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Xerophytic hardwood retention promotes competition over facilitation in longleaf pine woodlands in the absence of fire

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ABSTRACT

Recent reports of xerophytic hardwood facilitation of longleaf pine seedlings challenge the traditional paradigm that co-occurring hardwood tree species constrain longleaf pine (*Pinus palustris* Mill.) regeneration. To better understand this dynamic, we established an experiment examining the effects of hardwood retention duration (no retention, one-year retention, four-year retention), overstory basal area (2-to-41 m^2 ha^{-1}), and understory vegetation cover on microclimatic conditions and longleaf pine seedling survival, development, physiological performance, and brownspot needle blight (*Mycosphaerella dearnessii*) infection in the Sandhills Ecoregion of North Carolina, USA. Light availability (μmol m^{-2} s^{-1}) at the forest floor (~20 cm) was reduced by 27% in the four-year retention treatment which significantly exceeded reductions found in the one-year (<1%) and no retention (<1%) treatments, respectively, post midstory removal. However, midstory treatment had little effect on soil moisture and temperature at 15 and 30 cm depth. Longleaf pine seedling survival (85%), aboveground biomass (7.51 g dry weight), and root collar size (1.53 cm) were significantly highest in the no retention treatment compared to the four-year retention treatment. Between treatments with midstory retention (one-year vs. four-year retention), longleaf pine seedlings were statistically larger in the one-year retention treatment (5.37 g dry weight) compared to the four-year retention treatment (4.84 g dry weight). Seedling brownspot infection did not statistically vary among midstory retention treatments. Across all midstory treatments, overstory basal area had a stronger negative effect on longleaf pine seedling aboveground biomass development, root collar development and brownspot infection compared to midstory hardwood stem density or understory vegetation cover. Moreover, for most measured metrics, overstory basal area had a stronger negative effect on longleaf pine physiological performance compared to midstory hardwood stem density. Collectively, these results indicate that hardwood retention did not facilitate longleaf pine survival and development in the grass stage and that asymmetric competition from the overstory represents a stronger impediment to longleaf pine sapling recruitment than midstory hardwoods.

1. Introduction

Competition is a fundamental process in forest ecosystems. Without disturbance, resource demanding species are poorly adapted to compete with established vegetation leading to their eventual replacement by stress tolerant species (Gleason, 1927; Grime, 2006). Indeed, the effects of interspecific competitive exclusion have been documented in forests worldwide (Lewis and Tanner, 2000; Zhang et al., 2015; Ali, 2019). Nevertheless, competition is not the only biotic process influencing species composition, as facilitative interactions also contribute to forest stand dynamics (Wright et al., 2014; Abreu et al., 2021; Pretzsch, 2022).

Competitive interactions have been particularly well studied in the longleaf pine ecosystem of the southeastern United States (Ramsey et al., 2003; Pecot et al., 2007). Longleaf pine (*Pinus palustris* Mill.) is a foundational tree species due to its contribution to understory flammability but is a poor competitor for light during seedling development (Mitchell et al., 2006; Brockway et al., 2007; Varner et al., 2021). Rather than allocate resources to height growth following germination, longleaf pine seedlings begin life in a grass stage devoting carbohydrates to storage and root growth (Wahlenberg, 1946; Pile et al., 2017). The grass stage is

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thought to be an adaptation to fire, as it is often observed among pine species in frequently burned ecosystems (Rodríguez-Trejo and Fulé, 2003; Keeley, 2012; Pausas, 2015). Prior to European settlement, fire was a common occurrence in the longleaf pine ecosystem and helped limit the encroachment of fire-sensitive species (Glitzenstein et al., 1995; Stambaugh et al., 2011). Consequently, longleaf pine seedlings encountered modest competition for light and belowground resources. However, in the absence of burning, hardwood species compete with grass stage seedlings leading to the suppression of longleaf pine recruitment (Chapman, 1932).

While the effects of fire exclusion on longleaf pine recruitment are well-documented (Gilliam and Platt, 1999; Kush and Meldahl, 2000), evidence from the sandhills variant of the longleaf pine ecosystem suggests that xerophytic hardwood species may facilitate longleaf pine recruitment (Wahlenberg, 1946; Loudermilk et al., 2016; Johnson et al., 2021). Facilitation on xeric sites is generally consistent with the predictions of the stress tolerance hypothesis (Bertness and Callaway, 1994; Maestre et al., 2009), yet the underlying mechanisms for this pattern remain unclear. Recent studies demonstrate that facilitation is not occurring at the seed and seedling establishment phases, as hardwoods had no impact on seed predator preference and provided a poor substrate for longleaf pine germination (Willis et al., 2019 & 2021). However, reports on post-germination dynamics indicate that xerophytic hardwood species can facilitate longleaf pine seedlings by reducing chronic moisture stress through the nurse tree effect (Loudermilk et al., 2016). The presence of xerophytic hardwoods may also increase resource availability to longleaf pine seedlings through hydraulic lift or mineral nutrition addition from senesced leaf litter(Klemmedson, 1992; Espeleta et al., 2004; Madritch and Hunter, 2005). Nevertheless, facilitative interactions can become competitive over time or under acute stress (Bertness and Callaway, 1994; Michalet et al., 2014; Olsen et al., 2016), and, to our knowledge, no studies have empirically demonstrated that xerophytic hardwoods facilitate longleaf pine beyond the grass stage.

Little is also known about the effects of xerophytic hardwoods under varying structural conditions. Hardwood facilitation may be limited to stands with low overstory density, as longleaf pine overstory trees are strong competitors with longleaf pine seedlings (Brockway and Outcalt, 1998; McGuire et al., 2001; Kara et al., 2017). However, competition from understory vegetation is also likely to increase with decreasing overstory density potentially offsetting advantages wrought by reduced overstory competition or facilitative interactions with xerophytic hardwoods (McGuire et al., 2001; Gilliam and Platt, 1999).

Another factor to consider is the interactive effects of overstory and midstory density on fungal disease. In the absence of fire, longleaf pine seedlings often become infected with brownspot needle blight (BSNB; *Mycosphaerella dearnessii*) reducing growth and, in severe cases, contributing to mortality (Siggers, 1932; Wakeley, 1970; Van Der Nest et al., 2019). Infections generally increase with light availability, as longleaf pine seedlings become infected through open stomata (Parris and Killewbrew, 1969; Kais, 1975). This suggests that BSNB infection rates will increase with decreasing overstory density. Yet, the potential effect of overstory density on BSNB infection may depend on the absence of the midstory, which could reduce infection by shading longleaf pine seedlings on the forest floor. If so, reduced BSNB infection may be an additional mechanism through which xerophytic hardwoods facilitate longleaf pine seedling survival and development.

In this study, we followed the performance of planted longleaf pine seedlings over four- years under varying lengths of midstory hardwood retention and across a range of overstory basal area in North Carolina, USA. Our objectives were to determine whether: 1) midstory hardwoods facilitate or inhibit longleaf pine seedling survival and growth; 2) retention duration influences seedling survival and growth; 3) overstory basal area modifies the relationship between midstory hardwoods and longleaf pine seedlings; and) the relative influence of overstory basal area, midstory hardwood density, wiregrass (*Aristida stricta* Michx.) cover, forb cover, and shrub cover on longleaf pine seedling survival, growth, physiological performance, and BSNB infection rates. Collectively, this information will improve our fundamental knowledge of species interactions in xeric environments. Moreover, the information gleaned from this study will aid efforts to restore and conserve a threatened ecosystem.

2. Methods

2.1. Site description

Our study was established in a 104-ha mature longleaf pine stand (hereafter referred to as McCain) in the Sandhills Ecoregion of North Carolina, USA (35°3′ 34.6932″N, 79°22′ 22.0872″W). The local climate is considered humid-subtropical with average temperatures ranging from 1.0 −11.8 °C in January to 22.0–32.6 °C in July (Fayetteville Pope Air Force Base, NC; NCEI, NOAA). Precipitation in the region occurs primarily in the form of rain and averages 1234 mm annually (Fayetteville Pope Air Force Base, NC; NCEI, NOAA). Soils at our stand were classified under the Candor soil series in the sandy, kaolinitic, thermic Grossarenic Kandiudults family (Soil Survey Staff Natural Resources Conservation Service, 2019). The Candor series features rapid drainage capacity throughout the soil profile. Site index for longleaf pine growing on the Candor soil is 17.7 m height at age 50 (Soil Survey Staff Natural Resources Conservation Service).

McCain originated from an extensive clearcut in the 1920s. Following establishment, McCain developed under fire exclusion for nearly seven decades. Efforts to restore the historical woodland structure began in the 1990s and focused on removing encroaching hardwood species and reestablishing a frequent, low intensity fire regime. Currently, prescribed fire is applied to McCain in the dormant season on a three-year return interval. No other records of previous silvicultural activities are known to exist at McCain. Prescribed fire was excluded from our study areas for the duration of the experiment. Longleaf pine is the dominant tree species at McCain and comprises approximately 95% of the canopy. Overstory longleaf pine averaged 22.5 m in height and 31.7 cm in diameter. The midstory is comprised almost entirely of sprouts consisting of turkey oak (82%), a pyrophytic species, and minor components of mesophytic species including blackgum (*Nysssa sylvatica*) (9%) and sassafras (*Sassafras albidium*) (7%). Hardwood midstory average height was 1.2 m. Wiregrass is abundant throughout the understory and is augmented by a variety of shrubs (e.g., small cluster blueberry (*Vaccinium tenellum*)), forbs (e.g., sweet goldenrod (*Solidago odora*)) and graminoids (*Poaceae* spp.).

2.2. Experimental design

Our experiment was established as a randomized complete block. Fifteen blocks (0.17 ha) were installed throughout McCain in locations with varying longleaf pine overstory basal area (2-to-41-m^2 ha^{-1}). Each block contained nine plots (188 m^2). Plots were randomly assigned one of three midstory hardwood chemical control treatments (no retention, one-year retention, four-year retention) (Fig. 1). Each midstory treatment was replicated three times per block ($n = 45$). Midstory hardwoods were controlled with a cut stump treatment with Brushtox Brush Killer herbicide (61.6% ester triclopyr, Ragan and Massey, Inc., Gig Harbor, WA) mixed with methylated seed oil in a ratio of 1:9 (one part herbicide to nine parts oil). Hardwoods in the no retention and one-year retention treatments were cut with a brush saw in May of 2015 (no retention) and 2016 (one-year retention), respectively. Herbicide was applied to the cut stumps immediately post-cutting by hand with backpack sprayers. Hardwood sprouts surviving the cut stump treatment were foliar sprayed with the same herbicide mixture in the following May. In the center of each plot, we established a planted longleaf pine subplot (21 m^2). In the summer of 2015, planted subplot hardwood sprout density averaged 3 sprouts ± 1 in the no retention treatment (post-treatment),

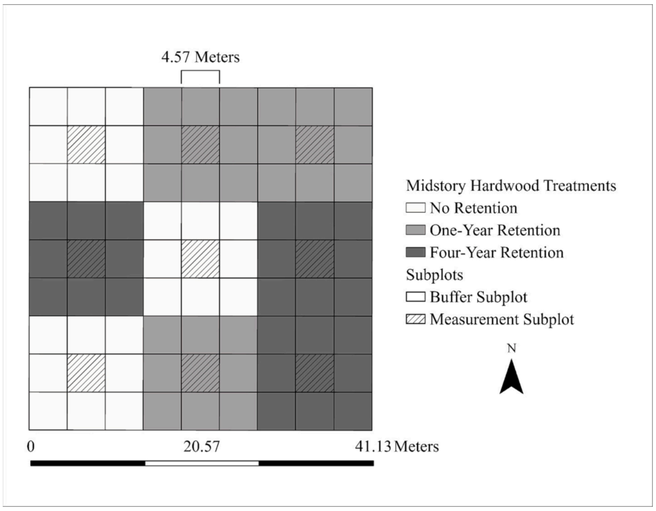

Fig. 1. Example layout of an experimental block (0.17 ha). Each block contained nine plots (188 m^2) and each block contained nine subplots (21 m^2). Treatments (no midstory hardwood retention (white), one-year retention (light grey), four-year retention (dark grey)) were randomly assigned at the plot level. Seedlings were planted within the measurement subplot (hashed) located in the center of each plot in the Sandhill ecoregion of North Carolina, USA.

46 stems ± 16 in the one-year retention treatment (pre-treatment), and 44 stems ± 18 in the four-year retention treatment. To minimize edge effect from neighboring plots with different midstory treatments, each planted subplot was buffered by at least one unplanted subplot on all sides (Fig. 1). Subplots were hand-planted in January 2016 with 12 one-year old containerized longleaf pine seedlings. The seedlings were planted approximately 1 m apart in a grid pattern. All seedlings were obtained from the North Carolina Forest Service Claridge Nursery. A seedling survival check was conducted in November 2016 to account for planting-associated mortality. Initial survival exceeded 90% in all treatments.

2.3. Field measurements

All measurements occurred within the planted subplots. Overstory basal area (all tree species included) was quantified with a one-factor metric prism at the center of each planted subplot. To determine the effects of residual vegetation on microclimatic conditions, we measured light availability in the growing season of 2017. Photosynthetic photon flux density (μmol m^{-2} s^{-1}) was quantified with a line quantum sensor (LI-COR, Lincoln NE) in the center of each planted subplot directly above the hardwood midstory (~2.0 m) and at the seedling level (~20.0 cm). All light measurements were taken on clear days during a two-hour window before and after solar noon to minimize light angle variability. Soil moisture (percent moisture content) and temperature (°C) were measured at planted subplot center at 0.0–15.0 cm and 15.0–30.0 cm depth with a TEMP-350 Digital Soil Moisture and Temperature Meter (Aquaterr, Costa Mesa, CA, USA). Measurements were taken during a single day between 11:00 a.m. and 1:00p.m. once per month (June-August 2017). All soil measurements occurred on a day that was at least one week removed from the last recorded rainfall. Logistical constraints limited soil moisture and temperature measurements to planted subplots within seven blocks across the range of basal area. Percent coverage of wiregrass, shrubs, forbs, and mineral soil were visually assessed to the nearest five percent in July 2017.

To further examine the effect of local vegetation on longleaf pine seedlings, we measured the physiological performance of planted seedlings in a subset of 11 blocks over one day in July 2019. Within each sampled block, we randomly selected 4–8 subplots across the range of midstory treatments. In each selected subplot, we collected foliar samples to determine foliar N (%) and measured mass-based photosynthesis (nmol g^{-1} s^{-1}), area-based transpiration (mmol m^{-2} s^{-1}), and stomatal conductance (gs; mol m^{-2} s^{-1}) on the largest and smallest seedling in the planted subplot with a LI-COR 6400XT Portable Photosynthesis System (LI-COR Biosciences Inc., Lincoln NE, USA) with a red-blue LED light source set between 800 and 1000 μmol m^{-2} s^{-1} depending on overstory density. Carbon dioxide concentrations were set to 400 ppm. Two to three needles from a fascicle were placed in the chamber and measurements were made once values reached equilibrium. Needles within the chamber were then cut, placed in zip-lock bags and returned to the lab so that their area could be measured using a flatbed scanner. These areas were then used to scale all area-based gas exchange data. Measurements of photosynthesis, transpiration, and stomatal conductance were also scaled to a common vapor pressure deficit to account for environmental differences associated with sampling time (9:00 AM – 4:00P.M.). Needles were then dried and weighed to determine leaf dry mass per unit area which was used to calculate mass-based photosynthetic rate and leaf nitrogen content. Dried leaves were then ground, placed in tin capsules, and sent to the UC Davis Stable Isotope Facility (Davis, CA, USA) for estimation of needle carbon and nitrogen concentrations, $\delta^{13}C$ (and estimate of spatially and temporally integrated water use efficiency) and $\delta^{15}N$. From these measurements, we calculated intrinsic water use efficiency (iWUE; μmol mol^{-1}) (ratio of photosynthesis and stomatal conductance), integrated water use efficiency based on isotopes ($\delta^{13}C$), and photosynthetic nitrogen use efficiency (PNUE) (ratio between photosynthesis and foliar N). All foliar N and physiological measurements were averaged at the subplot level.

Survival, development, and brown spot infection were assessed on each planted seedling in November 2019. BSNB was estimated to the nearest percent. No planted seedling had bolted from the grass stage at final measurement. Therefore, seedling development was assessed by obtaining a root collar diameter measurement with digital calipers on each surviving seedling in the subplot. In addition, we randomly selected four seedlings per planted subplot to destructively obtain an above ground biomass sample. Each selected seedling was cut at the groundline, placed in a plastic bag, and transported to the laboratory for further processing. Once at the laboratory, sampled seedlings were dried in an oven for 72 h at 70 °C and subsequently weighed. All performance metrics were averaged at the subplot level.

2.4. Statistical methods

A mixed-effects analysis of covariance (ANCOVA) was used to examine the influence of midstory treatment and overstory basal area on light availability above the midstory (2 m), light availability at the forest floor (~20 cm), soil moisture and temperature (15 and 30 cm), and longleaf pine seedling survival, root collar diameter development, aboveground biomass development, and BSNB. The main effects of midstory treatment (categorical factor), overstory basal area (continuous factor), and their interaction were considered fixed effects, while block was considered a random effect in the full model. The effects of block were modeled with a variance components covariance structure. Prior to modeling, we checked response variable distribution within midstory treatment groups to confirm an approximately normal distribution. In addition, we examined the relationship between regression slopes to check for homogeneity. Preliminary model runs consisted of a full factorial of fixed effects and the random effect. The interaction term was found to be insignificant in all preliminary runs. Thus, we removed the interaction term and ran a reduced model containing the residual main effects and the random effect. Model fit was assessed by examining plots of studentized residuals and quantile–quantile plots. Potential outliers were evaluated with a Cook's distance statistic. Points with a distance statistic exceeding one were evaluated for leverage strength by removing the point and re-running the model to check for changes in parameter significance (Ramsey and Schafer, 2012). Outlier removal had no effect on parameter significance; thus, all points were retained in the analyses. Models containing a significant treatment effect were further examined with Tukey's adjusted multiple comparison tests to identify differences among midstory treatments. Statistical significance was determined at $\alpha = 0.05$.

To evaluate the relative influence of understory and overstory factors on longleaf pine seedling survival, aboveground biomass development, root collar development, and brownspot infection, we ran multiple regression models containing wiregrass cover, forb cover, shrub cover, overstory basal area, and midstory hardwood stem density as factors within individual treatments. The full model was used in the one-year and four-year retention treatments. Midstory hardwood stem density was excluded from all analyses in the no retention treatment to account for their removal from the subplots prior to planting. Prior to modeling, scatter plots were examined to confirm a linear relationship between the independent and dependent variables. We then ran Pearson's bivariate correlation analyses to check for multicollinearity between the independent variables. No associations exceeded 0.40 indicating low-to moderate collinearity. Finally, we examined scatterplots of the residuals versus predicted values to evaluate model fit. Variables were considered statistically significant at $\alpha = 0.05$.

Based on the results of the above-described multiple regression analyses, and our interest in examining the relative effects of midstory hardwoods versus overstory basal area, we ran additional multiple regressions examining the effect of overstory basal area and midstory hardwood stem density on seedling physiological performance (foliar N, mass-based photosynthesis, area-based transpiration, stomatal conductance, intrinsic water use efficiency, water use efficiency, and photosynthetic nitrogen use efficiency, following the above-described procedures. Due to a reduced sample size, and the similarity between midstory treatments in the previous regression analyses, midstory treatments were pooled together. All analyses were conducted in SAS version 9.4 (SAS Institute, Cary, NC, U.S.A.).

3. Results

3.1. *Effects of midstory retention duration and overstory basal area on microclimatic conditions*

Light availability above the midstory (2 m) was similar among midstory treatments (1004–1176 ± 86 S.E. μmol m^{-2} s^{-1}), after accounting for overstory basal area, and did not statistically differ (Tables 1 & 2). Increases in overstory basal area reduced light availability (-11.45 μmol m^{-2} s^{-1}) above the midstory but was not statistically significant (Table 2). Midstory treatment significantly influenced light availability at the forest floor (~20 cm) (Table 2). Light availability at the forest floor was reduced by 27% in the four-year retention treatment which significantly exceeded reductions recorded in the one-year (<1%) and no retention (<1%) treatments, respectively, post midstory removal (Tables 1 & 2). Increasing overstory basal area reduced light availability (−8.34 μmol m^{-2} s^{-1}) at the forest floor but was not statistically significant (Table 2). Soil moisture at 15 cm depth ranged from 35.4% ± 1.2 in the no retention treatment to 38.0% ± 1.2 in the one-year retention treatment but did not significantly differ among treatments (Tables 1 & 2). Increasing overstory basal area modestly increased soil moisture at 15 cm (+0.08%) but was not statistically significant (Table 2). Like the trends found at 15 cm, soil moisture at 30 cm was lowest in the no retention treatment (30.9% ± 1.3) and highest in the one-year retention treatment (33.8% ± 1.3) but did not statistically differ among treatments (Tables 1 & 2). Soil moisture at 30 cm was not significantly affected by increases in overstory basal area (+0.02%) (Table 2). Soil temperature at 15 and 30 cm depth varied little (maximum difference 0.4 °C ± 0.2) among midstory treatments and was not statistically significant (Tables 1 & 2). In contrast, soil temperature at both sampled depths was significantly reduced (-0.03 °C) by increasing overstory basal (-0.03 °C) (Table 2).

Table 1
Results of mixed-effects analyses of covariance (ANCOVA) examining the influence of midstory treatments and overstory basal area on microclimatic conditions within planted subplots in the Sandhill ecoregion of North Carolina, USA. Presented values represent the average of three measurements taken at subplot center from June-August 2017 ± one standard error. All comparisons were made within rows. Values with different letters were considered statistically significant at $\alpha = 0.05$.

Metric	No Retention	One-Year Retention	Four-Year Retention
Light above the midstory (μmol m^{-2} s^{-1})	998 (88)^{a}	954 (88)^{a}	1007 (83)^{a}
Light at the ground (μmol m^{-2} s^{-1})	996 (88)^{a}	948 (88)^{a}	705 (74)^{b}
Soil moisture (15 cm) (% content)	35.6 (1.1)^{a}	37.8 (1.3)^{a}	35.5 (0.8)^{a}
Soil moisture (30 cm) (% content)	31.0 (1.2)^{a}	33.8 (1.1)^{a}	32.3 (1.0)^{a}
Soil temperature (15 cm) (°C)	25.0 (0.2)^{a}	25.4 (0.2)^{a}	25.1 (0.2)^{a}
Soil temperature (30 cm) (°C)	25.0 (0.2)^{a}	25.2 (0.2)^{a}	24.8 (0.2)^{a}

3.2. *Effects of midstory retention duration and overstory basal area on longleaf pine seedlings*

Longleaf pine seedling survival was significantly affected by midstory retention (Table 3). Seedling survival in the no retention (85% ± 4) and one-year retention (86% ± 4) treatments significantly exceeded that in the four-year retention treatment (76% ± 4) (Fig. 2) (Table 3). Increasing overstory basal area slightly increased longleaf pine seedling survival (<1%) but was not statistically significant (Table 3). Longleaf pine seedling aboveground biomass in the no retention treatment (7.51 g dry weight ± 0.65) significantly exceeded values found in the one-year (-26%) and four-year retention (- 33%) treatments (Fig. 2) (Table 3). Increasing overstory basal area significantly reduced (-0.30 g dry weight) longleaf pine seedling aboveground biomass (Table 3). Longleaf pine seedling root collar diameter also varied significantly among midstory treatments and was highest in the no retention treatment (1.53 cm ± 0.04) (Fig. 2) (Table 3). However, in this instance, the no retention treatment only significantly exceeded the four-year retention treatment (- 7%) in longleaf pine root collar diameter (Table 3). Longleaf pine seedling root collar diameter was significantly reduced (-0.02 cm) by increasing overstory basal area (Table 3). Brownspot infection percentage was similar (13–17% ± 3) among midstory treatments and did not statistically differ (Fig. 2) (Table 3). In contrast, increasing overstory basal area significantly reduced (- < 1%) longleaf pine seedling brownspot infection (Table 3).

3.3. *Relative influence of overstory and understory factors*

Longleaf pine seedling survival was not significantly affected by any investigated factor across all midstory treatments (Table 4). In contrast, longleaf pine seedling aboveground biomass, root collar diameter, and brownspot infection was significantly reduced by increasing overstory basal area across all midstory treatments (Table 4). Hardwood sprout density, shrub cover, forb cover, and wiregrass cover, did not significantly influence any performance metric in any midstory treatment (Table 4).

Within pooled midstory treatments, longleaf pine seedling foliar N (−0.0027 %), photosynthesis (−0.4897 nmol g^{-1} s^{-1}), transpiration (−0.0814 mmol m^{-2} s^{-1}), and stomatal conductance (−0.0018 gs; mol m^{-2} s^{-1}), were significantly reduced by increasing overstory basal area (Table 5). Alternatively, increasing basal area significantly increased longleaf pine seedling water use efficiency ($0.0096\delta\,^{13}C$) (Table 5). Increasing midstory hardwood stem density significantly reduced (−0.0005 gs; mol m^{-2} s^{-1}) longleaf pine seedling stomatal conductance but had no statistical effect on any other measured physiological metric (Table 5). Neither overstory basal area nor midstory hardwood stem

Table 2

Statistical results from multiple regression analyses examining the influence of midstory treatments and overstory basal area on microclimatic conditions within planted subplots in the Sandhill ecoregion of North Carolina, USA.

Planted Subplot Environment	Effect	Numerator DF	Denominator DF	Parameter Estimate	F-Test	P-Value
Light above the midstory (μmol m-2 s-1)	Basal Area	1	117	−11.45	3.48	0.0645
	Treatment	2	117		1.04	0.3576
Light at the ground (μmol m-2 s-1)	Basal Area	1	117	−8.34	1.97	0.1632
	Treatment	2	117		4.78	0.0101
Soil moisture (15 cm) (% content)	Basal Area	1	53	0.08	0.96	0.3322
	Treatment	2	53		1.79	0.177
Soil moisture (30 cm) (% content)	Basal Area	1	53	0.02	0.03	0.8576
	Treatment	2	53		1.79	0.1768
Soil temperature (15 cm) (°C)	Basal Area	1	53	−0.03	5.63	0.0213
	Treatment	2	53		0.74	0.4827
Soil temperature (30 cm) (°C)	Basal Area	1	53	−0.03	6.85	0.0115
	Treatment	2	53		1.4	0.2564

Table 3

Statistical results from multiple regression analyses examining the influence of midstory treatments and overstory basal area on microclimatic conditions within planted subplots in the Sandhill ecoregion of North Carolina, USA.

Longleaf Pine Seedling	Effect	Numerator DF	Denominator DF	Parameter Estimate	F-Test	P-Value
Survival (%)	Basal Area	1	117	0.21	1.19	0.2782
	Treatment	2	117		6.15	0.0029
Biomass (g)	Basal Area	1	117	−0.30	60.13	<0.0001
	Treatment	2	117		7.78	0.0007
Root collar diameter (cm)	Basal Area	1	117	−0.02	44.05	<0.0001
	Treatment	2	117		3.29	0.0405
Brownspot infection (%)	Basal Area	1	117	−0.71	19.14	<0.0001
	Treatment	2	117		1.2	0.3060

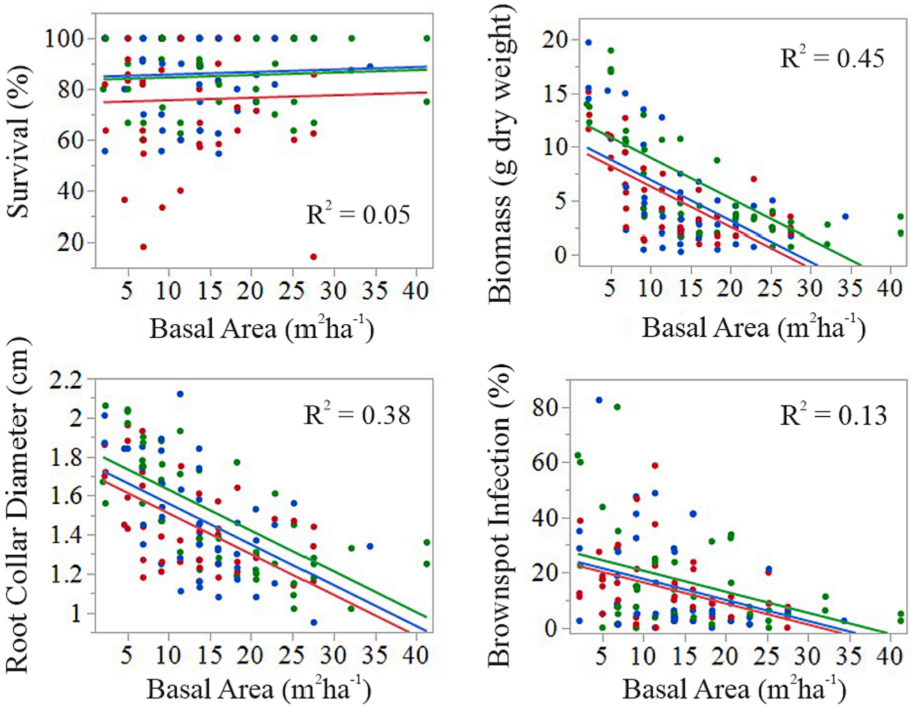

Fig. 2. Results of mixed-effects analyses of covariance (ANCOVA) examining the influence of midstory treatment (no retention (green), one-year retention (blue), four-year retention (red)) and overstory basal area on longleaf pine seedling survival, aboveground biomass, root collar diameter, and brownspot infection in the Sandhill ecoregion of North Carolina, USA. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 4

Statistical results from multiple regression analyses examining the effects of midstory hardwood stem density, overstory basal area, shrub cover, forb cover, and wiregrass cover, on longleaf pine seedling survival, aboveground biomass development, root collar development, and brownspot infection across midstory treatments in the Sandhills Ecoregion of North Carolina, USA. Bolded factors were considered significant at α = 0.05.

		Four-Year Retention			**One-Year Retention**			**No Retention**		
Longleaf Pine	Factor	Parameter Estimate	F-Test	P-Value	Parameter Estimate	F-Test	P-Value	Parameter Estimate	F-Test	P-Value
	H. Stems	0.36 (0.21)	2.84	0.0998	−0.23 (0.14)	2.52	0.1204	n/a	n/a	n/a
	B.Area	0.12 (0.56)	0.04	0.8256	0.40 (0.35)	1.3	0.2596	0.36 (0.24)	2.20	0.1458
Survival	Shrubs	0.49 (0.59)	0.67	0.4146	0.81 (0.52)	2.35	0.1329	0.31 (0.36)	0.73	0.3949
Adjusted R^2	Forbs	0.23 (0.84)	0.07	0.7805	0.39 (0.28)	1.89	0.1765	0.56 (0.29)	3.59	0.0653
<0.01,0.04, <0.01	Wiregrass	−0.16 (0.28)	0.33	0.5640	0.21 (0.22)	0.93	0.3408	0.13 (0.14)	0.84	0.3644
	H.Stems	0.02 (0.02)	0.89	0.3498	−0.01 (0.03)	0.07	0.7680	n/a	n/a	n/a
	B.Area	**−0.29 (0.07)**	**16.81**	**0.0002**	**−0.42 (0.09)**	**19.33**	**<0.0001**	**−0.32 (0.05)**	**30.44**	**<0.0001**
Biomass	Shrubs	0.09 (0.07)	1.44	0.2366	0.01 (0.14)	0.01	0.9255	−0.04 (0.08)	0.33	0.5645
Adjusted R^2	Forbs	0.15 (0.10)	2	0.1645	0.07 (0.07)	0.85	0.3606	0.05 (0.06)	0.59	0.4446
0.41, 0.30, 0.56	Wiregrass	-<0.01 (0.03)	0.01	0.9022	0.01 (0.06)	0.05	0.8207	0.03 (0.03)	1.29	0.2617
	H.Stems	<0.01 (<0.01)	4.01	0.0592	<0.01 (<0.01)	0.07	0.7908	n/a	n/a	n/a
	B.Area	**−0.01 (<0.01)**	**4.96**	**0.0317**	**−0.02 (<0.01)**	**20.71**	**<0.0001**	**−0.01 (<0.01)**	**24.99**	**<0.0001**
Root Collar	Shrubs	<0.01 (<0.01)	1.79	0.1879	-<0.01 (<0.01)	0.58	0.4495	<0.01 (<0.01)	0.52	0.4743
Adjusted R^2	Forbs	<0.01 (<0.01)	1.49	0.2293	<0.01 (<0.01)	0.71	0.4025	<0.01 (<0.01)	3.75	0.0597
0.27, 0.31, 0.52	Wiregrass	<0.01 (<0.01)	0.25	0.6141	-<0.01 (<0.01)	0.01	0.9314	<0.01 (<0.01)	0.36	0.5507
	H.Stems	−0.20 (0.11)	3.03	0.0892	−0.12 (0.16)	0.54	0.4649	n/a	n/a	n/a
	B.Area	**−0.87 (0.30)**	**8.41**	**0.0061**	**−0.89 (0.40)**	**4.97**	**0.0316**	**−0.69 (0.29)**	**5.73**	**0.0214**
Brownspot	Shrubs	−0.38 (0.31)	1.44	0.2360	−0.27 (0.59)	0.21	0.6452	−0.29 (0.32)	0.85	0.3597
Adjusted R^2	Forbs	−0.66 (0.44)	2.17	0.1487	−0.38 (0.32)	1.43	0.2383	−0.66 (0.46)	2.05	0.1595
0.11, 0.07, 0.20	Wiregrass	−0.04 (0.15)	0.09	0.7591	−0.08 (0.25)	0.1	0.7484	0.05 (0.14)	0.12	0.7275

*Adjusted R^2 values are listed in the following order: four-year retention, one-year retention, no retention.

density significantly affected longleaf pine seedling photosynthetic nitrogen use efficiency (Table 5).

4. Discussion

4.1. Hardwood facilitation

Results indicate that one-year of midstory hardwood retention had negligible effects on longleaf pine seedling survival but negatively affected aboveground biomass development. In contrast, four-year midstory hardwood retention negatively affected seedling survival and all growth metrics. Taken together, these findings indicate that facilitation is not occurring and suggest that the relationship between longleaf pine and xerophytic hardwood species becomes increasingly antagonistic over time. Our results also contradict observational evidence of longleaf pine facilitation on sandhill sites and theories of increased facilitation in stressful environments (Maestre et al., 2009; Loudermilk et al., 2016; Johnson et al., 2021). Nevertheless, with the exception of stomatal conductance, longleaf pine physiological performance was unaffected by hardwood stem density suggesting that competition between species is modest but cumulative in nature.

Several factors likely contributed to the expression of competition over facilitation. Part of this outcome may be related to the modest effect of hardwood retention on the microenvironment. Subplot measurements indicate that four-year hardwood retention reduced light availability at the forest floor by 27% but failed to increase moisture availability or decrease soil temperature compared to midstory removal treatment. This minimal shading effect on the growing environment, combined with the observed reduction in seedling stomatal conductivity to increasing midstory hardwood stem density, indicates that hardwood retention did not ameliorate chronic moisture stress. Moisture availability measurements also suggest that hydraulic lift was not promoted by hardwood retention as has been demonstrated by previous work on sandhill sites (Espeleta et al., 2004). We suspect that moisture dynamics are an important underlying factor to longleaf pine facilitation on sandhills sites given their low capacity for moisture retention, relatively open stand structure, and vulnerability to moisture stress while in the grass stage (Provencher et al., 2001; Hart et al., 2020). It should be recognized, however, that the midstory hardwoods examined in this study were relatively small sprouts, resulting from decades of repeated prescribed burning at McCain, and possessed relatively small crowns to shade the understory compared to a typical midstory tree. Nevertheless, xerophytic hardwood species such as turkey oak are known to maintain relatively open crowns on xeric sites potentially reducing the importance of crown size (Hiers et al., 2007).

Another plausible scenario is that our study did not examine the most important facilitative mechanism. Surface fire is a common disturbance in longleaf pine woodlands and may alter the interaction between longleaf pine and xerophytic hardwoods (Rother et al., 2020). Grass stage longleaf pine seedlings are generally fire resistant (Brethauer et al., 2021); however, high intensity burns can kill small seedlings (Knapp et al., 2018). Growing beneath a hardwood midstory may improve survival; even though xerophytic hardwood litter is highly flammable, it tends to produce lower fire intensity compared to longleaf pine litter (Fonda, 2001; Kane et al., 2008; Varner et al., 2021; Magee et al., 2022). Surviving longleaf pine seedlings would also benefit from an ephemeral reduction in hardwood competition providing an opportunity to initiate height growth (Rebertus et al., 1989). Future studies are encouraged to explore this biologically important process.

One surprising result was the unresponsiveness of BSNB to growing conditions. While minimal infection rates were anticipated in low light environments featuring heavy overstory basal area and midstory hardwood retention, we expected that the opening of stomates in response to elevated light availability would promote BSNB infection in areas with low overstory density and midstory hardwood removal (Parris and Killewbrew, 1969; Kais, 1975). We can only speculate on the cause of this unexpected result, but we suspect that drought induced stomatal closure may constrain BSNB on sandhill sites. To our knowledge, no studies have compared BSNB infection rates across light environments on sites with varying moisture holding capacity.

4.2. Overstory and understory effects

Asymmetric competition from mature trees is recognized as an

Table 5
Statistical results from multiple regression analyses examining the effects of overstory basal area and hardwood stem density on longleaf pine foliar N, photosynthesis, transpiration, stomatal conductance, intrinsic water use efficiency, water use efficiency, and photosynthetic nitrogen use efficiency in the Sand Hills Ecoregion of North Carolina, USA. Bolded factors were considered significant at $\alpha = 0.05$.

Longleaf Pine	Factor	Parameter Estimate	F-Test	P-Value	Adjusted R^2
Foliar N (%)	**Basal Area**	**−0.0027 (0.0012)**	**4.51**	**0.0376**	0.05
	Hardwood Stems	−0.0005 (0.0004)	1.57	0.2144	
Photosynthesis (nmol g^{-1} s^{-1})	**Basal Area**	**−0.4897 (0.1839)**	**7.08**	**0.0099**	0.10
	Hardwood Stems	−0.1186 (0.0684)	3.01	0.0878	
Transpiration (mmol m^{-2} s^{-1})	**Basal Area**	**−0.0814 (0.0247)**	**10.80**	**0.0017**	0.14
	Hardwood Stems	−0.0172 (0.0092)	3.51	0.0656	
Stomatal conductance (g_s; mol m^{-2} s^{-1})	**Basal Area**	**−0.0018 (0.0005)**	**9.65**	**0.0029**	0.15
	Hardwood Stems	**−0.0005 (0.0002)**	**5.90**	**0.0181**	
Intrinsic water use efficiency (iWUE; μmol mol^{-1})	Basal Area	0.0970 (0.1680)	0.33	0.5655	<0.01
	Hardwood Stems	0.0252 (0.0624)	0.16	0.6872	
Water use efficiency (d13C)	**Basal Area**	**0.0096 (0.0041)**	**5.50**	**0.0223**	0.01
	Hardwood Stems	−0.0004 (0.0015)	0.07	0.7854	
Photosynthetic nitrogen use efficiency (PNUE)	Basal Area	−0.0256 (0.0211)	1.46	0.2305	<0.01
	Hardwood Stems	−0.0088 (0.0078)	1.27	0.2633	

influential process in community assembly within forests and played a prominent role in this study (Pretzsch and Biber, 2010; Picard, 2019). Longleaf pine overstory cover has been reported to have facilitative, competitive, and neutral effects on seedling survival in studies examining gap dynamics (Palik et al., 2003; McGuire et al., 2001; Mitchell et al., 2006; Pecot et al., 2007). While our study did not investigate the influence of gap size, our results indicate that overstory basal area had little impact on seedling survival. This result is somewhat surprising considering that McCain is a drought-prone site where overstory facilitation is thought to potentially occur (Jack and Pecot, 2017). We suspect the duration of our study may have contributed to the neutral effects of overstory basal area, as longleaf pine seedlings can persist in the grass stage well-beyond the duration of this study (Wahlenberg, 1946). In contrast to survival, increasing overstory basal area negatively influenced longleaf pine seedling root collar and aboveground biomass development. Competitive overstory effects on seedling growth are well-documented in longleaf pine woodlands and have been identified as a potential cause of regeneration domes in the center of canopy gaps and likely contribute to the development of density-dependent recruitment patterns in longleaf pine woodlands (Schwarz, 1907; Kara et al., 2017; Brockway and Outcalt, 1998; Johnson et al., 2021).

Initial assessments of longleaf pine seedling performance across shrub and herbaceous vegetation indicated that neither vegetation type was exerting a strong competitive or facilitative effect. This result was somewhat surprising considering that understory vegetation can either facilitate or compete with longleaf pine seedlings depending on life history stage and stand conditions (McGuire et al., 2001; Pecot et al., 2007; Iacona et al., 2012; Miller et al., 2019). We suspect the presence of a relatively dense overstory across most of our blocks contributed to this result, as many previous studies reporting facilitative or competitive effects were conducted in harvest gaps or in savannas where the influence of overstory trees is reduced (Brockway and Outcalt, 1998; McGuire et al., 2001; Pecot et al., 2007; Miller et al., 2019). Consequently, our results suggest that interactions between longleaf pine seedlings and shrub and herbaceous vegetation are overwhelmed by the influence of the overstory in stands managed at or above a woodland density.

5. Conclusions

Reducing competition has been the focus of restoration efforts in longleaf pine woodlands. However, recent reports of hardwood facilitation of longleaf pine on xeric sites have brought this paradigm into question. Our results indicate that hardwood retention becomes detrimental to longleaf pine seedlings after four-years. Taken in consideration with previous investigations of minimal-to-inhibitory effects of hardwood retention on seed depredation and germination (Willis et al., 2019 & 2021), these results indicate that xerophytic hardwoods are not facilitative towards longleaf pine at the seed, seedling, or bolting phases on sandhill sites. Yet, it is important to recognize that this study only pertains to grass stage seedlings and was conducted in the absence of fire and thus may not be capturing important facilitative effects. Consequently, we encourage future studies to consider the use of prescribed fire and different life history stages when exploring interactions in longleaf pine woodlands.

While xerophytic hardwoods provided modest competition for longleaf pine seedlings, the presence of mature longleaf pine presented a stronger impediment to seedling development and physiological function compared to the midstory. Thus, restoration treatments aiming to promote longleaf pine emergence from the grass stage should prioritize treatments that reduce overstory density rather than the midstory.

CRediT authorship contribution statement

J.L. Willis: Conceptualization, Methodology, Formal analysis, Investigation, Data curation, Writing – original draft, Writing – review & editing, Visualization, Project administration, Funding acquisition. **H.J. Renninger:** Conceptualization, Methodology, Investigation, Writing – review & editing. **D.K. Schnake:** Investigation, Writing – review & editing. **H.D. Alexander:** Conceptualization, Writing – review & editing.

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

Data will be made available on request.

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