Canadian Science Publishing

ARTICLE

Assessment of natural regeneration of longleaf pine (*Pinus palustris*) 15 years post-regeneration control

Zhaofei Fan, W. Keith Moser, Cameron Poyner, Shaoyang Yang, Sunil Nepal, John S. Kush, and Dwight K. Lauer

Abstract: We assessed natural regeneration of longleaf pine (*Pinus palustris* Mill.) using the data collected from the Escambia Experimental Forest in southern Alabama. Fifteen years after the regeneration control, natural regeneration of longleaf pine remained patchy across a wide range of site and stand conditions; slightly more than half of all plots contained regeneration, but the density of seedlings and saplings varied significantly. The abundance of seedlings ≤1-year-old was positively related to stand age and time since last fire, but negatively related to overstory basal area. The abundance of seedlings and saplings was positively related to stand age, but negatively related to time since last fire and overstory basal area. The probability of achieving at least 15 000 seedlings·ha^{-1} that are older than 1 year but less than 1 m tall and at least 1250 saplings·ha^{-1} that are over 1 m tall was, respectively, positively related to the ratio of time since last fire to overstory basal area and the ratio of quadratic mean diameter to site index. A longer fire interval (> 2 to 3 years) should be adopted to naturally regenerate longleaf. We did not find clear zones of exclusion present in natural regeneration even though overstory trees, seedlings, and saplings tended to be repulsive spatially and >80% grass stage seedlings and saplings occurred outside tree crowns.

Key words: longleaf pine (*Pinus palustris* Mill.), natural regeneration, zero-inflated negative binomial model, point pattern data, spatial analysis.

Résumé : Nous avons évalué la régénération naturelle du pin des marais (*Pinus palustris* Mill.) en utilisant les données recueillies dans la Forêt expérimentale d'Escambia située dans le sud de l'Alabama. Quinze ans après une inspection de la régénération, la régénération naturelle du pin des marais était restée irrégulière malgré une large gamme de conditions de station et de peuplements; un peu plus de la moitié des placettes étaient régénérées, mais la densité des semis et des gaules variait considérablement. L'abondance des semis de moins d'un an était positivement liée à l'âge du peuplement et au temps écoulé depuis le dernier feu, mais négativement liée à la surface terrière du couvert dominant. L'abondance des semis et des gaules était positivement liée à l'âge du peuplement, mais négativement liée au temps écoulé depuis le dernier feu et à la surface terrière du couvert dominant. La probabilité d'obtenir au moins 15 000 semis·ha^{-1} plus vieux qu'un an mais d'une hauteur égale ou inférieure à 1 m, et au moins 1250 gaules·ha^{-1} d'une hauteur supérieure à 1 m était, respectivement, positivement corrélée au rapport entre le temps écoulé depuis le dernier feu et la surface terrière du couvert dominant et au rapport entre le diamètre quadratique moyen et l'indice de qualité de station. Un intervalle de feu plus long (plus de 2 à 3 ans) devrait être adopté pour régénérer naturellement le pin des marais. Nous n'avons pas trouvé de zones claires d'exclusion de la régénération naturelle même si les arbres du couvert dominant, les semis et les gaules avaient tendance à être spatialement répulsifs et que plus de 80 % des petits semis et des gaules étaient établis hors de la projection de la cime des arbres. [Traduit par la Rédaction]

Mots-clés : pin des marais (*Pinus palustris* Mill.), régénération naturelle, modèle binomial négatif à excès de zéro, données par patron de points, analyse spatiale.

Introduction

The longleaf pine (*Pinus palustris* Mill.) forest ecosystem in the southern United States is a unique ecological community that has experienced a drastic reduction in area, from approximately 37.2 million ha pre-European settlement (Boyer 1990*a*; Landers et al. 1995; Frost 2006) to today's 1.3 million ha (Oswalt et al. 2012). This reduction in area can be attributed to several key factors including large-scale exploitable logging, land conversion (e.g., urbanization, tree plantations of other pine species, and agriculture), regeneration failures, and fire suppression (Van Lear et al. 2005; Frost 2006). Among these factors, fire suppression following European settlement has significantly reshaped the historical vegetation and fuel structures and fire regimes (with a return interval of 2–10 years) and is recognized as the primary cause of decline of longleaf pine ecosystems (Christensen 1981; Glitzenstein et al. 2001). Fire can not only help reduce litter and understory woody components but can also stimulate fire-dependent species, with frequent surface fires particularly benefiting longleaf (Landers et al. 1995; Palmquist et al. 2015; Hammond et al. 2015).

Received 22 August 2020. Accepted 20 March 2021.

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There has been a growing interest in the use of prescribed fire in combination with vegetation management practices (e.g., removal of overstory and (or) midstory trees) to restore longleaf pine ecosystems through natural regeneration (Brockway and Outcalt 2000; Jose et al. 2006), although it has been proven difficult to achieve in the field (Croker and Boyer 1975).

The regeneration process of a tree species has two stages: (*i*) seedfall and germinant establishment and (*ii*) germinant survival and growth. Successful regeneration requires a fortunate combination of receptive site conditions and adequate seedfall (Pearson 1950; Ashton and Kelty 2018). Long gaps between good seed years and extreme sensitivity to competition from other ground-layer plants, plus years of fire suppression combined with conversion of land to other tree species, make restoring "natural" longleaf forests in its historical range a challenge (Boyer 1990*b*). Common causes of inadequate regeneration and regeneration failure include insufficient numbers of seed-bearing trees, infrequent seed crops, the limited distance that the heavy longleaf seeds can disperse, seeds dispersing but not reaching mineral soil or suitable seedbeds, brown spot fungus (*Mycosphaerella dearnessii*, formerly *Scirrhia acicola*), and competing species (Wahlenberg 1946; Croker and Boyer 1975; Boyer 1979; Brockway et al. 2006). Seeds may not germinate because those that do disperse do not reach mineral soil or suitable seedbeds (Boyer 1993*a*; Brockway et al. 2006). Germinants may succumb to brown spot fungus (Phelps et al. 1978) or to the effects of competing species (Wahlenberg 1946; Croker and Boyer 1975; Boyer 1979).

Competition from overstory trees

A particular source of uncertainty is the timing and conditions for longleaf pine emergence from the grass stage and the commencement of height growth, particularly given the species' extreme sensitivity to competition, whether it is from the overstory, at ground level, or belowground (Pessin 1944; Boyer 1990*a*; Brockway et al. 2006; Knapp et al. 2006). Longleaf pine is considered to be a very shade-intolerant species (Wahlenberg 1946; Boyer 1990*a*) (but see Samuelson and Stokes 2012). Neither regeneration nor older individuals tolerate competition well (Boyer 1990*a*, 1993*b*; Harrington 2006), particularly aboveground and belowground competition by overstory trees (Croker and Boyer 1975), although seedlings have been known to remain alive in the understory for many years (Croker and Boyer 1975). Overstory trees influence the surrounding microenvironment both directly and indirectly (but mainly indirectly) by consuming of resources such as light, water, and nutrients, by denying light to the understory, by the effects of needle fall on soil moisture and fire behavior, and by changing or otherwise buffering the temperature from ambient conditions (Harrington 2006). Due to the competition between and within species for sunlight, moisture, nutrients, and other resources (Spurr and Barnes 1980; Grace and Platt 1995; Oliver and Larson 1996), the density of the parent plants affects recruitment and survival of new plants (Harper 1977; Grace and Platt 1995), although there is often a particular range of densities that optimizes overstory influences on the environment and provides sufficient seedfall (Boyer 1993*a*).

Fire effect

More recently, studies of prescribed fire found that fire topkills aboveground hardwood brush if it occurs every 1–3 years with suitable site and stand conditions (Whelan et al. 2018). The dried, fluffed up fuels of longleaf pine needles and wiregrass (*Aristida stricta* Michx.) fuel more-intense fires and increase time of smoldering and burning, thereby better controlling hardwoods (Hiers et al. 2009; Whelan et al. 2018), although there can also be damage to both young and old longleaf (Boyer 1990*b*). The highest longleaf seedling mortality often occurs during the first growing season. A droughty spring alone can cause up to 50% mortality (Brockway et al. 2006). Fires occurring during the first two growing seasons can result in up to 90% mortality (Grace and Platt 1995; Provencher et al. 2001; Brockway et al. 2006). Longleaf's sensitivity to competition extends to juvenile diameter and height growth. At a root collar diameter (RCD) of 1.3 cm, longleaf starts to become fire resistant (Boyer 1974), and at 2.5 cm RCD, longleaf seedlings freed of competition can commence height growth (Boyer 1975, 1990*a*, 1993*a*; Haywood 2000; Brockway et al. 2006).

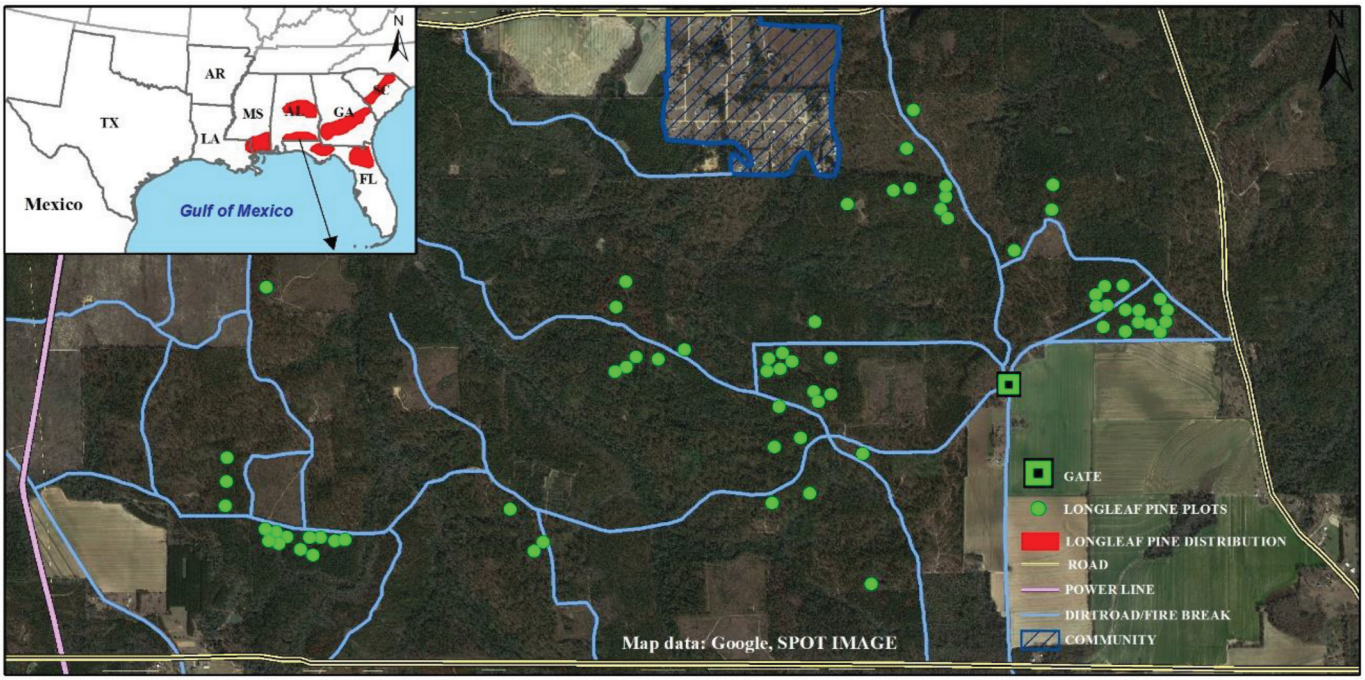
Spatial exclusion and gap size effect

Past research has found that regeneration of longleaf pine varied spatially, as shown by a zone of exclusion under mature longleaf trees where there is a significant reduction in the number of seedlings present (Wahlenberg 1946; Smith 1955); recruitment of new longleaf seedlings was less in areas that had high adult tree densities (Platt et al. 1988; Platt and Rathbun 1993; Brockway and Outcalt 1998). There have been two hypotheses to explain this phenomenon: the first being higher levels of sunlight available near the center of gaps, and the second being direct needle fall beneath the large mature trees leading to more intense prescribed fires and killing of the seedlings (Boyer 1974; Platt et al. 1988; Grace and Platt 1995; Farrar 1996). However, Brockway and Outcalt (1998) provided another plausible explanation, concluding that the most likely mechanism causing the zone of exclusion was due to the competition for soil moisture and nutrients between the root systems of seedlings and adults. According to the Janzen–Connell hypothesis, other factors such as host-specific herbivores, pathogens, intraspecific competition, or other natural enemies (seed predators) may also make the areas near a parent tree inhospitable for the survival and growth of seedlings (Comita et al. 2014). Yet, there have been conflicting conclusions about the influence of overstory trees. Some research has suggested that individual trees may increase the amount of soil nutrients and moisture available to the understory in a savanna-type environment, and as a result, naturally regenerated seedlings were frequently found within 4 m of a mature longleaf pine (McGuire et al. 2001). Schwarz (1907) concluded that regeneration can occur in any-sized gaps. Some have suggested that smaller gaps, such as those resulting from individual tree mortality, may be enough to successfully regenerate longleaf (McGuire et al. 2001; Jack et al. 2006), whereas others identified larger gaps as necessary for successful regeneration (Wahlenberg 1946; Walker and Davis 1956; Palik et al. 2002; Brockway et al. 2006).

In fact, the relationship between adult longleaf trees and regeneration is not well understood (McGuire et al. 2001). Although initial establishment of seedlings was related to the proximity of parent trees, Brockway et al. (2006) stated that there was little likelihood of these seedlings entering into the overstory as canopy dominants. Kara et al. (2017) looked at three different levels of overstory density (residual basal area, RBA) and the resultant number of surviving seedlings and the years to a projected mean RCD of 2.5 cm. They found no relationship between overstory density or intercepted photosynthetically active radiation and germinant numbers until after the third year and a prescribed fire, resulting in a significant negative relationship. They determined that low RBA was unnecessary, as the sites would create too many seedlings. The ideal was a medium RBA at 1000 seedlings per hectare in 17 years, closer to the optimal level of recruitment (Kara et al. 2017). Curtin et al. (2020) also found that a high overstory density inhibited tree recruitment. A study of planted longleaf pine seedlings found larger RCD near the center of gaps and smaller RCD near the edge (Gagnon et al. 2003). Given the relative influence of aboveground and belowground competition attributed to the overstory, one would expect growth rates to be higher with low overstory basal and lower with high overstory basal area (Palik et al. 1997, 2003). There is a tradeoff between basal area and having an adequate number of surviving saplings.

In an effort to help land managers identify more appropriate management techniques to promote natural regeneration of this critical species, we were specifically motivated to answer the

Fig. 1. Map of plots surveyed in the Escambia Experimental Forest (EEF), southern Alabama. The base map came from the Google SPOT IMAGE and was prepared by using ArcGIS 10.2. [Colour online.]



following questions: (*i*) What factors are significantly related to the recruitment of new seedlings (≤1 year old) and the development of seedlings and saplings under a 2- to 3-year fire return interval? (*ii*) What is the likelihood of a stand being stocked 15 years after the termination of regeneration control? (*iii*) What combination of factors — overstory basal area and density and distance from overstory trees — influences the placement and production of a sustainable number of saplings beyond grass stage (>1 m tall)?

Methods

Study site

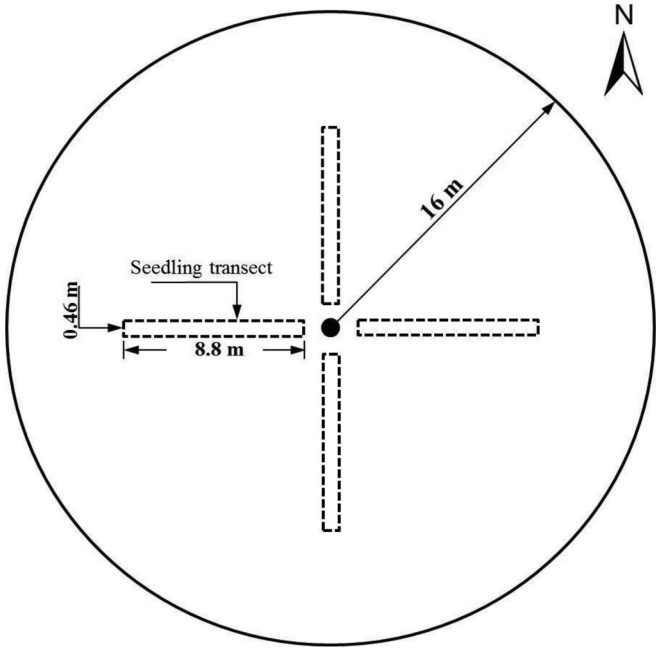
In 1964, the United States Forest Service established the Regional Longleaf Pine Growth Study (RLGS) in the Gulf states to collect data for the development of growth and yield predictions for naturally regenerated, even-aged longleaf stands (Farrar 1978). The RLGS plots are primarily concentrated in six sites distributed in central and southern Alabama, southern Mississippi, southwestern Georgia, northern Florida, and the Sandhills of North Carolina. Plots were installed to cover a range of ages, densities, and site qualities. There are five stand-age classes ranging from 20 to 120 years, five site-index classes ranging from 15.2 to 27.4 m at 50 years, and six density classes ranging from 7 to 34 $m^2 \cdot ha^{-1}$, plus plots left free to grow (controls). Densities are established and maintained by thinning from below, where the most suppressed trees are taken out. A set of new plots in younger age classes was added to the RLGS approximately every 10 years to account for potential changes in growth rates over time (Kush et al. 1998).

Situated near the center of the native range of longleaf pine distribution near Brewton, Alabama, USA (31°00′N–87°03′W) (Fig. 1), the 1215 ha Escambia Experimental Forest (EEF) was established in 1947 as a cooperative effort between the United States Forest Service in conjunction with T.R. Miller Mill Company to study longleaf pine forests as a whole, with a focus on trends in density, growth, and natural regeneration (Barlow et al. 2011). Primary management of the EEF is through the use of prescribed fire, with every unit having a fire return interval of no greater than 3 years. The basal area of each EEF plot is maintained in accordance with its initial target (7 to 34 $m^2 \cdot ha^{-1}$) by periodic thinning-from-below methods, thus providing an ideal opportunity to evaluate the efficiency of the prescribed treatments on natural regeneration of longleaf pine and quantify the effect of stand factors on the regeneration patterns of the longleaf pine in an area with a long time period of regeneration management. To study regeneration, a total of 305 permanent, circular plots approximately 0.08 ha in size were established (Connor et al. 2014). Each plot was surrounded by a similarly treated 10-m-wide isolation strip and a 10-m-wide protective buffer strip that received extensive management. Primary management of the EEF is through the use of prescribed fire, with every plot having a fire return interval of no greater than 3 years. The original objective of these plots was to develop growth and yield models, so all regeneration in the plots was mowed over until 2001. The prior mowing treatment provided a unique opportunity to evaluate regeneration during a fixed time (2001∼2017). Longleaf pine, unlike, for example, shortleaf pine (*Pinus echinata* Mill.), does not commonly resprout, so all seedlings and saplings that we found can be assumed to have originated in 2001 or later.

Data collection

A total of sixty-nine 0.08 ha plots were measured in June of 2016 and 2017 to assess natural regeneration 15 years following a regeneration control. To examine factors related to the recruitment of new seedlings and the development of older seedlings and saplings (objective 1), a new seedling was defined as an individual that germinated the prior fall or early winter from seed and is less than 1 year old by the measurement date. An older seedling was defined as anything >1 year old but ≤1 m tall and a sapling as >1 m tall but was not previously marked as a mature tree. The total height of saplings ranged from 1.1 to 12.2 m in the study plots. New seedling density was measured from four strips (8.8 m long and 0.46 m wide), which began 1.83 m from the plot center and extended in the four cardinal directions (Fig. 2). The

Fig. 2. Design of the approximately 0.08 ha plot used to examine the longleaf pine regeneration. The new seedlings (≤1 year old) were counted within four (north, east, south, west) of 8.8 m by 0.46 m transects, older seedlings (>1 year old but ≤1 m tall), saplings (>1 m tall but ≤12 cm diameter at breast height (DBH)), and overstory trees (>12 cm DBH) were counted and mapped within the entire plot.



density of seedlings (>1 year old) and saplings was measured directly from the 0.08 ha plot. For plots with seedlings and saplings (except for three plots with saplings >25 000·ha^{-1}), total height (m), diameter at breast height (DBH, cm) (if applicable), azimuth, and distance to the plot center of all overstory trees, seedlings, and saplings were measured to examine the spatial relationship between overstory trees and sapling recruitment using spatial statistics. In addition, site index (SI, m), time since last fire (TSLF, in days), overstory basal area (BA, m^2·ha^{-1}), quadratic mean diameter (QMD, cm), and mean tree age (AGE, year) were calculated as covariates from measurement data or management records to evaluate their effect on seedling and sapling regeneration. In addition, we installed a large plot (205 m × 52 m, or 1.07 ha) within which seedling and sapling density varied significantly. We mapped all overstory trees (n = 264), seedlings, and saplings (n = 2436) and measured their total height, DBH (if applicable), and crown width (in the east–west and south–north directions) to study the spatial relationship between overstory trees, seedlings, and saplings. A total of 77 overstory trees were cored to determine their age.

Data analysis

With the zero-inflated, overdispersed (variance ≫ mean) count data of longleaf new seedlings (≤1 year old), seedlings (>1 year old but ≤1 m tall), and saplings (>1 m tall) among the 69 plots, the zero-inflated negative binomial (ZINB) model was employed to address the first specified objective (Zeileis et al. 2008). The best ZINB model (minimum Akaike information criterion (AIC), significance of coefficients) out of several candidates examined was developed to evaluate factors contributing to longleaf regeneration. The mixture ZINB model including a logit model and a count model is given by

$$(1)\qquad P(Y=y|\mu,\theta)=\begin{cases} p+(1-p)\left(1+\dfrac{\mu}{\theta}\right)^{-\theta}, & y=0 \\ (1-p)\dfrac{\Gamma(\theta+y)}{y!\Gamma(\theta)}\left(1+\dfrac{\mu}{\theta}\right)^{-\theta}\left(1+\dfrac{\theta}{\mu}\right)^{-y}, & y=1,2,\ldots \end{cases}$$

where $\mu = E(Y)$ is the mean of the response variable Y (here, count of new seedlings or grass stage seedlings and saplings in a plot), and θ is a scale parameter quantifying the amount of overdispersion with $E(Y) = (1 - p)\mu$ and $\mathrm{Var}(Y) = (1+p)\mu\left(1+p\mu\dfrac{\mu}{\theta}\right)$, respectively. The variance of the response variable Y is a quadratic function of its mean, given by $\mu + (\mu^2/\theta)$. The ZINB regression model regresses p (the probability for the response variable Y to be zero) and μ (the mean of the response variable Y) on a set of covariates X and Z via

$$(2)\qquad \mathrm{logit}(p) = X\beta \quad \text{and} \quad \log(\mu) = Z\Upsilon$$

where β and Υ are the regression coefficients to estimate μ and p, respectively, using the maximum likelihood method. In the final model, X and Z may be different, representing a subset of significant variables selected from those measured or calculated for each plot. These variables include site index (SI), stand age (AGE), quadratic mean diameter (QMD), and basal area (BA) of overstory trees, and time since last fire (TSLF), respectively.

According to Croker and Boyer (1975), Boyer and White (1990), and Brockway et al. (2006), a reasonable standard for successful regeneration of longleaf pine should be at least 15 000 seedlings·ha^{-1} that are older than 1 year old but <1 m tall to get at least 1250 saplings·ha^{-1} that are ≥1 m tall likely free from brown spot infection and fire damage. Thus, plots were further divided into success (1) or failure (0) cases based on whether the count of longleaf regeneration was >15 000 stems·ha^{-1} for seedlings and >1250 stems·ha^{-1} saplings, respectively. Logistic regression was conducted to quantify the "success" probability of longleaf regeneration based on the best fit (minimum AIC, significance of coefficients) selected stepwise from the full model, which contains TSLF, BA, QMD, AGE, SI, 1/BA, 1/SI, and three "composite" variables — TSLF/BA, TSLF/SI, and QMD/SI — as the predictor variables (objective 2). With the best model, the Hosmer–Lemeshow test was conducted and McFadden's R^2 was calculated to evaluate the goodness of fit and the predictive power of the best model.

To address objective 3, the spatial distributions of mapped overstory trees, seedlings, and saplings in the 28 0.08 ha circular plots and in the 1.07 ha large, rectangular plot were examined using marked point pattern data with the x, y coordinates as the location and the status (overstory tree versus seedling and sapling) of longleaf pine as the "mark" (auxiliary data) in the spatstat package of R (Baddeley and Turner 2005). The cross-type (overstory trees versus seedlings and saplings) pair correlation function (pcfcross, labelled as $g(r)$) and a simulated Monte Carlo envelope were used to identify the spatial scales (r, measured by linear distance) at which both are significantly repulsive (dispelled) or attractive (clustered) against the null model that they are spatially random or independent (a spatial Poisson process) (Lutz et al. 2014). Then, the nearest distance from seedlings and saplings to overstory trees was calculated using the nncross function, and the smoothed probability density function (pdf) of the calculated nearest distances was plotted to visualize the placement of seedlings and saplings and their distances from overstory trees. The proportions of seedlings and saplings occurring in a distance of 1 (the dripline) to 5× crown radius from overstory trees were calculated to examine whether a zone of exclusion exists, as observed by other studies. Finally, we applied the rhohat function to the large rectangular plot to estimate local

Table 1. Summary statistics of the plots with regeneration surveyed in the Escambia Experimental Forest, southern Alabama.

Variable	Age (year)	BA ($m^2 \cdot ha^{-1}$)	QMD (cm)	SI (m)*	TSLF (days)	1-year-old seedlings ($trees \cdot ha^{-1}$)	Older seedlings and saplings ($trees \cdot ha^{-1}$)
Minimum	41	5.5	15.6	18.6	4	618	12
Mean	63	19.2	32.7	23.6	608.6	19 661	2718
Standard deviation	20.2	8.2	9.1	2.7	18.8	43 025	9829
Maximum	126	37.2	56.4	35.7	1065	223 630	56 217

Note: BA, basal area; QMD, quadratic mean diameter; SI, site index; TSLF, time since last fire. The number of sample plots to calculate summary statistics for 1-year-old seedlings, and older seedlings and saplings is $n = 40$ and $n = 35$, and $n = 69$ for other variables.

*Base age = 50 years.

Table 2. Estimated coefficients of the zero-inflated negative binomial model.

Variable	Estimate	Standard error	*z* value	*p* value
Count model to quantify the number of ≤1-year-old seedlings				
Intercept	2.57	1.341	1.917	0.055
Basal area	−0.019	0.009	−2.043	0.041
Time since last fire	0.001	0.001	1.795	0.073
Age	0.023	0.013	1.884	0.059
Log(θ)	−0.691	0.259	−2.663	0.008
Logit model to predict the probability with no ≤1-year-old seedlings				
Intercept	14.949	6.248	2.393	0.017
Basal area	0.039	0.015	2.534	0.011
Time since last fire	−0.003	0.001	−2.082	0.037
Age	−0.059	0.026	−2.224	0.026
Site index	−0.181	0.08	−2.26	0.024
Count model to quantify the number of older seedlings and saplings				
Intercept	4.56	1.042	4.375	0.000
Basal area	−0.063	0.009	−6.839	0.000
Time since last fire	−0.002	0.001	−2.202	0.028
Age	0.061	0.012	5.12	0.000
Log(θ)	−1.026	0.207	−4.963	0.000
Logit model to predict the probability with no older seedlings and saplings				
Intercept	144.363	254.998	0.566	0.571
Basal area	1.269	2.534	0.501	0.616
Time since last fire	0.061	0.131	0.462	0.644
Age	−1.402	7.423	−0.189	0.850
Site index	−2.874	7.548	−0.381	0.703

densities of seedlings and saplings established under varying overstory basal areas and tree densities, two critical variables to be manipulated mechanically in longleaf regeneration. The rhohat function computes the intensity of a point process (the development of seedlings and saplings) as a nonparametric function of a continuous spatial covariates (overstory basal area or tree density).

The ZINB and logistic regressions were conducted using the pscl package (Zeileis et al. 2008), and the spatial analysis of point pattern data through the spatstat package (Baddeley and Turner 2005). All analyses were done using the R language, with an α level of 0.05 used to determine statistical significance (R Development Core Team 2020).

Results

Natural regeneration across a wide range of site and stand conditions over this 15-year period was patchy, with 29 (42%) lacking new seedlings and 34 (49%) of 69 plots lacking older seedlings and saplings, respectively. For those plots with regeneration, the density varied significantly from 618 up to 223 630 new $seedlings \cdot ha^{-1}$ and from 12 up to 56 217 older seedlings and $saplings \cdot ha^{-1}$ (Table 1). The ZINB models suggest that overstory basal area, tree age, site index, and the time since the last fire may be limiting factors of longleaf regeneration (Table 2). The count models show that new seedling abundance was positively related to stand age and the time since last fire, but negatively related to basal area. Sapling abundance was positively related only to stand age, but negatively related to the time since last fire and basal area. The logit models show that the probability of having no new seedlings increases with basal area, but decreases with site index, stand age, and the time since last fire. Conversely, none of these factors were found to be significantly related to the probability of having no older seedlings and saplings (Table 2).

Of the 69 plots, only five (7.2%) and four (5.8%) plots reached the specified regeneration standards of ≥15 000 $seedlings \cdot ha^{-1}$ and ≥1250 $saplings \cdot ha^{-1}$, respectively. The stepwise logistic regression indicated that only TSLF/BA and QMD/SI were, respectively, statistically significant to predict the probability of regenerating ≥15 000 $seedlings \cdot ha^{-1}$ and regenerating ≥1250 $saplings \cdot ha^{-1}$. Both models fit the data well based on the Hosmer–Lemeshow test ($p > 0.05$) and have a moderate predictive power of 0.14 and 0.44 in terms of the McFadden's R^2 (Table 3; Fig. 3). This suggests that there are other factors not included in this study influencing longleaf regeneration.

Spatially, overstory trees, seedlings, and saplings are essentially repulsive over varying distances, with seedlings and saplings occurring

Table 3. Estimated coefficients of logistic regression models to predict the probability of ≥15 000 seedlings·ha^{-1} (>1 year old but ≤1 m tall) and ≥1250 saplings·ha^{-1} (>1 m tall) based on the 69 0.08 ha circular plots.

Variable	Estimate	Standard error	*z* value	*p* value	McFadden's R^2	Hosmer–Lemeshow test
15 000 seedlings·ha^{-1}						
Intercept	–3.461	0.766	–4.4519	<0.0001	0.1353	0.4706
TSLF/BA	0.024	0.009	2.463	0.0138	—	—
≥1250 saplings·ha^{-1}						
Intercept	–10.875	3.584	–3.035	0.0024	0.4449	0.6293
QMD/SI	4.419	1.658	2.666	0.0077	—	—

Note: TSLF/BA, ratio of time since last fire to basal area; QMD/ SI, ratio of quadratic mean diameter to site index.

mostly in canopy gaps of varying sizes (Figs. 4 and 5). The cross-type pairwise correlation curve based on the 1.07 ha plot confirmed this repulsive distribution pattern (Fig. 5A). Figure 5B shows the smoothed probability density of the distance from individual seedlings and saplings to their nearest overstory trees and the mean crown radius of overstory trees based on the mapped 28 0.08 ha circular plots and the 1.07 ha rectangular plot. With the calculated mean crown radius of 3.6 m, the calculated percentage of seedlings and saplings falling within 1 (3.6 m), 2 (7.2 m), 3 (10.8 m), 4 (14.4 m), and 5 (18 m) times the mean crown radius was 15%, 49%, 76%, 92%, and 100%, respectively. This means 85% of seedlings and saplings were outside the range of tree crowns but within 18 m of overstory trees. The number of seedlings and saplings decreased significantly as overstory density increased up to 200 trees·ha^{-1} or BA increased up to 10 m^2·ha^{-1} (Figs. 5C and 5D). To reach the regeneration level of ≥1250 saplings·ha^{-1}, the overstory tree density and basal area should be less than 145 trees·ha^{-1} and 8.3 m^2·ha^{-1}, respectively.

Discussion

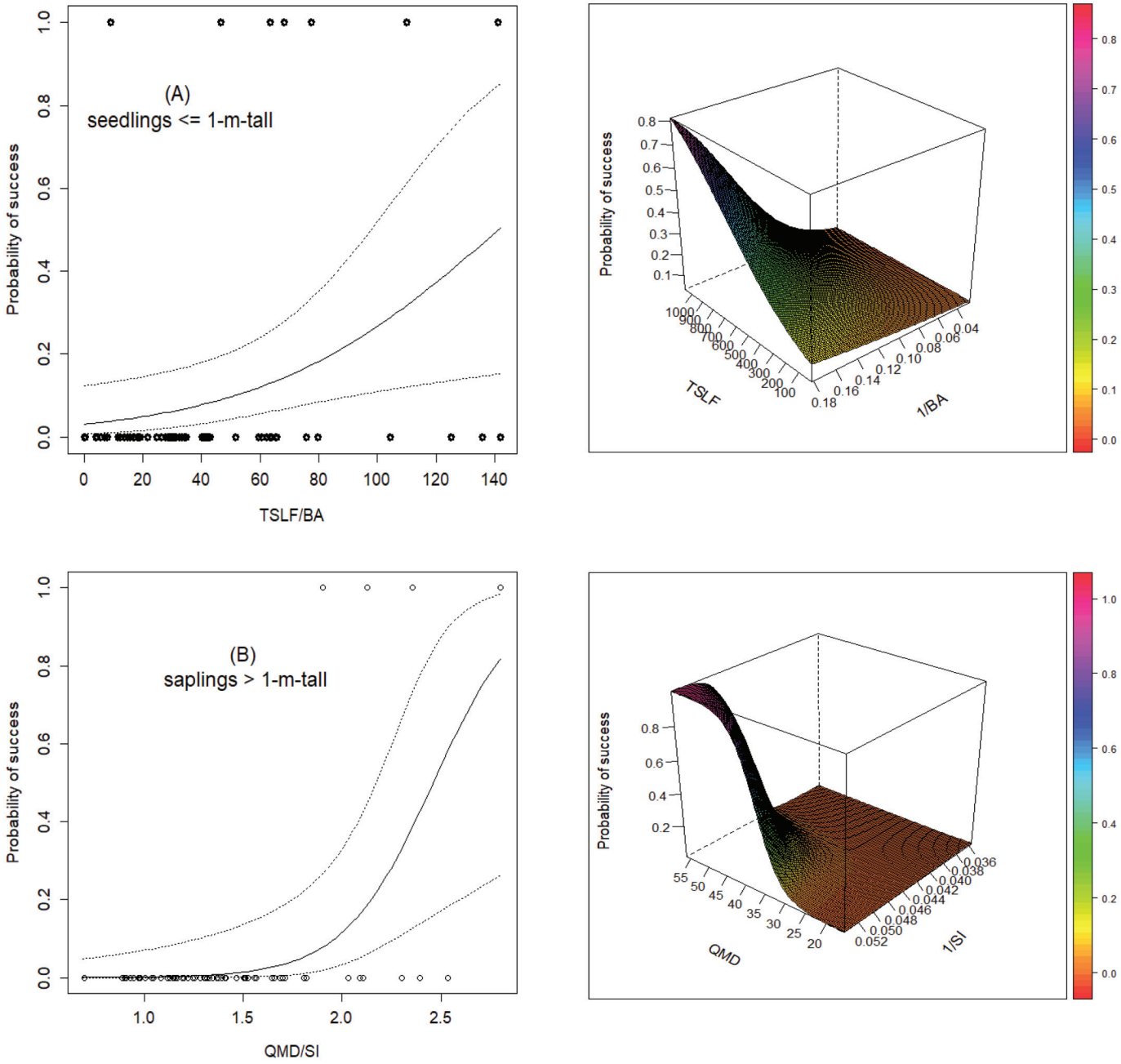
Intermittent and patchy regeneration patterns for longleaf pine are not atypical (Boyer 1990*a*), unlike the more prolific and consistent seeding of its fellow yellow pine, loblolly pine (*Pinus taeda* L.) (Baker and Langdon 1990). In our study, regeneration over the 15 years was patchy, with slightly more than half of all plots (58%, or 40 plots; and 51%, or 35 plots) containing new seedlings, older seedlings, and saplings, and only 7.2% (five plots) and 5.8% (four plots) achieving ≥15 000 seedlings·ha^{-1} and ≥1250 saplings·ha^{-1}, respectively. Numerous studies have reported the great uncertainty of natural regeneration and the effects of the extended 2+ year seed development process (Croker and Boyer 1975), climatic factors (e.g., Wahlenberg 1946; Shoulders 1967), and temporal changes in seed production (Croker 1973) on regeneration. The greatest influence of site and stand variables is most likely on seed development and production and seedling recruitment processes. However, many other factors that affect seed development and seedling recruitment are often beyond management control (Shoulders 1967). Therefore, site and stand variables such as overstory tree age and basal area could be used to predict the density of seedlings and saplings only when other related factors have been identified.

To ensure a future overstory component while accounting for the mortality that will naturally occur as a result of local stand dynamics, it is important to create enough seedlings to start the process (Oliver and Larson 1996). The targets of 15 000 seedlings·ha^{-1} and 1250 saplings·ha^{-1} reflect these dynamics (Croker and Boyer 1975; Boyer 1990*a*; Brockway et al. 2006). Of all stand factors examined, overstory tree age and basal area were the most significant determinants of seedling recruitment and seedling survival into future saplings (Croker and Boyer 1975). Increasing stand age increased the fecundity of the stand, resulting in more seed crops, which in turn provided more opportunities for seedling establishment. Basal area represents not only an influence on aboveground microclimate and seed-producing potential, but also an indicator of the intensity of belowground competition, particularly as faced by seedlings and saplings (Brockway et al. 2006; Kara et al. 2017). Other variables such as site index and burn interval (e.g., TSLF) also play critical roles in seedling recruitment, growth, and survival. Site index is usually viewed as a measure of site suitability or potential to regenerate longleaf pine, but TSLF influences not only the probability but also the amount of seedling recruitment and seedling survival (development of saplings) (Table 2). Therefore, given a specific site condition (e.g., SI), how to prescribe treatment, specifically, to determine optimal burn intervals and residual overstory basal area has been a critical issue in natural regeneration of longleaf.

Fire, whether natural or prescribed, is the single most important disturbance shaping the longleaf ecosystem (Brockway and Outcalt 1998). While some literature recommends longer burn-free period of up to 10 years as necessary to get the seedlings established (Ford et al. 2010), historical fire regimes on the Atlantic and Gulf Coastal Plains averaged 2–5 years (Noss 1988; Wade et al. 2000), an interval that conforms to the management on our study site. There are two vulnerable periods that seedlings must survive: the initial years until the longleaf seedlings assume the grass stage, and the period when the trees bolt from the grass stage until they reach a largely fire-safe height (Boyer 1990*a*). Intermittent fire regimes create stochastic disturbance patterns that allows some subset of the regeneration to make it through to the next stage. In a similar manner, land managed for wildlife, such as northern bobwhite quail (*Colinus virginianus*), employ temporary cover blocks as protection for quail during spring burns, and simultaneously permit longleaf pine to enjoy a fire-free interval to progress on to the next stage (Moser and Palmer 1997).

The influence of TSLF, a variable that can be controlled by forest managers, represents the fire-free window in which seedlings are established. Among all simple and composite variables examined, the ratio TSLF (in days)/BA (in m^2·ha^{-1}) was found to be the only variable that significantly determines the success likelihood to achieve the threshold (≥15 000 1-year-old seedlings·ha^{-1}) of seedling recruitment. Application of TSLF/BA offers forest managers two avenues to enhance seedling establishment and growth, by either increasing years since the last burn or reducing BA and subsequently fine fuel production or fire intensity. TSLF represents a fire-free period and thus the likelihood of fire destroying seedlings. Fire must occur infrequently enough for seedlings to reach the stage where they are fire resistant (grass stage or bolted saplings above 2 m), but in combination of mechanical treatments, frequently enough to control competing vegetation such as woody shrubs. Increased basal area reduces this composite variable, reducing the likelihood of successful fully stocked stands. Basal area also represents both the competition (aboveground and belowground) of the overstory and the fine fuels production of the overstory trees. As shown, the ratio TSLF/BA should be at least 140 if a mean success rate of >50% is

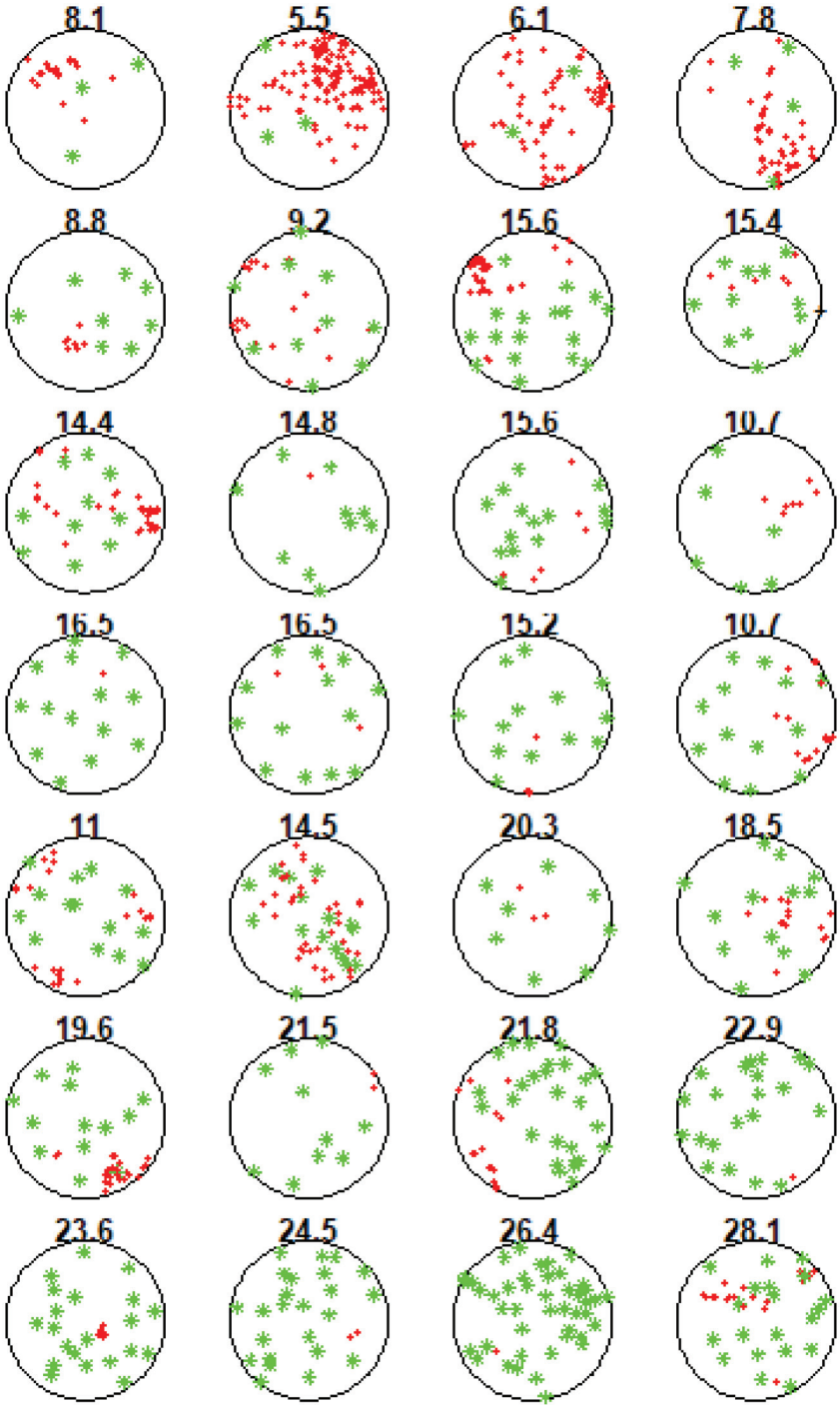
Fig. 3 Longleaf pine recruitment by identified key limiting factors. (A) The probability and 95% confidence interval of seedlings ≥15 000 trees·ha^{-1} by the ratio of time since the last fire (TSLF, day) over overstory basal area (BA, m^2·ha^{-1}). (B) The probability and 95% confidence interval of ≥1250 saplings·ha^{-1} by the ratio of quadratic mean diameter (QMD, cm) over site index (SI, m). The panels on the right show their corresponding three-dimensional plot of probability of success. [Colour online.]



expected (Fig. 3). If the fire return interval (here represented by TSLF) is shorter than the time between adequate or large seed crops, the forest will have difficulty maintaining a continuous forest cover over time. The impact of TSLF upon seedling survival can be partially offset by a robust seed source. To maintain a TSLF/BA ratio of 140, TSLF should be ≥2.68 years (980 days) for a stand with BA of 7 m^2·ha^{-1} and must be at least 5.75 years (2100 days) if BA is 15 m^2·ha^{-1}. One should note that this prescription is only valid and meaningful on suitable site and stand conditions (e.g., SI = 15.2∼27.4 m at 50 years, BA = 7∼34 m^2·ha^{-1}) (Fig. 3) and cannot be overly generalized to any site or stand. Meanwhile, the opposite effect of TSLF on the number of seedlings and saplings (Table 2) suggests that a tradeoff between seedling recruitment and growth and survival (development of saplings) exists, and TSLF should not be too long (e.g., more than 6 years) or too short (e.g., less than 2 years) for a recommended range of BA between 7 to 15 m^2·ha^{-1} (30 to 65 ft^2·acre^{-1}) to regenerate longleaf pine (Crocker and Boyer 1975).

The probability of achieving at least 1250 saplings·ha^{-1} was significantly influenced only by the ratio QMD (in cm)/SI (in m). QMD may be considered an expression of tree crown size, with larger trees more likely to be good seed producers (Boyer 1990*a*). QMD could also be a surrogate for needle fall, and thus fine fuels production, which is causally related to fire occurrence and intensity. If SI represents

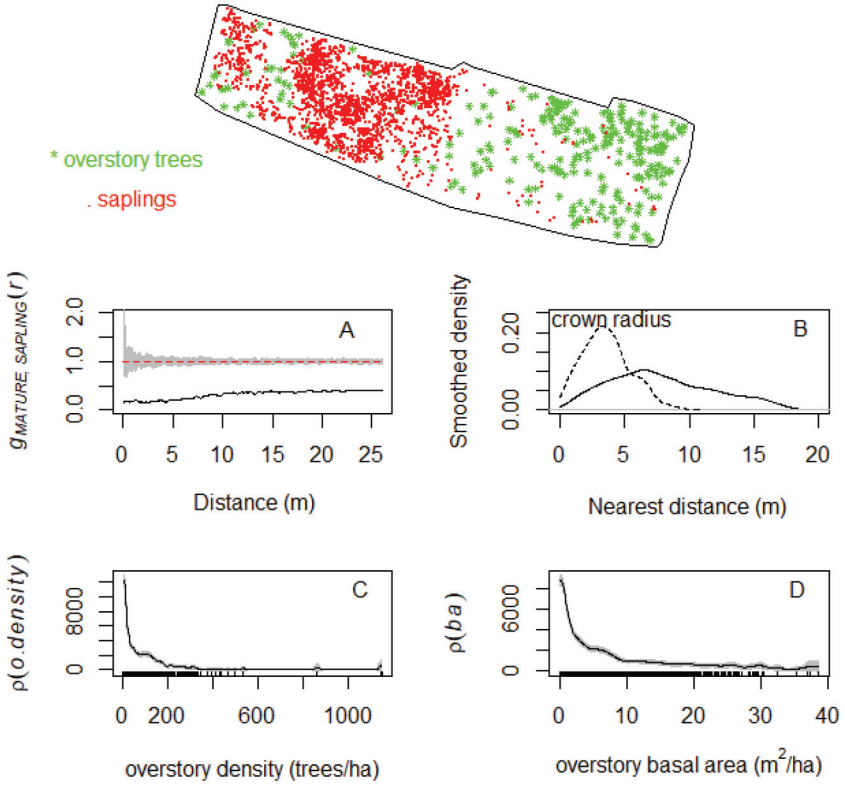
Fig. 4. Spatial distribution of longleaf seedlings and saplings (red cross) under overstory trees (green asterisk) in the twenty-eight 0.08 ha circular plots with varying basal areas (the number on top, $m^2 \cdot ha^{-1}$). The recruitment of seedlings and saplings is closely related to overstory density or basal area, or both. [Colour online.]



site suitability or potential to regenerate longleaf pine, then the ratio QMD/SI can represent the realized regeneration potential of a particular site. Longleaf will be more competitive than other tree species on sites with a low SI, but the regeneration potential (success rate) depends on the ratio QMD/SI, a combination of QMD and SI. The ratio should be at least 2.3 for a mean success rate of >50% (Fig. 3). With large variations (a wide confidence interval) of the predictive model due to the skewness of the data (i.e., 4 "success" plots versus 65 "failure" plots), we conservatively suggest the ratio should be slightly larger than the calculated values. With a suitable site condition (SI), forest managers can use both ratios through potentially manipulating TSLF, BA and QMD to quantify the likelihood of regeneration success (Fig. 3).

The general decreasing trend of saplings with overstory density and basal area reflected a 15-year cumulative effect on a 1.07 ha plot with a mean overstory tree age of 49 years (25∼93 years) under a regime of 2- to 3-year burn intervals since the regeneration event in 2001 (Figs. 5C and 5D). Croker (1973) observed that

Fig. 5. Regeneration patterns of longleaf pine in the 1.07 ha rectangular plot: spatial distribution of seedling and sapling recruitments (red cross, n = 2436) and overstory trees (green asterisk, n = 264). (A) The cross-type (overstory trees versus seedlings and saplings) pairwise correlation function ($g(r)$) curve, showing a repulsive relationship between overstory trees and the recruitment of seedlings and saplings across all spatial scales (distance or r = 0∼25 m). (B) The smoothed probability density of overstory tree crown radius (dashed line) and the nearest distance from seedlings and saplings to overstory trees (solid line), indicating only a small proportion of seedlings and saplings occurring underneath the crown. (C and D) An exponential decrease of seedling and sapling recruitment (ρ(.), stems·ha^{-1}) as local overstory tree density (o. density) and basal area (ba) increases, respectively. [Colour online.]



despite a decrease in seedlings on sites with higher basal area, there are still seedlings present. Situations may arise where a land manager may not want a large number of seedlings; therefore, thinning below 15 m^2·ha^{-1} is not recommended (but for saplings to survive and thrive, a considerably lower density is necessary). If a land manager wants a large amount of seedling recruitment, a seed cut to reduce overstory basal area down to about 7.5 m^2·ha^{-1} should be implemented. Mitchell et al. (2006) advocated a considerably higher minimal basal area (9 m^2·ha^{-1}) in order for those seedlings to survive until they are saplings and eventually mature trees. Similar results (∼8.3 m^2·ha^{-1} in BA or 145 trees·ha^{-1}) were observed in this study. Croker and Boyer (1975) suggested that the initial preparatory cut should be made at least three growing seasons prior to the manager's desired timeframe, since cone crops will not respond for several years.

As understory trees grow, the distance between them and overstory trees widens as a result of competitive pressure. Whereas seedlings can coexist with overstory trees, saplings need freedom from overstory tree competition (both aboveground and belowground) to be free to grow. This pattern is similar to that of Scots pine (*Pinus sylvestris* L.) trees, where saplings and small poles are clearly separated from overstory trees (Montes and Cañellas 2007). Given the heavy longleaf seeds, however, saplings must be somewhat near the overstory trees. Supporting Boyer's (1963) assertion that seedlings under the tree canopy are not likely to grow into the overstory, our study found only 15% of the saplings to be within one crown radius of an overstory tree stem (i.e., under the dripline), while approximately 34%, 26%, 16%, and 8% of saplings to be within the "ring" of from second to fifth crown radius. Therefore, if the goal of management is to recruit trees into the overstory, the optimal gap size appears to be 1∼2× crown widths beyond the dripline of the nearest overstory trees. Too close, and the seedlings do not grow into saplings because of competition. It is generally accepted that belowground competition can extend beyond crown width (Oliver and Larson 1996). Yet, longleaf regeneration will not be too far from overstory trees, as its seeds are heavier than those of the other southern pines (Bonner and Karrfalt 2008) and do not generally land far from parent trees (Boyer 1990*a*).

Numerous hypotheses have been proposed to interpret the repulsive relationship between overstory trees and seedlings or saplings, such as root competition, canopy cover, and higher mortality due to fire (Platt et al. 1988; Grace and Platt 1995; Brockway and Outcalt 1998; Montes and Cañellas 2007). Our data indicate that there is no clear zone of exclusion present in natural regeneration of longleaf pine, although overstory trees and seedlings or saplings are repulsive spatially, and >80% saplings fall within gaps of varying sizes (Figs. 4 and 5). This is in contrast to other studies (Wahlenberg 1946; Smith 1955; Brockway and Outcalt 1998) that have shown a 16 m gap between a mature tree and seedlings. In another study, however, McGuire et al. (2001) suggested mature longleaf overstory trees may increase, rather than decrease, the establishment of longleaf seedlings. Although our study did not examine the spatial relationship between overstory trees and seedlings, the finding that saplings were present immediately under and close to the overstory trees suggests that the recruitment of seedlings was affected by location relative to overstory trees and multiple limiting factors contribute to the diverse spatial regeneration patterns of longleaf pine.

Conclusions

Overstory basal area and age, time since last fire, and site index are important in determining the number of longleaf seedlings and saplings present in a stand. However, to determine the probability of achieving the desired number of seedlings and saplings (i.e., 15 000 seedlings·ha^{-1}, 1250 saplings·ha^{-1}) on a site, forest managers need to carefully examine two ratios: TSLF/BA and QMD/SI so that the desired goal can be maximized through intentionally manipulating individual factors, that is, TSLF, BA, and QMD on a given site condition (SI). The effect of fire on regeneration is related to the stage of regeneration: as the time since last fire increases, so does the amount of ≤1-year-old seedling recruitment, but the amount of older seedling and sapling recruitment tends to decrease. Our observations align with the idea that longleaf pine evolved with frequent surface fires. A return interval (e.g., >2 years) that favor both seedling recruitment and sapling development (passing the grass stage) is necessary to maximize regeneration. Frequent prescribed fires, in combination with necessary mechanical treatments can prevent hardwood tree species and other pines from encroaching and threatening to overtake the longleaf and make this species' habitat suitable for its own regeneration.

Our data indicate that there is no clear "zone of exclusion" under or around mature trees even though the spatial relationship between overstory trees and saplings has been approved to be repulsive at all spatial scales (e.g., 0∼30 m) tested. The distances between saplings and overstory trees follow a unimodal distribution, and approximately 15% of sapling recruitment was found to be within one crown radius (∼3.6 m) of an overstory tree stem (i.e., under the dripline) and additional 34%, 26%, 16%, and 8% of saplings to be within the "ring" of from second to fifth crown radius (7.2 ∼18 m). Therefore, if the goal of management is to recruit trees into the overstory, the optimal gap size appears to be 1∼2× crown widths beyond the dripline of the nearest overstory trees. In efforts to promote natural regeneration of this critical species, land managers can refer to the results of this study to inform their selection of appropriate management techniques.

Funding

Partial funding support for this study came from the US Department of Agriculture National Institute of Food and Agriculture's McIntire Stennis fund (project No. ALAZ00065) and Hatch fund (project No. ALA0031-1-17108) through the Alabama Agricultural Experimental Station.

Contributions

Fan analyzed the data and wrote the manuscript. Moser revised the manuscript. Poyner, Yang, and Nepal collected field data and formatted some figures and texts. Kush and Lauer provided guidance in field data collection and reviewed the manuscript.

Acknowledgements

This work originated from Poyner's thesis work. Lin Fan from Stanford University reviewed the manuscript. The constructive comments from two anonymous reviewers improved the revised version of this manuscript. We thank them all.

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