to overstory basal area (BA, $m^2\ ha^{-1}$) and stand age (years). After testing several equations, the model selected was:

$$GC_B = a_1 \cdot \exp^{(-a_2 \cdot BA)} + \varepsilon_1 \quad (1)$$

where a_1 and a_2 are curve fit parameter estimates, exp is base of natural logarithm and ε_1 is the error term, with $\varepsilon_1 \sim N(0, \sigma_1^2)$. Stand age was not a significant factor in the model.

2.2. Ground cover biomass for burned stands

2.2.1. Recovery following fire

In order to estimate GC_B for longleaf pine stands subjected to periodic prescribed burning, a biomass consumption recovery function was fitted using data from the Fire and Environmental Research Applications Team (FERA, http://depts.washington.edu/nwfire/dps/). The dataset consisted of B_{GC} sampled in seven stands in the sandhills and eight stands in the flatwoods (Ottmar et al., 2000, 2003). In addition, two plots from one experimental site in Alabama (Kush et al., 1999) and two plots from one experimental site in Louisiana (Haywood, 2011) were included into the dataset. Stands ranged in time since last prescribed fire (TSF) from 1 to 23 years and in pine BA from 1.5 to 24.6 $m^2\ ha^{-1}$. For each report, all data were expressed as a fraction of the GC_B of the unburned condition. For stands reported by Ottmar et al. (2000, 2003), the average GC_B at TSF = 20 years was assumed to be the unburned condition that had a value = 1. Assuming an asymtotic response within the range of fire intervals under consideration, a sigmoidal model was fit to data of GC_B recovery after fire ($recGC_B$, the proportion of ground cover biomass on burned stands relative to initial unburned biomass), and TSF:

$$recGC_B = \frac{1}{1 + b_1 \cdot \exp^{(-b_2 \cdot TSF)}} + \varepsilon_2 \quad (2)$$

where b_1 and b_2 are curve fit parameter estimates, exp is base of natural logarithm and ε_2 is the error term, with $\varepsilon_2 \sim N(0, \sigma_2^2)$.

2.2.2. Biomass partitioning

For stands with periodic prescribed burning, the partitioning of GC_B into herbaceous and woody components was analyzed using data collected from longleaf pine stands located on Fort Benning Georgia (GA), Fort Polk Louisiana (LA) and Camp Lejeune North Carolina (NC) (Fig. 1). Data were collected from five stands in GA in 2012, 14 stands in LA in 2013, and 9 stands in NC in 2014.

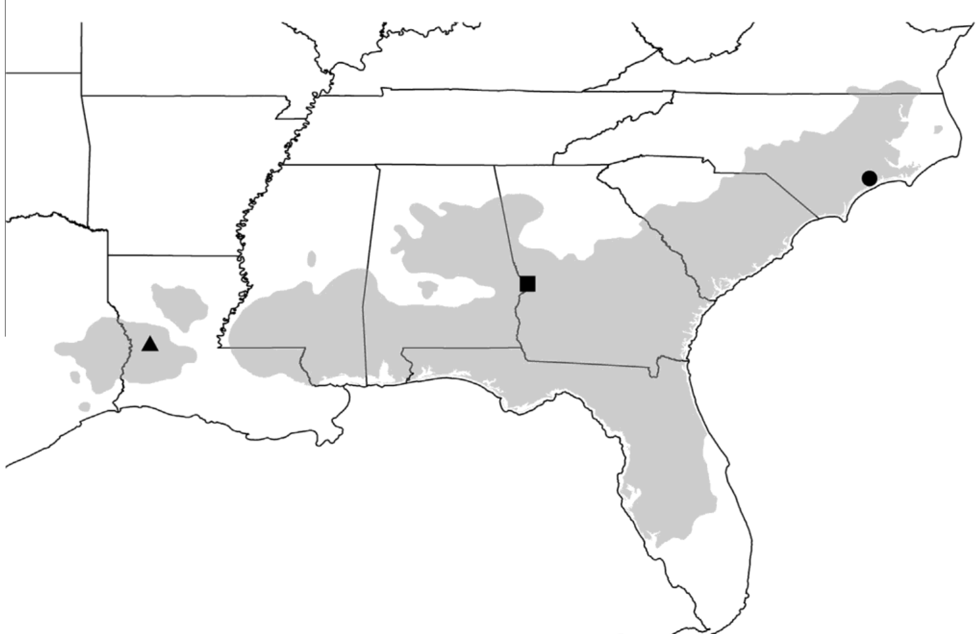

Fig. 1. Location of the sampling sites in Fort Polk Louisiana, LA (triangle), Fort Benning Georgia, GA (square), and Camp Lejeune North Carolina, NC (circle) within the species natural distribution range (shaded area).

Table 1
Parameter estimates and fit statistics of the selected functions to estimate GCB, recGCB, LHp and LWp for longleaf pine stands growing in southeastern U.S.

Variable	Model	Parameter	Parameter estimate	SE	n	R^2	RMSE	CV%
GC_B	$= a_1 \cdot \exp^{(-a_2 \cdot BA)}$	a_1	5.9272	0.3288	35	0.942	0.986	26.8
		a_2	0.0451	0.0061				
$recGC_B$	$= \frac{1}{1+b_1 \cdot \exp^{(-b_2 \cdot TSF)}}$	b_1	14.2946	8.5931	14	0.967	0.131	20.1
		b_2	1.2124	0.2615				
LHp	$= c_1 \cdot (TSF^{c_2}) \cdot (BA^{c_3}) \cdot (age^{c_4})$	c_1	0.3416	0.1399	28	0.832	0.139	49.4
		c_2	-1.1361	0.2376				
		c_3	-0.4461	0.1604				
		c_4	0.4316	0.1748				
LWp	$= \frac{1}{1+d_1 \cdot \exp^{(d_2 \cdot \ln(TSF)+d_3 \cdot \ln(BA))}}$	d_1	118.6	12.7600	28	0.850	0.175	50.4
		d_2	-2.4413	0.6345				
		d_3	-0.8725	0.3541				

Notation: 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; Age is stand age (years); BA is stand basal area (m^2 ha^{-1}); TSF is time since last prescribed fire (years); SE is standard error, n is number of observations; R^2 is coefficient of correlation; RMSE is root of mean square error; CV% coefficient of variation (percentage).

Table 2
Summary of model evaluation statistics for unburned southern pines and burned longleaf pine stands in Georgia, Louisiana and North Carolina.

Type of validation	Variable	$\overline{P}$	$\overline{O}$	n	RMSE	Bias	R^2
Leave-one-out cross-validation	GC_B [a]	4.05	4.02	27	1.07 (26.6)	-0.03 (-0.7)	0.63
	$GC_{B\text{-}LW}$	0.30	0.28	28	0.21 (75.1)	-0.018 (-6.4)	0.81
	$GC_{B\text{-}LH}$	0.35	0.35	28	0.19 (53.7)	-0.0006 (-0.2)	0.59
Overall	GC_B [b]	1.63	1.39	28	0.60 (43.3)	0.24 (17.1)	0.65
	$GC_{B\text{-}LW}$ [c]	0.58	0.51	28	0.40 (78.7)	0.07 (13.0)	0.48
	$GC_{B\text{-}LH}$ [d]	0.39	0.35	28	0.21 (60.4)	0.04 (12.3)	0.46
	$GC_{B\text{-}Dead}$ [e]	0.66	0.53	28	0.32 (60.0)	0.13 (24.3)	0.71

Note: GC_B is the total biomass of the ground cover vegetation (Mg ha^{-1}); $GC_{B\text{-}LW}$ is the biomass of living woody ground cover vegetation (Mg ha^{-1}); $GC_{B\text{-}LH}$ is the biomass of living herbaceous ground cover vegetation (Mg ha^{-1}); $GC_{B\text{-}Dead}$ is the biomass of dead ground cover vegetation (Mg ha^{-1}); $\overline{P}$ is the mean predicted value; $\overline{O}$ is the mean observed value; n is the number of observations; RMSE is the root of mean square error; Bias is the bias estimator; R^2 is the coefficient of determination. Values in parenthesis correspond to percentage to mean observed value.

[a] Using data for unburned southern pine stands shown in Table A1.
[b] Using functions 1 and 2.
[c] Using functions 1, 2 and 3.
[d] Using functions 1, 2 and 4.
[e] Computed as the difference between estimated GC_B and estimated ($GC_{B\text{-}LW} + GC_{B\text{-}LH}$).

Stands encompassed a range in soil drainage classes (https://soilseries.sc.egov.usda.gov/), age, forest structure and TSF at the time of sampling (Table A2). The herbaceous layer in GA stands was dominated by graminoids such as *Andropogon* spp. and *Schizachyrium scoparium* (Michx.) Nash, herbaceous species such as *Desmodium* spp., and *Lespedeza* spp., and composites such as *Eupatorium* spp., and *Solidago* spp. (Knapp et al., 2011). In LA stands, ground cover was dominated by *Schizachyrium* spp., *Panicum* spp., and *Dichanthelium* spp. (Haywood and Harris, 1999). The herbaceous ground layer in NC stands consisted of *Aristida* spp., *Andropogon* spp., *Schizachyrium* spp., *Panicum* spp., *Dichanthelium* spp., and *Rhynchospora* spp. (Knapp et al., 2008). Woody ground cover (<1 m in height) in GA stands was dominated by *Ilex glabra*, *Rubus cuneifolius* and *Quercus* spp. (Dale et al., 2002). In LA stands, woody ground cover was dominated by *Ilex vomitoria*, *Vaccinium* spp., *Myrica cerifera* and *Gaylussacia* spp. (Scott, 2014). The woody ground cover in NC stands was dominated by *Ilex* spp. and *Cyanococcus* spp. (Hu, 2011). All stands were even-aged and planted, with the exception of the 64 and 87-year-old stands in GA and the 65 and 79-year-old stands in NC, which were relatively even-aged but naturally regenerated. Data from GA were previously reported by Samuelson et al. (2014). Stands ranged in age from 5 to 87 years, in BA from 0.1 to 31.5 m^2 ha^{-1} and in TSF from 1 to 4 years. In each stand, ground cover samples were collected over the last week of May and first week of June from five to ten 1 m^2 sample rings in each of four 0.04 ha circular subplots established in a stand, following Samuelson et al. (2014). All vascular plants (including dead and living shrubs and herbaceous plants) <1 m in

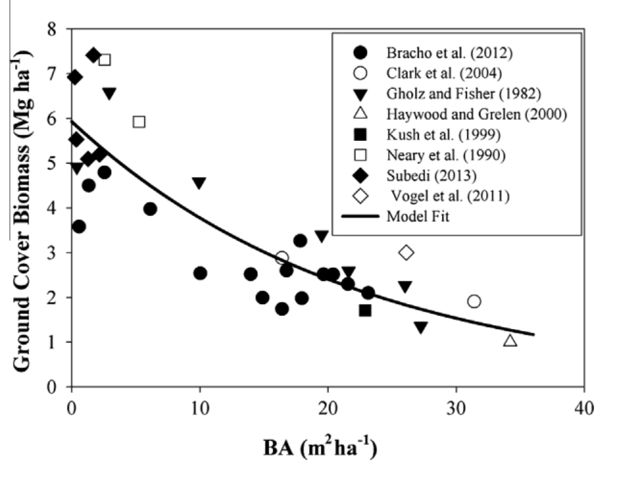

Fig. 2. Relationship between overstory basal area (BA) and ground cover biomass (GC_B) for southern pine stands without periodic prescribed burning.

height were clipped at the root collar. Biomass was oven-dried at 70 °C for 72 h and weighed and classified as $GC_{B\text{-}LW}$ (living woody plants including vines), $GC_{B\text{-}LH}$ (living forbs, ferns, graminoids and legumes), and $GC_{B\text{-}Dead}$ (all dead material pooled).

Using the data shown in Table A2, models to estimate GC_B partitioning into woody and herbaceous ground cover biomass were fitted using the ratios of living herbaceous to GC_B (LHp: $GC_{B\text{-}LH}/GC_B$) and living woody to total GC_B (LWp: $GC_{B\text{-}LW}/GC_B$). The proportion of dead ground cover to GC_B (Dp: $GC_{B\text{-}Dead}/GC_B$) was calculated as Dp = 1 – LHp – LWp. The variables considered as possible covariates were TSF, BA, SI (site index at base age 50 years) and stand age. In order to test which variables should be included in the final model, a logarithmic transformation of the response variable was carried out and a stepwise procedure was used. A threshold significance value of 0.15 and 0.05 was used for variable selection criteria for a variable to enter and stay, respectively; and the variance inflation factor (VIF) was monitored to detect multicollinearity among explanatory variables. Variables included in the model with VIF larger than 5 were discarded, as suggested by Neter et al. (1996). After testing several non-linear equations, the models selected were:

$$LHp = c_1 \cdot (TSF^{c_2}) \cdot (BA^{c_3}) \cdot (age^{c_4}) + \varepsilon_3 \qquad (3)$$

where c_1 to c_4 are curve fit parameter estimates and ε_3 is the error term, with $\varepsilon_3 \sim N(0, \sigma_3^2)$.

$$LWp = \frac{1}{1 + d_1 \cdot \exp^{(d_2 \cdot \ln(TSF) + d_3 \cdot \ln(BA))}} + \varepsilon_4 \qquad (4)$$

where d_1 to d_3 are curve fit parameter estimates and ε_4 is the error term, with $\varepsilon_4 \sim N(0, \sigma_4^2)$.

2.3. Comparison against published models

The results from the combination of equations to predict $GC_{B\text{-}LH}$ (Eqs. (1)–(3)) and $GC_{B\text{-}LW}$ (Eqs. (1), (2) and (4)) were compared against the models reported by Parresol et al. (2012). The authors presented equations to estimate separately ground cover living biomass in seedlings, shrubs and vines (grouped as $GC_{B\text{-}LW}$), as well as grasses and forbs (grouped as $GC_{B\text{-}LH}$).

2.4. Model fitting and evaluation

All statistical analyses were performed using non-linear model fitting in SAS 9.3 (SAS Inc., Cary, NC, USA). The predictive ability of Eqs. (1), (3) and (4) was evaluated by using leave-one-out cross-validation (Neter et al., 1996). An overall validation of the models was also carried out using data shown in Table 2. For each stand, of known TSF, BA and stand age, we used Eqs. (1)–(4) to estimate ground cover biomass. Estimated $GC_{B\text{-}Dead}$ was computed as the difference between estimated GC_B and estimated ($GC_{B\text{-}LW} + GC_{B\text{-}LH}$). We recognize that there is a lack of independency for the overall validation, as data used for validation was also used to fit the models to estimate LHp and LWp, but the estimations of GC_B, $recGC_B$, that are the basis to estimate $GC_{B\text{-}LW}$, $GC_{B\text{-}LH}$ and $GC_{B\text{-}Dead}$, are completely independent and provide a robust basis for validation.

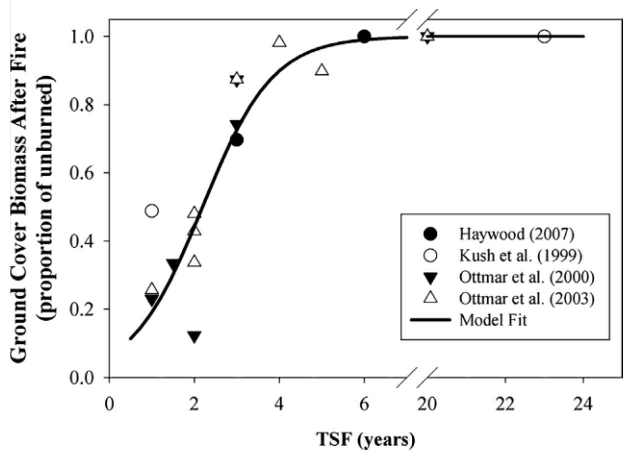

Fig. 3. Mean ratio of living herbaceous to total GC_B (LHp), ratio of living woody to total GC_B (LWp) and ratio of dead to total GC_B (Dp) for longleaf pine stands in Georgia, Louisiana and North Carolina (error bars represent standard error) with different times since last prescribed fire (TSF).

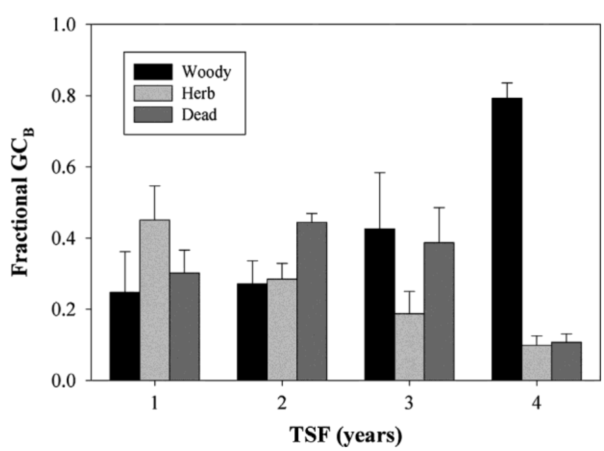

Fig. 4. Model fit to estimate ground cover biomass recovery from time since last prescribed fire (TSF) after fire as a proportion of initial biomass.

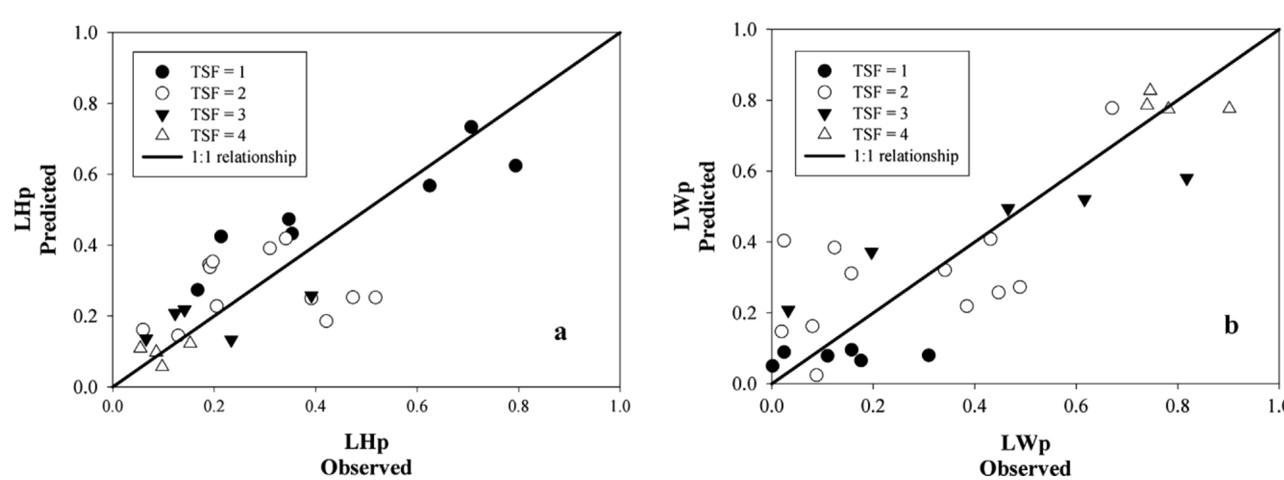

Fig. 5. Relationship between observed and predicted (a) ratio of living herbaceous (LHp) and (b) ratio of living woody (LWp) to total ground cover biomass for different time since last prescribed fire (TSF) for longleaf pine stands in Georgia, Louisiana and North Carolina.

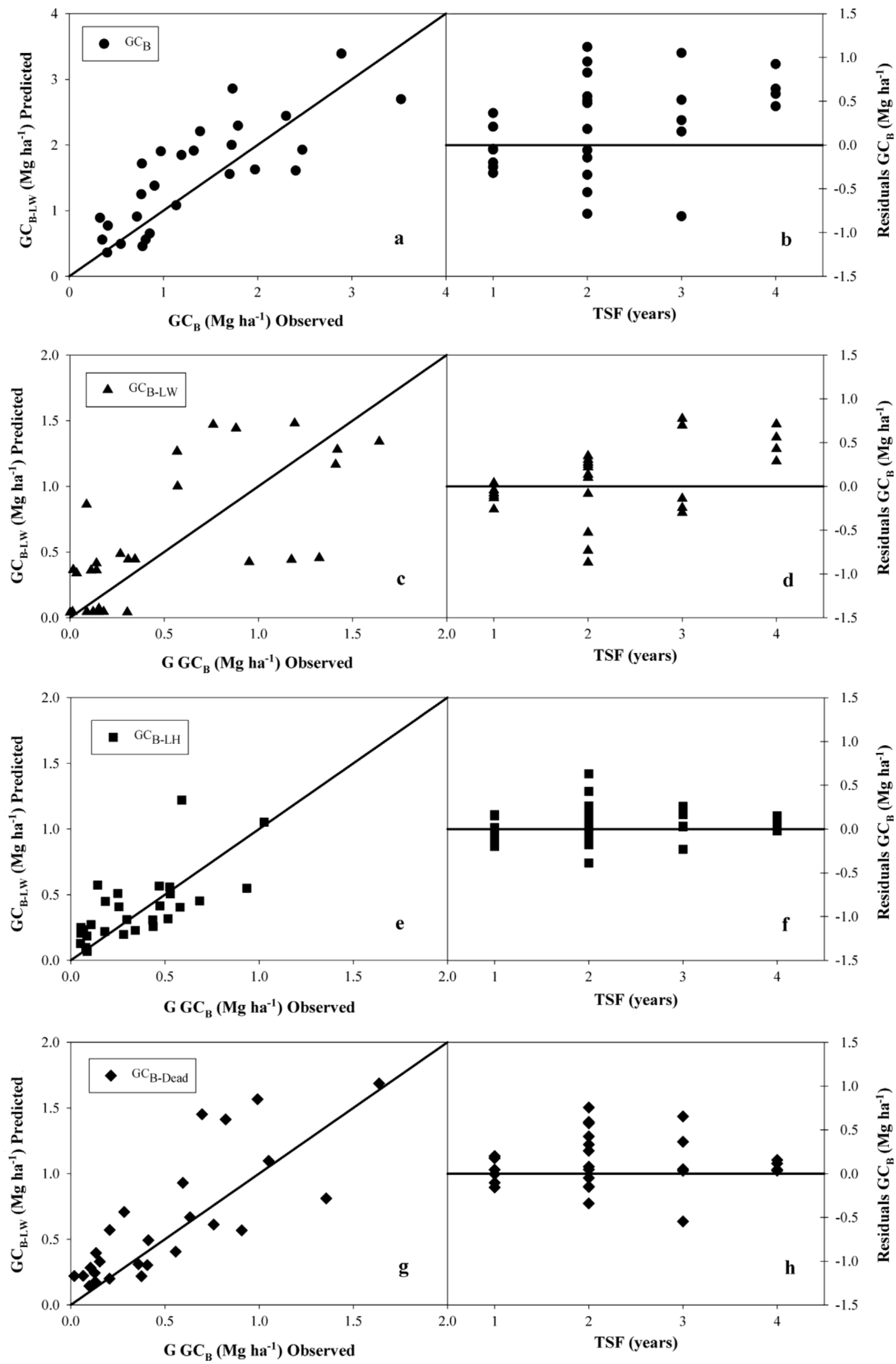

Fig. 6. Overall simulation validation of total ground cover biomass (GC_B) (a and b), living woody biomass ($GC_{B\text{-}LW}$) (c and d), living herbaceous biomass ($GC_{B\text{-}LH}$) (e and f) and dead ground cover biomass ($GC_{B\text{-}Dead}$) (g and h), for longleaf pine stands in Georgia, Louisiana and North Carolina. Observed versus predicted (simulated) values (a, c, e, d) and residuals (predicted-observed) versus time since last prescribed fire (TSF) (b, d, f, h) relationships. Solid line represents the 1-to-1 relationship. All calculations were based on known BA, stand age and TSF.

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:

$$R^2 = 1 - \frac{SSE/df_e}{SST/df_t} \quad (5)$$

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. Paired *t*-tests were conducted to compare estimates against reported models.

2.5. Modeling the effect of prescribed burning on GC_B

The effect of prescribed burning on GC_B was computed using the consumption standards reported by Reinhardt (2003) and Ottmar et al. (2006), where consumption factors of 0.93 and 0.85 were assumed for herbaceous and woody ground cover, respectively. The growth and yield model reported by Gonzalez-Benecke et al. (2012a,b) was used to simulate stand dynamics in BA. Initial parameters assumed were: Age = 40 yrs.; SI = 23 m, stand density = 250 trees ha^{-1}; BA = 16.5 m^2 ha^{-1}. Four burning frequencies were tested: 1, 3, 5 and unburned. The model was run for 10 years.

3. Results

3.1. Model fitting

The model parameter estimates for the selected functions to estimate ground cover biomass, ground cover biomass recovery after fire, ratio of living herbaceous to total GC_B and ratio of living woody to total GC_B are reported in Table 1. All parameter estimates were significant at $P < 0.05$, and all models showed $R^2 > 0.83$. The model selected to predict LHp depended on TSF, BA and stand age. On average, as TSF and BA increased, LHp decreased (negative sign of parameter estimates for TSF and BA). Older stands with the same TSF and BA had larger LHp (positive sign of parameter estimates for stand age). The model selected to predict LWp depended only on stand BA and TSF. On average, as TSF and BA increased, LWp decreased.

Fig. 2 shows the relationships between BA and GC_B for southern pine stands without periodic prescribed burning. As BA increased, GC_B of unburned stands decreased, and, on average, GC_B was 6 Mg ha^{-1} after the first year (BA < 1 m^2 ha^{-1}) and 2.4 Mg ha^{-1} at a BA of 20 m^2 ha^{-1}.

Fig. 3 shows the mean values of fractional GC_B for varying TSF for the 28 stands in GA, LA and NC. The relative abundance of woody (LWp) and herbaceous (LHp) ground cover biomass changed depending on the number of years since last fire. For example, on average, one year after prescribed fire (TSF = 1), living herbaceous and living woody ground cover biomass represented 25% and 45% of GC_B, respectively. Four years after prescribed fire (TSF = 4), living herbaceous and living woody ground cover biomass represented 79% and 10% of GC_B, respectively (Fig. 4).

Initially, we fit the model for recGC_B separately for each type of site (not shown). After pooling all data, a single model was finally selected due to no further improvement using separate models. Fig. 4 shows the relationship between TSF and recGC_B for all sites. On average, after one and four years since prescribed fire, ground cover recovered 19% and 90% of the pre-fire biomass, respectively.

3.2. Model validation

Fig. 5 shows the dynamics of observed and predicted LHp and LWp for TSF ranging between 1 and 4 years. There was a good correlation between observed and predicted LHp and LWp across all stands. As TSF increased, LHp decreased and LWp increased. The models captured most of the variability observed at different TSF. The inclusion of BA and stand age as co-variables allowed the models to capture more variability of LHp (Fig. 5a) and LWp (Fig. 5b) for

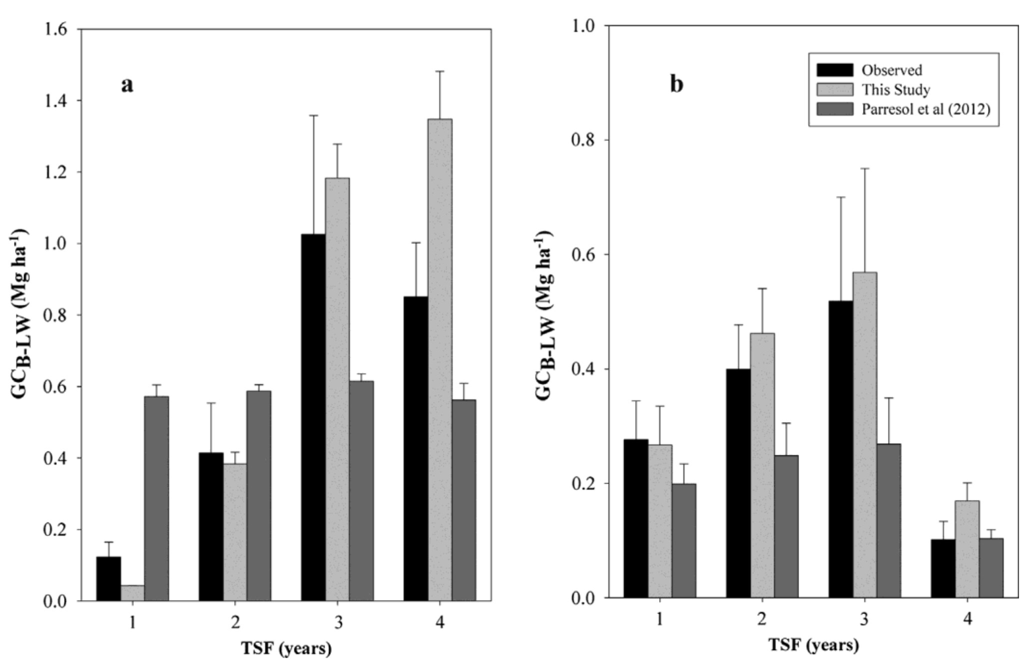

Fig. 7. Comparison between mean observed (black bars) and predicted (gray bars) living woody ($GC_{B\text{-}LW}$, left panel) and herbaceous ($GC_{B\text{-}LH}$, right panel) ground cover biomass after last prescribed fire (TSF) for longleaf pine stands in Georgia, Louisiana and North Carolina.

any given value of TSF, thus improving the agreement between observed and predicted values.

There was a good agreement between observed and predicted values of ground cover biomass for the 28 stands measured in GA, LA and NC. Even though predicted and observed values were moderately correlated for $GC_{B\text{-}LW}$ and $GC_{B\text{-}LH}$, bias was smaller than 13%. Larger error, but high correlation, was observed for $GC_{B\text{-}Dead}$ estimations, with a mean absolute bias of about 0.13 Mg ha^{-1} (Table 2).

When calculations of ground cover biomass were based only on known BA, stand age and TSF (overall validation), there was good correlation between observed and predicted values for the 28 stands measured in GA, LA and NC (Fig. 6). In all cases, the intercept of the relationship between observed and predicted values was not different from zero ($P > 0.29$). The slope of that relationship was not different from 1 only for $GC_{B\text{-}LW}$ ($P = 0.10$) and $GC_{B\text{-}LH}$ ($P = 0.08$). Paired *t*-tests indicated no difference between observed and predicted values for $GC_{B\text{-}LW}$ ($P = 0.13$) and $GC_{B\text{-}LH}$ ($P = 0.15$), but differences for GC_B ($P = 0.01$) and $GC_{B\text{-}Dead}$ ($P = 0.02$). For GC_B, $GC_{B\text{-}LH}$ and $GC_{B\text{-}Dead}$, residuals were centered on zero, but for $GC_{B\text{-}LW}$ the estimations were sensitive to TSF (Fig. 6d).

3.3. Comparison against reported functions

Fig. 7 shows the comparison between observed (black bars) and predicted living ground cover biomass using the models reported in this study (light gray bar) and the models reported by Parresol et al. (2012) (dark gray bar). There was a good agreement between observed and predicted values using the models reported in this study for stands with TSF < 4 years. It is interesting to note that for our dataset, the estimates of $GC_{B\text{-}LW}$ using the model of Parresol et al. (2012) were practically insensitive to changes in TSF (Fig. 7a). Even though there was moderate correlation ($R^2 = 0.37$) between observed and predicted $GC_{B\text{-}LW}$ using the model of Parresol et al. (2012), the estimates were underestimated by 37% ($P = 0.001$). For $GC_{B\text{-}LH}$ the correlation was nill ($R^2 = 0.00$), but there was no difference between observed and predicted values ($P = 0.25$), possibly because overestimation when TSF 6 2 was compensated with underestimation when TSF > 2.

3.4. Effect of fire frequency and BA on ground cover biomass

The interactive effect of fire frequency and BA on herbaceous and woody ground cover biomass is shown in Fig. 8. While TSF has little impact on $GC_{B\text{-}LH}$, BA has a major effect, reducing $GC_{B\text{-}LH}$ as BA increased, from about 0.3–0.4 Mg ha^{-1} for a stand with BA = 10 m^2 ha^{-1}, to around 0.1–0.2 Mg ha^{-1} for a stand with BA = 35 m^2 ha^{-1}. On the other hand, an opposite effect was observed for $GC_{B\text{-}LW}$, where BA has little impact when TSF < 3 and TSF has a major effect, reducing $GC_{B\text{-}LW}$ as fire frequency increased (smaller TSF). For example, independent of BA, when TSF = 1 $GC_{B\text{-}LW}$ ranged between 0 and 0.5 Mg ha^{-1}; when TSF = 2, $GC_{B\text{-}LW}$ ranged between 0.5 and 1.0 Mg ha^{-1}. When TSF P 3 there was an interactive effect; both TSF and BA affected ground cover biomass. For example, for TSF = 3, when BA was increased from 5 to 35 m^2 ha^{-1}, $GC_{B\text{-}LW}$ was reduced from about 1.5 to around 1.0 Mg ha^{-1}. For TSF = 5, when BA was increased from 5 to 35 m^2 ha^{-1}, $GC_{B\text{-}LW}$ was reduced from about 3.0 to around 1.0 Mg ha^{-1}.

3.5. Modeling prescribed burning effect on ground cover biomass

Fig. 9 shows the predicted dynamics of ground cover biomass for 40 to 50-year-old longleaf pine stands growing with different regimes of prescribed burning. Woody biomass was the component of ground cover most affected by prescribed burning.

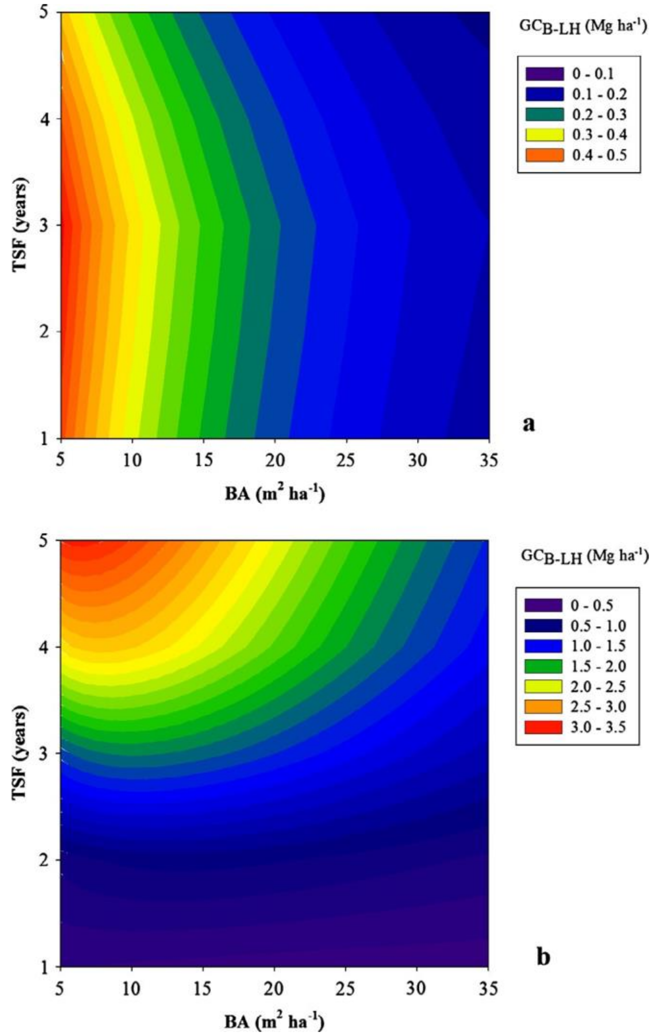

Fig. 8. Effect of basal area (BA) and prescribed burning frequency (TSF) on (a) living herbaceous ($GC_{B\text{-}LH}$) and (b) living woody ($GC_{B\text{-}LW}$) ground cover biomass.

Assuming the stand was burned every year (rough = 1 year), $GC_{B\text{-}LW}$ had a mean value of around 0.06 Mg ha^{-1} and $GC_{B\text{-}LH}$ was maintained at about 0.24 Mg ha^{-1}. If the modeled stand was burned every 3 years (rough = 3 years), $GC_{B\text{-}LW}$ reached around 1.1 Mg ha^{-1} at the time of the prescribed burning and $GC_{B\text{-}LH}$ was maintained at about 0.25 Mg ha^{-1}. When the modeled stand was burned every 5 years (rough = 5 years), GC_B was similar to an unburned stand (around 2.4 Mg ha^{-1}), reaching $GC_{B\text{-}LW}$ a mean value of around 1.9 Mg ha^{-1} at the time of the prescribed burning and maintaining $GC_{B\text{-}LH}$ at about 0.24 Mg ha^{-1}.

4. Discussion

Prescribed burning is the most important tool for managing understory density and species composition, and ground cover native plant diversity in longleaf pine forests (Brockway et al., 2006; Knapp et al., 2009; Haywood, 2005). In general, prescribed burning will stimulate graminoid and forb abundance and reduce the growth of hardwood sprouts (Lewis and Harshbarger, 1976; White et al., 1991; Heuberger and Putz, 2003). The density of the ground cover layer is not only important for plant biodiversity conservation, but also for prescribed fire planning (Hiers et al., 2003; Wright, 2013), wildlife habitat (Glitzenstein et al., 1995;

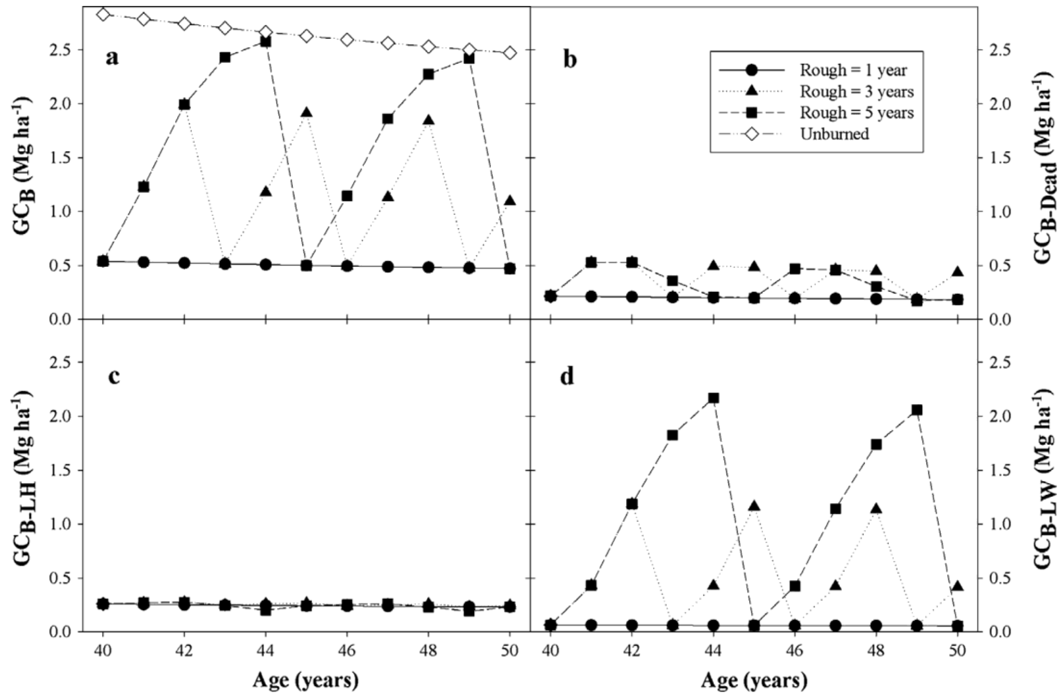

Fig. 9. Simulated effect of prescribed burning frequency on (a) total (GC_B), (b) dead ($GC_{B\text{-}Dead}$), (c) living herbaceous ($GC_{B\text{-}LH}$) and d) living woody ($GC_{B\text{-}LW}$) ground cover biomass. Prescribed burning was initiated at age 40 years with a frequency of 1 (filled circle), 3 (filled triangle), or 5 (filled square) years. In (a) GC_B for unburned stands is also shown (open diamond).

Means, 2006) and livestock management (Greene, 1935; Wahlenberg et al., 1939). In addition, it is important to assess the impact of frequent prescribed fires on carbon dynamics to better understand the role of longleaf pine forests in forest carbon sequestration.

Our study focused on ground cover biomass rather than percentage cover, the most common reported metric of ground cover abundance and horizontal fuel continuity (Abrahamson and Abrahamson, 1996; Brockway and Lewis, 1997; Brockway and Outcalt, 2005; Harrington, 2011; Haywood, 2011; Wright, 2013). Ground cover biomass can reflect differences in community dominance and diversity (Guo and Rundel, 1997; Chiarucci et al., 1999) and has been shown to be positively related to ground cover species richness in some longleaf pine systems (Brockway and Lewis, 1997; Kirkman et al., 2001).

We developed the models in this paper to estimate ground cover biomass for longleaf pine forests under varying stand age, basal area and fire management histories and, similar to Fernandes et al. (2006) and Parresol et al. (2012), we focused on models which used input information obtainable from simple inventories. The set of equations presented in this study provide a practical tool for researchers and land managers so they can analyze the impacts of varying management activities (thinning and burning frequency) on the dynamics of herbaceous and woody ground cover biomass. Our models are applicable for estimating fuel loading for fire simulation systems (Hiers et al., 2003; Ottmar et al., 2009; Wright, 2013), to study interactions between wildlife habitat and prescribed fire (Means and Campbell, 1982; Provencher et al., 2002), to study interactions between livestock (as pinewood cattle) and fire (Augustine and Milchunas, 2009; Albin, 2014), and to account for biomass and carbon emissions for carbon balance models (Gonzalez-Benecke et al., 2010, 2015).

Our estimates of ground cover biomass of burned longleaf pine stands are within the range reported by other authors. For example, Parresol et al. (2012) reported mean values for woody and herbaceous ground cover biomass of about 0.56 and 0.21 Mg ha^{-1}, respectively, for stands growing in South Carolina with a burning frequency between 1 and 5 years. Our overall mean values were 0.58 and 0.35 Mg ha^{-1}, respectively. For stands growing in South Carolina, Glitzenstein et al. (2003) reported mean values for $GC_{B\text{-}LW}$ of about 0.2, 0.4 and 0.8 Mg ha^{-1}, for stands with TSF of 1, 2 and 3 years, respectively. For the same TSF, our overall mean values were 0.15, 0.4 and 1.0 Mg ha^{-1}, respectively. The same authors also reported mean $GC_{B\text{-}LH}$ of 0.45, 0.35 and 0.20 Mg ha^{-1} for stands with TSF of 1, 2 and 3 years, respectively. Kirkman et al. (2001) reported a range in $GC_{B\text{-}LH}$ between 0.12 and 0.35 Mg ha^{-1} the year following a burn for longleaf pine on sites ranging from xeric to wet-mesic. Haywood et al. (1998) reported $GC_{B\text{-}LH}$ of 0.78 Mg ha^{-1} for a 34-year-old stand growing in Louisiana with TSF = 3 years. Our overall mean values were 0.3, 0.4 and 0.5 Mg ha^{-1}, for stands with TSF = 1, 2 and 3 years, respectively.

The model selected to estimate GC_B was similar to that reported by Gonzalez-Benecke et al. (2010), but used BA as an independent variable rather than leaf area index, in order to incorporate more published data into the dataset and expand the applicability of the model, as leaf area index is not a common metric reported for longleaf pine stands. Most longleaf pine stands are managed with frequent prescribed fire (Samuelson et al., 2014), so specific information on ground cover dynamics in unburned longleaf pine stands was not readily available. Of the existing reports, only understory percentage cover (Brockway and Lewis, 1997; Brockway and Outcalt, 2005); hardwood density and height (Haywood et al., 2001) or herbaceous biomass (Haywood, 2012a,b) were documented, rather than total ground cover biomass. In order to increase our sample size, we decided to include data from other southern pine stands (slash pine and loblolly pine), assuming that the general relationship between BA and GC_B holds for the three species. The model predicts a reduction in GC_B as pine overstory BA increases, which was expected since BA is coupled to dynamics in leaf area index and therefore to available light in the understory (Dougherty et al., 1995; Gonzalez-Benecke et al., 2012a,b).

When data were expressed as a fraction of unburned conditions, a unique sigmoidal response of ground cover biomass recovery following fire was determined. Our model predicts that on average, ground cover biomass returned to initial unburned conditions 4 to 5 years following the last burn. Lavoie et al. (2010) reported that the initial ground cover biomass was attained within three years following fire in longleaf pine flatwoods in North Florida. Hough (1982) reported that ground cover returned to pre-fire levels 6–8 years following a prescribed burn in natural slash/longleaf pine stands in Georgia and North Florida. Is important to note that the relationship shown in Fig. 2 represents the mean value of the recovery rate of ground cover biomass after fire, and site-to-site variability can be expected.

Frequent prescribed fire reduces the amount of woody ground cover biomass (Waldrop et al., 1987; Haywood, 2005), and in general, fire intervals of two to four years are recommended to properly control the woody midstory (Wade and Lunsford, 1989;). Our model to estimate $GC_{B\text{-}LW}$ is in agreement with those findings, having high sensitivity to fire frequency, and $GC_{B\text{-}LW}$ declined as TSF decreased. On the other hand, our model to estimate $GC_{B\text{-}LH}$ was insensitive to TSF, with $GC_{B\text{-}LH}$ ranging between 0.1 to 0.5 Mg ha^{-1} depending on BA. Glitzenstein et al. (1995) reported $GC_{B\text{-}LH}$ between 0.20 and 0.45 Mg ha^{-1} for stands with TSF between 1 and 3 years. Brockway and Lewis (1997) reported for a 39-year-old longleaf stand in Georgia with TSF ranging between 1 and 3 years, an average $GC_{B\text{-}LH}$ between 0.2 and 0.6 Mg ha^{-1}.

Even though our model predictions agreed with mean observed values, there are sources of variation not included in our study, such as variation in soils and drainage as well as weather (principally rainfall) both spatially and temporally, that could improve these estimates. Future targeted research incorporating plant physiology and climate and soil attributes, and their interactions under varying management and fire regimes, would improve our understanding of understory-overstory relationships and allow inferences to include behavior under a changing climate future.

Burning season and intensity are important factors that are also considered in fire management planning (Knapp et al., 2009). Our models do not include those effects and we assumed that our equations describe the average responses under varying conditions. Palik et al. (2002) concluded that in order to maintain understory biodiversity in longleaf pine systems burning frequency is more critical than burning season. Similar results were reported by Streng et al. (1993) who did not observe a change in biomass or percent cover of grasses and forbs in response to season of burn. Furthermore, fire frequency, fuel loading, and overstory canopy cover can confound the role of burning season (Haywood, 2005; Knapp et al., 2009).

5. Conclusion

We developed a novel set of functions to simulate ground cover biomass dynamics in response to timing of prescribed burning longleaf pine stands in southeastern U.S. The models incorporate the effects of burning frequency, stand age and basal area. Woody understory ground cover was highly reduced as fire frequency increased, and was also affected by stand basal area when time since the last burn was longer than two years. Herbaceous understory ground cover was little affected by burning frequency, but sensitive to basal area. The set of equations is a useful tool that can be incorporated into fire management models (Ottmar et al., 2009) as well as growth and yield (Gonzalez-Benecke et al., 2012b) and carbon balance models (Gonzalez-Benecke et al., 2015). Coupled with a model that simulates the dynamics of basal area under different thinning schemes, this set of equations allows analysis of the impacts of fire management regimes on ground cover biomass and diversity under varying stand age, basal area and productivity conditions.

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Appendix Appendix

See Tables A1 and A2.

Table A1
Mean stand characteristics and ground cover biomass (all live and dead plants <1 m in height) of unburned southern pine stands used for model fitting.

Age (years)	BA (m^2 ha^{-1})	GC_B (Mg ha^{-1})	Species (overstory)	Reference
0	–	0.90	Slash	1
1	0.58	3.58	Slash	2
2	0.40	4.91	Slash	3
2	0.26	6.92	Loblolly	4
2	1.28	5.09	Loblolly	4
2	0.37	5.53	Loblolly	4
2	2.17	5.20	Loblolly	4
2	1.70	7.41	Loblolly	4
2	1.33	4.50	Slash	2
3	2.56	4.79	Slash	2
4	6.13	3.97	Slash	2
5	2.93	6.58	Slash	3
5	10.04	2.54	Slash	2
6	2.56	7.31	Loblolly	5
6	5.25	5.92	Slash	5
6	13.98	2.52	Slash	2
7	16.41	1.74	Slash	2
8	9.93	4.58	Slash	3
8	17.96	1.98	Slash	2
9	20.40	2.51	Slash	2
11	16.40	2.88	Slash	1
13	14.89	1.99	Slash	2
14	19.50	3.40	Slash	3
14	16.76	2.60	Slash	2
15	17.83	3.26	Slash	2
16	19.65	2.52	Slash	2
17	21.56	2.30	Slash	2
18	21.60	4.59	Slash	3
18	23.13	2.10	Slash	2
23	22.90	1.71	Longleaf	6
25	31.40	1.91	Slash	1
25	26.10	3.20	Slash	7
26	27.23	1.36	Slash	3
27	34.20	1.00	Loblolly/Longleaf	8
34	26.00	4.27	Slash	3

Notation: Age is stand age; BA is stand basal area; GC_B is the biomass of live plus dead ground cover. References: 1: Clark et al. (2004); 2: Bracho et al. (2012); 3: Gholz and Fisher (1982); 4: Subedi et al. (2014); 5: Neary et al. (1990); 6: Kush et al. (1999); 7: Vogel et al. (2011); 8: Haywood and Grelen (2000).

Table A2
Mean stand characteristics and ground cover biomass of longleaf pine stands in Georgia, Louisiana and North Carolina used for BGC validation under burned conditions.

Site	Age (years)	Soil drainage	BA (m^2 ha^{-1})	SI (m)	TSF (years)	GC_B (Mg ha^{-1})	$GC_{B\text{-}LW}$ (Mg ha^{-1})	$GC_{B\text{-}LH}$ (Mg ha^{-1})	$GC_{B\text{-}Dead}$ (Mg ha^{-1})
GA[a]	5	Well drained	0.49	21.7	2	1.73	0.15	0.59	0.99
	12	Well drained	11.49	27.0	2	1.97	1.32	0.05	0.60
	21	Excessively drained	22.42	20.2	2	0.33	0.14	0.05	0.13
	64 [b]	Excessively to well drained	10.19	16.8	2	0.77	0.34	0.14	0.28
	87 [b]	Excessively drained	14.49	23.7	2	0.90	0.31	0.18	0.41
LA	8	Moderately well drained	5.23	21.9	2	1.39	0.11	0.58	0.70
	13[c]	Moderately well drained	4.59	17.1	2	1.79	0.04	0.93	0.82
	13[c]	Moderately well drained	6.04	21.6	3	2.89	0.57	0.68	1.64
	18	Moderately well drained	7.97	21.3	2	2.47	0.95	0.47	1.05
	22[c]	Moderately well drained	2.37	21.6	3	2.70	0.09	1.03	1.58
	24[c]	Moderately well drained	8.27	26.0	1	0.41	0.00	0.26	0.15
	26[c]	Moderately well drained	11.32	19.3	1	0.86	0.15	0.30	0.41
	34	Well drained	18.21	21.3	1	0.78	0.12	0.28	0.38
	50[c]	Moderately well drained	14.29	24.2	1	0.81	0.09	0.52	0.21
	60	Moderately well drained	19.97	19.3	2	1.14	0.14	0.44	0.56
	73[c]	Moderately well drained	16.68	23.6	1	0.55	0.01	0.44	0.10
	75[c]	Moderately well drained	21.94	23.3	2	0.72	0.02	0.34	0.36
	75[c]	Moderately well drained	12.13	25.4	3	2.30	1.42	0.25	0.63
	83	Moderately well drained	13.79	21.4	2	1.70	0.27	0.53	0.91
NC	15	Poorly drained	22.70	25.0	1	0.40	0.30	0.08	0.02
	19	Poorly drained	29.54	15.8	4	0.77	0.57	0.09	0.11
	25	Poorly drained	14.63	20.3	1	0.35	0.18	0.07	0.10
	37	Moderately well drained	15.99	22.0	3	1.72	1.41	0.11	0.21
	47	Well drained	20.26	16.7	4	0.97	0.76	0.09	0.13
	60	Moderately well drained	20.43	15.1	4	1.32	1.19	0.05	0.07
	65[b]	Poorly drained	10.76	17.3	3	3.52	1.64	0.53	1.36
	79 [b]	Moderately well drained	11.15	21.5	2	2.40	1.18	0.47	0.76
	81	Moderately well drained	21.81	23.3	4	1.19	0.88	0.18	0.13

Notation: age is stand age; BA is stand basal area; SI is site index at base age = 50 years; GC_B is the biomass of live plus dead ground cover; $GC_{B\text{-}LW}$ is the biomass of live woody ground cover biomass; $GC_{B\text{-}LH}$ is the biomass of live herbaceous ground cover; $GC_{B\text{-}Dead}$ is the biomass of dead ground cover; TSF is time since last prescribed fire.

[a] From Samuelson et al. (2014).

[b] Naturally regenerated stand.

[c] Indicates stands in which two subplots were measured in August, in all other stands four subplots were measured in late May to early June.

References

Abrahamson, W.G., Abrahamson, C.R., 1996. Effects of fire on long-unburned Florida uplands. J. Veg. Sci. 7, 565–574.

Albin, L.T., 2014. Restoring the Longleaf Pine (*Pinus palustris*) Forests Using Pineywoods Cattle Grazing in Conjunction with Prescribed Burning. Hattiesburg, MS, USA, The University of Southern Mississippi, PhD dissertation.

Augustine, D.J., Milchunas, D.G., 2009. Vegetation responses to prescribed burning of grazed shortgrass steppe. Rangeland Ecol. Manage. 62, 89–97.

Bracho, R., Starr, G., Gholz, H.L., Martin, T.A., Cropper Jr., W.P., Loescher, H.W., 2012. Controls on carbon dynamics by ecosystem structure and climate for southeastern U.S. slash pine plantations. Ecol. Monogr. 82, 101–128.

Brockway, D.G., Lewis, C.E., 1997. Long-term effects of dormant-season prescribed fire on plant community diversity, structure and productivity in a longleaf pine wiregrass ecosystem. For. Ecol. Manage. 96, 167–183.

Brockway, D.G., Outcalt, K.W., 2005. Understory vegetation response in longleaf pine forests to fire and fire surrogate treatments for wildfire hazards reduction and ecological restoration. In: National Fire and Fire Surrogate Study for Ecosystem Restoration, Fuel Treatments Workshop. pp. 38–48.

Brockway, D.G., Outcalt, K.W., Boyer, W.D., 2006. Longleaf pine regeneration ecology and methods. In: Jose, S., Jokela, E.J., Miller, D.L. (Eds.), The Longleaf Pine Ecosystem: Ecology, Silviculture, and Restoration. Springer, New York, NY, pp. 95–133.

Chapman, H.H., 1932. Is the longleaf type a climax? Ecology 13, 328–334.

Chiarucci, A., Wilson, J.B., Anderson, B.J., De Dominicis, V., 1999. Cover versus biomass as an estimate of species abundance: does it make a difference to the conclusions? J. Veg. Sci. 10, 35–42.

Clark, K.L., Gholz, H.L., Castro, M.S., 2004. Carbon dynamics along a chronosequence of slash pine plantations in north Florida. Ecol. Appl. 14, 1154–1171.

Dale, V.H., Beyeler, S.C., Jackson, B., 2002. Understory vegetation indicators of anthropogenic disturbance in longleaf pine forests at Fort Benning, Georgia, USA. Ecol. Ind. 1, 155–170.

Dougherty, P.M., Hennessey, T.C., Zarnoch, S.J., Stenberg, P.T., Holeman, R.T., Wittwer, R.F., 1995. Effects of stand development and weather on monthly leaf biomass dynamics of a loblolly pine (*Pinus taeda* L.) stand. For. Ecol. Manage. 72, 213–227.

Fernandes, P., Luz, A., Loureiro, C., Ferreira-Godinho, P., Botelho, H., 2006. Fuel modelling and fire hazard assessment based on data from the Portuguese National Forest Inventory. In: Viegas, D.X. (Ed.). Proceedings V International Conference Forest Fire Research. 27–30 November 2006. Figueira da Foz. Coimbra. Portugal. pp. 10.

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

Glitzenstein, J.S., Platt, W.J., Streng, D.R., 1995. Effects of fire regime and habitat on tree dynamics in north Florida longleaf pine savannas. Ecol. Monogr. 65, 441–476.

Glitzenstein, J.S., Streng, D.R., Wade, D.D., 2003. Fire frequency effects on longleaf pine (*Pinus palustris* P. Miller) vegetation in South Carolina and Northeast Florida, USA. Nat. Areas J. 23, 22–37.

Gonzalez-Benecke, C.A., Martin, T.A., Cropper Jr., W.P., Bracho, R., 2010. Forest management effects on *in situ* and *ex situ* slash pine forest carbon balance. For. Ecol. Manage. 260, 795–805.

Gonzalez-Benecke, C.A., Jokela, E.J., Martin, T.A., 2012a. Modeling the effects of stand development, site quality, and silviculture on leaf area index, litterfall, and forest floor accumulations in loblolly and slash pine plantations. Forest Sci. 58, 457–471.

Gonzalez-Benecke, C.A., Gezan, S.A., Leduc, D.J., Martin, T.A., Cropper Jr., W.P., Samuelson, L.J., 2012b. Modeling survival, yield, volume partitioning and their response to thinning for longleaf pine (*Pinus palustris* Mill.) plantations. Forests 3, 1104–1132.

Gonzalez-Benecke, C.A., Samuelson, L.J., Martin, T.A., Cropper Jr., W.P., Johnsen, K.H., Stokes, T.A., Butnor, J.R., Anderson, P.H., Jackson, J., 2015. Modeling the effects of forest management on *in situ* and *ex situ* longleaf pine forest carbon stocks. For. Ecol. Manage. http://dx.doi.org/10.1016/j.foreco.2015.02.029.

Greene, S.W., 1935. Relation between winter grass fires and cattle grazing in the longleaf pine belt. J. Forest. 33, 339–341.

Guo, Q., Rundel, P.W., 1997. Measuring dominance and diversity in ecological communities: choosing the right variables. J. Veg. Sci. 8, 405–408.

Harrington, T.B., 2011. Overstory and understory relationships in longleaf pine plantations 14 years after thinning and woody control. Can. J. For. Res. 41, 2301–2314.

Hartnett, D.C., Krofta, D.M., 1989. Fifty-five years of post-fire succession in a southern mixed hardwood forest. Bull. Torrey Bot. Club 116, 107–113.

Haywood, J.D., 2005. Effects of herbaceous and woody plant control on *Pinus palustris* growth and foliar nutrients through six growing seasons. For. Ecol. Manage. 214, 384–397.

Haywood, J.D., 2011. Influence of herbicides and felling, fertilization, and prescribed fire on longleaf pine growth and understory vegetation through ten growing seasons and the outcome of an ensuing wildfire. New Forest. 41, 55–73.

Haywood, J.D., 2012a. Pine straw harvesting, fire, and fertilization affect understory vegetation within a Louisiana longleaf pine stand. Southern J. Appl. Forestry 36, 130–135.

Haywood, J.D., 2012b. Frequency and season of prescribed fire affect understory plant communities in longleaf pine stands. In: Butnor, J.R., (Ed.), Proceedings of the 16th Biennial Southern Silvicultural Research Conference. e-Gen. Tech. Rep. SRS-156. Asheville, NC: U.S. Department of Agriculture Forest Service, Southern Research Station. pp. 137–143.
Haywood, J.D., Grelen, H.E., 2000. Twenty years of prescribed burning influence the development of direct-seeded longleaf pine on a wet pine site in Louisiana. Southern J. Appl. Forestry 24, 86–92.
Haywood, J.D., Harris, F.L., 1999. Description of vegetation in several periodically burned longleaf pine forest on the Kisatchie National Forest. In: Haywood, J.D. (Ed.), Proceedings of the 10th Biennial South. Silv. Res. Conf. USDA For. Serv. Gen. Tech. Rep. SRS-GTR-30. pp. 217–224.
Haywood, J.D., Tiarks, A.E., Elliott-Smith, M.L., Pearson, H.A., 1998. Response of direct seeded *Pinus palustris* and herbaceous vegetation to fertilization, burning, and pine straw harvesting. Biomass Bioenergy 14, 157–167.
Haywood, J.D., Harris, F.L., Grelen, H.E., 2001. Vegetative response to 37 years of seasonal burning on a Louisiana longleaf pine site. Southern J. Appl. Forestry 25, 122–130.
Heuberger, K.A., Putz, F.E., 2003. Fire in the suburbs: ecological impacts of prescribed fire in small remnants of longleaf pine (*Pinus palustris*) sandhill. Restor. Ecol. 11, 72–81.
Hiers, J.K., Laine, S.C., Bachant, J.J., Furman, J.H., Greene Jr., W.W., Compton, V., 2003. Simple spatial modeling tool for prioritizing prescribed burning activities at the landscape scale. Conserv. Biol. 17, 1571–1578.
Hiers, J.K., O'Brien, J.J., Will, R.E., Mitchell, R.J., 2007. Forest floor depth mediates understory vigor in xeric *Pinus palustris* ecosystems. Ecol. Appl. 17, 806–814.
Hough, W.A., 1982. Phytomass and nutrients in the understory and forest floor of slash/longleaf pine stands. Forest Sci. 28, 359–372.
Hu, H., 2011. Restoring Longleaf Pine (*Pinus palustris*) in Loblolly Pine (*P. taeda*) Stands on the coastal plain of North Carolina. Clemson, SC, USA, Clemson University, PhD dissertation.
Kirkman, L.K., Mitchell, R.J., Helton, R.C., Drew, M.B., 2001. Productivity and species richness across an environmental gradient in a fire-dependent ecosystem. Am. J. Bot. 88, 2119–2128.
Knapp, B.O., Wang, G., Walker, J.L., 2008. Relating the survival and growth of planted longleaf pine seedlings to microsite conditions altered by site preparation treatments. For. Ecol. Manage. 255, 3768–3777.
Knapp, E.E., Estes, B.L., Skinner, C.N., 2009. Ecological effects of prescribed fire season: a literature review and synthesis for managers. Gen. Tech. Rep. PSW-GTR-224. Albany, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station. 80p.
Knapp, B.O., Wang, G.G., Hu, H., Walker, J.L., Tennant, C., 2011. Restoring longleaf pine (*Pinus palustris* Mill.) in loblolly pine *Pinus taeda* L.) stands: effects of restoration treatments on natural loblolly pine regenerations. For. Ecol. Manage. 262, 1157–1167.
Kush, J.S., Meldahl, R.S., Boyer, W.D., 1999. Understory plant community response after 23 years of hardwood control treatments in natural longleaf pine (*Pinus palustris*) forests. Can. J. Forest Res. 29, 1047–1054.
Lavoie, M., Starr, G., Mack, M.C., Martin, T.A., Gholz, H.L., 2010. Effects of a prescribed fire on understory vegetation, carbon pools and soil nutrients in a longleaf pine – slash pine forest in Florida. Nat. Areas J. 30, 82–94.
Lewis, C.E., Harshbarger, T.J., 1976. Shrub and herbaceous vegetation after 20 years of prescribed burning in the South Carolina Coastal Plain. J. Range Manage. 29, 13–18.
Loudermilk, E.L., Cropper Jr., W.P., Mitchel, R.J., Lee, H., 2011. Longleaf pine (*Pinus palustris*) and hardwood dynamics in a fire-maintained ecosystem: a simulation approach. Ecol. Model. 222, 2733–2750.
Means, D.B., Campbell, H.W., 1982. Effects of prescribed burning on amphibians and reptiles. In: Wood, G.W., Belle, W. (Eds.), Prescribed Fire and Wildlife in Southern Forests. Proceedings of a Symposium. Baruch Forest Science Institute, Clemson University, Clemson, SC, pp. 89–97.
Means, D.B., 2006. Vertebrate faunal diversity of longleaf pine ecosystems. In: Jose, S., Jokela, E.J., Miller, D.L. (Eds.), The Longleaf Pine Ecosystem: Ecology, Silviculture, and Restoration. Springer, New York, NY, pp. 157–213.
Mitchell, R.J., Kirkman, L.K., Pecot, S.D., Wilson, C.A., Palik, B.J., 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, 743–751.
Myers, R.H., 2000. Classical and Modern Regression with Applications, 2nd ed. PWS and Kent Published, Boston.
Neary, D.G., Jokela, E.J., Comerford, N.B., Colbert, S.R., Cooksey, T.E., 1990. Understanding competition for soil nutrients – the key to site productivity on southeastern Coastal Plain Spodosols. In: Gessel, S.P., LaCate, D.S., Weetman, G.F., Powers, R.F. (Eds.), Sustained Productivity of Forest Soils. Proceedings of the 7th. North American Forest Soils Conference. University of British Columbia, Faculty of Forestry Publication, Vancouver, BC, Canada, pp. 432–450.
Neter, J., Kutner, M.H., Nachtsheim, C.J., Wasserman, W., 1996. Applied Linear Statistical Models, fourth ed. Irwin, pp. 770.
Ottmar, R.D., Vihnanek, R.E., 2000. Stereo photo series for quantifying natural fuels. Volume VI: Longleaf Pine, Pocosin, and Marshgrass in the Southeast United States. PMS 835. Boise, ID: National Wildfire Coordinating Group, National Interagency Fire Center. 85pp.
Ottmar, R.D., Vihnanek, R.E., Mathey, J.W., 2003. Stereo photo series for quantifying natural fuels. Volume VIa: Sand Hill, Sand Pine Scrub, and Hardwoods with White Pine Types in the Southeast United States with Supplemental Sites for Volume VI. PMS 838. Boise, ID: National Wildfire Coordinating Group, National Interagency Fire Center. 78pp.
Ottmar, R.D., Prichard, S.J., Vihnanek, R.E., Sandberg, D.V., 2006. Modification and Validation of Fuel Consumption Models for Shrub and Forested Lands in the Southwest, Pacific Northwest, Rockies, Midwest, Southeast and Alaska. Final Report to the Joint Fire Science Program. 97pp.
Ottmar, R.D., Wright, C.S., Prichard, S.J., 2009. A suite of fire, fuels, and smoke management tools. Fire Manage. Today 69, 34–39.
Palik, B.J., Mitchell, R.J., Hiers, J.K., 2002. Modeling silviculture after natural disturbance to sustain biodiversity in the longleaf pine (*Pinus palustris*) ecosystem: balancing complexity and implementation. For. Ecol. Manage. 155, 347–356.
Parresol, B.R., Blake, J.I., Thompson, A.J., 2012. Effects of overstory composition and prescribed fire on fuel loading across a heterogeneous managed landscape in the southeastern USA. For. Ecol. Manage. 273, 29–42.
Peet, R.K., Allard, D.J., 1993. Longleaf pine-dominated vegetation of the southern Atlantic and eastern Gulf Coast region, USA. Tall Timbers Fire Ecol. Conf. 18, 45–82.
Provencher, L., Galley, K.E.M., Litt, A.R., Gordon, D.R., Brennan, L.A., Tanner, G.W., Hardesty, J.L., 2002. Fire, herbicide, and chainsaw felling effects on arthropods in fire suppressed longleaf pine sandhills at Eglin Air Force Base, Florida. In: Ford, W.M., Russell, K.R. and Moorman, C.E. (Eds.), Proceedings: The Role of Fire for Nongame Wildlife Management and Community Restoration. Gen. Tech. Report NE-288. US For. Service Northeastern Research Station, Newtown, PA. pp. 24–33.
Quarterman, E., Keever, K., 1962. Southern mixed hardwood forest: climax in the southeastern coastal plain: U.S.A. Ecol. Monogr. 32, 167–185.
Reinhardt, E.D., 2003. Using FOFEM 5.0 to estimate tree mortality, fuel consumption, smoke production and soil heating from wildland fire. Page P5.2 in: Proceedings of the Second International Wildland Fire Ecology and Fire Management Congress and Fifth Symposium on Fire and Forest Meteorology. American Meteorological Society, 16–20 November 2003, Orlando, Florida, USA.
Samuelson, L.J., Stokes, T.A., Butnor, J.R., Johnsen, K., Gonzalez-Benecke, C.A., Anderson, P., Jackson, J., Ferrari, L., Martin, T.A., Cropper Jr., W.P., 2014. Ecosystem carbon stocks in *Pinus palustris* Mill. forests. Can. J. Forest Res. 44, 476–486.
Scott, J.H., Burgan, R.E., 2005. Standard fire behavior fuel models: a comprehensive set for use with Rothermel's surface fire spread model. Gen. Tech. Rep. RMRS-GTR-153. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 72p.
Scott, D.A., 2014. Initial ecosystem restoration in the highly erodible Kisatchie Sandstone Hills. Southeast. Nat. 13, 64–79.
Streng, D.R., Glitzenstein, J.S., Platt, W.J., 1993. Evaluating effects of season of burn in longleaf pine forests: a critical literature review and some results from an ongoing long-term study. In: Hermann, S.M. (Ed.), Proceedings 18th Tall Timbers Fire Ecology Conference. The longleaf pine ecosystem: ecology, restoration and management. Tallahassee, FL. Tall Timbers Research Inc, Tallahassee, FL. pp. 227–263.
Subedi, P., Jokela, E.J., Vogel, J.G., Martin, T.A., 2014. Inter-rotational effects of fertilization and weed control on juvenile loblolly pine productivity and nutrient dynamics. Soil Sci. Soc. Am. J. http://dx.doi.org/10.2136/sssaj2013.08.0345nafsc.
Vogel, J.G., Suau, L., Martin, T.A., Jokela, E.J., 2011. Long term effects of weed control and fertilization on the carbon and nitrogen pools of a slash and loblolly pine forest in north central Florida. Can. J. For. Res. 41, 552–567.
Wade, D.D., Lunsford, J.D., 1989. A guide for prescribed fire in southern forests. Tech. Publ. R8-TP11. Atlanta, GA: U.S. Department of Agriculture, Forest Service, Southern Region. 56pp.
Wahlenberg, W.G., Greene, S.W., Reed, H.R., 1939. Effects of fire and cattle grazing on longleaf pine lands as studied at McNeill, Mississippi. U.S. Dep. Agr. Tech Bull. 683. 52pp.
Waldrop, T.A., Van Lear, D.H., Lloyd, E.T., Harms, W.R., 1987. Long-term studies of prescribed burning in loblolly pine forests of the Southeastern Coastal Plain, U.S. Department of Agriculture, Forest Service, Southeastern Forest Experiment Station, Asheville, NC, Gen. Tech. Rep. SE-45. 23pp.
White, D.L., Waldrop, T.A., Jones, S.M., 1991. Forty years of prescribed burning on the Santee fire plots: effects on understory vegetation. In: Nodvin, S.C., Waldrop, T.A. (Eds.), Fire and the Environment: Ecological and Cultural Perspectives: Proceedings of an International Symposium. Gen. Tech. Rep. SE-69. Knoxville, TN: U.S. Department of Agriculture, Forest Service, Southeastern Forest Experiment Station. pp. 51–59.
Wright, C.S., 2013. Fuel consumption models for pine flatwoods fuel types in the southeastern United States. Southern J. Appl. Forestry 37, 148–159.