Relationships between plant biomass and cover in the ground cover layer of longleaf pine forests at Fort Benning, GA

by

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Abstract

Interest in restoring longleaf pine (*Pinus palustris* Mill.) ecosystems has recently grown but little information is available for estimating biomass in the highly diverse ground cover layer of longleaf pine forests. Aboveground biomass-cover relationships in the ground cover were examined by growth form (shrubs/tree seedlings, vines, graminoids, legumes, forbs, ferns) in five longleaf pine stands ranging in age (5, 12, 21, 64, and 87 years) and forest structure at Fort Benning, GA. Cover was visually estimated and live biomass was determined through destructive harvests. Total live biomass in the ground cover layer ranged from 28 to 171 g m^{-2}. Linear relationships were observed but different models were required for different growth forms and stands. The increase in biomass with increasing cover was greatest in the youngest stand for all growth forms except shrubs/tree seedlings, where the slope coefficient was highest for the 12-year-old stand. For forbs, the two oldest stands demonstrated a greater increase in biomass with increasing cover than the 12- and 21-year-old plantations. Live, herbaceous, graminoid, and dead biomass decreased linearly with increasing basal area. Results suggest that percent cover can be used to obtain a rapid estimate of biomass in the ground cover layer of longleaf pine forests.

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Computer Software Used:

- SAS version 9.2/9.3
- Microsoft Word 2010
- Microsoft Excel 2010
- Sigma Plot 10.0

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CHAPTER 1. INTRODUCTION

1.1. Background

Longleaf pine occurs over the large physiographic region of the Atlantic and Gulf Coastal Plain from southeastern Virginia to central Florida and west to east Texas (Ware et al., 1993). Woodlands, savannas and other ecosystems dominated by longleaf pine occupied approximately 37 million ha in the southeastern United States prior to European settlement (Frost, 1993). Since then, these communities have undergone a reduction in occurrence of longleaf pine to less than 3% of their overall original extent (Frost, 2006) due to logging, production of turpentine, interruption of natural fire regimes, and conversion of longleaf pine forests to crops, pasture or other southern pine species (Noss, 1989; Frost, 1993; Van Lear et al., 2005).

Longleaf pine forests are important ecosystems in terms of biological diversity (Sorrie and Weakley, 2001) and provide an essential habitat for sensitive animal and plant species (Van Lear et al., 2005). Longleaf pine ecosystems constitute a critical environment for federally listed animal species such as the red-cockaded woodpecker (*Picoides borealis* Vieillot). On frequently burned sites, plant species richness in the understory is among the highest in the world (Peet and Allard, 1993). Moreover, nearly 60% of the vascular plant taxa endemic to the entire Coastal Plain are obligate associates of the longleaf pine systems and occur almost only within the range of longleaf pine (Sorrie and Weakley, 2006). The loss of longleaf pine forests and the decline of many species that are found primarily in these habitats have recently led to increasing interest in restoring longleaf pine ecosystems. Furthermore, longleaf pine forests are considered ecosystems that can contribute to minimizing the effects of climate change and increasing carbon sequestration in the southern U.S. because of longleaf pine's higher longevity and longer rotations, wider ecological amplitude, and greater resistance to diseases, insects, and wind damage compared to other southern pine species (Stainback and Alavalapati, 2004; Stanturf et al., 2007; Johnsen et al., 2009).

The largest blocks of longleaf pine communities in the Coastal Plain remain on federal lands, principally National Forests, military installations, and National Wildlife Refuges (Sorrie and Weakley 2006). The Department of Defense is one of the largest federal land managers in the U.S. and is in charge of managing longleaf pine forests and protecting listed species. The Strategic Environmental Research and Development Program (SERDP) is the means through which the Department of Defense addresses environmental concerns. SERDP's objective is to improve military readiness and to manage the environment of military installations by supporting the development of new scientific knowledge and cost-effective technologies in areas such as resource conservation and climate change. This study was part of a project funded by the Department of Defense through the SERDP program. The goal of the overall project, called "Developing Tools for Ecological Forestry and Carbon Management in Longleaf Pine", was to create two carbon management models (an even-aged management model and an uneven-aged management model) and provide managers with the necessary knowledge to balance military training objectives with the maintenance of native biodiversity, sustainable yield of forest products and enhancement of forest carbon sequestration.

1.2 Objectives

The primary objective of this study was to investigate relationships between biomass, percent cover and forest structure in the ground cover layer of longleaf pine forests varying in age and stand structure in order to better understand forest carbon balance and provide land managers in military installations with tools to efficiently estimate carbon pools in the ground cover layer of longleaf pine ecosystems. Biomass and carbon pool data will be used to develop even-aged and uneven-aged longleaf pine ecosystem models and information about the relationships between ground cover biomass, percent cover, and stand structure will be incorporated into the models to better describe important ecosystem processes. Five longleaf pine stands of the ages of 5, 12, 21, 64, and 87 years with different stand structures were selected for this study. The three youngest stands were plantations while the two oldest stands were naturally regenerated. Specific objectives were to:

1. Examine the relationship between percent cover and biomass in the ground cover layer by growth form (shrubs/tree seedlings, vines, graminoids, legumes, forbs, and ferns) in order to determine whether the relationship varied among stands and whether percent cover can be used to estimate ground cover biomass in longleaf pine forests, and
2. Develop relationships between ground cover biomass and forest structure in order to assess whether biomass in the ground cover can be estimated by basic forest indices, such as basal area.

CHAPTER 2. RELATIONSHIPS BETWEEN BIOMASS AND COVER IN THE GROUND COVER LAYER OF LONGEAF PINE FORESTS AT FORT BENNING, GA

2.1 - Introduction

Though the ground cover normally constitutes less than 1% of the total aboveground forest biomass in the Northern Hemisphere (Gilliam, 2007; Muller, 2003), this layer is an ecologically important component in forest ecosystems (Augusto et al., 2003; Gilliam, 2007). In most temperate forests, the ground cover is a species-rich stratum (Whigham, 2004) and it is two to 10 times more diverse than the overstory (Gilliam, 2007). In southern temperate zone forests, while understory plants and herbs are on average 4% of the forest community biomass, the herbaceous litter can account for approximately 9% of the annual foliar litter fall (DeAngelis et al., 1981; Muller, 2003). Furthermore, the high proportion of nutrient uptake and recycling in this layer is important to overall forest productivity (Yarie, 1980; Moore et al., 2007). The ground cover layer is generally a small fraction of the overall forest biomass in many forest ecosystems (Peichl and Arain 2006; Cao et al., 2012) and therefore it has received little attention in carbon (Nabuurs et al., 2003) and forest process modeling (Loudermilk et al., 2011). However, values of ground cover biomass reported by some studies in temperate forests suggest that the aboveground portion in the ground cover may not be negligible during early successional stages when stands still lack a well-developed tree canopy and in low-density forests, such as longleaf pine (*Pinus palustris* Mill.) forests (Litton et al., 2004; Lavoie et al., 2010).

Longleaf pine forests, which were once an important ecosystem in the Southeast, are now the focus of restoration (Brockway et al., 1998, 2005; Harrington et al., 2003; Aschenbach et al., 2010. These provide ecosystem services (e.g. biodiversity) and refugia for rare species, and also there is the opportunity to use longleaf pine which is a long-lived species (up to 400 years) in carbon sequestration projects. Naturally developed longleaf pine ecosystems are characterized by a dense and diverse ground cover layer (Kirkman et al., 2001; Peet, 2006). Mitchell *et al.* (1999) determined that across a soil drainage gradient of longleaf pine-wiregrass sites, net primary productivity of the understory (all herbaceous vegetation and woody plants with basal diameter of 1 cm or smaller) was on average 68% of total aboveground productivity. Plant species richness in longleaf pine forests can be considerable, especially at the small scale, with up to 42 species per 0.25 m^2 (Walker and Peet, 1984; Drew et al., 1998), and species associated with longleaf pine forests make up the majority of the endemic plant taxa of the Coastal Plain (Sorrie and Weakley, 2006). The ground layer of a longleaf pine forest is particularly well-developed in open woodlands, where longleaf pine tree crowns in the overstory typically do not overlap (Brockway and Outcalt, 1998). Frequent burning increases cover of grasses and forbs (Glitzenstein et al., 2003; Brockway et al., 2009; Outcalt and Brockway, 2010) and keeps shrubs and woody understory species from increasing in dominance (Outcalt and Brockway, 2010). In the absence of a hardwood midstory, the open canopy of longleaf pine forests allows a substantial amount of light to reach the ground cover and therefore vegetation abundance is higher in this layer than in closed canopy forests (Harrington and Edwards, 1999; McGuire et al., 2001; Pecot et al., 2007). Given the renewed interest in longleaf pine restoration by land managers and the opportunities that these forests may offer to sequester carbon, more information on the proportion of forest biomass stored in the ground cover of these ecosystems is needed.

Biomass is used to quantitatively describe ground cover vegetation and is considered the species variable that best reflects differences in community dominance and diversity (Wilson, 1991; Guo and Rundel, 1997; Chiarucci et al., 1999). However, collecting biomass data through direct destructive methods is labor intensive and time-consuming; therefore, indirect methods have been sought to estimate biomass in ground cover. Cover is suitable to predict biomass because cover is repeatable, can assess different plant life forms in comparable terms, and is more closely related to biomass than are other measures of abundance, such as density and frequency (Muller-Dombois and Ellemberg, 1974). A visual estimate of cover is a popular method to predict biomass since it only requires a small set of field tools (Daubenmire, 1959; Peet et al., 1998). In addition, the visual estimate is considered reliable (Bråkenhielm and Qinghong, 1995; Vanha-Majamaa et al., 2000), is precise in estimating cover of growth forms in the understory, and requires reasonable sample sizes (3-36 replicates for growth form groups) (Abrahamnson et al., 2011). Significant linear and nonlinear relationships between biomass and cover have been demonstrated in different ecosystems at the level of species (Ohmann et al., 1981; Alaback, 1986; Halpern et al., 1996; Halpern and Lutz, 2013), life form or growth form (Mitchell et al., 1987), and understory layer (Joyce and Mitchell, 1989; Gilliam and Turrill, 1993). For example, allometric regressions for the prediction of ground cover biomass based on percent cover have been developed for understory growth forms in boreal forests (MacDonald et al., 2012; Muukkonen et al., 2006), southern Appalachian spruce-fir forests (Moore et al., 2007), and ponderosa pine forests (*Pinus ponderosa* Douglas ex Lawson & C. Lawson) (Rose and Eddleman, 1994; Mitchell et al., 1987). In the southern U.S., relationships between biomass and cover have been studied for some broad forest types, such as planted mixed pine, natural mixed pine, oak-pine, and upland hardwoods (Joyce and Mitchell, 1989). Linear relationships between cover and biomass were reported for three-year-old longleaf pine plantations on hydric soils in North Carolina (Walker and Cohen, 2009) and were described by logarithmic functions. However, there is no study we are aware of that has investigated biomass-cover relationships in the ground cover layer in longleaf pine dominated forests varying in age. As a faster and non-destructive method of estimating ground cover biomass, cover analysis may be better suited to land managers who are interested in managing for biodiversity and carbon in longleaf pine forests.

The biomass versus cover relationship is influenced by plant traits and characteristics such as plant physiognomy, carbon content, and biomass distribution, therefore it varies between growth forms but it is likely to be comparable among species of the same growth form (Röttgermann et al., 2000; Diaz and Cabido, 1997; Chapin, 1993; Frank and McNaughton, 1990; Hermy, 1988). For example, biomass per unit of cover is higher in woody than in herbaceous growth forms. The biomass-cover relationship in the ground layer is expected to be linear whenever ground cover height and composition are similar (Hermy, 1988; Muukkonen et al., 2006). In general, growth forms with multilayered canopies accumulate more biomass per unit of cover than prostrate monolayer growth forms (Alaback, 1986). The ratio of biomass to cover can decrease with decreasing light availability, because plants living under dense overstory canopies show higher specific leaf area, higher leaf area ratio, lower leaf thickness, and reduced branching compared to plants growing in open vegetation (Hutchings and de Kroon, 1994; Pearcy, 1999). Moreover, where light is a limiting factor and ground cover vegetation is sparse or less stratified, such as in high-density forests, plants may tend to explore space more with plagiotropic (horizontal) stems rather than by vertical growth, thus decreasing the biomass-cover ratio (Hutchings and de Kroon, 1994; Liira et al., 2002).

The objective of this study was to examine the relationship between biomass and percent cover in the ground cover layer of longleaf pine forests varying in age and stand structure. To achieve this objective, percent cover was estimated and biomass was harvested by growth form (shrubs and tree seedlings, vines, graminoids, legumes, forbs, and ferns) in five stands dominated by longleaf pine at Fort Benning, GA. Stands varied in age from 5 to 87 years. We tested the hypothesis that ground cover biomass will be linearly related to cover in each stand and for each growth form. We expected to find linearity between biomass and cover because: i) plant height and composition of each growth form were probably homogeneous within stands; and ii) data were collected in Spring and the prediction of biomass by means of cover has been shown to be more accurate when not at the peak of standing crop (Hermy, 1988). We tested the null hypothesis that the biomass-cover relationship of each growth form will be the same for all stands in each growth form. Lastly, we expected biomass will decline with increasing basal area.

2.2 – Materials and Methods

Study Site

The study was conducted at the Fort Benning Army Base, on the Coastal Plain-Piedmont Fall-Line of west-central Georgia and eastern Alabama. Fort Benning is a United States military installation serving as a basic training site for infantry. The majority of the soil on the installation is represented by highly weathered Ultisols, originated by Coastal Plain material and few alluvial deposits from the Piedmont (Garten, 2006). Average annual precipitation is 1180 mm, and temperatures range from an average minimum of 12.8ºC to an average maximum of 24.6ºC, with an average annual temperature of 18.7ºC (data from the Columbus Airport weather station, for the years 1982-2011; http://www.ncdc.noaa.gov). Soil series were: Nankin sandy clay loam (5-year-old stand), Nankin sandy loam (12-year-old), Troup loamy sand (21- and 87-year-old), and Troup Springhill Luverne Complex (64-year-old) (USDA NRCS, 1997, 1999).

Fort Benning is located in the central-interior portion of the range of longleaf pine, but is outside the range of wiregrass. Five different age longleaf pine stands were selected. Stand ages were: 5, 12, 21, 64, and 87 years. The three youngest stands were plantations, whereas the 87-year-old and the 64-year-old stands were natural. Planting density was 1494 trees ha^{-1} in the 5-year-old stand, 1494 trees ha^{-1} in the 12-year-old stand, and 2240 trees ha^{-1} in the 21-year-old stand. Basal area of all overstory trees ranged from 0.5 m^2 ha^{-1} in the 5-year-old stand to 22.4 m^2 ha^{-1} in the 21-year-old stand. Total overstory density also was highest in the 21-year-old stand at 1982 trees ha^{-1} and lowest in the 5-year-old stand at 214 trees ha^{-1}. Understory density varied between 500 trees ha^{-1} in the 21-year-old stand to 2500 trees ha^{-1} in the 12-year-old stand. All stands were last burned in winter or early spring 2010. The actual burning history is unknown therefore, variation in burn history may confound the results, in addition to variation in stand structure among stands.

Study Design

Research plots 1-ha in size were selected. In each research plot, four 0.04-ha circular subplots were established (Figure 2.2.1). Overstory 1 was defined as all woody stems ≥10 cm dbh (main trees) and Overstory 2 was woody stems > 2 m height and < 10 cm dbh. Understory was all stems between 1 and 2 m height, except in the 5-year-old stand where understory included all planted longleaf pine < 2 m height. Ground cover was defined as trees and shrubs < 1 m in height and all herbaceous species. Five 1-m^2 circular plots were located within each 0.04-ha subplot for a total of 20 1-m^2 sample plots per stand. In order to avoid over-sampling the inner one-half of the plot area, the stratified-random polar coordinates method described by Gaiser (1951) was used. Cover was defined as the percentage of ground surface obscured by the vertical projection of all live aboveground parts of a given growth form onto that surface. Relatively small gaps between plant live material were ignored. Cover classes followed the ten-point scale of Peet *et al.* (1998): 1 = trace (< 0.1%), 2 = 0-1%, 3 = 1-2%, 4 = 2-5%, 5 = 5-10%, 6 = 10-25%, 7 = 25-50%, 8 = 50-75%, 9 = 75-95%, 10 = > 95%.

A stand inventory was conducted in February 2012 (Table 2.2.1). Cover and biomass data were collected during May and June 2012. Cover was estimated for six plant growth forms: (1) tree seedlings and shrubs < 1 meter in height, (2) vines, (3) graminoids, (4) legumes, (5) forbs, and (6) ferns. Although no growth form category may exceed 100% cover, total percent cover estimates across all categories exceeded 100% when multiple overlapping plants occurred. After visual estimation of cover, plant biomass was harvested by hand clipping all plants at the root collar. Plant biomass was sorted by growth form and live biomass was separated from dead biomass. Plant material was then dried at 70°C for 72 h and weighed. Plants were identified at the species level when possible. Some species could only be identified at the genus level. A total of 73 plant taxa was encountered, 27 woody and 46 herbaceous (Table 2.2.2). Sixty three taxa were identified at the species level and 10 taxa only at the genus level.

Statistical methods

Effects of stand age on cover and biomass

Average cover and biomass of each growth form, total biomass, and dead standing biomass were determined for each stand age. Data from 1-m^2 plots were averaged by subplot and used to calculate an overall mean and standard error by stand age.

The influence of stand age on mean cover and biomass was examined using a mixed linear model. The model was in the following form:

$$y = \mathbf{X}\beta + \mathbf{Z}\gamma + \varepsilon \qquad (3)$$

where β is the fixed-effect parameter and γ the random parameter. Stand age was the fixed-effect parameter and subplot was the random parameter. Total biomass was defined as the sum of each growth form's biomass in the 1-m^2 plots. The mean cover for each growth form was the mid-point of each cover class (Peet et al., 1998). Midpoints of cover classes were 0.05, 0.5, 1.5, 3.5, 7.5, 17.5, 37.5, 62.5, 85, and 97.5. The Bonferroni adjustment was applied since after fitting the model residuals showed heteroscedasticity.

Cover-biomass relationships by growth form

The relationship between biomass and cover was determined by pooling all stands by each growth form using data from the 1-m^2 plots. Cover values were the same cover class midpoints that were used to test the effect of stand age on cover. Regressions were forced through 0 (model without intercept) because this regression function is known to pass through it (biomass = 0 g m^{-2} will always correspond to cover = 0%). Simple linear regressions run separately for each stand and that included an intercept showed that the intercept did not differ from zero in almost all cases. Data points with very unusual relative proportion of growth forms and that produced a change of more than 20% on the regression slope were considered outliers, therefore those points were taken out and the models were re-fitted. These outliers were excluded from the other analyses as well. Since dead biomass was not sorted by growth forms and outliers could not be excluded, we used dead biomass data with outliers for analyses.

To determine effect of the different stands on the relationship between biomass and cover for each growth form, the likelihood-ratio test was used. Under this test procedure, a full model and a reduced model were compared, as in the general linear test (Kutner et al., 2004). The full model represents the scenario in which all the slopes of the relationship between biomass and cover are different from each other and therefore every stand age has a different model. The full model was compared to the reduced model that describes the relationship between biomass and cover as being the same for all stand ages, in order to determine if there were any differences between any of the stand ages. The full model was:

$$Y_i = \beta_1 X_{i1} + \beta_2 X_{i2} + \beta_3 X_{i3} + \beta_4 X_{i4} + \beta_5 X_{i5} + \varepsilon \qquad (1)$$

where Y_i is the aboveground biomass measurements, $X_{i1}, X_{i2}, X_{i3}, X_{i4},$ and X_{i5} are the dummy variables that represent five different stands, and $\beta_1, \beta_2, \beta_3, \beta_4,$ and β_5 the slope terms of the dummy variables. The hypothesis tested was:

$H_0: \beta_1 = \beta_2 = \beta_3 = \beta_4 = \beta_5$ H_a: at least one β_k is different from the others

The null hypothesis was the reduced model and the alternative hypothesis the full model. The test statistic for the likelihood-ratio test was:

$$G = -2log_eL(R) - (-2log_eL(F)) \qquad (2)$$

where $-2log_e(F)$ is the log-likelihood for the full model and $-2log_eL(R)$ is the log-likelihood for the reduced model. If H_0 holds, G is approximately distributed as χ^2. The $log_e(F)$ and the $log_eL(R)$ were calculated using the maximum likelihood (ML) estimation method [Proc Mixed (SAS version 9.2; SAS Institute, Inc., Cary, NC)]. The level of significance was set at 0.05. If G (d.f.=4) $\leq \chi^2$ was not significant then H_0 was not rejected. Whenever H_0 was rejected, combinations of stands were tested against the full model using the appropriate degrees of freedom in order to determine whether a coarser group of stands could share the same slope. Smallest number of groups in each growth form was the criterion through which the most satisfactory combinations were selected.

Biomass - basal area relationships

The relationship between ground cover biomass and total basal area of trees > 2 m in height was determined by pooling subplots and stands (n=20). Both linear and non-linear models were tested (SAS version 9.2; SAS Institute, Inc., Cary, NC). Live total biomass, herbaceous biomass, biomass by growth form, and dead biomass were averaged by subplot. Basal area data from the forest inventory were also averaged by subplot. Linear functions fit the data. The linear function was in the form of $Y = a + bX$ where y is biomass, x is total basal area of trees > 2 m in height, and a and b estimated regression coefficients.

Fig. 2.2.1. Representative schematic of the 1-ha field plot sampling structure for each longleaf pine stand at Fort Benning, GA. Within each subplot five circular 1-m^2 plots were randomly selected.

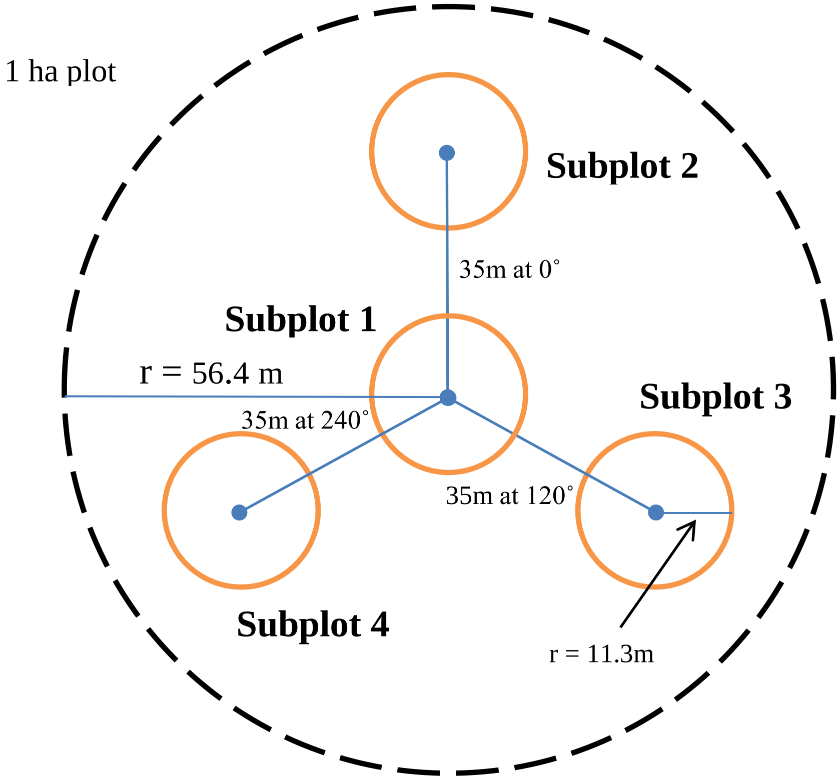


Table 2.2.1. Structure of longleaf pine (LLP) stands sampled at Fort Benning, GA. Overstory1 includes all woody stems ≥10 cm dbh and Overstory2 is woody stems > 2 m height and < 10 cm dbh. The 5-year-old stand understory includes all planted longleaf < 2 m height and is included only for the 5-year-old stand to account for all planted trees.

Age	Stand Type	Canopy Layer	Species	Basal Area ($m^2 ha^{-1}$)	Density (trees ha^{-1})	Dbh (cm)	H (m)
5	Planted	Overstory1	LLP	0.0	0.0	-	-
			Other	0.0	0.0	-	-
		Overstory2	LLP	0.4	150	6.6	2.4
			Other	0.04	64	3.2	2.7
		Understory	LLP	-	625	-	<2
			Other	-	1,000	-	<2
12	Planted	Overstory1	LLP	3.7	300	12.2	9.2
			Other	4.4	219	14.6	8.6
		Overstory2	LLP	2.7	619	7.2	6.2
			Other	0.6	159	6.6	5.8
21	Planted	Overstory1	LLP	18.6	1,331	13.2	11.8
			Other	0.9	75	12.0	9.3
		Overstory2	LLP	2.3	481	7.7	8.7
			Other	0.6	95	9.3	8.0
64	Natural	Overstory1	LLP	7.5	94	29.7	18.3
			Other	2.4	37	29.5	18.3
		Overstory2	LLP	0.3	159	4.5	3.1
			Other	0.1	127	2.3	2.3
87	Natural	Overstory1	LLP	13.4	87	42.5	28.9
			Other	0.0	0.0	-	-
		Overstory2	LLP	1.1	765	4.1	3.7
			Other	0.0	0.0	-	<2

Table 2.2.2. Ground cover plant species in longleaf pine stands at Fort Benning, GA.

Scientific Name	**Family**	**Common Name**
Andropogon/*Schizachyrium*	Poaceae	bluestem
Asimina parviflora (Michx.) Dunal	Annonaceae	smallflower pawpaw
Callicarpa americana L.	Verbenaceae	American beautyberry
Carya alba (L.) Nutt.	Juglandaceae	mockernut hickory
Centrosema virginianum (L.) Benth	Fabaceae	spurred butterfly pea
Chamaecrista spp.	Fabaceae	partridge pea
Chrysopsis mariana (L.) Elliott	Asteraceae	Maryland goldenaster
Cnidoscolus urens (L.) Arthur var. *stimulosus* (Michx.) Govaerts	Euphorbiaceae	finger rot
Coreopsis major Walter	Asteraceae	greater tickseed
Danthonia sericea Nutt.	Poaceae	downy danthonia
Desmodium lineatum DC.	Fabaceae	sand ticktrefoil
Desmodium obtusum Muhl. ex Willd.) DC	Fabaceae	stiff ticktrefoil
Desmodium paniculatum (L.) DC.	Fabaceae	panicledleaf ticktrefoil
Desmodium rotundifolium DC.	Fabaceae	prostrate ticktrefoil
Dichanthelium aciculare (Desv. ex Poir.) Gould & C.A. Clark	Poaceae	needleleaf rosette grass
Dichanthelium acuminatum (Sw.) Gould & C.A. Clark	Poaceae	tapered rosette grass
Dichanthelium commutatum (Schult.) Gould	Poaceae	variable panicgrass
Diospyros virginiana L.	Ebenaceae	common persimmon
Eupatorium compositifolium Walter	Asteraceae	yankeeweed
Eupatorium hyssopifolium L.	Asteraceae	hyssopleaf thoroughwort
Euphorbia pubentissima Michx.	Euphorbiaceae	false flowering spurge
Galium hispidulum Michx.	Rubiaceae	coastal bedstraw
Galium pilosum Aiton	Rubiaceae	hairy bedstraw
Gelsemium sempervirens (L.) W.T. Aiton	Loganiaceae	evening trumpetflower
Hypericum gentianoides (L.) Britton, Sterns & Poggenb.	Clusiaceae	orangegrass
Hypericum hypericoides (L.) Crantz	Clusiaceae	St. Andrew’s cross
Ipomoea pandurata (L.) G. Mey.	Convolvulaceae	man of the earth
Lespedeza cuneata (Dum. Cours.) G. Don	Fabaceae	sericea lespedeza
Lespedeza procumbens Michx.	Fabaceae	trailing lespedeza
Lespedeza repens (L.) W.P.C. Barton	Fabaceae	creeping lespedeza

Lespedeza stuevei Nutt.	Fabaceae	tall lespedeza
Liquidambar styraciflua L.	Hamamelidaceae	sweetgum
Lygodium japonicum (Thunb.) Sw.	Lygodiaceae	Japanese climbing fern
Mimosa quadrivalvis L.	Fabaceae	fourvalve mimosa
Morella cerifera (L.) Small	Myricaceae	wax myrtle
Opuntia sp.	Cactaceae	
Oxalis spp.	Oxalidaceae	woodsorrel
Packera anonyma (Alph. Wood) W.A. Weber & Á. Löve	Asteraceae	Small’s ragwort
Parthenocissus quinquefolia (L.) Planch.	Vitaceae	Virginia creeper
Physalis virginiana Mill.	Solanaceae	Virginia groundcherry
Pinus palustris Mill.	Pinaceae	longleaf pine
Pinus spp.	Pinaceae	pine
Pityopsis spp.	Asteraceae	silkgrass
Pseudognaphalium spp.	Asteraceae	cudweed
Pteridium aquilinum (L.) Kuhn	Dennstaedtiaceae	western brackenfern
Quercus falcata Michx.	Fagaceae	southern red oak
Quercus hemisphaerica W. Bartram ex Willd.	Fagaceae	Darlington oak
Quercus incana W. Bartram	Fagaceae	bluejack oak
Quercus marilandica Münchh.	Fagaceae	blackjack oak
Quercus nigra L.	Fagaceae	water oak
Rhus copallinum L.	Anacardiaceae	winged sumac
Rhynchosia reniformis DC.	Fabaceae	dollarleaf
Rubus cuneifolius Pursh	Rosaceae	sand blackberry
Rubus sp.	Rosaceae	blackberry
Scleria ciliata Michx. var. *ciliata*	Cyperaceae	fringed nutrush
Sericocarpus tortifolius (Michx.) Nees	Asteraceae	Dixie whitetop aster
Smilax bona-nox L.	Smilacaceae	saw greenbrier
Smilax glauca Walter	Smilacaceae	cat greenbrier
Solidago odora Aiton	Asteraceae	anisescented goldenrod
Stylosanthes biflora (L.) Britton, Sterns & Poggenb.	Fabaceae	sidebeak pencilflower
Symphyotrichum patens (Aiton) G.L. Nesom	Asteraceae	late purple aster
Sisyrinchium sp.	Iridaceae	blue-eyed grass
Tephrosia spicata (Walter) Torr. & A. Gray	Fabaceae	spiked hoarypea
Tephrosia virginiana (L.) Pers.	Fabaceae	Virginia tephrosia
Toxicodendron pubescens Mill.	Anacardiaceae	Atlantic poison oak
Tragia urens L.	Euphorbiaceae	wavyleaf noseburn
Triodanis perfoliata (L.) Nieuwl.	Campanulaceae	clasping Venus’ looking-glass
Ulmus alata Michx.	Ulmaceae	winged elm

Vernonia angustifolia Michx.	Asteraceae	tall ironweed
Vaccinium arboreum Marshall	Ericaceae	farkleberry
Vaccinium myrsinites Lam.	Ericaceae	shiny blueberry
Vaccinium stamineum L.	Ericaceae	deerberry

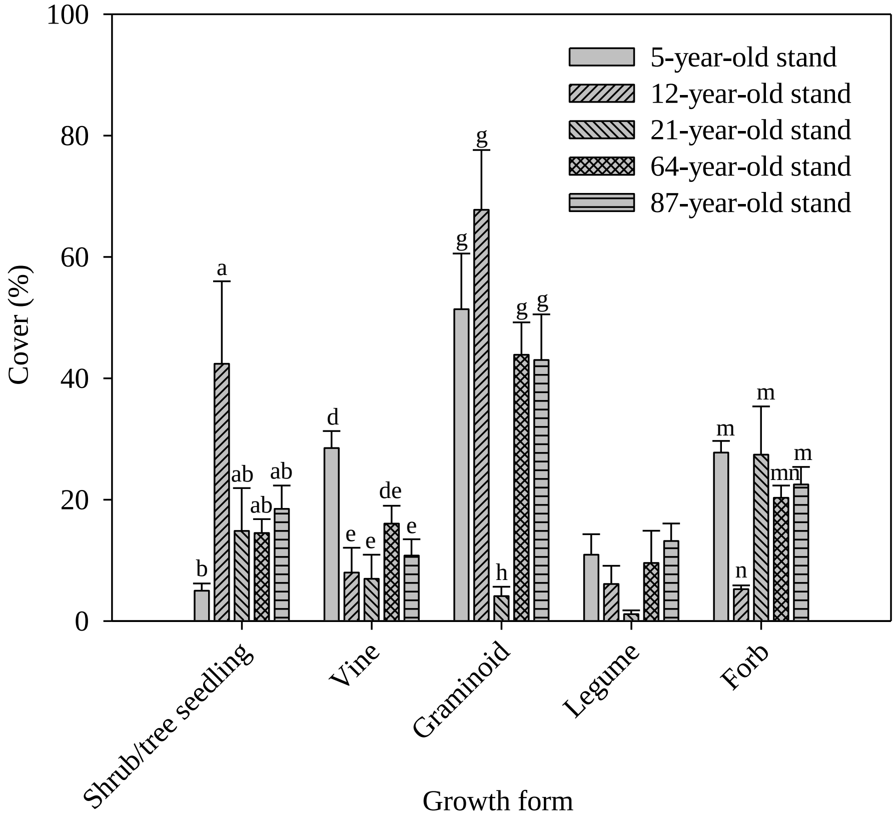
2.3 - Results

Cover of shrubs/tree seedlings, vines, graminoids, and forbs varied significantly among stands (Table 2.3.1). Stand age had no significant effect on cover of legumes. Ferns occurred only in the 64-year-old stand. Within the shrub/tree seedling growth form, cover ranged from 5% in the 5-year-old stand to 42% in the 12-year-old stand (Figure 2.3.1). Shrub/tree seedling cover in the 12-year-old stand was significantly higher than in the 5-year-old stand but neither stand was significantly different from the other stands (Figure 2.3.1). Vine cover varied between 7% in the 21-year-old stand to 29% in the 5-year-old stand and was higher in the 5-year-old stand than in the 12-, 21-, and 87-year-old stands (Figure 2.3.1). Cover of graminoids was lowest in the 21-year-old stand (4%) but was similar among the other stands and was on average 42% (Figure 2.3.1). Average legume cover was 8%. Forb cover was lower in the 12-year-old stand compared to the 5, 21, and 87-year-old stands and forb cover was similar among the 5, 21, 64, and 87-year-old stands (Figure 2.3.1).

Table 2.3.1. Observed probability values for the effect of stand age on groundcover layer variables in longleaf pine stands at Fort Benning, GA. Total live and dead biomass is the sum of biomass of all growth forms within each 1-m^2 plot.

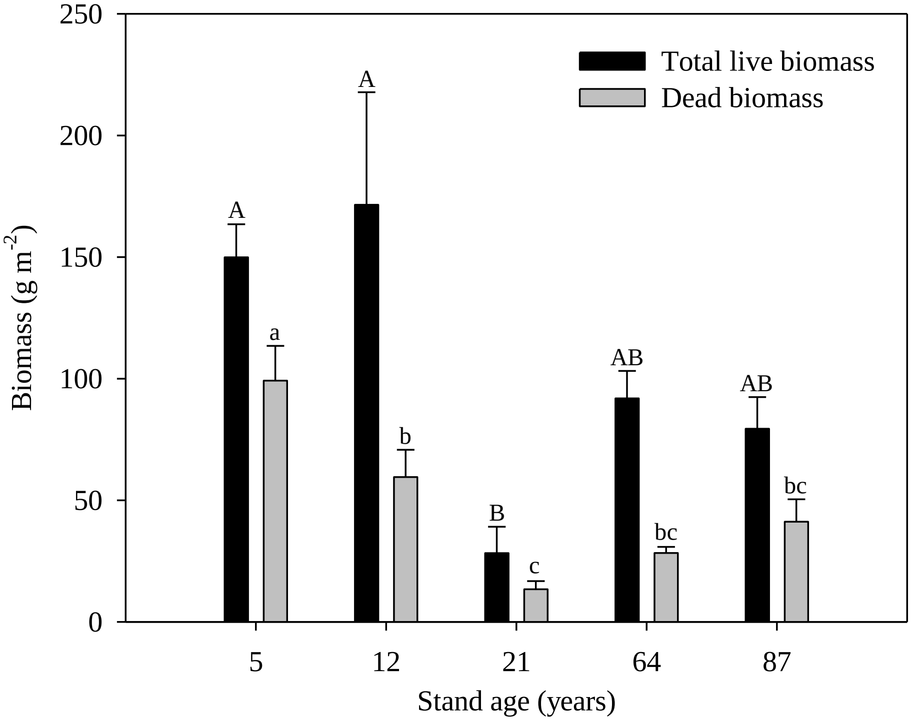
Variable	Stand age (*P*>*F*)
Shrub/tree seedling cover	0.009
Vine cover	0.001
Graminoid cover	< 0.001
Legume cover	0.080
Forb cover	0.002
Shrub/tree seedling biomass	0.003
Vine biomass	< 0.001
Graminoid biomass	< 0.001
Legume biomass	0.187
Forb biomass	< 0.001
Total live biomass	0.001
Dead biomass	< 0.001

Figure 2.3.1. Mean (SE) cover by growth form in the ground cover layer in longleaf pine stands at Fort Benning, GA. Standard errors represent variability among subplots. Within each growth form, different letters indicate significant differences in least square means among stands at α=0.05.



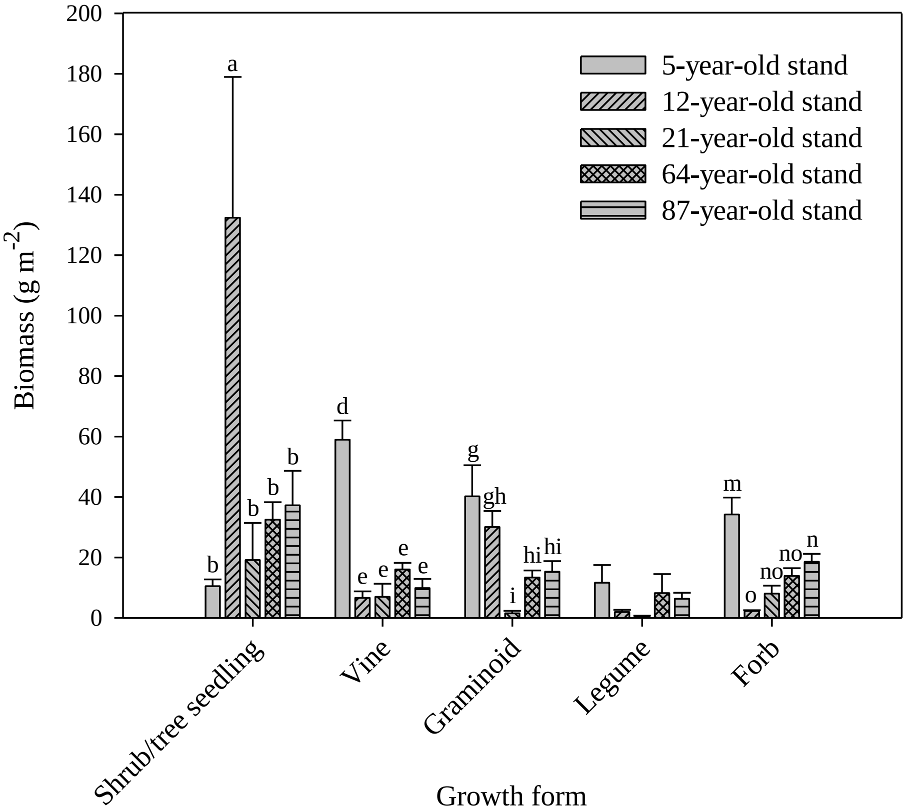
Total live biomass in the ground cover layer varied among stand ages and values ranged from 28.3 g m^{-2} in the 21-year-old stand to 171.5 g m^{-2} in the 12-year-old stand (Table 2.3.1; Figure 2.3.2). Total live biomass was significantly lower in the 21-year-old stand than in the 5- and 12-year-old stands but similar to live biomass in the two oldest stands (Figure 2.3.2). Dead biomass also varied among stands (Table 2.4.1). Dead biomass was highest in the 5-year-old stand and higher in the 12-year-old stand than in the 21-year-old stand (Figure 2.3.2).

Figure 2.3.2. Mean (SE) total live biomass (sum of all growth forms) and dead biomass in the ground cover layer in longleaf pine stands at Fort Benning, GA. Standard errors represent variability among subplots. Different capital letters, for live biomass, and different lowercase letters, for dead biomass, indicate significant differences in least square means between stands at α=0.05.



Live biomass by growth form differed among stand ages except for legumes (Table 2.3.1). Shrub/tree seedling biomass was highest in the 12-year-old stand, 132.3 g m^{-2}, compared to an average of 24.8 g m^{-2} in the other stands, which were similar (Figure 2.3.3). Biomass of vines ranged between 6.6 g m^{-2} in the 12-year-old stand to 58.9 g m^{-2} in the 5-year-old stand, which had the highest vine biomass (Figure 2.3.3). Graminoid biomass in the 21-year-old stand was 1.5 g m^{-2} and lower than graminoid biomass in the two youngest stands, which had an average graminoid biomass of 35.1 g m^{-2} (Figure 2.3.3). Average legume biomass across all stands was 5.3 g m^{-2}. Biomass of forbs varied between 2.2 g m^{-2} in the 12-year-old stand and 34.2 g m^{-2} in the 5-year-old stand, and was highest in the 5-year-old stand (Figure 2.3.3). The 12-year-old stand had lower forb biomass than the 87-year-old stand (Figure 2.3.3).

Figure 2.3.3. Live biomass by growth form in the ground cover layer in longleaf pine stands at Fort Benning, GA. Standard errors represent variability among subplots. Within each growth form, different letters indicate significant differences in least square means of biomass between stands at $\alpha=0.05$.



At the stand level, the linear relationship between biomass and cover in the form of $y = \beta x + \varepsilon$ was significant for almost all growth forms and stands. The regression for ferns in the 64-year-old stand was also significant. For shrubs, vines and graminoid growth forms a reduced model with two equations was as good as the full model in estimating biomass (Tables 2.3.2 and 2.3.3). For legume and forb growth forms the relationship between biomass and cover was explained by three different functions (Table 2.3.2 and 2.3.3). For shrub/tree seedlings, the 12-year-old stand demonstrated a greater slope compared to all the other stands combined (Table 2.3.2; Figure 2.3.4). The slope of the 5-year-old stand was greater compared to all other stands combined for vine and graminoid growth forms (Table 2.3.2; Figure 2.3.4). For legumes, slopes of the 12-, 21-, and 87-year-old stands were similar and smaller than the 64-year-old stand and the 5-year-old stand which were grouped separately (Table 2.3.2; Figure 2.3.5). In the forb growth form, three equations were necessary to describe the relationship between cover and biomass with the slope of the two oldest stands combined being higher than the 12- and the 21-year-old stands combined slope and smaller than 5-year-old stand (Table 2.3.2; Figure 2.3.5).

Table 2.3.2. Slopes of the relationship ($y= \beta_1 x+\varepsilon$) between biomass (g m^{-2}) and ground cover (%) by growth form in longleaf pine stands varying in age at Fort Benning, GA.

Growth form	β_1	S.E. of β_1
Shrubs/tree seedlings		
12-year-old stand	3.180	0.112
All other stands	2.021	0.176
Vines		
5-year-old stand	1.932	0.101
All other stands	0.877	0.110
Graminoids		
5-year-old stand	0.829	0.048
All other stands	0.391	0.027
Legumes		
5-year-old stand	1.344	0.082
64-year-old stand	1.014	0.087
12-, 21-, and 87-year-old stands	0.509	0.067
Forbs		
5-year-old stand	1.163	0.072
64-and 87-year-old stands	0.663	0.078
12-and 21-year-old stands	0.241	0.078

Table 2.3.3. Relationship between biomass and percent cover in the ground cover layer in longleaf pine stands at Fort Benning, GA. Likelihood ratio tests were used to test reduced models against the full five-parameter model by different growth forms. *G* is the test statistic for the likelihood ratio test. Non-significant *p*-values at α=0.05 indicate that the reduced model is as appropriate as the full model.

Growth form	Reduced model	*G*	df	*P>G*
Shrubs/tree seedlings	1 function for all stands	32.7	4	< 0.001
	1) 12-year-old stand 2) All the other stands	6.8	3	0.079
Vines	1 function for all stands	39.9	4	< 0.001
	1) 5-year-old stand 2) All the other stands	0.0	3	0.873
Graminoids	1 function for all stands	56.2	4	< 0.001
	1) 5-year-old stand 2) All the other stands	7.3	3	0.06
Legumes	1 function for all stands	55.5	4	< 0.001
	1) 12, 21, and 87-year-old stands 2) 5 and 64-year-old stands	11.4	3	0.001
	1) 12, 21, and 87-year-old stands 2) 5-year-old stand 3) 64-year-old stand	3.7	2	0.157
Forbs	1 function for all stands	64.2	4	< 0.001
	1) 5-year-old stand 2) All the other stands	18.8	3	< 0.001
	1) 5-year-old stand 2) 12 and 21-year-old stands 3) 64 and 87-year-old stands	1.5	2	0.472

Fig. 2.3.4. Biomass of shrubs/tree seedlings, vines, and graminoids in relation to cover in the ground cover layer in longleaf pine stands at Fort Benning, GA.

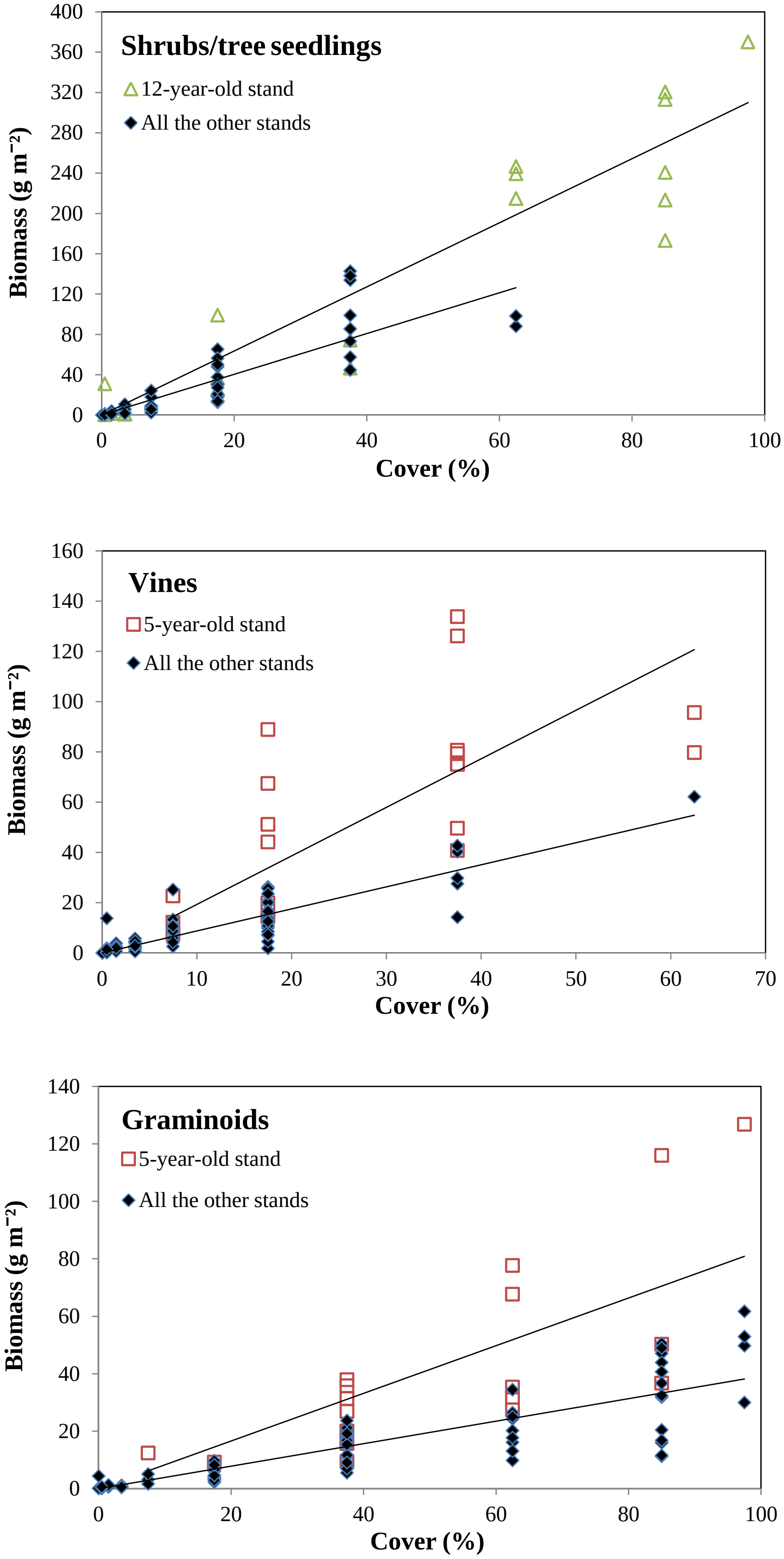
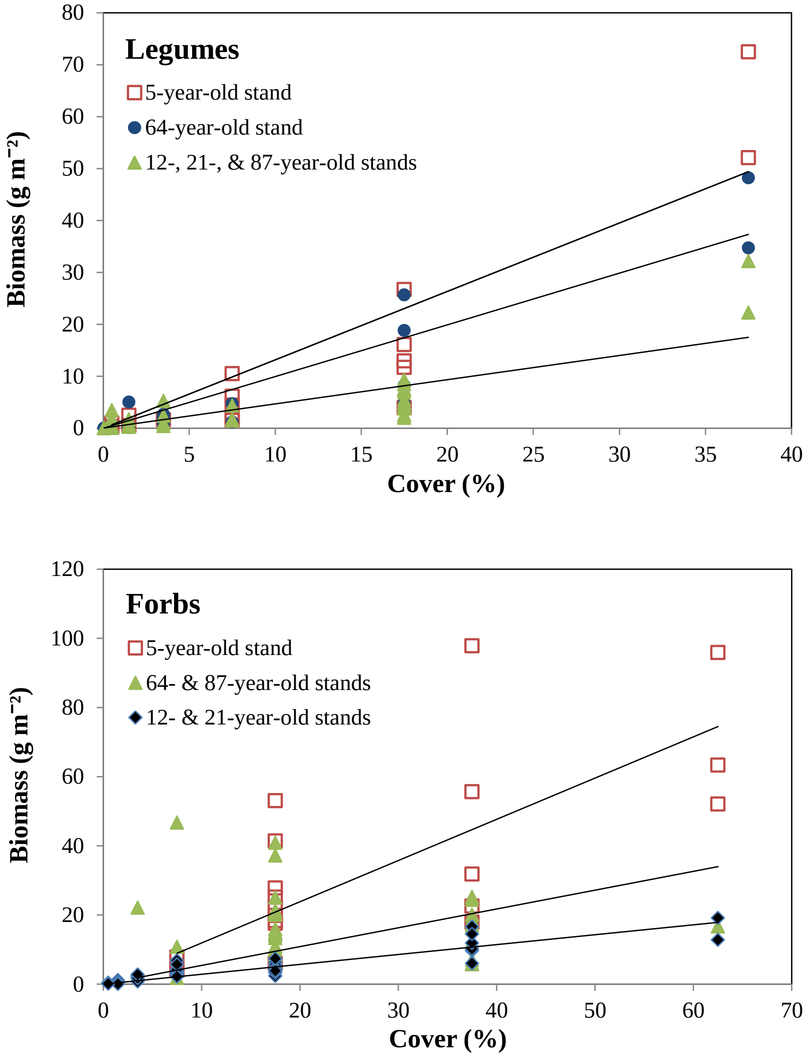


Fig. 2.3.5. Biomass of legumes and forbs in relation to cover in the ground cover layer in longleaf pine stands at Fort Benning, GA.

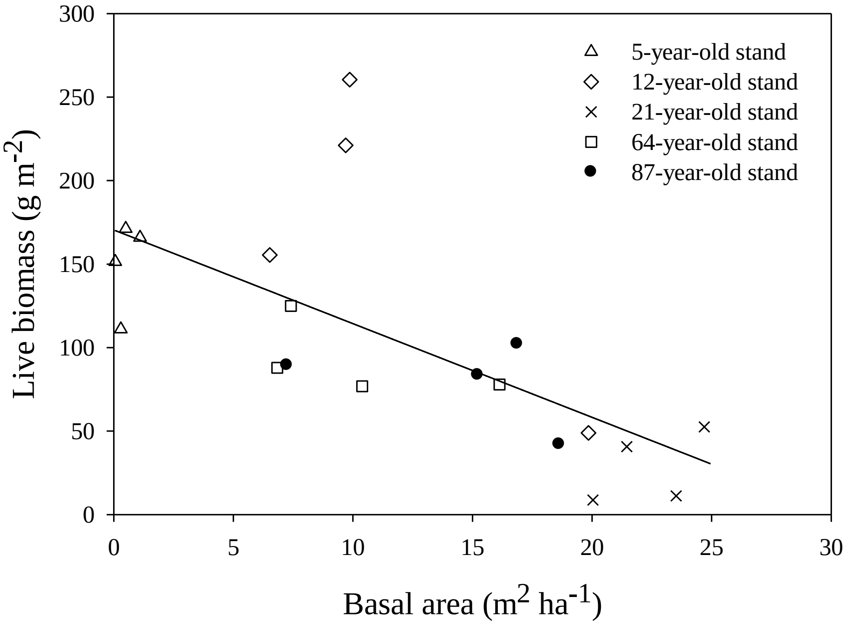


Total live, dead, herbaceous, and graminoid biomass at the 1-m^2 plot level were averaged by subplot and relationships between biomass and stand basal area were explored. Total live and dead biomass were linearly and negatively related to basal area and basal area explained 46 and 65% of the variability in live and dead biomass, respectively (Table 2.3.4, Fig. 2.4.6). Herbaceous biomass, which included graminoids, legumes, forbs, and ferns, declined linearly with increasing basal area (Fig. 2.3.7). Graminoid biomass was also significantly and negatively related to basal area (Fig. 2.3.7).

Table 2.3.4. Regression functions for relationships between ground cover biomass (g m^{-2}) variables and total basal area (m^2 ha^{-1}) of woody stems > 2m in height in longleaf pine stands at Fort Benning, GA (α=0.05). Herbaceous biomass is total live biomass without shrub/tree seedling biomass and vine biomass. Regression coefficients are indicated by *a* and *b*. The number of observations is 20 for all models.

Biomass	Model equation	*a*	*b*	R²	*P>F*
Total live	$y = a + bx$	170.44	-5.61	0.46	0.001
Dead	$y = a + bx$	88.95	-3.44	0.65	< 0.001
Herbaceous	$y = a + bx$	79.88	-3.01	0.68	< 0.001
Graminoid	$y = a + bx$	39.03	-1.60	0.58	< 0.001

Figure 2.3.6. Total live biomass (sum of all growth forms) and dead biomass in the ground cover layer as a function of basal area of all woody stems ≥ 2 m in height in longleaf pine stands at Fort Benning, GA.



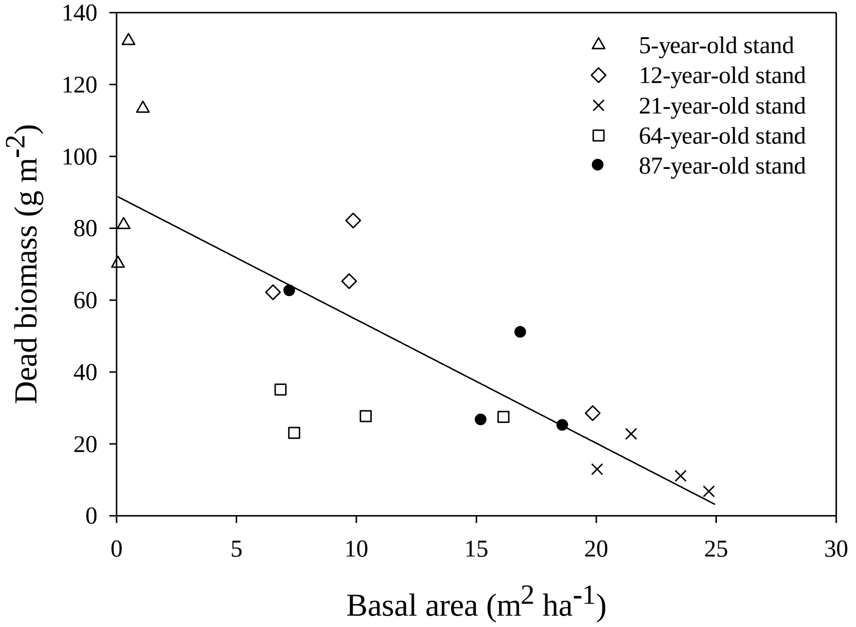
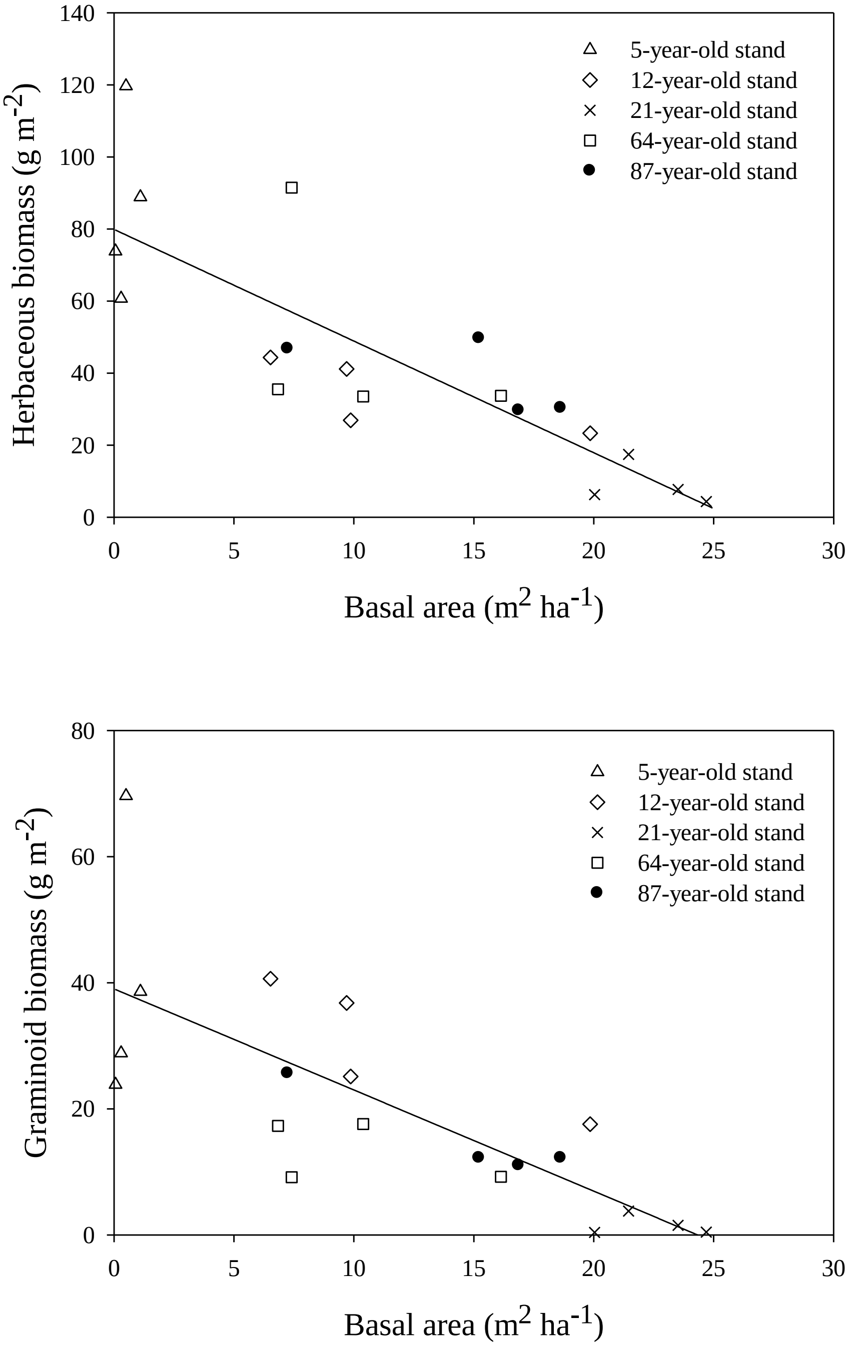


Figure 2.3.7. Herbaceous biomass (total of graminoids, legumes, forbs, and ferns) and graminoid biomass in the ground cover layer as a function of basal area of all woody stems ≥ 2 m in height in longleaf pine stands at Fort Benning, GA.



2.4 - Discussion

Biomass Production

Aboveground biomass in the ground cover of forests dominated by loblolly pine (*Pinus taeda* L.), longleaf pine (*Pinus palustris* Miller), and shortleaf pine (*Pinus echinata* Miller) was studied at Fort Benning by Lajeunesse *et al.* (2006). Mean total live biomass in the third season following fire was 88 g m^{-2}, which was lower than the average (104 g m^{-2}) across all stands observed in this study. Herbaceous, graminoid, and legume biomass was on average higher and forb biomass lower than in Lajeunesse *et al.* (2006). Total live biomass in this study (104 g m^{-2}) was within the range of biomass values found in a longleaf pine-wiregrass woodland of southern Georgia, where total live biomass in ground cover varied from approximately 81 g m^{-2} in xeric sites to 157 g m^{-2} in wet-mesic sites and basal area of overstory trees was lower in xeric sites than in wet-mesic sites (Kirkman et al., 2001). However, total live and herbaceous biomass by stand at Fort Benning, GA, was generally lower than biomass values reported in the literature for longleaf pine forests, especially in the 21-year-old plantation. For example, a 21-year-old stand in Louisiana had higher herbaceous biomass (41.8 g m^{-2}) than the stand of same age at Fort Benning, GA (10 g m^{-2}), even though basal area was similar between the two studies (Wolters, 1982). In the West Gulf region, herbaceous biomass in a 37-year-old longleaf pine stand with a basal area of 22 m^{2} ha^{-1} was 94 g m^{-2} (Haywood et al., 2001) and higher than in the 21-year-old plantation at Fort Benning, GA, which had similar basal area but higher density. Differences between studies in the literature and this study in graminoid, total live, and herbaceous biomass can be attributed not only to differences in stand structure but also to the contribution of wiregrass, which normally constitutes a high proportion of ground cover biomass in longleaf pine-wiregrass woodlands (Kirkman et al., 2001). Moreover, ground cover biomass was measured in May and June and was likely lower than values at the peak biomass of herbaceous plants, which comes in July/August at Fort Benning, GA (Lajeunesse et al., 2006). In the 21-year-old stand, specifically, high planting density has led to a closed canopy structure and to less available space for plants to grow in the ground cover compared to the stands in Louisiana and West Gulf Region.

Basal Area Influence

In longleaf pine forests, herbaceous plant production has been shown to decrease linearly with increasing overstory basal area and to increase with increasing seasonal precipitation (Grelen and Lohrey, 1978; Wolters, 1973, 1982). At Fort Benning, herbaceous biomass and graminoid biomass of all stands pooled together decreased linearly with increasing basal area. The regression coefficient of 3 g m^{-2} for herbaceous biomass was substantially lower than the slope obtained in longleaf pine plantations in Louisiana varying in age from 8 to 23 years, where biomass decreased 10 g m^{-2} with each m^2 ha^{-1} increase in tree basal area (Wolters, 1982). Precipitation at Fort Benning in Spring 2012 (12 mm in April and 85 mm in May) was below average (101 mm in April and 95 mm in May), particularly in April, and was lower compared to the average rainfall at the Louisiana site (195 mm in April and 175 mm in May between 1969 and 1975) (http://www.ncdc.noaa.gov; accessed October 2013). Differences in precipitation between the two sites therefore may have accounted for the lower decrease in biomass with increasing basal area in this study. The relationship between live biomass (herbaceous plus woody) and tree basal area was significant but basal area explained less variation in biomass compared to the relationship with herbaceous vegetation. Pecot *et al.* (2007), for a longleaf pine woodland in west central Georgia, showed that growth of herbaceous vegetation increased with overstory tree removal while woody understory did not. The authors suggest that herbaceous plants may be competing primarily for light while shade-tolerant understory woody plants and canopy trees competed mostly for soil nitrogen. The equations to estimate biomass from basal area can be particularly useful in fuel and carbon models where separate quantifications of herbaceous and dead biomass in the ground cover are needed.

Plant Cover-Biomass relationships

As hypothesized, and consistent with similar studies in the literature, biomass and cover at Fort Benning, GA were positively and linearly related for all growth forms and stands. For example, in the understory of Canadian riparian forests, MacDonald *et al.* (2012) found that percent cover varied linearly with biomass in dwarf shrubs and graminoids. Similarly, Muukkonen *et al.* (2006) reported significant linear biomass-cover relationships for dwarf shrubs and herbaceous plants (forbs and grasses) in boreal coniferous upland forests. According to Muukkonen *et al.* (2006), a linear relationship was suitable because species composition in the ground cover did not vary with total percent cover. In southern forests, understory herbaceous biomass has been reported to increase linearly with percent cover. For example, in Alabama, slopes of the regressions for relationships between cover and biomass were 1.9 g m^{-2}, 1.7 g m^{-2}, and 1.1 g m^{-2} respectively for planted pine, natural pine, and oak-pine forest types (Joyce and Mitchell, 1989). Significant linear relationships between biomass and cover were reported for herbs and shrubs in a 2-year-old longleaf pine plantation on hydric soils at Camp Lejeune, NC (Walker and Cohen, 2009) and were best described by a log-transformed equation.

Models and Prediction

A single model was not sufficient to describe the relationship between biomass and cover in the ground cover layer. For shrubs/tree seedlings, vines, and graminoids two models were needed while for legumes and forbs three different models were necessary. The slope of the relationship of biomass versus cover was highest in the 5-year-old stand for vines, graminoids, legumes, and forbs. In the ground cover layer, the ratio of biomass to cover within a growth form can vary with stand age or seral stage (Alaback, 1986), because of different light conditions determined by stand structure. Higher light availability can allow plants to produce more biomass per unit of cover and also can influence plant architecture and species composition. In the youngest stand, there was no overstory canopy. In order to limit the effect of stand age on understory biomass-cover relationships, Muukkonen *et al.* (2006) did not include very young stands in their analyses. In contrast to our results, the increase in biomass with increasing percent cover did not differ between early and late seral stages for graminoids and dwarf shrubs in riparian boreal forests (MacDonald et al., 2012). In riparian forests, the relationship between biomass and cover for such growth forms may be driven more by hydrologic processes.

While differences between the 5-year-old stand and the other stands can be explained by light limitation under tree canopies compared to an early seral stage, further separations into three models for legumes may reflect a difference in species composition between the 64-year-old stand and the younger stands. The legume species *Tephrosia* *virginiana* (L.) Pers., which is denser and taller than most legume species we encountered, occurred and was abundant only in the 64-year-old stand. In forbs, higher slope for the natural stands compared to the 12- and 21-year-old stands suggest an influence of stand origin, and possibly past land use, on the biomass cover ratio. Within the shrub/tree seedling growth form, the slope of the biomass versus cover relationship was higher in the 12-year-old stand than in all other stands. The slope for the 12-year-old stand was similar to that of dwarf shrubs in Muukkonen *et al.* (2006) and MacDonald *et al.* (2012) (both coefficients were 2.1 g m^{-2}). A separate model for the 12-year-old stand was the result of generally higher biomass but not higher cover in the 12-year-old stand compared to the other stands. The two different models may be a result of differences in species composition within the growth form, because dense and many branched shrub species with high biomass per unit cover, such as *Vaccinium myrsinites* Lam. and other species in the Ericaceae family, were more common in the 12-year-old stand compared to all other stands. These results suggest that a single linear relationship in the graminoid and vine growth forms could be used to estimate biomass from cover for longleaf pine forests similar in ground cover species composition and growth forms to the stands at Fort Benning, GA, regardless of stand age and structure. However, graminoid and vine biomass will be probably underestimated in very young plantations without a tree canopy.

Results from this study provide a better understanding of the relationship between aboveground biomass and cover of plant growth forms in the ground cover of longleaf pine stands. In shrubs/tree seedlings, vines, graminoids, legumes, and forbs, biomass was linearly related to percent cover. Two different equations for shrubs/tree seedlings, vines, and graminoids and three equations for legumes and forbs were developed. In the 5-year-old stand, which lacked overstory trees, the slopes of the regressions were generally higher than in the other stands, suggesting that a lower slope under tree canopy was determined by light limitation. Other changes in biomass-cover relationships between some stands for shrubs/tree seedlings, legumes, and forbs may be related to stand-specific differences in species composition and dominant species and to stand origin (planted versus naturally regenerated stands). Through its influence on species composition, a different fire history among stands may have also indirectly affected the relationships between biomass and cover. Live, herbaceous, graminoid, and dead biomass were linearly and inversely related to basal area. Biomass-basal area equations developed in this study can be used to obtain a rapid estimate of herbaceous, dead, and graminoid biomass when stand structure data are available but ground cover data are not.

CHAPTER 3. CONCLUSIONS

Results from this study provide information useful for estimating ground cover biomass in longleaf pine ecosystems. Evidence supports use of the fast and non-destructive method of visual cover estimate to predict biomass of growth forms in the ground cover layer. Relationships between biomass and cover were linear but different models were needed for different growth forms and stands. Regression slopes were highest in the youngest stand, which did not have a tree canopy, for all three herbaceous growth forms and for vines. Other slope differences in biomass-cover relationships seemed to be linked to differences in ground cover composition, as in the case of shrubs/tree seedlings and legumes, or to stand origin (planted versus natural) as in the case of forbs. Live, herbaceous, graminoid, and dead biomass in the ground cover layer can be estimated by using linear relationships with basal area. Further research should investigate the relationship between biomass and cover in other areas of the longleaf pine range, especially in areas of bluestem and wiregrass, and the influence of plant height, which is probably more variable within each growth form in other seasons. Our results also support the findings of other studies indicating that herbaceous biomass can be efficiently estimated by basal area.

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