INSIGHT INTO THE ROLES OF PRESCRIBED FIRE AND HARDWOOD COMPETITION IN THE SURVIVAL AND GROWTH OF SHORTLEAF PINE THROUGHOUT ITS EARLY LIFE

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The undersigned, appointed by the dean of the Graduate School, have examined the dissertation entitled

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ABSTRACT

Shortleaf pine is an economically and ecologically important species that was once prevalent across the southeastern United States, and there is growing interest in its restoration throughout its former range. One challenge with restoring shortleaf pine is competition from hardwoods. In Missouri specifically, many sites formerly occupied by shortleaf pine are now dominated by oak species with established and highly competitive advanced regeneration. Prescribed fire is a tool often used in shortleaf pine management, with varying effects at different life stages. This dissertation incorporates results from four studies on the early life stages of shortleaf pine in the Missouri Ozarks. The first study examined the direct and indirect effects of fire on shortleaf pine seeds. The second study focuses on survival, sprouting, and growth following prescribed burning of shortleaf pine and oak seedlings and saplings of various sizes from 0-15 cm basal diameter, and can be used to help managers determine the best time to use prescribed fire to manage for shortleaf pine success in mixed oak-pine forests. The third focuses on the growth and survival of planted shortleaf pine seedlings under a range of overstory conditions and highlights the importance of competitive status relative to hardwood competition for survival of shortleaf pine regeneration during their first decade. The fourth study uses tree-ring analysis to study growth response of shortleaf pine planted following a 2002 tornado in two stands with different known histories of management activities, specifically prescribed burning and mechanical release, across a range of competition levels. Taken together these findings provide insight into the roles of prescribed fire and hardwood competition in the survival and growth of shortleaf pine throughout its early life.

Chapter 1: Literature review

General information

Shortleaf pine (*Pinus echinata*) is one of the most important and commercially valuable of the southern pine species. Shortleaf pine is a tall tree with a long trunk and broad crown. It has thick, dark, plated bark, needles 7.5-12.5 cm long in clusters of two or three, and approximately 5 cm egg-shaped cones with spikes. *Pinus echinata* translates roughly to prickly pine, referring to the cones. Like many pines, shortleaf pine is shade intolerant. It has slow initial shoot growth, and early development focuses on root establishment (Williston, 1972; Guldin 1986). Shortleaf pine has its highest growth rate in early spring and moderate growth in early summer (Byram and Doolittle, 1950), though favorable late growing season conditions and precipitation can facilitate renewed growth (Guldin, 1986).

Shortleaf pine's natural range covers 22 states, from northern Florida to New York and New Jersey, and from eastern Texas and Oklahoma to the east coast (Little, 1971) though more recent inventory found it in only 21 states (Oswalt et al., 2012). It is the most widespread pine species in the eastern United States. It often grows on south and west facing slopes. Shortleaf pine occurs in two main forest types, the shortleaf pine and shortleaf pine-oak forest types. Approximately 18% of shortleaf pine trees are in the mixed oak forest type (Moser et al., 2007). Shortleaf pine also grows in loblolly – shortleaf forest types, and is a minor component of at least 15 other forest types (Burns, 1990). Shortleaf ecosystems can range from closed canopy forests to open woodlands, depending on the disturbance regime. Shortleaf pine is the only native pine in Missouri.

Current and historic abundance

Shortleaf pine has declined from historic prevalence. Shortleaf pine currently covers 25,000 km^2 in the United States (Oswalt al., 2012), though it is estimated to have covered approximately 283,000- 324,000 km^2 pre-colonization (Anderson et al., 2016). The majority (62%) of current shortleaf pine-dominated forests are privately owned (Oswalt al., 2012). In addition to departure from historic abundance, shortleaf pine has also experienced more recent declines, with every state in which shortleaf pine is present seeing a decrease in abundance since the 1980s (Moser et al., 2007). Seventy one percent of shortleaf pine-dominated forests are large diameter stands (defined as stands in which greater than 50 percent of stocking is in large and medium diameter trees, and the majority of stocking is in large diameter trees. Large diameter trees have a diameter at breast height (DBH) of at least 28 cm for hardwoods and 23 cm for softwoods, and medium diameter trees have a DBH of at least 13 cm. Only 7% are in small diameter stands (Oswalt et al., 2012). The size distribution of shortleaf forests hints at a lack of regeneration. Further evidence of shortleaf pine regeneration issues was provided by Moser (2007), who compared the percent of shortleaf pine in the overstory to the percent of shortleaf pine in the seedling population. In every state where shortleaf pine was at least 1% of the overstory, the proportional abundance of shortleaf was lower in the seedling layer than in the overstory.

The decline of shortleaf pine in Missouri began with rapid human population growth in the 1860s followed by intensive logging from the 1880s to 1920s. The logging practices used were unsustainable, leaving an inadequate seed source for shortleaf regeneration. In addition to the insufficient seed quantity, overly frequent burning to promote grass for grazing prevented shortleaf seedlings from becoming established in the years following the initial logging era. Later, fire suppression policies allowed vigorous hardwood sprouts to outcompete shortleaf pine on areas where it had formerly been present. Excluding plantations, it is estimated that the current abundance of shortleaf pine in Missouri is 22% of historic levels (Guyette et al., 2007).

Restoration motivation

Wildlife habitat is one of the reasons for the interest in restoring shortleaf pine woodlands and forests. Shortleaf pine provides habitat for several species of mammals and birds, though the species composition varies with successional stage and fire frequency (Masters, 2007). For example, sapling stands provide bedding and browse for white tailed deer (*Odocoileus virginianus*) and elk (*Cervus canadensis*), who also prefer pine saplings over hardwood saplings for antler rubbing and marking territory. Prescribed fire extends the length of time young pine woodlands and forests are suitable for these uses. Mid successional stands begin to provide habitat for flying squirrels (*Glaucomys* spp.*)*, grey squirrels (*Sciurus carolinensis*), gray foxes (*Urocyon cinereoargenteus*) and various songbirds. Without fire, midstory hardwoods develop during this stage and lead to the decline of small mammal and songbird use. Late successional stands provide habitat for several bird species including multiple species of woodpecker. Mature shortleaf pine - bluestem woodlands provide habitat for deer, elk, small mammals, and birds. Though no species require shortleaf pine specifically, some bird species found in shortleaf ecosystems are pine obligates, including pine warbler (*Setophaga pinus*), brown-headed nuthatch (*Sitta pusilla*), and red-cockaded woodpecker (*Leuconotopicus borealis*). In fact, the brown headed nuthatch was recently reintroduced to Missouri in restored shortleaf pine areas in the Mark Twain National Forest. Other wildlife species found in shortleaf ecosystems include Bachman's sparrow (*Peucaea aestivalis*), red-headed woodpecker (*Melanerpes erythrocephalus*), ringed salamander (*Ambystoma annulatum*), northern fence lizard (*Sceloporus undulatus*), wood frog (*Lithobates sylvaticus*), plains spotted skunk (*Spilogale putorius*), turkey (*Meleagris gallopavo*), white tailed deer (*Odocoileus virginianus*), and elk (*Cervus canadensis*).

Starbuck et al. (2015) studied bats in the Ozark highlands on sites actively managed for savanna and woodland restoration, as well as unmanaged sites, and found that evening bats respond well to such management, including the use of prescribed fire, while northern long eared bats do better on unmanaged sites, and big brown, eastern red, and tri-colored bats did not show a preference. They also found that these relationships between bat occupancy and site type were on a relatively large (16 km radius) scale, indicating that landscape scale management could be important for bat conservation. Stanton et al. (2015) studied brown headed nuthatches in the Ouachita and Ozark St. Francis National Forests and found that nuthatch occupancy increased with snag density and decreased with percent stocking, concluding that shortleaf pine woodland restoration might extend habitat range.

In addition to providing habitat, shortleaf pine can improve forest health and resistance to climate change and other forest threats such as oak decline. Specifically in Missouri, reintroducing shortleaf pine in areas where it was formerly present can help address the oak decline facing many of the red oaks that replaced shortleaf pine. Fan et al. (2012) found that red oak mortality was correlated with drought in the Ozark Highlands. Similarly, Dwyer et al. (1995) found that red oaks with current crown die back began to show decreased growth in tree rings in the 10 years following major droughts. Kabrick et al. (2008) found greater overall mortality for red oaks on droughty and nutrient poor sites but concluded that this was due to greater red oak abundance on these sites, as they were prone to colonization by red oaks after the heavy harvesting of shortleaf pine and the farming practices of the early 1900s, rather than due solely to environmental factors.

More generally, mixed woods are less susceptible to forest pests, and mixed shortleaf-oak forests are better adapted to climate change than pure oak forests (Kabrick et al., 2017). Shortleaf has several attributes that provide advantages in the changing climate. It is drought resistant as well as fire tolerant and in favorable conditions can continue to photosynthesize in winter months (Guldin, 1986), taking advantage of warming winter temperatures. Shortleaf pine's response to climate change will vary throughout its range.

The drought tolerance of shortleaf pine has been demonstrated even in comparison to other pine species. A Texas study compared loblolly (*Pinus taeda*), slash (*Pinus elliottii*), and shortleaf pine seedling survival in simulated drought conditions, both with and without ground cover competition. After 7 months, in the absence of competition the three species all had at least 95% survival, but with competition shortleaf pine seedlings had 63% survival, significantly higher than loblolly pine at 19% and slash pine at 8% (Stransky, 1966). Shortleaf pine can both absorb more water and hold more water in its leaves than loblolly pine when at the soil moisture is at the wilting coefficient (Schopmeyer, 1939).

Shortleaf pine has several adaptations that have made it well-suited to past fire regimes and current fire management tactics. These adaptations will be advantageous into the future as well, as Guyette et al (2014) predict the probability of wildfire to increase across most of the range of shortleaf pine. Shortleaf pine has a morphological feature referred to as a basal crook that allows it to re-sprout following top-kill. The basal crook is a J-shaped curve at the root collar of shortleaf pine seedlings where dormant buds are protected from fire or other types of damage, primarily by their location in mineral soil. The crook forms in the first year of growth for open-grown seedlings but can take 3-9 years for shaded seedlings (Little et al., 1956). Larger shortleaf pine also have thicker bark, which helps protect the cambium from fire damage.

Shortleaf pine also has economic value. According to the U.S. Forest Service, shortleaf pine is the second most harvested softwood species in the southeastern United States by volume. It can be used for lumber, plywood, utility poles, fencing, and pulpwood. Shortleaf pine is one of the top 5 most harvested tree species in Missouri, with most of it being processed in state and used for sawlogs (Treiman et al., 2007).

Regeneration ecology

Shortleaf pine seed production varies regionally and yearly. A study of eight stands from Georgia to North Carolina over ten years found that only three of the years had adequate seed production, which was estimated by the authors to be 40,469 seeds per ha, and two stands in Virginia measured for five years had no adequate seed production (Bramlett, 1965). There was also evidence that seed production is negatively correlated with latitude in the Piedmont region. A five-year study in Louisiana of loblolly-shortleaf pine stands found that a closed canopy stand produced 1,653,875 sound seeds per ha over the five-year period while an open canopy stand produced 2,396,426 sound seeds per ha (Campbell, 1967). A ten-year study in Texas found that four of the ten years produced ample sound seeds, ranging from 667,184 per ha to >2,471,052 per ha, while in the other six years they produced very few seeds (Stephenson, 1963). The percentage of seeds produced that are sound can vary widely even in similar areas, with one study finding a range of 6-100% (Bramlett, 1965).

In the Ozark and Ouachita Mountains, studies indicate there is often adequate seed source for regeneration. Shelton and Wittwer (1996) studied seed production in the Ouachita and Ozark Mountains from 1965 to 1974. They observed notable year to year variation in seed production, as well as a positive correlation with stand age and a negative correlation with stand basal area. They concluded that shortleaf seed production would usually be adequate for natural regeneration. Wittwer and Shelton (2004) reported similar results in a more recent study in which seed production ranged from 0 to 7,413,155 seeds per ha over an eight year period. They again concluded that production would usually be adequate. Cain and Shelton (2001) studied shortleaf pine seed production in southeastern Arkansas and observed that yearly seed production ranged from 0 to 4,942,103 seeds per ha over 20 years. In their study, six years were considered to have bumper seed crops, nine years good seed crops, and five years poor seed crops. No poor seed crops occurred in consecutive years. The overall seed production was considered adequate for natural regeneration over the monitoring period.

For regeneration to occur, the seedbed must be free enough from litter to allow seeds to reach mineral soil (Baker, 1992). In southern Arkansas, Cain (1991) studied shortleaf pine seedling abundance in relation to seed production for areas treated with hardwood control and seedbed preparation. He found that while generally seedling counts were correlated with seed production, the number of seeds required for adequate seedling establishment decreased with hardwood control and decreased further with the combination of hardwood control and raking. In the Ouachita National Forest, Shelton (1995) found that shortleaf pine seedling density was positively correlated with seed production and negatively correlated with litter depth and overstory basal area. Looking at gap openings in Missouri forests, Stambaugh and Muzika (2007) found a gradual decrease in shortleaf pine regeneration as litter depth increased from 2.5 – 6 cm, and none when litter depth exceeded 6 cm. Prescribed fire can be an effective tool for reducing litter and achieving a suitable seedbed. Yocom and Lawson (1977) found that burning increased the ratio of seedlings established to seed produced. Grano (1949) however found that though there were more seedlings established in logging and skid roads than in undisturbed areas, litter of an average depth of 3.3 cm did not prevent adequate seedling establishment on an Arkansas site following a bumper seed crop.

Disturbance is required for the establishment and recruitment of shortleaf pine. The disturbance could be stand-replacing, resulting in an even aged stand of shortleaf pine. Traditionally, shortleaf pine has been described as being adapted to stand-replacement fires (Keeley and Zedler, 1998). This type of disturbance can be simulated by clearcutting or seed tree management strategies. Another pathway for shortleaf pine development is through more localized disturbances. Dendrochronological evidence from the Missouri Ozarks indicates that canopy disturbances causing gap openings were important to the growth of historic shortleaf pine and oaks, along with periodic fire. These canopy disturbances released the pines and oaks from competition, with the effects lasting on average 6 years. Most trees sampled experienced multiple releases (King and Muzika, 2014). In contemporary forests in Missouri, Stambaugh and Muzika (2007) found that the average age of shortleaf pine trees in canopy gaps ranged from 43 – 59 years, the size ranged from 1.7 – 25 cm DBH and 2 - 7 m tall. In the Cumberland Plateau of Tennessee, Goode et al. (2021) found that a combination of both stand-wide and more localized canopy disturbances catalyzed the establishment and growth of shortleaf pine in a mixed pine-oak forest. They concluded that 38% of the shortleaf pine trees they sampled were established due to stand-wide disturbance, and 41% were established due to local canopy gap disturbances. They also found that 83% of the shortleaf pines had experienced at least one release event, and 49% experienced at least two such events. Stambaugh et al. (2006) suggests a fire frequency of 1 to 4 years is appropriate for promoting pine regeneration, and an 8- to 14-year interval is needed for survival and recruitment.

Management for shortleaf pine regeneration

There is interest across the eastern United States in managing for hardwood-softwood mixtures due to their high diversity and resilience (Kabrick et al., 2020). In Missouri, the hardwood- softwood mixture is composed of shortleaf pine-oak forests and woodlands, which were historically common. In many cases, restoring these ecosystems involves trying to establish shortleaf pine on areas currently dominated by hardwoods. Several strategies have been tested, including manipulating forest density and competing vegetation, using prescribed fire to favor shortleaf pine and restore open ecosystem structure, and planting shortleaf pine seedlings where natural regeneration has not been successful.

An early strategy was to harvest the overstory and plant shortleaf pine. This has been tested in both the Sumter National Forest in South Carolina (Phillips and

Abercrombie, 1987) and in Tennessee (Clabo and Clatterbuck, 2020). Both studies included burns following harvest and the mechanical removal of woody competition. Both studies reported moderate success, with Phillips and Abercrombie (1987) finding 68-92% of planted seedlings alive and free-to-grow after four growing seasons, and Clabo and Clatterbuck (2020) finding around 50% survival after three growing seasons.

Others have experimented with planting shortleaf pine under a hardwood canopy, with varying degrees of overstory cover. Two studies (Schnake et al., 2021; Kabrick et al., 2015) found that height growth of shortleaf pine seedlings is negatively correlated with overstory density, though neither study found a meaningful correlation between overstory density and early survival. Measuring the success of planted bareroot shortleaf pine seedlings under different overstory treatments including clearcut, uneven-aged management, and thinning to B- and C-level stocking, Jensen et al. (2007) found the greatest stocking of shortleaf pine seedlings in the clearcut areas (63%) and the lowest in the uneven-aged management areas (28%). Similarly, they reported that the height of pine seedlings in the clearcut areas averaged 2.68 m, 1.22 m in the uneven-aged management areas, and 0.45 m in the B-level areas.

Others asked whether burning alone would be sufficient to establish a mixed pine-hardwood ecosystem. Elliot and Vose (2005) aimed to restore a shortleaf pine mixed hardwood bluestem ecosystem in the Appalachian Mountains. They concluded that a single spring burn was not sufficient to reduce the overstory basal area, prepare the seedbed for shortleaf regeneration, or change the diversity of ground vegetation. Jin et al. (2018), using a modeling approach, similarly concluded that a combination of burning and harvesting would be required to restore pine – oak woodlands to the central United

States. In areas where shortleaf pine and loblolly pine grow together and hybridization is a concern, burning can select for shortleaf pine by killing both loblolly pine and hybrid seedlings, as both lack the basal crook needed for sprouting (Stewart et al., 2015).

Seedling stock type and quality is important for the success of artificial regeneration of shortleaf pine. Schnake et al. (2021) compared bareroot, small containerized, and large containerized shortleaf pine seedlings planted under residual overstory of 0-10 m^2/ha. There was a strong relationship between seedling stock and survival, with survival ranging from 77% for large containers, 64% for small containers and 40% for bareroot seedlings after 5 years. The large containerized seedlings also showed greater height growth than the small containerized and bareroot seedlings (Schnake et al., 2021). Kabrick et al. (2015) examined bareroot shortleaf pine seedlings planted under 0-73% stocking in the Missouri Ozarks and found a significant, positive correlation between the initial seedling size and survival. They reported an overall survival of 67% after one growing season and 50% after 5 growing seasons. Clabo and Clatterbuck (2020) planted bareroot shortleaf pine seedlings in clusters in canopy openings following a harvest to 12 m^2/ha. After 4 growing seasons, survival was 35 – 43%, similar to the bareroot seedlings from Schnake et al. (2021), and competition from overtopping understory hardwood seedlings was believed to be an issue. In the Ozark National Forest in Arkansas, Barnette and Brissette (2004) found survival of 90 – 96 % of both bareroot and containerized pine seedlings after 10 years on sites that were clear-cut and site prepped.

Planting can cause changes in root structure compared to seeded trees. Planting results in a smaller percentage of trees with downward facing root systems (Harrington et al., 1989). This might pose a problem for the success of shortleaf pine restoration, as shortleaf seedlings lacking a major tap root, and with lateral roots primarily extending outward rather than downward, had poor growth compared to other root orientations (Harrington et al., 1987). There is a larger distance between the groundline and the uppermost lateral roots in planted trees, and fewer first order lateral roots per tree. In addition, more spiraling and turning of major lateral roots is found in planted trees (Harrington et al., 1989). Despite potentially damaging changes in root orientation, planting shortleaf pine can also have advantages. It can be the only option when a seed source is lacking and also allows the regeneration process to bypass the many potential problems associated with relying on seed, such as the condition of the seed bed, seed predation, and annual variations in seed production. Additionally, by the 1980s, shortleaf pine tree improvement programs had advanced enough so that nearly all seedlings used for planting could be of genetically improved stock (Kitchens, 1986).

Prescribed burning

While prescribed burning is often used to promote shortleaf pine success, several studies indicate that the size and/or age of shortleaf pine seedlings is an important factor in fire survival, with the general trend being that larger and older seedlings are more likely to survive without top-kill. A study in the Big Piney Ranger District of the Ozark-St. Francis National Forest, Arizona looking at shortleaf pine seedlings from 0.3 to 9 cm in basal diameter found that the group of seedlings that were not top-killed by a prescribed fire had an average pre-fire ground line diameter (GLD) of 4.1 cm, the group of seedlings that were top-killed by the fire and sprouted had an average GLD of 2.1 cm, and the seedlings that were killed completely by the fire had an average GLD of 1.5 cm

(Lilly et al., 2012). A study of prescribed burning at the Chilton Creek Preserve in southern Missouri found that for both shortleaf pine and oak species, mortality following fire decreased with increasing basal diameter (Dey and Hartman, 2005). A study on planted shortleaf seedlings' response to burning in the Cumberland Plateau of Tennessee found that all one-year-old seedlings and nearly all two-year-old seedlings were top-killed by burning, while some of the three-year-old seedlings were not. The total survival was 43% for one-year-old seedlings, 54% for two-year-old seedlings, and 57% for three-year-old seedlings (Clabo and Clatterbuck, 2019). In a mixed pine-hardwood stand in East Texas, Ferguson (1957) found that mortality decreased with increasing DBH for both shortleaf pines and associated oaks, though shortleaf pine was less susceptible, with negligible mortality when DBH exceeded 10 cm. At the Sinkin Experimental Forest, Phares and Crosby (1962) found 83% top-kill of three-year-old planted shortleaf seedlings following a prescribed burn. Only 7% were initially killed completely, though 11.5 % sprouted post burn but did not survive the growing season. They also found that taller trees were less susceptible to top-kill and that taller trees developed taller sprouts.

The fire conditions have also been shown to effect seedling survival. Lilly et al. (2012) found that fire surface temperature and percent crown scorch were significant factors in determining mortality. One study suggests that wildfire might produce more shortleaf pine seedlings than prescribed burns (Gnehm and Hadley, 2007), though this was purely a survey of seedlings post fire, not a study of whether pre-fire seedlings survived.

Season of burning also plays a role. A study simulating prescribed burns on raised beds found that 95% of 1 year old planted shortleaf pine seedlings resprouted after a winter burn, but none resprouted after a summer burn (Cain and Shelton, 2000). Sparks et al. (2002) found that fuel loads were higher in the dormant season and fuel consumption was less in the growing season. A study of a shortleaf-loblolly stand in Texas experimented with different seasons of burns to control understory hardwoods (Ferguson, 1961). They found that winter burns top-killed significantly fewer hardwoods (sweetgums and oaks) than other seasons, and that spring and summer burns caused complete mortality for significantly more oaks than other seasons. Summer burns also top-killed significantly more pines. For all species, smaller stems experienced significantly more top-kill (Ferguson, 1961).

For artificially regenerated shortleaf pine, planting decisions can affect the response to burning. Planting the seedlings deeper in the soil can increase the percent that resprout following fire when burned 1 year after planting (Meek and Will, 2020). Two studies showed that bareroot seedlings responded better to fire than containerized seedlings. Meek and Will (2020) found that bareroot seedlings were more likely to resprout than containerized when burned 1 year after planting (50% v 17%), and Chiriro (2019) found that overall survival was greater for bareroot seedlings (70%) than containerized seedlings (60%) when burned two years after planting.

Prescribed fire also can affect older trees. Using tree ring analysis Adhikari et al. (2021) found that shortleaf pine radial growth was reduced 21–33% during the growing season following prescribed burning for treatments with a 2- and 3-year fire return interval. Prescribed fire could increase the density of shortleaf pine wood by repeatedly heating the trees, promoting resin production (Guyette et al., 2008). Prescribed fire can also cause fire scars on mature trees. The size of scars increases with greater flame heights and are also larger and more common on exposed slopes. A study of several oak species, hickories, and shortleaf pine in the Missouri Ozarks found that following prescribed burning shortleaf pine had both fewer and smaller fire scars than the other species (Stevenson et al., 2008). A similar study across the Mark Twain, Hoosier, Daniel Boone, and Wayne National Forests found that shortleaf pine was among the least frequently scarred trees, with scars being relatively small when they did occur (Saunders et al., 2023). Another study in the Missouri Ozarks found that following two prescribed burns, for trees ≤ 11cm DBH, shortleaf pine showed 17.9% mortality compared to 36.5% for white oak, 45% for post oak, 71.4% for black oak, and 65% for scarlet oak; for trees ≥ 11 cm DBH shortleaf pine had 7.7% mortality compared with white oak at 9%, post oak at 9.1%, black oak at 15.2%, and scarlet oak at 32.6% (Kinkead et al., 2017).

Study overview

This project has multiple studies to provide a comprehensive assessment of key factors that can affect the success of shortleaf pine regeneration and recruitment, from seed germination to sapling survival and growth. The first study examines the timing of prescribed fire with regard to seed germination and germinant survival, and also examines the direct effects of heat and smoke on seed germination. The second and third studies look at shortleaf seedling growth and survival in mixed pine oak forests. The second compares survival and growth of both shortleaf pine and oak seedlings of various sizes following prescribed fire, and the third analyzes the effect of hardwood competition on survival and growth of shortleaf pine seedlings planted under a range of overstory densities. The final study uses tree ring analysis to study growth patterns of shortleaf pine during the first 18 years of growth in response to release events, competition level, and prescribed burning. Together this work provides a picture of the early life of shortleaf pine, with focus on the role fire and competition in shortleaf pine’s success.

Chapter 2: Direct and indirect effects of fire on shortleaf pine seeds and implications for natural regeneration

Background

Fire is an important ecosystem process that affects forest structure, composition, and function. In the eastern United States, changes in forest ecosystems over the past century have been attributed, in part, to changes in fire regimes, commonly reported to have resulted in increased tree densities and shifts to more fire-sensitive, mesic species (Nowacki and Abrams, 2008; Hanberry et al., 2020). The effects of fire on forest composition may be related to several factors, such as differential rates of removal through mortality (Huddle and Pallardy, 1996) or impacts on the success of tree establishment during the regeneration process (Brose, 2014). Tree regeneration is a complicated process that includes several stages (seed production; germination; seedling survival; sustained growth) (Dey et al., 2019; Grubb, 2021). Failure at any of these stages can result in undesirable regeneration outcomes. Following seed production, fire may affect regeneration outcomes by: 1) having direct effects on seeds, such as stimulating or inhibiting germination through heat or smoke; 2) affecting the seedbed conditions; and 3) moderating the competitive environment for developing seedlings. Effectively incorporating fire into regeneration prescriptions requires understanding of the prevailing fire regime on each stage of the regeneration process (Arthur et al., 2012).

In the eastern United States, shortleaf pine (*Pinus echinata*) occurs in fire-adapted ecosystems that have greatly decreased in abundance and extent over the past few centuries. Prior to European colonization, shortleaf pine covered approximately 300,000 km^2 (Anderson et al., 2016) but has been reduced to current estimates of 25,000 km^2

(Oswalt al., 2012), in large part due to overharvesting followed by nation-wide fire exclusion that facilitated conversion to hardwood species following harvest. Many areas with mature shortleaf pine remaining in the overstory lack shortleaf pine seedlings and saplings, indicating that natural regeneration of shortleaf pine is generally not adequate to replace existing stands (Moser et al., 2007; Vickers et al., 2019), even following timber harvest that increase understory light levels (Olson et al., 2017). Given evidence of the historical role of fire in shortleaf pine ecosystems, prescribed burning is commonly recommended for improving regeneration success, yet specific prescriptions that consider different stages of regeneration are lacking.

Past studies have demonstrated that prescribed burning can increase the abundance of shortleaf pine seedlings. Germination of shortleaf pine seed requires contact with mineral soil, and the accumulation of leaf litter on the forest floor reduces seedling establishment (Grano, 1949; Baker, 1992). In Missouri, Stambaugh and Muzika (2007) found that the number of regenerating shortleaf seedlings decreased as litter depth increased from 2.5 – 6 cm, and no shortleaf pine seedlings were found when litter depth exceeded 6 cm. Increased abundance of shortleaf pine seedlings following fire is often attributed to improved seedbed conditions, but no information is available about possible direct effects of heat or smoke on shortleaf pine germination. Shortleaf pine disperses seeds primarily in November and December (Bramlett, 1965; Cain, 1991), and seeds are then cold stratified during the winter and germinate in early spring (Lawson, 1990). Prescribed burns applied prior to seed-fall would reduce leaf litter without direct effects on the seed, whereas prescribed burns during the winter and spring dormant seasons may have additional, direct effects on seeds.

The direct effects of fire on plant seeds vary by species, with examples of germination triggered by fire-related cues for some species in fire-adapted ecosystems. This may be caused by exposure to heat, as for bay cedar (*Guazuma ulmifolia*) (Dayamba et al., 2008), Shittimwood (*Acacia seya*) and multiple *Desmodium* species in Ethiopian savannas (Gashaw and Michelsen, 2002), or by exposure to smoke, as seen in species of *Cistaceae, Poaceae*, *Fabaceae*, and *Asteraceae* in Spanish woodlands (Pérez-Fernández and Rodríguez-Echeverría, 2003) and *Pinus douglasiana* in Mexican montane forests (Zuloaga-Aguilar et al., 2011). However, the opposite effect also occurs, as heat can damage seeds and reduce germination, which has been observed for white oak (*Quercus alba*), Shumard oak (*Quercus shumardii*), and northern red oak (*Quercus rubra*) acorns in the U.S. (Greenberg et al., 2012, Nation et al., 2021). Direct effects of fire on shortleaf pine seeds have not been studied.

This study is designed to improve the understanding of the fire ecology of shortleaf pine regeneration and has two objectives. The first is to determine the direct effects of heat and smoke exposure on shortleaf pine seeds through a greenhouse experiment. We hypothesize that smoke and heat exposure may stimulate greater germination of shortleaf pine seeds, but that there may be a heat exposure threshold at which seeds are damaged and germination decreases. The second objective is to determine the effect of the time of year of prescribed burning on the germination of shortleaf pine seeds in the field. We hypothesized that burning in the fall, prior to seed dispersal, increases germination compared to unburned controls by improving the seedbed, while burning in the late spring kills young germinants. Burning in the early spring may decrease germination by damaging the seeds with heat or increase germination by improving the seedbed, so the overall impact of early spring burns will depend on the trade-off between these factors and is of particular interest.

Methods

Greenhouse study

Experimental design

The greenhouse study was designed to test effects of heat exposure and smoke exposure on germination of shortleaf pine seed. The study included heat exposure treatments that combine five temperatures (60, 80, 120, 200, and 270 ° C) with each of three durations (1, 5, and 10 minutes). It also includes an untreated control, for 16 total temperature and time combinations. These heat exposure treatments were applied by placing shortleaf pine seeds in a Yamato DKN602C oven for each specific combinations of temperature and time. Smoke exposure treatments were applied separately and included four treatments: an untreated control and smoke exposure (without heat) for 5, 10, and 90 minutes. The smoke was generated using a TMKEFFC electric portable smoke infuser, designed for flavoring food without cooking it. Shortleaf pine needles gathered from local stands were used as the fuel for the smoker, and the smoke infused into sealed containers of seeds via rubber tubing. The heat exposure or smoke treatments were each applied to sets of 30 shortleaf pine seeds, replicated three times per treatment (90 total seeds within each treatment) on March 17-19, 2021. The seeds used were produced from Missouri trees grown in a seed orchard on the Ouachita National Forest in Arkansas. They were collected in 1986 and stored in a -15.5 °C (4 °F) freezer since then at the George O. White Nursery, managed by Missouri Department of Conservation in Licking, MO.

After treatment, the seeds were planted in 98 cell propagation trays in a mixture of 40% peat, 40% vermiculite, and 20% perlite. One seed was planted within each cell on March 19, 2021. Treatments were randomly assigned to trays, and each tray contained three treatments with the exception that no tray could have two of the same treatment. The propagation trays were kept in greenhouses on the University of Missouri campus, and the trays were watered daily.

Data collection and analysis

For 40 days following planting, trays were monitored for germination daily, and cells with live germinants were recorded. The number of total germinants peaked on day 30, and only one seed germinated after day 35, so the experiment was ended on day 40. The probability of a seed germinating by the end of the 40-day sampling period was modeled using logistic regression, with a generalized linear mixed model that used a binomial distribution and logit link function. The binary response of germination status (yes or no) was the response variable, and the heat exposure and smoke exposure treatments, respectively, were the independent variables in separate models. Each model included random terms to specify the replicate experimental unit (set of 30 seeds to which treatments were applied) and the planting tray used in the greenhouse. For significant effects of heat exposure or smoke exposure, pair-wise comparisons among treatment levels were tested using Tukey’s HSD adjustment for multiple comparisons.

Field study

Study site

The field study was conducted at the Baskett Wildlife Research and Education Center (BWREC), a University of Missouri property located five miles east of Ashland, MO. The land where BWREC currently exists was private farms, with much of the area cleared of trees, prior to consolidation under federal ownership in the 1930s. Since that time, the area has been managed by the University of Missouri. Agricultural reclamation practices included widespread tree planting in the late 1930s and early 1940s, including several plantations of shortleaf pine. There are no records of management activities (thinning, prescribed burning, etc.) in the plantations after the time of planting. The average temperature in Boone County, MO from 1991-2021 was 18 °C and the average precipitation was 107.49 cm (NOAA, 2021). The soils of the study were mapped as Weller silt loam, 5-9% slopes. The Weller soils are deep, moderately well-drained, and formed of loess (Soil Survey Staff, 2021).

Table 2.1: Characteristics of the four shortleaf pine stands used in the field study.

	Block 1	**Block 2**	**Block 3**	**Block 4**	**Average**
BA (m^2/ha)	49.1	49.3	43.9	59.6	**50.5**
Trees per Hectare	1001	420	803	988	**803**
QMD (cm)	24.8	38.3	26.2	27.5	**29.2**
Litter (dry g/m^2)	978.3	1018.7	1185.2	1136.7	**1079.7**
Burned Litter (dry g/m^2)	962.0	610.0	667.8	827.9	**766.9**
Establishment Year	1942	1939	1942	1940	

Experimental design

We used a randomized complete block design, with four treatments applied in each of four shortleaf pine plantations (i.e., blocks). Treatments include a control (no fire), a fall burn (applied prior to seed dispersal), an early spring burn (applied following seed dispersal but prior to germination), and a late spring burn (applied after germination). The study plots were 0.01-ha rectangles with dimensions of 8.35 m x 17.25 m. Within a block, the study treatments were randomly assigned to the plots.

Study treatments were applied to each plot by establishing fire breaks around plot boundaries. The fall burns took place on November 5, 2020, between 1:40 pm and 4:30 pm. Plots were ignited in a ring pattern, with the two plots burned later in the day also ignited centrally as temperatures cooled. Air temperatures were between 10.5 and 23.3 °C. Flame lengths were generally around 30 cm. The early spring burn occurred on March 6, 2021, between 12:30 pm and 4:00 pm. Air temperatures were between 0 and 16 °C. Plots were ignited in a ring pattern, and flame lengths were generally around 30 cm. The late spring burn was conducted on May 1, 2021, between 12:30 pm and 4:00 pm. Air temperatures were between 18 and 29 °C and flame lengths were generally around 30 cm.

Shortleaf pine seeds (of the same origin as in the greenhouse experiment) were scattered by hand across all plots on November 11, 2020, at a rate of ~ 74,000 seeds/ha. The seeding rate was determined based on a 10-year study in Oklahoma, Arkansas, and Missouri (Shelton and Wittwer, 1996). In the study, shortleaf pine produced a range of 5000-1,846,000 seeds/ha during the study years. In most years (7 of the 10 years), at least 66,700 seeds/ha were produced, and no two consecutive years had less than 79,000 seeds/ha produced.

Data collection and analysis

In late May 2021, plots were surveyed for germination. In each plot, three parallel transects were established across the length of the plot (17.25 m), and all germinants within 0.38 m on each side of the transect were counted. The total sampling area was 40.5 m^2 in each plot. Natural regeneration was assessed outside the seeded plots, using three non-parallel transects of equal length within each of the stands. All transects were re-surveyed in October 2021.

The abundance of shortleaf pine germinants (number per hectare) was modeled using generalized linear mixed models, with burn treatment as the independent variable and stand (i.e., block) included as a random effect. Spring and fall germinant counts were analyzed separately. For significant effects of burn treatment, pair-wise comparisons were tested using Tukey's HSD adjustment. For all models, statistical significance was determined when $p < 0.05$. All analyses were conducted using SAS 9.4 software (SAS Institute, Cary, NC, USA).

Results

Greenhouse study

Germination began 12 days after planting and peaked approximately 20 days after planting (Figure 2.1). The patterns of germination through time were generally similar among treatments, with the exception that the 80 ºC treatments with 5 and 10 minute durations had later germination (day 18). After the 40-day monitoring period, the germination rate for the untreated shortleaf pine seeds was 81.1% (Figure 2.2), and the heat exposure treatments had significant effects on germination ($p < 0.001$). No seeds germinated when exposed to 120 ºC or higher, regardless of the duration, and therefore treatments greater than 80 ºC were excluded from the model. Seeds exposed to 60 ºC did not differ significantly from controls, regardless of the duration of exposure. For seeds exposed to 80 ºC, the duration of exposure was important. Seeds with exposure to 80 ºC for 1 minute and 5 minutes did not significantly differ from controls, but seeds exposed to 80 ºC for 10 minutes had significantly lower germination than all other treatments except for 80 ºC for 5 minutes (Figure 2.2).

There were no significant effects of smoke exposure (p=0.814). The model estimated 79.9% germination for the controls and 79.5%, 82.7%, and 75.5% germination for 5 minutes, 10 minutes and 90 minutes of smoke exposure, respectively.

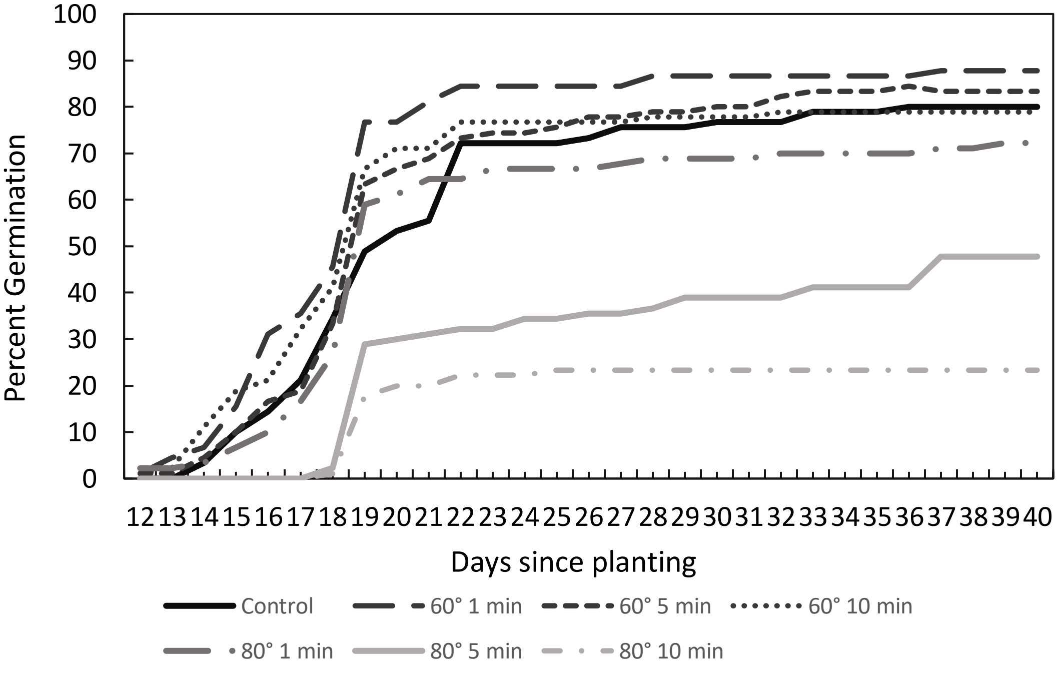


Figure 2.1: Cumulative percent germination through time for shortleaf pine seeds following exposure to various temperatures for 1, 5, or 10 minutes. No germination occurred for exposure to temperatures > 80 °C.

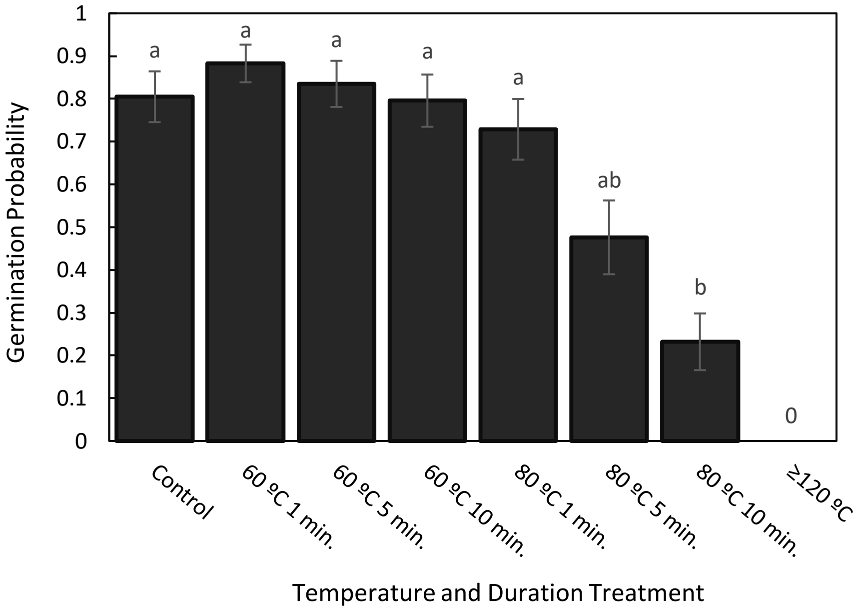


Figure 2.2: Germination probability (modeled mean ± standard error) of shortleaf pine seeds by heat exposure treatment. Different letters represent Tukey -adjusted significant differences between pairwise comparisons. No germination occurred for any treatment with temperature ≥ 120 °C.

Field study

For the May sampling, the fall burn resulted in the most germinants and was significantly greater than all other treatments (Figure 2.3). The abundance of germinants in the early spring burn treatment did not differ from the control, and the late spring burn had significantly fewer germinants than all other treatments. After the end of the first growing season (i.e., the October sampling), the abundance of germinants was lower than in the May sampling for all treatments but still differed among the burn treatments. The fall burn had the greatest abundance of germinants but was only significantly different from the late spring burn. The control and early spring burn treatments were not significantly different from any other treatments. Unseeded areas had approximately 1606 shortleaf pine germinants per hectare when surveyed in May and 371 germinants per hectare when surveyed in October.

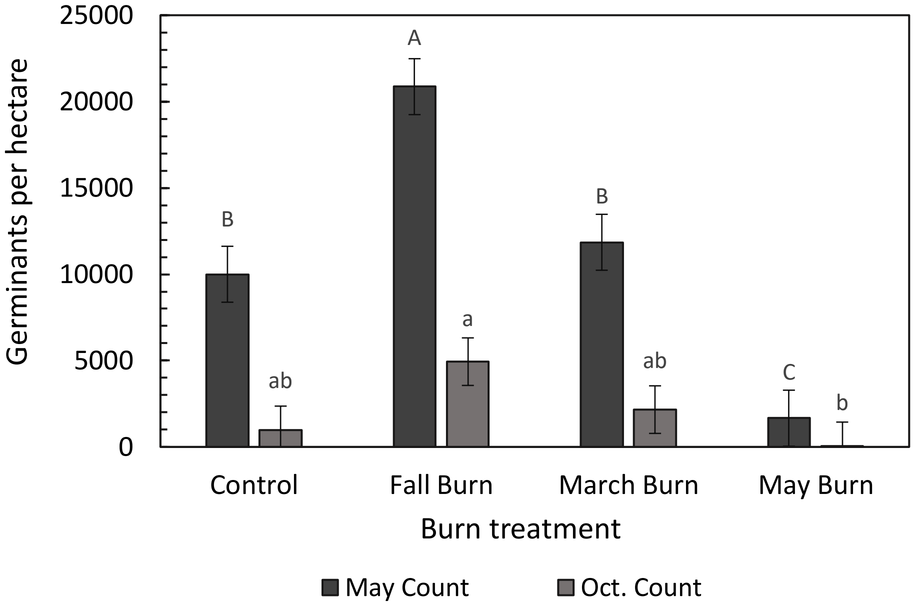


Figure 2.3: Least squared means (± standard error) of germinant counts across four shortleaf pine stands by burn treatment for May (dark grey) and October (light grey) sampling periods. Different letters represent significant differences between treatments within each sampling period.

Discussion

This study demonstrates the potential for prescribed burning to have both direct and indirect effects on germination success of shortleaf pine seeds. Exposure of seeds to temperatures of 80 °C or greater can partially or completely inhibit shortleaf pine germination. We found that burning prior to seed dispersal increased germination in the field, an indirect effect of fire that was likely due to combustion of forest floor material and exposure of mineral soil. Burning following dispersal but before germination, which would represent the period during much of the dormant season burn window in the region, resulted in germinant abundance similar to the unburned control. It is possible this treatment was a balance of direct effects of heat exposure that reduced germination for affected seeds with the indirect effects of improved germination sites through forest floor removal. We found poor success when burning occurred following germination, likely due to direct effects of fire on mortality of new germinants.

Some previous studies have documented direct positive effects of fire on seed by stimulating germination. For six legume species that occur in longleaf pine (*Pinus palustris*) ecosystems, heat treatments stimulated germination at low levels of exposure but inhibited germination at high levels of exposure, although there were variations in the stimulation and inhibition thresholds among the species (Wiggers et al., 2017). Heat exposure between 70 and 150 °C stimulated germination in six of seven Mediterranean legumes tested (Herranz et al., 1998). Exposure to both fire and smoke in the absence of fire enhanced germination of seeds of four common tree species of the deciduous forests of India, with the effects of fire being greater than the effects of smoke alone for all species, indicating that heat provides an additional stimulatory effect for these species (Singh and Raizada, 2010).

Similar to our results, however, past studies have found that applying heat directly to seeds of pine species reduces germination. Seeds of seven Spanish pine species, Aleppo pine (*Pinus halepensis*), stone pine (*P. pinea*), maritime pine (*P. pinaster*), mountain pine (*P. uncinate*), black pine (*P. nigra*), Scotch pine (*P. sylvestris*), and Canary Island pine (*P. canariensis*) were exposed to temperatures between 50 – 150 °C for 1-15 minutes (Escudero et al., 1999). Germination was decreased rather than stimulated by heat exposure for all species, although the thresholds varied among species. For the least heat-tolerant species, germination suppression began at 70 °C and for the most tolerant species, germination was significantly lower only at 130 °C (Escudero et al., 1999). In a different study, Turkish red pine (*P. brutia*) showed no effect of exposure to temperatures up to 130 °C, at which point the duration of exposure became more important than increased temperature up to 170 °C (Boydak and Caliskan, 2016).

For some species, including a few tree species, smoke stimulates germination (see Brown and van Staden, 1997 for review). Scientists have isolated the compound butenolide 3-methyl-2H-furo[2,3-c]pyran-2-one, now referred to as karrikinolide (Dixon et al., 2009), as the main component within smoke that stimulates germination (Flematti et al., 2004). In previous studies, seeds have been experimentally germinated in aqueous smoke solution (Todorović et al., 2005), on smoked filter papers (Singh and Raizada, 2010), with direct application of the butanolide compound (Kulkarni et al., 2007), and with direct smoke application as in this study. We found no effects of direct smoke exposure on shortleaf pine seeds in our study. Similarly, applying smoke to seeds of Scotch pine, black pine, mountain pine, and maritime pine for 5 to 20 minutes had no effect on germination (Reyes and Casal, 2006). However, Douglas pine (*Pinus douglasiana*) germination was increased with application of an aqueous smoke solution (Zuloaga-Aguilar et al., 2011), and it is possible that shortleaf pine seeds may respond to different applications of the compounds within smoke.

Collectively, our results and those of past studies indicate that germination is not commonly stimulated by heat or smoke for pine species. Instead, pines use other adaptive strategies suited for specific fire regimes (Schwilk and Ackerly, 2001). Keeley (2012) used common fire-adaptation traits of pines to describe general life history strategies in relation to fire regimes. Species adapted to frequent surface fires often exhibit thick bark, persistence of seedlings with fire, and self-pruning, whereas species adapted to stand replacement fire may exhibit serotiny and short, dense needles (Keeley, 2012). Shortleaf pine has been described as being adapted to stand-replacement fires (Keeley and Zedler, 1998) but exhibits traits of species tolerant to frequent surface fires, such as thick bark and sprouting from the basal crook of seedlings (Matoon, 1915; Bradley et al., 2016). Fire history studies from shortleaf pine stands in the Missouri Ozarks indicate frequent, low to mixed intensity fire regimes, with mean fire returns intervals ranging from 4 – 18 years (Guyette and Bruce, 1997; Batek et al., 1999). Like many other pines species, shortleaf pine seeds require mineral soil for germination, which can be created by fires that vary in intensity from surface to crown (Keeley, 2012).

Prescribed burning can be a useful site preparation for shortleaf pine regeneration by reducing the forest floor and exposing mineral soil. Past studies have shown that the depth of the forest floor is inversely related to the abundance of shortleaf pine seedlings (Grano, 1949) and that practices that disrupt the forest floor can increase the abundance of shortleaf pine seedlings. Site preparations that improve seedbed conditions effectively increase the number of seedlings established per sound seeds produced (or seeded), also referred to as seedling percent (Yocom and Lawson, 1977; Cain, 1991; Shelton, 1995). Seedling percents estimated for our field study, from the May and October sampling, respectively, were: control – 11.3%, 1.1%; fall burn – 26.0%, 5.8%; March burn – 13.8%, 3.1%; May burn – 0.1%, 0.0%. Boggs and Wittwer (1993) observed seedling percents (measured in December for seeds sown in January) of 4.0%, 1.9%, and 1.0% in areas that had been treated the previous July with a hot burn, a medium burn, or no burn respectively. Yocum and Lawson (1977) reported 3-year seedling percents for naturally regenerated shortleaf pine of 0.42% for unburned, unlogged areas, 0.98% in both burned only and logged only areas, and 1.29% in areas both logged and burned. By improving seedbed conditions, prescribed burning can be a tool for increasing natural regeneration success despite the interannual variability in shortleaf pine seed production (Bramlett, 1965; Stephenson, 1963; Wittwer and Shelton, 2004).

While the results of our greenhouse study show that heat exposure can reduce germination of shortleaf pine seed, we were not able to quantify the level of heat exposure experienced by seeds in our field study. The position of the seeds within the leaf litter profile may affect their vulnerability to heat exposure and germination success. This has been experimentally tested for acorns; Greenberg et al. (2012) placed northern red oak and white oak acorns on the leaf litter surface, in the duff layer, or in the mineral soil during winter prescribed burns and then germinated the acorns in a greenhouse. They found that for all acorns on the litter surface germination rates decreased with increasing fire temperature, but acorns in the duff layer and mineral soil were not generally affected. For shortleaf pine seedlings, it is possible that the timing of prescribed burning may interact with the position of seeds in the litter to affect heat exposure experienced by seeds. Bogs and Wittwer (1993) suggested that shortleaf pine seeds move from the surface of the litter layer to the mineral soil in the months following dispersal. Therefore, a burn in December or January might damage more seeds than an early spring burn (e.g., the March burn in our study), because the seeds might be closer to the litter surface in the earlier burn. More generally, local variability in fuels and fire behavior can have important implications for fire effects on litter consumption and heat exposure to seeds. Our field study used low-intensity burns that may have generally dampened the effects of the burns, on both the reduction of the forest floor in the fall burn (the indirect positive effect) and the heat exposure to shortleaf pine seeds in the March burn (the direct negative effect).

Conclusions

Our study provides evidence that prescribed burning can be used to increase the success of natural regeneration of shortleaf pine, but the time of year of the burns can affect the outcomes. Fall burning, prior to seed dispersal, maximized the number of new germinants during the next growing season by preparing the seedbed but avoiding direct damage to seeds through heat exposure. Burning during the winter or early spring, after seed dispersal, is likely to reduce viable seed through heat exposure but also consume the litter layer to improve the seedbed. The burns in our study were done in a small area and were low-intensity, so higher intensity burns in early spring could result in more damage to seeds. Late spring burns, following germination, drastically reduced regeneration success. Forest managers specifically interested in shortleaf pine natural regeneration can use this information to better time prescribed burning to improve regeneration outcomes.

Chapter 3: Sprouting dynamics of shortleaf pine and oak regeneration following prescribed fire in the Missouri Ozarks

Background

Shortleaf pine (*Pinus echinata*) was once more abundant than it is currently, both across its range and in Missouri specifically. Shortleaf pine covered an estimated 283,000- 324,000 km^2 across what is now the southeastern United States prior to European colonization (Anderson et al., 2016). Shortleaf pine currently occupies 25,000 km^2 in the United States (Oswalt al., 2012). Guyette et al. (2007) estimate that, excluding plantations, shortleaf pine in Missouri is currently at only 22% of historic abundance. There is growing interest in restoring shortleaf pine within its former range. The former prevalence of shortleaf pine across the eastern United States can be in part attributed to past fire regimes, so prescribed fire is often used as a management tool in the shortleaf pine restoration effort.

Shortleaf pine has two important traits making it well adapted to fire. The first is a morphological feature referred to as a basal crook that allows it to re-sprout following top-kill. The basal crook is a J-shaped curve at the root collar of shortleaf pine seedlings, often located at or under the mineral soil surface, where dormant buds are protected from fire and other types of damage. The crook forms in the first year of growth for open-grown seedlings but can take 3-9 years to form for shaded seedlings (Little et al., 1956). The second factor is the thickness of shortleaf pine's bark, which helps protect the cambium from fire damage. Reifsnyder et al. (1967) examined several thermophysical properties of the bark of shortleaf, longleaf (*Pinus palustris*), and red pine (*Pinus resinosa*) including conductivity, thermal diffusivity, and specific heat, and found that bark thickness was the most important factor in determining a tree's fire resistance. Harmon (1984) found a significant correlation between bark thickness and likelihood of surviving a prescribed burn for pitch pine (*Pinus rigida*), Virginia pine (*P. virginiana*), and chestnut oak (*Quercus prinus*) and also found a significant correlation between bark thickness and diameter at breast height (DBH) for 27 species including shortleaf pine. Using Harmon's bark thickness findings, Stevenson et al. (2008) ranked shortleaf pine as the most fire tolerant of 7 species included in a fire scar study in the Missouri Ozarks.

In the Ozarks, shortleaf pine is often managed in mixed oak-pine stands, so understanding both oak and pine seedling response to burning, and how they may differ, is of interest if managers hope to use fire to promote healthy pine-oak mixtures. In Missouri, much of the area historically occupied by shortleaf is now dominated by oaks. Like shortleaf pine, the oaks of the Ozarks re-sprout following top-kill from burning. On oak dominated sites, oak regeneration can die-back and resprout several times, developing robust root systems. The energy stored in these roots often gives resprouting oaks a competitive advantage over shortleaf pine seedlings in terms of early growth (Dey, 2002).

Despite several fire related adaptations, shortleaf seedlings can still be damaged or killed by fire. Thus, understanding the factors contributing to shortleaf pine seedling survival after a fire is important to managers. Using a combination of methods including historic fire scar and growth data, fire effects data from studies at Chilton Creek Preserve in Missouri, and modeling, Stambaugh et al. (2007) suggested a fire frequency of 1 to 4 years is appropriate for promoting pine regeneration, and an 8- to 14-year interval is needed for survival and recruitment into the overstory. However, the specific factors affecting the likelihood of success of shortleaf pine seedlings relative to those of competing oaks are not clear.

In general, woody plants become less susceptible to top-kill or mortality from fire as stem size increases. A study in the Big Piney Ranger District of the Ozark-St. Francis National Forest, AR found that shortleaf pine seedlings with greater basal diameters were less likely to be top-killed or experience complete mortality (Lilly et al., 2012) and a study at the Chilton Creek Preserve in southern MO found that for both shortleaf pine and oak species, mortality following fire decreased with increasing basal diameter (Dey and Hartman, 2005).

The fire conditions have also been shown to effect pine seedling survival. For example, Lilly et al. (2012) found that surface fire temperature and percent crown scorch were significant factors in determining mortality. Season of burning also plays a role. One study, using simulated prescribed burns on raised beds with evenly distributed litter from a nearby forest and box fans, found that 95% of 1-year-old planted shortleaf pine seedlings resprouted after a winter burn, but none resprouted after a summer burn (Cain and Shelton, 2000).

Species differences in survival after fire have also been studied. The Chilton Creek study found that after a single prescribed burn, shortleaf pine seedlings had greater mortality, at around 38%, than did oak seedlings (Dey and Hartman, 2005). There were also differences among oak species, with white (*Quercus alba*), post (*Quercus stellata*), black (*Quercus velutina*), and scarlet oak (*Quercus coccinea*) having slightly greater mortality, at 5-10%, than chinkapin (*Quercus muehlenbergii*) and blackjack oak (*Quercus marilandica*), at less than 5%. After 3 or more burns, shortleaf pine mortality stayed about the same, while white and post oak mortality increased to about 20%, and scarlet and blackjack oak mortality increased to around 40%. Looking at the same study site 7 years later after subsequent burns, Fan et al. (2012) observed greater overall mortality for shortleaf pine, 69%, than for oak species, 36-54%, though shortleaf pine was the only species to increase in mean height. Oaks primarily survived by resprouting, whereas larger (greater than 4 cm basal diameter) shortleaf pine seedlings resisted top-kill.

As previous research indicates differences in post-fire responses between shortleaf pines and oaks, the goal of this research is to directly compare the survival rates and strategies of shortleaf pine and oak seedlings and saplings after prescribed burning. Specifically, we aim to: 1) find size thresholds at which shortleaf pine and oak can either resist top-kill or survive through sprouting following prescribed burning, 2) determine the relationship between fire intensity (measured through temperature-sensitive paint tags) and survival for pine and oak seedlings, 3) compare the growth of sprouts and surviving stems of shortleaf pine and oaks following burning, and 4) determine whether there is a specific timing during the development of shortleaf pine and oak regeneration during which a burn would give shortleaf pine a competitive advantage over oaks through different survival or top-kill rates.

Methods

Study site

In 2000, the Missouri Department of Conservation (MDC) established the 5000 ha Midco Shortleaf Pine Restoration Area (referred to as Midco) within the southern part of the Peck Ranch Conservation Area in Carter County, Missouri. The elevation of Midco ranges from 190-295 m above sea level with rolling topography and dry to dry-mesic, cherty Ultisol and Alfisol soils (Olson and Olson, 2016). The predominant soils in the study area are mapped as Clarksville and Alred-Rueter and Alred-Gepp soil series, which are very deep, well drained to somewhat excessively drained soils, composed of hillslope sediments over clayey residuum (Soil Survey Staff). Slopes range from 0 to 35 %. Carter County has a 30-year (1991-2020) average precipitation of 1247 mm and temperature of 13.8 °C (NOAA, 2022). The Missouri ecological classification system uses ecological and geological information to categorize landscapes into landtype associations (LTAs). Midco is described as a Current River Oak-Pine Woodland/ Forest Hills LTA (Nigh and Schroeder, 2002; Olson and Olson, 2016) and as a Current-Eleven Point Oak-Pine Woodland Dissected Plains LTA (Tuttle and Houf, 2007, Olson and Olson, 2016).

The original project at Midco was designed to compare the effectiveness of multiple management strategies for pine establishment and included ten management units. The management units received different treatments through time, and the timing of management actions for each unit are listed in Table 3.1. All management units were harvested. Harvests focused on salvaging declining red oaks and were done with the goal of leaving approximately 4.6 m^2/ha basal area of white and post oak, with shortleaf pine seed trees. Following harvest, the stands were slashed by cutting remaining suppressed oak and hickory trees (Tuttle and Houf, 2007). One management unit was kept as a control following harvest, and the remaining nine were planted with shortleaf seedlings. Shortleaf pine seedlings planted in the units were from the George O. White State Nursery and planted at a spacing of 3.6 x 3.6 m. The remaining nine management units were then divided into groups of three and treated with either herbicide application, mechanical release, or prescribed burning. The current study focuses on the three units within the Midco Shortleaf Pine Restoration Area treated with prescribed fire. Unit 1 received a light-intensity burn in February 2002, and units 4 and 6 received a moderate-to-intense burn in April 2002. Unit 1 was burned again in September of 2007, March 2010, and in 2014. Units 4 and 6 were burned again in 2013 and 2012 respectively, and also received mechanical release treatments, which were done either with chainsaws by cutting all woody competition within 1.83 m of pine seedlings or with a bull-hog, which generally cleared the entire area among pine seedlings. As a result of various treatments applied through time, the Midco Shortleaf Pine Restoration Area has both shortleaf pine and oak seedlings and trees of various ages and sizes. Oak species include post, white, black, and blackjack.

Table 3.1: History of management treatments in three burn units at the Peck Ranch Conservation Area since 1999.

	Unit 1	**Unit 4**	**Unit 6**
Harvest	2001, 2003	2001	2001
Plant	2005, 2006	2006	2005
Prescribed Burn	2002, 2007, 2010, 2014	2002, 2013	2002, 2012
Slash	2007	2007	2005
Mechanical Release		2011	2009

Experimental design

The experimental design consisted of 30 plots in each of three burn units (units 1, 4, and 6) at Midco, with 2 species groups (shortleaf pine and oaks) and 5 size classes of seedlings/saplings within each plot. The size classes were separated by basal diameter and include: 0-1.5 cm, 1.5-4 cm, 4-6.5 cm, 6.5-10 cm, 10-15 cm.

In each of the burn units, sampling plots were established in the fall/ winter of 2019. The location of each plot was determined by using GIS to overlay a grid over the areas determined by the Missouri Department of Conservation to be suitable for shortleaf pine within each of the three burn units, and randomly selecting points along the grid. Initially 50 points were generated for each unit; these were examined and those without the appropriate size classes of trees within 30 m of the point were excluded. Because the first random grid of 50 points failed to generate the 30 sample plots within each burn unit, a second set of 50 points were randomly selected, randomly numbered, and visited in order until 30 suitable plots were found. At each plot, one shortleaf pine and one oak in each of the 5 size classes were tagged. Plots were 10 m in diameter.

Pre-fire sampling

The height and basal diameter, measured 2.5 cm from ground, of all tagged trees were measured and recorded in the fall / winter of 2020. Oaks were identified and species recorded.

To quantify a surrogate for fire intensity, an aluminum tag painted with temperature sensitive paints designed to melt at specific temperatures (Tempil® Temperature Indicating Liquids) was staked by each tagged tree at a height of 10 cm above the ground. Paint temperatures included: 80, 121, 149, 177, 204, 232, 260, 288, 316, 343, and 399 °C. Temperature paint tags were installed adjacent to all seedlings in Units 1 and 4. In Unit 6, 25 of the 30 plots had at least 1 temperature painted tag, with most at the smallest size class of pine and oak seedlings only, due to time constraints. All tags were collected 1 – 2 days following burning, and I determined the highest temperature indicated by melting.

Post-fire sampling

Following the burns, paint tags were collected, and any plots that did not burn were noted. In June 2021, all tagged trees were re-visited, and status was recorded as: alive (resisted top-kill), sprouted (survive with top-kill), or dead. In fall of 2021, the number of sprouts and height and basal diameter of the largest sprout for each seedling were recorded, and trees not top-killed were re-measured for height and basal diameter.

Burns

Unit 6 was burned 2/3/21. Ignition began at 11:40 am and was complete at 3:46 pm. Air temperature was between 5 and 13 °C. Relative humidity was between 43% and 68%. Wind was from the south, and less than 8 km per hour. The estimated flame height was 24 cm and the estimated rate of spread was 36 m/hour. The average temperature indicated by painted tags was 92 °C. Twenty-two of the 30 plots were at least partially burned.

Units 1 and 4 were burned on 3/3/21. Ignition began in unit 4 at 10:58 am and was complete at 12:51pm. Ignition of unit 1 began at 1:51 pm and was complete at 4:03 pm. The air temperature was 16 – 23 °C, with winds primarily from the west, up to 13.8 km per hour. The relative humidity was in the mid-30s throughout. The average estimated flame height was 37 cm in unit 1 and 27 cm in unit 4. The average estimated rate of spread was 46 m/hour in unit 1 and 27 m/hour in unit 4. The average temperature indicated by painted tags was 288 °C in unit 1 and 215 °C in unit 4. All plots were burned in both units. Note that rate of spread and flame heights were estimated visually by different fire crew members with 5 – 12 observations per burn.

Data analysis

Our first objective was to find size thresholds at which shortleaf pine and oak seedlings can either resist top-kill or survive through sprouting following prescribed burning. However, because complete mortality was extremely low over the course of the experiment (~1%), analysis was conducted on a tree's ability to resist top-kill rather than on overall survival. A generalized linear mixed model with a binomial distribution and logit link function was used with the liklihood of resisting top-kill as the dependant variable, and basal diameter and species type, as well as their interaction as fixed effects. The random effects of plot within unit were initially included, but no models would converge, so no random terms were used.

To address our second objective, determining the relationship between fire intensity and seedling survival, generalized linear mixed models with a binomial distribution and a logit link function were used, with fire temperature range, basal diameter, and species type, the interaction between species and temperature, and the interaction between species and basal diameter as fixed effects, and the liklihood of resisting top-kill as the dependant variable. In the event of significant interactions between species type and temperature or diameter, separate models were then run for each species type. Again, models that included pines would not converge when any random effects were included, however oak-only models include the random effects of plot within unit. Note that models including temperature were run seperately from models without temperature because the sample size that included temperature measurements was somewhat smaller and excluded much of unit 6. Measured fire temperatures were pooled into temperature ranges and treated as catagorical for analysis.

To address our third objective, comparing post-fire growth of shortleaf pine and oak seedlings, generalized linear mixed models with a lognormal distribution were used, with height growth after 1 growing season as the dependant variable, pre-fire basal diameter, top-kill status, and species group as fixed effects, as well as the interactions between them, and plot within unit as a random effect. These were run on trees in the smallest two size classes, which had the majority of the top-kill. Because of many significant interactions, the same analysis was run seperately for the survivors and sprouts of both species groups.

To address our fourth objective, of finding a specific timing of burn to give shortleaf pine seedlings an advantage, a Chi square analysis was conducted, to test whether observed frequencies match expected frequencies in the four possible outcomes for oak-pine tree pairs (both resist, both top-killed, only oak resists, or only pine resists) by size class, and a Bonferroni adjusted alpha value of 0.0025 was used. Statistical tables are in the appendix.

Results

Overall survival following burns was very high for both oaks and pines, with 99% alive in some form after one growing season. Smaller seedlings were more likely to survive through sprouting, while larger trees were more likely to resist top-kill (Table 3.2).

Table 3.2: The percent of shortleaf pine and oak seedlings that resisted top-kill, sprouted, or died immediately following a prescribed burn by basal diameter class, n=82 for each species group in each size class.

Size Class (cm)	Shortleaf Pine			Oaks		
	Resisted Top-Kill	**Sprouted**	**Dead**	**Resisted Top-Kill**	**Sprouted**	**Dead**
1 (0-1.5)	5	92.5	2.5	7.3	92.7	0
2 (1.5-4)	64.1	34.6	2.5	34.6	66.7	0
3 (4-6.5)	100	0	0	92.6	7.4	0
4 (6.5-10)	100	0	0	96.3	3.7	0
5 (10-15)	100	0	0	100	0	0

For both shortleaf pine and oaks, basal diameter was a significant predictor of ability to resist top-kill ($p<0.001$ for both) with increasing probability with increasing diameter (Figure 3.1A). For pine models including temperature, both basal diameter and temperature were significant predictors of resisting top-kill ($p<0.001$ for both), with the likelihood increasing with larger diameters and decreasing with higher temperatures, and there was no interaction between diameter and temperature ($p=0.678$) (Figure 3.1B). For oak models including temperature, both basal diameter ($p<0.001$) and temperature ($p=0.008$) were significant predictors of resisting top-kill, and there is weak evidence for an interaction between the two ($p=0.104$) (Figure 3.1C).

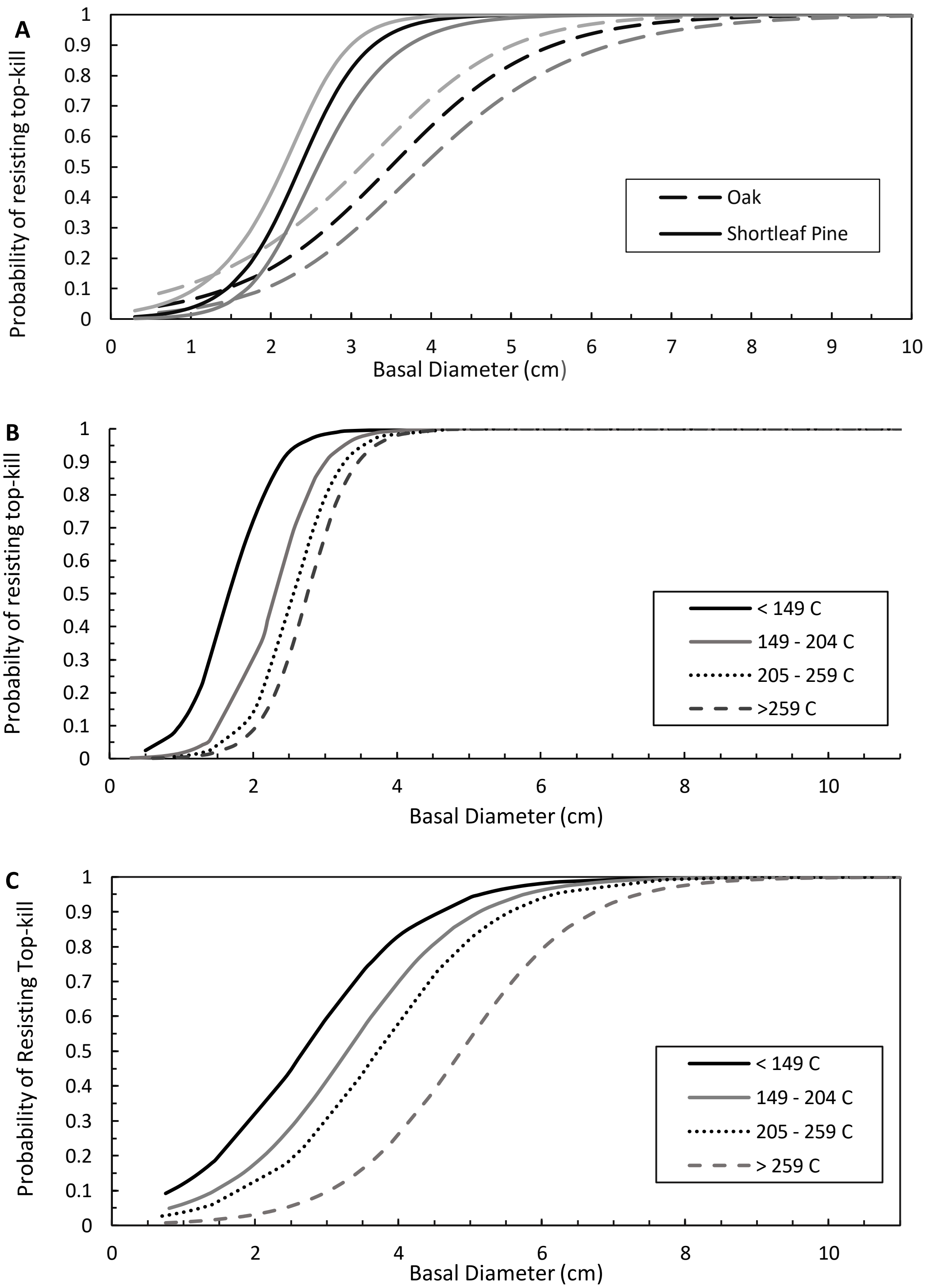


Figure 3.1: A) Predicted probability of resisting top-kill for shortleaf pine and oak seedlings and saplings following a prescribed burn, with 95% confidence intervals in grey bracketing the black lines for pine (solid) and oak (dashed). B) predicted probability of resisting top-kill for shortleaf pine seedlings and saplings following a prescribed burn for four temperature ranges. C) predicted probability of resisting top-kill for oak seedlings and saplings following a prescribed burn for four temperature ranges.

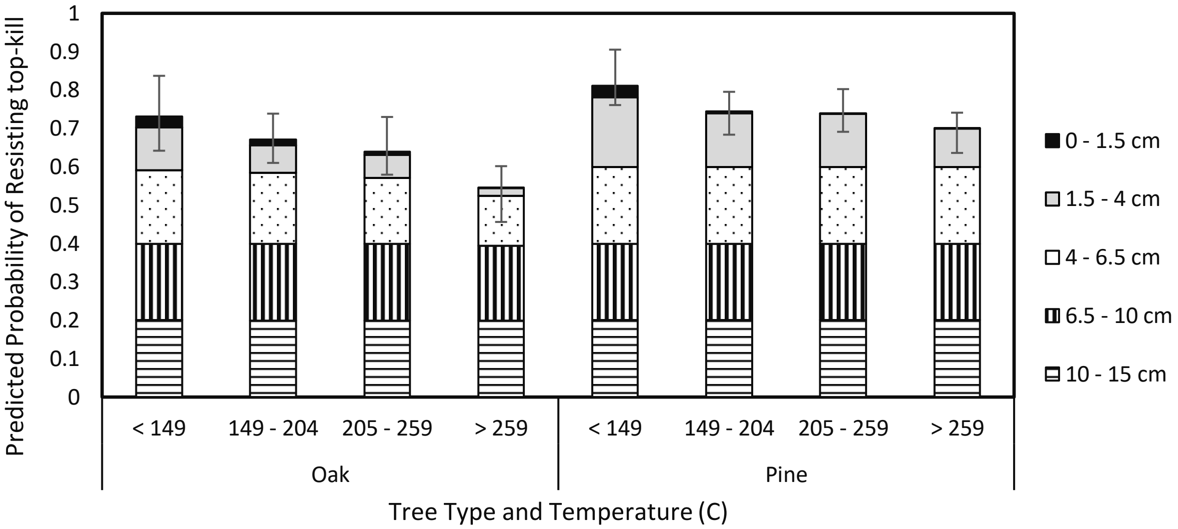


Figure 3.2: Predicted probability of resisting top-kill for oak and pine seedlings by temperature range. Whole bars represent total survival probability by temperature range. Bars are vertically divided by size class, with each size class representing ~20% of the total sample size. Error bars are the 95% confidence interval for all size classes combined.

Chi square analysis showed that for size classes 1 and 2, the likelihood of both species types resisting top-kill was significantly lower than expected ($p<0.00001$ for both, alpha for all tests = 0.0025), and for size class 1 the likelihood of both being top-killed was significantly higher than expected ($p<0.00001$). For size classes 3, 4, and 5 the likelihood of both resisting top-kill was significantly higher than expected and the likelihood of both being top-killed was significantly lower than expected ($p<0.00001$). For size class 2, the likelihood of the pine resisting top-kill while the oak does not was significantly higher than expected ($p<0.00001$) (Figure 3.3).

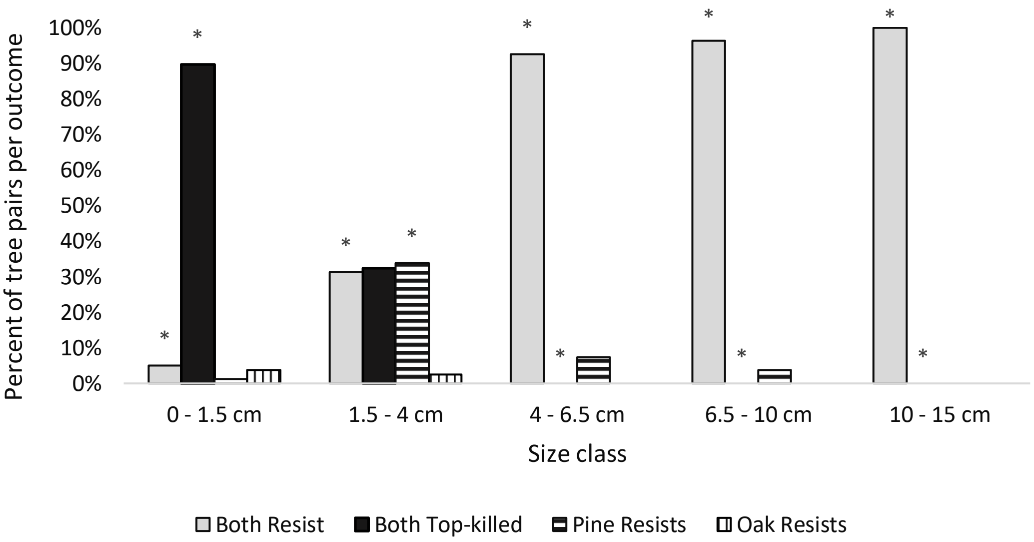


Figure 3.3: The percent of shortleaf pine – oak pairs that fall into each of four categories following prescribed burning: Both resist top-kill, both are top-killed, only the pine resists top-kill, or only the oak resists top-kill. Stars represent outcomes significantly different from the expected according to a chi square analysis with Bonferroni adjustment.

Analysis of post-fire heights of seedlings (in size classes 1 and 2) indicated that both basal diameter (p=0.002) and top-kill status (p=0.002) were significant variables in predicting height, while species group shows only weak evidence for predicting height (p=0.104). However, there were significant interactions between top-kill status and species group (p<.0001) and basal diameter and species group (p=0.033). When analyzed separately, the heights of sprouts of oaks (p<0.001) were significantly correlated with pre-fire basal diameter, and there was weak evidence that heights of shortleaf pine were as well (p=0.053) (Figure 3.4). Of seedlings that were top-killed and sprouted, oaks had taller sprouts on average while shortleaf pine had more sprouts on average (Table 3.3). For seedlings that were not top-killed, height growth during the first growing season after burning was significantly correlated with pre-fire basal diameter for both shortleaf pine (p<0.001) and oaks (p<0.001). The number of sprouts per top-killed stem was significantly correlated with pre-fire basal diameter (p<0.001), and species group (p<0.001), and there was a significant interaction between basal diameter and species group (p=0.004).

Table 3.3: The average height of the tallest sprout and average number of sprouts for shortleaf pine and oak seedlings that were top-killed by a prescribed burn and sprouted.

Average Height (cm) of Tallest Sprout	**Oaks**	**59**
	Shortleaf Pine	**29**
Average Number of Sprouts	**Oaks**	**4**
	Shortleaf Pine	**13**

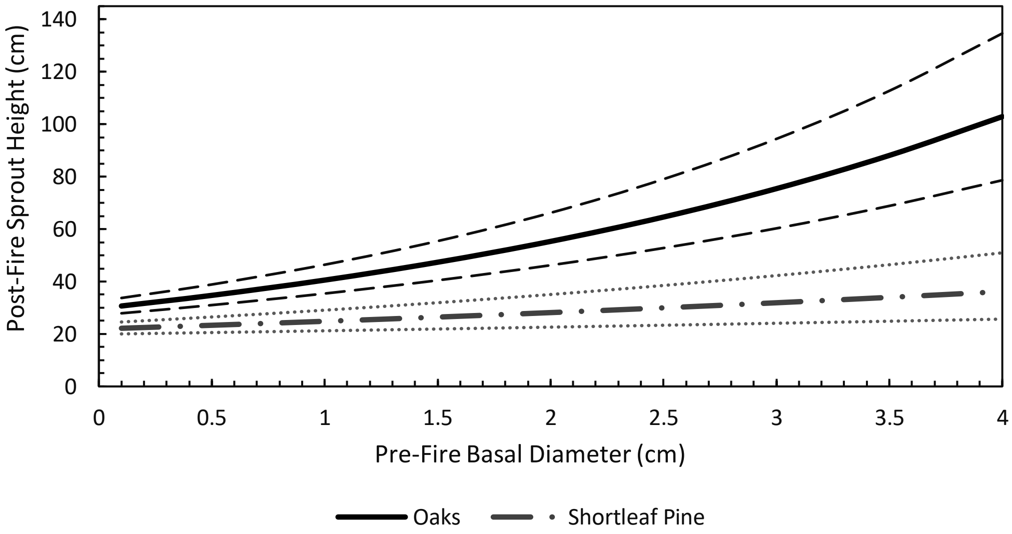


Figure 3.4: Height of shortleaf pine and oak sprouts from seedlings top-killed by prescribed burning by pre-fire basal diameter. The relationship is statistically significant for oaks but only marginally so for shortleaf pine. Standard error of the models is represented by dashed lines bracketing the main relationship line for each species.

Discussion

This study has several key findings. The first is that shortleaf pine and associated oaks can have very high overall survival following prescribed burning. The second is that the probability of shortleaf pine and oak trees resisting top-kill by prescribed burning increases with increasing basal diameter and decreases with increasing fire temperature. The third is that the height of oak sprouts from stems top-killed by burning is positively correlated with pre-fire basal diameter, but there is only weak evidence for that trend in shortleaf pine. Overall oak sprouts are taller while shortleaf pine sprouts are more numerous.

The amount of complete mortality seen in this study was lower than other studies of shortleaf pine and oak seedlings following fire. Lily et al (2012) found 37% total mortality immediately following the burns, 56% top-killed and sprouted, and only 7% that resisted top-kill, with an additional 20.5% of seedlings that had initially sprouted experiencing complete mortality following one growing season for shortleaf pine seedlings with basal diameters from 0.3 – 9 cm. Dey and Hartman (2005) report that after one spring burn white oak, post oak, and black oak experienced approximately 5 to 10% mortality, while more than 33% of shortleaf pine died. Phares and Crosby (1962) found 83% top-kill with 18% complete mortality of three-year-old planted shortleaf seedlings following a prescribed burn.

Multiple factors could explain the lower mortality seen in this study. Phares and Crosby (1962) studied planted seedling, whereas in this study the tagged seedlings were likely mostly natural regeneration and may have previously resprouted following earlier top-kill, though the area was planted in 2005-2006. Because the sites in this study had been burned previously, some of the tagged seedlings were likely advance regeneration with developed root systems, which could improve survival. The seedlings that Lilly et al. (2012) studied were a mix of 5-year-old planted seedlings and natural regeneration, with the possibility of some resprouting from one previous burn. The range of fire temperatures they reported was also similar to those in our study. One factor that may have contributed to the higher mortality seen by Lilly et al. (2012) is the timing of the burns in mid-April, compared to the early February and early March burns in this study. Cain and Shelton (2000) found that shortleaf pine seedlings had higher mortality following growing season burns compared with dormant season, and Harrington (1993) found the same result for Ponderosa pine (*Pinus ponderosa*). Glitzenstein et al. (1995) however, found that season of burn did not affect longleaf pine (*Pinus palustris*) survival, but growing season burns did result in higher mortality for three associated oak species.

The finding that pre-fire basal diameter was positively correlated with resisting top-kill is consistent with other studies. Lilly et al. (2012) found the same trend for shortleaf pine seedlings and Dey and Hartman (2005) found the same trend for both shortleaf pine and several oak species, including white and black oak. Ferguson (1957) found that hardwood seedlings, including post oak, southern red oak (*Quercus falcata*), and sweetgum (*Liquidambar styraciflua*), under 3.81 cm were more likely to be top-killed by burning. Survival prediction curves for scarlet, black, white, and post oak from Loomis (1973) identified diameter at breast height as a significant predictor of survival, as well as season of burn.

The finding that increased fire temperature correlates with an increase in top-kill is also consistent with the literature. Lilly et al. (2012) found that seedlings with less crown scorch and lower fire temperatures (measured at the basal crook) were more likely to resist top-kill. Holmes et al. (2011) found that fire temperature was a significant predictor of the severity of damage to five to six-year-old valley oak (*Quercus lobata*) saplings. Ferguson (1957) found that head fires were more likely to result in top-kill for white and black oak (and sweetgum (*Liquidambar styraciflua*)) than backing fires.

Other studies have looked at the behavior of sprouts following top-kill. Lilly et al. (2012) found that following one growing season, shortleaf pine sprout counts ranged from 1 – 28 per seedling, with an average height of 19.7 cm. The range of sprouts per stem was greater in the present study, ranging from 1 to 104, and the average height was slightly higher at 29 cm. Clabo and Clatterbuck (2019) studied sprouting of planted shortleaf pine at different ages and found that for one year old seedlings the average number of sprouts following an April burn was 2.6, for two year old seedlings was 5, and for three-year old seedlings was 21.4, suggesting that shortleaf pine’s ability to produce sprouts following top-kill increases with age. Cane and Shelton (2000) studied sprouting responses of first year shortleaf pine and white oak seedlings subjected to simulated prescribed fire. By the end of the first growing season following fire the sprouts of white oak seedlings top-killed by the burn were equal in height to the white oak seedlings in the unburned control plots, while for shortleaf pine seedlings, the heights of the unburned seedlings were 82% greater than the heights of sprouts. After two growing seasons despite their shorter heights, shortleaf pine sprouts had eight times more biomass than oak sprouts, probably due to a larger number of sprouts per stem.

Combined with the results of this study, the evidence suggests different strategies for coping with top-kill displayed by shortleaf pine compared to oak seedlings. Shortleaf pine responds by sprouting prolifically, increasing live biomass as well as surface area available for photosynthesis, while oaks respond by producing few sprouts with rapid height growth, putting them at a competitive advantage over shortleaf sprouts in mixed oak-pine forests.

There may be a broader pattern related to oak and pine fire survival strategies. A study in Madrean forests in southeastern Arizona compared responses to moderate intensity fires of two pine species, Chihuahua pine (*Pinus leiophylla*) and Arizona longleaf pine (*P. engelmannii*), and four oak species, silverleaf oak (*Quercus hypoleucoides*) Arizona white oak (*Q. arizonica*) Emory oak (*Q. emoryi*) and netleaf oak (*Q. rugosa*), and concluded that the pines and oaks in these ecosystems had different strategies for surviving these fire regimes, with the pines more likely to resist top kill and the oaks more successful at post fire sprouting (Barton, 1999). The same general pattern of differing survival strategies was seen at the Chilton Creek study in Missouri. After repeated burning short leaf pine was more likely to survive by resisting top kill while associated oak species were more likely to survive through sprouting (Dey and Hartman, 2005; Fan et al., 2012)

This study has implications for managing shortleaf pine and oak mixed forests. First, it indicates that dormant season prescribed burns with similar fuels and weather conditions to those in this study are unlikely to cause mass complete mortality for shortleaf pine and oak seedlings, regardless of size. Managers can also reduce mortality by burning when seedlings are larger. Because fire temperature is positively correlated with the probability of top-kill, managers could control the amount of mortality somewhat by selecting burn conditions likely to result in desired fire temperature. There was weak indication in this study that oaks may be more sensitive to top-kill at higher temperatures, so more research into different temperature thresholds between species groups may provide information helpful in selective management.

Finally, the paired nature of this study can give some insights into managing for shortleaf pine in oak-pine mixtures. There seems to be a period in growth, when seedlings are between 1.5 and 4 cm, during which shortleaf pines are more likely to resist top-kill than oaks, giving them a competitive advantage that could be important when selectively managing for shortleaf pine. Burning when shortleaf pine is able to resist top-kill is important, because shortleaf pine sprouts have a height disadvantage compared with oak sprouts, and are unlikely to compete successfully.

Appendix of statistical tables:

Table A1: The liklihood of resisting top-kill by basal diameter and species type. No random effects are included as the models would not converge. (Num DF = numerater degrees of freedom, Den DF = denominatior degrees of freedom throughout)

EFFECT	NUM DF	DEN DF	F VALUE	P VALUE
BASAL DIAMETER (CM)	1	802	97.87	< .0001
SPECIES GROUP	1	802	5.50	0.0192
INTERACTION	1	802	15.23	0.0001

Table A2: The liklihood of resisting top-kill by basal diameter for pines only. No random effects are included as the models would not converge.

EFFECT	NUM DF	DEN DF	F VALUE	P VALUE
BASAL DIAMETER	1	396	52.59	<.0001

Table A3: The liklihood of resisting top-kill by basal diameter for oaks only. With random effects of plot within unit

EFFECT	NUM DF	DEN DF	F VALUE	P VALUE
BASAL DIAMETER	1	322	88.41	<.0001

Table A4: The liklihood of resisting top-kill by basal diameter and temperature for oaks only, with random effects of plot within unit**.**

EFFECT	NUM DF	DEN DF	F VALUE	P VALUE
BASAL DIAMETER	1	230	29.85	<.0001
TEMPERATURE	3	230	4.02	0.0082
INTERACTION	3	230	2.08	0.1040

Table A5: The liklihood of resisting top-kill by basal diameter and temperature for pines only. No random effects are included as the models would not converge.

EFFECT	NUM DF	DEN DF	F VALUE	P VALUE
BASAL DIAMETER	1	300	1955.25	<.0001
TEMPERATURE	3	300	30.88	<.0001
INTERACTION	2	300	0.39	0.6784

Table A6: Post-fire height by pre-fire basal diameter, species group, and sprouting status, with plot within unit as random effect

EFFECT	NUM DF	DEN DF	F VALUE	P VALUE
SPECIES GROUP	1	216	2.66	0.1043
BASAL DIAMETER	1	216	9.78	0.0020
SPROUTING STATUS	1	216	10.31	0.0015
BD*SG	1	216	4.61	0.0330
SPROUT*SG	1	216	14.41	0.0002
BD*SPROUT	1	216	0.39	0.5339

Table A7: The number of sprouts per sprouted seedling by pre-fire basal diameter and species group, with plot within unit as random effect

EFFECT	NUM DF	DEN DF	F VALUE	P VALUE
BASAL DIAMETER	1	145	34.86	<.0001
SPECIES GROUP	1	145	13.64	0.0005
INTERACTION	1	145	8.60	0.0039

Table A8: Oak height growth for non-top-killed seedlings one growing season post-fire by pre-fire basal diameter and species group, with plot within unit as random effect

EFFECT	NUM DF	DEN DF	F VALUE	P VALUE
BASAL DIAMETER	1	25	63.09	<.0001

Table A9: Shortleaf pine height growth for non-top-killed seedlings one growing season post-fire by pre-fire basal diameter and species group, with plot within unit as random effect

EFFECT	NUM DF	DEN DF	F VALUE	P VALUE
BASAL DIAMETER	1	42	71.70	<.0001

Chapter 4: Competition dynamics of shortleaf pine planted for restoring oak – pine mixtures

Background

Shortleaf pine (*Pinus echinata*) was estimated to cover 2.7 million hectares in Missouri historically (Fletcher and McDermott, 1957). Recent Forest Inventory and Analysis (FIA) data indicate that shortleaf pine currently occupies 72,000 hectares in Missouri (Moser et al., 2007). Much of the area previously covered by shortleaf pine is now dominated by red oak species, which have been declining (Kabrick et al., 2008; Fan et al., 2012). The recent effort to restore shortleaf pine, combined with the need to improve forest health, has motivated foresters to plant shortleaf pine where it once grew, on land now dominated by oaks. However, it is challenging to establish shade-intolerant shortleaf pine seedlings under the residual oak canopy with heavy competition from oak advance regeneration. In addition to recent interest in shortleaf pine restoration, there is interest in managing for mixedwood forests (Kabrick et al., 2017), or mixtures of pines and hardwoods, especially mixed pine-oak forests and woodlands in Missouri. In many cases, as in Missouri, this involves trying to establish shortleaf pine on areas currently dominated by hardwoods. Several strategies have been tested.

An early strategy for establishing shortleaf pine in mixedwood forests was to harvest the overstory and plant shortleaf pine seedlings. Phillips and Abercrombie (1987) used this method in the Sumter National Forest in South Carolina. They harvested the overstory, felled all remaining trees greater than 0.3 m tall, and conducted a growing season prescribed burn the summer before planting 1112 shortleaf pine seedlings per ha. They found 95% survival after 1 year, and after 4 years reported there were 751-1023 “free to grow” seedlings per hectare. Clabo and Clatterbuck (2020) used a similar strategy, with additional testing of various site preparation and release methods for establishing planted shortleaf pine on clear-cut areas in Tennessee. All study areas were burned in late fall, drum chopped, and burned again in spring. Other treatments were herbicide release, done immediately after planning and again the following growing season, a fall burn two growing seasons after planting, and a combination of the two. After three growing seasons, seedling survival was greatest in the control (site preparation only) and herbicide treatments, 49 and 51%, but the authors concluded the burn-herbicide combination was most likely to grow into a successful mixed stand, as the other treatments had high levels of invasive species.

Others have experimented with planting shortleaf pine under a hardwood canopy. Schnake et al. (2021) planted shortleaf pine seedlings under residual basal areas of 0, 3, 7, and 10 m^2/ha of mostly oak and hickory. They compared bareroot seedlings to small and large containerized seedlings. After five growing seasons, they found a slight but statistically significant relationship between overstory basal area and survival, with the 10m^2/ha plots having the greatest survival, though the authors did not believe this to be scientifically meaningful. There was a strong relationship between seedling stock and survival, with large containers having 77%, small containers 64%, and bareroot 40% survival. They also found that height growth of shortleaf seedlings was negatively correlated with overstory density. Clabo and Clatterbuck (2020) planted bareroot shortleaf pine seedlings in clusters in canopy openings following a harvest to 12 m^2/ha. After four growing seasons, survival was 35 – 43 %, and competition from overtopping understory hardwood seedlings was believed to be an issue. At the Clearwater

Conservation Area in Missouri, Jensen et al. (2007) planted bareroot shortleaf pine seedlings under overstory treatments including clearcut, uneven-aged management, and thinning to B- and C-level stocking. After seven years, they found the greatest stocking of shortleaf pine seedlings in the clearcut areas (63%), and the lowest in the uneven-aged management areas (28%). The height of seedlings in the clearcut areas averaged 2.68 m, 1.22 m in the uneven-aged management areas and 0.45 m in the B-level stocking thinned areas.

Overall, these studies highlight two important factors to consider when managing for shortleaf pine in a mixedwood situation: the availability of understory light modified by overstory conditions, and the control of competition in the regeneration layer during the seedling stage. Generally, shortleaf pine seedlings tend to grow faster with lower overstory densities, and in some but not all situations, survive better with lower overstory densities as well. The role of competition from other seedlings seems to have been less frequently studied but does seem to be important in some instances.

This chapter follows up on the 2015 paper by Kabrick et al. on early results from a study conducted at the Sinkin Experimental Forest evaluating the effect of overstory stocking and initial size on the growth and survival of planted shortleaf seedlings after 5 growing seasons. The overall survival was 67% after the first growing season and 50% after the fifth growing season (Kabrick et al., 2015). Key findings of the study include: the probability of seedling survival was positively correlated with initial basal diameter; overstory stocking did not affect shortleaf seedling survival; and both the height and basal diameter of seedlings were negatively correlated with overstory stocking, to a greater degree after each additional growing season (Kabrick et al., 2015).

The following analysis includes three additional data collections, extending the study to 13 growing seasons. We aim to determine if the trends observed over the first 5 growing seasons continue through time. Additionally, we aim to analyze the effects of understory competition on shortleaf pine growth and survival. Specific research questions include: 1) does the initial size of planted shortleaf pine continue to increase the probability of survival 10 and 13 growing seasons after planting? 2) does overstory density continue to inhibit planted shortleaf pine growth after 10 and 13 growing seasons? 3) does overstory density reduce survival of shortleaf pine growth after 10 and 13 growing seasons? 4) does the relative size of hardwood competitors to planted shortleaf pine trees at 3 and 5 growing seasons after planting affect the survival of planted shortleaf pine trees 10 and 13 growing seasons after planting? 5) does the relative size of hardwood competitors to shortleaf pine at 3 and 5 growing seasons after planting affect the height of planted shortleaf pine seedlings 10 and 13 growing seasons after planting?

Methods

Study site

This study took place in southern Missouri at the Sinkin Experimental Forest, which is located within the Mark Twain National Forest. The average daily temperature was 24° C in the summer and 1° C in the winter, with 1118 mm of annual precipitation. The site index (*Q. velutina* equivalent) was 17 m. The areas selected for the study were on summit or shoulder slope positions and deemed well-suited for managing shortleaf pine or pine-oak mixtures. Soils are derived from sandstones or cherty dolomites, are very deep, well to somewhat excessively drained, and have low available water holding capacity (Kabrick et al., 2015). Soil series include Nixa, Coulstone, and Clarksville.

Experimental design

The study consisted of 48 square experimental units measuring 0.4 ha each, uniform in forest type, soil properties, slope, and aspect. At the center of each experimental unit was a 0.08 ha circular plot, and within those circular plots a 0.0004 ha circular plot. Four basal area ranges, <2, 4-9, 10-14, and >14 m^2 per hectare, were randomly assigned to experimental units, resulting in 12 replicates each, for a completely randomized design.

Harvest

The harvests to establish assigned basal areas were conducted in the fall and winter of 2006 – 2007. Preferred retention trees were shortleaf pine, white oak (*Q. alba*), post oak (*Q. stellata*), northern red oak (*Q. rubra*), scarlet oak (*Q. coccinea*), black oak (*Q. velutina*), and hickories (*Carya* spp.) >25 cm diameter at breast height (DBH). A windstorm in May 2009 blew down many canopy trees, resulting in a loss of basal area across most of the experimental units. The resulting basal areas ranged from 0 – 22 m^2/ha, and stocking (Rogers, 1983) ranged from 0 – 73%.

Planting

In April 2008, 30 1-0 bareroot shortleaf pine seedlings were hand planted in each 0.08 ha circular plot in each experimental unit at a spacing of 3.7 x 7.3 m. Following planting, seedlings were tagged, and basal diameter (measured 1 cm above root collar) and height were recorded. Seedlings were from the George O. White State nursery.

Data collection

Planted shortleaf pine seedlings were re-inventoried during the dormant seasons of 2009, 2010, 2011, and 2013, 2017, and 2020. The tallest competing hardwood within a 1.37 m radius of each planted shortleaf pine seedling was also measured for height and basal diameter, and the species was recorded during the dormant seasons of 2010, 2013, and 2017.

Data analysis

To address question 1 regarding the influence of initial diameter on survival, generalized linear mixed models with a binomial distribution and a logit link function were used, with the survival of planted shortleaf pine trees in 2017 and 2020 as the dependent variables, initial seedling size as the fixed effect, and the plot specified as the random effect. To address question 2 regarding the influence of overstory stocking on growth, linear regressions were used, with the height and basal diameter of planted shortleaf pine trees 2017 and 2020 as the dependent variables, and overstory stocking (as measured in 2013, at the plot level) as the fixed effect. To address question 3 regarding the influence of overstory stocking on survival, generalized linear mixed models with a binomial distribution and a logit link function were used, with the survival of planted shortleaf pine trees in 2017 and 2020 as the dependent variables, and overstory stocking (as measured in 2013, at the plot level) as the fixed effect, with the random effect of plot.

Questions 4 and 5 address the impact of the hardwood competitors on the planted shortleaf pine trees. For these analyses, the difference in height between the nearest competitor and the planted shortleaf pine was calculated (competitor height – shortleaf pine height) for each shortleaf pine in 2010 and 2013 and used as predictor variables (competitor relative size) for later survival or growth. To address questions 4, generalized linear mixed models with a binomial distribution and a logit link function were used with the probability of survival of shortleaf pine as the dependent variables, competitor relative size and stocking of experimental unit as fixed effects, and the plot as a random effect. To address question 5 regarding the relationship between shortleaf height and the height difference with hardwood competitors, generalized linear mixed models with a lognormal distribution were used, with the height of planted shortleaf pine trees as the dependent variables, competitor relative size and stocking of experimental unit as fixed effects, and the plot as a random effect. For questions 4 and 5, separate models were run for survival and shortleaf pine height in 2017 and in 2020, and separate models were run using competitor relative size from 2010 and from 2013. For question 4, a model using survival in 3013 and competitor relative size in 2010 as well. Statistical tables are in the appendix.

Results

Survival

After 10 growing seasons, overall survival of planted shortleaf pine trees was 26%. Survival was positively correlated with initial basal diameter (at the time of planting) after 10 growing seasons (p=0.033) (Figure 4.1). After 13 growing seasons, the survival of planted shortleaf pine seedlings was 15% and was no longer significantly correlated with initial basal diameter (p=0.168).

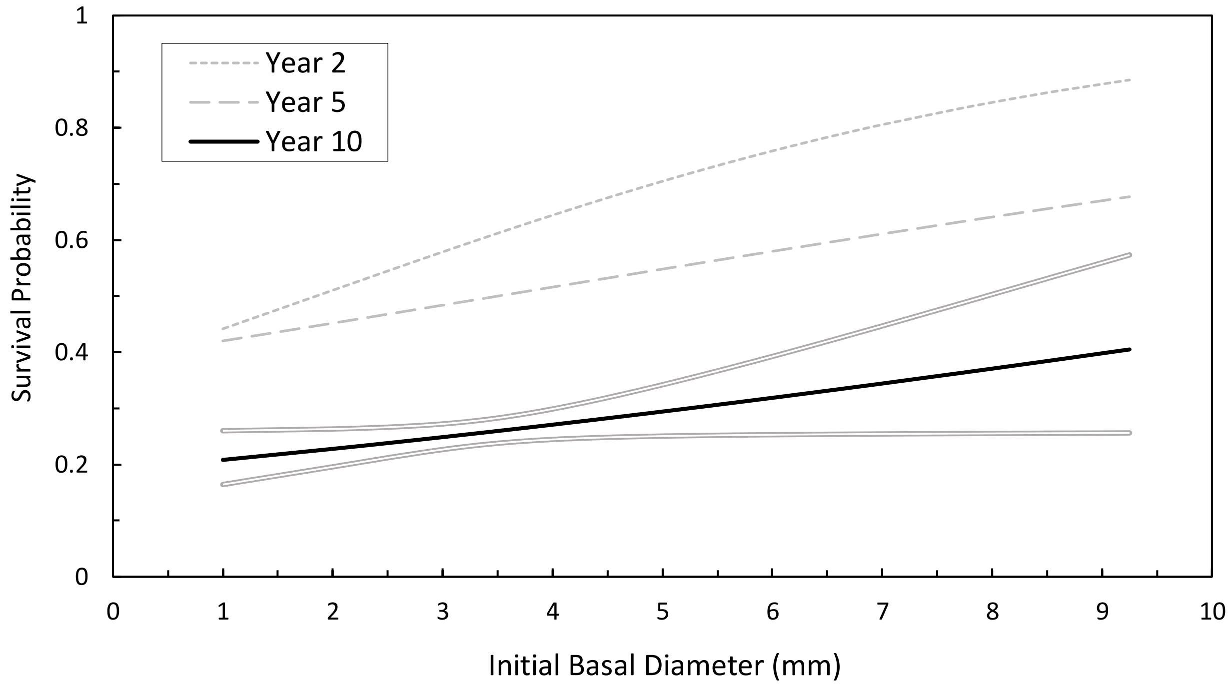


Figure 4.1: The predicted probability of survival in 2017 (after 10 growing seasons) for planted shortleaf pine trees based on initial basal diameter. Ten-year results (black solid line) with 95% confidence intervals (gray solid lines) analyzed in this chapter. Results from years 2 and 5 from Kabrick et al. (2015) are also shown for reference.

Overstory effects on survival varied by year. Ten years after planting overstory stocking was not a significant predictor of seedling survival (p=0.437). Thirteen years after planting, survival was significantly correlated with overstory stocking (p=0.009) (Figure 4.2).

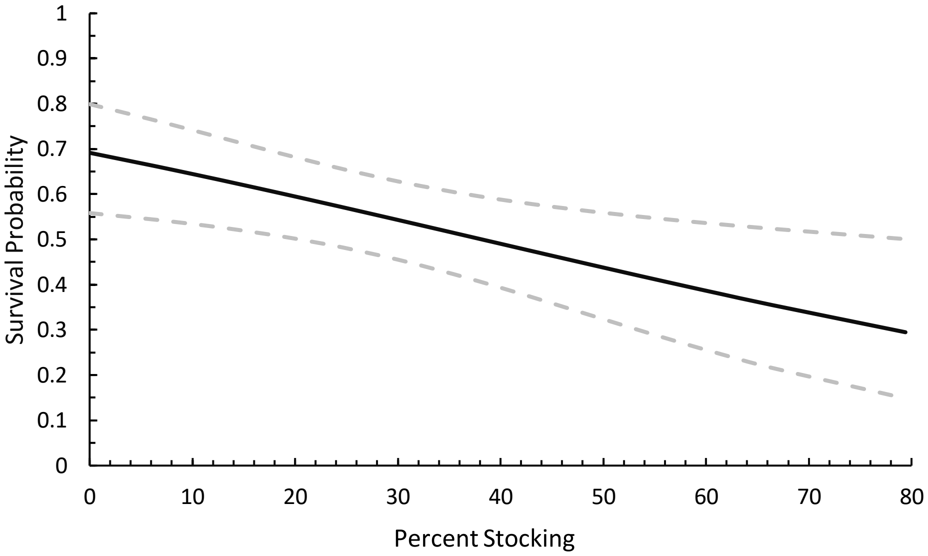
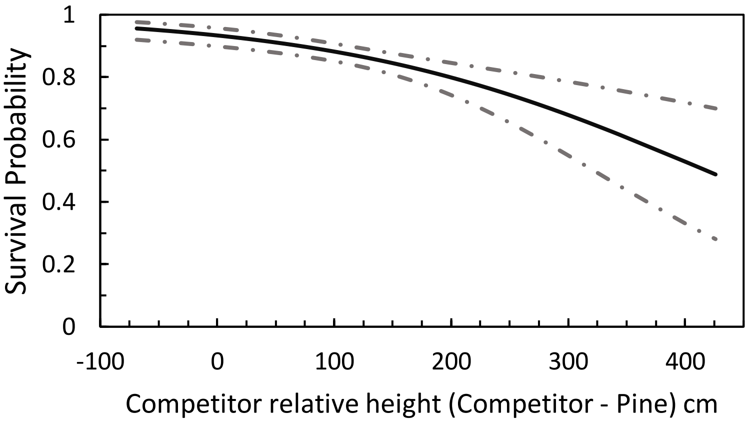


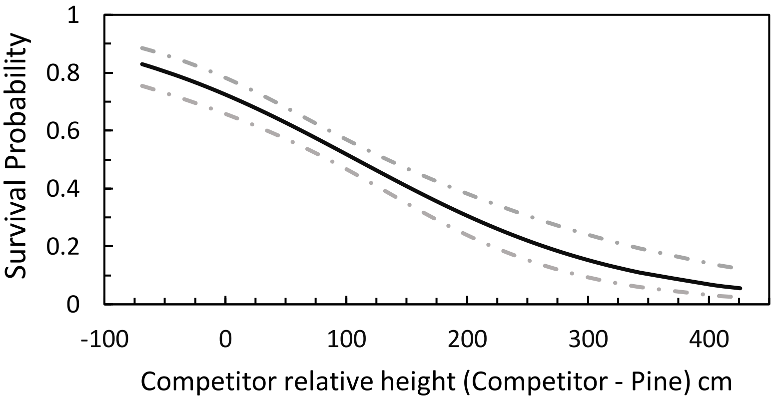
Figure 4.2: Survival probability of shortleaf pine trees 13 years after planting by overstory stocking (black) with 95% confidense intervals (grey).

At several points throughout its life, shortleaf pine survival is related to the difference in height between the shortleaf seedling at its primary hardwood competitor (the tallest hardwood competitor within 1.37 m). Shortleaf pine seedling survival after 5 years was significantly correlated with relative competitor heigh 2 years after planting, with shortleaf pine survival probability decreasing as competitor relative size increased ($p<0.001$) (Figure 4.3a). Shortleaf pine seedling survival after 10 years was also significantly correlated with competitor relative height 2 and 5 years after planting ($p<0.001$) (Figure 4.3b&c). Survival after 13 years was also negatively correlated with competitor relative height after 2 and 5 years ($p<0.001$ for both).

a. Shortleaf survival after 5 years by height difference after 2 years



b. Shortleaf survival after 10 years by height difference after 2 years



c. Shortleaf survival after 10 years by height difference after 5 years

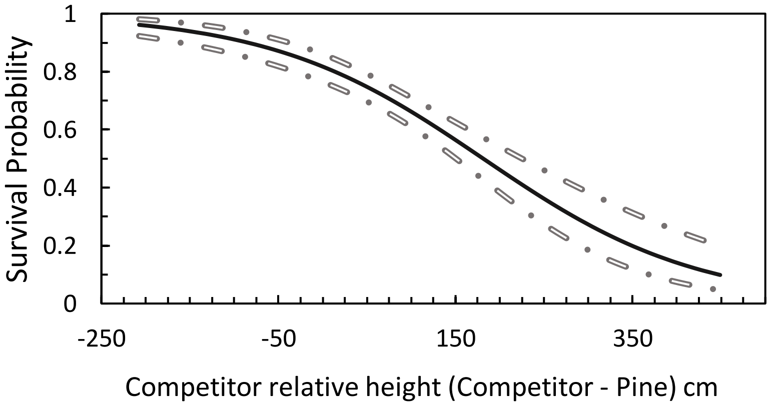


Figure 4.3: Predicted probability of survival of shortleaf pine trees 5 or 10 years after planting based on competitor relative height at 2 or 5 years post-planting.

When overstory and understory were examined together, shortleaf pine survival after 10 years was significantly correlated with competitor relative height 2 years after planting (p<0.001) and overstory stocking (p=0.001), and there was a significant interaction between stocking and height difference 2 years post planting (p=0.001) (Figure 4.4). Shortleaf pine seedling survival after 10 years was also significantly correlated with overstory stocking (p<0.001), competitor relative height after 5 years (p<0.001), and their interaction (p=0.023).

Shortleaf pine survival after 13 years was significantly correlated with competitor relative height 2 years after planting (p<0.001) and overstory stocking (p<0.001), and there was a significant interaction between stocking and competitor relative (p=0.003). Shortleaf pine survival after 13 years was also significantly correlated with overstory stocking (p<0.001) and competitor relative height 5 years after planting (p<0.001), and there was a significant interaction between stocking and competitor relative height (p=0.005).

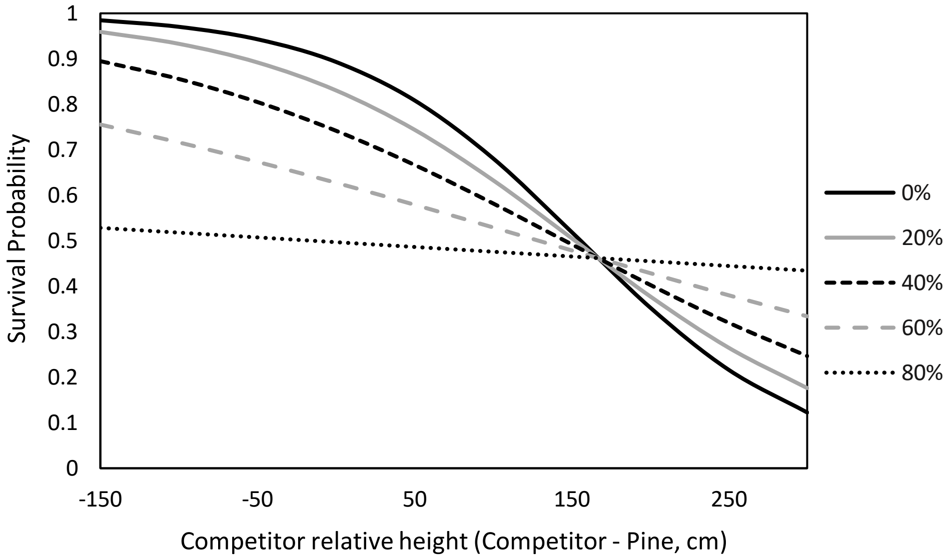


Figure 4.4: Survival probability of planted shortleaf pine after 10 years by competitor relative height after 2 years, separated by overstory stocking.

Height

Shortleaf pine growth, in terms of both height and basal diameter, was negatively correlated with overstory stocking after 10 years ($p < 0.001$) (Figure 4.5). The growth of hardwood competitors also was negatively correlated with overstory stocking after 10 years ($p=0.003$ for basal diameter and $p<0.001$ for height). Shortleaf pine height was no longer correlated with stocking alone after 13 growing seasons ($p=0.716$).

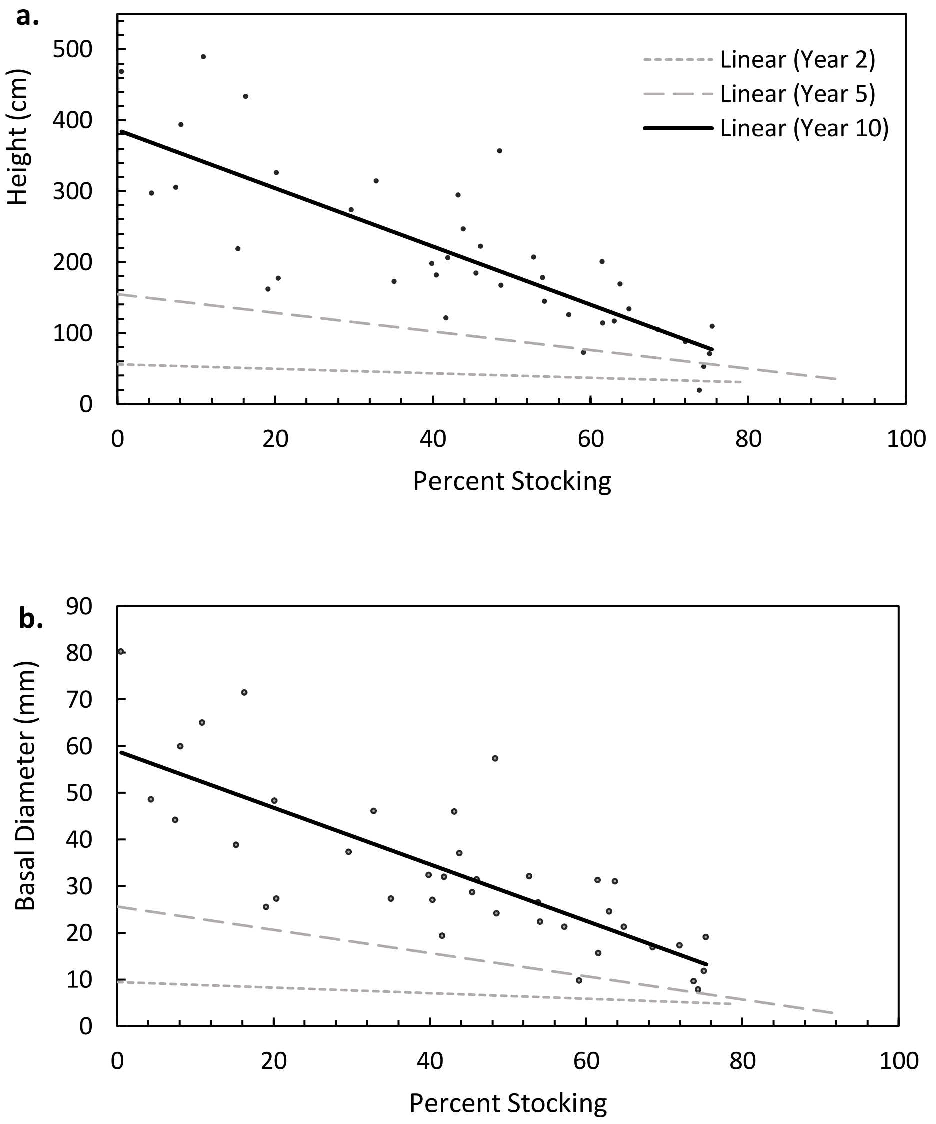


Figure 4.5: Shortleaf pine height (A) and basal diameter (B) growth 10 years after planting (solid black lines shows the trend and black dots represent data points) in relation to overstory percent stocking. Results from years 2 and 5 from Kabrick et al. (2015) are also shown for reference in grey.

When considering the overstory and understory together, the height of shortleaf pine 10 growing seasons after planting was significantly correlated with competitor relative height 2 years after planting ($p<0.001$) and overstory stocking ($p<0.001$), and there was a significant interaction between the two variables ($p<0.001$) (Figure 4.6). The height of shortleaf pine seedlings 10 growing seasons after planting was also significantly correlated with both overstory stocking ($p<0.001$) and competitor relative height 5 growing seasons after planting ($p<0.001$), and there was a significant interaction between the two variables ($p=0.023$).

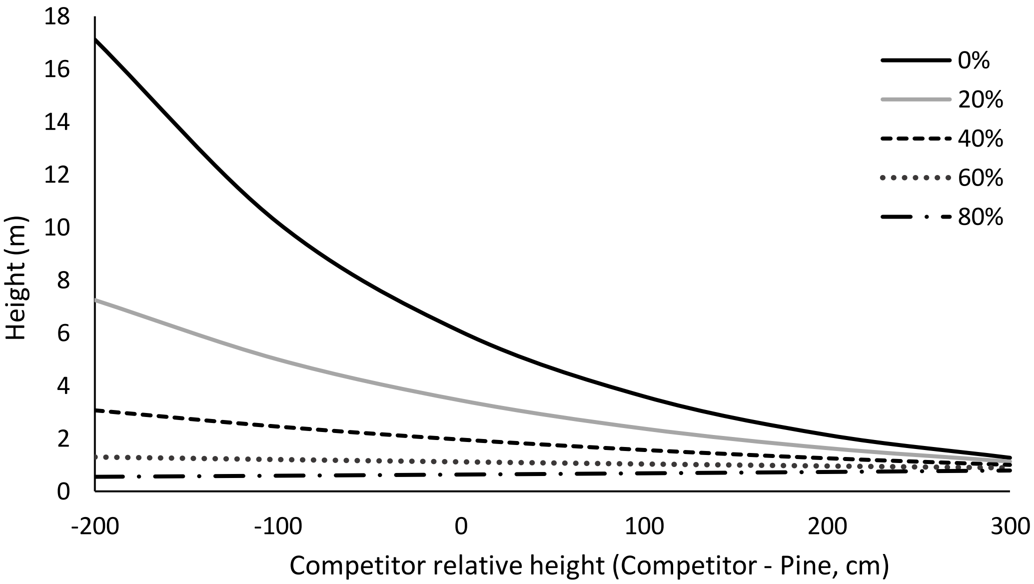


Figure 4.6: Height of planted shortleaf pine seedlings after 10 years by competitor relative height after 2 years, separated by overstory stocking (different line styles).

The height of the shortleaf pine trees after 13 growing seasons was significantly correlated with overstory stocking ($p<0.001$) and competitor relative height 2 years after planting ($p=0.028$). The height of the shortleaf pine seedlings after 13 growing seasons was also significantly correlated with overstory stocking ($p<0.001$) and competitor relative height 5 years after planting ($p<0.001$), and there was a significant interaction between stocking and relative height ($p=0.006$).

Discussion

This study has several findings important for understanding the growth and survival of underplanted shortleaf pine. The first is that planting larger seedlings provides an advantage in terms of survival for the first 10 growing seasons. Secondly, this study shows that being over-topped by understory hardwood competitors during the first decade after planting significantly reduced shortleaf pine growth and survival, highlighting the importance of early release from understory competition. The third is that after 13 growing seasons, greater overstory stocking reduces survival of underplanted shortleaf pine, though this is not seen in early years. Finally, greater overstory stocking reduces height growth of planted shortleaf pine starting in the first growing season following planting and continuing through the 13th.

The importance of the size at planting to the survival of shortleaf pine is somewhat supported in the literature. Franklin and Buckley (2009) found that the initial root collar diameter of planted shortleaf pine seedlings was significantly correlated with survival after 1 growing season on a mining reclamation site in Tennessee. Hayford et al. (2022) recently found the same positive relationship between basal diameter at the time of planting and survival for bareroot pin oaks after 15 growing seasons. Schnake et al. (2021) found greater survival after 5 years for underplanted containerized shortleaf seedlings than for bareroot seedlings. The initial basal diameter of seedlings in this study could correspond with more developed root systems, pointing to the general conclusion that planting more developed seedlings leads to greater early survival, which would be a relatively simple principle to adopt from a management standpoint, if doing so were economically viable.

The findings in this study that overstory stocking reduced the growth of shortleaf pine seedling growth is consistent with published research. In the Piedmont region of North Carolina, Schnake et al. (2021) found that greater overstory basal areas had significant negative effects on the height of planted shortleaf pine seedlings after five years, and similar to in this study, saw that the effect increased with time since planting. In the Ouachita mountains of Arkansas, Guldin and Heath (2001) also found that height of planted shortleaf pine seedlings was lower under greater residual basal area treatments after seven growing seasons. In Clark County Georgia, Reukema (1959) found that shortleaf pine seedlings planted in in gap openings 1.52 - 16.76 m in diameter were taller in larger gap openings six years post planting. In the Missouri Ozarks, Blizzard et al. (2007) found that both the basal diameter and height of natural shortleaf pine reproduction decreased with increasing overstory basal area.

The literature regarding overstory effects on shortleaf seedling survival is not as straight-forward as that of its effects on seedling height. Jensen et al. (2007) planted shortleaf pine under various overstory treatments including clear-cut, B and C level stocking, and uneven aged, and reported significantly higher seedling stocking of shortleaf pine after seven years in the clearcut areas, indicating greater survival. Reukema (1959) found that shortleaf pine seedlings planted in gap openings 1.52 - 16.76 m in diameter had greater survival in larger gap openings six years post planting, with only the 13.72 and 16.76 m gaps having greater that 50% survival. Kramer et al. (1952) found that survival of shortleaf pine seedlings planted under a pine stand was significantly lower than for seedlings planted in the open after 3 growing seasons, though seedlings planted in the margins of the pine stand did not differ significantly in survival from those planted in the open. However, Schnake et al. (2021) found that overstory retention levels of 0 - 10 m^2/ha did not affect survival of planted shortleaf pine seedlings after seven years, and an earlier publication of this study (Kabrick et al., 2015) found that overstory basal of 0 – 25 m^2/ha area did not affect shortleaf seedling survival after 5 years.

In this study, it seems that the way the overstory effects shortleaf pine seedling changes over time. Through 10 years after planting, overstory stocking alone significantly reduced growth of shortleaf pine, but did not significantly affect survival. However, 13 years after planting, overstory stocking alone significantly reduced shortleaf seedling survival, but was no longer correlated with seedling height. From a management perspective, this could indicate that shortleaf seedlings planted under higher overstory stocking can persist for a period of approximately 10 years, though growing more slowly, before they need to be released to survive.

The effects of understory competition are less thoroughly examined in the literature, but there is evidence of its importance in some studies. Cain (1991), studying shortleaf and loblolly pine (*Pinus taeda*) natural regeneration in clearcut stands in Arkansas, found that after 5 years, pines growing on plots with herbaceous vegetation control were significantly taller and had greater ground line diameters than pines in areas without herbaceous vegetation control, though there was no significant difference in survival.

Kramer et al. (1952) found that survival and growth of shortleaf pine seedlings were significantly reduced by canopy cover even when water stress was compensated for, indicating light reduction itself was critical in limiting growth and survival. It seems logical this same principle should apply whether light reduction comes from overstory or understory competition, as seen by the significant reductions in shortleaf seedling survival and growth seen in this study from both overstory stocking and understory competition, as well as their interactions. Knapp et al. (2016) found that root collar diameter increments for longleaf pine seedlings planted under loblolly overstory were positively correlated with the level of light transmittance and were better predicted by including both sub-canopy and canopy light transmittance than by using canopy light transmittance alone. This study highlighted the importance of relative competitive position in the understory for shortleaf pine seedlings as early as 2 years after planting in determining long-term growth and survival. This study also revealed noteworthy interactions between the overstory stocking and the relative height of understory competitors, with understory competition decreasing in importance at higher levels of overstory stocking, indicating that total light competition is likely more important for shortleaf pine regeneration than any single component.

Management recommendations

We recommend that when planting bareroot shortleaf selecting seedlings with larger basal diameters to improve survival over the first decade. This study found a significant correlation between basal diameter at the time of planting and survival through the first ten growing seasons. Basal diameter (Franklin and Buckley, 2009) and root development (Schnake et al., 2021) of planted shortleaf seedlings have been correlated with survival in other studies as well.

We recommend releasing planted shortleaf pine from understory hardwood competition early to improve growth and survival over the first 13 growing seasons. In this study the relative competitive position two years after planting of the shortleaf pine seedling compared with its tallest hardwood competitor (within 1.37 meters) was significantly correlated with the survival of the planted shortleaf pine seedling after 5, 10, and 13 years. The relative competitive position five years after planting of the shortleaf pine seedling and its tallest hardwood competitor was significantly correlated with the survival of the shortleaf pine seedling after 10 and 13 years. We therefore recommend releasing shortleaf pine seedlings from understory competition 2 – 5 years after planting.

A caveat to the above recommendation is that the degree to which release from understory competition will impact shortleaf pine seedling growth and survival is dependent upon overstory stocking. The effects of understory release are stronger at lower stocking levels, while at higher stocking levels the improvements in growth and survival following release are more marginal, and may not be worth the cost or effort of the release treatment.

Finally, we recommend that underplanted shortleaf pine seedlings be released from overstory competition after 10 years to improve survival, or sooner to improve growth. In this and other studies (Guldin and Heath, 2001; Schnake et al., 2021) the growth of planted shortleaf pines was negatively correlated with overstory stocking for the first decade after planting. In this study, after 13 years shortleaf pine survival was negatively correlated with overstory stocking, indicating that between 10 and 13 years after planting overstory competition begins to cause mortality. We therefore recommend not waiting longer than 10 years to release underplanted shortleaf seedlings from overstory competition.

Appendix of statistical tables:

2017 Data

Table A1: Height in 2017 by overstory stocking.

	SUM OF SQUARES	DF	MEAN SQUARE	F VALUE	P VALUE
REGRESSION	313785.5	1	313785.5	64.859	<.001
RESIDUAL	179005.4	37	4837.985		
TOTAL	492791	38			

Table A2: Basal Diameter in 2017 by overstory stocking.

	SUM OF SQUARES	DF	MEAN SQUARE	F VALUE	P VALUE
REGRESSION	6860.785	1	6860.785	58.513	<.001
RESIDUAL	4338.366	37	117.253		
TOTAL	11199.15	38			

Table A3: Height in 2017 by overstory stocking and height difference with hardwood competitor 5 years post planting.

EFFECT	NUM DF	DEN DF	F VALUE	P VALUE
STOCKING	1	307	93.1	<.0001
HEIGHT DIFF	1	307	95.66	<.0001
INTERACTION	1	307	5.22	0.0230

Table A4: Height in 2017 by overstory stocking and height difference with hardwood competitor 2 years post planting.

EFFECT	NUM DF	DEN DF	F VALUE	P VALUE
STOCKING	1	329	35.90	<.0001
HEIGHT DIFF	1	329	104.35	<.0001
INTERACTION	1	329	11.92	0.0006

Table A5: Survival in 2017 by initial basal diameter.

EFFECT	NUM DF	DEN DF	F VALUE	P VALUE
INITIAL BD	1	371	4.56	0.0334

Table A6: Survival in 2017 by overstory stocking.

EFFECT	NUM DF	DEN DF	F VALUE	P VALUE
STOCKING	1	699	0.24	0.6255

Table A7: Survival in 2017 by overstory stocking and height difference with hardwood competitor 5 years post planting.

EFFECT	NUM DF	DEN DF	F VALUE	P VALUE
STOCKING	1	557	61.47	<.0001
HEIGHT DIFF	1	557	14.35	0.0002
INTERACTION	1	557	19.54	<.0001

Table A8: Survival in 2017 by overstory stocking and height difference with hardwood competitor 2 years post planting.

EFFECT	NUM DF	DEN DF	F VALUE	P VALUE
STOCKING	1	661	39.72	<.0001
HEIGHT DIFF	1	661	10.80	0.0011
INTERACTION	1	661	10.63	0.0012

2020 Data:

Table A9: Height in 2020 by overstory stocking and height difference with understory hardwood competitor 5 years post planting.

EFFECT	NUM DF	DEN DF	F VALUE	P VALUE
HEIGHT DIFF	1	153	18.03	<.0001
STOCKING	1	153	34.28	<.0001
INTERACTION	1	153	7.84	0.0058

Table A10: Height in 2020 by overstory stocking and height difference with understory hardwood competitor 2 years post planting.

EFFECT	NUM DF	DEN DF	F VALUE	P VALUE
HEIGHT DIFF	1	171	4.95	0.0275
STOCKING	1	171	24.48	<.0001
INTERACTION	1	171	0.48	0.4904

Table A11: Survival in 2020 overstory stocking.

EFFECT	NUM DF	DEN DF	F VALUE	P VALUE
STOCKING	1	327	6.95	0.0088

Table A12: Survival in 2020 overstory stocking and height difference with understory hardwood competitor 5 years post planting.

EFFECT	NUM DF	DEN DF	F VALUE	P VALUE
HEIGHT DIFF	1	293	30.43	<.0001
STOCKING	1	293	13.25	0.0003
INTERACTION	1	293	9.41	0.0024

Chapter 5: Tree ring response to competition and prescribed fire in planted shortleaf pine

Background

Shortleaf pine (*Pinus echinata*) covered approximately 300,000 km^2 across what is now the southeastern United states prior to European colonization (Anderson et al., 2016) but has been reduced to approximately 25,000 km^2 currently (Oswalt et al., 2012). Interest in restoring shortleaf pine and shortleaf pine-oak mixedwood forests, or mixtures of hardwoods and softwoods, is challenged by issues with recruiting shortleaf pine from the forest understory to competitive positions in the midstory Planting shortleaf pine seedlings can provide a solution to regeneration shortages caused by potential problems with seed production or germination. However, newly planted shortleaf pine seedlings struggle to compete with hardwoods (Kabrick et al., 2015), often because the hardwood stems are larger advance reproduction or have recently resprouted from an established root system.

Competition from understory hardwoods can inhibit the growth of shortleaf pine, but removing the hardwoods provides an effective release to which shortleaf pine responds well (Brinkman and Smith, 1968). A study in Arkansas found that a shortleaf pine stand with the hardwood understory removed had greater growth over 5 years than stands with the understory left intact (Bower and Ferguson, 1968). A similar study at the Sinkin Experimental Forest in MO found that hardwood control increased shortleaf pine growth by 2 m^2 per hectare over 10 years (Rogers and Brinkman, 1965).

Prescribed burning provides another option to manage hardwood abundance in the understory and midstory layers. Properly timed prescribed fire may provide an advantage to shortleaf pine recruitment by top-killing hardwood competitors while shortleaf pine stems are not top-killed. Repeated prescribed burning can also be used as a maintenance treatment to prevent development of abundant hardwood stems in the midstory. Once shortleaf pine stems are large enough that vulnerability to top-kill is low, prescribed burning may be effective for keeping open stand conditions. By reducing competition with hardwood stems and maintaining lower stand density, growth rates of recruiting shortleaf pine trees could be increased with frequent prescribed burning. However, a recent study in southeast Oklahoma found that radial growth of shortleaf pine trees was reduced by 21–33% in the growing season following prescribed fire (Adhikari et al., 2021), suggesting that fire may also have direct effects on tree growth.

Because prescribed fire is often a tool used to control hardwood competition in shortleaf pine stands, the relative importance of both prescribed burning and hardwood competition in affecting shortleaf pine growth is important for understanding best management approaches for favoring shortleaf pine. The objective of this study is to use tree ring analysis to examine the radial growth of shortleaf pine in response to known management activities and local competition levels. Specific research questions include: 1) How does repeated prescribed burning affect stand development (structure and composition) following release of planted shortleaf pine? 2) How does shortleaf pine radial growth respond to release? 3) Does prescribed burning affect the radial growth of shortleaf pine? 4) Does the level and composition of local competition affect the radial growth of shortleaf pine?

Methods

Study site

The study was located in the Poplar Bluff District of the Mark Twain National Forest in southeast Missouri. The area was affected by a tornado in 2002, and a salvage harvest was conducted in 2003. Scattered residual overstory trees, consisting of primarily shortleaf pine and white oak (*Quercus alba*), survived the tornado and remain in the stands. The area affected by the tornado was divided into several management units, and this study focused on two adjacent units, separated by a gravel road. In both units a site preparation burn was conducted in 2004, and bareroot shortleaf pine seedlings were planted in spring of 2005 at 3 m by 3 m spacing. In 2011, a release and weed treatment was done on both units between June and December. The release objectives were to cut any hardwood within 1.83 m of a shortleaf pine tree except those that were less than half the height of the shortleaf pine. In one of the two units, prescribed burns were conducted on March 4, 2011, April 5, 2013, March 23, 2015, April 11, 2018, March 22, 2021. The burned unit is ~5 ha and the unburned unit is ~7 ha.

Soils series for both units are mapped as predominately (~93%) Captina silt loam, which are very deep, moderately well drained soils (Soil Survey Staff). The units are fairly flat, with slopes of 1-8 %. The average annual temperature from 2005 to 2021 was 14 °C and the average annual precipitation for the same period was 1286 mm (NOAA, 2023).

Experimental design

In each of the two units, henceforth called “burned” and “unburned” despite both having a site preparation burn, 30 shortleaf pine trees were selected as focal trees to quantify growth patterns in relation to the competitive environment. Around these trees the overstory and midstory basal area were calculated, and understory stems that reached at least breast height were tallied.

Tree selection and overstory sampling

In the summer of 2022, 4-5 parallel transects were established in each management unit, with sampling points set every 15 m along each transect, for a total of 45 sampling points per unit. At each point, the closest overstory (diameter at breast height (DBH) ≥ 11.4 cm) shortleaf pine was selected and flagged as a potential focal tree and DBH was measured. All overstory trees within a 7.3 m radius (~3x the average crown radius, as recommended by Lorimer (1983)) of the focal pine were identified and DBH was recorded.

The level of local competition surrounding each potential focal tree was quantified using the following competition index (CI): $(\Sigma D_j)/D_i$ as recommended by Lorimer (1983), where D_j is the diameter of the competitor and D_i is the diameter of the subject tree.

Competition indexes measured across the initial 45 potential focal trees for each unit ranged from 1.5 to 23.5, with fewer than 10 trees having CIs greater than 15. From this range six competition classes were established, with the goal of randomly selecting 5 focal trees from each stand per class for a total of 30 focal trees per stand covering a range of competition levels. The competition classes are: <5, 5-7.5, 7.5-10, 10-12.5, 12.5-15, and >15. If a competition class did not have sufficient trees to select from, additional trees from the closest class were randomly selected. In the burned unit, both of the highest competition classes had insufficient representation, so all available trees within the classes were used an additional tree from each of the 3 smaller competition classes were used. In the unburned unit, only 3 trees were included in the 12.5 – 15 CI class, so all 3 were used and one extra tree from the class immediately higher and lower were used.

Midstory and understory sampling

Within a 7.3 m radius of the 30 focal trees per unit, the midstory trees, classified as trees with a DBH of 2.5 cm – 11.4 cm, were identified and DBH was measured. The understory trees ≥ 1.37 m tall but < 2.5 cm DBH were also identified and tallied by species within the same radius.

Tree coring

Two cores were taken from each focal tree, as close to the base of the trees as possible. All tree cores were mounted to wooden blocks and sanded with increasingly fine (up to 1200) grit sandpaper. Images of each core were scanned and imported into the CooRecorder software (Cybis Electronik & Data AB, Sweden) for determination of ring boundaries and measurement of ring widths. The best core per tree was used for analysis.

The distance to pith was estimated in the CooRecorder software for each core used in analysis, and ring widths were converted to Basal Area Increment (BAI) for analyses.

Data analysis

Because this study is comparing two adjacent management units and does not have true replication at the stand level, the first research question regarding stand composition and repeated burning was addressed with descriptive statistics only. Composition for each unit is reported by grouping white oak species, in this study white oak (*Quercus alba*) and post oak (*Quercus stellata*), and red oak species, in this study scarlet oak (*Quercus coccinea*), black (*Quercus velutina*), blackjack (*Quercus marilandica*), and northern red oak (*Quercus rubra*). Hickory (*Carya*) species were also grouped, but not identified to the species level. Sumac species were predominately fragrant sumac (*Rhus aromatica*), with a smaller component of winged sumac (*Rhus copallinum*).

To address questions 2 and 3, regarding growth response to release and prescribed burning, a repeated measures ANOVA was used with ring width or BAI as the response variable, year as the within-subject variable, and treatment (burned v. unburned) as the between-subject variable. Because repeated measures ANOVA requires listwise deletion of missing values (meaning any sample missing ring width measurements for any year is deleted entirely from the dataset), analysis included only years with full replication, which began in 2011. To address question 4 regarding growth response to competition, a generalized linear model with a lognormal distribution was used with the average ring width or BAI of 2019-2021 as the response variable and plot-level basal area, stocking, or competition index as fixed effects. Because the results of the repeated measures ANOVA showed separation starting in 2019, the years 2019-2021 were used to analyze competition.

Results

Stand level

In the unburned area, the average overstory basal area was 15 m^2/ha and the average midstory basal area was 6 m^2/ha for a total of 21 m^2/ha. The average number of understory stems (≥ 1.37 m tall) was 2060 stems per hectare. In the burned area the average overstory basal area was 12 m^2/ha and the average midstory basal area was 1.4 m^2/ha for a total of 13.4 m^2/ha. The average number of understory stems was 3291 stems per hectare. Species composition was similar in the overstory but differed in the midstory and understory (Tables 5.1 – 5.3).

Table 5.1: Overstory species composition in the burned and unburned management unit.

Burned **Species**	**Percent of BA**	***Unburned*** **Species**	**Percent of BA**
Shortleaf Pine	73	Shortleaf Pine	74
White Oak Sp.	12	White Oak Sp.	12
Hickory Sp.	11	Red Oak Sp.	8
Red Oak Sp.	4	Hickory Sp.	4

Table 5.2: Midstory species composition in the burned and unburned management unit.

Burned Species	Percent of BA	***Unburned*** Species	Percent of BA
Shortleaf Pine	59	Red Oak Sp.	21
White Oak Sp.	12	White Oak Sp.	19
Red Oak Sp.	10	Hickory Sp.	17
Hickory Sp.	6	Winged Elm	13

Table 5.3: Understory species composition in the burned and unburned management unit.

Burned Species	Percent of stems	***Unburned*** Species	Percent of stems
Sumac Sp.	48	Winged Elm	40
Black Cherry	21	Hickory Sp.	28
Red Oak Sp.	14	White Oak Sp.	8
Black Gum	5	Red Oak Sp.	8
Hickory Sp.	4	Black Cherry	4

Annual ring width

Analysis of raw ring width data revealed a significant effect of year (p<0.001) and a significant interaction between year and treatment (p<0.001) on ring width. Years in which treatments were significantly different included 2013 (p<0.001), 2019 (p=0.002), 2020 (p<0.001), and 2021 (p<0.001) (Figure 5.1). Year differences within units were somewhat complex and are listed fully in Table 5.4. In the burned unit, generally years after 2014 had greater ring widths than years before, with the exception of 2018 being similar to early years. The unburned areas had fewer significant differences, with 2016 being significantly higher than some early years.

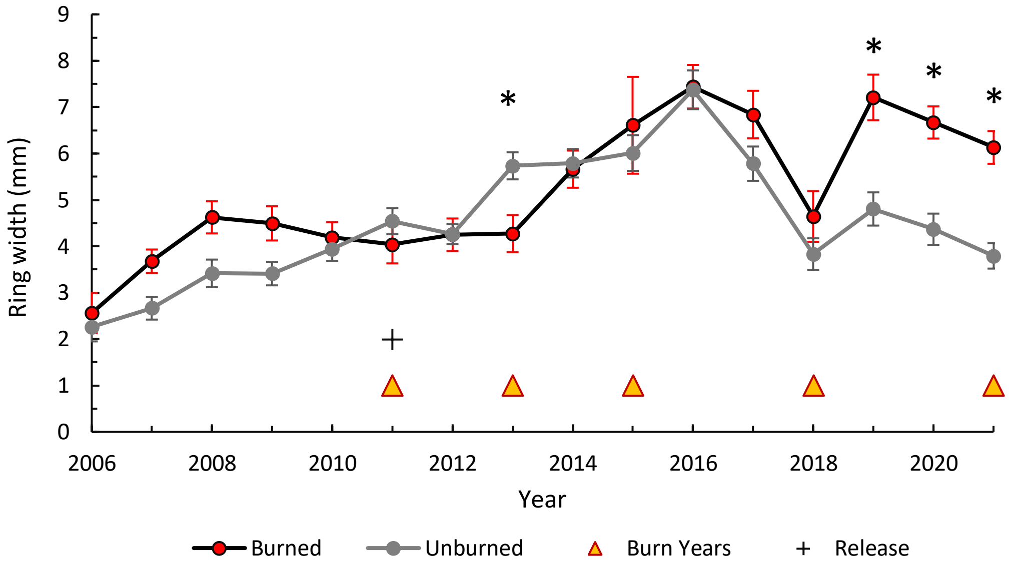


Figure 5.1: Average ring width for shortleaf pine tree cores taken from the burned and unburned management unit by year. * indicate years with treatment differences. Error bars are standard error. Orange triangles indicate burns.

Table 5.4: Differences between ring widths by year within the burned and unburned units. Significantly different years at alpha=0.05 are shown.

Year	**Significantly different years – Burned**	**Year**	**Significantly different years – Unburned**
2011	2016, 2017, 2019, 2020, 2021	**2011**	
2012	2017, 2019, 2020, 2021	**2012**	
2013	2016, 2019	**2013**	
2014	2006, 2007, 2010, 2018	**2014**	2007
2015		**2015**	
2016	2006, 2007, 2008, 2009, 2010, 2011, 2012, 2013, 2018	**2016**	2006, 2007, 2008, 2009
2017	2006, 2007, 2008, 2009, 2010, 2011, 2012, 2018	**2017**	
2018	2014, 2016, 2017, 2019, 2020, 2021	**2018**	
2019	2006, 2007, 2008, 2009, 2010, 2011, 2012, 2013, 2018	**2019**	
2020	2006, 2007, 2008, 2009, 2010, 2011, 2012, 2013, 2018	**2020**	
2021	2006, 2007, 2008, 2009, 2010, 2011, 2018	**2021**	

Analysis of BAI also revealed significant effects of year (p<0.001) and a significant interaction between year and treatment (p<0.001). Years in which BAI differed significantly between treatments were 2019 (p=0.012), 2020 (p=0.003), and 2021 (p<0.001) (Figure 5.2). Year differences within are listed in Table 5.5. In both the burned and unburned units, later years were generally higher than earlier years.

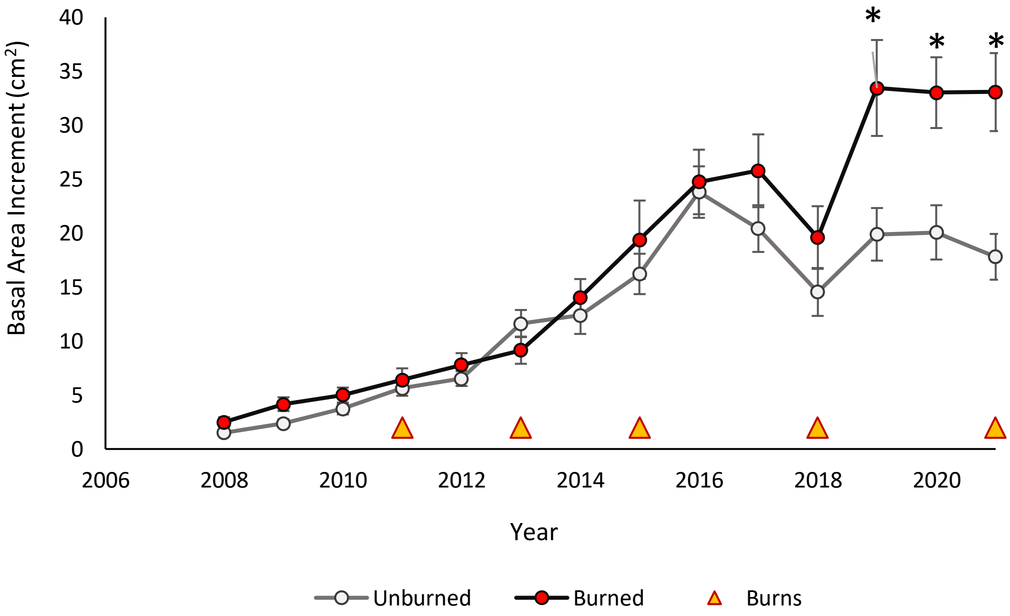


Figure 5.2: Average BAI for shortleaf pine tree cores taken from the burned and unburned management unit by year. * indicate years with treatment differences. Error bars are standard error. Orange triangles indicate burns. A release occurred in 2011.

Table 5.5: Differences between BAI by year within the burned and unburned units. Significantly different years at alpha=0.05 are shown.

Year	**Significantly different years – Burned**	**Year**	**Significantly different years – Unburned**
2011	2014, 2015, 2016, 2017, 2018, 2019, 2020, 2021	**2011**	2013, 2014, 2015, 2016, 2017, 2018, 2019, 2020, 2021
2012	2014, 2015, 2016, 2017, 2018, 2019, 2020, 2021	**2012**	2013, 2014, 2015, 2016, 2017, 2018, 2019, 2020, 2021
2013	2015, 2016, 2017, 2018, 2019, 2020, 2021	**2013**	2011, 2012, 2016, 2017, 2020
2014	2011, 2012, 2016, 2017, 2019, 2020, 2021	**2014**	2011, 2012, 2016, 2017
2015	2011, 2012, 2013, 2019, 2020, 2021	**2015**	2011, 2012
2016	2011, 2012, 2013, 2014, 2019, 2020, 2021	**2016**	2011, 2012, 2013, 2014
2017	2011, 2012, 2013, 2014, 2019, 2020, 2021	**2017**	2011, 2012, 2013, 2014
2018	2011, 2012, 2013, 2019, 2020, 2021	**2018**	2011, 2012
2019	2011, 2012, 2013, 2014, 2015, 2016, 2017, 2018	**2019**	2011, 2012
2020	2011, 2012, 2013, 2014, 2015, 2016, 2017, 2018	**2020**	2011, 2012, 2013
2021	2011, 2012, 2013, 2014, 2015, 2016, 2017, 2018	**2021**	2011, 2012

Effects of competition

The cumulative BAI from 2019 to 2021 was negatively correlated with basal area ($p<0.001$), stocking ($p<0.001$), and competition index ($p<0.001$) (Fig. 5.3). The raw ring width data averaged across the years 2019 to 2021 was also negatively correlated with basal area ($p<0.001$), stocking ($p<0.001$), and competition index ($p<0.001$).

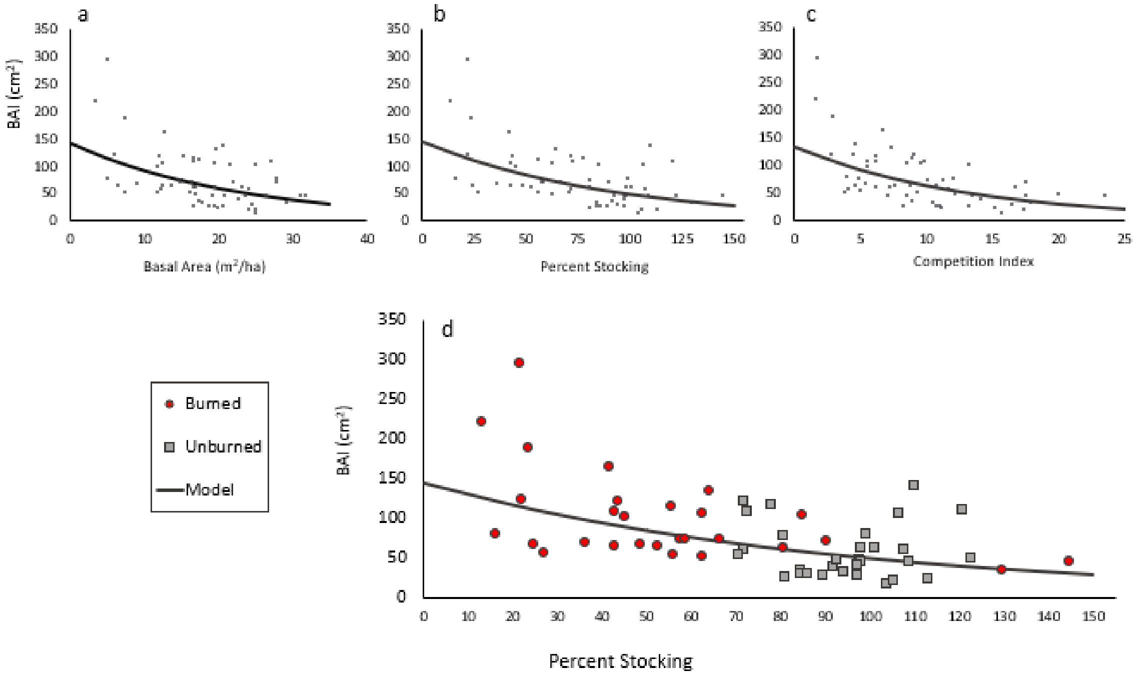


Figure 5.3: Cumulative BAI from 2019 to 2021 across both burned and unburned units by basal area (a), stocking (b), and competition index (c). BAI by stocking is shown again magnified (d) with data points separated by unit.

Cumulative BAI for 2019-2021 was significantly correlated with basal area (p=0.002) and the interaction between basal area and percent of basal area composed of hardwoods (p<0.001) (Fig 5.4). This pattern is true for ring width data averaged from 2019-2021 as well, with significant effects of basal area (p=0.048) and the interaction between basal area and percent hardwoods (p=0.018). There was not a significant interaction between stocking and percent hardwoods for either BAI (p=0.210) or ring width (p=0.068).

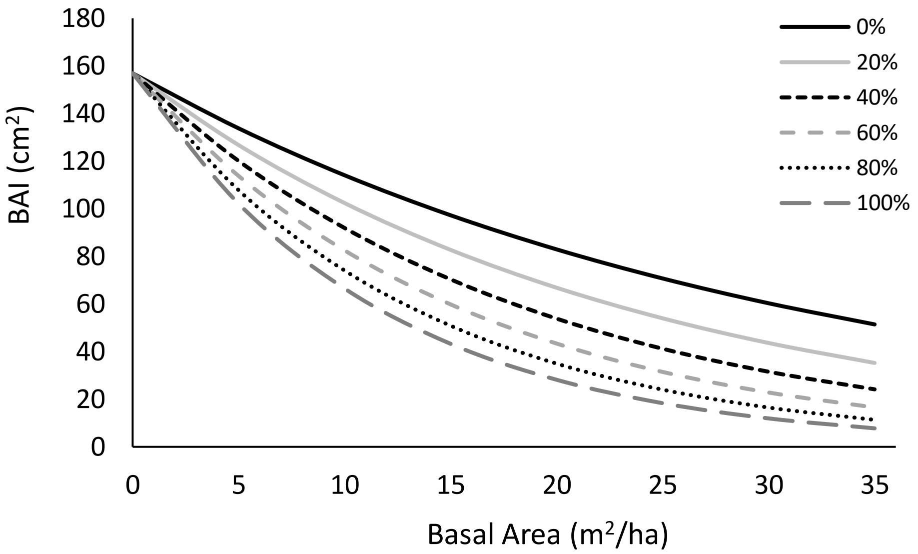


Figure 5.4: Cumulative BAI from 2019 to 2021 across both burned and unburned units by basal area and percent of the basal area composed of hardwoods.

Discussion

In this study, descriptive statistics of the midstory and understory composition pointed to differences in the burned and unburned units. Similar compositional changes have been seen in other studies. In uneven-aged loblolly-shortleaf pine stands in southeastern Arkansas, burn intervals of 3, 6, and 9 years were compared with unburned areas. While there was no difference of the basal area of the saplings (2.5-8.9 cm DBH) across treatments, there was significantly lower sapling diversity in the 3-year burn interval than in the other treatments, which was explained by the elimination of fire sensitive species (Cain et al., 1998). A 53-year study of loblolly and shortleaf pine woodlands in northern Florida found that 1-2 year burn intervals maintained pine dominance, while stands with a 3 year return interval showed signs of converting to a hardwood forest (Robertson et al., 2021). The authors also emphasized tailoring burn regimes to specific sites and land use histories forests (Robertson et al., 2021). In the Mark Twain tornado area, over a shorter time frame and with less replication, an approximately 3-year return interval seems to maintain shortleaf dominance for now, but of course continued monitoring remains important. In pine-oak forests in the southern Appalachians, the effects of a single March prescribed burn were studied. While the burn reduced the basal area of fire-sensitive midstory hardwoods, the density (stems per area) of these hardwoods increased due to prolific sprouting, indicating that repeated burns were warranted (Elliott and Vose, 2005).

There are several methods established in the literature for detecting release events using tree ring data. Several of these are reviewed in Trotsiuk et al. (2018). One of the early methods is called radial growth averaging, which was first described by Lorimer (1985) and used the procedure of averaging the radial growth over the 15 years preceding the potential release event as well as the radial growth for the 15 years following the potential release, and then calculating the percent growth change by subtracting the pre-event average from the post-event average and dividing that by the pre-event average.

Lorimer (1985) defined an event as a major release if the percentage growth change was greater than or equal to 100% and a defined a moderate release as a percentage growth change between 50% and 99%. The method was later modified by Nowacki and Abrams (1997) by using 10-year averages and by expanding the definition of a moderate release to include growth percent increases of 25% or higher. In this chapter I modified the method to use an average of only five years prior to and following release because of the young age of these trees. Using averages for the years 2006-2010 and 2012-2016 (I did not include the year 2011 in the averaging, as the release treatment was ongoing from June – December, so parts of each unit could be either pre or post release during most of the growing season), the percent growth change for the unburned unit was 69%, the burned unit was 38%, and combined was 52%, so there is evidence that the 2011 release was effective.

Another method for detecting release is the absolute increase method developed by Fraver and White (2005). This method also uses 10-year averages, but uses a species specific threshold value rather than a percent. They recommend thresholds for several species, but for other species suggest to use the formula of 1.25 times the standard deviation of all absolute increases to calculate the threshold. To attempt to detect release using the absolute increase method in this chapter I once again used 5-year averages. I calculated the threshold value of 1.8 millimeters using the standard deviation method. The differences between the five-year post release average and the pre-release average were 2.38 mm in the unburned unit, 1.65 mm in the burned unit, and 2.02 mm when data were combined, indicating a detectable release from the treatment in 2011 in the unburned unit and when looking at the units together. Both units show a decline in growth from 2016 to 2018, then in 2019 the burned area begins to have significantly higher ring widths for the remainder of the measurements. It is possible that the 2018 burn acted as a release from midstory competition in the burned unit, but with only 3 years following the 2018 burn, this was not calculated.

In this study, 2013 was the only year in which prescribed burning resulted in significantly lower growth in the burned unit, and only when analyzing raw ring width data, while other burn years did not show differences. In the western Ouachita Mountain in southeastern Oklahoma tree rings were analyzed in cores collected from shortleaf pine trees in oak-pine forest burned periodically since 1985. In areas burned on 2 or 3-year intervals, the radial growth in the year following fire was reduced by 21 to 33% (Adhikari et al., 2021). A reduction in growth following prescribed burning was not seen in the 4-year return interval stands, which the authors attributed to differences in fuel characteristics (Adhikari et al., 2021). Both this study and Adhikari et al. (2021) seem to indicate that fire behavior affects possible growth reductions in shortleaf. The 2013 burn was anecdotally described as being "hot," and took place in April, a bit later than the typical dormant season burns in this unit. Further research on prescribed burning and radial growth reduction, including data on fire timing and behavior, would likely be useful.

There is evidence that summer drought conditions slow the growth of shortleaf pine. In Georgia, Grissino-Mayer and Butler (1993) found significant negative relationships between growth and temperature in April, June, July, August, and September. They also found significant positive relationships between growth and precipitation during May, June, and July. These same trends were observed when using seasonal averages of temperature and precipitation, and the strongest predictor of growth was growing season precipitation. In Oklahoma, on the western edge of shortleaf pine's range, Adhikari et al. (2021), found that annual growth was positively correlated with growing season precipitation and negatively correlated with maximum summer temperature. They also found evidence that higher minimum temperatures the previous October correlate with higher growth and that trees growing in open savanna conditions were less sensitive to annual variation in precipitation than trees growing in closed forests. Using long term data from the Missouri Ozark Forest Ecosystem Project, Stambaugh and Guyette (2004) found that shortleaf pine growth was sensitive to a 21-year drought cycle, and also that growth was correlated with the minimum winter temperature prior to the growing season.

The year 2012 was a drought year in Missouri. Looking at NOAA county climate data, Carter County had the highest maximum growing season temperature (for the period of 2000 – 2021) in 2012 (29.8 °C) as well as the lowest precipitation (401 mm). The 2012 drought likely reduced shortleaf growth, so a potentially greater response to release may have been seen were the release not immediately followed by drought. The combined effects of the drought in 2012 and a hot April burn in 2013 could explain any reduction in growth in the burned unit in 2013.

The effects of competition, especially from hardwoods, on shortleaf pine growth have been noted before. In southeastern Arkansas, shortleaf pine and loblolly pine growth was examined in naturally regenerated stands with different types of competition control. From ages 5 to 13, pine diameter growth increased on plots with woody competition control compared with plots with only herbaceous competition control because of hardwood competition in the herbaceous control areas (Cain, 1997). In the Pisgah National Forest, McNab (2021) found that shortleaf and pitch pines planted in a clearcut hardwood stand were significantly taller when growing in groups of at least two pines than when surrounded by hardwood species. They concluded that the pine groups provided a buffer from interspecific competition, which was more detrimental than the intraspecific competition of pine groups (McNab, 2021). The increased effects of hardwoods to growth reduction in this study were not seen when analyzing growth by stocking, as the stocking equations themselves account for the greater growing space required by hardwoods (Rogers, 1983; Gingrich, 1967). When predicting radial growth of shortleaf pine in response to competition, managers should use stocking measurements or account for the differential effects of hardwoods if using basal area measurements.

Overall, this study shows that repeated burning may change midstory composition by reducing fire sensitive species and promoting shortleaf pine. One of the burn years in this study resulted in lower ring widths in the burned unit, while the others did not, indicating factors such as burn conditions and fire behavior may mediate the effects of burning on shortleaf pine growth, but burning does not necessarily reduce BAI. Local competition density reduced shortleaf pine radial growth in this study, and this was especially true for hardwood competition. Additionally, the hardwood midstory may have contributed to lower growth in the unburned area in the later years of this study. Further research into the ways prescribed fire effect shortleaf growth and the roles of inter and intra specific competition on shortleaf growth may be of interest.

Chapter 6: Conclusions

This project includes multiple studies to provide a comprehensive assessment of key factors that can affect the success of shortleaf pine regeneration and recruitment, from seed germination to sapling survival and growth, focusing especially on the roles of hardwood competition and prescribed burning. A summary of the role of prescribed fire at different life stages of shortleaf pine is included in Table 6.1.

It has been well established in the literature that shortleaf pine regeneration from seed strongly benefits from a seed bed free of litter and that prescribed burning is one tool for establishing a suitable seedbed (Grano, 1949; Baker, 1992). The first study of this dissertation examined the tradeoffs between improvement to the seed bed and direct effects on shortleaf pine seed when prescribed burning. Heat applied directly to seeds reduced germination starting at 80 ° C and completely inhibited germination at 120 ° C or higher. Shortleaf pine seeds fall in autumn, so the early spring prescribed burns which are common in management likely have direct effects on seeds in addition to the effects on seedbeds. This study showed that prescribed burning in the fall prior to seed dispersal resulted in significantly more first year seedlings than with not burning or burning in early or late spring. Burning in early spring while seeds were on the ground did not result in significantly different first year seedling counts then an unburned plots, suggesting that the improvement in the seed bed offset any negative effects direct effects of fire on shortleaf pine seeds. Prescribed burning in late spring after seed germination resulted in significantly lower counts then all other treatments.

The second study of this dissertation focuses on the fate of shortleaf pine and oak seedlings and saplings of different sizes following prescribed fire. As shown in other studies, the probability of resisting top-kill increased with basal diameter for both oaks and shortleaf pine (Dey and Hartman, 2005). Also in line with previous studies, this research showed that increasing fire temperature increases the risk of top-kill at a given size (Lilly et al., 2012). Unique to this research is a paired approach that shows that, for a range of basal diameters between 1.5 and 4 cm, shortleaf pine was more likely to resist top-kill than similarly sized oaks. This study also showed different sprouting strategies for shortleaf pine and oaks following top-kill. For oaks, the height of sprouts following fire was significantly correlated with pre-fire basal diameter, but for pine there was only weak evidence for this relationship. Oaks tended to have taller sprouts, while shortleaf pine had more sprouts per stem.

The third study of this research focuses on the survival and growth of planted shortleaf pine trees under different residual overstory stocking levels, and with relation to understory hardwood composition. As is seen in other literature, overstory stocking reduced height growth of planted shortleaf (Jensen et al. 2007; Schnake et al. 2021), an effect which increased with time in this study, and eventually caused increased mortality. This study also showed directly that being overtopped by a hardwood competitor 2 – 5 years after planting causes decreased growth and survival in shortleaf pine seedlings evident even 10 years later.

Finally, the fourth study examines the radial growth of planted shortleaf pine in relation to burning and competition over the first 16 years of life. It showed that burning only reduced shortleaf pine growth under certain conditions and that shortleaf growth was reduced by competition, especially by hardwood competition.

Collectively, the findings in this dissertation can lead to some overall conclusions and management recommendations for the early life of shortleaf pine.

Hardwood competition is a crucial factor regulating the growth and survival of shortleaf pine, and must be managed for shortleaf pine to be successful in mixed woods situations. The difference between the height of shortleaf pine and its closest hardwood competitor as early as two years post planting has long-term implications for both growth and survival, so release from competition is key for seedling success. Hardwood competition reduces the radial growth of shortleaf pine even at almost 20 years after planting, so a onetime release is likely not enough to ensure shortleaf pine success in stands with fast-growing hardwoods.

Prescribed fire is an effective tool for managing shortleaf pine, and can be used to obtain multiple objectives at different stages of shortleaf pine's life. Prescribed fire done in early fall before seed-fall is effective at preparing the seedbed and promoting natural regeneration from seed. If timed correctly to seedling size, prescribed burning during the dormant season may provide a release for shortleaf pine seedlings, by top-killing competitors while shortleaf pine seedlings are able to resist top-kill. Prescribed burning can also be used as a maintenance treatment for older shortleaf pine stands, to reduce hardwood encroachment in the midstory and possibly increase shortleaf radial growth by reducing hardwood competition.

Table 6.1: Pros and cons of burning at various life stages of shortleaf pine

Shortleaf Life Stage	Prescribed Fire Pros	Prescribed Fire Cons
Seed	Improve seed bed and increase germination (fall)	Damage to seeds (early spring) Mortality of germinants (late spring)
Seedling	Release from hardwood competition if timed correctly (seedlings between 1.5–4 cm BD) with possible lasting effects on growth and survival	Possible top-kill of shortleaf pine seedlings with loss of competitive position due to short sprouts Possible complete mortality
Established (~15 yo)	Prevents hardwood midstory development Possible increased growth from reduced competition	May slow shortleaf growth in some years following fire

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