

Rarity of shortleaf, slash, and longleaf pine seedlings in oak-pine forest types: An assessment of associated environmental, stand, site, and disturbance factors

Santosh K. Ojha^a, Kozma Naka^{a,*}, Luben D. Dimov^{a,b}, Dilli Bhatta^c

^a Department of Biological and Environmental Sciences, Alabama A&M University, Normal, AL 35762, United States

^b Rubenstein School of Environment and Natural Resources, University of Vermont, Burlington, VT 05405, United States

^c Division of Mathematics and Computer Science, University of South Carolina Upstate, Spartanburg, SC 29303, United States



ARTICLE INFO

Keywords:

FIA
Logistic modeling
Pine seedlings, regeneration
Penalized maximum likelihood estimation
Oak-pine forest
Forest disturbances
Site productivity

ABSTRACT

Determining the factors that influence the regeneration of pine in oak-pine forests is crucial for understanding natural regeneration dynamics and for planning forest management strategies. We investigated the vegetation structure and seedling dynamics of shortleaf, slash, and longleaf pine in oak-pine forest types of the southeastern United States. We used logistic regression with penalized maximum likelihood estimation because of the rarity of the regeneration from these pines. We performed canonical correlation, analysis of variance, and community structure analysis to produce multivariate relationships and statistical inferences. The classification accuracy of the logistic regression models for shortleaf, slash, and shortleaf pine were 96.0%, 96.7%, and 97.7%, respectively. The models indicated that environmental, climatic, stand, site productivity, and disturbance factors, or their combinations, had a significant influence on seedling occurrence. The probability of occurrence of seedlings of the three pine species increased with the increase in the overstory basal area from these species: one unit increase in overstory purity ratio of shortleaf, slash, and longleaf pine increased the odds of occurrence of their seedlings by approximately 51, 24, and 7 times, respectively.

The probability of occurrence of shortleaf pine seedlings increased with increasing canopy openness in stands with a substantial proportion of shortleaf pine in the overstory. The increase in mean annual temperature and overstory basal area of slash pine increased the probability of occurrence of slash pine seedlings on wetter sites that had disturbance through harvesting and silvicultural treatments. The chances of occurrence of longleaf pine seedlings increased with increasing overstory basal area of longleaf pine, species diversity, and mean annual temperature in low density stands on low productive sites. The findings can help forest managers in designing and implementing silvicultural treatments to promote the natural regeneration of the three pines in oak-pine forests.

1. Introduction

In the southeastern United States, oak-pine forests cover about 9.3% of the 99 million hectares of forest in the region (Oswalt et al., 2014). The United States Department of Agriculture (USDA), Forest Inventory and Analysis (FIA) classifies the southern forests into several forest type groups (Moser et al., 2006), among which the oak-pine forest type consists of stands with about 25–50% pine mixed with hardwoods (usually upland oaks) across a broad range of sites (Oswalt et al., 2014; Smith et al., 2004). The four most important pine species in terms of commercial and ecological significance are loblolly (*Pinus taeda* L.), shortleaf (*Pinus echinata* Mill.), slash (*Pinus elliotii* Engelm.), and

longleaf (*Pinus palustris* Mill.) (Coyle et al., 2015). Loblolly is the most dominant pine species in the oak-pine forest type, and it is also the most commonly planted and commercially managed. The occurrence of shortleaf, slash, and longleaf pine has diminished substantially after the early 1950s, mostly due to the preferential planting of loblolly pine on sites previously occupied by these pines, fire suppression, and urbanization (Clabo and Clatterbuck, 2005). Moreover, some pine-hardwood forests are converting to hardwood-only forests due to natural succession assisted by southern pine beetle outbreaks and lack of significant canopy disturbances needed for the survival of the regeneration of these shade-intolerant pines (South and Buckner, 2004).

The natural regeneration success of pines in the upland oak-pine

* Corresponding author.

E-mail address: kozma.naka@aamu.edu (K. Naka).

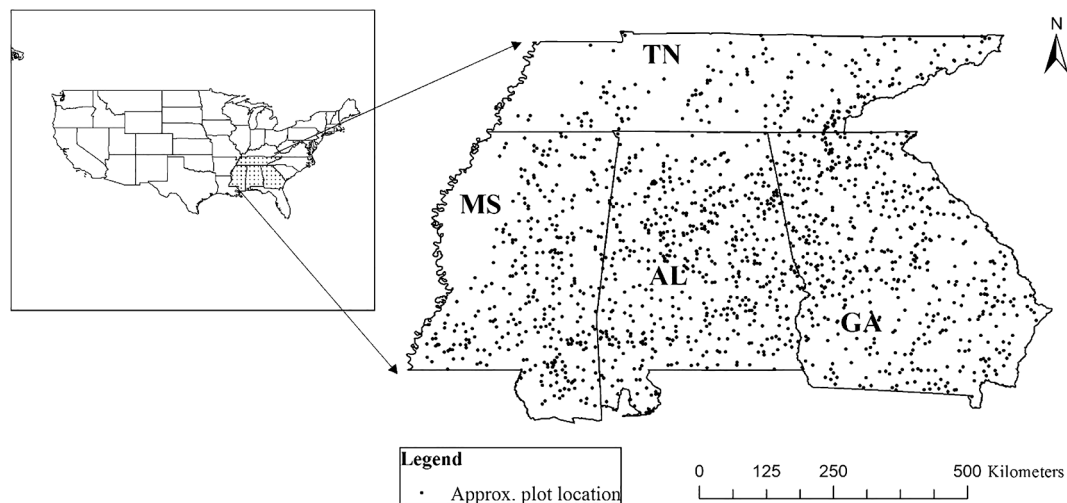


Fig. 1. Study area included states of Alabama (AL), Georgia (GA), Mississippi (MS), and Tennessee (TN).

forests of the southeastern United States is affected by a number of common factors, such as the composition and silvical characteristics of these species, local environmental conditions, initial stand structure and composition, competing vegetation, insects, diseases, deer browsing, invasive species, and other disturbances (Dey et al., 2012; Dey and Fan, 2009). Additionally, climate change and associated disturbances are having a significant impact on the distribution of oak-pine forests and associated species (Hansen et al., 2016; Iverson et al., 2008).

Natural fires occur very infrequently in upland forests, so they do not play a significant role in forest dynamics, while the role and the extent of human-induced fires as an ecological force for regeneration is still a matter of investigation (Dey et al., 2012). All pine species are more fire resistant than hardwoods, and some have developed unique adaptations to fire that influence seedling recruitment, establishment, and development. A low-intensity surface fire can kill shortleaf pine seedlings, but their ability to survive or resprout due to a j-shaped crook in the stem at the ground level rises with the increase in seedling diameter (Dey and Hartman, 2005). Frequent fires are beneficial for the establishment and development of early grass-stage seedlings of longleaf pine because fire controls some diseases, while the dense needles protect the terminal bud (Dey et al., 2012).

As a result of fire exclusion in oak-pine forests, pines are under successional replacement by mesophytic hardwoods, including red maple (*Acer rubrum* L.), common persimmon (*Diospyros virginiana* L.), sweetgum (*Liquidambar styraciflua* L.), yellow poplar (*Liriodendron tulipifera* L.), black cherry (*Prunus serotina* Ehrh.), and winged elm (*Ulmus alata* Michx.) (Cannon and Brewer, 2013; Dey and Fan, 2009; Nowacki and Abrams, 2008). Gaps created by disturbances such as storms, insect and disease outbreaks, late-season frosts, and harvesting, have a positive impact on pine regeneration dynamics, structure and species diversity of these stands (Cannon and Brewer, 2013; Dey et al., 2012; Dey, 2014; Dey and Fan, 2009). However, these disturbances are often not large enough to have a considerable impact, so there is still a need for silvicultural treatments to achieve establishment and maintenance of pine component in natural pine-hardwood stands (Clabo and Clatterbuck, 2005).

Regeneration dynamics in mixed stands has been the subject of increasing interest for the restoration of longleaf and shortleaf pine in the South (Guldin, 2011; Oswalt et al., 2012). A substantial amount of descriptive information about the ecology and the regeneration of shortleaf, slash, and longleaf pine is available, but there is much less quantitative information regarding the probability of seedling occurrence and consequent regeneration success in response to environmental, stand, site and disturbance factors, especially in southeastern

oak-pine forests.

Forest regeneration dynamics is associated with several random temporal and spatial processes, and statistical modeling is often used to predict the intricate relationships among all of these processes (Miina and Heinonen, 2008; Olson and Wagner, 2011). Logistic regression analysis has been widely used in modeling the probability of occurrence in ecological studies (Manly et al., 2002; Phillips and Elith, 2013). Quantifying the effects of ecological processes on regeneration dynamics is useful in determining appropriate silvicultural treatments to increase structural variability and species diversity, as well as biomass productivity of the forest ecosystem.

This study investigated the vegetation structure and seedling dynamics of shortleaf, slash, and longleaf pine in oak-pine forest types. We used logistic models for the three pines of interest to estimate the probability of seedlings occurrence depending on a variety of factors. Specifically, the study objectives were to (i) assess vegetation structure and seedling distribution status of the three pine species, (ii) model the likelihood of seedling occurrence of the three pine species of interest in relation to environmental, stand, site and disturbance factors, (iii) identify significant factors that predict the seedlings occurrence of the three pine species, and (iv) quantify the role of these factors on pine seedling occurrence.

2. Methods

2.1. Study area

The study was conducted in four of the southeastern states in the US: Alabama, Georgia, Mississippi, and Tennessee (Fig. 1), which have a temperate climate characterized as humid mesothermal (Thornthwaite, 1948). The study area is distributed across many geomorphological sections such as Southern Appalachian Piedmont, Coastal Plain-Middle, Southern Cumberland Plateau, Southern Ridge and Valley, and Mid Coastal Plains-Western (McNab et al., 2007). The topography and landform of the area vary from dissected irregular plains and high hills to rolling and mountainous landscapes, and from gentle sloping hills to highly folded sandstone and limestone formations. Soils vary in physical and chemical properties significantly across the area, but in general, they are deep and fine textured, with clay or loamy subsoil (McNab et al., 2007). The vegetation consists of both mixed and pure forests, such as upland hardwood forests, planted pine, natural pine, bottomland hardwoods, and oak-pine forests (McNulty et al., 2013).

2.2. Data and variables

We used oak-pine dominated plots from the national forest inventory data of the USDA Forest Service, Forest Inventory and Analysis (FIA), which is publicly available at FIA DataMart (2018). The oak-pine group, according to FIA classifications, includes many forest types, such as eastern white pine (*Pinus strobus* L.)-northern red oak (*Quercus rubra* L.)-white ash (*Fraxinus Americana* L.), longleaf pine-oak, shortleaf pine-oak, Virginia pine (*Pinus virginiana* Mill.)-southern red oak (*Quercus falcata* Michx.), loblolly pine-hardwood, and slash pine-hardwood. FIA uses a nationally standard quasi-systematic plot design covering all types of land ownership in the nation with current plot intensity (Phase 2) of one plot for every 2428 ha of land (Bechtold and Patterson, 2005). The FIA standard plot design is triangular and consists of four 7.3 m radius (0.0168 ha) subplots, one at each corner and one at the center of the triangle, totaling 0.067 ha (Woudenberg et al., 2010). The subplot data consists of measuring all the trees with a diameter at breast height (dbh, 1.37 m above the ground) ≥ 12.7 cm. A microplot with a radius of 2.07 m is nested in each subplot for measuring regeneration (seedlings and saplings) with a dbh < 12.7 cm. Each plot represents the stand in which it is located.

We used a total of 1503 plots from the most recent inventory cycles of the four states, collected between 2005 and 2013, if they had at least 10% tree cover and contained seedlings, regardless of which tree species (Fig. 1). All the plots were in naturally regenerated stands and under various ownership (private, public, industrial, and others). All tree species in each plot were categorized for analyses as seedlings, saplings, and trees. We used the FIA classification, in which the term *seedling* refers to stems < 2.54 cm in dbh, but ≥ 30.5 cm in height for hardwoods and ≥ 15.25 cm in height for conifers (Woudenberg et al., 2010), *sapling* refers to stems between 2.54 and 12.70 cm in dbh, and *tree* refers to stems ≥ 12.70 cm in dbh forming the overstory layer.

Data variables were classified into four broad groups: environmental, stand structure, site productivity, and disturbance condition. Environmental variables included topographical and climatic factors, such as slope, aspect, elevation, mean annual precipitation, mean annual temperature, mean annual maximum temperature, mean annual minimum temperature, and mean annual dew temperature. An arcsine transformation was applied to slope data (expressed in percentage) to improve normality (Legendre and Legendre, 1998). The Beers transformation (Beers et al., 1966) was applied to the aspect to change azimuth from 0 to 360° into values ranging from 0 to 2, where 0 represents southwest facing slopes (xeric), and 2 represents northeast facing slopes (mesic). The climatic data were the 1981–2010 climate normals extracted from an 800 m spatial resolution data set (“PRISM Climate Group,” n.d.). The PRISM climatic data is based on a digital elevation model (DEM) that uses the predictor grid and interpolation method to cover the conterminous United States and is publicly available for download (“PRISM Climate Group,” n.d.).

Stand structure variables were factors that represented stand characteristics based on the measurements from each plot and included seedling density, sapling density, stand (tree) density, average dbh, basal area per hectare, average height, average compacted live crown ratio (CCR), species purity ratio, and stand age. Stand density was calculated as trees per hectare for all species and for each of the three pine species (shortleaf, slash, and longleaf). CCR is the ratio of the length of tree bole supporting live foliage to the total height of the tree (Woudenberg et al., 2010) and it is used as a proxy for tree photosynthetic potential in stand growth modeling (Toney and Reeves, 2009). Purity ratio for each study species on each plot was assessed as the ratio of the overstory basal area of the species to the total basal area of all the trees. The purity ratio value ranges from 0 to 1, where 1 represents a pure stand. The occurrence of shortleaf, slash, and longleaf pine seedlings was identified as an event variable in the form of presence (1) or absence (0).

To assess diversity, we used Shannon's diversity index and

calculated it based on the basal area of the trees. Basal area accounts for size variation, unlike the number of trees (McMinn, 1992). Site productivity was included to describe the quality of the site. FIA classifies plots into seven site productivity classes based on industrial wood yield capacity of the land (Woudenberg et al., 2010). The site productivity classes range from the highest, class 1, to the lowest, class 7. We had no plots in classes 1 and 7. Site productivity was included as a categorical variable in our analysis. Thus, our five site productivity classes were: (1) site productivity class 2-very high (wood growth potential between 11.5 and 15.7 m³ ha⁻¹ yr⁻¹), (2) site productivity class 3-high (wood growth potential between 8.4 and 11.5 m³ ha⁻¹ yr⁻¹), (3) site productivity class 4-medium (wood growth potential between 5.9 and 8.3 m³ ha⁻¹ yr⁻¹), (4) site productivity class 5-low (wood growth potential between 3.5 and 5.9 m³ ha⁻¹ yr⁻¹), and (5) site productivity class 6-very low (wood growth potential between 1.4 and 3.4 m³ ha⁻¹ yr⁻¹).

The selected disturbance variables represented factors influencing stand dynamics. We took into account the visible disturbance that had happened since the last measurement or over the previous five years due to natural and anthropogenic causes, including stand treatments and harvesting activities. The disturbance conditions were broadly classified into four groups, (1) plots with fire disturbance including silvicultural treatments and harvest after fire (FDT), (2) plots with natural disturbances, such as diseases, insect outbreaks, animal grazing, blowdown, or ice (DND), (3) plots that had both harvesting and other silvicultural treatments (CST), and (4) plots with no visible disturbance or treatment (NDT). Silvicultural treatments included site preparation, fertilizing, girdling, pruning, and use of herbicides. Disturbance conditions were also coded as a categorical variable.

2.3. Data analysis

For the overstory trees (dbh ≥ 12.7 cm), we calculated the mean and the standard error of stand dbh, stand height, stand compacted crown ratio, stand density, stand basal area, Shannon's diversity index, and stand age for each site productivity class and disturbance condition. The mean and the standard error were also calculated for seedling density and sapling density. We used analysis of variance (ANOVA) to determine whether the difference between the means of the variables was significant for different site productivity classes and disturbance conditions.

We calculated the importance value percent (IVP) of the species separately for seedlings, saplings, and trees. The IVP of each species across the plots was the average of relative frequency percent, relative density percent, and relative dominance percent (Curtis and McIntosh, 1951). A descending ranking of IVP values was performed to identify the dominance of the species in each layer of the vegetation cover. The IVP is commonly used in plant community analysis because it is not influenced by large trees or a large number of small trees from a particular species (McCune and Grace, 2002).

We used canonical correlation analysis (CCA) to correlate simultaneously (Hair et al., 1998) site productivity class (independent variable) with stand variables (dependent variables). The CCA measures the strength of the overall relationship between the canonical variates (linear composites) for the dependent and independent variables (Hair et al., 1998; Prera et al., 2014).

Because the outcome variable Y is dichotomous ($Y = 1$, in case of seedling presence of shortleaf pine, slash pine or longleaf pine and $Y = 0$ otherwise), we modeled our data using logistic regression. Given a collection of n independent variables X_1, X_2, \dots, X_n , the logit of the multiple logistic regression model is given as:

$$\text{Log} \left[\frac{P(Y = 1|X_1 = x_1, \dots, X_n = x_n)}{1 - P(Y = 1|X_1 = x_1, \dots, X_n = x_n)} \right] = \log \left(\frac{P}{1 - P} \right) \\ = \alpha + \beta_1 x_1 + \beta_2 x_2 + \dots + \beta_n x_n \quad (1)$$

where $\frac{p}{1-p}$ is an odds ratio of the probability of seedling occurring with the probability of seedling not occurring for shortleaf, slash, or longleaf pine.

$$\text{Here, } \frac{P}{1-P} = e^{\alpha + \beta_1 x_1 + \beta_2 x_2 + \dots + \beta_n x_n} \quad (2)$$

Note here that the coefficient β_i measures the changes in odds ratio per unit change in the predictor X_i . Simplifying (2), the multinomial logistic regression in terms of P can be written as

$$P = \frac{e^{\alpha + \beta_1 x_1 + \beta_2 x_2 + \dots + \beta_n x_n}}{1 + e^{\alpha + \beta_1 x_1 + \beta_2 x_2 + \dots + \beta_n x_n}} \quad (3)$$

To fit the logistic regression model in (1), we obtained maximum likelihood estimates (MLE) of the unknown parameters $\alpha, \beta_1, \dots, \beta_n$ using SAS procedure PROC Logistic. Since there were many predictors, not all of them were significant in estimating the probability of seedling occurrence, so we applied a stepwise logistic regression procedure with Fisher's scoring method to select significant predictor variables.

Many authors (Allison, 2012a; Firth, 1993; King and Zeng, 2001) have discussed the problem of rare event data in logistic regression. MLE estimates of logistic regression are biased in small samples, and the bias amplifies with rare events (King and Zeng, 2001). Thus, simple logistic regression with MLE can sharply underestimate the probability of rare events. When simple logistic regression does not produce finite and consistent estimates of regression parameters due to the rarity of events, the logistic regression with penalized maximum likelihood estimation (PMLE) can reduce small-sample bias in MLE (Allison, 2012b; Firth, 1993; Heinze and Schemper, 2002). Due to the rarity of the event (proportion of 1's is relatively small) in the data, we also used PLME. In the case of separation in logistic regression with rare event data, PMLE allows convergence to finite estimates and reduces the bias seen in simple logistic models (Allison, 2012b).

We applied a goodness-of-fit test on the logistic models to compare the Akaike Information Criterion (AIC) values between the simple logistic regression model with MLE (full model) and the logistic regression model with Firth's PMLE (full model). The best model is the one that has the smallest AIC value among the candidate models (Hair et al., 1998). The Chi-square test was applied to determine the significance of the model ($\alpha = 0.05$). We also used the Hosmer & Lemeshow goodness of fit test to compare the observed and expected rates between presence and absence of seedlings of the plots (Hosmer et al., 2013). Classification accuracy percentage of the model was calculated to determine the percent of the plots (event = 1) classified correctly at the default cut-off value of 0.5 (Hosmer et al., 2013). We performed the Receiver Operating Characteristic (ROC) curve analysis to evaluate the predictive strength of the model (Hosmer et al., 2013). When the area under the ROC curve (AUC) is close to 1, it indicates a good fit.

The descriptive statistics, CCA, and binary logistic regression were analyzed using the IBM SPSS® 21 and SAS® 9.3 statistical packages, whereas Shannon's diversity index and species importance value percent were calculated using PC-ORD® Version 6.12.

3. Results

3.1. Vegetation structure and seedling distribution status of three pine species

The total number of tree species in the seedling, sapling, and tree layer across the plots was 119, 111, and 121, respectively (Table 1). The seedlings of shortleaf pine, slash pine, and longleaf pine were present only on 58, 47 and 32 plots, respectively, out of a total of 1503 plots. Similarly, saplings of shortleaf pine, slash pine, and longleaf pine were also found on 47, 44, and 37 plots, respectively, out of 1389 plots that had saplings. However, the occurrence of overstory shortleaf, slash, and longleaf pine trees was comparatively more frequent – they were present on 408, 181 and 121 plots, respectively, out of 1482 plots that had

Table 1
Occurrence and dominance ranking of seedlings, saplings, and trees of shortleaf, slash, and longleaf pine across plots in oak-pine forest types.

[illegible]

Where, IVP is the Importance Value Percent and is calculated as the average of relative frequency percent, relative density percent, and relative dominance percent. In the case of seedlings, IVP is the relative frequency percent because only the count data were available.

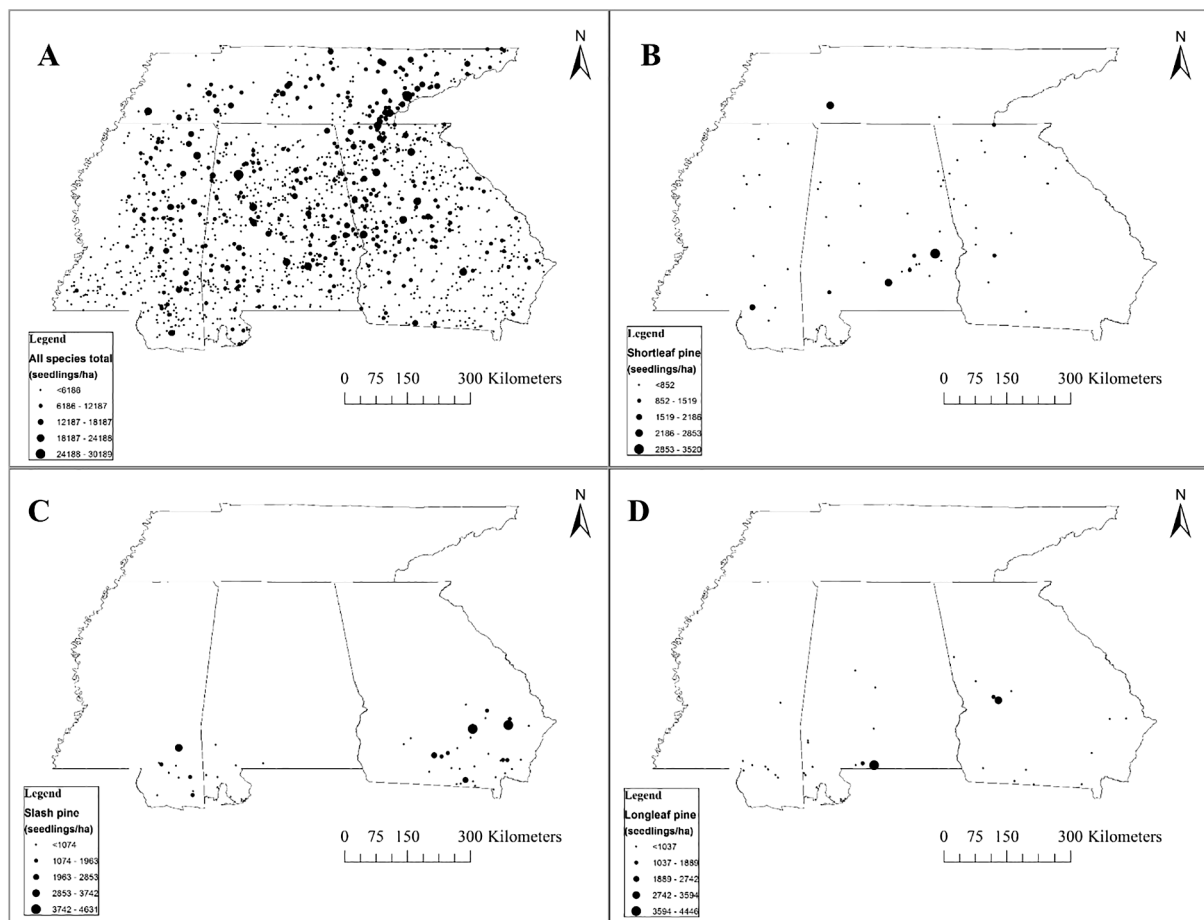


Fig. 2. Spatial distribution of naturally regenerated seedlings across 1503 FIA plots in oak-pine forest types for (A) all species, (B) shortleaf pine, (C) slash pine, and (D) longleaf pine.

trees.

Based on the IVP, seedling regeneration of shortleaf pine had the 41st, slash pine had the 33rd, and longleaf pine had the 50th dominance ranking among 119 species. Among the seedlings, red maple was the most dominant species with an IVP value of 11.7 (Table 1). Sweetgum was the most dominant species in the saplings layer with an IVP of 13.68, while loblolly pine was the dominant species in the overstory with an IVP of 19.48. Based on IVP, the dominance ranking of shortleaf pine, slash pine, and longleaf pine in the overstory was 7th, 9th and 23rd, respectively, among 121 tree species (Table 1).

There was a high variation in the number of seedlings of all species per plot, ranging from 185 to 30,189 per hectare (Fig. 2A). While natural seedlings of shortleaf pine were found in many plots in Mississippi, Alabama, and Georgia, they were present in only two plots in Tennessee (Fig. 2B). Slash and longleaf pine seedlings were present only in some southern localized pockets in Mississippi, Alabama, and Georgia, but they were not found in Tennessee (Fig. 2C and D).

Most of the naturally established seedlings of shortleaf pine were found in rolling upland mesic sites. Narrow floodplains or bottomlands contained some naturally regenerated shortleaf pine seedlings. Natural seedlings of slash pine were abundant in flatwoods and rolling uplands on mesic sites but not on hydric sites, such as swamps, bogs, bays and pocosins. Longleaf pine seedlings were found in xeric sites (deep sands), but they were predominantly located in mesic areas in rolling uplands and flatwoods.

On the 58 plots that contained shortleaf pine seedlings, loblolly pine, sand post oak (*Quercus margarettae* (Ashe) Small), mockernut hickory (*Carya alba* (L.) Nutt.), sweetgum and southern red oak were the most frequent associates of shortleaf pine in the overstory. On the

47 plots where slash pine seedlings were present, species that were frequent associates of overstory slash pine included longleaf pine, loblolly pine, pond cypress (*Taxodium ascendens* Brongn.), red maple, black gum (*Nyssa sylvatica* Marshall), swamp tupelo (*Nyssa biflora* Walter), laurel oak (*Quercus laurifolia* Michx.), water oak (*Quercus nigra* L.), sand post oak, and black willow (*Salix nigra* Marshall). Similarly, on the 32 plots with longleaf pine seedlings, the most frequent longleaf pine associates in the overstory were loblolly pine, turkey oak (*Quercus laevis* Walter), sweetgum, slash pine, water oak, mockernut hickory, and southern red oak.

Based on relative basal area density, the five most dominant species of sapling-size on the 58 plots where shortleaf pine seedlings occurred, were sweetgum, loblolly pine, shortleaf pine, water oak, white oak (*Quercus alba* L.) and red maple. Similarly, slash pine, red maple, pond cypress, swamp tupelo, and sweetgum were the most dominant species among the sapling size stems on the 47 plots that contained slash pine seedlings, whereas longleaf pine, loblolly pine, turkey oak, post oak and sourwood (*Oxydendrum arboreum* (L.) DC) were the most dominant species on the 32 plots that contained longleaf pine seedlings.

3.2. Relationship between stand variables and site productivity

As may be expected, site productivity explained a significant variation in diameter, height, compacted crown ratio, and basal area of the overstory trees (Table 2). While the mean stand age of the overstory trees varied significantly among the five site productivity classes, stand density, Shannon's diversity index, seedling density, and sapling density did not (Table 2).

The results of the relationship between site productivity class and

Table 2

Variation (mean \pm SE) in height, compacted crown ratio, stand density, stand basal area, Shannon's diversity index, stand age seedling density, sapling density by site productivity class.

Site productivity class	Plots	Overstory tree diameter (cm)	Overstory Tree height (m)	Overstory compacted crown ratio	Overstory stand density (trees ha ⁻¹)	Overstory basal area (m ² ha ⁻¹)	Overstory Shannon's diversity index	Stand age (year)	Seedling density (stems ha ⁻¹)	Sapling density (stems ha ⁻¹)
		$p < 0.001$	$p < 0.001$	$p = 0.011$	$p = 0.213$	$p < 0.001$	$p = 0.603$	$p < 0.001$	$p = 0.831$	$p = 0.045$
Very high	95	23.74 \pm 0.49	18.52 \pm 0.39	0.37 \pm 0.01	355 \pm 17.66	18.02 \pm 0.98	1.36 \pm 0.05	37.95 \pm 2.08	4179 \pm 380.51	1433 \pm 115.19
High	224	24.36 \pm 0.41	18.58 \pm 0.28	0.38 \pm 0.01	325 \pm 11.35	17.45 \pm 0.66	1.34 \pm 0.03	43.92 \pm 1.55	4081 \pm 246.40	1206 \pm 70.57
Medium	507	22.95 \pm 0.25	17.19 \pm 0.17	0.39 \pm 0.00	328 \pm 7.16	16.10 \pm 0.40	1.36 \pm 0.02	41.61 \pm 1.01	4332 \pm 169.11	1392 \pm 52.31
Low	585	21.96 \pm 0.24	15.84 \pm 0.15	0.40 \pm 0.00	316 \pm 7.48	13.95 \pm 0.36	1.32 \pm 0.02	38.09 \pm 0.95	4340 \pm 154.42	1502 \pm 56.69
Very low	92	21.20 \pm 0.45	14.97 \pm 0.31	0.38 \pm 0.01	345 \pm 16.86	13.76 \pm 0.72	1.40 \pm 0.05	47.45 \pm 2.46	4583 \pm 418.27	1353 \pm 116.37
Total	1503	22.72 \pm 0.15	16.82 \pm 0.10	0.39 \pm 0.00	326 \pm 4.42	15.44 \pm 0.23	1.35 \pm 0.01	40.71 \pm 0.59	4303 \pm 97.12	1407 \pm 31.89

Table 3

Canonical correlations between the site productivity class and stand attribute variables of shortleaf, slash, and longleaf pine.

Stand attributes	Site Productivity Class
	Canonical variate 1
Seedling density of shortleaf pine (stems ha ⁻¹)	0.02
Sapling density of shortleaf pine (stems ha ⁻¹)	0.04
Overstory stand density of shortleaf pine (stems ha ⁻¹)	0.05
Seedling density of slash pine (stems ha ⁻¹)	0.04
Sapling density of slash pine (stems ha ⁻¹)	0.06
Overstory stand density of slash pine (stems ha ⁻¹)	0.08
Seedling density of longleaf pine (stems ha ⁻¹)	0.05
Sapling density of longleaf pine (stems ha ⁻¹)	0.02
Overstory stand density of longleaf pine (stems ha ⁻¹)	0.16
Site Productivity Class	Stand attributes
	Canonical variate 1
Very high	-0.08
High	-0.09
Medium	-0.05
Low	0.07
Very low	0.17

stand attribute variables related to shortleaf pine, slash pine and longleaf pine using canonical correlation analysis are presented in Table 3. The hypotheses of independence of two sets of variables (site productivity and stand variables where the three pine species were present), was rejected (Wilks' lambda, $\lambda = 0.95$, $p < 0.001$). The first canonical correlation was only significant among the canonical variate pairs (canonical correlation, $r = 0.21$, $p < 0.001$). The value 0.21 of the first canonical correlation represented the highest possible correlation between any linear combination of the site productivity class and selected stand attribute variables of the three species. The overstory stand density of longleaf pine was positively correlated with site productivity ($r = 0.16$). The seedling density of shortleaf pine, slash pine and longleaf pine was weakly correlated with site productivity. Very low site productivity was positively correlated ($r = 0.17$), while very high site productivity was negatively correlated ($r = -0.08$) with the first canonical variate of the stand variables (Table 3). Thus, seedling density, sapling density and tree density of the three pine species of interest increased with decreasing the productivity of the site, because other species, primarily hardwoods, are less competitive in such conditions.

3.3. Impact of disturbances on seedling and sapling density

We took into account disturbances of the plots that occurred between the two consecutive measurements of each plot. When all species on the plots were considered, the occurrence of disturbances was significantly associated with the variation in seedling density ($p = 0.015$) and sapling density on the plots ($p < 0.001$, Table 4) – the presence of disturbances increased seedlings recruitment. Plots that experienced

disease and natural disturbance (DND) had the greatest seedling density (5889 ha⁻¹), while plots with no visible disturbance and treatment (NDT) had the lowest seedling density (4197 ha⁻¹, Table 4). However, mean sapling density was larger on plots with no visible disturbance than on disturbed plots.

Among the plots where shortleaf pine seedlings were present, plots with cutting and silvicultural treatments (CST) had the greatest percent of shortleaf pine seedlings (24.6%), while the tree to seedling ratio was 1:17, albeit this scenario occurred only on four plots (Table 5). Plots with fire disturbance and treatment (FDT) had shortleaf pine tree- to seedling ratio of 1:55, whereas the percent of shortleaf pine seedlings was 17.4% on the plots where shortleaf pine seedlings were present. Among the plots where slash pine seedlings were present, plots with fire disturbance and treatment (FDT) had the greatest percent of slash pine seedlings (61.3%) with a tree to seedling ratio of 1:17 (Table 5). Similarly, for longleaf pine, plots with no visible disturbance and treatment (NDT) contained the greatest percent (18.4%) of longleaf pine seedlings with a tree to seedling ratio of 1:22 (Table 5). No seedlings of shortleaf, slash, or longleaf pine were found on plots that experienced disease or natural disturbance (DND), and those plots did not contain trees of the three pines in the overstory either.

3.4. Factors associated with the rarity of seedlings of the three pine species

We selected a total of 23 explanatory variables, consisting of environmental, stand, site productivity, and disturbance variables. After removal of collinear variables such as mean dew temperature, maximum annual temperature, minimum annual temperature, and stand basal area density, we analyzed a total of 19 variables in a stepwise logistic regression to predict the presence of seedlings of shortleaf, slash, and longleaf pine (Table 6).

The simple binary logistic regression with stepwise selection procedure retained four significant explanatory variables in the model for shortleaf, four for slash pine and six for longleaf pine. The binary logit estimates for the parameters in the model are presented in Tables 7–9. Live crown ratio, overstory shortleaf pine density, and overstory purity ratio of shortleaf pine were all positive significant factors for the occurrence of shortleaf pine seedlings, while the overall tree stand density had a negative relationship with seedling occurrence (Table 7). For shortleaf pine, the overstory purity ratio and crown ratio had the most significant impact on the probability of occurrence of seedlings – for one unit increase in overstory purity ratio of shortleaf pine, the odds of shortleaf pine seedling occurrence increased by approximately 51 times (Table 7).

Mean annual temperature, aspect, overstory purity ratio, and CST disturbance had a significantly positive relationship with the occurrence of slash pine seedlings – for one unit increase in mean annual temperature, the odds of slash pine seedling occurrence increased by more than five times (Table 8). Similarly, one unit increase in overstory purity ratio of slash pine increased the odds of slash pine seedling occurrence approximately 24 times. The odds of the presence of slash pine

Table 4
Variation (mean \pm SE) in seedling and sapling density of all species on the plots by disturbance conditions.

Disturbance conditions	Plots	Seedlings density (stems ha ⁻¹) <i>p</i> = 0.015	Saplings density (stems ha ⁻¹) <i>p</i> < 0.001
Fire disturbance and treatment (FDT)	80	4615 \pm 369.97	891 \pm 107.00
Disease and natural disturbance (DND)	45	5889 \pm 903.23	1120 \pm 125.59
Cutting and silvicultural treatments (CST)	119	4621 \pm 392.62	943 \pm 86.34
No visible disturbance and treatment (NDT)	1259	4197 \pm 102.08	1494 \pm 35.77
Total	1503	4303 \pm 97.12	1407 \pm 31.89

seedlings was three times greater for plots with cutting and silvicultural treatments (CST) compared to plots with no visible disturbance and treatment (NDT).

Mean annual temperature, Shannon's diversity index, longleaf pine density, and overstory longleaf pine purity ratio had a significantly positive relationship with the occurrence of longleaf pine seedlings (Table 9). One unit increase in mean annual temperature, Shannon's diversity index, stand density, longleaf pine stand density, and longleaf pine overstory purity ratio increased the odds of longleaf pine seedling occurrence by 1.77, 2.65, 0.99, 1.02 and 7.43 times respectively. The odds of occurrence of longleaf pine seedlings were lower for high, medium and low productivity sites compared to very low productive sites (Table 9).

According to the odds ratio estimate in the models, the purity ratio of each of the three pine species was an important factor for their seedlings occurrence. While keeping other significant variables constant, overstory purity ratio was used as a predictor variable to construct the probability curve for seedling occurrence with 95% profile-likelihood confidence limits (Fig. 3).

The goodness of fit of the models showed that the AIC values of the simple logistic regression with MLE model for shortleaf pine, slash pine, and longleaf pine were 430.9, 238.7 and 220.8, respectively, which were reduced to 402.7, 231.3 and 187.5, respectively in logistic regression with Firth's PMLE (Table 10). The lower AIC value of models with Firth's PMLE indicates the greater robustness of the models. The likelihood ratio was significant and had a greater value than tabulated Chi-square value for all three models. The classification accuracy of models with Firth's PMLE for shortleaf, slash, and shortleaf pine was 96.0%, 96.7%, and 97.7%, respectively. The non-significant value of Hosmer & Lemeshow test of three models indicated that these models were well fitted to the data. Receiver Operating Characteristic (ROC) or Area Under Curve (AUC) was 0.80, 0.96 and 0.93 for shortleaf pine, slash pine and longleaf pine models, respectively. The goodness of fit of models indicate that the models were significant and robust for predicting the probability of seedling occurrence for shortleaf, slash, and longleaf pine in oak-pine forest types of the southeastern United States (see Table 10).

4. Discussion

Our analysis of the FIA data confirmed the rarity of occurrence of natural regeneration of shortleaf, slash, and longleaf pine in oak-pine forests of the southeast United States. Seedlings from these three pines were found in far fewer plots than overstory trees from the same species.

While variation in site productivity had a significant influence on the overall growth of overstory trees, it showed no influence on the overall seedling density. The overall abundance of seedlings was nearly the same for different site productivity levels. However, canonical correlation analysis indicated that the density of seedlings, saplings, and trees of the three pines was positively correlated with the decrease in site productivity. Hardwoods can outcompete the pines and dominate on highly productive sites compared to low productivity sites (Barnett and Baker, 1991). The availability of exposed mineral soil and abundant sunlight create favorable conditions for pine establishment,

but the reduced competition allows them to persist on low productivity sites. In addition, disturbances had a significant influence on overall seedling and sapling density. Although the overall seedling density from other species was greater in the plots affected by DND, no seedlings, saplings, and trees of the three pines were found on these plots. Windthrow, insect outbreak, and animal grazing were the main DND damaging agents that influenced the regeneration dynamics in these plots. However, the lack of mature trees of the three pine species, and therefore seed source, was likely the main cause for the absence of seedlings.

The probability of occurrence of shortleaf pine seedlings increased with the increase of overstory shortleaf pine basal area. The natural regeneration of shortleaf pine occurs if a significant number of mature shortleaf trees (seed source) are present near the area to be regenerated (Stambaugh and Muzika, 2007), which is rare in the southeastern forests (Clabo and Clatterbuck, 2005). Further decline of shortleaf pine regeneration in the eastern United States is expected in the future because of the low proportion of mature shortleaf pine trees in the overstory (Moser et al., 2007).

Stand live crown ratio had a positive correlation with the occurrence of shortleaf pine seedlings, while stand density had a negative association with it. The recruitment of shortleaf pine seedlings was abundant in relatively sparse stands. Shortleaf pine is a shade intolerant species, yet its seedlings can tolerate some shade better than slash and longleaf pine (Dey et al., 2012; Guldin, 2011).

Controlling competing hardwoods is necessary for the maintenance of shortleaf pine stands, especially on better sites where shortleaf pine comprises less than 50% of the stand (Clabo and Clatterbuck, 2005). KC et al. (2016) reported a decline of shortleaf pine regeneration because of competing regeneration of red maple and several oak species in the Ozark and Ouachita National Forests. We found several hardwood associates of shortleaf pine in the midstory and overstory of our plots, such as sand post oak, mockernut hickory, sweetgum and southern red oak, which would likely have to be controlled with prescribed fire or herbicide, to increase the establishment and survival rate of shortleaf pine seedlings. Thinning and canopy opening enhance the growth and development of shortleaf pine seedlings because of the increased sunlight and nutrients, conditions that favor its performance relative to the competitors (Stambaugh and Muzika, 2007). Shortleaf pine sometimes occurs more often with hardwood species than with loblolly pine, especially on the dry, better-drained ridgetops (Clabo and Clatterbuck, 2005).

Although disturbances are key drivers for natural regeneration of shortleaf pine, we found no significant relationship of disturbance with the occurrence of shortleaf pine seedlings in our plots over the previous five years. Variation in site productivity had also no significant impact on the establishment of shortleaf seedlings, probably because shortleaf pine grows well on a variety of soils, including on relatively dry rocky uplands (Clabo and Clatterbuck, 2005).

As with shortleaf, the occurrence of slash pine in the overstory was vital for its natural regeneration. Good seed crops of slash pine occur every three to four years, and about 90% of seeds fall within 50 m of the source tree (Lohrey and Kossuth, 1990). We found that slash pine frequently associates with longleaf pine, loblolly pine, pond cypress, red maple, black gum, swamp tupelo, laurel oak, water oak, sand post oak,

Table 5
Seedling, sapling, and stand (tree) density of all species on plots from four disturbance conditions. The number of plots indicates the plots on which regeneration was present, regardless of the species. The density in each condition is provided separately for plots on which the species of interest, shortleaf, slash, and longleaf pine is either present or absent.

Disturbance condition	Plots with any regeneration	Seedling density (stems ha ⁻¹)	Saplings density (stems ha ⁻¹)	Stand density (trees ha ⁻¹)	Tree: seedling ratio	Plots with any regeneration	Seedling density (stems ha ⁻¹)	Saplings density (stems ha ⁻¹)	Stand density (trees ha ⁻¹)	Tree: seedling ratio	Percent seedlings*
Shortleaf pine	Shortleaf seedlings not present					Shortleaf seedlings present					
FDT	74	4514	956	277	1:16	6	5864	93	107	1:55	17.4
DND	45	5889	1120	292	1:20	4	2824	1806	171	1:17	24.6
CST	115	4684	913	236	1:20	48	6111	1520	271	1:23	7.3
NDT	1211	4121	1493	342	1:12	58	5858	1392	247	1:24	8.9
Total	1445	4241	1408	329	1:13						
Slash pine	Slash seedlings not present					Slash seedlings present					
FDT	77	4646	892	266	1:17	3	3827	865	223	1:17	61.3
DND	45	5889	1120	292	1:20	8	2593	671	167	1:16	17.0
CST	111	4768	963	238	1:20	36	4141	1611	301	1:14	21.0
NDT	1223	4198	1491	341	1:12	47	3857	1403	273	1:14	23.1
Total	1456	4318	1408	327	1:13						
Longleaf pine	Longleaf seedlings not present					Longleaf seedlings present					
FDT	71	4585	986	286	1:16	9	4856	144	96	1:51	5.9
DND	45	5889	1120	292	1:20	5	2888	630	122	1:24	17.9
CST	114	4698	957	238	1:20	18	4207	1605	193	1:22	18.4
NDT	1241	4197	1493	342	1:12	32	4184	1042	155	1:27	14.2
Total	1471	4306	1415	329	1:13						

Where, FDT = Fire disturbance and treatment, DND = Disease and natural disturbance, CST = Cutting and silvicultural treatments, NDT = No visible disturbance and treatment.

* The percent seedlings refers to the proportion of the number of seedlings from the particular species of interest (shortleaf, slash, longleaf pine, respectively) out of the total number of seedlings from all species.

Table 6

List of predictor variables selected for the logistic regression. The stepwise forward selection procedure with Fisher's scoring method retained shown significant variables for shortleaf, slash, and longleaf pine at $\alpha = 0.05$.

Variables	Variable type	Shortleaf pine		Slash pine		Longleaf pine	
		Score (χ^2)	<i>p</i>	Score (χ^2)	<i>p</i>	Score (χ^2)	<i>p</i>
<i>Environmental variables</i>							
Mean annual precipitation	Continuous						
Mean annual temperature	Continuous			30.24	< 0.0001 (+)	8.63	0.0033 (+)
Elevation	Continuous						
Slope	Continuous						
Aspect	Continuous			5.27	0.0217 (+)		
<i>Stand variables</i>							
Mean height (overstory)	Continuous						
Mean compacted crown ratio (overstory)	Continuous	12.48	0.0004 (+)				
Shannon's diversity index	Continuous					4.3	0.0381 (+)
Stand density per ha (overstory)	Continuous	5.62	0.0177 (–)			18.59	< 0.0001 (–)
Sapling density per ha	Continuous						
Stand age (overstory)	Continuous						
Shortleaf pine density per ha (overstory)	Continuous	4.4	0.036 (+)				
Slash pine density per ha (overstory)	Continuous						
Longleaf pine density per ha (overstory)	Continuous					10.02	0.0016 (+)
Overstory purity ratio of shortleaf pine	Continuous	89.68	< 0.0001 (+)				
Overstory purity ratio of slash pine	Continuous			353.29	< 0.0001 (+)		
Overstory purity ratio of longleaf pine	Continuous					207.6	< 0.0001 (+)
Site productivity class	Categorical					11.51	0.0214
Very high site productivity (versus very low)							(–)
High site productivity (versus very low)							(–)
Medium site productivity (versus very low)							(–)
Low site productivity (versus very low)							(–)
Disturbance	Categorical			8.71	0.0334		
FDT (versus NDT)					(–)		
DND (versus NDT)					(–)		
CST (versus NDT)					(+)		

Where, FDT = Fire disturbance and treatment, DND = Disease and natural disturbance, CST = Cutting and silvicultural treatments, NDT = No visible disturbance and treatment.

Signs + or - in parenthesis indicate the positive or negative effect of a predictor variable on outcome variable (seedling occurrence), which was determined based on odds ratio estimate from the logistic regression model.

and black willow, both in midstory and overstory. The control of competing hardwoods through silvicultural treatments can increase recruitment and growth of slash pine seedlings. The occurrence of slash pine seedlings in mixed forests can be increased by the use of the shelterwood method with the retention of mature slash pine trees as a seed source and the removal of other competing tree species (Guldin, 2011).

Harvesting followed by site preparation and silvicultural treatments (CST disturbance) had a significant impact on the occurrence of slash pine seedlings. Slash pine seeds germinate rapidly when in contact with mineral soil (Dey et al., 2012). Aspect was a significant factor for slash pine regeneration because seedlings occurred only on slopes with a northeast aspect, which have the most moisture. Slash pine grows well in a wide variety of site conditions, but it grows best on deep, well-aerated soils that contain ample moisture (Barnett and Sheffield, 2004; Guldin, 2011). Soil moisture content is likely more important than site quality, as we found no significant influence of site productivity on the occurrence of slash pine seedlings.

The increase in mean annual temperature corresponded to an increased probability of occurrence of slash pine seedlings. Iverson et al. (2008) modeled potential response of 134 tree species of the eastern US to several scenarios of climate change and found that in the hottest scenario, southeastern oak-pine forests would expand and slash pine potentially would move northward up to 800 km. Similarly, Hansen et al. (2016) projected a large expansion of the range of slash pine by 2055 under a high emissions scenario.

Similar to the other two pines, the presence of parent seed trees in the overstory increased the chances of occurrence of longleaf pine seedlings. While longleaf pine masts every seven to ten years, it produces abundant seed crops every three to four years (Carey, 1992). Most of the seeds are dispersed by wind to a short distance (about 20 m) from the source tree (Boyer, 1990). Longleaf pine is intolerant of shade and competition, but grass-stage longleaf pine seedlings are nevertheless able to survive in the absence of overstory disturbances. We found that loblolly pine, slash pine, turkey oak, sweetgum, water oak, mockernut hickory, and southern red oak were frequent associates of

Table 7

Penalized maximum likelihood estimates and odds ratios for the shortleaf pine model.

Parameter	DF	Estimate	SE	<i>p</i> > χ^2	Odds Ratio Estimate	Profile-Likelihood 95% CL of Odds Ratio	
Intercept	1	–4.204	0.771	< 0.0001			
Mean compacted crown ratio (overstory)	1	3.559	1.422	0.0123	35.110	2.193	634.259
Stand density per ha (overstory)	1	–0.004	0.001	0.0022	0.996	0.994	0.999
Shortleaf pine stand density per ha (overstory)	1	0.011	0.005	0.0273	1.011	1.001	1.021
Overstory purity ratio of shortleaf pine	1	3.926	1.171	0.0008	50.677	5.833	579.263

Where, SE = Standard Error, CL = Confidence limit.
Algorithms converged.

Table 8
Penalized maximum likelihood estimates and odds ratios for the slash pine model.

Parameter	DF	Estimate	SE	$p > \chi^2$	Odds Ratio Estimate	Profile-Likelihood 95% CL of Odds Ratio	
Intercept	1	−36.9533	6.3506	< 0.0001			
Mean annual temperature	1	1.6448	0.3277	< 0.0001	5.180	2.780	10.701
Aspect	1	1.6052	0.7475	0.0318	4.979	1.412	35.122
Overstory purity ratio of slash pine	1	3.1963	0.6088	< 0.0001	24.442	7.582	83.133
FDT (versus NDT)	1	−0.4787	0.7166	0.5041	0.620	0.126	2.223
DND (versus NDT)	1	−0.8251	1.5897	0.6037	0.438	0.003	4.031
CST (versus NDT)	1	1.1899	0.4809	0.0134	3.287	1.216	8.284

Where, SE = Standard Error, CL = Confidence limit.

FDT = Fire disturbance and treatment, DND = disease and natural disturbance, CST = Cutting and silvicultural treatments, NDT = No visible disturbance and treatment.

Algorithms converged.

longleaf pine in the midstory and overstory. The recruitment and establishment of longleaf pine seedlings can be achieved by combining frequent fire with silviculture methods that mimic the pattern of natural disturbance and develop a conducive environment for natural regeneration, such as group selection and irregular shelterwood (Brockway et al., 2005). To increase the availability of light and nutrients for longleaf pine regeneration, competing hardwoods and shrubs should be reduced significantly by treatments such as injection with herbicides, girdling or cutting (Jose et al., 2007).

The increase in mean annual temperature also increased the probability of occurrence of longleaf pine seedlings on the plots. According to Iverson and Prasad (1998), longleaf pine is projected to expand northward from the southern Coastal Plains under climate change scenarios of increasing atmospheric temperature. We also found that the probability of occurrence of longleaf pine seedlings decreased with the increase in site productivity. Longleaf pine grows well in a warm, wet and temperate climate and it is commonly found on sandy, infertile and well-drained soils (Carey, 1992), where they face less competition from associated hardwood and shrub species than on high productivity sites (Brockway et al., 2005).

Our results indicate that logistic models with penalized maximum likelihood estimation predict the rare event of seedlings occurrence more robustly than simple logistic regression. Understanding of seedling establishment dynamics of the three pines of interest in oak-pine forest types can benefit land managers and landowners who want to design and implement silvicultural treatments that facilitate the regeneration of these pines in mixed oak-pine forests.

5. Conclusions

Poor regeneration and establishment of pines in mixed forests have been a growing concern to silviculturists. Nowadays, silvicultural

methods that emulate natural disturbance regimes are used to fulfill both ecological and economic objectives of forest management. It is vital to identify significant factors that affect the establishment of seedlings of shortleaf, slash, and longleaf pine to implement appropriate management actions suitable for different site conditions. Regeneration occurrence logistic models are potentially valuable tools in forestry for understanding and quantifying regeneration dynamics. Natural regeneration of the three pines of interest has become a rare event in the southeastern oak-pine forests. The use of anthropogenic disturbances (e.g., prescribed fire, tree stand improvement, and site preparation) can create an environment conducive not only for enhancing the natural regeneration of pines but also for preventing the conversion of pine associated subclimax communities into hardwood communities. Maintaining the stand structure and species composition with sufficient overstory trees of shortleaf, slash, and longleaf pine in oak-pine forest types can substantially increase the abundance of their natural regeneration. Understanding the role of the environmental, stand, site and disturbance factors is critical for selecting appropriate sites and silvicultural treatments that can facilitate the natural regeneration of these three pines in the oak-pine forests.

Acknowledgments

Partial support for this work was provided by USDA Forest Service Cooperative Agreement 15-CA-11330124-080, McIntire-Stennis Cooperative Forestry Program ALAX-011-4415, and Tennessee Valley Authority Contract 12846. We are grateful to the USDA, Forest Inventory and Analysis, National Forest Inventory crews who collected the data. We are also thankful to two anonymous reviewers for their reviews and valuable suggestions.

Table 9
Penalized maximum likelihood estimates and odds ratios for the longleaf pine model.

Parameter	DF	Estimate	SE	$p > \chi^2$	Odds Ratio Estimate	Profile-Likelihood 95% CL of Odds Ratio	
Intercept	1	−11.6077	3.2169	0.0003			
Mean annual temperature	1	0.5715	0.1721	0.0009	1.771	1.272	2.606
Shannon's diversity index	1	0.9727	0.4758	0.0409	2.645	1.021	7.289
Stand density per ha (overstory)	1	−0.0103	0.0025	< 0.0001	0.990	0.984	0.994
Longleaf pine stand density per ha (overstory)	1	0.0150	0.0070	0.033	1.015	1.000	1.029
Overstory purity ratio of longleaf pine	1	2.0055	1.0541	0.0571	7.430	1.001	59.468
Very high site productivity (versus very low)	1	−2.4484	1.5123	0.1055	0.086	< 0.001	0.858
High site productivity (versus very low)	1	−1.5076	0.7137	0.0346	0.221	0.051	0.893
Medium site productivity (versus very low)	1	−1.8730	0.6304	0.003	0.154	0.043	0.545
Low site productivity (versus very low)	1	−1.4415	0.5699	0.0114	0.237	0.078	0.761

Where, SE = Standard Error, CL = Confidence limit.

Algorithms converged.

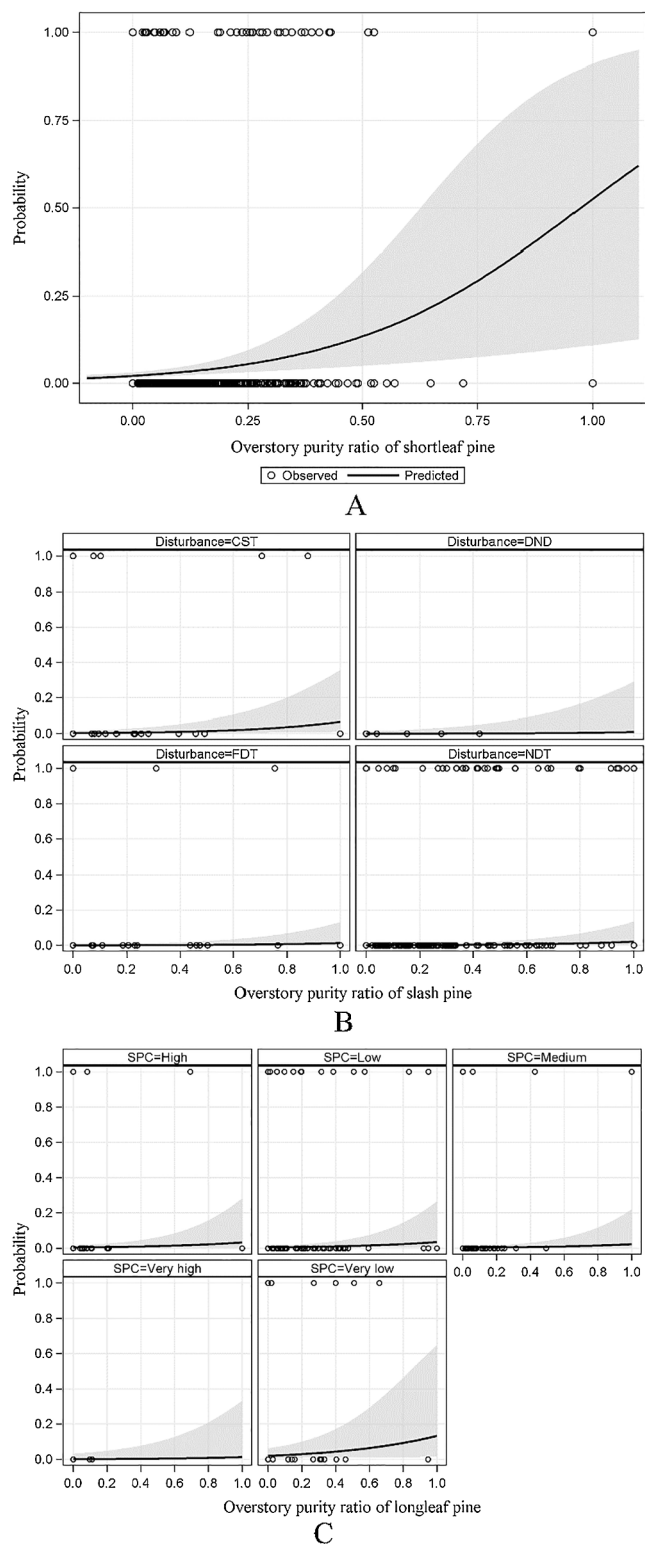


Fig. 3. Predicted probabilities for seedlings occurrence (event = 1) with 95% confidence limits, (A) for shortleaf pine fitted at mean crown ratio = 0.39, overstory mean stand density = 326 trees ha⁻¹ and overstory shortleaf pine mean stand density = 12 trees ha⁻¹, (B) for slash pine fitted at mean annual temperature = 17.02° and aspect = ~327°/123°, and (C) for longleaf pine fitted at mean annual temperature = 17.02°, mean Shannon's diversity index = 1.35, overstory mean stand density = 326 trees ha⁻¹ and overstory longleaf pine mean stand density = 4 trees ha⁻¹. (FDT = Fire disturbance and treatment, DND = Disease and natural disturbance, CST = Cutting and silvicultural treatments, NDT = No visible disturbance and treatment, and SPC = Site productivity class).

Table 10
Goodness of fit of the models.

Criterion	Shortleaf pine		Slash pine		Longleaf pine	
	df	Value	df	Value	df	Value
Simple logistic regression with MLE						
Deviance	1497	420.9	1495	224.7	1492	200.8
Pearson χ^2	1497	1256.6	1495	410.0	1492	753.7
AIC		430.9		238.7		220.8
Cox and Snell R ²		0.05		0.12		0.07
Nagelkerke R ²		0.16		0.50		0.38
Logistic regression with Firth's PMLE						
Deviance	1098	387.4	1495	226.0	1493	202.4
Pearson χ^2	1098	1029.4	1495	367.9	1493	642.4
AIC		402.7		231.3		187.5
Cox and Snell R ²		0.05		0.12		0.07
Nagelkerke R ²		0.18		0.50		0.41
Log-likelihood full model		392.7		217.3		167.5
Log-likelihood null model		464.3		404.3		274.2
Likelihood ratio [-2 Log L (null model) - 2 Log L (full model)]	4	71.6*	6	187.0*	9	106.7*
χ^2 value (F-Table value), $p < 0.05$	4	9.49	6	12.59	9	16.92
Hosmer & Lemeshow test of full model (# of groups = 10)		$p = 0.46$		$p = 0.97$		$p = 0.95$
Classification accuracy of full model (cut-off value = 0.5)		96.0%		96.7%		97.7%
ROC/AUC Mann-Whitney statistics						
Area under ROC curve		0.80		0.96		0.93
Std. error		0.027		0.007		0.019
95% confidence limits		0.74, 0.85		0.95, 0.97		0.89, 0.97

Where, MLE = maximum likelihood estimate; PMLE = penalized maximum likelihood estimate; ROC = Receiver Operating Characteristic; AUC = Area Under Curve.

The sign * indicates that tested models were statistically significant at $p < 0.0001$.

Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2019.02.013>.

References

- Allison, P.D., 2012a. Logistic Regression for Rare Events. Stat. Horiz. < <https://statisticalhorizons.com/logistic-regression-for-rare-events> > (accessed 7.17.18).
- Allison, P.D., 2012b. Logistic Regression Using SAS: Theory and Application. SAS Institute.
- Barnett, J.P., Baker, J.B., 1991. Regeneration methods. In: Duryea, M.L., Dougherty, P.M. (Eds.), Forest Regeneration Manual. Springer Netherlands, Dordrecht, pp. 35–50. https://doi.org/10.1007/978-94-011-3800-0_3.
- Barnett, J.P., Sheffield, R.M., 2004. Slash pine: characteristics, history, status and trends. In: Dickens, E.D., Barnett, J.P., Hubbard, W.G., Jokela, E.L. (Eds.), Proceedings of the Slash Pine Symposium. Presented at the Slash Pine: Still Growing and Growing! Department of Agriculture, Forest Service, Southern Research Station, Asheville, NC, pp. 1–6.
- Beers, T.W., Dress, P.E., Wensel, L.C., 1966. Aspect transformation in site productivity research. J. For. 64, 691–692.
- Bechtold, William A., Patterson, Paul, L., (Eds.), 2005. The Enhanced Forest Inventory and Analysis Program—National Sampling Design and Estimation Procedures. Gen. Tech. Rep. SRS-80. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southern Research Station. 85 p.
- Boyer, W.D., 1990. *Pinus palustris* Mill. Longleaf Pine. In: Burns, R.M., Honkala, B.H. (Eds.), Silvics of North America. Conifers, vol. 1. U.S. Department of Agriculture, Forest Service, Washington, DC, pp. 405–412.
- Brockway, D.G., Outcalt, K.W., Tomczak, D.J., Johnson, E.E., 2005. Restoration of Longleaf Pine Ecosystems (General Technical Report No. SRS-83). USDA Forest Service, Southern Research Station, Asheville, NC.

- Cannon, J.B., Brewer, J.S., 2013. Effects of tornado damage, prescribed fire, and salvage logging on natural oak (*Quercus* spp.) regeneration in a xeric Southern USA coastal plain oak and pine forest. *Nat. Areas J.* 33, 39–49. <https://doi.org/10.3375/043.033.0105>.
- Carey, J.H., 1992. *Pinus palustris*. Fire Effects Information System. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer). [WWW Document]. URL < <https://www.fs.fed.us/database/feis/plants/tree/pinpal/all.html> > (accessed 3.12.18).
- Clabo, D.C., Clatterbuck, W. (Eds.), 2005. A Tennessee Landowner and Practitioner Guide for Establishment and Management of Shortleaf and Other Pines. University of Tennessee, Institute of Agriculture, Extension Publication Number 1751.
- Coyle, D.R., Klepzig, K.D., Koch, F.H., Morris, L.A., Nowak, J.T., Oak, S.W., Orosina, W.J., Smith, W.D., Gandhi, K.J.K., 2015. A review of southern pine decline in North America. *For. Ecol. Manage.* 349, 134–148. <https://doi.org/10.1016/j.foreco.2015.04.007>.
- Curtis, J.T., McIntosh, R.P., 1951. An upland forest continuum in the prairie-forest border region of Wisconsin. *Ecology* 32, 476–496. <https://doi.org/10.2307/1931725>.
- Dey, D.C., 2014. Sustaining oak forests in eastern North America: regeneration and recruitment, the pillars of sustainability. *For. Sci.* 60, 926–942. <https://doi.org/10.5849/forsci.13-114>.
- Dey, D.C., Brissette, J.C., Schweitzer, C.J., Guldin, J.M., et al., 2012. Silviculture of forests in the eastern United States. *Cumul. Watershed Eff. Fuel Manage. East. U.* 7–40.
- Dey, D.C., Fan, Z., 2009. A review of fire and oak regeneration and overstory recruitment. In: Hutchinson, T.F. (Ed.), *Proceedings of the 3rd Fire in Eastern Oak Forests Conference*. 2008 May 20–22; Carbondale, IL. Gen. Tech. Rep. NRS-P-46. U.S. Department of Agriculture, Forest Service, Northern Research Station, Newtown Square, PA, pp. 2–20.
- Dey, D.C., Hartman, G., 2005. Returning fire to Ozark Highland forest ecosystems: effects on advance regeneration. *For. Ecol. Manage.* 217, 37–53. <https://doi.org/10.1016/j.foreco.2005.05.002>.
- FIA DataMart, 2018. Forest Inventory and Analysis Database, St. Paul, MN: U.S. Department of Agriculture, Forest Service, Northern Research Station [WWW Document]. FIA DataMart. < <https://apps.fs.usda.gov/fia/datamart/datamart.html> > (accessed 11.8.18).
- Firth, D., 1993. Bias reduction of maximum likelihood estimates. *Biometrika* 80, 27. <https://doi.org/10.2307/2336755>.
- Guldin, J.M., 2011. Silvicultural considerations in managing southern pine stands in the context of southern pine beetle. In: Coulson, R.N., Klepzig, K.D. (Eds.), *Southern Pine Beetle II*. Gen. Tech. Rep. Department of Agriculture, Forest Service, Southern Research Station, Asheville, NC: U.S., pp. 317–352.
- Hair, J.F., Tatham, R.L., Anderson, R.E., Black, W., 1998. *Multivariate Data Analysis*, fifth ed. Prentice Hall.
- Hansen, A.J., Monahan, W.B., Theobald, D.M., Olliff, S.T., 2016. *Climate Change in Wildlands: Pioneering Approaches to Science and Management*. Island Press.
- Heinze, G., Schemper, M., 2002. A solution to the problem of separation in logistic regression. *Stat. Med.* 21, 2409–2419.
- Hosmer, D.W., Lemeshow, S., Sturdivant, R.X., 2013. *Applied logistic regression*. Wiley series in probability and statistics, third ed. Wiley, Hoboken, New Jersey.
- Iverson, L.R., Prasad, A.M., 1998. Predicting abundance of 80 tree species following climate change in the eastern United States. *Ecol. Monogr.* 68, 465–485.
- Iverson, L.R., Prasad, A.M., Matthews, S.N., Peters, M., 2008. Estimating potential habitat for 134 eastern US tree species under six climate scenarios. *For. Ecol. Manage.* 254, 390–406. <https://doi.org/10.1016/j.foreco.2007.07.023>.
- Jose, S., Jokela, E.J., Miller, D.L. (Eds.), 2007. *The Longleaf Pine Ecosystem: Ecology, Silviculture, and Restoration*, first ed. Springer, New York.
- KC, A., Lynch, T.B., Guldin, J.M., 2016. Shortleaf pine (*Pinus echinata* mill.) and hardwood regeneration after thinning natural shortleaf pine forests in southern United States. In: Schweitzer, C.J., Clatterbuck, W.K., Oswalt, C.M. (Eds.), *Proceedings of the 18th Biennial Southern Silvicultural Research Conference*. e-Gen. Tech. Rep. SRS-212. U.S. Department of Agriculture, Forest Service, Southern Research Station, Asheville, NC, pp. 553–554.
- King, G., Zeng, L., 2001. Logistic regression in rare events data. *Polit. Anal.* 9, 137–163.
- Legendre, P., Legendre, L., 1998. *Numerical Ecology*, second english ed. Elsevier Science B.V., Amsterdam.
- Lohrey, R.E., Kossuth, S.V., 1990. *Pinus elliotii* Engelm. Slash Pine. In: Burns, R.M., Honkala, B.H. (Eds.), *Silvics of North America. Conifers*, vol. 1. U.S. Department of Agriculture, Forest Service, Washington, DC, pp. 338–347.
- Manly, B.F.J., McDonald, L.L., Thomas, D.L., McDonald, T.L., Erickson, W., 2002. *Resource Selection by Animals: Statistical Design and Analysis for Field Studies*. Kluwer Academic Publishers, Dordrecht; Boston.
- McCune, B., Grace, J.B., 2002. *Analysis of Ecological Communities*. MjM Software Design Glenden Beach, Oregon USA.
- McMinn, J.W., 1992. Diversity of woody species 10 years after four harvesting treatments in the oak-pine type. *Can. J. For. Res.* 22, 1179–1183.
- McNab, W.H., Cleland, D.T., Freeouf, J.A., Keys Jr., J.E., Nowacki, G.J., Carpenter, C.A., 2007. Description of “ecological subregions: sections of the conterminous United States” First Approximation (Gen. Tech. Report No. WO-76B). United States Department of Agriculture, Forest Service, Washington, DC.
- McNulty, S., Caldwell, P., Doyle, T.W., Johnsen, K., Liu, Y., Mohan, J., Prestemon, J., Sun, G., 2013. Forests and climate change in the Southeast USA. In: Ingram, K.T., Dow, K., Carter, L., Anderson, J. (Eds.), *Climate of the Southeast United States: Variability, Change, Impacts, and Vulnerability*. Island Press, Washington, DC, pp. 165–189.
- Miina, J., Heinonen, J., 2008. Stochastic simulation of forest regeneration establishment using a multilevel multivariate model. *For. Sci.* 54, 206–219.
- Moser, W.K., Hansen, M., McWilliams, W., Sheffield, R., 2006. Oak composition and structure in the eastern United States. In: Dickinson, M.B. (Ed.), *Proceedings of a Conference; 2005 November 15–17; Columbus, OH*. Gen. Tech. Rep. NRS-P-1. Presented at the Fire in eastern oak forests: delivering science to land managers, U.S. Department of Agriculture, Forest Service, Northern Research Station, Newtown Square, PA, pp. 49–61.
- Moser, W.K., Hansen, M., McWilliams, W.H., Sheffield, R.M., 2007. Shortleaf pine composition and structure in the United States. In: Kabrick, J.M., Dey, D.C., Gwaze, D. (Eds.), *Shortleaf Pine Restoration and Ecology in the Ozarks: Proceedings of a Symposium*. 2006 November 7–9; Springfield, MO. Gen. Tech. Rep. NRS-P-15. U.S. Department of Agriculture, Forest Service, Northern Research Station, Newtown Square, PA, pp. 19–27.
- Nowacki, G.J., Abrams, M.D., 2008. The demise of fire and “mesophication” of forests in the eastern United States. *BioScience* 58, 123–138.
- Olson, M.G., Wagner, R.G., 2011. Factors affecting species richness of tree regeneration in mixed-wood stands of central Maine: factors affecting tree species richness during regeneration. *J. Veg. Sci.* 22, 303–311. <https://doi.org/10.1111/j.1654-1103.2011.01258.x>.
- Oswalt, C.M., Cooper, J.A., Brockway, D.G., Brooks, H.W., Walker, J.L., Connor, K.F., Oswalt, S.N., Conner, R.C., 2012. History and Current Condition of Longleaf Pine in the Southern United States (General Technical Report No. SRS-166). United States Department of Agriculture, Forest Service, Southern Research Station, Asheville, NC: U.S.
- Oswalt, S.N., Smith, W.B., Miles, P.D., Pugh, S.A., 2014. Forest Resources of the United States, 2012: A Technical Document Supporting the Forest Service 2015 Update of the RPA Assessment.
- Phillips, S.J., Elith, J., 2013. On estimating probability of presence from use-availability or presence-background data. *Ecology* 94, 1409–1419.
- Prera, A.J., Grimsrud, K.M., Thacher, J.A., McCollum, D.W., Berrens, R.P., 2014. Using canonical correlation analysis to identify environmental attitude groups: considerations for national forest planning in the Southwestern US. *Environ. Manage.* 54, 756–767. <https://doi.org/10.1007/s00267-014-0349-0>.
- PRISM Climate Group [WWW Document], n.d. < <http://www.prism.oregonstate.edu/normals/> > (accessed 4.28.16).
- Smith, W.B., Miles, P.D., Vissage, J.S., Pugh, S.A., 2004. Forest resources of the United States, 2002. A Technical Document Supporting the USDA Forest Service 2005 Update of the RPA Assessment. U.S. Department of Agriculture, Forest Service.
- South, D.B., Buckner, E.R., 2004. In: *Population Growth and the Decline of Natural Southern Yellow Pine Forests* (Gen. Tech. Rep. SRS-75. Chapter 29). U.S. Department of Agriculture, Forest Service, Southern Research Station, Asheville, NC, pp. 347–358.
- Stambaugh, M.C., Muzika, R.-M., 2007. Successional trends of six mature shortleaf pine forests in Missouri. In: Kabrick, J.M., Dey, D.C., Gwaze, D. (Eds.), *Shortleaf Pine Restoration and Ecology in the Ozarks: Proceedings of a Symposium*, 2006 November 7–9. U.S. Department of Agriculture, Forest Service, Northern Research Station, Springfield, MO, pp. 59–67.
- Thornthwaite, C.W., 1948. An approach toward a rational classification of climate. *Geogr. Rev.* 38, 55–94.
- Toney, C., Reeves, M.C., 2009. Equations to convert compacted crown ratio to un-compacted crown ratio for trees in the Interior West. *West. J. Appl. For.* 24, 76–82.
- Woudenberg, Sharon W., Conkling, Barbara L., O’Connell, Barbara M., LaPoint, Elizabeth B., Turner, Jeffery A., Waddell, Karen L., 2010. *The Forest Inventory and Analysis Database: Database description and users manual version 4.0 for Phase 2*. Gen. Tech. Rep. RMRSGTR-245. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, 336 p.