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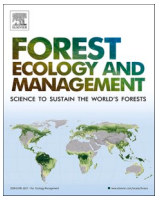

Plant growth forms influence sandhill longleaf pine regeneration

Seth W. Bigelow [a,*], J. Kevin Hiers [b], Scott Pokswinski [c], Douglas P. Aubrey [d], E. Louise Loudermilk [e], Joseph J. O'Brien [e]

[a] Tall Timbers Research, Inc., 13093 Henry Beadel Road, Tallahassee, FL 32312, USA
[b] Texas A&M Natural Resources Institute, 1747 Pennsylvania Ave., NW, Suite 400, WA, D.C. 20006, USA
[c] New Mexico Consortium, 4200 W. Jemez Rd., Los Alamos, NM 87544, USA
[d] University of Georgia, Warnell School of Forestry and Natural Resources, Savannah River Ecology Laboratory, Aiken, SC 29802, USA
[e] United States Department of Agriculture, Forest Service, Southern Research Station, 320 E. Green St., Athens 30602, Georgia

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ABSTRACT

Longleaf pine researchers have quantified many aspects of regeneration, growth and yield, but have focused on productive sites such as pine flatwoods and upland pine. Sandhill longleaf pine woodlands represent >40 % of remnant stands of longleaf pine ecosystems; most have no history of agriculture due to poor site productivity, yet many have been degraded by resin collection, grazing and fire exclusion. Restoration of structure and function of sandhill longleaf pine depends on understanding early stand-development processes, which are governed by fire, propagule availability, and competition from a range of overstory tree species not limited to longleaf pine. We analyzed a 16-year monitoring dataset from Eglin Air Force Base in northwest Florida, USA, focusing on how four tree growth forms influenced longleaf pine juvenile stages of seedling and sapling numbers and ingrowth to the subadult size class. Analyses were done with generalized linear mixed models using Poisson, normal, or negative binomial error distributions according to the response variable.

Restoration activities were effective at reducing numbers of sapling evergreen hardwoods, and basal area of overstory sand pine and other non-longleaf conifers was reduced by 35 % over the 16-year study. We observed threshold values for adult longleaf pine effects on seedlings and ingrowth; seedling numbers were maximized at 7.8 m^2/ha, and ingrowth was maximum at 5.1 m^2/ha. Seedling density was strongly governed by mast year. Sand pine, an invasive native pine, was detrimental to longleaf pine at all juvenile life stages even at low basal area. Deciduous oaks, which have been observed to facilitate longleaf pine seedling establishment, instead facilitated ingrowth to the subadult size class. Evergreen hardwoods, which may dampen fire behavior, only decreased longleaf pine density at the sapling stage. Ongoing silvicultural restoration activities should continue to focus on frequent fire and sand pine removal; deciduous oaks should be retained for their facilitative value; and removal of evergreen hardwoods should not be a high priority as long as prescribed fire can propagate in these lower productivity sites.

1. Introduction

Longleaf pine (*Pinus palustris* Mill.) ecosystem restoration has been a major public and private initiative in recent decades (Noss, 1989, Landers et al., 1995), and restoration projects can benefit from greater understanding of early stand development processes as they apply to varying community types (Mitchell et al. 2009). Longleaf pine community types include upland, montane, flatwoods, and sandhill (Boring et al., 2017). Sandhill, a distinctive community which develops in deep sand ridges, is the most nutrient-poor and arid of these community types; the stress-gradient hypothesis predicts that positive, facilitative interactions should be common in such plant communities (Maestre et al., 2009). Indeed, interspecific facilitation has been found in sandhill longleaf woodland (Wahlenberg, 1946, Loudermilk et al., 2016, Johnson et al., 2021), but these studies were limited in range of longleaf pine life stages and/or the number of plant life forms investigated. We use data from a large-scale, long-term restoration project in sandhill longleaf pine woodland to understand how a range of plant life forms influences growth of juvenile longleaf pine.

Arboreal plant life forms in sandhill beyond longleaf pine include

* Corresponding author.
E-mail address: sbigelow@talltimbers.org (S.W. Bigelow).

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other conifers such as the invasive Choctawhatchee sand pine [*P. clausa* (Chapm. ex Engelm.) Vasey ex Sarg. var. *immuginata* D.B. Ward], deciduous oaks such as turkey oak (*Q. laevis* Walt.), and evergreen hardwoods such as sand live oak (*Q. geminata* Small). Interactions among juvenile longleaf pine and these other sandhill plant life forms are deduced from spatial relationship and other kinds of evidence and are likely mediated in part by fire. Sand pine has small needles which form a dense, tightly packed forest floor which burns poorly and can prevent longleaf pine seeds from contacting bare mineral soil which they require for establishment (McCay and Parker, 2001). Turkey oaks are commonly found in association with longleaf pine seedlings (Johnson et al., 2021); proposed mechanisms include protection of seedlings from the high heat release of burning longleaf pine litter by cooler-burning hardwood litter (Kane et al., 2008), and thermal buffering by shade cast by hardwoods (Loudermilk et al., 2016). Sand live oak has not been the subject of laboratory burning studies but leaves of its relative coast live oak (*Q. virginiana* Mill.) burn less readily and often produce unburned areas which limit establishment opportunities for longleaf pine (Kane et al., 2008). Although the influence each of these three plant life forms on longleaf pine is broadly recognized, how the influence may change across the early life stages of longleaf pine is not known.

Here, we examine factors that influence early life stages of longleaf pine as they pass from seed to seedling to sapling to subadult. We use monitoring data from a 16-year study on pristine and degraded longleaf pine stands on the dry, infertile soils of a sandhill longleaf pine woodland; the study area underwent restoration treatments during the study. We focus on the roles that competing vegetation (intra-specific and from other plant life forms) play on regulating transitions between life stages (Fig. 1). We hypothesized that deciduous oaks would benefit longleaf seedlings but would become competitors to older life stages and that sand pine and evergreen hardwoods would be detrimental to all longleaf pine juvenile life stages. We also addressed hypotheses suggested by principles of tree population dynamics of frequent-fire forests: first, that fire would be beneficial to all longleaf pine juvenile life stages; second, that high densities of longleaf pine in the preceding developmental stage would be correlated with high densities in the succeeding one; and third that adult longleaf pine would be beneficial at low density and detrimental at high density for juvenile longleaf pine at all life stages. The objective was to learn how factors under the control of managers (e.g., fire, competing vegetation) might be manipulated to improve restoration outcomes in a sandhill longleaf pine woodland.

2. Methods

2.1. Study site

Eglin Air Force Base (AFB), located on Florida's western panhandle, has ~1500 km^2 of sandhill longleaf pine woodland. Gently rolling hills, 0–60 m above sea level, are dissected by steephead drainages where clay-rich layers of the Alum Bluff Group inhibit drainage of water (McCay, 2000). Average annual precipitation is 1640 mm; ca. 40 % falls during summer in convection thunderstorms. Soils are predominantly of the Lakeland series, which are deep, coarse textured, rapidly draining sands classified as typic Quartzipsamments (Provencher et al., 2001a).

The longleaf pine community type is classified as xeric or sandhill (Myers, 1990). Compared to upland (also known as clayhill) and flatwoods longleaf communities, sandhill longleaf has smaller trees, lower productivity, and lower fuel bed continuity (Fig. 2). Like other longleaf pine community types, sandhill longleaf pine regeneration is episodic and driven by infrequent seed years (Guo et al., 2016). Sand pine is the

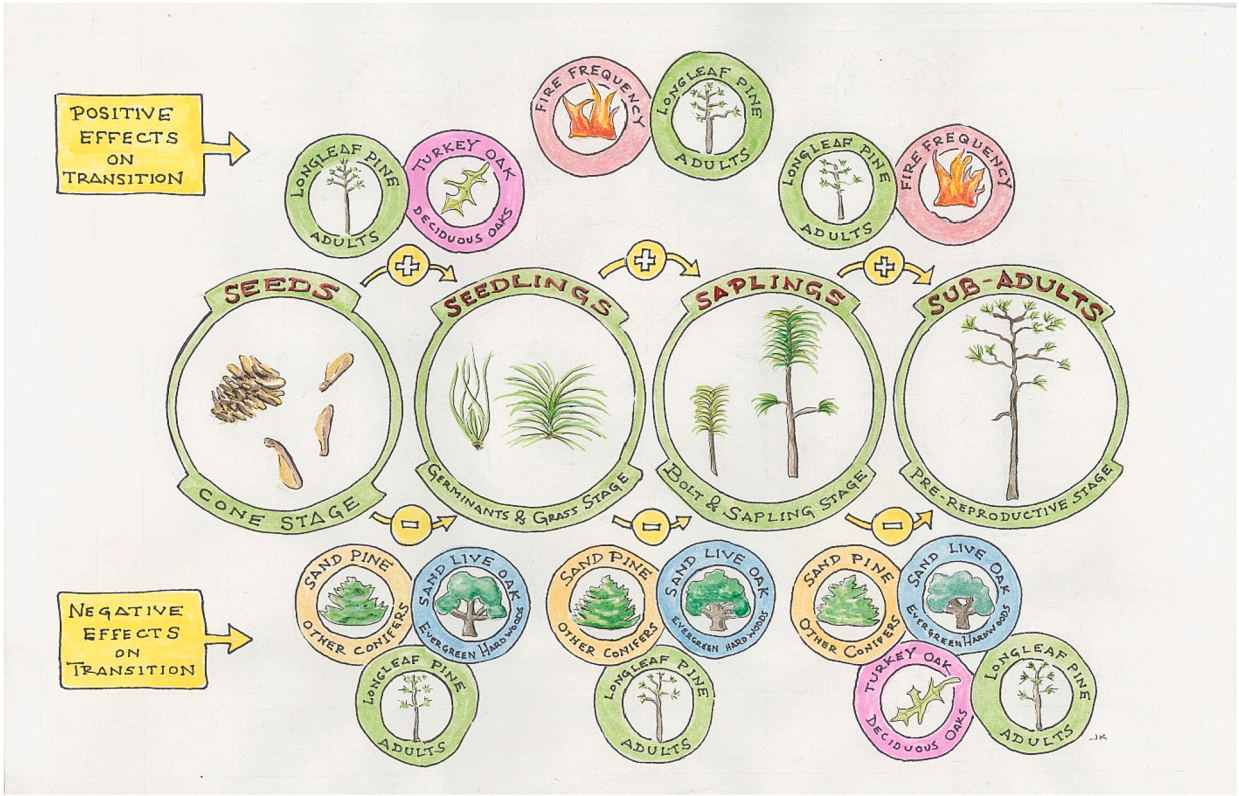

Fig. 1. Hypothesized effects of factors influencing progression of sandhill longleaf pine through seed, seedling, sapling, and sub-adult life stages. Adult longleaf pine is hypothesized to have a positive effects at low density and a negative effect at high density for all life stage; other conifers, especially sand pine, are hypothesized to have negative effects for all life stages; deciduous oaks like turkey oak are hypothesized to have positive effects at early life stages and negative effects at later ones; and evergreen hardwoods are hypothesized to have negative effects. The influence of fire frequency is hypothesized to be positive after the transition from seed to seedling (illustration by Jack Kruse).

Fig. 2. Photograph of sandhill longleaf woodland at Eglin AFB in northwest Florida, USA, several days after a prescribed fire in March 2023. Note bare mineral soil near turkey oak (left foreground), dark incompletely burned duff near evergreen hardwoods (center background), and bolting juvenile longleaf pine (center midground; photo Seth W. Bigelow).

second most common conifer and has been the subject of removal efforts at Eglin AFB (Provencher et al., 2000). Common hardwood trees at Eglin AFB include deciduous or briefly deciduous oaks characteristic of sandhill such as turkey oak and sand post oak [*Q. margaretta* (Ashe) Sarg.]; nomenclature follows Wunderlin and Hansen (2011). The evergreen sand live oak is common as a large mature tree; other evergreen hardwoods, often restricted to a smaller stature by frequent fire, include persimmon (*Diospyros virginiana* L.) and black cherry (*Prunus serotina* Ehrh.). There are also oaks characteristic of mesic habitat such as hardwood hammocks such as laurel oak (*Q. laurifolia* Michx.) and water oak (*Q. nigra* L.). The ground flora consists of graminoids including wiregrass (*Aristida stricta* Trin. & Rupr.), broom sedge (*Andropogon virginicus* L.), and little bluestem [*Schizachyrium scoparium* (Michx.) Nash]; low shrubs such as gopher apple (*Licania michauxii* Prance); and forbs like goat's rue [*Tephrosia virginiana* (L.) Pers.](Rodgers and Provencher, 1999).

Historic fire regimes in longleaf pine – wiregrass types in the southeastern USA consisted of frequent low-intensity fire (Rother et al., 2020); woodlands of Eglin AFB likely were formed in this type of fire regime. These lands underwent fire suppression and exclusion starting in the early 1900s, when they were known as the Chickasawhatchee Unit of the Florida National Forest, through the early 1970s (McCay, 2000). Since Eglin AFB was established in 1940 as a bombing and artillery range the land has experienced periodic fire, mostly unintentionally via aerial ignitions. Prescribed fire management began in 1972 and fire application intensity increased in 1999. Currently, Eglin AFB is divided into burn units from 1 ha to 1500 ha. Since 2000, most fires at Eglin AFB have occurred in February (Fig. 3), and the fewest fires have occurred in September.

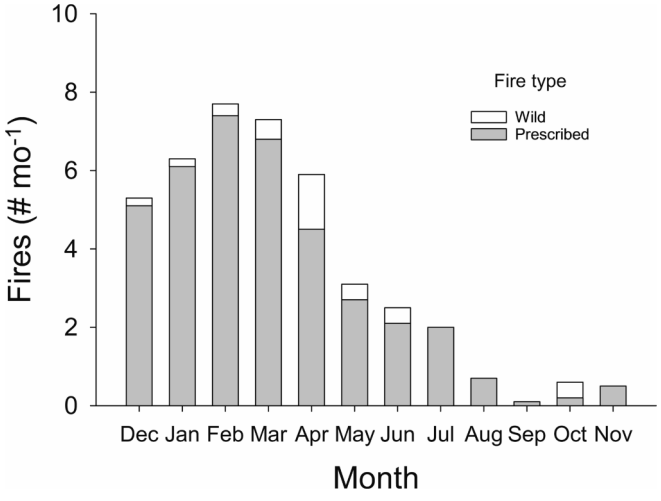

Fig. 3. Mean number of fires per month at Eglin AFB in northwest Florida, USA, from 2000 to 2016; includes wildfires (9% of total) and prescribed fires (Data courtesy of Eglin AFB natural resources management staff).

2.2. Plot establishment and monitoring

Our study relied on existing variation in stand structure, and variation caused by management actions, to infer effects of predictor variables such as basal area of overstory tree functional groups. Studies such as ours which involve manipulations but lack a formal design have been classified as non-observational, quasi-experimental (Cunningham and Lindenmayer, 2017). The present study included pristine reference areas without a history of fire exclusion and with little hardwood midstory or sand pine, and degraded areas in which fire exclusion had allowed a dense hardwood midstory and/or substantial numbers of sand pine trees. We did not distinguish between pristine and degraded areas in experimental analyses.

Large (0.64 ha) vegetation plots were placed at random within naturally regenerated longleaf pine stands which were distinguished from planted pine stands using aerial imagery. Our study used 120 large plots in sandhill (Dell et al., 2017); 15 of these plots were in areas classified as pristine. Median fire return interval for the plots was 3.2 years from 2000 through 2015. A system of smaller nested plots was

developed based on Peet et al., (1998; see figure in Hiers et al., 2007). Large plots were oriented north–south; dimensions were 106 m × 60 m. Three 20 m × 50 m (0.1 ha) sample-units were oriented west-to-east in the northern, central, and southern portion of the large plot. A 5 m × 50 m (0.025 ha) belt transect was established in the northern and southern 0.1 ha sample-units. A 20 m × 20 m (0.04 ha) area in the central 0.1 ha sample-unit was composed of four 10 m × 10 m (0.01 ha) modules. Two 1 m × 1 m sub-quadrats were established in each 0.01 ha module.

Longleaf seedlings were defined as <1.4 m tall and included individuals in germinant, grass, and early bolting stages. These were tallied in the eight 1 m^2 sub-quadrats. An average 3.6 (1.7 standard deviation) surveys per plot were carried out from 2000 through 2015. Saplings (pines with *dbh* of >0 cm to <10 cm and hardwoods with *dbh* of >0 cm to <16 cm) and larger sand pine were enumerated in the 0.1 ha sample-units. Longleaf pine was surveyed in all three 0.1 ha sample-units, and other species were surveyed in the central 0.1 ha sample-unit and the northern and southern 0.025 ha belt transects. Saplings of longleaf and other pines were identified to species and tallied in *dbh* intervals of 0 cm to 5 cm and 5 cm to 10 cm. Hardwoods were tallied in the same intervals plus a 10 cm to 16 cm *dbh* interval. Sand pine was tallied in 5 cm *dbh* intervals to 40 cm, a 40 cm to 47.5 cm *dbh* interval, and a >47.5 cm *dbh* interval. Surveys of 0.1 ha sample-units were done more frequently and at different times than surveys of the 0.64 ha plots. Pines ≥10 cm *dbh* (except sand pine) and hardwoods ≥16 cm *dbh* were surveyed in the large 0.64 ha plots; trees were identified to species, measured for *dbh* with a tape, and tagged. Tree coordinates were obtained from GPS (±2 m accuracy). From 1 to 4 (mean 1.7) overstory censuses were done on each plot through 2015. Censuses were often done after a management activity such as prescribed fire or midstory removal. Trees ≥10 cm *dbh* detected after the first census in each plot were classified as ingrowth.

Trees other than longleaf pine in overstory plots were classified in 3 functional groups: 1) pines and other gymnosperms ("other conifers": sand pine, southern red cedar (*Juniperus virginiana* var. *silicicola* (Small) E. Murray), slash pine (*P. elliottii* Engelm.), pond pine (*Pinus serotina* Michx.), loblolly pine (*Pinus taeda* L.), and pond cypress (*Taxodium ascendens* Brongn.); 2) deciduous oaks: turkey oak, sand post oak, southern red oak (*Q. falcata* var. *falcata* Michx.), bluejack oak, blackjack oak (*Q. marilandica* Muench.), and Arkansas oak (*Quercus arkansana* Sarg.); and 3) evergreen hardwoods such as sand live oak and other hardwoods such as persimmon and black cherry.

Estimates of cone crop were provided by USDA-Forest Service, Southern Research Station (Guo et al., 2016). In April of each year, binocular counts were done on adult longleaf pine trees to enumerate green cones that would drop seed in the fall. Surveys were done in several locations at Eglin AFB which were not co-located with the plots of the present study. The data set comprised 52 trees and dated to 1995.

2.3. Stand structure metrics

Stand structure metrics were calculated to facilitate comparisons with other longleaf pine woodlands, to document the impact of restoration actions, and to provide a benchmark for future management actions. We used Reineke's (1933) stand density index (SDI_r) to improve upon stand basal area as a description of occupied space. The metric version takes the form

$$SDI_r = TPH \bullet (Dq/25)^{1.6}$$

where *TPH* is stem density (trees ha^{-1}), and *Dq* is quadratic mean diameter (cm). SDI_r was designed for use in even-aged stands but an additive version

$$SDI_a = \frac{1}{25}\frac{1}{A}\sum_{i=1}^{n} D_i^{1.6},$$ where D_i, is diameter of the i^{th} tree and *A* is plot area, is more appropriate for uneven or mixed stands (Shaw and Long, 2007). We calculated SDI_a for the study stands and calculated a stand complexity index (*SCI*) based on the ratio between the two SDI formulations which diverge as diameter distributions increase in complexity (Ducey, 2009). The index

$$SCI = 1 - (SDI_a/SDI_r)$$

takes minimum values of zero for uniform stands and a maximum value of 0.14 for stands with highly irregular diameter distributions. Inner-bark volume of longleaf pines was estimated from allometry based on height and *dbh* (Gonzalez-Benecke et al., 2014).

2.4. Statistical analysis

Inferential statistical models were developed to find the factors that predicted longleaf pine seedling density, sapling density, and ingrowth to the ≥10 cm *dbh* size class. We tested whether longleaf seedling density was influenced by cone count in the previous spring, or basal area or sapling density of four tree functional groups. We used sapling density rather than sapling basal area as a predictor variable because longleaf pine seedlings are more sensitive to sapling density than sapling basal area (Loudermilk et al., 2016). We used x-y coordinates to select adult trees in 30 m x 30 m square areas that were centered on the area where seedlings were counted. Basal area of adult longleaf pine, scaled by division of 10, was entered in the model as a 2nd-degree polynomial to test the hypothesis that high levels of longleaf basal area would inhibit seedling density. We used the most recent tree survey data available as predictors in any given year.

2.4.1. Seedlings

We applied a generalized linear mixed model in which 0.64 ha plot was the random variable (Bolker et al., 2009). A negative binomial error probability density function was used because of the right-skewed frequency distribution of the seedling data and because many plots lacked seedlings. A log-link function was used to ensure that the response variable was linear. The form of the fixed effects of the statistical model was

$$\log(D) = B_0 + B_1 \bullet cc + B_2 \bullet ll + B_3 \bullet ll^2 + B_4 \bullet oc + B_5 \bullet eh + B_6 \bullet do + B_7 \bullet mll + B_8 \bullet moc + B_9 \bullet meh + B_{10} \bullet mdo,$$

where *D* is seedling density (# m^{-2}) and *cc* is cone count in previous spring (# per tree, scaled by dividing by 10). Basal area of functional groups is indicated by *ll* (longleaf pine), *oc* (other conifers, mainly sand pine), *eh* (evergreen hardwoods, mainly sand live oak), and *do* (deciduous oaks, mainly turkey oak). Stem density (# 100 m^{-2}) of saplings (0< *dbh* <10 cm) of the same groups is denoted by *m* to indicate midstory.

Seedling counts from the eight sub-quadrats were averaged and rounded to the nearest whole number to meet the assumptions of the negative binomial distribution. The sample consisted of 417 observations. The likelihood function in the generalized linear mixed model was integrated with Gauss-Hermite adaptive quadrature, and maximum likelihood was found with the *EM* algorithm (Wu, 1983, Pinheiro and Chao, 2006). Analyses were done with the *GLMMadaptive* package in the *R* statistical program (Rizopoulos, 2012, R Development Core Team, 2018). A probability of type I error of 0.1 was used as the threshold for statistical significance.

2.4.2. Midstory/Saplings

Density of sapling (0< *dbh* <10 cm) longleaf pine in the three 0.1 ha sample-units was averaged to provide a single value per plot (units of stems 0.1 ha^{-1}) for each survey. We tested for influence of basal area of longleaf pine, other conifers, deciduous oaks, and evergreen hardwoods in the 0.64 ha overstory plot, and for density of saplings in the 0.1 ha sample units. We tested the influence of number of fires since the previous survey.

Variables were entered in a linear mixed model with plot and survey year as random effects and with Normal error structure. The statistical model was

$$J = B_0 + B_1 \bullet ll + B_2 \bullet oc + B_3 \bullet do + B_4 \bullet eh + B_5 \bullet mll + B_6 \bullet moc + B_7 \bullet meh + B_8 \bullet mdo + B_9 \bullet fires,$$

where J is sapling density (in # 0.1 ha^{-1}), *ll*, *og*, *eh* and *do* are basal areas as described for the seedling analysis, *fires* is number of fires that occurred during the survey interval, and B_0 through B_9 are parameters that are estimated from the data. Seven high values of J (mean 114 per 0.1 ha^{-1}) were weighted by changing to 50 per 0.1 ha^{-1}. Analyses were done in the *lme4* R package (Bates et al., 2015).

2.4.3. Ingrowth

Longleaf pine trees reaching 10 cm *dbh* between sampling periods were classified as ingrowth; we analyzed ingrowth numbers per 0.64 ha plot recorded in the second and third overstory surveys and one fourth survey. We asked whether ingrowth was affected by basal area of overstory trees of four functional groups and numbers of fires between surveys. We used a generalized linear model with a Poisson probability density function and a log link. Poisson probability was used because the response variable, number of ingrowth stems per survey in a plot, was an integer and variance increased with the mean. No random effect was modeled because more than half of ingrowth records consisted of a single observation from a plot. Basal area of overstory trees was modeled identically to the seedling analysis, and we omitted the density of saplings because of the low probability that small trees would affect the growth of larger ones. The statistical model was

$$log(I) = B_0 + B_1 \bullet ll + B_3 \bullet ll^2 + B_4 \bullet oc + B_5 \bullet do + B_6 \bullet eh + B_7 \bullet ll + B_8 \bullet fires,$$

where I is ingrowth (0.64 ha)$^{-1}$, and other symbols are as described above. The *glm* function in base *R* was used.

3. Results

3.1. Stand structure

Mean basal area at the beginning of monitoring between 2000 and 2003 was 9.5 m^2•ha^{-1} (standard deviation 6.8), and mean stem density was 217 (194) ha^{-1}. Mean stand density index (SDI_a) was 148 (67), and mean structural complexity index (*SCI*) was 0.029 (0.011). Mean inner bark volume of longleaf pines was 38.7 (28.0) m^3 ha^{-1}. A Gingrich-style stocking diagram based on *SDI* for stocking guidelines indicated that 96 % of stands were below the B-line and would be classified as understocked from a timber production perspective (Fig. 4).

Longleaf pine was the dominant species, making up 61 % of basal area (Table 1). Other conifers was the next most dominant group (20 % of basal area), 88 % of which was composed of sand pine. The high coefficient of variation of other conifers, 290 %, indicates the patchy distribution of sand pine. Evergreen hardwoods had the next highest mean basal area (12 % of total), and deciduous oaks had the smallest basal area (7 % of total). Mean basal area of overstory trees changed little during the 16-year monitoring period except for sand pine and other non-longleaf conifers which declined by 36 % (Fig. 5A).

In contrast to overstory basal area, sapling density changed markedly during the study: longleaf pine sapling density increased but sapling density of the other groups decreased (Fig. 5B). Evergreen hardwood midstory stem density underwent the steepest drop, from 899 (1720) ha^{-1} in 2000 to 22 (84) ha^{-1} in 2015. Mean density of longleaf pine saplings was 67 (88) ha^{-1} in 2000, increasing to 105 (160) ha^{-1} in 2015. Other-conifer sapling density was 656 (1812) ha^{-1} in 2000, decreasing to 324 (697) ha^{-1} in 2015. Deciduous oak sapling density was 1126 (1309) ha^{-1} in 2000 decreasing to 734 (719) ha^{-1} in 2015.

3.2. Seedling density predictors

Seedling density varied from 0 to 35 m^{-2} (average of eight 1 m^2 quadrats). Elevated seedling counts occurred in the year after masting events (indicated by cone counts, Fig. 6A) at ~3-year intervals; few seedlings were seen in years that did not follow masting events (Fig. 6B). Consequently, cone count in spring of the prior year was a highly

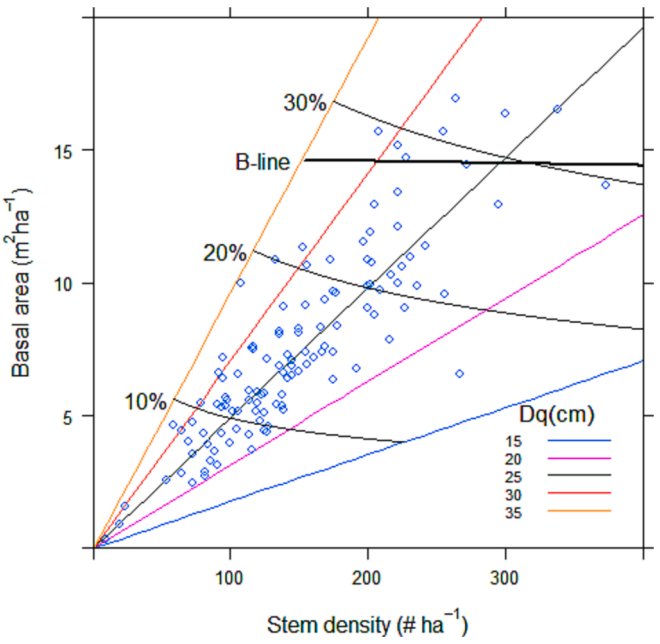

Fig. 4. Stand basal area (blue circles; includes all species) versus stem density for longleaf woodland on deep sand soils in northwest Florida, USA, with superimposed Gingrich-style stocking diagram. Colored rays extending from origin indicate quadratic mean diameter (*Dq*) ranges, curved black lines indicate stocking based on Reineke's stand density index (SDI_r) and maximum SDI of 1000, and B-line is the theoretical onset of full site-occupancy.

Table 1
Structure of longleaf pine woodland on deep sand soils from surveys at Eglin Air Force Base from 2000 to 2003, based on pines ≥10 cm breast-height diameter (*dbh*) and hardwoods ≥16 cm *dbh*; values are means with standard deviation in parentheses.

Functional Group or species	Density (# ha^{-1})	Basal area (m^2 ha^{-1})	Height (m)	90th qtl Height (m)
Longleaf pine	103 (61)	5.77 (3.61)	15.9 (2.2)	19.4 (2.7)
Other conifers	67 (179)	1.92 (5.57)	13.8 (4.5)*	15.4 (5.4)*
Deciduous oaks	23 (29)	0.70 (0.82)	9.0 (1.5)	10.7
Evergreen hardwoods	24 (30)	1.11 (1.40)	10.5 (1.7)	12.9

* Does not include sand pine.

significant predictor of seedling density ($p < 0.001$; Table 2). The cone-count parameter estimate, $b_1 = 1.01$, indicates that if cones per tree were to increase from 10 to 20 and all other factors were constant, the predicted increase in seedling density would be 4.79 m^{-2} = exp(1.01 x 20/10) – exp(1.01 x 10/10); Fig. 7A. Longleaf pine basal area was a highly significant predictor: both terms in the second-degree polynomial were significant ($p < 0.1$); the basal area effect increased to a maximum at *BA* = 7.8 m^2/ha then decreased at higher values (Fig. 7B). The confidence interval for the maximum is 0.4 m^2/ha to 15.2 m^2/ha based on the formula for quotients involving error terms (Barry, 1978). The basal area of other conifers, primarily sand pine, in the overstory was negatively associated with longleaf pine seedling density ($p < 0.001$); even a small quantity of sand pine was associated with a dramatic decrease in longleaf seedling density (Fig. 7C). At maximum other-conifer BA of 15.6 m^2/ha the output from the predictive expression exp(B_4•*OC*) [Eq. 1] was 0.02, indicating a 98 % reduction of seedling density. Seedling density was not influenced by basal area of deciduous oaks or evergreen hardwoods, or of stem counts of midstory trees of these or other tree functional groups.

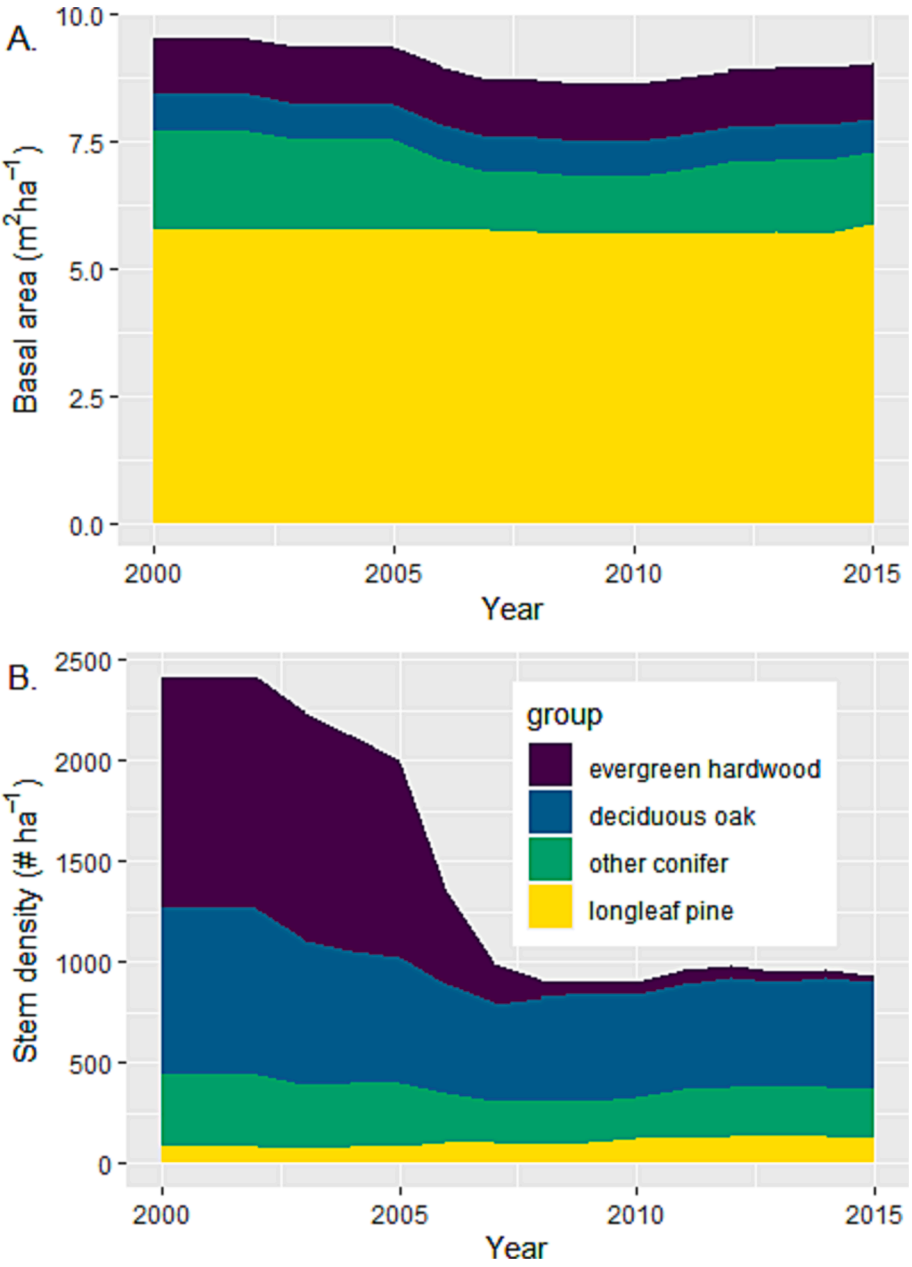

Fig. 5. Trends in four functional groups of trees during 15 years of restoration management at Eglin AFB in northwest Florida (annual averages from 120 plots; no growth was assumed to have occurred between surveys). A. Basal area of overstory trees (conifers, *dbh* ≥10 cm; hardwoods, *dbh* >16 cm). B. Stem density of mid-story trees (0< *dbh* ≤10 cm).

The generalized linear mixed model with negative binomial error structure used for the seedling analyses performed well. The marginal r^2 (r^2_m), which is due to fixed effects, was 0.46 and the conditional r^2 (r^2_c) which is due to fixed and random effects, was 0.65, indicating that the random effect of plot was responsible for a large portion of variance. A likelihood ratio test comparing models with Poisson error variance to models with negative binomial error supported use of the latter error structure ($p < 0.001$). Standard deviation of random effects for plot was 0.879, and dispersion parameter was estimated at 0.984, indicating that model error structure was appropriate.

3.3. Influences on longleaf pine saplings and ingrowth

Sapling (0 cm < *dbh* < 10 cm) longleaf pine density varied from 0 to 169 0.1 ha^{-1} (median 6, mean 10). Basal area of other conifers, mostly sand pine, and basal area of evergreen hardwoods, mostly sand live-oak, had negative effects on longleaf sapling density ($p < 0.1$; Table 3). A 1 m^2 ha^{-1} increase in other-conifer basal area was associated with a decrease in longleaf pine saplings of 0.29 0.1 ha^{-1}, and a 1 m^2 ha^{-1} increase in sand live-oak basal area was associated with a decrease in saplings of 1.65 0.1 ha^{-1}. No other factors, including overstory longleaf pine basal area and sapling functional group density, had a significant effect on longleaf pine sapling density. The general linear mixed model, which used sapling density as a response variable, had r^2_m of 0.07 and r^2_c of 0.65, indicating that fixed effects explained little variation compared to the random effects of plot and survey year.

A sample size of 84 plots was available for ingrowth detection because even though 120 plots formed the structure of the study, only 88 of these underwent two or more overstory surveys, and four of the 88 lacked sapling survey data. Longleaf pine ingrowth was sensitive to most of the influences tested (Table 4). Positive influences on ingrowth included density of longleaf pine saplings in the most recent midstory

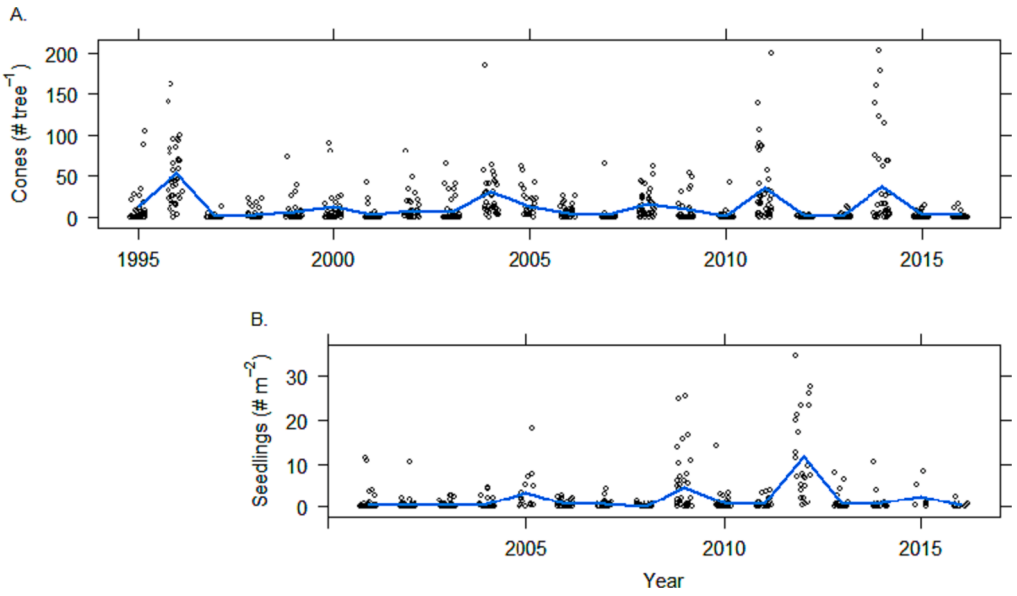

Fig. 6. Longleaf pine regeneration over time on sandhill at Eglin AFB, northwest Florida; lines connect negative-binomial means. A. Green cone counts in spring (data courtesy of D. Brockway and USDA-Forest Service Southern Research Station). B. Seedling counts in monitoring plots.

Table 2
Effect of previous year cone-count and neighboring vegetation on longleaf pine seedling density in sandhill longleaf pine woodland in northwest Florida, USA. Data are parameter estimates and 90 % confidence intervals for a generalized linear mixed model which incorporates basal area of longleaf pine in quadratic form. Other variables include basal area of other conifers (mainly sand pine), evergreen hardwoods (mainly sand live oak), and deciduous oaks (mainly turkey oak); and sapling stem density of these functional groups. Bold font indicates statistical significance at $\alpha = 0.1$ probability of type I error.

Effect	Estimate [§,†]	CI [†]
Intercept	**−2.04*****	**−2.78 – −1.30**
Cone Count	**1.01*****	**0.86 – 1.15**
Longleaf BA	**2.63*****	**1.25 – 4.01**
Longleaf BA^2	**−1.27*****	**−1.99 – −0.56**
Other conifer BA	**−1.23****	**−1.89 – −0.57**
Evergreen hardwood oak BA	−0.070	−0.09 – 0.23
Deciduous oak BA	−0.202	−0.425 – 0.022
Longleaf pine saplings	−0.028	−0.101 – 0.045
Other conifer saplings	0.005	−0.063 – 0.073
Evergreen hardwood saplings	−0.006	−0.024 – 0.011
Deciduous oak saplings	0.018	−0.013 – 0.050

§ * $p < 0.1$, ** $p < 0.01$, *** $p < 0.001$.

† Error structure is negative binomial and estimates are based on natural logarithm of response variable (i.e., a log-link function). Per-tree cone count and basal area of overstory tree functional groups (m^2/ha) were scaled by division by 10; sapling density units were individuals 100 m^{-2}.

survey; overstory longleaf pine at low basal area (< ~5 m^2 ha^{-1}); deciduous oak basal area; and number of fires since the previous survey (Fig. 8). Negative influences on ingrowth included overstory longleaf pine at high basal area (>5 m^2 ha^{-1}), and basal area of other conifers, mostly sand pine. This latter effect indicated that ingrowth stems per ha^{-1} rapidly approached zero as other conifer BA increased. Evergreen hardwoods, mostly sand live-oak, did not have a significant effect on ingrowth.

Mean and median time elapsed between overstory surveys was respectively 4.6 and 3 years. Thirty-seven plots had ingrowth, i.e., longleaf pine trees that grew into the ≥ 10 cm *dbh* class during the study. Maximum number of ingrowth stems in any survey was 40 0.64 ha^{-1}.

4. Discussion

Our long-term study of juvenile longleaf pine life stages on deep-sand soils confirmed some paradigms but also produced surprises. As expected, sand pine was devastating to juvenile longleaf pine, and adult longleaf pine were helpful to longleaf seedlings and ingrowth at low density and harmful at high density. The effect of turkey oak and other deciduous oaks across longleaf life stages, although beneficial, was the opposite of our prediction; their effect was not significant on early longleaf pine life stages and positive at later stages. The effects of sand live oak and other evergreen hardwoods, which we predicted to be negative at all juvenile life stages, were also surprising in that effects were non-significant except at the sapling stage. The results highlight the complexity of interaction between juvenile longleaf pine and other plant life forms as the pine cohorts progress through life stages.

Our study was subject to the limitations of non-observational, quasi-experimental studies (Cunningham and Lindenmayer, 2017). Plots were usually surveyed the year following management actions such as prescription burning or restoration thinning. This monitoring approach limited inferential power because of the absence of randomized, no-action controls. Large random effects due to plot, for longleaf pine saplings, imply that individuals persisted in the sapling size class over multiple censuses. Although this random effect of plot should not have biased the results, it suggests a lack of sensitivity in the sapling measurements.

4.1. Facilitative and competitive effects of other tree species

Facilitation of longleaf pine establishment by other plant species is an emerging paradigm in longleaf pine ecology (Wahlenberg, 1946, Loudermilk et al., 2016, Johnson et al., 2021). Regenerating pines in longleaf pine woodland are sometimes found clustered around mature hardwoods and away from mature pines (Magee et al., 2022). This spatial pattern of suggests longleaf pine establishment is facilitated by hardwoods and inhibited by excessive proximity of mature longleaf pines (Wahlenberg, 1946, Loudermilk et al., 2016, Johnson et al., 2021). Proposed mechanisms for such apparent facilitation include different energy release from burning litter (Williamson and Black, 1981); hydraulic redistribution of soil water by hardwoods (Espeleta et al., 2004); and different shading (Wright et al., 2015). This study on sandhill longleaf woodland at Eglin AFB, though, did not yield evidence for

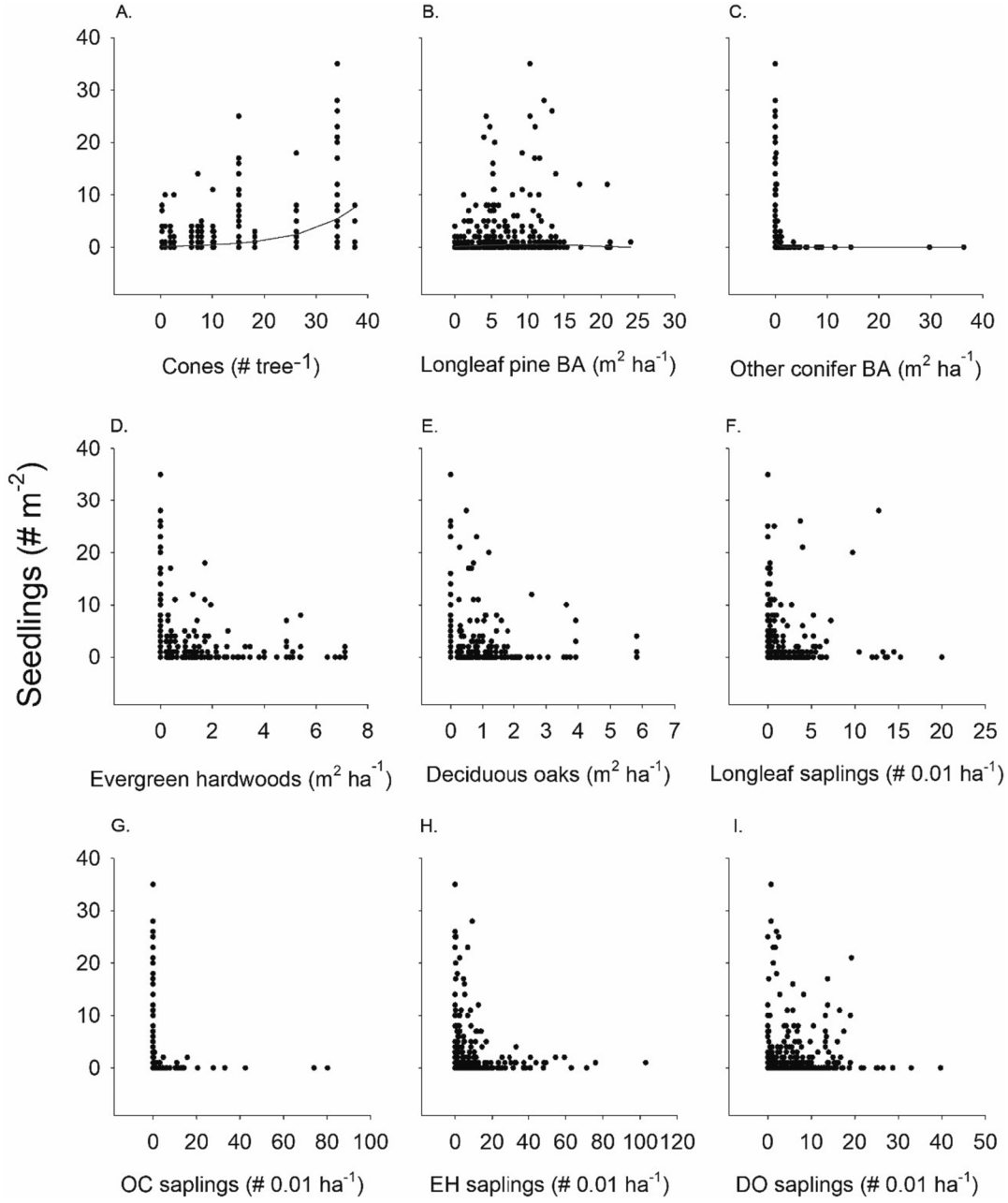

Fig. 7. Longleaf pine seedling counts with respect to other factors in sandhill longleaf pine in northwest Florida. Lines show predictions from a generalized linear mixed model with negative binomial error and a log link; predictions are only shown for significant ($p < 0.1$) factors. A. Cone counts per tree in preceding spring B. Basal area of overstory longleaf pine trees. C. Basal area of other conifers, mainly sand pine. D. Basal area of evergreen hardwoods, mainly sand live oak. E. Basa area of deciduous oaks, mainly turkey oak. F. Stem density of longleaf pine sapling. G. Stem density of other conifer saplings. H. Stem density of evergreen hardwood saplings. I. Stem density of deciduous oak saplings.

hardwood facilitation of longleaf pine during life-stage transitions other than ingrowth. The timing of our sampling may have some bearing on this discrepancy with other studies. Most of the seedlings we tallied were probably pre-grass stage, newly germinated from seeds dropped the previous autumn. Such seedlings are more sensitive to environmental conditions than seedlings in the grass stage (Grace and Platt 1995a). Because our field censuses were mostly conducted in late spring the demanding conditions of summer would not yet have produced the differential mortality that is the primary signature of facilitation. In contrast, the 1996 seed cohort studied by Provencher et al., (2001b) and Loudermilk et al. (2016) was measured in winter of 1997–1998 and would therefore have experienced facilitation. We conjecture, then, that facilitation of longleaf pine seedling establishment by deciduous oaks in longleaf sandhill may be a transient process that occurs mainly in the pre-grass stage seedlings and depends on subsequent summer drought.

The densely packed moist litter and deep shade under sand live oak is likely to prevent longleaf pine germination and establishment; sand live oak has thick unlobed leaves like its relative coast live oak whose leaves burn poorly (Kane et al., 2008). In contrast, hardwoods and sand pine can establish within the unburned zone (Guerin, 1993). By the same token the transition zone between the unburned and burned area around individual sand live oaks suggests the possibility of safe sites (Fig. 2; Rebertus et al., 1989). We conjecture that the lack of significant relationship between sand live oak and juvenile longleaf (other than the negative effect in the sapling stage) does not indicate an absence of influence. Instead, a negative effect directly under the crown of sand live

Table 3
Effect of tree growth form (basal area of adults and density of saplings) and number of fires since previous survey on density of longleaf pine saplings (0 cm < *dbh* < 10 cm) surveyed over 15 years in a sandhill longleaf pine woodland in northwest Florida, USA. Other conifers, mostly sand pine, and evergreen hardwoods, mostly sand live oak, were negatively correlated with longleaf pine sapling density. Bold font indicates statistical significance at α = 0.1 probability of type I error.

Effect †	Estimate §	90 % CI
Intercept	**13.9*** **	**10.4 – 17.3**
Longleaf pine BA	−3.48	−7.05 – 0.90
Other conifer BA	**−0.29***	**−0.566 – −0.006**
Deciduous oak BA	1.35	−0.19 – 2.88
Evergreen hardwood BA	**−1.65****	**−2.56 – −0.74**
Other conifer sapling density	−1.09	−2.64 – 0.45
Deciduous oak sapling density	−0.84	−2.05 – 0.34
Evergreen hardwood sapling density	0.45	−0.15 – 0.32
Number of fires	−0.54	−0.22 – 2.25

† The mixed statistical model used plot and survey year as random effects; error function was Normal. Basal area units of overstory tree functional groups was m^2/ha except for longleaf pine which was scaled by division by 10; sapling density units were individuals 0.1 ha^{-1}.

§ R_m^2 (fixed effects) = 0.07, R_c^2 (fixed and random effect) = 0.65; σ^2 = 36.43; standard deviation of random effect of plot = 7.59; of year, 1.75; residual, 6.036. Level of significance, * $p < 0.1$, ** $p < 0.01$, *** $p < 0.001$.

Table 4
Effect of tree growth form (basal area of adults), number of sapling longleaf, and number of fires since previous survey on ingrowth (trees reaching *dbh* ≥ 10 cm) of longleaf pine in plots surveyed over 15 years in a sandhill longleaf pine woodland in northwest Florida, USA. Other conifers are mainly sand pine, deciduous oaks are mainly turkey oak, and evergreen hardwoods are mainly sand live oak. Bold font indicates a significant parameter estimate at α = 0.1 probability of type I error.

Effect§	Estimate †	90 %CI
Intercept*	**−1.42**	**−2.32 – −0.523**
Longleaf sapling density***	**0.060**	**0.047 – 0.072**
Longleaf BA***	**0.600**	**0.315 – 0.885**
Longleaf BA^2***	**−0.058**	**−0.083 – −0.033**
Other conifer BA*	**−1.13**	**−2.11 – −0.41**
Deciduous oak BA*	**0.323**	**0.112 – 0.534**
Evergreen hardwood BA	−0.070	−0.234 – 0.095
Number of fires***	**0.146**	**0.080 – 0.212**

§ * $p < 0.1$, ** $p < 0.01$ *** $p < 0.001$.

† Estimates are for a generalized linear model with Poisson distribution and log link.

oak may be counterbalanced by a positive effect on the outer margin of the crown. Such conjecture requires explicit spatial study to be confirmed or refuted.

There were few longleaf pine seedlings in the vicinity of sand pines in our study. The sensitivity of predicted longleaf pine seedling numbers to the presence of sand pine was striking; the model predicted almost total failure of longleaf pine regeneration when sand pine was present at basal area of only ~2 m^2/ha. Essentially, stands with almost any amount of sand pine were virtually devoid of juvenile longleaf. We do not know for certain whether sand pines invaded first, subsequently preventing longleaf seedlings from establishing, but this sequence of events seems likely. Similarly, the mode of suppression of longleaf pine regeneration is not apparent but is probably a combination of densely packed litter that keeps longleaf pine seedling radicles from reaching mineral soil; and deep shade that leads to poor growth and high mortality of longleaf pine seedlings that may have been present prior to invasion. Sand pine stands at the study site can have basal area >20 m^2/ha (McCay and Parker, 2001). Presence of sand pine is indicative of long periods of fire suppression, and young sand pine may outcompete longleaf pine that germinate at the same time.

4.2. Longleaf pine intraspecific interactions

The early stages of seedling establishment are critical for determining the composition and cohort structure of the future stand. The tight coupling between cone production and seedling counts in the following year, and the periodic masting behavior (Guo et al., 2016), emphasized the origin of the seedling cohorts. Natural regeneration requires a seed source, and given the large size and limited dispersal distance of longleaf pine seeds (Boyer, 1963) we expected to find seedlings associated with mature trees. Seedling counts did display the predicted relationship with longleaf pine basal area: seedlings increased with increasing longleaf pine basal area up to a threshold then declined. Studies have identified a negative, repulsion-type spatial relationship between adult longleaf pine dominance (basal area) and numbers of seedlings and saplings (Grace and Platt 1995b, Brockway and Outcalt, 1998, Fan et al., 2021), and there is little documentation of the positive effects found in our study at low values. Others have suggested post-thinning residual basal area values of 7.5 m^2/ha to 9 m^2/ha for maximum seedling recruitment (Mitchell et al., 2006, Fan et al., 2021); these values may be regarded as thresholds. The threshold longleaf pine basal area, 7.8 m^2/ha, can be regarded as a tipping point beyond which increased stocking results in decreased regeneration although the wide confidence intervals surrounding this estimate indicate that the tipping point is not sharply defined. This tipping point is roughly half of the *B*-line at which full stocking is approached and intraspecific competition begins in stands of similar-age trees (Fig. 3; Shaw and Long, 2007). We interpret the rise in seedling counts as showing that more adult longleaf pine meant more seeds for seedling establishment. Transient facilitation may also be occurring: mature longleaf enhance survival of first year seedlings prior to application of fire (McGuire et al., 2001, Pecot et al., 2007).

At higher basal area, competition likely overwhelms any effects of seed source and intraspecific facilitation; several mechanisms may be responsible. Longleaf pine litter can adversely affect survival of longleaf seedlings by releasing energy during fire (Williamson and Black, 1981), but most of the seedlings we observed were probably in their first year and had not undergone burning based on the sampling protocol. Other possible mechanisms are competition for soil water and nutrients (Pecot et al., 2007) and excessive shading (Battaglia et al., 2002). Regardless of mechanism it was clear that mature longleaf pine suppressed seedlings once a basal area threshold was exceeded.

Sapling density is determined by many processes and factors including recruitment (i.e., height growth initiation of grass-stage seedlings), survival and ingrowth to the >10 cm *dbh* (i.e., subadult) height class. Longitudinal analyses have showed that adult longleaf pines decrease growth, recruitment, and survival of sapling longleaf pine (Rathbun and Cressie, 1994, Magee et al., 2022). Initiation of height growth of grass-stage longleaf pine seedlings is inversely correlated with pine overstory density (Knapp et al., 2013), so we expected higher counts of saplings with lower longleaf pine basal area. Nevertheless, there was no relationship between longleaf pine sapling density and overstory longleaf pine. Reasons for the lack of relationship could be that factors that contribute to recruiting seedlings to this size class are also responsible for recruiting saplings to the subadult size class, resulting in an equilibrium.

Ingrowth of saplings to the subadult (10 cm ≤ *dbh* < 30 cm) stage is sensitive to competition from overstory longleaf pine; for example, thinned longleaf pine stands show reduced ingrowth in any but the lightest residual overstory (e.g., basal area 2 m^2/ha; Boyer, 1993). Ingrowth was negatively spatially related to adult trees in a second-growth longleaf pine woodland in southwest Georgia (Cannon et al., 2022), and adult trees influenced growth of subadult trees in old-growth longleaf woodland (Rathbun and Cressie, 1994). In the present study findings were consistent with expectations, i.e., ingrowth increased at levels of adult longleaf pine basal area up to 5.1 m^2/ha and decreased at higher levels. The context of the present study led to slightly different

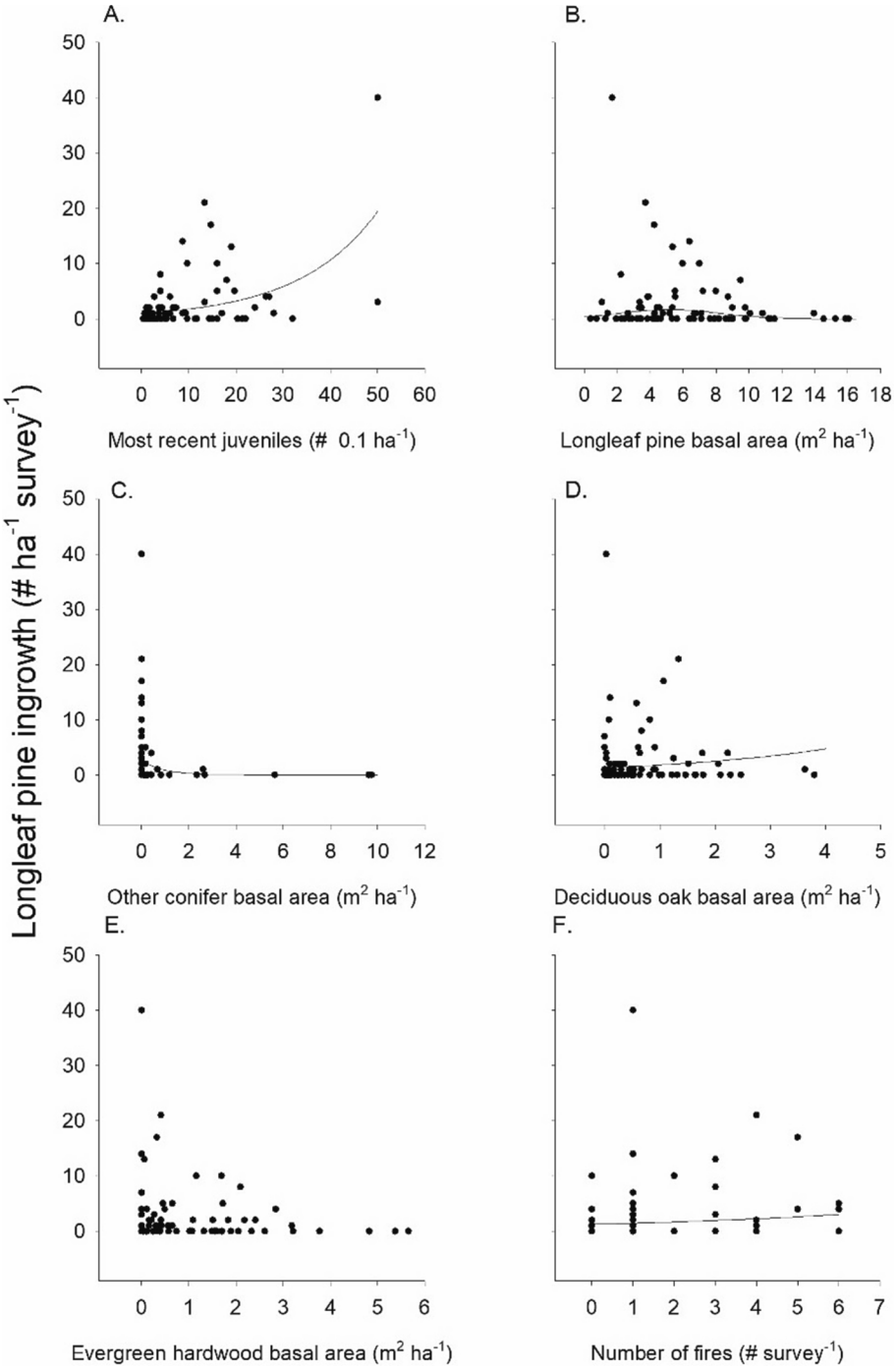

Fig. 8. Longleaf pine ingrowth (stems growing > 10 cm *dbh* in recent survey) in monitoring plots in longleaf pine sandhill in northwest Florida, USA, from 2000 to 2015. Lines show predictions from a generalized linear mixed model with Poisson error and a log link; predictions are only shown for significant ($p < 0.1$) factors. A. Saplings in most recent survey. B. Basal area of longleaf pine; prediction line shows a quadratic function. C. Basal area of other conifers, mainly sand pine. D. Basal area of deciduous oaks, mainly turkey oak. E. Basal area of evergreen hardwoods, mainly sand line oak. F. Number of fires since previous survey.

results than earlier studies; i.e., there is a positive relationship between adult longleaf BA (at low levels) and ingrowth because adult longleaf pines are necessary to produce the saplings whose transition to sub-adults constitutes ingrowth. Again, there is large uncertainty around this value.

4.3. Management implications: Restoration of sandhill longleaf pine woodland

Efforts to restore longleaf pine across its historic range are supported by federal, state, and non-governmental groups, who have put forth a goal of increasing longleaf pine woodland area from 1.4 million ha to 3.2 million ha (Regional Working Group for America's Longleaf, 2009). The extensive longleaf pine woodland at the study site was protected from conversion to other land uses, the fate of most longleaf pine woodland in the historic range, partly by the establishment of the Choctawhatchee Unit of the Florida National Forest in 1908 and then transfer to the Department of Defense in 1940 (McCay, 2000). Live-ammunition military exercises led to wildfires that helped to preserve longleaf pine woodland structure, but prescribed fire was not applied systematically

until 1972. Despite the early innovative prescribed fire program, considerable hardwood and off-site pine establishment occurred prior to the reinvigorated restoration program beginning in the 1990s (Provencher et al., 2001a). Our study took place against a backdrop of restoration activities undertaken by the natural resource managers of Eglin AFB from 2000 to 2015, and offers insights into silviculture and restoration.

Longleaf pine has wide ecological amplitude and achieves dominant status on many soils of the southeastern coastal plain under frequent prescribed fire regimes (Hedman et al. 2000, Boring et al., 2017). Threshold values for control of stand structure on regeneration processes are likely to differ on soils of varying productivity because of differences in tree allometry and ground cover. Mean longleaf pine basal area at the study site, 5.4 m^2/ha, was just above the value at which we estimated ingrowth was maximum (5.1 m^2/ha) but below the basal area threshold at which seedling production was inhibited (7.8 m^2/ha). Other basal area thresholds proposed for longleaf pine management include 7 m^2/ha value of maximum residual post-harvest density in planted stands to avoid inhibition of ingrowth while providing a seed source for regeneration and needle fuel for prescribed fire for hardwood control (Croker, 1973, Boyer, 1993). The present study, on deep-sand soils, suggests that the corresponding basal area thresholds for sandhill longleaf are lower than those suggested by Croker (1973) and Boyer (1993), whose thresholds were derived from studies on Ultisols with fine-texture subsurface horizons that result in higher productivity.

Silvicultural management often relies on residual basal area targets, but such absolute values have been criticized as providing less insight into stand conditions than stocking indices (Kara et al., 2017). Density management diagrams are a common tool for interpreting stand density and regeneration relationships (Jack and Long, 1996); the Gingrich-style stocking diagram applied in the present study depicts stocking as a proportion of a maximum stand density index (*SDI*). Stand density index combines number of trees and basal area, and expresses stand structure as equivalent number of 10 cm *dbh* trees per ha (Kush et al., 2006, Kara et al., 2017). Restored second-growth upland longleaf pine woodland on Ultisols with clay subsoil horizons had *SDI* of ~200 (Bigelow et al., 2021), compared to mean *SDI* of 148 in the deep-sand Entisols of the present study. The stocking index for the current study was based on the assumption of 100 % stocking at *SDI* = 1000 (Reineke, 1933). The vast majority of stands in the present study were below the *B*-line representing onset of full site occupancy; the *B*-line, however, has not been adjusted for the different allometry of trees on deep sand soils, raising the question of whether a stand density diagram tailored to sandhill longleaf should be developed because these trees tend to be shorter for a given diameter than trees on more fertile (e.g., soils of higher clay content in subsurface horizons) soils (Addington et al., 2006).

Longleaf pine forest maintained by frequent fire has a typically bimodal diameter distribution (Moser et al., 2002), and the longleaf pine woodland at Eglin AFB has strongly bimodal diameter distribution (Provencher et al., 2001b). The stand complexity index is a quantitative reflection of stem diameter distributions; stands with Normal diameter distributions have *SCI* of 0.01 and a simulated extreme bimodal diameter distribution has *SCI* of 0.14 (Ducey, 2009). Our data indicated that mean *SCI* in pre-treatment stands was 0.029, a value close to the 0.028 *SCI* of second-growth longleaf woodland in southwest Georgia managed with frequent fire and treated with removal of evergreen hardwoods (Bigelow et al., 2021). We did not estimate post-restoration *SCI* because we lacked complete surveys of stands after 15 years of restoration treatments. Our *SCI* value, then, represents a data point which may be used for comparison, e.g., where planted pines are being restored to diverse natural woodlands, a common scenario for longleaf pine.

The utility of retaining or recruiting isolated or small clusters of hardwoods in longleaf pine woodland continues to be debated among public and private land managers (Willis et al., 2023). Paucity of reference sites with uninterrupted fire regimes means that target species compositions are elusive; the effect of hardwoods on longleaf pine, therefore, is an important metric for guiding silvicultural actions. Our study largely supports the paradigm that deciduous oaks are potentially beneficial, and evergreen hardwoods may be detrimental, to longleaf regeneration in the demanding environment of deep sand soils (Hiers et al., 2014, Loudermilk et al., 2016). There are some differences with Loudermilk et al. (2016) who found facilitative effects of midstory deciduous hardwoods during the longleaf germinant phase, rather than facilitative effects of adult deciduous hardwoods during the longleaf ingrowth phase as in the present study. Still, deciduous oaks are an important functional component of longleaf sandhill woodlands whose preservation and retention should be included in management planning.

Evergreen hardwoods such as sand live oak are a minor component of reference condition longleaf sandhill at best, occurring as scattered individuals or clumps (Myers, 1990). Above-ground portions of small sand live oaks are readily killed by prescribed fire and large individuals or clusters may be a result of past periods of fire exclusion (Guerin, 1993). The small, moisture-absorbing senesced leaves of adult individuals create local fire-free zones which may allow persistence of plant species that are not adapted to fire but which may provide habitat benefits such as soft mast (Seth W. Bigelow, *personal observation*); unfortunately these fire-free areas may also have the undesirable effect of allowing reinvasion of sand pine (Guerin, 1993). Identification of threshold levels of evergreen hardwood encroachment that impede reintroduction of fire may help to diminish the application of expensive treatments such as mechanical removal or herbicide during restoration (Hiers et al., 2007, Kirkman et al., 2013). Implications of the present study are that to maximize longleaf pine regeneration, adult sand live oak should be removed, e.g., by girdling and herbicide, yet such an action would need to be undertaken cautiously in light of the potential wildlife habitat benefits of this species.

Unlike the evergreen hardwoods and deciduous oaks, sand pine and other conifers have an unequivocally negative impact on every life stage phase of juvenile longleaf pine (Provencher et al., 2000, McCay, 2001, Hiers et al., 2007). These studies and the present one support efforts to restore sandhill by sand pine removal. Monitoring plot data at Eglin AFB show that although progress was made in this regard over the 15 years of the study, more remains to be done particularly because of indications of a small increase in sand pine basal area during the latter years of the monitoring study (Fig. 5). Sand pine produce seed prolifically and are able to reproduce under closed canopies in the absence of prescribed fire, so frequent fire is essential for control (McCay, 2000).

The need for frequent prescribed fire in sandhill restoration is unquestioned (Gilliam and Platt, 1999, Kirkman et al., 2013, Shappell and Koontz, 2015) and the ability of longleaf pine to persist for many years in the grass stage is central to its fire ecology (Aubrey, 2021). Despite their adaptation to fire not all grass stage seedlings survive fire (Knapp et al., 2018), and recruitment from the bolting stage may also be adversely affected with very frequent fires (e.g., 1 to 2 y return interval; Ford et al., 2010). Mean fire return interval in the study was 3.2 years. We did not test the seedling stage and found no influence of fire on the sapling stage, but more frequent fires enhanced ingrowth to the subadult stage. Subadult longleaf pine are sensitive to overstory competition (Rathbun and Cressie, 1994, Curtin et al., 2020) and increased ingrowth could have arisen through fire-driven mortality of competing vegetation. Prescribed fire is the preeminent controlling process for these woodlands and should retain the highest priority among ecosystem management actions.

4.4. Conclusions

Restoration of structure and function of fire-excluded sandhill longleaf pine woodland depends not only on reintroduction of frequent prescribed fire but also managing the balance among plant growth forms other than longleaf pine. Our study, which was focused on life stages of juvenile longleaf pine and was based on monitoring during a 16-year period of restoration of the largest remaining sandhill longleaf pine

woodland, confirmed the value of removing sand pine and provided support for retaining deciduous oaks. Our study also supported the view that evergreen hardwoods can be detrimental to juvenile longleaf pine survival, yet we caution that wholesale removal of evergreen hardwoods may compromise other ecosystem values such as wildlife habitat. The thorough removal of juvenile evergreen hardwoods at the study site, implemented as part of restoration activities, may provide information on this idea as stand dynamics unfold in the future.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The data that has been used is confidential.

Acknowledgments

Dr. Dale Brockway of USDA-Forest Service, Southern Research Station provided data on cone counts. Eglin AFB natural resource management staff carried out restoration activities, conducted prescribed fires, maintained a data base of fire occurrences, and collected plot monitoring data.

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