

The path back: oaks (*Quercus* spp.) facilitate longleaf pine (*Pinus palustris*) seedling establishment in xeric sites

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Abstract. Understanding plant–plant facilitation is critical for predicting how plant community function will respond to changing disturbance and climate. In longleaf pine (*Pinus palustris* Mill.) ecosystems of the southeastern United States, understanding processes that affect pine reproduction is imperative for conservation efforts that aim to maintain ecosystem resilience across its wide geographic range and edaphic gradients. Variation in wildland fire and plant–plant interactions may be overlooked in “coarse filter” restoration management, where actions are often prescribed over a variety of ecological conditions with an assumed outcome. For example, hardwood reduction techniques are commonly deemed necessary for ecological restoration of longleaf pine ecosystems, as hardwoods are presumed competitors with longleaf pine seedlings. Natural regeneration dynamics are difficult to test experimentally given the infrequent and irregular mast seed events of the longleaf pine. Using a long-term, large-scale restoration experiment and a long-term monitoring data site at Eglin Air Force Base, Florida (USA), this study explores the influence of native fire-intolerant oaks on longleaf regeneration. We test for historical observations of hardwood facilitation against the null hypothesis of competitive exclusion. Our results provide evidence of hardwood facilitation on newly germinated longleaf pine seedlings (<2 yr old) after two mast seeding events (1996, 2011). Using regression-tree and Kaplan–Meier survival analyses, we found that deciduous oak midstory density was the most significant variable associated with longleaf pine seedling survival rates in the first 2 yr after germination. We found that as few as 43 oak midstory stems ha⁻¹ were sufficient to facilitate seedling survival, but as many as 1400 stems ha⁻¹ maintained facilitation without competitive exclusion of seedlings. We found that 1.5-yr-old pine seedlings were more moisture stressed under more open canopy conditions when compared to those immediately adjacent to a midstory oak canopy. Recognition that deciduous oaks are important facilitators of longleaf seedling establishment on xeric sites represents a significant departure from conventional wisdom and current management practices that has largely focused on competitive exclusion. This points to a critical role of a deciduous oak midstory of moderate densities for long-term ecosystem resilience in xeric longleaf pine ecosystems in light of climate uncertainty.

Key words: deciduous oaks; Eglin Air Force Base; Kaplan–Meier; longleaf pine; management; plant facilitation; regression trees; restoration; seed masting; turkey oak; xeric sandhill.

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INTRODUCTION

There has been a renewed focus on the role of positive interactions among species, such as facilitation in influencing community dynamics (e.g., Bruno et al. 2003). In fact, Brooker et al. (2008) proposed that the understanding of facilitation is critical for both ecological restoration and predicting how plant community function will respond to climate change. In the face of climate uncertainty, with potentially hotter temperatures, longer growing seasons, extended droughts (Cook et al. 2015), and more variable rainfall predicted (particularly in the southeastern United States, *sensu* Mitchell et al. 2014), understanding key processes that are responsible for maintaining foundation and keystone species will be critical for managing native biodiversity and restoring ecosystems (e.g., Ross et al. 2010). These ecosystem processes, which include wildland fire and plant–plant interactions, may be overlooked in “coarse filter” restoration management, where actions are prescribed over a wide range of conditions with an assumed ecological outcome.

In longleaf pine (*Pinus palustris* Mill.) ecosystems of the southeastern United States, hardwood reduction is commonly considered necessary for ecological restoration (Provencher et al. 2001*b*, Jose et al. 2006, Menges and Gordon 2010) and maintenance of native biodiversity. Hardwoods invade or are released from their shrub state in the absence of frequent fire, and their removal by chemical and mechanical methods is extensively used across a wide edaphic range of longleaf pine communities to increase native groundcover (Hiers et al. 2014) and promote pine regeneration success (Provencher et al. 2001*a,b*, Menges and Gordon 2010). This intensive hardwood removal is a top priority because of the focus on oak–pine competition (Pecot et al. 2007), where oaks reduce light availability for seedling growth (but see, for example, Stoddard 1931, Wahlenberg 1946). Given its widespread use, the conventional wisdom of removing midstory oaks—those typically less than 16 cm dbh—has the potential to affect the ecosystem’s resiliency in response to future novel climates by removing these native species that at least partly interact with pines through facilitation (e.g., Fig. 1, McGuire et al. 2001, Pecot et al. 2007).

Longleaf pine mast seeds regionally every 6–15 yr, therefore processes governing successful reproduction are critical to its persistence on the landscape and are linked to regional climate patterns (Koenig and Knops 1998, Pederson et al. 2000). The infrequent and irregular mast events have challenged experimental manipulations in understanding regeneration dynamics (Pecot et al. 2007). Studies of regeneration of this fire-tolerant species have concentrated on the effect of fire in preparing a microsite of bare mineral soil necessary for seedling establishment (Wahlenberg 1946, Jose et al. 2006). Longleaf pine occupies a wide edaphic gradient from hydric to xeric sites (Kirkman et al. 2004), but key processes at play along this gradient could differ substantially (Hiers et al. 2007, Veldman et al. 2013). For example, processes driving seedling establishment are much more critical to the persistence of longleaf pine on xeric sites because adults are capable of hydraulic lift and are less vulnerable to droughty conditions (Espeleta et al. 2004), but adults do create fuel conditions conducive to high fire intensity and long duration (Williamson and Black 1981) often intolerable to new recruits (Grace and Platt 1995). The native oak midstory, particularly turkey oak (*Quercus laevis*), has been found to be associated with longleaf pine regeneration, both natural (Wahlenberg 1946) and underplanted (Pecot et al. 2007), but as of yet, no studies have investigated the mechanisms of facilitation.

Although facilitation challenges fundamental competitive (e.g., niche) theories in ecology (Bruno et al. 2003), there is significant support for facilitative mechanisms within many plant communities around the world (Callaway et al. 2002, Brooker et al. 2008, de la Luz Avendaño-Yáñez et al. 2014). Facilitation often occurs under established plants where they act as nurses for new germinants, especially in harsh environments (Turner et al. 1966, Callaway 1992, Flores and Jurado 2003). These nurse plants have been found to create a more ideal microenvironment by reducing plant moisture stress (Vetaas 1992, Lloret et al. 2005, Sthultz et al. 2007) and creating more favorable soil conditions through hydraulic lift (Ludwig et al. 2003, Espeleta et al. 2004). There have been suggestions of facilitation in longleaf pine systems for some time (Wahlenberg 1946, Allen 1956, Boyer 1963, Rebertus et al. 1989, McGuire et al. 2001, Espeleta



Fig. 1. Example of facilitation of the oak midstory on longleaf pine regeneration. Picture taken Nov. 13, 2012 by author Loudermilk in a longleaf pine sandhills area of Eglin AFB, FL.

et al. 2004, Pecot et al. 2007), with evidence of facilitation by the overstory (McGuire et al. 2001, Pecot et al. 2007, Knapp et al. 2013). Several broad-scope longleaf pine ecosystem dynamic studies have presented several pieces to the puzzle, particularly in relation to the habitat structure and burning regime on seedling dynamics (e.g., Glitzenstein et al. 1995, Grace and Platt 1995, Provencher et al. 2001b), but none have directly tested a longleaf seedling facilitation hypothesis. As such, there has not been a study quantifying facilitation by oaks, nor examining potential mechanisms of facilitation of initial seedling establishment when seedlings are most sensitive to mortality (<2 yr old). We chose to focus on initial establishment and survival, since through time, other agents of mortality such as fire, disease, plant competition, and predation may obscure patterns driven by facilitation.

This study explores the influence of native oaks on longleaf pine regeneration and tests anecdotal observations of oak facilitation. If facilitation by oaks does occur, the concentrated removal of midstory oaks, as is often prescribed for the management of xeric longleaf sites, could compromise the recruitment of longleaf, a foundation species. The objective of our study was to determine if

midstory oaks facilitate survival of recently established longleaf pine seedlings (<2 yr old) on xeric sandhills in the southeastern United States. We analyzed two independent data sets after two separate mast seeding events that occurred in the years 1996 and 2011 at Eglin Air Force Base, Florida, USA. We also analyzed field measurements of 1.5-yr-old seedling moisture stress and environmental conditions (i.e., surface temperature, canopy openness, soil moisture) that identify mechanisms driving oak midstory facilitation.

METHODS

Study site

The study area is located on Eglin Air Force Base (EAFB) in southern Santa Rosa, Okaloosa and Walton counties in the Florida panhandle. EAFB sandhill habitats are characterized by xeric, well-drained Lakeland series soils. These sandhills are dominated by an open longleaf pine canopy with a hardwood midstory and understory not only made up of predominantly turkey oak but also blue jack oak (*Q. incana*), sand post oak (*Q. margaretta*), sand live oak (*Q. geminata*), and persimmon (*Diospyros virginiana*).

EAFB represents one of the largest remnant tracts of longleaf pine in the southeastern United States. These portions of EAFB were not subjected to agricultural disturbance and were not entirely logged at the turn of the 20th century, when most harvesting took place. Like many sites in the southeastern United States, fire suppression at Eglin began in the 1950s, but were only marginally successful due to military-caused fires. Nonetheless, these sites received less fire than is required to manage a healthy stand of longleaf, with each site averaging less than two fires in the 30 yr prior to 1994. No previous restoration had been conducted on this study’s experimental sites prior to 1994.

For this study, we focused on data from the two most recent seed mast years (1996, 2011) at EAFB. Mean cone production for years 1996 (88 cones per tree) and 2011 (65 cones per tree) was the highest on record since 1966 at EAFB (Brockway and Boyer 2014). Based on longleaf overstory density of 144–178 trees ha⁻¹ (from 1996 data below) and assuming 32 seeds per cone (average from Boyer 1990), we estimated that seed density was approximately 300,000–500,000 seeds ha⁻¹, or 30–50 seeds m⁻². Given these large seed densities and our large area sampled (77 0.5 m × 40 m belt transects = 20 m², or 1540 m² total) within each treatment (methods described below), we were able to minimize issues associated with spatial variability in overstory masting and seed dispersal across each treatment area.

1996 seed masting: sampling design and analysis

Long-term monitoring plots of vegetation characteristics were established in 1994 for a previous study (Provencher et al. 2001a, b), within five management units (blocks), using three treatments of hardwood removal (mechanical, chemical, and prescribed burning) and treatment control. The management units were relatively uniform in longleaf pine overstory density of 144–178 tree ha⁻¹, with two units having slightly higher productivity than the other three (Provencher et al. 2001a, b). Treatments included a burn only treatment with 20% removal of overstory and midstory hardwoods (‘burn only’, also see Hiers et al. 2007), a mechanical treatment with 99% removal of understory and midstory hardwoods (“mechanical”), a herbicide treatment using hexazinone with 90% removal of oaks (“chemical”), and a control with no hardwood removal (“control”). All hardwood

Table 1. Importance values (IV) of the top 20 significant input variables from the regression tree analysis of vegetation characteristics (density and BA: basal area) on longleaf pine seedling density (response variable) 1 yr after the 1996 seed masting event at Eglin AFB, FL.

Input variable	IV
Deciduous hardwood midstory density	15
<i>Quercus laevis</i> midstory density	12
<i>Quercus laevis</i> midstory BA	11
Deciduous hardwood midstory BA	10
Hardwood midstory density	10
Treatment	10
<i>Pinus palustris</i> overstory BA	7
Management Unit	4
Evergreen hardwood midstory density	2
<i>Ilex vomitoria</i> midstory density	2
<i>Ilex vomitoria</i> midstory BA	2
<i>Quercus geminata</i> midstory density	2
Evergreen hardwood overstory BA	2
<i>Quercus geminata</i> overstory BA	2
Evergreen hardwood midstory BA	2
Evergreen hardwood overstory density	1
<i>Ilex Ambigua</i> midstory density	1
<i>Quercus geminata</i> overstory density	1
<i>Pinus palustris</i> overstory density	1
Deciduous hardwood overstory density	1

reduction treatments were conducted in 1995 before seed release in Fall of 1996. At the time of masting and data collection for this study (next paragraph), only the ‘burn only’ treatment had received fire in the previous 10 yr. All hardwood reduction treatments were prescribed burned in 1997 after data collection (see next paragraph) with the exception of the control which were not burned until the end of the experiment in 2001. Experimental data and analysis are detailed in previous work (Provencher et al. 2001a, b, Kirkman et al. 2013).

In 1997 prior to burning but less than 1 yr after the 1996 seed masting event, 73 vegetation characteristics were measured (Provencher et al. 2001a, b), however, only 20 of these were relevant to the current work (Table 1). They included density and basal area (BA) of the overstory and midstory vegetation as well as density of longleaf pine seedlings. Longleaf pine seedlings were counted in 80 0.5 m × 40 m belt transects per treatment. To distinguish overstory species from midstory, all nonpine species with less than 16 cm DBH were classified as midstory while all pine species with less than 10.16 cm DBH were characterized

as midstory. Hardwoods and pines were identified by species as well as grouped as deciduous or evergreen hardwoods. Only two conifers were present: longleaf pine and sand pine (*P. clausa*). Data aggregation and density and basal area calculations are described in Kirkman et al. (2013).

We used a Classification and Regression Tree (CART) approach to analyze relationships between seedling density and vegetation characteristics. A CART analysis was chosen over a more traditional approach (i.e., multiple regression), as it is nonparametric and can be used for large complex data sets that have many independent, and possibly correlated variables (Breiman et al. 1984, De'ath and Fabricius 2000). Both continuous and categorical independent variables can be used in CART to explain model variation. CART models use a binary recursive partitioning approach, where the variation within and between variables is iteratively split into relatively homogeneous (low-deviation) terminal nodes, which then determine their predictive ability (Grunwald et al. 2009). A regression tree is used when the response variable is continuous and a classification tree is used when the response variable is categorical. We conducted a regression tree analysis using the "rpart" (v 4.1-5) package (Therneau et al. 2013) in the R programming language (v3.0.1, R Core Team 2013). Longleaf pine seedling density was used as the response variable, while all other 73 vegetation characteristics (density and BA) plus management unit (5 categories, A–E) and treatment type (4 categories, A–D) were included as 75 input independent variables (Appendix S1). From the model output, we determined which variables were most important in explaining the variation in mean longleaf pine seedling density. Although model fit and error statistics provided overall model evaluation, the model's variable importance values (IV), which range from 0 to 100, were used to determine the relative explanatory power of each input variable in the full regression tree.

To determine the statistical significance of treatment on seedling survival (density) 1 yr after masting, we performed an Analysis of Variance (ANOVA) on longleaf pine seedling density in response to treatment. We used a Tukey's multiple comparisons of means to determine which treatments were contributing to seedling survival. Both analyses were run in R using the "aov" and "TukeyHSD" functions with an alpha of 0.05.

2011 seed masting: sampling design and analysis

Since 2001, Eglin's vegetation monitoring program has collected understory, midstory, and overstory vegetation data in approximately 200 one ha monitoring plots distributed across the base (Hiers et al. 2007). Following the fall 2011 mast year, 15 plots with eight 1 m² quadrats were selected that contained longleaf pine seedlings. Initial seedling counts were collected in understory quadrats during the monitoring season following the mast year (summer 2012). Following the initial counts, plots were revisited in winter 2012 and summer 2013. There was no prescribed burning in these plots during this data collection period. The seedlings were therefore approximately 6 months, 18 months, and 24 months of age when sampled. Species, DBH, and distance to quadrat center were recorded to the nearest midstory tree and overstory tree within 5 m. Species and distance was recorded for all understory trees (<1.4 m high) within 3 m.

We used Kaplan–Meier estimate (Kaplan and Meier 1958) to compare survivorship curves in overstory, midstory, and understory categories. These categories were similar to the ones used for the CART analysis. Overstory categories included longleaf pine overstory (DBH > 10.16 cm), and no overstory. Only three sampling points had oaks that were large enough to be considered overstory so the oak overstory category was eliminated. Midstory categories included longleaf pine midstory (DBH < 10.16 cm), deciduous oak midstory (DBH < 16 cm), and no midstory (may contain other hardwoods). Understory analysis compared the presence or absence of understory (trees and shrubs < 1.4 m in height). Curves were generated using the survival (v 2.37-7) package (Therneau 1999) in the R programming language. To compare Kaplan–Meier survival curves across categories, a nonparametric Tarone–Ware test (Tarone and Ware 1977) was conducted using the survival package. Tarone–Ware tests were used because the analysis is weighted more evenly through the curves than other nonparametric tests.

Mechanisms of facilitation: May 2013 measurements

To begin exploring the environmental factors that may contribute to mechanisms of facilitation, we collected predawn and midday plant moisture stress (PMS) using a Scholander

Pressure Chamber (Turner 1988) in May 2013. On a xeric sandhill site at Eglin AFB, 21 seedlings established in the 2011 seed mast were randomly chosen within a 40 × 40 m area, 12 in “open canopy” conditions (no direct canopy obstruction within at least 3 m), and nine “mid-story canopy” conditions (less than 1 m from a turkey oak midstory shrub). Five seedlings of the 21 seedlings were measured for predawn moisture stress; three in open canopy conditions, two near midstory canopy. In the field, seedlings were removed entirely from the ground and were verified as 1.5 yr old by a lack of secondary needle growth, small stature, and one growth ring visible below the root collar. For the midday measured seedlings ($n = 16$, 9 = open canopy, 7 = midstory canopy), we took hemispherical digital photos ~1 m above each seedling and used WinScanopy 2014a (Regent Scientific, Quebec, Canada) to determine overstory canopy openness. In addition, an infrared image was taken downward from 1 m height above the seedlings (e.g., Appendix S2)

to measure soil surface temperature (°C) at midday (12 to 2 pm) on May 29–30, 2013. Next to each seedling, we also measured soil moisture from 0 to 20 cm depth, the deepest root depth of seedlings measured. Root collar diameter (RCD) and total (above and below ground) biomass was measured as well. We used an unpaired, two-tailed Student’s t test (unequal variance) to test for significant differences between measurements (mean PMS, RCD, total biomass, mean IR image surface temperature, and canopy openness) taken for or at open canopy and midstory canopy seedlings, using a critical value of alpha of 0.05. We ran linear regressions of seedling PMS vs. canopy openness and PMS vs. midday temperature.

RESULTS

1996 seed masting

The regression tree indicated a significant relationship between pine seedling density and vegetation characteristics ($R^2 = 0.67$). The most

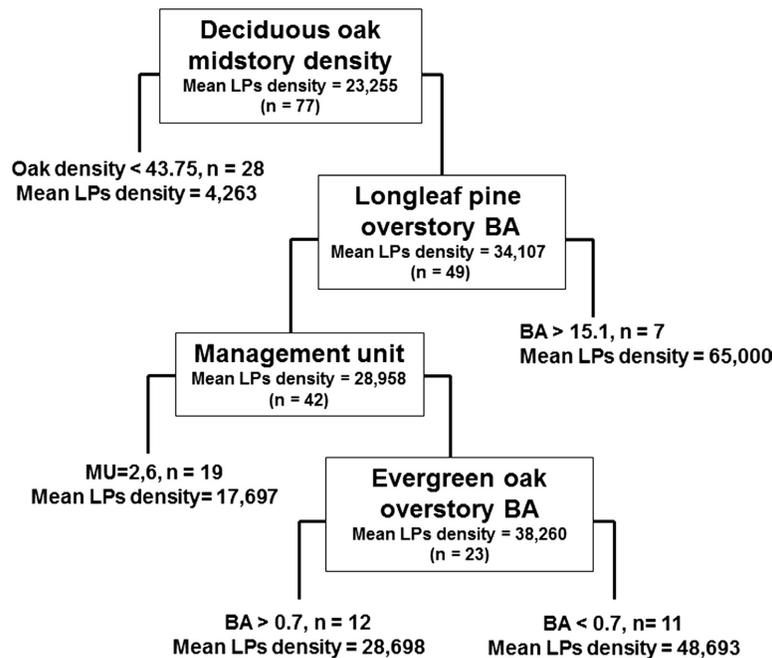


Fig. 2. Regression tree, for the 1996 seed masting analysis, illustrating the primary variables used to split the variability accounting for pine seedling density (response variable). Primary splits: Deciduous oak midstory density (IV: 17), then longleaf pine overstory BA (IV: 7), management unit (MU, IV: 4), and evergreen oak overstory BA (IV: 2). IV: importance value (total: 100). See Table 1 for all significant (20) predictor variables within the model. Mean LPs density: mean longleaf pine seedling density at that tree node. BA: basal area.

important predictors of longleaf pine seedling density (Fig. 2, Table 1) were, in descending order, (1) deciduous hardwood midstory density (IV = 15), which explained most of the variation (0.35 contributing power), (2) longleaf pine overstory BA (IV = 7, 0.17 contributing power), (3) management unit (IV = 4, 0.10 contributing power), and (4) evergreen hardwood overstory BA (IV = 2, 0.06 contributing power). A higher mean density of first year pine seedlings (34,107 ha⁻¹) was found in plots with denser (>43.75 individuals ha⁻¹) deciduous hardwood midstory, compared to less dense areas (4263 seedlings ha⁻¹, <43.75 hardwood individuals ha⁻¹).

The importance values provide more detailed information about the predictive ability of the input variables in the full model. We found that 20 of the 76 input vegetation characteristics were significantly related to pine seedling density. Variables of midstory hardwood density and basal area were the top five predictors of the model (Table 1, IVs = 10–15), which mainly consisted of turkey oak. Treatment was also a strong predictor (IV = 10) and was a primary predictor in the first tree split. Here, the variation was partitioned between the burn only and control treatments vs. the mechanical and chemical treatments, where higher seedling density was found in the burn only and control treatments (mean seedling density: 38,260 vs. 17,697 ha⁻¹). Longleaf pine overstory basal area (IV = 7) and management unit (IV = 4) were the next significant predictors. The remaining predictors (Table 1) had a low IV = 1–2 and consisted of evergreen midstory and overstory groups and species (e.g., sand live oak). All other vegetation characteristics were not significant in the model.

The ANOVA results showed treatments significantly determined pine seedling density ($F[3,73] = 10.26, P < 0.0001$). From Tukey’s test, all mean seedling densities were significantly

different between treatments ($P < 0.02$), except between the burn treatment and control and the chemical and mechanical treatments ($P > 0.69$, Table 2). The burn only treatment and control had 2.5–6 times the mean seedling density than the mechanical and chemical treatments (Table 2). As deciduous oak midstory density and longleaf pine overstory BA were significant predictors in the regression tree, an ANOVA and Tukey’s test of treatment effect was run on these variables as well. From the ANOVA, there was a significant treatment effect on deciduous oak midstory density ($P < 0.0001, F(3,73) = 20.52, P < 0.0001$). From Tukey’s test, there was a significantly larger density of deciduous oak midstory in the control ($P < 0.0001$), compared to any treatment, with no differences between the burn only, mechanical, and chemical treatments ($P > 0.12$, Table 2). There was no difference in longleaf pine overstory BA among treatments.

2011 seed masting

Tarone–Ware tests confirmed a strong influence of midstory deciduous oaks on survivorship probability of longleaf seedlings up to 24 months post germination. Seedling survival was greatest in the presence of midstory oaks and least in quadrats with no midstory and longleaf pines in the midstory throughout the length of the curve ($P < 0.001$, Fig. 3A). Survival was also greater in quadrats greater than 5 m from overstory longleaf pines ($P < 0.001$, Fig. 3B). There was no significant difference in the presence or absence of understory in longleaf pine seedling survivorship.

Mechanisms of facilitation

The *t* test on PMS illustrated that seedlings in the open canopy experienced significantly greater moisture stress during the day than

Table 2. Summary statistics from ANOVA and Tukey’s tests for pine seedling and oak midstory density among treatments 1 yr after the 1996 seed masting event at Eglin AFB.

Treatment	Longleaf pine seedling density in 1997 (ha ⁻¹)		Deciduous oak midstory density in 1997 (ha ⁻¹)	
	Mean	SD	Mean	SD
Burn only	36,406 ^a	27,057	238 ^a	160
Control	35,093 ^a	24,143	731 ^b	494
Mechanical	13,823 ^b	20,069	160 ^a	318
Chemical	6281 ^b	6003	20 ^a	22

Note: Statistical differences between treatments are noted by different letters (a, b).

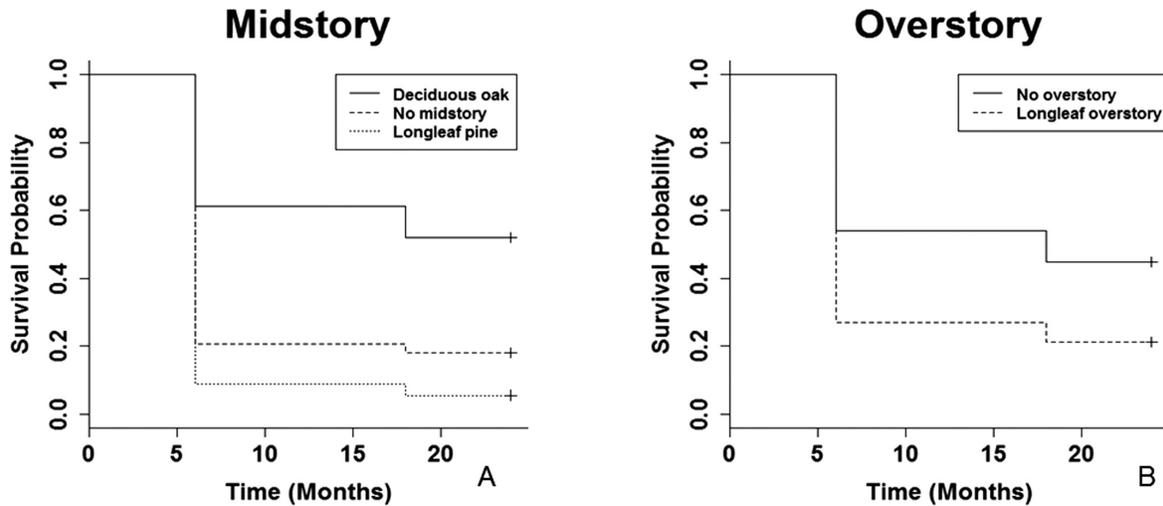


Fig. 3. Midstory Kaplan–Meier longleaf pine seedling survival for the 2011 seed masting analysis, by (A) midstory classes and (B) overstory classes. For the midstory analysis (A), these were categorized by the closest tree within 5 m, with midstory oaks <16 cm DBH and midstory longleaf pines <10.16 cm DBH. For the overstory analysis (B), there was no oak overstory category (see text for details). These were categorized by the closest pine tree (>10.16 cm DBH) within 5 m. All curves were significantly different using Tarone–Ware analysis ($P < 0.001$).

those underneath oak shrubs ($P < 0.009$, Fig. 4A). Furthermore, mean IR image surface temperatures and canopy openness were different for the open canopy seedlings compared to the seedlings underneath oak shrubs ($P < 0.0005$, $P < 0.0003$ and Fig. 4B, C, respectively). PMS was linearly related to canopy openness ($R^2 = 0.34$, $RMS = 0.987$, $P < 0.017$) and mean surface temperature ($R^2 = 0.28$, $RSE = 1.03$, $P < 0.035$), despite the observation of no difference in mean soil moisture 0–20 cm deep between seedling groups. There were no differences in mean RCD and total biomass between seedling groups ($P < 0.152$, $P < 0.094$, respectively). Canopy openness ranged between 32 and 68% open. Mean IR image surface temperatures ranged between 35.8° to 55.3°C.

DISCUSSION

Recognition that deciduous oaks are important facilitators of longleaf seedling establishment represents a significant departure from conventional wisdom and current management practices, which largely focus on competitive limitation of longleaf regeneration by broadleaved species (e.g., Brockway and Outcalt 1998, Provencher et al.

2001a). Furthermore, since our study was able to capture the influence of historic midstory reduction treatments on a longleaf pine mast seeding in 1996, this study provides a unique perspective on ecosystem resilience and recovery not explored in the current conservation management paradigm.

On xeric longleaf pine sites, we found that the oak midstory facilitates pine seedling survival, particularly in the first 1–2 yr post germination when seedlings are most susceptible to drought mortality in xeric conditions (Wahlenberg 1946, Rodríguez-Trejo et al. 2003, Pecot et al. 2007). Longleaf pine is known for its ability to persist along a wide range of edaphic conditions, and its grass stage confers survival advantage in a frequent fire regime (Mitchell et al. 1999). While individuals in the grass stage may persist up to 20 yr, germination and early survival are poorly understood (Mitchell et al. 2006) and likely have major impact on future stand development (O’Brien et al. 2008). Often the first 2 yr of life are ignored in seedling studies and are likely the most vulnerable life stage. This study provides quantitative evidence from two distinct seed masting events that midstory oaks were facilitating longleaf seedling survival in xeric longleaf

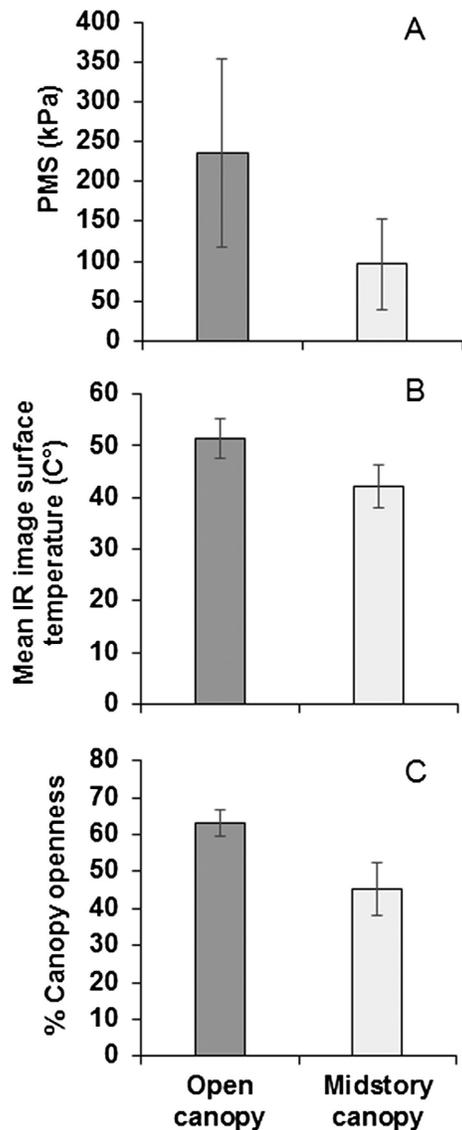


Fig. 4. Mean and standard deviation (error bars) of field measurements for longleaf pine seedlings found in the 'open canopy' (no canopy within 3 m from seedling, dark gray) and a 'midstory canopy' (within 1 m of midstory oak, light gray); (A) midday plant moisture stress (PMS) of 1.5-yr-old longleaf pine seedlings, (B) mean surface (vegetation and soil) temperature using infrared (IR) image at 1 m above ground from seedling, (C) percent canopy openness from hemispherical photos taken 1 m above seedling. For all three (A–C), measurements taken on or by open canopy seedlings ($n = 9$) were significantly different ($P < 0.02$) from those nearby midstory oaks ($n = 7$). (A and B) were taken in May 2013.

ecosystems. For the 1996 mast, our results showed a clear effect of hardwood midstory that contributed to a higher seedling density (higher survival rate) in denser hardwood stands (Fig. 2). For the 2011 mast, the survival analysis illustrated a facilitation effect at least through 24 months of age (Fig. 3A). While the facilitative effects were pronounced in both masting events (Fig. 2, Fig. 3A, Fig. 4), the proximity of overstory pine had a negative effect on survival, potentially showing some intraspecific competitive exclusion by adult pines (Fig. 3B). It should be noted that proximity (distance to nearest adult pine) is different than overstory longleaf density, which was a strong predictor of seedling survival following the 1996 mast (Fig. 2). This distinction suggests that while sufficient overstory density is required to supply seed during a mast, the strong facilitation of seedling survival in proximity to oaks is not present under adult pine trees. This effect may simply be related to the relatively large size of pines vs. deciduous oaks in longleaf sandhills.

This study also found that while only low hardwood midstory density is critical for early pine establishment, high midstory densities are not an impediment for facilitation during the critical phase of seedling establishment (e.g., Fig. 1). As few as 43 stems ha^{-1} were found sufficient to facilitate seedling survival, but as many as 1400 stems ha^{-1} maintained facilitation without competitive exclusion on these xeric sites. For instance, although untreated areas had a significantly higher density of oak midstory than the burn only treatment, the oak abundance in the burn only treatment supported similar pine seedling densities (Table 2). This threshold of 43 oak stems ha^{-1} (first tree split in regression tree) could represent a starting threshold density for maintaining an oak midstory on xeric longleaf sites. Other management objectives, such as red-cockaded woodpecker recovery or understory restoration, could still be met, using prescribed burning without removing hardwoods below this threshold (Hiers et al. 2014).

Midstory facilitation was at least in part driven by reduced plant moisture stress in hot and dry conditions (Fig. 4), although other mechanisms of facilitation by the midstory, and perhaps the overstory adult pines (Fig. 2) should be explored

further. Previous studies, however, provide some insights regarding the mechanisms, with at least two studies pointing to water and light availability driving enhanced survival of artificial regeneration (McGuire et al. 2001, Pecot et al. 2007). Although longleaf pine is highly drought tolerant, McGuire et al. (2001) documented that germination, survival, and growth is sensitive to water availability, especially on xeric sites (Wahlenberg 1946, McGuire et al. 2001). Hydraulic lift from adult tree root systems has been measured in longleaf pine (Espeleta et al. 2004, Addington et al. 2006) and other tree-grass communities (Ludwig et al. 2003, Espeleta et al. 2004). Pine litter accumulation underneath adult longleaf trees has been found to be a source of nitrogen and to physically retain soil water and maintain water holding capacity of the soil (Harrington 2006). It is unknown whether during periods of drought, if adult pines facilitate early recruitment. From our field survey in May 2013, we documented significantly higher mean surface (vegetation and soil) temperatures in open canopies (>3 m from any canopy) conditions (Fig. 4B), with higher temperatures (upwards 60°C) occurring on bare sand with direct solar radiation (Appendix S2). A more open canopy may provide a better light environment for early stage growth (Palik et al. 2003), but may create conditions of extreme heat stress, especially for new germinants, that could affect regeneration success during periods of extended drought.

Regeneration dynamics in longleaf pine have often been portrayed as a function of competition for germination microsites (Brockway and Outcalt 1998), where fire is used to remove understory vegetation in advance of a mast year (Brockway et al. 2005). The role of hardwood-induced facilitation on xeric sites may play a dominant role in successful regeneration. Longleaf pine is known to be a shade-sensitive species with respect to growth rates, but seedlings and saplings have been found to have at least some leaf morphological and physiological plasticity related to their light environment (Battaglia et al. 2002, 2003). This suggests that although seedling growth is a function of light availability (Wahlenberg 1946, McGuire et al. 2001, Harrington 2006), their initial reproductive success could have more to do with facilitation by the oak midstory than their light environment, particularly during drought years. Based on our moisture stress measurements, it

appears the advantage of reduced evaporative demand outweighs any competitive interaction for light or bare mineral soil, although the interaction between fire and oaks on seedling establishment may be qualitatively different for more mesic sites.

It remains unclear how this tradeoff of facilitation and competition drives reproduction dynamics along the full edaphic gradient occupied by longleaf pine. In more mesic conditions in a planted longleaf pine stand, the dense canopy facilitated seedling survival during severe drought years (McGuire et al. 2001, Pecot et al. 2007). Such a response suggests that climatic variability may alter the facilitative interactions between hardwoods and pine seedlings on more mesic sites, and potentially on xeric sites during years with higher rainfall. With predictions of increasingly variable rainfall and shifts toward winter precipitation (Mitchell et al. 2014), climate change will likely increase drought stress in more mesic communities, which already show greater sensitivity to severe drought than xeric sites (Wright et al. 2013).

This window of facilitation may not be the only critical process in seedling survival, but certainly a foundational feature of xeric demography that has not been explored before. Future work would benefit from understanding other processes that govern longleaf stand development in these early years of life, particularly in relation to gap and hardwood dynamics (Loudermilk et al. 2011). Given the mast response of longleaf, regeneration success appears to be limited by seed consumption and mortality of very young (newly established) seedlings (Boyer 1964, Grace and Platt 1995). The critical importance of facilitation at early life stages likely disappears as seedlings rapidly invest in deep taproots that provide long-term drought resistance and ability to survive fire during the grass stage and beyond (Heyward 1933). We argue that while there is a need to understand longer term survival dynamics, widespread regeneration failure in an infrequent masting species would have far reaching consequences to the other processes and long-term stand development.

ECOLOGICAL AND MANAGEMENT IMPLICATIONS

The path back

Facilitation of seedling establishment within longleaf sandhill ecosystems is also useful in understanding the resilience of the community

to canopy disturbance events due to hurricanes, tornados, hotspots within wildfires, tree harvest, and insect outbreaks. Large-scale overstory mortality in response to high severity portions of surface fire regimes have been observed even in frequently burned longleaf old growth stands and have eliminated significant portions of the pine overstory (Varner et al. 2007, O'Brien et al. 2010). With the loss of the pine overstory, hardwoods are released from competition (primarily belowground, *sensu* McGuire et al. 2001, Pecot et al. 2007, Mitchell et al. 2009), and can then occupy the midstory or canopy (Mitchell et al. 2009). In the case of xeric longleaf sandhills, the resulting dense stands of turkey oak would continue to accumulate on the landscape, unless there were ecological mechanisms, such as facilitation, for the re-establishment of young longleaf through time (Mitchell et al. 2009, Hiers et al. 2014). Facilitation of seedling establishment documented in this study suggests released midstory oaks may be responsible for long-term longleaf pine recovery from larger scale canopy disturbances, such as wildfire and hurricanes. This recovery likely operates over decadal timescales, as larger canopy openings give way to a turkey oak-dominated midstory that in turn facilitates longleaf regeneration. As such, we propose that facilitation of seedling establishment by the oak midstory provides the "path back" after larger canopy disturbances and increasing resilience of this ecosystem to canopy disturbance and drought.

Such a dynamic of hardwood-facilitated longleaf reforestation would be increasingly important across a wider portion of the edaphic gradient occupied by longleaf if climate conditions lead to extended droughts and more intense hurricanes (Mousavi et al. 2011, Mitchell et al. 2014). Moreover, seedlings occupying the driest longleaf communities are likely the most vulnerable to the impacts of climate change, especially any alteration in the moisture regime due to excessively drained soil and constant water stress (Addington et al. 2006). Wholesale removal of hardwoods would compromise the ecological function on those sites. Climate projections already predict increased temperature, more variable rainfall, and higher water stress (Mitchell et al. 2014), and recent research on mesic sites have already documented vulnerability to even short-term drought (Starr et al. 2015).

Considering oaks in longleaf management

A recent review of longleaf management (Hiers et al. 2014) has challenged the current management focus on hardwood reduction. Targeting for the near complete elimination of hardwoods from longleaf ecosystems, particularly through the use of broadcast herbicide, may ultimately compromise longleaf pine resilience to climate change and undermine conservation of associated biodiversity.

Herbicide, chemical, or other site preparation techniques may be useful restoration tools, and may be necessary in conditions where a tipping point has been reached, for example, evergreen shrub conversion (Hiers et al. 2007). If fire is already used as a management technique, but the area is not "pristine" or close to known reference conditions, additional hardwood reduction techniques are often applied to further enhance ecosystem structure (Menges and Gordon 2010). However, it has been recently found (Kirkman et al. 2013) that regardless of treatment (herbicide, mechanical removal, fire), longleaf stands will converge to reference conditions in terms of native plant diversity in as little as a decade, as long as fire was applied regularly (2–3 yr return interval). Although forest structural differences may be observed, function and processes were restored. Data from this study offer a case for understanding the role of hardwoods in longleaf pine ecosystems, and provide management guidance for threshold densities of midstory hardwoods needed to facilitate longleaf recruitment.

Although research has documented the influences of competition, disease, predation, invasive species, and fire mortality on longleaf pine reproductive success, facilitation by oaks on xeric sites appears to be a missing and critical component to our understanding. We suggest managers consider facilitation in their long-term ecosystem management strategies, especially when planning site restoration techniques in light of climate uncertainty.

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