Forest Ecology and Management 589 (2025) 122782

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Longleaf and shortleaf pine seedling fire tolerance is more sensitive to shade than encroaching hardwood species

John L. Willis [a,*], Ajay Sharma [b], Timothy M. Shearman [b], J. Morgan Varner [c], Justin McKeithen [d]

[a] USDA Forest Service, Southern Research Station, 521 Devall Drive, Auburn, AL 36849, USA
[b] College of Forestry, Wildlife and Environment, Auburn University, 602 Duncan Drive, Auburn, AL 36849, USA
[c] Tall Timbers Research Station, 13093 Henry Beadel Drive, Tallahassee, FL 32312, USA
[d] West Florida Research and Education Center (WFREC), University of Florida, 5988 Highway 90, Building 4900, Milton, FL 32583, USA

ARTICLE INFO

Keywords:
Mesophication
Non-structural carbohydrates
Quercus, *Pinus*
Restoration
Shortleaf pine
Sprouting

ABSTRACT

Traits enabling fire tolerance are essential for plant persistence in fire-prone ecosystems. Yet, fire tolerance alone fails to account for other pre-existing forms of stress that could modify species tolerance of fire. Shade is an increasingly important form of stress on the contemporary forested landscape, as widespread fire exclusion has hastened the transition of many open woodlands into closed canopy forests. To investigate the interaction of fire and shade in the longleaf pine ecosystem, we established a shade house experiment examining seedling mortality and recovery of six native subtropical tree species from prescribed fire applied under four levels of shade (unshaded, 63 %, 73 %, 90 %) in northwest Florida, USA. Longleaf and shortleaf pine mortality consistently increased with shade and were best predicted by shade intensity and degree of crown scorch. Resprouting became the primary survival mechanism of longleaf and shortleaf pine under increasing shade. Among encroaching species, mockernut hickory maintained the highest pre-fire non-structural carbohydrates (NSC) and experienced the lowest post-fire mortality; loblolly pine maintained the lowest pre-fire NSC and suffered the highest mortality. Survival of encroaching hardwood species was entirely dependent on resprouting across shade levels. Post-fire NSC recovery of northern red oak and mockernut hickory increased with shade intensity, while shortleaf pine NSC recovery declined with shade. Collectively, these results demonstrate that reducing pre-fire shade below 63 % will minimize longleaf and shortleaf pine mortality and accelerate post-fire NSC recovery compared to encroaching hardwood species.

1. Introduction

Interspecific differences in stress tolerance are foundational for predicting changes in forest demographics (Albert et al., 2015; McDowell et al., 2020; Adams et al., 2023). While no species directly benefits from stress, those capable of persisting benefit indirectly from reduced competition following local conspecific or interspecific mortality (Chin et al., 2023). Tolerance is acquired through the development of functional traits and life history strategies that mitigate the effects of chronic stress (Šímová et al. 2017). Nevertheless, long-lived species often experience interacting forms of stress (i.e. herbivory and drought or drought and shade) potentially eroding their tolerance to any individual form of stress (Valladares and Pearcy, 2002; Niinemets, 2010; Barton and Shiels, 2020). Consequently, studies incorporating multiple forms of stress are needed to accurately predict how species will respond to disturbance.

Low-intensity surface fire was a common form of stress shaping the structure and species composition of savannas and woodlands of North America (hereafter referred to as “open forests”) (Brown and Sieg, 1996; Wolf 2004; Guyette et al., 2012; Ryan et al., 2013; Hanberry et al., 2018;). Open forests were historically dominated by a limited number of tree species capable of surviving under a frequent fire regime and high light environments (Peterson and Reich 2001; Collins, 2020). Longleaf pine (*Pinus palustris*) and shortleaf pine (*P. echinata*) are among the most fire tolerant species in the world and dominated over 60 million hectares in the southeastern United States prior to European settlement (Frost 1993; Keeley, 2012; Anderson et al., 2016). Both species derive fire tolerance from their conservative early height growth strategy, rapid

* Corresponding author.
E-mail address: john.willis@usda.gov (J.L. Willis).

https://doi.org/10.1016/j.foreco.2025.122782
Received 31 October 2024; Received in revised form 31 March 2025; Accepted 2 April 2025
Available online 7 May 2025

bark growth, and ability to resprout as a seedling following top-kill (Farrar 1975; Jackson et al., 1999; Lilly et al., 2012). Longleaf pine has the additional advantage of beginning life in a "grass stage" where needles and buds are the only exposed tissues (Keeley and Zedler, 1998; He et al., 2012). Moreover, during the grass stage, longleaf pine maintains large reserves of non-structural carbohydrates (NSC) in its roots, which can be mobilized to facilitate tissue recovery following top-kill (Pile et al., 2017; Aubrey, 2022).

However, in many historically open forests, fire tolerance is not the primary factor affecting contemporary survival, as decades of fire exclusion have allowed fire-sensitive species to establish increasing resource competition (Hanberry et al., 2020; Tatina et al., 2024). Without fire, longleaf and shortleaf pine are rapidly outcompeted for growing space by shade intolerant encroaching species (e.g., loblolly pine (*P. taeda*), yellow-poplar (*Liriodendron tulipifera*)) creating closed canopy positions, while species more tolerant of shade (e.g., northern red oak (*Quercus rubra*), mockernut hickory (*Carya tomentosa*)) are better adapted to persist in sub-canopy positions (Niinemets and Valladares 2006). Consequently, longleaf and shortleaf pine seedlings fail to recruit in degraded open forests without subsequent disturbance (Hanberry, 2021; Pile-Knapp et al., 2024).

Efforts to restore degraded open forests generally involve reintroducing prescribed fire to improve the competitiveness of longleaf and shortleaf pine seedlings (Provencher et al., 2001; Varner et al., 2005; Guldin, 2019). However, the capacity of prescribed fire to alter competitive hierarchies may be compromised under shade, as any stress factor that restricts carbon assimilation may reduce fire tolerance (Drus et al., 2014). Potential effects of shade on fire tolerance include reductions in bark growth, stem size and NSC storage (Scott et al., 2013). The presence of shade may also shift resource allocation toward leaf area production over root growth further compromising fire tolerance (Chmura et al., 2017). Longleaf and shortleaf pine may be particularly vulnerable to reduced fire tolerance in low light environments, as neither species can tolerate deep shade for extended periods (Groninger et al., 1996; Niinemets and Valladares 2006; Samuelson and Stokes, 2012). Yet, little is known about the degree of shading longleaf and shortleaf pine can endure before fire tolerance begins to decline.

Prescribed fire efficacy is also affected by the traits of encroaching species. For example, temperate hardwood species are more likely to resprout following fire-induced top-kill than loblolly pine (Del Tredici, 2001; Bradley et al., 2016; Keyser, 2019). Encroaching species post-fire recovery may also correspond with interspecific differences in shade tolerance, as tolerant species invest heavily in carbohydrate storage at the expense of aboveground growth to maximize survival and resprouting ability in shaded environments (Kobe, 1997; Poorter and Kitajima, 2007; Poorter et al., 2010). Consequently, mockernut hickory and northern red oak may be better adapted for tolerating the combined effects of fire and shade than loblolly pine and yellow-poplar based on their respective shade tolerance (Groninger et al., 1996; Niinemets and Valladares 2006; Rebbeck et al., 2012; Knapp et al., 2021). If true, this finding could explain why restoration efforts utilizing prescribed fire alone often struggle to control shade tolerant species in degraded open forests with a long history of fire exclusion (Hutchinson et al., 2005; Alexander et al., 2008; Schweitzer et al., 2016; Howie et al., 2024).

To explore these tradeoffs, we established a shade house experiment examining the interactive effects of prescribed fire and shade on six southeastern tree species in northwest Florida, USA. Our objectives were to quantify interspecific differences in pre-fire NSC storage and post-fire survival mechanism (stem vs. resprout), growth, and NSC recovery. Specifically, we predicted: 1) pre-fire NSC storage would increase with species shade tolerance across shade levels; 2) post-fire mortality of shade intolerant species would increase with shade; 3) sprouting would become the dominant survival mechanism for all species with increasing shade; and 4) growth and NSC recovery of burned seedlings of all species would decrease with increasing shade intensity. The results of this study will improve our fundamental understanding of how interacting forms of stress alter forest stand dynamics and can inform efforts to restore longleaf and shortleaf pine within degraded southeastern woodlands.

2. Materials and methods

2.1. Study site

Our study was conducted at the University of Florida Jay Research Facility located in Santa Rosa County, Florida, USA (30.773000 −87.143950). The research facility is located within the Southeastern Plains Ecoregion. Annual temperature and precipitation average 19 °C and 1700 mm, respectively (NCEI 2024). Temperature and precipitation peak during the warm, humid summer months (June-August). The site is located approximately 62 m above sea level on Orangeburg series soils (Fine-loamy, kaolinitic, thermic Typic Kandiudults) (USGS, 2020; Soil Survey Staff). The Orangeburg series features loamy sand that is very deep, well-drained, and moderately permeable. The site was previously used to grow pumpkins before sitting fallow for one growing season. Slope at the research facility is negligible (<1 %).

2.2. Experimental design

Our experiment was conducted within three shade houses and one unshaded area (20.1 m × 20.1 m). A series of chemical and mechanical treatments were conducted to provide experimental control over weedy vegetation prior to planting. In July 2021, each area was sprayed with a mixture of imazapyr (1 % solution) and glyphosate (2 % solution) to kill existing vegetation. We then mowed and lightly tilled the soil in August to stimulate seedbank germination. Herbaceous vegetation arising from the seedbank was then sprayed with a mixture of glyphosate (2 % solution) sulfometuron methyl (140.1 g ha^{-1}) in October to minimize competition in the planted areas. Weeding and spot spraying (glyphosate, 2 % solution) were periodically conducted throughout the experiment to control herbaceous competition.

To capture a range of shade and fire tolerance, we selected six native southeastern tree species: longleaf pine, shortleaf pine, loblolly pine, northern red oak, yellow-poplar, and mockernut hickory (Table 1). All seedlings were obtained from local nurseries. Each area was hand planted in January 2022 (Fig. 1). Bare root (1–0 stock) seedlings were planted for all species except longleaf pine (containerized seedlings (1–0 stock). All deciduous species were established with planting shovels. Loblolly and shortleaf pine were planted with a standard Dibble bar while longleaf pine was planted with a Dibble bar designed for plugs.

Table 1
Interspecific differences in seedling light compensation point, sapling bark thickness, and seedling sprouting potential.

Species	Seedling Light Compensation Point (μmol $m^{-2}.s^{-1}$)	Sapling Bark Thickness (cm)	Seedling Sprouting Potential
Northern red oak	15.7[1]	0.06[5]	High[7]
Yellow-poplar	31.2[2]	0.24[6]	Moderate[7]
Mockernut hickory	8.4[−3]	0.18[6]	N/A
Shortleaf pine	N/A	0.37[5]	High[8]
Loblolly pine	42.3[2]	0.38[5]	Low[8]
Longleaf pine	9.5[4]	0.49[5]	Moderate[9]

[1] Rebbeck et al. (2012)
[2] Groninger et al. (1996)
[3] Knapp et al. (2021)
[4] Samuelson and Stokes (2012)
[5] Jackson et al. (1999)
[6] Shearman et al. (2018)
[7] Keyser (2019)
[8] Will et al. (2013)
[9] Knapp et al. (2018)

Fig. 1. Seedlings planted in the unshaded area and one of the three shade houses in January 2022.

Seedlings were planted randomly at a 0.9 m × 1.2 m spacing within a grid pattern. Each area was planted with 176 seedlings (~ 29 seedlings per species) and left unshaded for two months to aid seedling establishment. Soil moisture (10 cm depth) was monitored regularly throughout the experiment with a time domain reflectometry soil moisture meter (Fieldscout 150, Spectrum Technologies, Aurora, Illinois, USA). Seedlings were watered to saturation at any point in the experiment once soil moisture reached 10 percent to control for drought stress. At the end of March (two months after planting), each shade house was covered with one level of shade cloth (63 % (low), 73 % (medium), and 90 % (high)). Photosynthetically active radiation was measured with a quantum sensor (Apogee Instruments, Logan, Utah, USA) at four locations in each planted area and declined predictably with increasing shade (1618 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (unshaded), 594 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (low), 443 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (medium), and 158 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (high)). Approximately one meter, on the sides, and three meters, on the ends, of each hoop house was left open to promote air circulation. Seedlings were grown in their respective environments for one growing season without manipulation.

We conducted an initial seedling census in May 2023 to establish a baseline population (Table 2). All seedlings were surveyed for living status and their collar diameter (RCD) (mm) and height (cm) were measured. Following the census, we added longleaf pine needles (4481 kg ha^{-1}) to each planting area approximating fuels in nearby mature forests to standardize fuel conditions (Ottmar and Vihnanek, 2000). Complete ground cover was targeted for the fuel additions to promote consistent fire behavior. Fuel was added one month prior to burning to allow it to settle and equilibrate with ambient environmental conditions (McDaniel et al., 2021). All longleaf pine needles were purchased in bundles from a local pine straw vendor.

On the morning of the burn, we removed the shade cloth from each treatment. Fire lines were installed around the southwest corner of each planted area to create an unburned control containing 3–5 seedlings of each species (Table 2). Seedlings growing on the edge of the unburned controls were shielded from heat with fire shelters.

Each planted area was burned between 10:50 AM and 12:48 PM local time on 25 May 2023 (Fig. 2) (Table 3). One-hour woody fuel moisture at the time of burning ranged from 5 % to 11 % (dry weight basis). Ambient air temperature, relative humidity (50.6–56.6 %), wind speed (5.5–6.9 $km.hr^{-1}$) and wind direction (NE) were measured with a Kestrel 3000 pocket weather meter immediately preceding ignition and were similar across burns (Kestrel Instruments, Neilsen-Kellerman Company, Boothwyn, Pennsylvania, USA) (Table 3). A drip torch (3:2 diesel-to-gasoline mix) was used to ignite the entire east side of the planted areas with the intent of creating a head fire. Rate of spread (ROS) was measured using rebar positioned at one-meter intervals from the ignition line and was similar across burns (0.005–0.012 $m.s^{-1}$). Extinguishment time was recorded as the time at which flames were no longer visible. Flame length was visually estimated every 30 seconds with the aid of height poles positioned near the burn boundary and was representative of surface fire (e.g., 0.7–0.9 m height) across burns (Table 3). Measurements of ROS and flame length were not taken until the flaming front had traveled one meter from the ignition point to better represent within treatment fire behavior. Fire temperature was measured at six equally spaced interior locations in each planted area. Four thermocouple probes (K-type thermocouples, Omega Engineering, Inc., Stratford, Wisconsin, USA) were fastened to rebar at four heights (ground level, 0.5 m, 1.0 m, and 1.5 m) at each measurement location. Temperature data were recorded with a HOBO® datalogger (HOBO UX120 Data Logger, Onset Computer Corporation, Cape Cod, Massachusetts, USA). Ground-level maximum thermocouple temperature averaged 401°C across all treatments and declined by 78 % at 1.5 m height. Shade cloth was reattached to each shade house within five hours of the burn.

Table 2
The initial starting population of northern red oak, yellow poplar, mockernut hickory, shortleaf pine, loblolly pine, and longleaf pine seedlings one-year post planting. Numbers in parentheses detail the number of seedlings grown in the unburned controls.

Species	Unshaded (0 %)	Low Shade (63 %)	Medium Shade (73 %)	High Shade (90 %)
Northern red oak	19 (4)	19 (4)	18 (4)	24 (5)
Yellow-poplar	10 (4)	13 (4)	7 (4)	8 (3)
Mockernut hickory	17 (5)	20 (4)	23 (5)	23 (5)
Shortleaf pine	23 (4)	17 (4)	21 (4)	17 (4)
Loblolly pine	16 (4)	14 (3)	10 (3)	15 (5)
Longleaf pine	21 (4)	18 (4)	22 (4)	14 (5)

2.3. Post-fire measurements

Each seedling was assessed for fire damage one week after the burn. Specifically, we measured percent crown scorch, percent crown consumption (Varner et al., 2021), and a binary sprouting status. A final census was conducted in February 2024 to assess seedling mortality, RCD growth, and height growth.

2.4. Non-structural carbohydrates

One day prior to burning, we randomly selected four seedlings of each species in each planted area to assess pre-burn NSC storage (n = 92). Yellow-poplar seedlings were not sampled in the medium shade area due to low initial survival. Selected seedlings were unearthed with shovels, cut at the root collar, and stripped of all foliage. Tissue

Fig. 2. Post burn environment under low, moderate, and high shade. Seedlings in the unburned control can be seen in the rear of the shade house.

Table 3
Fire weather and behavior in each planted area taken one minute prior to ignition.

Climatic Conditions	Unshaded (0 %)	Low Shade (60 %)	Medium Shade (70 %)	High Shade (85 %)
Ignition time	10:50	11:22	11:48	12:20
Extinguish time	11:07	11:38	12:08	12:48
Air temperature (°C)	27.1	26.1	27.5	28.8
Relative humidity (%)	56.6	50.6	51.3	52.4
Wind speed (km.hr^{-1})	6.9	6.4	6.0	5.5
Wind direction	NE	NE	NE	NE
Rate of spread (m.s^{-1})	0.010	0.012	0.012	0.005
Flame length (cm)	25.8	34.8	42.3	25.5

samples were then obtained from the first 10 cm of the tap root, two first order lateral roots, and the main stem. All tissue samples were combined within five minutes (at the seedling level) in a paper bag and placed in a drying oven for one hour at 100 °C. Thereafter, we reduced oven temperature to 55 °C for an additional 48 hours of drying to deactivate enzyme activity (Pelletier et al., 2010). Dried tissues were then ground to < 0.5 mm in a Wiley Mill. Samples were then shipped to the United States Forest Service Analytical Laboratory in Raliegh North Carolina for analysis. Sample starch and sugar content was determined with an Astoria 2 micro-segmented flow analyzer (Astoria-Pacific, Inc., Clackamas, Oregon USA) using the methods detailed in Ward and Deans (1993).

One-week following the final measurement in February 2024 (nine months post-burn), we harvested additional seedlings to determine NSC recovery. Between two and six burned and control seedlings of each species were sampled in each planted area based on the remaining population. High levels of mortality precluded harvesting yellow-poplar and loblolly pine. Sample processing and analysis followed the above-described procedures.

2.5. Statistical analyses

Our analyses consisted of multiple tests exploring different aspects of seedling mortality and recovery across species and shade treatments. All analyses were conducted using R Studio version 4.4.1 (R Studio Team 2020). Seedling mortality was modeled with exact logistic regression in the logistf package to account for complete separation (Heinze and Schemper, 2002; Heinze et al., 2023). The full model contained the main effects of species (nominal), shade (nominal), and the interaction between species × shade on seedling mortality. While shade had an inherent order to its levels, we considered it a nominal factor to investigate its interactive effects with fire directly related to our study objectives. Moreover, the specific order of the shade levels was inconsequential to our interpretation of the analysis. Model fit was evaluated through examining plots of studentized residuals and quantile–quantile plots. Outlier influence was assessed with a Cook's distance statistic. Points with a distance statistic > 1 were evaluated for leverage strength by removing the outlier and re-running the model to check for changes in factor significance (Ramsey and Schafer, 2012). Outlier removal had no effect on parameter significance; thus, all points were retained in the final analyses. Statistically significant ($p < 0.05$) main effects or interactions were further explored with Tukey's post-hoc tests in the emmeans package (Lenth, 2016).

To develop a mechanistic understanding of seedling mortality, we first assessed the relative influences of fire injury, shade, and seedling morphological characteristics in species-specific LASSO (Least Absolute Shrinkage and Selection Operator) models using the glmnet package (Friedman et al., 2010). A k-fold cross-validation approach was used to select a λ value. Factors included in the models included shade, pre-burn RCD, pre-burn height, percent crown scorch, and percent crown consumption. Shade was considered a continuous factor in these analyses to assess its relative effect compared to other factors measured on a common scale. Then, using the factors identified in the Lasso models, we constructed multiple logistic regression models to identify the most parsimonious explanation for seedling mortality. The suite of models evaluated varied in complexity from a full model containing the main effects of all factors identified by the Lasso model to a null model containing only an intercept. We then used Akaike's information criterion (AICc) to select the best fitting model (Burnham and Anderson, 2004). Mortality models were not constructed for mockernut hickory (which had minimal mortality) and loblolly pine (which had minimal survival).

In addition to mortality, we also examined seedling pre-burn NSC using a linear model (R Studio Team 2020). The statistical model was a full factorial involving species (categorical) and shade (categorical) and followed the same procedures as previously described. However, pre-burn NSC required a square root transformation to satisfy the assumptions of normality.

To assess seedling recovery, we used exact logistic regression to examine whether residual seedlings survived fire through sprouting or resisting top-kill. This model contained the same factorial structure of species (categorical), shade (categorical), and their interaction and followed the previously described fitting procedures. Loblolly pine was excluded from this test due to low post-fire survival, Additionally, all hardwood species were excluded, as all residual seedlings survived via sprouting.

High interspecific variation in residual survival among species across the shade gradient compelled us to develop species-specific models exploring the growth and NSC status of surviving burned and unburned seedlings. We used linear models to the growth (diameter and height) and NSC storage of burned and unburned seedlings. The full model included the main effects of shade (categorical), fire (categorical), and the interaction between fire and shade. Model assumptions were checked following the above-described procedures. Loblolly pine and yellow-poplar were not included from these analyses due to low post-fire survival.

3. Results

3.1. Post-fire seedling mortality

Mortality varied significantly among species across shade levels (F=1.77, p = 0.0380). Loblolly pine experienced the highest post-fire mortality rate (88–96 %) of any species and had significantly higher post-fire mortality than mockernut hickory under each shade level (69–87 %) (Fig. 3). Moreover, loblolly pine was 75–76 % more likely to be killed by fire in the absence of shade than either shortleaf or longleaf pine, respectively (Fig. 3). Consistent with our initial hypothesis, mockernut hickory experienced minimal post-fire mortality (7–19 %) across shade levels and was significantly less likely to be killed by fire under low, medium, and high shade (64–79 %) than shortleaf pine (Fig. 3). Additionally, yellow-poplar mortality was 67 percent higher than mockernut hickory under low shade (Fig. 3).

Crown scorch (0.007), crown consumption (0.005), and shade (0.002) were identified as factors increasing the likelihood of longleaf pine mortality. In contrast, increasing pre-fire root collar size decreased (-0.001) longleaf pine post-fire mortality. The most parsimonious model predicting longleaf pine mortality contained the main effects of crown scorch and shade (Appendix 1) ($R^2 = 0.25$); within which, a ten percent increase in crown scorch and shade increased longleaf pine mortality by 1.1 and 0.3 percent, respectively (Table 4).

Like longleaf pine, shade (0.006) and crown scorch (0.005) were identified as mortality promoting factors for shortleaf pine, while increasing RCD (-0.006) reduced mortality. Shortleaf pine post-fire mortality was also best predicted by the model containing the main effects of crown scorch and shade (Appendix 1) ($R^2 = 0.45$). With shortleaf pine, increasing crown scorch and shade by 10 percent increased seedling mortality by 0.8 and 0.4 percent, respectively (Table 4).

Pre-fire seedling height (-0.003) was the only factor found to influence northern red oak seedling mortality. However, the model containing pre-fire seedling height was less effective at predicting northern red oak mortality than the null model. Similarly, no factors were identified as having a strong impact on yellow-poplar mortality.

3.1.1. Seedling recovery

All living hardwood seedlings survived fire through sprouting. In contrast, longleaf and shortleaf pine survived fire through a combination of sprouting and resisting top-kill depending on the light environment (Fig. 4). Shade significantly affected the survival mechanism of both species, as seedlings were 46 and 65 percent more likely to survive fire through resisting top-kill in the absence of shade compared to medium and high shade, respectively (F = 4.71, P = 0.0053) (Fig. 4).

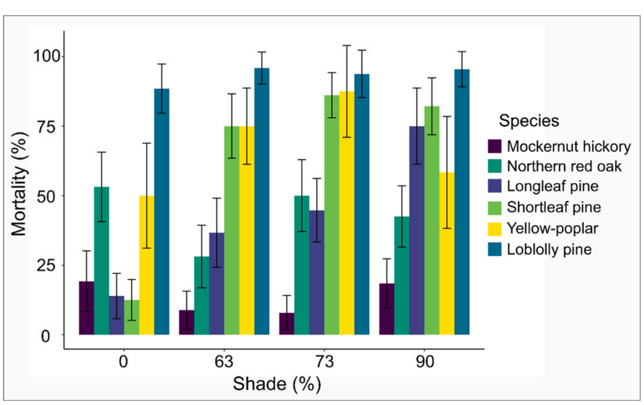

Fig. 3. The effect of shade intensity on the mortality of burned and unburned mockernut hickory, longleaf pine, northern red oak, shortleaf pine, loblolly pine, and yellow-poplar seedlings. Note that mortality does not include individuals that were top-killed by fire and then sprouted. Mortality was estimated from the exact logistic regression model. Error bars are one standard deviation from the mean.

Table 4
Logistic regression models describing the effects of shade and crown scorch on longleaf and shortleaf pine mortality.

Species	Coefficients	Estimate	Standard Error	Z -Value	P > Z	R^2
Longleaf Pine	Intercept	−12.17	3.94	−3.09	0.0019	0.25
	Shade	0.03	0.01	2.56	0.0104	
	Crown Scorch	0.11	0.04	2.63	0.0086	
Species	Coefficients	Estimate	Standard Error	Z -Value	P > Z	R^2
Shortleaf Pine	Intercept	−9.23	3.79	−2.44	0.0149	0.45
	Shade	0.04	0.01	3.49	0.0005	
	Crown Scorch	0.08	0.04	2.03	0.0422	

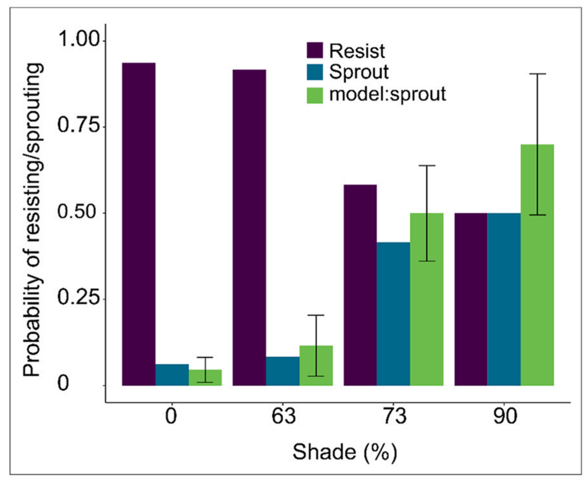

Fig. 4. The effect of shade on longleaf and shortleaf pine sprouting post-fire. Resist and sprouting probability are total proportions observed. Model:sprout probability is based on exact logistic regression model. Error bars are one standard deviation from the mean.

Post-fire growth varied widely among species. Longleaf pine was significantly affected by the combination of fire and shade, as the average RCD of unburned seedlings grown under full sun, low shade, and moderate shade was consistently 33 percent larger than those recovering from fire (Fig. 5; F = 3.74, P = 0.0181). However, the difference in RCD between burned and unburned longleaf pine seedlings was nearly identical under high shade (Fig. 5). A similar pattern emerged with height growth, as unburned longleaf pine seedlings grown under full sun and low shade were more than twice the height of burned seedlings (Fig. 6; F = 2.85, P = 0.0485); however, the height differential between burned and unburned longleaf pine seedlings became statistically undetectable under medium and low shade (Fig. 6).

In contrast to longleaf pine, shortleaf pine RCD was affected solely by shade (data not shown) (F = 8.40, P = 0.0002). The RCDs of shortleaf pine seedlings grown under full sun were 29 and 48 percent larger than those grown under medium and high shade, respectively. Trends in shortleaf pine height growth also differed from longleaf pine. Fire and shade significantly interacted to affect shortleaf pine height (F = 3.39, P = 0.0302), but, unlike longleaf pine, the height advantage of unburned seedlings was greatest under medium and low shade (Fig. 6).

Mockernut hickory RCD size was statistically affected by the combination of fire and shade (F= 2.82, P = 0.0463). Seedlings growing under full sun and low shade had comparable RCD size regardless of fire, but unburned seedlings RCD was approximately twice the size of burned

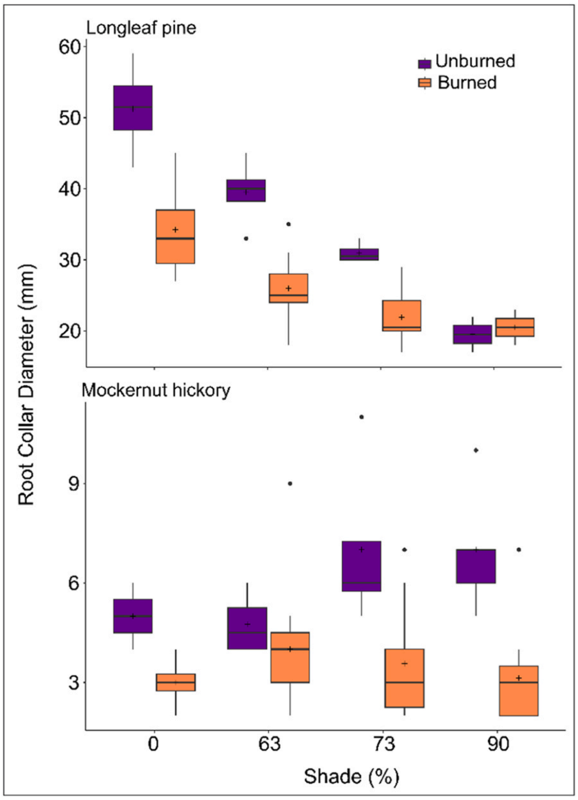

Fig. 5. The effect shade intensity on root collar diameter (RCD) size for burned and unburned longleaf pine and mockernut hickory seedlings. Horizontal bars within box plots represent the median RCD. Whiskers extend to the highest/lowest value within 1.5 times the inter-quartile range (IQR). Points represent values beyond 1.5 * IQR. Crosses represent mean root collar diameter.

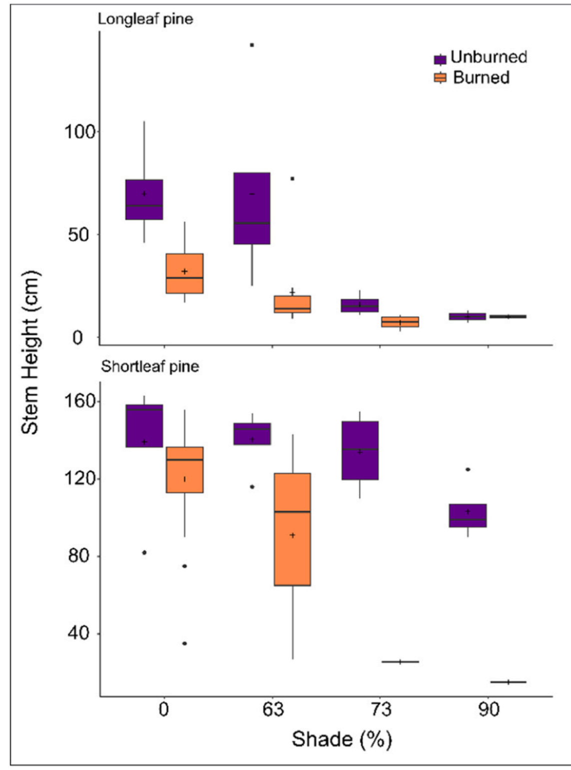

Fig. 6. The effect shade intensity on stem size for burned and unburned longleaf pine and shortleaf pine seedlings. Horizontal bars within box plots represent the median stem height. Whiskers extend to the highest/lowest value within 1.5 times the inter-quartile range (IQR). Points represent values beyond 1.5 * IQR. Crosses represent mean stem height.

seedlings under moderate and high shade (Fig. 5). In contrast, mockernut seedling height was solely affected by fire, as unburned seedlings were 37 percent larger than burned seedlings (Fig. 7) (F= 25.65, $P < 0.0001$).

Northern red oak RCD (data not shown) and height (Fig. 7) were significantly affected by fire (RCD: $F = 70.72$, $P < 0.0001$; Height: $F = 47.37$, $P < 0.0001$). For both metrics, unburned northern red oaks seedlings were 3.5 times larger than burned seedlings.

3.1.2. NSC dynamics

Pre-fire NSC varied significantly among species (Fig. 8) (F=17.81, $P < 0.0001$). Mockernut hickory had the highest pre-fire NSC reserves (15.0 %) and significantly exceeded the reserves of every other species except longleaf pine (11.4 %) (Fig. 8). Among the other species, longleaf pine NSC reserves were more than 2 × shortleaf pine and northern red oak, and nearly 5 × the reserves of loblolly pine (Fig. 8). Yellow-poplar maintained the second highest NSC reserves (8.1 %) among hardwood species, more than 3 × those of loblolly pine (Fig. 8).

The combination of fire and shade significantly affected shortleaf pine (F=11.99, $P = 0.0008$), northern red oak (F=3.72, $P = 0.0257$), and mockernut hickory (F=7.99, $P = 0.0006$) NSC recovery, but the pattern of NSC recovery differed among tree species. Unburned northern red oak and mockernut hickory grown under full sun maintained biologically higher NSC reserves than burned seedlings (Fig. 9). However, under medium shade, burned northern red oak seedlings maintained nearly twice the NSC reserves compared to unburned seedlings (Fig. 9). A similar pattern emerged with mockernut hickory, as unburned seedlings grown under low shade possessed three times more NSC reserves of burned seedlings; however, under high shade, burned seedlings maintained over twice the NSC reserves of unburned seedlings (Fig. 9). In contrast to the hardwood species, burned shortleaf pine seedlings maintained nearly 60 percent more NSC reserves compared to unburned seedlings. Nevertheless, under medium shade, unburned seedlings were found to have 3 × the NSC reserves of burned seedlings (Fig. 9). Shade was the sole factor influencing longleaf pine NSC reserves, as seedlings grown under full sun maintained more than 3 × the amount of NSC reserves compared to those grown under high shade (F=3.77, $P = 0.0239$).

4. Discussion

4.1. Seedling mortality

After controlling for fuel abundance and seedling age, longleaf and shortleaf pine post-fire mortality consistently increased under shade, indicating a decline in fire tolerance. Moreover, shortleaf pine experienced significantly higher post-fire mortality than mockernut hickory under 63–90 % shade illustrating that forest species can be more fire tolerant than savanna species under closed canopy conditions (Gignoux et al., 2016). This result is particularly unexpected because shortleaf pine resprouts vigorously following fire and other forms of top-kill (Mattoon 1915; Clabo and Clatterbuck, 2019). Our mechanistic investigation identified crown scorch and shade intensity as the two most parsimonious factors contributing to longleaf and shortleaf pine post-fire mortality after controlling for seedling size. In both models, crown scorch had the strongest effect; however, model explanatory power was nearly twice as strong for shortleaf pine, likely reflecting the low carbon demands of longleaf pine in the grass stage (Samuelson and Stokes, 2012). Comparatively low NSC reserves further indicate that shortleaf pine was under greater pre-fire carbon stress than longleaf pine. Nevertheless, the disparity in pre-fire NSC between these fire

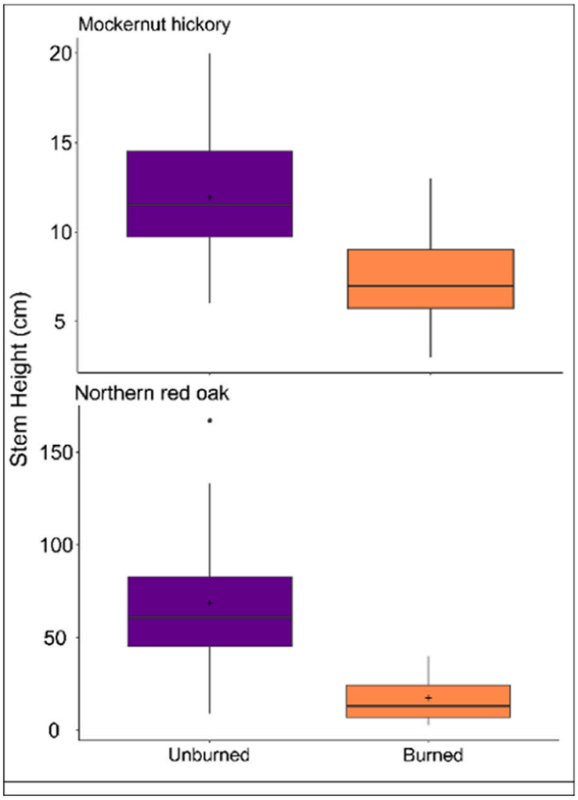

Fig. 7. The effect of fire on northern red oak and mockernut hickory seedling height. Horizontal bars within box plots represent the median stem height. Whiskers extend to the highest/lowest value within 1.5 times the inter-quartile range (IQR). Points represent values beyond 1.5 * IQR. Crosses represent mean stem height.

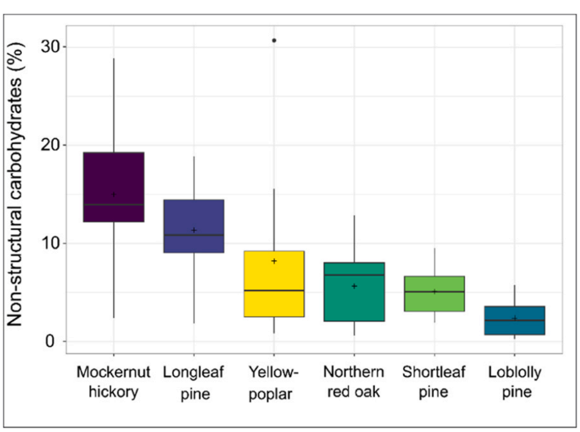

Fig. 8. Pre-fire non-structural carbohydrate storage of mockernut hickory, longleaf pine, northern red oak, yellow-poplar, shortleaf pine, and loblolly pine seedlings averaged across all shade levels. Horizontal bars within box plots represent the median Non-structural carbohydrate concentration. Whiskers extend to the highest/lowest value within 1.5 times the inter-quartile range (IQR). Points represent values beyond 1.5 * IQR. Crosses represent mean non-structural carbohydrate concentrations.

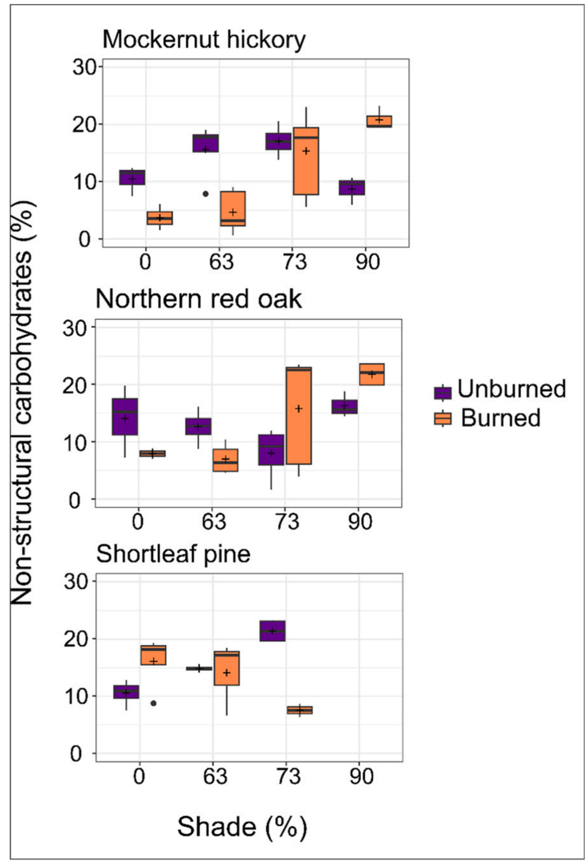

Fig. 9. The effect of shade intensity on non-structural carbohydrate storage of burned and unburned mockernut hickory, longleaf pine, northern red oak, and shortleaf pine total one-year after the burn. Horizontal bars within box plots represent the median Non-structural carbohydrate concentration. Whiskers extend to the highest/lowest value within 1.5 times the inter-quartile range (IQR). Points represent values beyond 1.5 * IQR. Crosses represent mean non-structural carbohydrate concentrations.

tolerant species may be caused by the conservative allocation strategy of longleaf pine in the grass stage (Jose et al., 2003; Knapp et al., 2021; Aubrey 2022).

While longleaf pine post-fire mortality was lower than shortleaf pine at most shade levels, mortality steadily increased with shade intensity. Crown scorch was the strongest factor contributing to longleaf pine post-fire mortality, which is surprising considering that grass stage seedlings and small saplings are often completely scorched by surface fire. One plausible explanation for this result could be related to changes in crown architecture under shade, as longleaf pine needle thickness decreases with shade intensity (Niinemets et al., 2002). Thus, the terminal bud of longleaf pine seedlings likely became increasingly exposed to heat under shade, elevating the risk of mortality. Collectively, this result adds further evidence demonstrating that longleaf pine seedlings are not impervious to surface fire and may explain why post-fire mortality increases with overstory basal area (Kara et al., 2017; Knapp et al., 2018; Brethauer et al., 2021).

Post-fire mortality was highest among shade intolerant species with low carbohydrate reserves. Loblolly pine provided the best example of this trend, experiencing consistently high fire-induced seedling mortality across shade levels demonstrating a lack of fire tolerance. Indeed, few loblolly pine seedlings possessed sufficient RCD size to resist surface fire prior to burning (> 3.8 cm RCD) (Ward 1993). Fire seasonality may also have increased mortality, as loblolly pine seedlings rarely resprout following growing season fire (Shelton and Cain, 2002; Will et al., 2013; Pile et al., 2017; Willis et al., 2024). Regardless of the underlying cause, this result broadly supports studies from other ecosystems demonstrating that prescribed fire can inhibit conifer encroachment if used at the seedling stage of development (Clark et al., 2018; van Mantgem et al., 2021).

In contrast to loblolly pine, encroaching hardwoods post-fire mortality varied considerably across shade levels, corresponded with shade tolerance (mockernut hickory > northern red oak > yellow-poplar), and generally matched pre-fire NSC storage rankings (mockernut hickory > yellow poplar > northern red oak) (Groninger et al., 1996; Rebbeck et al., 2012; Knapp et al., 2021). Comparable persistence of mockernut hickory, and other shade tolerant, encroaching species (e.g., winged elm (*Ulmus alata*) and red maple (*Acer rubrum*), have also been found after multiple prescribed fires under varying light environments (Fan et al., 2012; Schweitzer et al., 2016; Iverson et al., 2017; Zeitler et al., 2025). These collective results suggest that prescribed fire may fail to reduce mockernut hickory advance regeneration density in degraded woodlands. However, from a competition control perspective, mockernut hickory rarely recruits beyond the midstory under a frequent fire regime, as its relatively thin bark and short stature provide little protection from top-kill (Shearman et al., 2018; Knapp et al., 2022). Thus, mockernut hickory encroachment presents few problems for longleaf and shortleaf pine recruitment if prescribed fire is regularly applied.

4.1.1. Recovery

Non-structural carbohydrate storage allows species to persist through periods of minimal photosynthate production and recover from aboveground disturbance (Myers and Kitajima, 2007). However, investment in NSC storage decreases growth potential in high resource environments (Kobe, 1997). Diverging patterns in NSC recovery emerged between surviving shortleaf pine, northern red oak, and mockernut hickory. Contrary to our initial hypothesis, burned mockernut hickory and northern red oak resprout NSC storage steadily increased with shade, and surpassed that of unburned stems under high shade. Trends in aboveground tissue further demonstrate increased allocation to storage, as, apart from medium shade, burned mockernut hickory resprouts had smaller RCDs than unburned stems. Similarly, burned resprouts of both encroaching hardwood species were consistently shorter than unburned stems regardless of shade intensity. Collectively, these results indicate that shade tolerant species preferentially allocate towards NSC storage and demonstrate that resprouts become increasingly conservative under increasing shade(Kobe, 1997; Poorter et al., 2010).

In contrast to the hardwood species, burned shortleaf pine resprout and stem NSC storage steadily declined with shade intensity, but was significantly higher than unburned seedlings. Relatedly, burned shortleaf pine resprout and stem height consistently decreased with shade intensity. High NSC storage in burned shortleaf pine sprouts and stems indicate that burning may have triggered a conservative shift in growth strategy under full sun and low shade, which could be interpreted as an adaptation for surviving frequent fire in open forests (Pausas et al., 2017). However, burned shortleaf pine resprout and stem NSC storage dropped dramatically under increasing shade. We suspect much of this reduction can be attributed to the mobilization of NSC to facilitate resprouting and subsequent regrowth of aboveground tissues (Wigley et al., 2009; Sayer et al., 2020). Nevertheless, shade also played a role, as NSC storage also decreased among unburned seedlings. What remains unclear is why northern red oak and mockernut hickory recovered NSC reserves more effectively than shortleaf pine under increasing shade intensity, as sprouting was the primary survival mechanism for all species under high shade.

5. Conclusion and management implications

The legacy of fire exclusion has transformed many open forests into dense, closed canopy forests featuring species of varying fire and shade tolerance. Prescribed fire is applied to combat this trend through killing fire-sensitive species, thereby increasing light availability and longleaf and shortleaf pine seedling competitiveness. Our results demonstrate that increasing shade intensity reduces fire tolerance and particularly so for shade intolerant conifer species. In contrast, shade tolerant hardwoods became increasingly conservative with NSC under shade, waiting for the opportunity to capture growing space. Collectively, these results offer a plausible explanation for why initial attempts to reintroduce prescribed fire into degraded open forests often fail to alter species composition in the eastern United States (Alexander et al., 2008; Goode et al., 2024).

Like all shade house studies, readers should recognize that our experiment was conducted under semi-controlled conditions complicating their extrapolation to the field. For example, our seedlings were the same age and were regularly watered to prevent drought stress. Moreover, the fuelbeds used in this study does not account for the loss of fuel connectivity existing under canopy gaps (Mitchell et al., 2009). Therefore, our management recommendations should be considered cautiously.

Overcoming the influence of shade will require the use of other silvicultural tools in concert with prescribed fire. Overstory harvesting or thinning from above should be used to increase longleaf and shortleaf pine seedling vigor prior to burning, whether residual advance regeneration is present, or seedlings are planted beneath the existing overstory. Variable density thinning could also benefit longleaf and shortleaf pine seedlings if advance regeneration is patchy. The importance of increasing pre-fire light availability will be particularly important in natural stands, where seedlings exist under shaded conditions for multiple years.

The optimal pre-fire harvesting or thinning strategy to accentuate the competitiveness of longleaf and shortleaf pine is situationally dependent. Prescribed fire will likely be successful at eliminating loblolly pine competition under any residual overstory structure if seedlings are smaller than 3.8 cm RCD (Wade 1993). In contrast, burning is unlikely to reduce the density of mockernut hickory seedlings regardless of overstory structure. Burning in the absence of shade produced the biggest relative reduction in competition for longleaf and shortleaf pine seedlings. However, clearcutting is generally reserved for scenarios where seed sources and advance regeneration of longleaf and shortleaf pine are absent (Willis et al., 2024). Burning under 65 % shade was generally effective at reducing yellow-poplar competition on longleaf pine seedlings. In a longleaf pine woodland, this corresponds with a residual basal area target of approximately 19 m^2ha^{-1} or a 0.11 ha harvest gap (Palik et al., 1997; McGuire et al., 2001). A more aggressive pre-fire harvesting or thinning approach (7–10m^2ha^{-1} or 0.41 ha harvest gap) will be required for prescribed fire to release longleaf pine from competition with northern red oak seedlings. A similarly aggressive pre-fire harvesting approach will be necessary to improve the competitiveness of shortleaf pine against yellow-poplar or northern red oak seedlings. Collectively, these findings provide guidance for land managers looking to increase the efficacy of prescribed fire in degraded southeastern woodlands. We encourage future studies to explore the combined effects of fire and shade on advance regeneration with mature root systems and to further investigate broader species compositions that reflect contemporary management and restoration conundrums.

CRediT authorship contribution statement

Shearman Tim: Writing – review & editing, Writing – original draft, Methodology, Investigation. **Varner Morgan:** Writing – review & editing, Writing – original draft, Methodology, Conceptualization. **Willis John L.:** Writing – review & editing, Writing – original draft, Validation, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation. **Sharma Ajay:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization. **McKeithen Justin:** Writing – review & editing, Resources, Project administration, Methodology, Investigation, Conceptualization.

Funding

Partial funding for this study was provided by the USDA Forest

Service Southern Research Station (21-JV-11330170-031) and the USDA NIFA McIntire Stennis Project #1014653.

Declaration of Competing Interest

The authors have nothing to declare.

Acknowledgements

The authors thank Edward Andrews, Caden Shows, and John Tracy for their help with field work. We thank Karen Sarsony for her assistance in processing the tissue samples. The lead author would like to dedicate this manuscript to the memory of his longtime field assistant Sasha. This paper was written and prepared in part by U.S. Government employees on official time, and therefore it is in the public domain and not subject to copyright. The findings and conclusions in this publication are those of the authors and should not be construed to represent an official USDA, Forest Service, or United States Government determination or policy.

Appendix 1. Candidate models predicting longleaf and shortleaf pine mortality

Longleaf Pine Mortality Models	AICc
Shade + Crown Scorch + RCD + Crown Consumption	65.39
Shade + RCD + Crown Consumption	64.62
Shade + Crown Scorch + Crown Consumption	64.07
Scorch +RCD + Crown Consumption	64.60
Shade + Crown Scorch	**62.87**
Shade + RCD	68.63
Shade + Crown Consumption	63.51
Crown Scorch + RCD	65.86
Crown Scorch + Crown Consumption	64.73
RCD + Crown Consumption	62.95
Shade	69.68
Crown Scorch	69.40
RCD	70.23
Crown Consumption	62.93
Null	77.09
Shortleaf Pine Mortality Models	
Shade + RCD + Crown Scorch	53.44
Shade + RCD	55.81
RCD + Crown Scorch	58.04
Shade + Crown Scorch	**52.19**
Shade	55.56
Crown Scorch	65.54
RCD	64.11
Null	84.82

Data availability

Data will be made available on request.

References

Adams, W.W., Stewart, J.J., Polutchko, S.K., Cohu, C.M., Muller, O., Demmig-Adams, B., 2023. Foliar phenotypic plasticity reflects adaptation to environmental variability. Plants 12 (10), 2041. https://doi.org/10.3390/plants12102041.

Albert, M., Hansen, J., Nagel, J., Schmidt, M., Spellmann, H., 2015. Assessing risks and uncertainties in forest dynamics under different management scenarios and climate change. For. Ecosyst. 2, 1–21. https://doi.org/10.1186/s40663-015-0036-5.

Alexander, H.D., Arthur, M.A., Loftis, D.L., Green, S.R., 2008. Survival and growth of upland oak and co-occurring competitor seedlings following single and repeated prescribed fires. For. Ecol. Manag. 256 (5), 1021–1030. https://doi.org/10.1016/j.foreco.2008.06.004.

Anderson, M., Hayes, L., Keyser, P.D., Lituma, C., Sutter, R.D. and Zollner, D., 2016. Shortleaf pine restoration plan: Restoring an American forest legacy. Shortleaf Pine Initiative. Available online at ⟨http://shortleafpine.net/shortleaf-pine-initiative/shortleaf-pine-restoration-plan⟩; last accessed 2/6/2025.

Aubrey, D.P., 2022. Grass (stage) root movement to ensure future resilience of longleaf pine ecosystems. N. For. 53 (6), 971–982. https://doi.org/10.1007/s11056-021-09870-1.

Barton, K.E., Shiels, A.B., 2020. Additive and non-additive responses of seedlings to simulated herbivory and drought. Biotropica 52 (6), 1217–1228. https://doi.org/10.1111/btp.12829.

Bradley, J.C., Will, R.E., Stewart, J.F., Nelson, C.D., Guldin, J.M., 2016. Post-fire resprouting of shortleaf pine is facilitated by a morphological trait but fire eliminates shortleaf× loblolly pine hybrid seedlings. For. Ecol. Manag. 379, 146–152. https://doi.org/10.1016/j.foreco.2016.08.016.

Brethauer, D.K., Sharma, A., Vogel, J.G., Miller, D.L., van Santen, E., 2021. Longleaf pine seedling growth and survival: effects of season and intensity of simulated prescribed burning. For. Ecol. Manag. 502, 119719. https://doi.org/10.1016/j.foreco.2021.119719.

Brown, P.M., Sieg, C.H., 1996. Fire history in interior ponderosa pine communities of the Black Hills, South Dakota, USA. Int. J. Wildland Fire 6 (3), 97–105. https://doi.org/10.1071/WF9960097.

Burnham, K.P., Anderson, D.R., 2004. Multimodel inference: understanding AIC and BIC in model selection. Sociol. Methods Res. 33 (2), 261–304. https://doi.org/10.1177/0049124104268644.

Chin, A.R., Lambers, J.H.R., Franklin, J.F., 2023. Context matters: natural tree mortality can lead to neighbor growth release or suppression. For. Ecol. Manag. 529, 120735. https://doi.org/10.1016/j.foreco.2022.120735.

Chmura, D.J., Modrzyński, J., Chmielarz, P., Tjoelker, M.G., 2017. Plasticity in seedling morphology, biomass allocation and physiology among ten temperate tree species in response to shade is related to shade tolerance and not leaf habit. Plant Biol. 19 (2), 172–182. https://doi.org/10.1111/plb.12531.

Clabo, D.C., Clatterbuck, W.K., 2019. Shortleaf pine (Pinus echinata, Pinaceae) seedling sprouting responses: clipping and burning effects at various seedling ages and seasons. J. Torrey Bot. Soc. 146 (2), 96–110. https://doi.org/10.3159/TORREY-D-18-00004.1.

Clark, P.E., Williams, C.J., Pierson, F.B., 2018. Factors affecting efficacy of prescribed fire for western juniper control. Rangel. Ecol. Manag. 71 (3), 345–355. https://doi.org/10.1016/j.rama.2018.02.002.

Collins, L., 2020. Eucalypt forests dominated by epicormic resprouters are resilient to repeated canopy fires. J. Ecol. 108 (1), 310–324. https://doi.org/10.1111/1365-2745.13227.

Del Tredici, P., 2001. Sprouting in temperate trees: a morphological and ecological review. Bot. Rev. 67, 121–140. https://doi.org/10.1007/BF02858075.

Drus, G.M., Dudley, T.L., D'Antonio, C.M., Even, T.J., Brooks, M.L., Matchett, J.R., 2014. Synergistic interactions between leaf beetle herbivory and fire enhance tamarisk (Tamarix spp.) mortality. Biol. Control 77, 29–40. https://doi.org/10.1016/j.biocontrol.2014.04.010.

Fan, Z., Ma, Z., Dey, D.C., Roberts, S.D., 2012. Response of advance reproduction of oaks and associated species to repeated prescribed fires in upland oak-hickory forests. Mo. For. Ecol. Manag. 266, 160–169.

Farrar, Jr, R.M., 1975. Sprouting ability of longleaf pine. For. Sci. 21 (2), 189–190. https://doi.org/10.1093/forestscience/21.2.189.

Friedman, J., Hastie, T., Tibshirani, R., 2010. Regularization paths for generalized linear models via coordinate descent. J. Stat. Softw. 33 (1), 1. https://doi.org/10.18637/jss.v033.i01.

Frost, C.C., 1993. May. Four centuries of changing landscape patterns in the longleaf pine ecosystem. Proc. Tall Timbers Fire Ecol. Conf. 18 (18), 17–43.

Gignoux, J., Konaté, S., Lahoreau, G., Le Roux, X., Simioni, G., 2016. Allocation strategies of savanna and forest tree seedlings in response to fire and shading: outcomes of a field experiment. Sci. Rep. 6 (1), 38838. https://doi.org/10.1038/srep38838.

Goode, J.D., Hart, J.L., Dey, D.C., LaFevor, M.C., Torreano, S.J., 2024. Restoration of low-intensity fire in Quercus-Pinus mixedwoods following a prolonged period of fire exclusion. Can. J. For. Res. 54 (1), 97–109. https://doi.org/10.1139/cjfr-2023-0116.

Groninger, J.W., Seiler, J.R., Peterson, J.A., Kreh, R.E., 1996. Growth and photosynthetic responses of four Virginia Piedmont tree species to shade. Tree Physiol. 16 (9), 773–778. https://doi.org/10.1093/treephys/16.9.773.

Guldin, J.M., 2019. Restoration of native fire-adapted southern pine-dominated forest ecosystems: diversifying the tools in the silvicultural toolbox. For. Sci. 65 (4), 508–518. https://doi.org/10.1093/forsci/fxz005.

Guyette, R.P., Stambaugh, M.C., Dey, D.C., Muzika, R.M., 2012. Predicting fire frequency with chemistry and climate. Ecosystems 15, 322–335. https://doi.org/10.1007/s10021-011-9512-0.

Hanberry, B.B., 2021. Transition from fire-dependent open forests: alternative ecosystem states in the southeastern United States. Diversity 13 (9), 411. https://doi.org/10.3390/d13090411.

Hanberry, B.B., Abrams, M.D., Arthur, M.A., Varner, J.M., 2020. Reviewing fire, climate, deer, and foundation species as drivers of historically open oak and pine forests and transition to closed forests. Front. For. Glob. Change 3, 56. https://doi.org/10.3389/ffgc.2020.00056.

Hanberry, B.B., Bragg, D.C., Hutchinson, T.F., 2018. A reconceptualization of open oak and pine ecosystems of eastern North America using a forest structure spectrum. Ecosphere 9 (10), e02431. https://doi.org/10.1002/ecs2.2431.

He, T., Pausas, J.G., Belcher, C.M., Schwilk, D.W., Lamont, B.B., 2012. Fire-adapted traits of Pinus arose in the fiery Cretaceous. N. Phytol. 194 (3), 751–759. https://doi.org/10.1111/j.1469-8137.2012.04079.x.

Heinze, G., Ploner, M., Dunkler, D., Southworth, H. and Heinze, M.G., 2023. Package 'logistf'.

Heinze, G., Schemper, M., 2002. A solution to the problem of separation in logistic regression. Stat. Med. 21 (16), 2409–2419. https://doi.org/10.1002/sim.1047.

Howie, N.A., Goode, J.D., Hart, J.L., Dey, D.C., 2024. Prescribed fire effects on understory woody plants and fuels in Quercus-Pinus mixedwoods. Can. J. For. Res. 54 (10), 1100–1113. https://doi.org/10.1139/cjfr-2024-0027.

Hutchinson, T.F., Sutherland, E.K., Yaussy, D.A., 2005. Effects of repeated prescribed fires on the structure, composition, and regeneration of mixed-oak forests in Ohio. For. Ecol. Manag. 218 (1-3), 210–228. https://doi.org/10.1016/j.foreco.2005.07.011.

Iverson, L.R., Hutchinson, T.F., Peters, M.P., Yaussy, D.A., 2017. Long-term response of oak-hickory regeneration to partial harvest and repeated fires: influence of light and moisture. Ecosphere 8 (1), e01642. https://doi.org/10.1002/ecs2.1642.

Jackson, J.F., Adams, D.C., Jackson, U.B., 1999. Allometry of constitutive defense: a model and a comparative test with tree bark and fire regime. Am. Nat. 153 (6), 614–632. https://doi.org/10.2307/2463619.

Jose, S., Merritt, S., Ramsey, C.L., 2003. Growth, nutrition, photosynthesis and transpiration responses of longleaf pine seedlings to light, water and nitrogen. For. Ecol. Manag. 180 (1-3), 335–344. https://doi.org/10.1016/S0378-1127(02)00583-2.

Kara, F., Loewenstein, E.F., Brockway, D.G., 2017. Effects of basal area on survival and growth of longleaf pine when practicing selection silviculture. pp.e005-e005 For. Syst. 26 (1). https://doi.org/10.5424/fs/2017261-10043.

Keeley, J.E., 2012. Ecology and evolution of pine life histories. Ann. For. Sci. 69 (4), 445–453. https://doi.org/10.1007/s13595-012-0201-8.

Keeley, J.E., Zedler, P.H., 1998. Evolution of life histories in *Pinus*. In: Richardson, D.M. (Ed.), Ecology and Biogeography of Pinus. Cambridge Press, Cambridge, United Kingdom, pp. 219–251.

Keyser, T.L., 2019. Resprouting by seedlings of four North American deciduous broadleaved tree species following experimental burning. Oecologia 190 (1), 207–218. https://doi.org/10.1007/s00442-019-04397-x.

Knapp, B.O., Maginel, C.J., Graham, B., Kabrick, J.M., Dey, D.C., 2022. Escaping the fire trap: does frequent, landscape-scale burning inhibit tree recruitment in a temperate broadleaf ecosystem? For. Ecol. Manag. 513, 120191. https://doi.org/10.1016/j.foreco.2022.120191.

Knapp, B.O., Pile, L.S., Walker, J.L., Geoff Wang, G., 2018. Fire effects on a fire-adapted species: response of grass stage longleaf pine seedlings to experimental burning. Fire Ecol. 14 (2), 1–16. https://doi.org/10.1186/s42408-018-0003-y.

Knapp, L.S.P., Snell, R., Vickers, L.A., Hutchinson, T., Kabrick, J., Jenkins, M.A., Graham, B., Rebbeck, J., 2021. The 'other'hardwood: growth, physiology, and dynamics of hickories in the Central Hardwood Region, USA. For. Ecol. Manag. 497, 119513. https://doi.org/10.1016/j.foreco.2021.119513.

Kobe, R.K., 1997. Carbohydrate allocation to storage as a basis of interspecific variation in sapling survivorship and growth. Oikos 226–233. ⟨https://www.jstor.org/stable/3546590⟩.

Lenth, R.V., 2016. Least-squares means: the R package lsmeans. J. Stat. Softw. 69, 1–33. https://doi.org/10.18637/jss.v069.i01.

Lilly, C.J., Will, R.E., Tauer, C.G., Guldin, J.M., Spetich, M.A., 2012. Factors affecting the sprouting of shortleaf pine rootstock following prescribed fire. For. Ecol. Manag. 265, 13–19. https://doi.org/10.1016/j.foreco.2011.10.020.

Mattoon, W.R., 1915. Life History of Shortleaf Pine (No. 244). US Department of Agriculture. ⟨https://catalog.hathitrust.org/Record/010668745⟩.

McDaniel, J.K., Alexander, H.D., Siegert, C.M., Lashley, M.A., 2021. Shifting tree species composition of upland oak forests alters leaf litter structure, moisture, and flammability. For. Ecol. Manag. 482, 118860. https://doi.org/10.1016/j.foreco.2020.118860.

McDowell, N.G., Allen, C.D., Anderson-Teixeira, K., Aukema, B.H., Bond-Lamberty, B., Chini, L., Clark, J.S., Dietze, M., Grossiord, C., Hanbury-Brown, A., Hurtt, G.C., 2020. Pervasive shifts in forest dynamics in a changing world. Science 368 (6494), eaaz9463. https://doi.org/10.1126/science.aaz9463.

McGuire, J.P., Mitchell, R.J., Moser, E.B., Pecot, S.D., Gjerstad, D.H., Hedman, C.W., 2001. Gaps in a gappy forest: plant resources, longleaf pine regeneration, and understory response to tree removal in longleaf pine savannas. Can. J. For. Res. 31 (5), 765–778. https://doi.org/10.1139/x01-00.

Mitchell, R.J., Hiers, J.K., O'Brien, J., Starr, G., 2009. Ecological forestry in the Southeast: understanding the ecology of fuels. J. For. 107 (8), 391–397. https://doi.org/10.1093/jof/107.8.391.

Myers, J.A., Kitajima, K., 2007. Carbohydrate storage enhances seedling shade and stress tolerance in a neotropical forest. J. Ecol. 383–395. ⟨https://www.jstor.org/stable/4495991⟩.

NCEI National Centers for Environmental Information Climate Data Online. Climate Data Online. Avaialble online at ⟨https://www.ncdc.noaa.gov/cdo-web/⟩ (accessed July 24, 2024).

Niinemets, Ü., 2010. Responses of forest trees to single and multiple environmental stresses from seedlings to mature plants: past stress history, stress interactions, tolerance and acclimation. For. Ecol. Manag. 260 (10), 1623–1639. https://doi.org/10.1016/j.foreco.2010.07.054.

Niinemets, Ü., Ellsworth, D.S., Lukjanova, A., Tobias, M., 2002. Dependence of needle architecture and chemical composition on canopy light availability in three North American Pinus species with contrasting needle length. Tree Physiol. 22 (11), 747–761. https://doi.org/10.1093/treephys/22.11.747.

Niinemets, Ü., Valladares, F., 2006. Tolerance to shade, drought, and waterlogging of temperate northern hemisphere trees and shrubs. Ecol. Monogr. 76 (4), 521–547. https://doi.org/10.1890/0012-9615(2006)076[0521:ttsdaw]2.0.co;2.

Ottmar, R.D. and Vihnanek, R.E. 2000. Stereo photo series for quantifying natural fuels. Volume VI: Longleaf pine pocosin, and marshgrass types in the southeastern United States. PMS 835. National Wildfire Coordinating Group, National Interagency Fire Center, Boise, ID. 56 pp.

Palik, B.J., Mitchell, R.J., Houseal, G., Pederson, N., 1997. Effects of canopy structure on resource availability and seedling responses in a longleaf pine ecosystem. Can. J. For. Res. 27 (9), 1458–1464. https://doi.org/10.1139/x97-08.

Pausas, J.G., Keeley, J.E., Schwilk, D.W., 2017. Flammability as an ecological and evolutionary driver. J. Ecol. 105 (2), 289–297. https://doi.org/10.1111/1365-2745.12691.

Pelletier, S., Tremblay, G.F., Bertrand, A., Bélanger, G., Castonguay, Y., Michaud, R., 2010. Drying procedures affect non-structural carbohydrates and other nutritive value attributes in forage samples. Anim. Feed Sci. Technol. 157 (3-4), 139–150. https://doi.org/10.1016/j.anifeedsci.2010.02.010.

Peterson, D.W., Reich, P.B., 2001. Prescribed fire in oak savanna: fire frequency effects on stand structure and dynamics. Ecol. Appl. 11 (3), 914–927. https://doi.org/10.1890/1051-.

Pile, L.S., Wang, G.G., Knapp, B.O., Liu, G., Yu, D., 2017. Comparing morphology and physiology of southeastern US Pinus seedlings: implications for adaptation to surface fire regimes. Ann. For. Sci. 74, 1–12. https://doi.org/10.1007/s13595-017-0666-6.

Pile-Knapp, L.S., Dey, D.C., Stambaugh, M.C., Thompson, F.R., Varner, J.M., 2024. Managing forward while looking back: reopening closed forests to open woodlands and savannas. Fire Ecol. 20 (1), 72. https://doi.org/10.1186/s42408-024-00312-9.

Poorter, L., Kitajima, K., Mercado, P., Chubina, J., Melgar, I., Prins, H.H., 2010. Resprouting as a persistence strategy of tropical forest trees: relations with carbohydrate storage and shade tolerance. Ecology 91 (9), 2613–2627. https://doi.org/10.1890/09-0862.1.

Poorter, L., Kitajima, K., 2007. Carbohydrate storage and light requirements of tropical moist and dry forest tree species. Ecology 88 (4), 1000–1011. https://doi.org/10.1890/06-0984.

Provencher, L., Herring, B.J., Gordon, D.R., Rodgers, H.L., Tanner, G.W., Hardesty, J.L., Brennan, L.A., Litt, A.R., 2001. Longleaf pine and oak responses to hardwood reduction techniques in fire-suppressed sandhills in northwest Florida. For. Ecol. Manag. 148 (1-3), 63–77. https://doi.org/10.1016/S0378-1127(00)00525-9.

Ramsey, F. and Schafer, D., 2012. Student Solutions Manual for Ramsey/Schafer's The Statistical Sleuth: A Course in Methods of Data Analysis, 3rd. Brooks/Cole Publishing Co.

Rebbeck, J., Scherzer, A., Gottschalk, K., 2012. Do chestnut, northern red, and white oak germinant seedlings respond similarly to light treatments? II. Gas exchange and chlorophyll responses. Can. J. For. Res. 42 (6), 1025–1037. https://doi.org/10.1139/x2012-057.

RStudio Team 2020. RStudio: Integrated Development for R. RStudio, PBC, Boston, MA URL ⟨http://www.rstudio.com/⟩.

Ryan, K.C., Knapp, E.E., Varner, J.M., 2013. Prescribed fire in North American forests and woodlands: history, current practice, and challenges. Front. Ecol. Environ. 11 (s1), e15–e24. https://doi.org/10.1890/120329.

Samuelson, L.J., Stokes, T.A., 2012. Leaf physiological and morphological responses to shade in grass-stage seedlings and young trees of longleaf pine. Forests 3 (3), 684–699. https://doi.org/10.3390/f3030684.

Sayer, M.A.S., Tyree, M.C., Kuehler, E.A., Jackson, J.K., Dillaway, D.N., 2020. Physiological mechanisms of foliage recovery after spring or fall crown scorch in young longleaf pine (Pinus palustris Mill.). Forests 11 (2), 208. https://doi.org/10.3390/f11020208.

Schweitzer, C.J., Dey, D.C., Wang, Y., 2016. Hardwood-pine mixedwoods stand dynamics following thinning and prescribed burning. Fire Ecol. 12, 85–104. https://doi.org/10.4996/fireecology.1202085.

Scott, A.C., Bowman, D.M., Bond, W.J., Pyne, S.J. and Alexander, M.E., 2013. Fire on Earth: an Introduction. John Wiley & Sons.

Shearman, T.M., Wang, G.G., Ma, P.T., Guan, S., 2018. Patterns of bark growth for juvenile trees of six common hardwood species in the eastern United States and the implications to fire-tolerance. Trees 32, 519–524. https://doi.org/10.1007/s00468-017-1649-9.

Shelton, M.G., Cain, M.D., 2002. Recovery of 1-year-old loblolly pine seedlings from simulated browse damage. Can. J. For. Res. 32 (2), 373–377. https://doi.org/10.1139/x01-193.

Šímová, I., Rueda, M., Hawkins, B.A., 2017. Stress from cold and drought as drivers of functional trait spectra in North American angiosperm tree assemblages. Ecol. Evol. 7 (18), 7548–7559. https://doi.org/10.1002/ece3.3297.

Soil Survey Staff, Natural Resources Conservation Service, United States Department of Agriculture. Web Soil Survey. Available online at ⟨https://websoilsurvey.nrcs.usda.gov/⟩. Accessed [July/24/2024].

Tatina, R., Hanberry, B.B., Willis, J.L., 2024. Differentiating historical open forests and current closed forests of the Coastal Plain, Southeastern USA. Forests 15 (3), 532. https://doi.org/10.3390/f15030532.

USGS United States Geological Survey 2020. 3D Elevation Program. Available online at ⟨https://www.usgs.gov/core-science-systems/ngp/3dep⟩ (accessed July 24, 2024).

Valladares, F., Pearcy, R.W., 2002. Drought can be more critical in the shade than in the sun: a field study of carbon gain and photo-inhibition in a Californian shrub during a dry El Niño year. Plant, Cell Environ. 25 (6), 749–759. https://doi.org/10.1046/j.1365-3040.2002.00856.x.

van Mantgem, P.J., Wright, M.C., Engber, E.A., 2021. Patterns of conifer invasion following prescribed fire in grasslands and oak woodlands of Redwood National Park, California. Restor. Ecol. 29 (4), e13366. https://doi.org/10.1111/rec.13366.

Varner, J.M., Gordon, D.R., Putz, F.E., Hiers, J.K., 2005. Restoring fire to long-unburned Pinus palustris ecosystems: novel fire effects and consequences for long-unburned ecosystems. Restor. Ecol. 13 (3), 536–544. https://doi.org/10.1111/j.1526-100x.2005.00067.x.

Varner, J.M., Hood, S.M., Aubrey, D.P., Yedinak, K., Hiers, J.K., Jolly, W.M., Shearman, T.M., McDaniel, J.K., O'Brien, J.J., Rowell, E.M., 2021. Tree crown injury from wildland fires: causes, measurement and ecological and physiological consequences. N. Phytol. 231 (5), 1676–1685. https://doi.org/10.1111/nph.17539.

Wade, D.D., 1993. Thinning young loblolly pine stands with fire. Int. J. Wildland Fire 3 (3), 169–178. https://doi.org/10.1071/WF9930169.

Ward, E., Deans, J.D., 1993. A simple method for the routine extraction and quantification of non-structural sugars in tree tissues. For. Int. J. For. Res. 66 (2), 171–180. https://doi.org/10.1093/forestry/66.2.171.

Wigley, B.J., Cramer, M.D., Bond, W.J., 2009. Sapling survival in a frequently burnt savanna: mobilization of carbon reserves in Acacia karroo. Plant Ecol. 203, 1–11. https://doi.org/10.1007/s11258-008-9495-x.

Will, R.E., Lilly, C.J., Stewart, J., Huff, S., Tauer, C.G., 2013. Recovery from topkill of shortleaf pine× loblolly pine hybrids compared to their parent populations. Trees 27, 1167–1174. https://doi.org/10.1007/s00468-013-0866-0.

Willis, J.L., Bragg, D.C., Cannon, J.B., Gandhi, K.J., Kidd, K.R., Polinko, A.D., Puhlick, J. J., Saenz, D., Sayer, M.A., Schalk, C.M., Self, A.B., 2024. Assessing the potential impact of retaining native off-site tree species in woodland restoration. Restor. Ecol., e14119 https://doi.org/10.1111/rec.14119.

Wolf, J., 2004. A 200-year fire history in a remnant oak savanna in southeastern Wisconsin. Am. Midl. Nat. 152 (2), 201–213. https://doi.org/10.1674/0003-0031(2004)152[0201:AYFHIA]2.0.CO;2.

Zeitler, E.F., Robertson, K.M., Dixon, C.M., Lashley, M.A., 2025. Fire season differentially affects resprouting vigor of pyrophytic and mesophytic hardwoods in a southeastern US pine savanna. For. Ecol. Manag. 578, 122478. https://doi.org/10.1016/j.foreco.2024.122478.