

RESEARCH ARTICLE

Effects of longleaf pine planting density and other factors on stand structure and associated wildlife habitat

Evan A. Wheeler¹, William D. Gulsby^{1,2}, John S. Kush¹, Robert A. Gitzen¹

The primary objective of many longleaf pine (*Pinus palustris*) restoration programs is to enhance or restore habitat for wildlife dependent on herbaceous plant communities. Because herbaceous cover is inversely related to canopy cover, restoration programs often place restrictions on longleaf pine planting density. However, the influence of planting density on understory plant communities has been inadequately evaluated. Therefore, we initiated a study to examine the relative influences of planting density and other factors on overall understory composition and forage availability for white-tailed deer (*Odocoileus virginianus*) and northern bobwhite (*Colinus virginianus*) in nine longleaf pine stands throughout the Coastal Plain of Alabama during 2017–2018. We found that coverage of herbaceous plants decreased 3.5%, coverage of woody plants decreased 2.4%, and coverage of northern bobwhite forage plants decreased 1.9% for each 1 m²/ha increase in longleaf pine basal area. However, planting density was not a significant predictor of current basal area, nor coverage of any functional group of plants we examined, likely because current longleaf pine density averaged only 46% (range = 30–64%) of seedling planting density. We did not detect an effect of prescribed fire on stand condition or understory plant communities, likely due to variability in fire timing and frequency. Our findings related to planting density were likely a function of low longleaf pine survival, which is not uncommon. Because of this and the inherent variability in growth rates for young longleaf pine stands, restoration programs should consider placing greater emphasis on post-planting monitoring and management than planting density.

Key words: basal area, herbaceous, longleaf pine, *Pinus palustris*, planting density, prescribed fire, understory, wildlife habitat

Implications for Practice

- Restoration of longleaf pine ecosystems may be accomplished via plantation forestry, but variability in seedling survival makes it difficult to predict the relationship between planting density and understory plant community composition and structure.
- It is important to monitor longleaf pine plantings post-establishment to determine whether stands are currently meeting wildlife habitat or other ecological objectives because inherent and management-driven differences among sites will determine stand conditions over time.
- Longleaf pine restoration programs should focus more on post-establishment monitoring than pre-establishment prescriptions when longleaf pine ecosystem restoration is the goal.

INTRODUCTION

Though longleaf pine (*Pinus palustris*) forests once covered as much as 37 million hectares of the southeastern United States, coverage was reduced to approximately 3.5% (1.3 million hectares) of this original extent by 1995 (Landers et al. 1995). Reasons for the decline include unsustainable logging,

conversion of lands to other uses or faster growing pine species (e.g. loblolly pine [*P. taeda*]), and fire suppression (Landers et al. 1995; Outcalt 2000; Stainback & Alavalapati 2004). The decline in longleaf pine coverage has resulted in a significant decline in associated flora and fauna and, as of 2006, 66% of species classified as declining, threatened, or endangered in the southeastern United States were associated with the longleaf pine ecosystem (Mitchell et al. 2006).

However, increasing awareness of both the economic and ecological benefits of longleaf pine has increased interest in restoration. For example, America's Longleaf Initiative, a group led by several federal agencies, was founded in 2007 with the goal of more than doubling coverage of longleaf pine across the Southeast within a 15-year period. Concomitantly, financial assistance programs have encouraged longleaf pine restoration

Author contributions: EAW, WDG, JSK, RAG conceived and designed the research and contributed to writing and editing the manuscript; EAW collected and analyzed the data; WDG, RAG contributed to data analysis.

¹School of Forestry and Wildlife Sciences, Auburn University, Auburn, Alabama U.S.A.

²Address correspondence to W. D. Gulsby, email wdg0010@auburn.edu

© 2019 Society for Ecological Restoration

doi: 10.1111/rec.13108

Supporting information at:

http://onlinelibrary.wiley.com/doi/10.1111/rec.13108/supinfo

on private lands, and plantation forestry has been proposed as a viable means of wide-scale longleaf restoration (Harrington 2011). For example, the Natural Resources Conservation Service (NRCS) offers longleaf planting assistance to private landowners through the Environmental Quality Incentives Program (EQIP; NRCS 2017).

The major emphasis of these efforts centers around the ecological benefits associated with maintaining vegetative diversity and promoting an herbaceous understory, both of which are affected by planting density. Planting density affects the structure and species composition of understory vegetation in a variety of tree plantation systems. For example, wider tree spacing resulted in greater species richness and cover of herbaceous plants in red pine (*P. resinosa*), black spruce (*Picea mariana*), and white spruce (*P. glauca*) plantations in Canada (Newmaster et al. 2006). Similarly, lower stocked Monterey pine (*P. radiata*) stands in New Zealand had greater understory cover (Brockhoff et al. 2003). Based on these, and other, results Carnus et al. (2006) recommended increasing tree spacing in plantations where maintaining biodiversity is an objective.

Accordingly, many longleaf pine restoration programs restrict maximum planting density. However, from a silvicultural perspective, planting density influences stocking rates, planting costs, wood quality and volume, and timing of operational factors such as harvesting and thinning (Huang et al. 2005). Greater planting densities provide a buffer against seedling mortality associated with competition and herbivory, and increase potential timber revenues (Harrington 2011). Further, Albritton (2012) suggested that greater planting densities (e.g. $\geq 1,483$ seedlings/ha) allow stands to reach canopy closure and naturally prune lower limbs sooner, resulting in a greater number of high-quality trees. Others (Demers et al. 2000) have recommended even greater longleaf pine planting densities if timber production is a primary objective.

However, because canopy closure occurs sooner in densely planted stands, coverage of understory vegetation and duration of its availability will decline earlier in the life of the stand (Harrington 2006). Specifically, denser stands compete with understory vegetation through the combined effects of overstory shading, needle-fall, and belowground competition (Harrington 2011). Therefore, wildlife-focused longleaf pine restoration generally calls for decreased planting densities. For example, Demers et al. (2000) recommended planting from 742 to 1,236 seedlings/ha if the goal is longleaf ecosystem restoration and/or wildlife habitat. Further, South (2006) suggested that a planting density of 1,100 seedlings/ha would be more optimal than 2,200 seedlings/ha where providing herbivore forage is an objective. Even in bottomland hardwood forests, planting fewer seedlings is recommended to increase suitability of afforested sites for wildlife (Twedt & Wilson 2002). Although the literature is replete with examples of the relationship between canopy cover and understory vegetation, few have explored this relationship in a wildlife context as it pertains to afforestation efforts, outside of these few examples.

However, prescribed fire is also an important driver of wildlife habitat quality in a variety of systems, including longleaf pine forests. Coupled with the more open canopy

associated with this species, prescribed fire encourages a species-rich herbaceous understory (Van Lear et al. 2005). Specifically, frequent (i.e. every 1–3 years), low-intensity fire limits invasive plant coverage, prepares the seedbed for natural longleaf pine regeneration, increases understory plant diversity, and stimulates seed production of native species (Frost 1993; Aschenbach et al. 2009). In the absence of frequent fire, woody shrubs and trees will eventually develop a midstory, suppressing herbaceous plant coverage by shading plants near ground level (Kush et al. 1999; Loudermilk et al. 2011). In contrast, frequent fire in longleaf pine stands can result in some of the most species-rich plant communities outside of the tropics (Hedman et al. 2000), and plant species densities as great as 42/0.25 m² have been recorded in longleaf pine savannas (Drew et al. 1998). Therefore, even in relatively low-density longleaf pine stands, absence of frequent prescribed fire may preclude occupancy or limit abundance of both flora and fauna.

Nonetheless, wildlife-focused longleaf pine restoration programs generally place greater emphasis on planting densities than prescribed fire. Specifically, planting densities are restricted to a range of 989–1,691 seedlings/ha under the EQIP in Alabama (NRCS 2014). Anecdotally, these guidelines may be overly restrictive as abundant herbaceous vegetation may be maintained, even in densely planted stands, when frequent prescribed fire is applied. Further, the response of understory vegetation to planting density may differ among species. For example, Newmaster et al. (2006) found that the impact of tree spacing on understory vegetation was greater for spruce than pine plantations. Given the role of fire and variable effects of tree spacing on understory vegetation among species, some longleaf pine restoration programs may be unnecessarily restrictive, decreasing landowner participation and ultimately limiting longleaf pine restoration efforts. However, research on longleaf pine planting regimes and resulting wildlife habitat is limited (Harrington 2011). More broadly, plantation establishment for objectives other than wood production is increasing, but little is known about the effects of this practice on biodiversity (Bremer & Farley 2010) or, more specifically, wildlife habitat.

Therefore, we conducted a study to examine the relative influences of planting density, prescribed fire, and other factors on stand structure and understory composition in plantation longleaf pine stands throughout the Coastal Plain of Alabama. We also examined how these factors affected coverage of preferred seed-producing and forage plants for northern bobwhite (*Colinus virginianus*) and white-tailed deer (*Odocoileus virginianus*). White-tailed deer are the most sought-after game species in the southeastern United States, and many private landowners in the region implement hunt-lease programs to provide an annual revenue source to offset land management costs (Barlow et al. 2007; Davis et al. 2017). Northern bobwhites are also a game species, but they are a common bird in steep decline, largely due to habitat fragmentation and loss (Hernández et al. 2013). Further, northern bobwhite populations in the southeastern United States are strongly linked to the longleaf pine ecosystem, and areas that support robust northern bobwhite populations may also provide habitat for Bachman's sparrow (*Peucaea aestivalis*), gopher tortoises (*Gopherus polyphemus*), and the

red-cockaded woodpecker (*Picoides borealis*), all species of conservation concern in the longleaf pine ecosystem (Van Lear et al. 2005). Therefore, we considered white-tailed deer and northern bobwhites indicators of financially and ecologically motivated wildlife objectives, respectively, in this system.

We hypothesized that coverage of understory vegetation (including forage plants) would be inversely related to planting density. We also hypothesized that coverage of herbaceous plants, northern bobwhite forage, and white-tailed deer forage would increase with increasing fire frequency, and that coverage of woody vegetation would decrease with increasing fire frequency.

METHODS

We conducted our study in nine unthinned longleaf pine stands on private lands in the Coastal Plain of Alabama (Fig. 1). All stands were ≥ 5 years old, planted to a specific density (i.e., not regenerated naturally) using containerized seedlings, prepared for planting via broadcast herbicide application, and ≥ 4 ha in area. All stands were treated with prescribed fire at least once prior to our study, mostly during the dormant season. However, season and recency of burn relative to sampling varied among stands.

Stand 1 was in Escambia County and had Orangeburg fine sandy loam and Benndale-Orangeburg complex soils. Stand 2 was in Conecuh County and had Greenville sandy loam and Troup-Orangeburg association soils. Stand 3 was in Barbour County and had Luverne sandy loam, Goldsboro loamy fine sand, Mantachie, Kinston, and Iuka soils. Stand 4 was in Bullock County and had Conecuh sandy loam soils. Stand 5 was in Macon County and had Bonifay loamy fine sand and Lucy-Luverne complex soils. Stand 6 was in Barbour County and had Luverne-Springhill complex and Conecuh sandy loam soils. Stand 7 was in Lowndes County and had Nankin-Springhill-Lucy complex, Cowarts sandy loam, Bonifay loamy sand, and Lucy loamy sand soils. Stand 8 was in Lowndes County and had Nankin-Springhill-Lucy complex and Bonifay loamy sand soils. Stand 9 was in Barbour County and had Luverne sandy loam, Troup-Alaga complex, Mantachie, Kinston, Iuka, and Luverne-Springhill complex soils (NRCS 2019).

The study region generally had hot summers, mild winters, and year-round precipitation. Specifically, daytime high summer temperatures typically ranged from 29 to 35°C, average winter low temperatures ranged from -1 to 7°C, and average annual statewide precipitation totals were 137 cm (Runkle et al. 2017).

Prior to sampling, we mapped stand boundaries in ArcMap10.4.1 (Environmental Systems Research Institute, Inc., Redlands, CA, U.S.A.). We subset stands > 8 ha into 8 ha units and randomly selected one 8 ha unit for sampling using a random number generator in program R (R Core Team 2019). We used a fishnet grid to systematically locate a series of points spaced 50 m apart within each stand and randomly selected sample points from the grid at a density

of 2.5 ha⁻¹. Points were distributed proportionately (based on area) between interior (> 50 m from boundary) and edge (≤ 50 m from boundary) portions of the stand. We performed vegetation sampling at each point during the summers of 2017 and 2018. Specifically, we established a 30-m transect along a random azimuth originating at each point and identified each species of plant that intersected the transect at 3-m increments (10 total points) according to the FIREMON Point Intercept Sampling Method (Caratti 2006). When multiple plants intersected a single point, we recorded a hit for each independent plant; therefore, it was possible to have total cover values $> 100\%$ for a transect.

For each transect, we calculated the percent cover of herbaceous (i.e. grasses and forbs) and woody plants (i.e. trees, shrubs, and woody vines). We also calculated the percent cover of plants considered moderate to highly preferred white-tailed deer (*Odocoileus virginianus*) forage based on available literature (Warren & Hurst 1981; Miller & Miller 1999). We did the same for plants considered valuable seed and soft mast producers for northern bobwhite (*Colinus virginianus*), according to the literature (Landers & Johnson 1976; Rosene & Freeman 1988; Miller & Miller 1999). We also quantified longleaf pine basal area (m²/ha) and density (trees/ha), as well as basal area of all non-longleaf pine species (m²/ha), at every other vegetation sampling transect during 2018. Specifically, we counted and measured diameter at breast height (DBH) of all longleaf pine trees ≥ 1.4 m in height and all non-longleaf pine trees ≥ 7.6 cm DBH within 5 m of either side of the transect, such that area sampled constituted an approximately 5% cruise. We defined planting density for each stand as the target longleaf pine planting density based on information provided by landowners and managers.

We used the linear regression in program R (R Core Team 2019) to estimate the effects of stand-level parameters (i.e. longleaf pine planting density, stand age, and average prescribed fire return interval [stand age \div number of prescribed fires]) on percent cover of each category of plants, current longleaf pine density, and longleaf pine and non-longleaf pine (i.e. all other species) basal areas. We compared stand-level models (i.e. response variables averaged across transects within each stand) using Akaike's information criterion (AICc) (Burnham & Anderson 2004), and considered those within ≤ 2 Δ AICc points of the top model competitive. We generated parameter estimates and associated 95% confidence intervals for each fixed effect parameter in each competitive model. We considered parameter estimates from competing models with 95% confidence intervals not overlapping zero informative (Arnold 2010).

We also constructed linear mixed-effects models in the *nlme* package (Pinheiro et al. 2018) to estimate the effect of longleaf pine basal area on our response variables at the transect level, because we collected both basal area and vegetation data for a subset of transects. To account for the structure of our data and differences among stands due to inherent factors like soil characteristics, sample point was nested within stand as a random effect in each model. We considered parameter estimates with 95% confidence limits not overlapping zero informative.

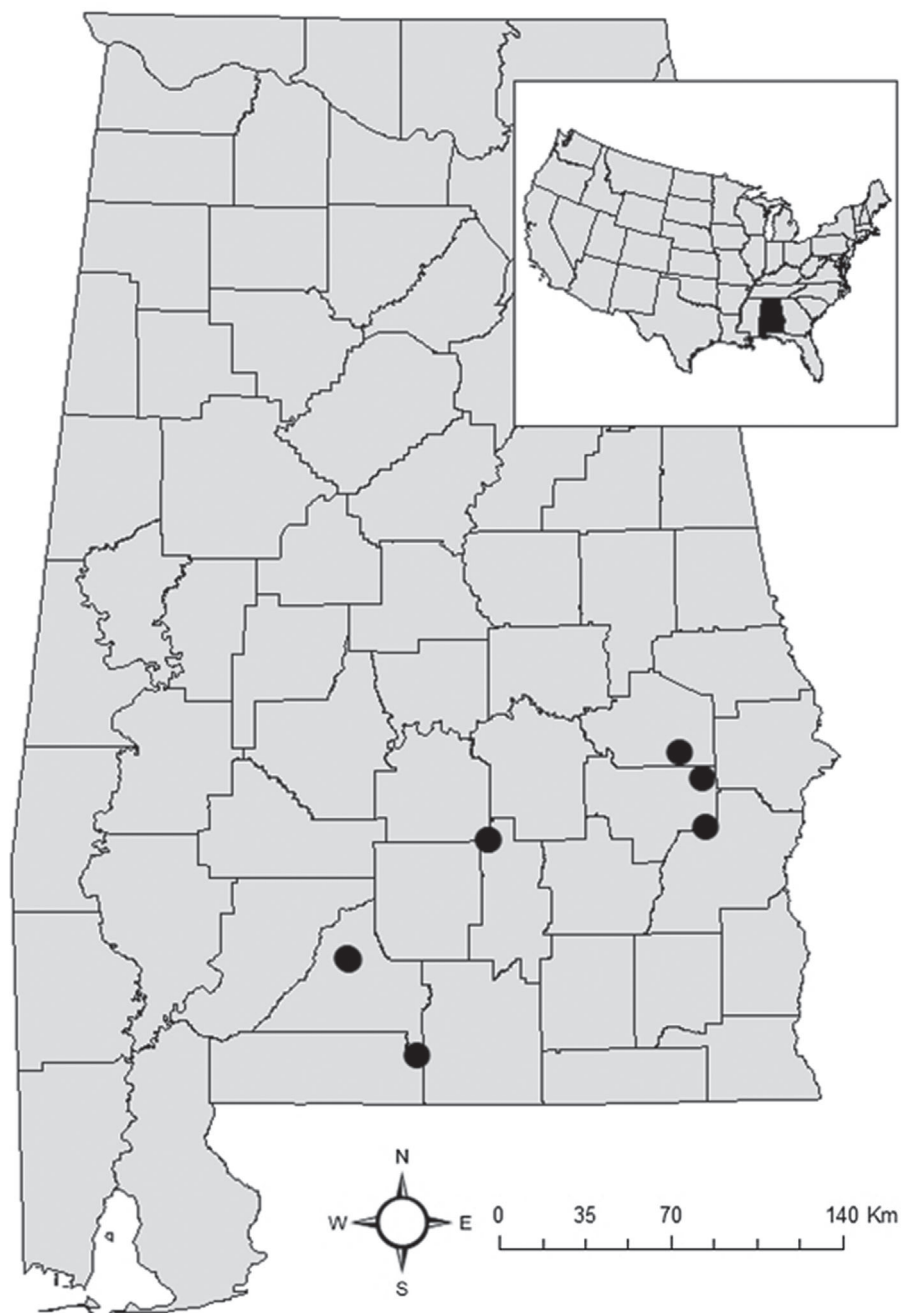


Figure 1. General locations of longleaf pine (*Pinus palustris*) stands in the Coastal Plain of Alabama where we evaluated the effects of longleaf pine planting density and stand management on coverage of herbaceous and woody plants, white-tailed deer (*Odocoileus virginianus*) forage plants, and valuable seed and soft mast producers for northern bobwhite (*Colinus virginianus*) during 2017–2018.

RESULTS

We collected data from a total of nine stands that met our criteria. Stand size ranged from 5 to 8 ha and planting density ranged from 1,078 to 1,538 longleaf seedlings/ha. On average, longleaf pine density in stands was 46% of the reported planting density (range = 30–64%). During 2017, stand age ranged from 6 to 16 years, and average fire return interval ranged from 2 to 7 years (Table 1). Although stand age, prescribed fire return,

and planting density (stand-level factors) were contained in the confidence set of models describing coverage of some vegetation types (Table S1), none of these predictors were informative (i.e. their confidence intervals overlapped zero).

The stand-level models for the effects of fire and planting density on longleaf pine basal area, non-longleaf pine basal area, and current longleaf pine density were similarly uninformative (Table S2). Specifically, the intercept only (i.e. null) model

Table 1. Management history for longleaf pine (*Pinus palustris*) stands in the Coastal Plain of Alabama where we evaluated the effects of planting density and stand management on coverage of herbaceous and woody plants, white-tailed deer (*Odocoileus virginianus*) forage, and seed and soft mast producers for northern bobwhite (*Colinus virginianus*) during 2017–2018. We calculated average fire return by dividing stand age by the number of prescribed fires applied.

Stand	Age	Average Fire Return	Planting Density (seedlings/ha)	Current Density (trees/ha)
1	8	2.7	1,077	332
2	10	3.3	1,122	629
3	8	2.7	1,196	608
4	12	2.0	1,344	637
5	14	7.0	1,345	854
6	16	4.0	1,347	764
7	14	3.5	1,359	415
8	6	3.0	1,483	584
9	6	3.0	1,537	597

carried most of the weight for each of these models. Although average fire return was included in the confidence set of models predicting both longleaf pine density and basal area, the confidence limits for these parameter estimates overlapped zero.

In contrast, at the transect level, longleaf pine basal area was a significant predictor of percent cover of herbaceous and woody plants, as well as northern bobwhite forage plants (Fig. 2). Specifically, for each 1 m²/ha increase in longleaf basal area, percent cover of herbaceous plants decreased 3.5% (95% CI = -6.18 to -0.73), percent cover of woody plants decreased 2.3% (95% CI = -4.54 to -0.02), and percent cover of northern bobwhite forage plants decreased 1.9% (95% CI = -3.28 to -0.47).

DISCUSSION

Although tree spacing influences understory vegetation in a variety of systems (e.g. Twedt & Wilson 2002; Brokerhoff et al. 2003; Carnus et al. 2006; Newmaster et al. 2006), we did not detect an effect of longleaf pine planting density on coverage of any category of plant, nor on current longleaf pine density or basal area in our stands. We believe this finding is likely attributable to two major factors, the first being post-planting mortality. Specifically, longleaf pine density in our stands was, on average, only 46% of the original planting density. Although some have reported longleaf pine seedling survival rates >80% (Cram et al. 2010; Hu et al. 2012), reports of low survival are not uncommon. For example, Knapp et al. (2006) reported longleaf pine survival was as low as 57%, 20 months post-planting for plots prepared with herbicide, and Knapp et al. (2015) reported longleaf pine survival in clearcuts was 40% at the end of the fifth growing season. In addition, Jack et al. (2010) measured survival of longleaf pine seedlings for two years after application of prescribed fire and found that survival was only 30–50%, depending on the season of burn. Finally, South et al. (2012) reported that average survival across a number of studies was 51% for plantation longleaf pine stands ranging in age from 10

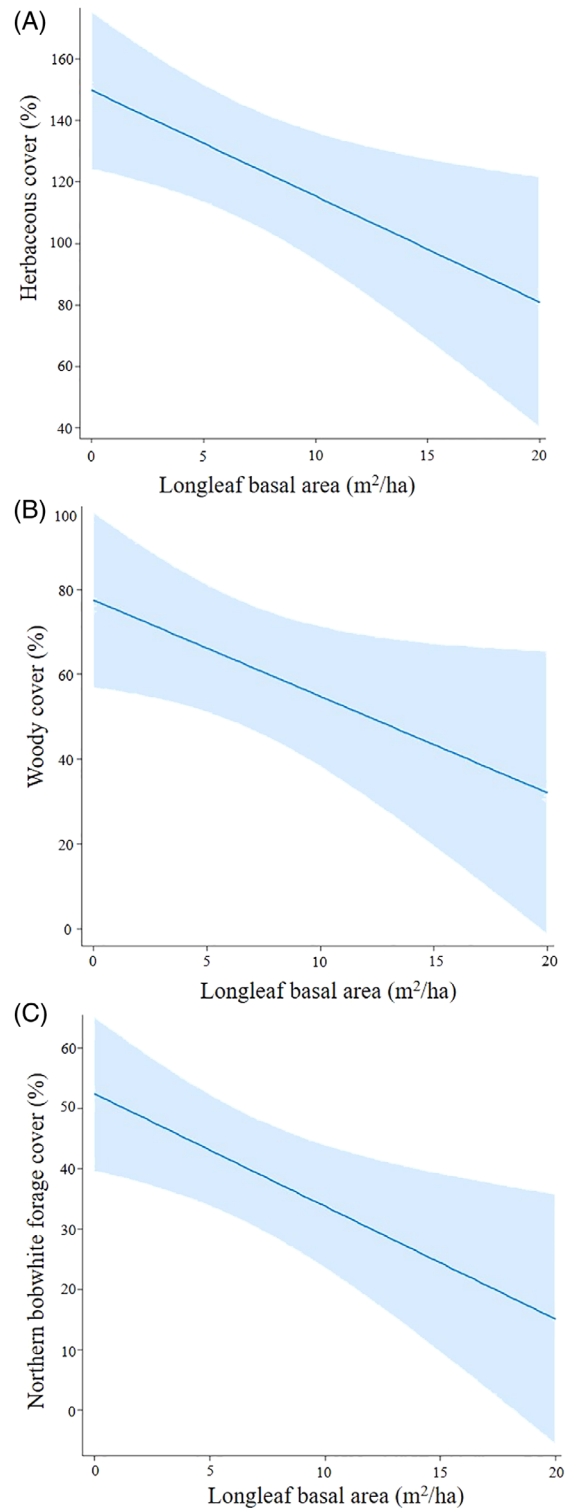


Figure 2. Plots predicting the effects of longleaf pine (*Pinus palustris*) basal area on the understory percent cover of (A) herbaceous plants, (B) woody plants, and (C) plants valuable as seed and soft mast producers for northern bobwhite (*Colinus virginianus*) for longleaf pine stands in the Coastal Plain of Alabama sampled during 2017–2018. Bands represent 95% CI.

to 28 years. Common sources of longleaf pine mortality include fire (Cram et al. 2010), competition with herbaceous vegetation (Hu et al. 2012), and drought (Rodríguez-Trejo et al. 2003). Although our study design did not allow us to directly determine the factors that contributed to low survival, planting density was not a good predictor of current density and, by extension, a poor predictor of canopy cover, which could interfere with understory vegetation development.

The second major factor influencing the lack of a correlation between planting density and understory vegetation in our study was likely the physical characteristics of longleaf pine. Even in mature longleaf pine stands, canopy closure may average as low as 50% (Palik & Pederson 1996). Longleaf pine crowns, especially in young trees, are more sparse and open than that of loblolly pine (*P. taeda*), the most commonly planted pine species in the southeastern United States. This suggests that longleaf pine may be another example of a tree species for which planting density has a lesser impact on understory vegetation, similar to Newmaster et al. (2006).

Nonetheless, we did find that longleaf pine basal area was negatively correlated with coverage of herbaceous, woody, and northern bobwhite forage plants. In general, this is consistent with much of the literature. For example, in a study of young plantation longleaf and slash pine (*P. elliottii*), biomass of herbaceous plants decreased 73 kg/ha for each 1 m²/ha increase in pine basal area (Wolters 1973). Similarly, Harrington and Edwards (1999) reported a 21% increase in herbaceous coverage in response to thinning young longleaf pine plantations from 9 to 5 m²/ha. Specifically regarding northern bobwhite habitat requirements, Stransky (1971) recommended a maximum longleaf pine basal area of 14 m²/ha, and Little et al. (2009) suggested pine basal area should not exceed 9 m²/ha when northern bobwhite habitat is a primary management objective. However, Wolters (1982) found that coverage of herbaceous vegetation in longleaf pine stands was not significantly impacted until 17 years post-planting. In contrast, we found a negative effect of longleaf pine basal area in our stands, which averaged only 10 years in 2017.

Given the importance of light availability to herbaceous plants (Pecot et al. 2007), it is possible that the influence of basal area on understory vegetation may vary with the age and size of trees, attributable to differential light attenuation. For example, Gaines et al. (1954) suggested that there may be an upward trend of herbaceous production in older stands with greater basal area but fewer trees, where side light is increased due to taller trees. However, rates of crown closure in plantation stands often exceed those of natural stands (Harrington 2006), and our results may indicate that the negative influences of increasing basal area may be apparent in plantation stands at a younger age than in naturally regenerated longleaf pine stands.

It is well established that prescribed fire promotes herbaceous vegetation by reducing litter accumulation, reducing or removing competing vegetation, and influencing overstory structure (Boyer 1990; Boyer 1993; Harrington & Edwards 1999). Prescribed fire can also benefit longleaf pine stands by suppressing encroachment of hardwood and other southern yellow pine species that threaten longleaf pine recruitment and slow growth

(Brockway & Lewis 1997; Provencher et al. 2001; Shappell & Koontz 2015). Conversely, many managers are concerned with fire-associated mortality, even in longleaf pine stands, and Boyer (1993) found that frequent fire can reduce longleaf pine growth rates. Although we did not detect a negative effect of fire on longleaf pine density or basal area, there was no evidence to suggest fire return interval decreased non-longleaf basal area either. However, the effect of average fire return interval on herbaceous vegetation in our study approached statistical significance. Fire frequency is more important than season in maintaining understory vegetation structure consistent with longleaf pine ecosystem restoration objectives (Glitzenstein et al. 2008; Addington et al. 2015). However, a 1–3-year fire return is necessary for limiting woody plant abundance in longleaf pine understories (Addington et al. 2015), and Glitzenstein et al. (2003) suggested that even slight reductions in fire frequency can stimulate sprouting and proliferation of shrubs, reduce space available for herbaceous plants, and decrease species richness. Therefore, the absence of a statistically significant effect of fire on woody vegetation in our study may be attributable to the fact that the average fire return interval in our stands was 3.5 years and 3.7 years during 2017 and 2018, respectively. Further, the lack of a wide range in fire return intervals represented among our stands likely limited our ability to detect an effect of this factor on woody vegetation and other parameters of interest.

Similarly, we did not detect an influence of prescribed fire return on northern bobwhite forage plants. One potential reason is that the majority of these plants are promoted by growing season fire, whereas the majority of prescribed fire events on our sites occurred during the dormant season. Specifically, early growing season fire promotes both native warm season grasses and forbs, whereas late growing season fire may promote additional forb coverage and decrease woody encroachment (Harper 2007). Further, Haywood (2009) found that month of burning significantly affected herbaceous plant cover in young longleaf pine stands, with July-burn plots having significantly greater grass and forb cover than March-burn or May-burn plots. In addition to the potential influences of season of burn, our stands were exposed to prescribed fire less frequently than is generally recommended (i.e. 2 years; Burke et al. 2008) for northern bobwhite habitat management. Regardless, our finding does not necessarily imply that our stands were not suitable for northern bobwhite. Specifically, although we did not evaluate cover, it has been established that native, perennial grasses, which were abundant in our stands, are important for northern bobwhite nesting material and cover (Greenfield et al. 2002). Therefore, our stands may have provided adequate nesting and predator concealment cover for this species.

None of the factors we evaluated significantly influenced coverage of preferred white-tailed deer forage plants. This is not surprising given that most preferred deer forage plants are either forbs or woody browse species (Warren & Hurst 1981; Miller & Miller 1999). Many of our sites were dominated by grasses, which have little to no food value for deer, and may preclude more preferred forb species (Felix et al. 1986). In addition, the increased coverage of woody browse species in the less frequently burned stands may have been counteracted by

the increased coverage of herbaceous plants in more frequently burned stands. Therefore, deer forage was spread out between more and less frequently burned stands, and there was a lack of a detectable directional effect of fire on overall deer forage availability.

These findings have important implications for advancing our understanding of the primary drivers of understory structure and associated wildlife habitat quality not only in young plantation longleaf pine stands, but potentially in other systems as well. Specifically, the absence of any detectable effects of planting density on understory responses of interest, combined with previously observed variation in growth and survival common among young longleaf pine plantations, suggests that post-planting monitoring and management guidelines may be more important than those related to planting density for government-subsidized longleaf pine restoration programs. In addition, these data offer further evidence that the effects of planting density on ecological restoration objectives may vary according to the physical characteristics and silvics of the tree species being planted.

Nonetheless, several researchers have reported negative effects of greater stocking rates or planting densities on understory vegetation (Twedt & Wilson 2002; Brockerhoff et al. 2003; Carnus et al. 2006; Newmaster et al. 2006), and we observed a negative influence of increasing longleaf pine basal area on herbaceous, woody, and northern bobwhite forage plants. Therefore, in longleaf pine systems, managers should actively monitor understory vegetation and use thinning and prescribed fire to maintain preferred understory conditions, as necessary. In addition, although relatively high coverage of herbaceous vegetation generally benefits a number of longleaf pine-associated wildlife species, it is important to be aware that high herbaceous coverage does not necessarily provide optimal habitat for all species throughout the year. Rather, stand management, including management actions like prescribed fire, should be prescribed and periodically evaluated on a case-by-case basis to ensure habitat conditions for focal species are being met (Harper 2007).

Acknowledgments

We thank S. Saloom, T. Bowden, and B. Shepherd for allowing access to their properties for a portion of this work. We also thank T. Albritton, R. Johnson, J. Stivers, N. Hatch, T. DeVos, A. Nix, A. Pritchett, B. Gray, J. Martin, and J. Gilbert for technical and logistical assistance throughout the project. K. Keene, D. Penfold, J. Goethlich, S. Rankins, J. Graves, T. Mershon, L. Hancock, M. Gomes, N. Deig, J. Osborn, G. Hepp, and A. Gauci assisted with data collection. Funding for this project was provided by the United States Department of Agriculture National Institute of Food and Agriculture Hatch Project 1009794 and the Auburn University School of Forestry and Wildlife Sciences.

LITERATURE CITED

Addington RN, Knapp BO, Sorrell GG, Elmore ML, Wang GG, Walker JL (2015) Factors affecting broadleaf woody vegetation in upland pine forests

- managed for longleaf pine restoration. *Forest Ecology and Management* 354:130–138
- Albritton T (2012) The longleaf planting density debate. *Alabama's Treasured Forests Magazine* Fall 2012:10–11
- Arnold TW (2010) Uninformative parameters and model selection using Akaike's Information Criterion. *Journal of Wildlife Management* 74:1175–1178
- Aschenbach TA, Foster BL, Imm DW (2009) The initial phase of a longleaf pine-wiregrass savanna restoration: species establishment and community responses. *Restoration Ecology* 18:1–10
- Barlow R, Grado S, Miller D, Grebner D (2007) Opportunity costs of managing for wildlife habitat in the North Central Hills region of Mississippi. *Southern Journal of Applied Forestry* 31:39–46
- Boyer WD (1990) *Growing-season burns for control of hardwoods in longleaf pine stands*. Research Paper SRS-256. United States Department of Agriculture, Forest Service, Southern Forest Experiment Station, New Orleans, Louisiana
- Boyer WD (1993) Eighteen years of seasonal burning in longleaf pine: effects on overstory growth. Pages 602–610. In: *Fire, Meteorology, and the Landscape: 12th Conference on Fire and Forest Meteorology*. Society of American Foresters, Jekyll Island, Georgia
- Bremer LL, Farley KA (2010) Does plantation forestry restore biodiversity or create green deserts? A synthesis of the effects of land-use transitions on plant species richness. *Biodiversity and Conservation* 14:3893–3915
- Brockway DG, Lewis CE (1997) Long-term effects of dormant-season prescribed fire on plant community diversity, structure, and productivity in a longleaf pine wiregrass ecosystem. *Forest Ecology and Management* 96:167–183
- Brockerhoff EG, Ecroyd CE, Leckie AC, Kimberley MO (2003) Diversity and succession of adventive and indigenous vascular understorey plants in *Pinus radiata* plantation forests in New Zealand. *Forest Ecology and Management* 185:307–326
- Burke JD, Chamberlain MJ, Geaghan JP (2008) Effects of understory vegetation management on brood habitat for northern bobwhites. *Journal of Wildlife Management* 72:1361–1368
- Burnham KP, Anderson DR (2004) Multimodel inference: understanding AIC and BIC in model selection. *Sociological Methods & Research* 33:261–304
- Caratti JF (2006) Point intercept sampling method. FIREMON: Fire Effects Monitoring and Inventory System. Pages PO-1–PO-12. In: Lutes D C (ed) *General Technical Report RMRS-GTR-164-CD*. United States Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado
- Carnus JM, Parrotta J, Brockerhoff E, Arbez M, Jactel H, Kremer A, Lamb D, O'Hara K, Walters B (2006) Planted forests and biodiversity. *Journal of Forestry* 104:65–77
- Cram MM, Outcalt KW, Zarnoch SJ (2010) Growth of longleaf and loblolly pine, planted on South Carolina sandhill sites. *Southern Journal of Applied Forestry* 34:79–83
- Davis PB, Munn IA, Henderson JE, Strickland BK (2017) Economic tradeoffs of managing for timber production or wildlife habitat. *Journal of Wildlife Management* 81:1363–1371
- Demers CA, Long A, Minogue PJ (2000) Longleaf pine regeneration. Document SS-FOR-13: School of Forest Resources and Conservation Department, UF/IAS Extension. Revised 2010, 2017
- Drew MB, Kirkman LK, Gholson AK Jr (1998) The vascular flora of Ichauway, Baker County, Georgia: a remnant longleaf pine/wiregrass ecosystem. *Castanea* 63:1–24
- Felix AC III, Sharik TL, McGinnes BS (1986) Effects of pine conversion on food plants of northern bobwhite quail, eastern wild turkey, and white-tailed deer in the Virginia Piedmont. *Southern Journal of Applied Forestry* 10:47–52
- Frost CC (1993) Four centuries of changing landscape patterns in the longleaf pine ecosystem. Pages 17–43. In: Hermann S M (ed) *The longleaf pine ecosystem: ecology, restoration and management*. Vol. 18. Proceedings of the Tall Timbers Fire Ecology Conference, Tallahassee, Florida

- Gaines EM, Campbell RS, Brasington JJ (1954) Forage production on longleaf pine lands of southern Alabama. *Ecology* 35:59–62
- Glitzenstein JS, Streng DR, Wade DD (2003) Fire frequency effects on longleaf pine (*Pinus palustris* P. Miller) vegetation in South Carolina and northeast Florida, USA. *Natural Areas Journal* 23:22–37
- Glitzenstein JS, Streng DR, Masters RE, Platt WJ (2008) Clarifying long-term impacts of fire frequency and fire season in southeastern Coastal Plain pine savannas. Pages 13–18. In: Stringer W C, Andrae J, Yarrow G (eds) *Proceedings of the Sixth Eastern Native Grass Symposium: Managing and Ecosystem on the Edge*, Columbia, South Carolina
- Greenfield KC, Burger LW Jr, Chamberlain MJ, Kurzejeski EW (2002) Vegetation management practices on conservation reserve program fields to improve northern bobwhite habitat quality. *Wildlife Society Bulletin* 30:527–538
- Harper CA (2007) Strategies for managing early successional habitat for wildlife. *Weed Technology* 21:932–937
- Harrington TB (2006) Plant competition, facilitation, and other overstory-understory interactions in longleaf pine ecosystems. Pages 135–156. In: Jose S, Jokela EJ, Miller DL (eds) *The longleaf pine ecosystem: ecology, silviculture, and restoration*. Springer, New York
- Harrington TB (2011) Overstory and understory relationships in longleaf pine plantations 14 years after thinning and woody control. *Canadian Journal of Forest Research* 41:2301–2314
- Harrington TB, Edwards MB (1999) Understory vegetation, resource availability, and litterfall responses to pine thinning and woody vegetation control in longleaf pine plantations. *Canadian Journal of Forest Research* 29:1055–1064
- Haywood JD (2009) Eight years of seasonal burning and herbicidal brush control influence sapling longleaf pine growth, understory vegetation, and the outcome of an ensuing wildfire. *Forest Ecology and Management* 258:295–305
- Hedman CW, Grace SL, King SE (2000) Vegetation composition and structure of southern coastal plain forests: an ecological comparison. *Forest Ecology and Management* 134:233–247
- Hernández F, Brennan LA, DeMaso SJ, Sands JP, Wester DB (2013) On reversing the northern bobwhite population decline: 20 years later. *Wildlife Society Bulletin* 37:177–188
- Hu H, Wang GG, Walker JL, Knapp BO (2012) Silvicultural treatments for converting loblolly pine to longleaf pine dominance: effects on planted longleaf pine seedlings. *Forest Ecology and Management* 276:209–216
- Huang CH, Kronrad GD, Morton JD (2005) The financially optimal loblolly pine planting density and management regime for nonindustrial private forestland in east Texas. *Southern Journal of Applied Forestry* 29:16–21
- Jack SB, Hiers JK, Mitchell RJ, Gagnon JL (2010) Fuel loading and fire intensity—effects on longleaf pine seedling survival. Pages 275–279. In: Stanturf J A (ed) *Proceedings of the 14th Biennial Southern Silvicultural Research Conference. General Technical Report SRS-121*. U.S. Department of Agriculture, Forest Service, Southern Research Station, Asheville, North Carolina
- Knapp BO, Wang GG, Walker JL, Cohen S (2006) Effects of site preparation treatments on early growth and survival of planted longleaf pine (*Pinus palustris* Mill.) seedlings in North Carolina. *Forest Ecology and Management* 226:122–128
- Knapp BO, Wang GG, Walker JL, Hu H (2015) From loblolly to longleaf: fifth-year results of a longleaf pine restoration study at two ecologically distinct sites. Pages 470–472. In: Holley A G, Connor K F, Haywood J D (eds) *Proceedings of the 17th Biennial Southern Silviculture Research Conference. Technical Report SRS-203*. U.S. Department of Agriculture, Forest Service, Southern Research Station, Asheville, North Carolina
- Kush JS, Meldahl RS, Boyer WD (1999) Understory plant community response after 23 years of hardwood control treatments in natural longleaf pine (*Pinus palustris*) forests. *Canadian Journal of Forest Research* 29:1047–1054
- Landers JL, Johnson AS (1976) *Bobwhite quail food habits in the southeastern United States with a seed key to important foods*. Miscellaneous Publication No. 4. Tall Timbers Research Station, Tallahassee, Florida
- Landers JL, Van Lear DH, Boyer WD (1995) The longleaf pine forests of the Southeast: requiem or renaissance? *Journal of Forestry* 93:39–44
- Little IT, Wellendorf SD, Palmer WE, Carroll JP (2009) Effects of timber density on northern bobwhite autumn abundance. Pages 178–183. In: Cederbaum S B, Faircloth B C, Terhune T M, Thompson J J, Carroll J P (eds). *Gamebird 2006: Quail VI and Perdix XII*. Warnell School of Forestry and Natural Resources, Athens, Georgia
- Loudermilk EL, Croper WP Jr, Mitchell RJ, Lee H (2011) Longleaf pine (*Pinus palustris*) and hardwood dynamics in a fire-maintained ecosystem: a simulation approach. *Ecological Modelling* 222:2733–2750
- Miller JH, Miller KV (1999) Forest plants of the southeast and their wildlife uses. The Southern Weed Science Society, Champaign, Illinois
- Mitchell RJ, Hiers JK, O'Brien JJ, Jack SB, Engstrom RT (2006) Silviculture that sustains: the nexus between silviculture, frequent prescribed fire, and conservation of biodiversity in longleaf pine forests of the southeastern United States. *Canadian Journal of Forest Research* 36:2724–2736
- Newmaster SG, Bell FW, Roosenboom CR, Cole HA, Towill WD (2006) Restoration of floral diversity through plantations on abandoned agricultural land. *Canadian Journal of Forest Research* 36:1218–1235
- NRCS (Natural Resources Conservation Service) (2014) Restoration and management of rare and declining habitats and tree/shrub establishment: establishment of longleaf pine stands. Alabama Job Sheet Nos. AL490B, AL612C, and AL643-1
- NRCS (Natural Resources Conservation Service) (2017) Environmental Quality Incentives Program (EQIP). <https://www.nrcs.usda.gov/wps/portal/nrcs/main/national/programs/financial/eqip/> (accessed 27 Mar 2017)
- NRCS (Natural Resources Conservation Service) (2019) Web soil survey. <https://websoilsurvey.sc.egov.usda.gov/> (accessed 27 Jan 2019)
- Outcalt KW (2000) The longleaf pine: ecosystem of the south. *Native Plants Journal* 1:42–53
- Palik BJ, Pederson N (1996) Overstory mortality and canopy disturbances in longleaf pine ecosystems. *Canadian Journal of Forest Research* 26:2035–2047
- Pecot SD, Mitchell RJ, Palik BJ, Moser EB, Hiers JK (2007) Competitive responses of seedlings and understory plants in longleaf pine woodlands: separating canopy influences above and below ground. *Canadian Journal of Forest Research* 37:634–648
- Pinheiro JD, Bates D, DebRoy S, Sarkar D, R Core Team (2018) nlme: linear and nonlinear mixed effects models. R Package version 3.1-131. <https://CRAN.R-project.org/package=nlme> (accessed 28 Dec 2019)
- Provencher LB, Herring J, Gordon DR, Rodgers HL, Tanner GW, Hardesty JL, Brennan LA, Litt AR (2001) Longleaf pine and oak responses to hardwood reduction techniques in fire-suppressed sandhills in northwest Florida. *Forest Ecology and Management* 148:63–77
- R Core Team (2019) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/> (accessed 28 Dec 2019)
- Rodríguez-Trejo DA, Duryea ML, White TL, English JR, McGuire J (2003) Artificially regenerating longleaf pine in canopy gaps: initial survival and growth during a year of drought. *Forest Ecology and Management* 180:25–36
- Rosene W, Freeman JD (1988) *A guide to and culture of flowering plants and their seed important to bobwhite quail*. Morris Communications Corporation, Augusta, Georgia
- Runkle JK, Kunkel K, Stevens L, Frankson R (2017) Alabama state climate summary. NOAA Technical Report NESDIS 149-AL
- Shappell LJ, Koontz SM (2015) Fire reintroduction increased longleaf pine (*Pinus palustris* L.) recruitment and shifted pine demographics in a long-unburned xeric sandhill assemblage. *Forest Ecology and Management* 354:344–352
- South DB (2006) Planting longleaf pine at wide spacings. *Native Plants Journal* 7:79–88
- South DB, Johnson EE, Hains MJ, VanderSchaaf CL (2012) Restoring longleaf pine on an agricultural site by planting alternating rows of slash pine: a case study. *Southern Journal of Applied Forestry* 36:118–125

- Stainback GA, Alavalapati JRR (2004) Restoring longleaf pine through silvopasture practices: an economic analysis. *Forest Policy and Economics* 6:371–378
- Stransky JJ (1971) Texas forestry paper No. 9: managing for quail and timber in longleaf pine forests. *Texas Forestry Papers No. 1-29, 1970–1976*:1–8
- Twedt DJ, Wilson RR (2002) Development of oak plantations established for wildlife. *Forest Ecology and Management* 162:287–298
- Van Lear DH, Carroll WD, Kapeluck PR, Johnson R (2005) History and restoration of the longleaf pine-grassland ecosystem: implications for species at risk. *Forest Ecology and Management* 211:150–165
- Warren RC, Hurst GA (1981) Ratings of plants in pine plantations as white-tailed deer food. *Mississippi Agriculture and Forestry Experiment Station, Information Bulletin 18*. Mississippi State University, Mississippi
- Wolters GL (1973) Southern pine overstories influence herbage quality. *Journal of Range Management* 26:423–426

- Wolters GL (1982) Longleaf and slash pine decreases herbage production and alters herbage composition. *Journal of Range Management* 35:761–763

Supporting Information

The following information may be found in the online version of this article:

Table S1. Number of parameters (K), Akaike's information criterion (AICc), difference from lowest AICc (Δ AICc), and model weights (w_i) for the confidence set of models.

Table S2. Number of parameters (K), Akaike's information criterion (AICc), difference from lowest AICc (Δ AICc), and model weights (w_i) for the confidence set of models.

Coordinating Editor: Stuart Allison

Received: 18 October, 2019; First decision: 16 November, 2019; Revised: 19 December, 2019; Accepted: 19 December, 2019