

RESTORATION TREATMENTS AND REGENERATION DYNAMICS
IN EAST TEXAS MIXED WOOD FORESTS

A Thesis

presented to

the Faculty of the Graduate School
at the University of Missouri-Columbia

In Partial Fulfillment

of the Requirements for the Degree

Master of Science

by

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JULY 2023

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RESTORATION TREATMENTS AND REGENERATION DYNAMICS
IN EAST TEXAS MIXED WOOD FORESTS

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ACKNOWLEDGEMENTS

First, I would like to acknowledge Dr. Ben Knapp for all the hard work he put into guiding me through the research and writing process. I have certainly felt out of my element at many points in this process, and I could not have gotten luckier in terms of a research advisor. Thank you for all your advice, and probably most importantly your patience!

Next, I would like to thank the T.L.L. Temple Foundation for funding this research and providing me with an opportunity to learn more about forestry while spending time in beautiful East Texas and Missouri as the first Buddy Temple Graduate Fellow. I am sure that my experience will be the first in a long line of individuals who achieve great personal growth while contributing valuable knowledge to the management and conservation of East Texas lands in the memory of Buddy Temple.

Thank you to Steve Jack and Robert Sanders for making this research possible at Boggy Slough, for your welcoming nature, and your good communication. Knowing that you all were there to help me out if I needed it made a big difference, and hearing your perspectives on the management of Boggy Slough was invaluable. Additionally, thanks to the Temple family for their hospitality, and to Ellen Temple specifically for a couple good conversations. The beautiful accommodations during field work were a luxury that many researchers do not have.

Thank you to Dr. Samniqueka Halsey for being a calm and collected voice of reason in the face of my statistical struggles and in advance of my defense. Your input helped me feel more confident about my process and findings.

Thank you to the other members of the Knapp Lab who made this experience much more enjoyable and interesting through happy hours and good conversations. Ian Vaughan, George Jensen, Hope Fillingim, Abby Huffman, Trystan Harpold, Dacoda Maddox, Isaac Hayford, Ian Goldberg, Sloane Scott, Kendra Esparza-Harris, Dacoda Maddox, and Raelin Kronenberg, thank you for making lab lunches interesting.

Lastly, I need to thank the people outside of Mizzou and Boggy Slough who helped me through this process. Of course, I would like to thank my family for planting the seed of my love for forestry, and for putting up with my subsequent preoccupation with everything tree related. Thank you to the whole HH crew from OCD for being so encouraging as I embarked on this process, and to Keely Dunham in particular for her friendship and support throughout the process. And a huge thank you to Gwen Keller, who was without a doubt as integral as anyone in this process. I owe you so much for listening to all my complaints and worries, for your steadfast support, and for your regular visits. I'll do my best to return the favor over the years to come.

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ABSTRACT

Extensive harvesting, fire exclusion, and plantation forestry altered composition and structure, and thus function and habitat values of east Texas Pineywoods uplands. Upland restoration efforts are made difficult by the abundance of sprouting mesophytic species and by the complex silvics of the historical mixed wood types. This study evaluated the effects of restoration sequences on regeneration dynamics at the Boggy Slough Conservation Area, in Trinity County, TX, USA. A chronosequence was used to evaluate population-level changes in four species groups: historically dominant oaks and pines and contemporary competitors yaupon holly and sweetgum. Individual seedlings were tracked to evaluate the effects of harvesting, dormant season prescribed burning, foliar herbicide application, and growing season prescribed burning on growth, topkill, and mortality. None of the treatment sequences caused significant mortality of yaupon holly, but its growth rate was reduced by herbicide applied soon after prescribed burning. Mortality was also low among oak species, which remained intermediate in abundance to other species in the study and maintained a growth rate which was relatively unaffected by treatments. Treatment sequences involving herbicide led to high mortality of both sweetgum and pine species. The treatments successfully re-established the desired two-layered woodland structure by topkilling large yaupon holly, however, resprouts were abundant. Overall, results indicated the need for continued management to maintain a two-layered woodland structure and allow the successful recruitment of the desired pine and oak species to the midstory and overstory.

Chapter I – Literature Review

Welcome to the Pineywoods

The Pineywoods is a largely forested ecological region that spans approximately 117,000 km² of East Texas, western Louisiana, southeastern Oklahoma, and southern Arkansas (NRCS, 2006). The Pineywoods of East Texas are characterized by rolling uplands interspersed by flat bottomlands and elevations from 25 to 200 meters above sea level (LBJ School of Public Affairs, 1978; NRCS, 2006). Average precipitation ranges from 990 to 1600 millimeters annually across the region, and the mean annual air temperature ranges from 16 to 20 °C (NRCS, 2006). Throughout the region, soils are deep and of marine origin in uplands and alluvial origin in bottomlands, ranging from well to poorly drained, with siliceous, smectitic, or mixed minerology (NRCS, 2006).

Historical Conditions and Land Use Change

The Pineywoods region has been occupied by humans for thousands of years, although there is little knowledge of population distributions, agricultural patterns and practices, or land management practices before the relatively recent “Late Prehistory” period (Story, 1981). Archaeologists assume that mast bearing trees such as oaks and hickories have been important sources of food throughout the occupation of this region, and there is some evidence of permanent “sedentary” villages and cultivation of maize as early as C.E. 780 (Story, 1981)

Precise information about presettlement vegetation and structure is not available for much of the Pineywoods, but Original Texas Land Survey notes and accounts by early explorers have been used to describe pre-settlement vegetation in general terms

(Komarek, 1974; Srinath 2012). Extensive timber harvesting and land clearing for agriculture had already begun before any detailed surveys of the natural resources of East Texas, but William L. Bray compiled information about unharvested forests and what was known of the native vegetation for the United States Forest Service in 1904 (Bray, 1904). Native vegetation in the Pineywoods region of Texas ranged from bayous of bald cypress (*Taxodium distichum*), sweetgum (*Liquidambar styraciflua*), water oak (*Quercus nigra*), and tupelos (*Nyssa* spp.), to alluvial valleys dominated by oaks (*Quercus* spp.) and ashes (*Fraxinus* spp.), and uplands dominated by longleaf pine (*Pinus palustris*) in the southeast and loblolly pine (*Pinus taeda*) in the southern portion of the region (Bray, 1904). The most extensive forest type was dominated by varying proportions of shortleaf pine (*Pinus echinata*) and upland oaks, especially post oak (*Quercus stellata*), and occupied the northern two-thirds of the region (Bray, 1904).

Prior to the widespread logging of the Pineywoods, most sawmills were small and served local markets for fuelwood and building materials (Maxwell and Martin, 1970). Trees were harvested using axes and were often floated down rivers to mills, and naval stores operations tended living trees or extracted stumps of harvested trees (Bray, 1904). During the logging boom in the Pineywoods, all marketable timber was extracted using diameter-limit cutting, generally to eight inches, in concert with temporary tram lines and steam-powered skidders that were notoriously destructive to all residual trees and advanced regeneration (Maxwell and Martin, 1970). Products including lumber, barrel staves, railroad ties, crates, boxes, naval stores, and more were processed at large facilities and shipped by rail to fast-growing areas of the country (Bray, 1904; Maxwell and Martin, 1970). After the easily accessible timber was harvested, smaller operations

and mills continued to operate and harvested more difficult to access or poorer quality timber in smaller quantities for local use (Bray, 1904). By 1930, most virgin timber had been harvested, and large companies that preferred to purchase only stumpage rights sold what land they had purchased, leading to the creation of the four National Forests in Texas and leaving the nascent Texas forest industry to those who invested in acquiring land (Maxwell and Martin, 1970; Burka, 1982). One such individual was Thomas Lewis Latané Temple, who acquired 2800 hectares of cutover pineland in 1883 and acquired over 81,000 hectares of land in East Texas over the course of his life (Burka, 1982). This represented an investment in forests managed for future production, rather than simply extracting the existing timber. Temple's land was located around the confluence of three major timber types described by Bray (1904): loblolly pine, longleaf pine, and shortleaf pine-oak, near Diboll, Texas (Burka, 1982).

Bray (1904) described uncut upland woodlands as having a grassy understory and lacking a developed midstory, with bottomland species maintaining a foothold in ravines and drainages that extended deep into these stands, whereas most cutover stands were described as overrun by "scrub oaks" and oak thickets. Subsequent research has made clear that fire played a key part in the maintenance of these longleaf and mixed pine-oak uplands (Abrams, 1992; Chapman, 1932; Komarek, 1974). Stambaugh *et al.* (2014) synthesized multiple sources of evidence to estimate a mean fire return interval from one to six years across the region prior to Euro-American settlement. While direct evidence of anthropogenic burning in this region is limited, Guyette *et al.* (2002) documented patterns in fire frequency that paralleled population changes in the Ozark Mountains. Fire regimes

driven by native people appeared to dominate pre-Euro-American settlement, and these practices were then adopted and altered by settlers (Guyette *et al.*, 2002).

Throughout the 1900s, disturbances that maintained pine on the landscape, primarily fire and abandonment of agricultural land, declined over time with increasing permanent settlement and the desire to protect property, including trees as crops, from the effects of fire (Quarterman and Keever, 1962). Bray (1904) noted that some forests were already being harvested a second time, and Foster (1917) reported on rapid conversion of forested land to agricultural use. Bray (1904) further emphasized the importance of fire suppression initiatives to securing regeneration, stating “The renewal of the forest is made impossible by the agencies which prevent the growth of seedlings. The worst of these is fire.” This perception of the deleterious effect of fire fueled a desire for a widespread fire suppression program, leading to the passage of the Weeks Law and Clarke-McNary Act (Peirce *et al.* 1964). These policy changes succeeded in largely taming the issue of frequent and catastrophic fire that had disrupted the regeneration process in many Pineywoods stands and worried professional foresters about the future of the forests of the region (Cruikshank and Eldredge, 1939). By the time of later USDA Forest Service reports regarding Pineywoods resources and management concerns in 1967 and 1988, fire was no longer mentioned as a persistent problem facing East Texas forests (Sternitzke, 1967; McWilliams and Lord, 1988).

As the exploitation of the virgin timber in the Pineywoods wound down in the 1930s, the industry turned to naturally regenerated second-growth timber but also needed to address regeneration failures that resulted from destructive harvesting practices and severe slash fires that followed the initial logging (Mann, 1969). Selection harvest

systems were adopted to provide a consistent supply of sawlogs and ensure regeneration in small gaps created by harvesting, particularly in the loblolly-shortleaf pine types, and plantations became an ever more popular means to secure reliable regeneration of desired species, especially loblolly and slash pines (Mann, 1969). By 1986, 30% of pine stands were plantations, largely loblolly pine, followed by slash pine (McWilliams and Lord, 1988). Rosson (2000) reported that, by 1992, clear-cut and replant methods had largely supplanted even-aged shelterwood and seed tree methods of harvest, which themselves had replaced prior selection systems (Mann, 1969). Site preparation including prescribed burning and disking for increased mineral soil seedbed exposure, bedding and draining for increased site productivity, and herbicides and chopping for control of competition also came into common practice in this era (Mann, 1969).

Following the initial logging boom in the Pineywoods the forest products industry needed to adapt to utilizing the smaller diameter, second-growth forests that now occupied the landscape. The founding of the Champion Paper and Fiber Company in 1937 and the renewed production at a pulp mill in Orange in 1939 helped mark this shift in the East Texas forest products industry (Cruikshank and Eldredge, 1939; Power, 1998). Lumber from softwood sawtimber continued to be the highest-volume product for decades, but pulpwood quickly became an important source of revenue through the production of paper products. In fact, by 1965, pulpwood accounted for one third of the volume produced in the Pineywoods (Sternitzke, 1967), and by 1985 it comprised over half of production in the region (McWilliams and Lord, 1988). In 1964, what would become another key product for East Texas forest industries was introduced by the opening of two pine plywood plants (Bertelson, 1975). Lumber, paper products, plywood,

and later reconstituted wood products such as oriented strand board became the foundation of the Texas forest products industry, allowing continual improvements in the use of residual materials and reduced wastage (Bertelson, 1975; McWilliams and Lord, 1988). Although important in the early days of East Texas forestry, fuelwood and naval stores rapidly declined in importance (Cruikshank and Eldredge, 1939; Robinson, 1953; Sternitzke, 1967). By 2009, 42% of volume produced was in sawlogs for lumber, 19% in roundwood for veneer (especially softwood veneer for plywood), and 39% was for posts, poles, pilings, and paper products (Li *et al.* 2009).

Present Conditions and Restoration

The history of management and the evolution of industry in East Texas has shaped its modern-day landscape. Land ownership is largely stable, and agriculture and timber production remain important industries in the region (Brandeis, 2015; Dooley, 2017). The majority (61%) of land in the contemporary Pineywoods is forested, with cropland and grassland comprising 25% of the region and 6% of the area converted to urban land uses (USDA NRCS, 2006). In the forests that remain, loblolly pine is now the most abundant species and sweetgum is second, surpassing shortleaf pine, which is now third most abundant (Dooley, 2017). Longleaf pine, once a dominant species across much of Southeast Texas, no longer ranks among the ten most abundant species in East Texas (Dooley, 2017). Without frequent fire and other processes to maintain an open forest structure, dense midstories and overstories have developed in many East Texas pine stands.

In addition to the changes wrought through forest management and industrialization in the region, global trade and climate change are having an impact on East Texas forests. Drought has become an issue of note in East Texas, with the potential to affect forest structure and composition in the future (Dooley, 2017; Klockow *et al.*, 2020; Schwantes *et al.*, 2017). Since the early 1900s, Chinese tallow (*Triadica sebifera*), privets (*Ligustrum* spp.), and more recently Japanese climbing fern (*Lygopodium japonicum*) have become increasingly abundant and troublesome invasive plant species in East Texas forests (Klepzig *et al.* 2014).

The changes in East Texas forests have motivated several restoration initiatives focused on the structure and function of these forests. The widespread reduction in longleaf and shortleaf pine stands through the exploitative harvesting practices of the early logging era, fire suppression, conversion to loblolly pine plantations, and urbanization led to the creation of multi-state cooperative efforts for their restoration (Guldin and Black, 2018; ALRI 2009). Contemporary forests with dense midstories create an unfavorable environment for the success of red-cockaded woodpeckers, which are adapted to nesting in large, old pines and foraging in open pine woodlands and savannas (Conner and Rudolph, 1989; Macey, 2016). These conditions were common prior to widespread logging and fire suppression and have deteriorated over time with hardwood encroachment, midstory development, and even-aged silvicultural practices (Conner and Rudolph, 1989; Macey, 2016). The interest in restoring habitat for this endangered species has beneficial knock-on effects for other threatened and endangered species like the Texas trailing phlox (*Phlox nivalis* ssp. *texensis*) and others associated with this habitat.

In addition to habitat considerations, forest health and resiliency motivate restoration efforts. With projected increases in water stress to forests due to increased temperature and decreased precipitation, managing forests for continued provisioning of forest products, habitat value, and other ecosystem services is paramount (Klepzig *et al.* 2014). Historical forest composition and structure (higher overstory diversity, lower density, or a combination thereof) have the potential to confer resistance in the face of water stress (Klockow *et al.*, 2020). The maintenance of healthy, vigorous forests in the face of changing climate conditions and economic conditions will also be key in resistance and resilience to forest pests and pathogens of increasing concern across the continent (Ramsfield *et al.* 2016). The Southern Pine Beetle Prevention Program demonstrates the potential efficacy of management tailored to these concerns and provides an example of how historical conditions and processes may be beneficial in the face of contemporary and future challenges to forest health (Nowak *et al.* 2015).

Structure and Function of Pineywoods Uplands

Restoration and conservation efforts in the region commonly focus on the historical structure and function of the Pineywoods uplands. Restoring these key components is expected to create the conditions necessary for the success of species of conservation concern including red-cockaded woodpecker, Texas trailing phlox, longleaf pine, shortleaf pine, and others. Our knowledge of historical composition and processes in these forests is limited, but research attempts to illuminate key structural and functional components that can be reintroduced through well-planned management.

The overstory composition of the Pineywoods uplands at the time of European settlement was dominated by longleaf pine in the southeast, mixed shortleaf pine and oak in the northern two thirds, and loblolly pine in the south and southwest of the ecoregion (Bray, 1904). These dominant species were indicative of varying edaphic, topographic, and pyrogenic features across the landscape. While all of these dominant pine species benefit from the exposed mineral seedbeds that fire creates, each species requires a different length of time to become resistant to the top-killing effects of fire (Chapman, 1932; Komarek, 1974). The varied fire regime that supported these different forest types is reflected in the synthesis of Stambaugh *et al.* (2014), which estimated the mean pre-settlement fire return interval of the Pineywoods ranged from one to six years but varied by region.

In the southeastern Pineywoods, droughty soils and a relatively level topography encouraged frequent fire. These were nearly pure forests of longleaf pine, requiring very frequent fire to suppress competitors and maintain this composition (Bray, 1904; Chapman, 1932). Once established, these open-structured pine forests and savannas provided ideal conditions for future burning. Longleaf pine needles are very long, allowing them to be at least partially suspended from the soil surface, to dry rapidly, and to remain highly flammable (Platt, 1991). In addition, the open structure and plentiful understory light conditions of these forests allow a profusion of understory grasses and forbs, fine fuels which readily carry fire, as well as a favorable low-humidity microclimate relative to denser forests (Komarek, 1974). These longleaf pine-dominated forests are dependent upon frequent fire to overcome longleaf pine's slower growth and tendency to be permanently suppressed by competitors, especially oaks (Crocker and

Boyer, 1976). Longleaf pine's resistance to mortality from fire allow it to capture overstory gaps without an extended fire-free interval (Croker and Boyer, 1976). Under a sufficiently frequent fire-return interval, longleaf pine-dominated forests and savannas were self-perpetuating and provided vital habitat to fire adapted herbaceous flora, their invertebrate associates, and vertebrate animals, including the now-endangered red-cockaded woodpecker (Engstrom, 1993; Engstrom and Sanders, 1997; Folkerts *et al.* 1993; Walker, 1993).

The northern two-thirds of the Pineywoods uplands were historically dominated by mixedwood forests of shortleaf pine and hardwood species, predominantly oaks and hickories (Bray, 1904; Mattoon, 1915). Like longleaf pine forests, understory grasses and forbs were abundant in shortleaf pine dominated woodlands and forests (MacRoberts and MacRoberts, 2009). Fire in interaction with the soils and topography of this region was once again critical in creating and maintaining this forest type. The northern portion of the landscape features moderately-well to well-drained soils that are highly dissected by drainages that can act as natural firebreaks (Bray, 1904). Frequent fire was necessary to maintain the dominance of shortleaf pine in this forest type. Shortleaf pine is very resistant to the effects of fire at maturity and can accumulate as advance reproduction due to its ability to resprout after topkill as a seedling (Mattoon, 1915). Although the fire-free period required for shortleaf pine to develop resistance to topkill is variable and not well known, it likely is more resistant at smaller diameters than associated hardwoods, increasing the likelihood that fires would prove advantageous to accumulated shortleaf pine regeneration relative to hardwood associates (Stambaugh *et al.* 2007; Walker and Wiant, 1966). Associated oak species, especially post oak and blackjack oak (*Quercus*

marilandica) provide significant competition to shortleaf pine in these stands. Oaks can also accumulate in the understory by resprouting after fire, and they are less light-demanding than pines, so they may take advantage of smaller canopy gaps than pines. Given a sufficient fire-free period, oaks develop thick bark and become highly resistant to the effects of surface fires, allowing them to recruit to the overstory and persist in the stand through periods of more frequent fire (Arthur *et al.* 2012).

The lower flammability of shortleaf pine and oak foliage relative to that of longleaf pine and the dissected landscape of the region may have caused greater variability in the natural fire return interval (Komarek, 1974). In addition, Gerland (2022) synthesizes from multiple sources how native peoples of this region, especially the Hasinai of the Caddo Confederacy, used fire as a management tool to achieve their objectives of maintaining open forests with rich herbaceous understories, hard-mast bearing hardwood trees, and soft-mast bearing shrubs. These natural and anthropogenic factors could provide varied fire-free periods to maintain different elements of this complex mixedwood forest type. Extended periods of frequent fire may have reduced the abundance faster-growing hardwood competitors (Waldrop, 1987), while brief fire-free periods may have allowed the recruitment of shortleaf pine, and longer fire-free periods may have allowed recruitment of hardwood associates to the overstory (Arthur *et al.*, 2012). The intersection of soils, topography, natural disturbance, and human management maintained these systems.

Loblolly pine dominated uplands in an undulating landscape of swampy depressions and sandy ridges in the southwestern portion of the Pineywoods (Bray, 1904). Hardwoods were more abundant in the depressions, and loblolly pine occurred in

nearly pure stands on the ridges (Bray, 1904). This is the region known as the “Big Thicket” of Texas (Bray, 1904). The native Bidai people of this region were less active in the use of prescribed fire as a management tool than the Hasinai, thereby favoring loblolly pine (Sjoberg, 1951). While pole-sized and mature loblolly pines are resistant to mortality from fire, and fire creates a favorable mineral seedbed for loblolly, it is less well-adapted to frequent fire regimes than shortleaf or longleaf pines (Baker and Langdon, 1990; Komarek, 1974). Loblolly pine does not resprout as a seedling, meaning that given a frequent fire regime, loblolly pine will not accumulate as advanced regeneration (Baker and Langdon, 1990). However, given infrequent fire, thick-barked mature loblolly pine readily survive fire and regularly produce large seed crops, allowing them to capitalize on favorable seedbeds when they occur (Baker and Langdon, 1990). Loblolly pine’s rapid growth rate in uplands and lowlands makes it more competitive with oaks than shortleaf or longleaf pines, even in this region of lower fire-frequency (Baker and Langdon, 1990; Bray, 1904). Loblolly pine occurred nearest the gulf coast, exposing it to more wind disturbance than the shortleaf and longleaf dominated systems, as illustrated by a destructive windstorm reported by Bray (1904). While pine dominated, the historical loblolly pine-oak forests of the southwestern Pineywoods provided much different habitat than the more open woodland and savanna ecosystems typical of shortleaf and longleaf pines.

Ecological Concepts in Restoration

Ecological restoration is defined by the Society for Ecological Restoration (SER) as “The process of assisting the recovery of an ecosystem that has been degraded,

damaged, or destroyed.” (Clewell *et al.* 2004). Restoration is motivated by the ecological imperative to protect and promote threatened species and landscapes, as well as aesthetic, cultural, economic, and other motivations. Human values derived from ecosystems and the goods and services they provide are the fundamental inspiration for restoration activities, while scientific knowledge and criteria are used to carry out and evaluate management for restoration (Davis and Slobodkin, 2004; Martin, 2017). The ability of the system to be self-replacing, or autogenic, is regarded as a core element of a “restored” ecosystem, which necessitates the presence of species and functional groups and their reciprocal relationship with key structural processes for the sustenance of that system (Holling, 1992; Clewell *et al.* 2004). Reference ecosystems include intact contemporary or recorded historical ecosystems that share climatic, edaphic, topographic, cultural, and other attributes with the degraded, damaged or destroyed ecosystem such that they can serve as an example of that system in a healthy, functioning state (Clewell *et al.* 2004). The success of restored ecosystems is evaluated against these reference systems in terms of composition, function, and developmental trajectory (Clewell *et al.* 2004).

Although it is well understood that reference systems ranged in composition, disturbance regime, climate, and other characteristics over time, given spatially and temporally extensive direct and indirect anthropogenic alterations of ecosystems across the globe, even many reference systems now likely lie outside their historic range of variability in some or all these characteristics (Hobbs *et al.* 2006; Landres *et al.* 1999; Seastedt *et al.* 2008). As such, managers are tasked with restoring “novel ecosystems” with only historical records of intact examples, or less altered “novel ecosystems” as benchmarks (Hobbs *et al.* 2006; Willard and Cronon, 2007). These novel systems and

circumstances may require restoration actions outside of simply reinstating the historical species composition or disturbance regimes and will require adaptive management strategies over time as these new and not fully understood systems continue to develop (Seastedt *et al.* 2008). Despite new and changing conditions, considerable existing knowledge of the species, functions, and processes that drove historical ecosystems provide helpful guides to preventing further deviation from reference ecosystems while knowledge is gained about novel ecosystems and the effects of management on them (Jackson and Hobbs, 2009).

Restoration objectives are often centered on moving the ecosystem back into its theoretical historical or natural range of variability, as this range of variability is expected to promote or preserve characteristics of interest such as critical habitat and other ecosystem services (Landres, 1999). Intensive management action will likely be required until the ecosystem is restored to its natural range of variability, whereafter management that replicates the historic management and disturbance regimes must be upkept in a “natural variability-based maintenance approach” (Landres, 1999). Depending upon the condition of the ecosystem at the outset of management activity, intensive management may be required for decades (Landres, 1999). The degree to which human action was a key factor in maintaining specific community types is a matter of debate, and the ability of a system to maintain itself without specific human interactions over time will require site and community-specific monitoring and knowledge-building (Seastedt *et al.* 2008; SER, 2004; Vale, 1998).

Ecosystems are dynamic but may be relatively autogenic depending upon species composition, disturbance regime, and other abiotic and biotic factors, leading to the

potential for multiple “stable states” or successional trajectories in a given ecosystem depending on those variables (Holling, 1973; Watt, 1947; White and Pickett, 1985). As disturbance regimes or other factors including those biotic (e.g., species invasions) and abiotic (e.g., climatic variability) change, ecosystems can transition from one stable state or trajectory to another (Levine *et al.* 2003; Schwantes *et al.* 2017). Ecosystems may undergo gradual or sudden changes in composition and function, which are associated with the ecosystem crossing a threshold after which their tendency is to maintain a new composition and trajectory along with new functional traits (Holling, 1973).

Ecosystem thresholds are consequential in the practice of restoration, because once crossed the functional traits of the new ecosystem state are self-reinforcing (Groffman *et al.* 2006). For this reason, guiding a system back across an abiotic or biotic ecosystem threshold requires a more intensive intervention than preventing the ecosystem from crossing the threshold in the first place (Groffman *et al.* 2006). In some cases, the alterations that led the system to cross a threshold may create changes that can not be reversed or remediated, necessitating novel management approaches to rehabilitate key functional processes and ecosystem services within the new and persistent system (Groffman *et al.* 2006; Hobbs *et al.* 2006).

Empirical information regarding the mechanisms that drive threshold behavior is limited, which leaves managers to practice adaptive management informed by historical functions and conditions until desired functional traits are restored and sustainable (Groffman *et al.* 2006). Martin and Kirkman (2009) applied this approach to restoring depressional wetlands embedded in a longleaf pine ecosystem. In this case, the depressional wetlands were thought to be historically dominated by a diverse mix of

herbaceous species that were maintained by the same frequent fires that maintained the adjacent uplands. However, a change in the disturbance regime allowed for the establishment of fire-suppressing oak species in the center of the wetlands, which created a feedback loop allowing these oak species to exclude fire and dominate the wetlands, extirpating most of the herbaceous wetland species. The reinstatement of the historic disturbance regime in the adjacent uplands was not sufficient to reverse the biotic change in the depressional system, so the authors conducted a study to evaluate the effect of more intensive intervention by mechanically and chemically removing all oaks and suppressing their regeneration. The more intensive intervention appeared to be successful in moving the system back across the threshold to a fire-maintained, herbaceous wetland ecosystem (Martin and Kirkman, 2009). The significant biotic alteration of fire-adapted communities is a widespread phenomenon, and extensive research is being done to attempt to understand how thresholds suppressing the reinstatement of a fire-maintained system may be overcome using varied treatment intensities (Nowacki and Abrams, 2008; Jin *et al.* 2018; Schweitzer *et al.* 2016).

The study of the interactions between organisms in ecosystems is dominated by the investigation of competitive relationships; however, facilitative relationships have garnered increasing interest given their potential for improving restoration efforts and understanding of ecosystem dynamics, species persistence, and other concerns (Brooker, 2008). Facilitation is “an interaction in which the presence of one species alters the environment in a way that enhances growth, survival or reproduction of a second, neighbouring species.” (Bronstein, 2009). The facilitation may be direct: Species A changes the environment in a way that directly benefits Species B, or indirect: Species A

changes the environment in a way detrimental to Species C, reducing Species C's negative effect on Species B (Species B indirectly benefits from changes induced by Species A) (Brooker, 2008; Miller, 1994). Facilitation has long been a subject of interest in ecology, however, the growing and urgent need for strategic improvement to restoration practices has initiated additional research into its applicability to the field (Pearson, 1914; Brooker, 2008).

A facilitation concept of particular interest and utility in the field of restoration is that of “nurse plants”, plants which modify the environment in such a way that they allow for the establishment or growth of other species (Niering *et al.* 1963; Gómez-Aparicio *et al.* 2004). Direct facilitation of this fashion is thought to be most common in high-stress environments, such as arid environments with extreme water stress, as laid out in the stress gradient hypothesis of Bertness and Callaway (1994). Alternatively, the primary form of facilitation on sites of higher productivity and diversity is likely indirect facilitation and may buoy the diversity of these systems by reducing the level of competitive exclusion (Brooker, 2008; Laird and Schamp, 2006). An understanding and promotion of nurse plants is suggested for the restoration of harsh environments but not necessarily for higher-productivity sites (Gómez-Aparicio *et al.* 2004; Padilla and Pugnaire, 2006). However, given that indirect facilitation is less well understood than direct facilitation, and that indirect facilitation may be the primary sort of non-hierarchical plant interaction in higher productivity communities, it is likely a productive pursuit to investigate the potential to exploit indirect facilitative effects in the restoration of degraded diverse and high productivity sites (Brooker, 2008). Interspecific interactions in diverse ecosystems will be extremely difficult to disentangle, so developing a broad

base of knowledge about the indirect facilitation effects in productive systems will likely be very difficult. In the meantime, indirect facilitation should be included when interpreting the ecosystem effects of management actions in order to properly implement an adaptive management regime (Brooker, 2008).

Management for the Restoration of Pineywoods Uplands

Practices commonly used in the restoration of forest communities such as those of the Pineywoods include timber harvesting, reintroducing prescribed fire, applying herbicides, mechanically controlling vegetation, and planting desired species (Stanturf *et al.* 2014). Practices are limited by their financial and operational feasibility, as well as by their social acceptability (Landres, 1999). For example, restoring fire to ecosystems adjacent to highways can present safety concerns, and restoring stand-replacing catastrophic fire to systems in which they historically occurred may be unsafe or socially unacceptable (Landres, 1999; Seastedt *et al.* 2008).

Foresters have long used silvicultural practices like harvesting and natural or artificial regeneration to affect the species composition and density of forest stands (Nyland, 2016). Regeneration harvesting can occur across a gradient of intensities and spatial extents, depending on the management objective. At one end of the spectrum is clearcutting—a silvicultural practice that removes the entire tree community to create a fully exposed site benefitting the regeneration of species that require characteristics of open sites, like abundant sunlight, to regenerate (Nyland, 2016). At the other end of the spectrum is single-tree selection harvesting, which involves the creation of small gaps by the removal of individual trees from the forest canopy and is better suited to the

regeneration of shade-tolerant species (Nyland, 2016). Between the extremes of a fully exposed and minimally exposed site are many harvesting methods that vary in their spatial arrangement and extent and can be selected based on the desired species and age structure. While regeneration harvests create the appropriate conditions for regeneration, thinning is a silvicultural treatment that is applied to control stand density and composition while not explicitly targeting regeneration.

Silvicultural treatments involving harvesting, thinning, and regeneration practices are well suited to the task of restoration, since a primary consideration in many restoration efforts is the re-establishment of historical species composition, structure, and function (Muzika, 2017). Artificial regeneration by seeding or planting nursery-grown stock can be necessary where propagules of desired species are absent or insufficient to practically recolonize a site (Aschenbach *et al.* 2010; Looney *et al.* 2015). Harvesting can be used to alter understory light conditions to favor the natural or artificial regeneration of desired woody and herbaceous plant species as well as animal species (Hayford *et al.* 2023; Looney *et al.* 2015; Van Lear *et al.* 2005). Herbicide application can reduce the abundance of species anachronistic to the reference condition, including invasive species and off-site species (McMahon *et al.* 1993). Site preparation techniques including prescribed fire and mechanical scarification can replicate natural disturbances that created appropriate seedbeds for species like pine and reduced vegetative competition in the understory (Löf *et al.* 2012; Vose *et al.* 1995). While altering hydrology through site preparation methods like bedding can be used to increase the productivity of a site in plantation forestry, drainage or impoundment can also be used to restore hydrological regimes disrupted by road construction, the loss of ecosystem engineers like beavers, and

other manipulations of the environment (Catton *et al.* 2007; Law *et al.* 2017; Wohl, 2021).

In the early stages of professional forestry, fire was considered a purely detrimental and destructive force, but as fire's role in the maintenance of many desirable communities became clear over time, it became an important tool for traditional forestry and restoration (Bray, 1904; Foster, 1917; Heyward, 1939; Little and Moore 1949; Wall *et al.* 2019). Intentional burning of forests varied in application through time, from mixed intervals applied by indigenous peoples and very frequent fire applied by settlers for land clearance and pasture management, to targeted applications by professional forestry practitioners in the modern era (Pyne, 2017; Guyette *et al.* 2002; Ryan *et al.* 2013). Today, fire is understood to be a driving force in many ecosystems, especially fire-adapted southern pine ecosystems such as those dominated by longleaf and shortleaf pine (Guldin, 2019). Fire can play an important role in producing mineral seedbeds conducive to pine reproduction, reducing woody debris that increases the danger of severe fire and may harbor pests and pathogens, and controlling the composition and density of forest understories and overstories (Knapp *et al.* 2015; Wade and Lundsford, 1990). However, while seasonality and burn weather conditions can be planned for to target vulnerabilities of undesirable species or promote desired species, the nuances of simultaneously managing for many taxa with fire are not well understood (Arthur *et al.* 2012; Hamman *et al.* 2011; Stambaugh *et al.* 2007). While fire is now appreciated as a key functional trait of many systems, and thus an important component of restoration in those systems, knowledge is limited and research to better understand how to successfully employ fire as a management tool in many contexts is needed.

The chemical or mechanical control of vegetation outside of timber harvesting is common for industrial forestry and has similar applicability in the restoration of desired species compositions and structures (Nyland, 2016). Extensive control of competition is an integral part of intensive southern pine silviculture, with the objective to reduce competition from associated hardwoods while maintaining the most productive pine plantation possible (Stanturf *et al.* 2003). Herbicide can be seen as preferable in this context due to the potential of some mechanical vegetation control, like root raking, to reduce plantation productivity, and others, like chopping, to result in vigorous resprouting in the understory (Knapp *et al.* 2008; Stanturf *et al.* 2003). While vegetation control is often employed in plantation forestry to eliminate competition and maximize growth of the target species, it can be applied in a diverse range of management scenarios and for diverse objectives (Shepard *et al.* 2004). Under very intensive management regimes, the use of herbicides and mechanical control can result in significant losses to biodiversity and habitat qualities (Miller and Miller, 2004). However, mechanical treatments can be used in conjunction with herbicides to treat aggressive invasive species to restore habitat quality and other ecosystem attributes (Pile *et al.* 2017). In addition, mechanical treatments like mastication can be used to restore structural attributes and prepare systems for the reintroduction of processes like periodic fire with reduced risk of catastrophic fire (Reiner *et al.* 2009). The use of chemical and mechanical vegetation control methods in natural landscapes is a contentious issue that generates some public concern, but it has garnered widespread use due to the flexibility and utility of both methods (Shepard *et al.* 2004). As with the great variety of harvest and thinning

applications employed by forest managers, chemical and mechanical vegetation control can be implemented in a variety of ways, with associated costs and benefits.

Reintroduction of fire, harvesting, and vegetation control are all widely used in the restoration of southern mixed pine-oak forests. Schweitzer *et al.* (2016) implemented thinning and prescribed fire treatments in conjunction to restore unmanaged loblolly pine plantations to mixed pine-oak forests but found that in the absence of additional vegetation control, achieving the desired species composition was challenging. In the Missouri Ozarks, harvesting, mechanical and chemical vegetation control, as well as prescribed fire were used to guide the restoration of an oak-dominated stand toward a more historically prevalent mixed shortleaf pine-hardwood system with positive initial results (Olson and Olson, 2016). Clabo and Clatterbuck (2020), after cluster-planting shortleaf pine, found that the combined effects of herbicide application and prescribed fire resulted in more desirable species composition than either of those treatments alone. Planting in conjunction with the reintroduction of frequent prescribed fire has been an important component of longleaf pine restoration, particularly in areas where mature trees are absent and cannot provide a seed source (McIntyre *et al.* 2018). These applications of silviculture in restoration demonstrate the importance, when planning restoration, of varied silvicultural interventions based upon the locality, existing stand conditions, and desired future composition and structure.

Chapter II – Introduction

The Pineywoods is a largely forested ecological region that spans much of East Texas, western Louisiana, southeastern Oklahoma, and southern Arkansas. The region is composed of a mosaic of upland forests dominated by pine and mixed pine-hardwood types, dissected by rich bottomland types on flats along rivers and drainages (LBJ School of Public Affairs, 1978; Van Kley, 2020). Historically, fires in the uplands of the Pineywoods maintained largely pure stands of longleaf pine (*Pinus palustris* Mill.) in areas with the most frequent fire regime grading to stands of mixed composition including longleaf pine, shortleaf pine (*Pinus echinata* Mill.), loblolly pine (*Pinus taeda* L.), and oaks such as southern red oak (*Quercus falcata* Michx.), post oak (*Quercus stellata* Wangenh.), and blackjack oak (*Quercus marilandica* Muenchh.) (LBJ School of Public Affairs, 1978). The historic fire regime that maintained these mixed pine-hardwood forests is not well known, but the fire return interval has been estimated to vary between one and six years (Stambaugh *et al.* 2014). It is estimated that over 49,000 km² of the East Texas Pineywoods were composed of this forest type prior to European settlement (LBJ School of Public Affairs, 1978; Stambaugh *et al.* 2014). The open structure of these fire-maintained ecosystems allowed for the development of diverse ground flora and served as ideal habitat for the cavity-nesting red-cockaded woodpecker (*Leuconotopicus borealis* Vieillot.) (Texas Parks and Wildlife Department).

Boggy Slough Conservation Area (BSCA) is a roughly 7700-hectare complex of mixed pine-oak upland forests and hardwood-dominated bottomland forests along the Neches River in the Pineywoods of Trinity and Houston Counties, Texas, USA. The land

was acquired in 1902 by the founder of the Southern Pine Lumber Company, T.L.L. Temple. Since that time the land has been managed for multiple objectives including timber production, wildlife and forest management research, and two white-tailed deer (*Odocoileus virginianus* (Zimmermann) hunting clubs. However, the Temple family's connection to and investment in Boggy Slough never changed, and, in recent years, Arthur "Buddy" Temple III and the Temple Foundation acquired the land from International Paper Company and created the Conservation Area (T.L.L. Temple Foundation). In keeping with the BSCA's founding principles, the Temple Foundation manages the forests for timber production, restoration of Pineywoods natural communities, education and outreach, and quality white-tailed deer habitat (S. Jack, personal communication, October 11, 2021).

Since European settlement, large portions of the Pineywoods, including portions of Boggy Slough, have been converted to pastureland and intensive plantation management, especially of loblolly pine (Rosson, 1992). Fire regimes have been dramatically altered from their historic condition through a policy of fire suppression implemented to control wildfires following the timber harvesting boom of the late 1800s and early 1900s (McWilliams and Lord, 1988). Management history in the Pineywoods, including fire suppression, has led to the development of dense understory and midstory vegetation, a departure from the more open vertical and horizontal structure in the historic forests of the region (Oswald *et al.* 2017). Thickets of yaupon holly (*Ilex vomitoria* Sol. ex Aiton.) and increasingly abundant species like sweetgum (*Liquidambar styraciflua* L.) and invasive exotic plants like Chinese tallow (*Triadica sebifera* (L.) Small) constitute significant competition to the regeneration of upland oaks and pines and

may alter the behavior of fire, a key element to the maintenance of these fire-adapted communities. Formation of yaupon holly (yaupon) thickets and encroachment by species historically restricted to moist forests, like sweetgum, have degraded upland Pineywoods forests by altering forest structure, complicating regeneration, and reducing appropriate habitat for endemic plant and animal species, particularly the red-cockaded woodpecker (Macey *et al.* 2016).

Managers at BSCA are interested in restoring contemporary forests to their historical upland pine-oak woodland composition and structure. Most of these forests are naturally regenerated, mixed stands of loblolly pine, shortleaf pine, southern red oak, and post oak in the overstory, while less historically abundant species including yaupon holly and sweetgum have become established in the understory and midstory.

Management and restoration of the native pine-oak forests of the Pineywoods is challenging due to the varied silvics of component species (Kabrick *et al.* 2020). These “mixedwood” forests, defined as forests of hardwoods and softwoods in which neither exceeds 75-80% of the stand’s composition (Helms, 1998), are the subject of significant research interest due to the lack of empirical information on best practices in balancing these competing silvics (Kabrick *et al.* 2020; Kenefic *et al.* 2021). In the Pineywoods, the oaks exceed the pines in shade tolerance, while the pines can more readily colonize areas after a severe disturbance due to their light seeds and fast early growth. Both the pines and oaks are adapted to fire. Fire prepares a mineral seedbed for pine seedling germination, and the sprouting ability of shortleaf pine and oaks allow them to persist through repeated fires. However, loblolly pine cannot resprout if top-killed by fire, and all three species require fire-free periods of different lengths to develop thick, fire-

resistant bark and crowns high enough to escape surface fires (Baker and Langdon, 1990; Stambaugh *et al.* 2007; Arthur *et al.* 2012). The existing closed-canopy forests with dense understories and midstories are poorly suited to the regeneration of both the softwood and hardwood components of these forests, but no single silvicultural treatment is the obvious choice for the restoration and maintenance of the historical woodland structure and composition.

Reaching Boggy Slough's management objectives in these forests is further complicated by competition from yaupon and sweetgum. These species change fire dynamics, as considered in discussions of "mesophication" (Nowacki and Abrams, 2008). Thereby, yaupon and sweetgum make the applicability of historical fire regimes in the restoration process of present-day forests, as opposed to the maintenance of restored forests, more ambiguous. Both species sprout aggressively after being cut or top-killed, necessitating the use of herbicides to kill the root systems (Mitchell *et al.* 2005). However, the broadcast application of herbicides may also impact desirable advance regeneration of shortleaf pine or oak and herbaceous vegetation. Shifts in species composition due to herbicide application may affect the fuel environment, and place advance regeneration-dependent oak species and, to some degree shortleaf pine, in an unfavorable competitive dynamic with more pioneering and light-seeded species such as sweetgum, yaupon, and loblolly pine (Stambaugh *et al.* 2007; Larsen and Johnson, 1998).

The presence of yaupon and sweetgum in these stands, however, may have the potential to facilitate the establishment and growth of the desired pine and oak species. By inhibiting the spread and intensity of fires, yaupon and sweetgum may allow small pines and oaks to escape topkill while they themselves, having little adaptation to fire, are

topkilled. Large, overtopping yaupon and sweetgum may also shield smaller pines and oaks from herbicide applications and thereby facilitate greater responses to release than they could demonstrate in the absence of these shielding plants.

To the goal of restoring native open-structured forests of mixed species, Boggy Slough's stands are being rehabilitated using a series of treatments including a harvest to favor desired oaks and pines followed by a dormant season prescribed burn, an herbicide application, and a growing season prescribed burn. These treatments are intended to eliminate the abundant understory yaupon holly and sweetgum and to offer a competitive advantage to regenerating desirable, fire-adapted oak and pine species (Abrams, 1992; Keeley, 2012). However, neither the current abundance and distribution of desired species nor the effects of these treatments individually and in combination on desirable species and competitors are well known. To better prescribe treatments for the restoration of mixed pine-oak forests through thinning and release from competitors, more thorough understanding of the effects of each step of the prescription is needed. This study will focus on the regeneration dynamics across the prescription's steps and alternatives. The study's results are intended to provide insights into the regeneration phase of the silvicultural system being implemented in the mixedwood forests of BSCA, to which future management and research refining regeneration practices and investigating best tending and harvesting practices can be added.

Specifically, this study aimed to:

- 1.) Determine the pre-treatment stem counts of the four species groups of interest: pines, oaks, yaupon holly, and sweetgum in four height classes: 1-49 centimeters, 50-99 centimeters, 100-136 centimeters, and the midstory, and how stem counts

change through the three treatment series. A treatment series without an herbicide application and with an herbicide application delayed by one year were also evaluated. We expected that treatments involving prescribed fire would promote fire-adapted oaks and pines while herbicide treatments would not have a selective effect, thereby reducing the abundance of all the species.

- 2.) Better understand the drivers of the patterns seen in Objective 1 by investigating rates of topkill, mortality, and growth following each treatment. Prescribed fire was expected to cause higher rates of topkill and mortality among yaupon and sweetgum than oak and pine, while treatment with herbicide was expected to increase mortality and reduce growth across all species.
- 3.) Describe the fine-scale drivers of variability in the results of Objective 2 by evaluating the rates of fuel consumption, likelihood of topkill or mortality, and the likelihood of stem char, reflecting the effects of local environmental variables and potential facilitation of oak and pine survival and growth by yaupon and sweetgum competitors. Greater densities, sizes, and closer proximity of yaupon and sweetgum were expected to moderate fire behavior, and subsequently topkill and mortality rates in a way that would benefit oak and pine more than yaupon and sweetgum.

Chapter III – Methods

Study Design

This study was located on Boggy Slough Conservation Area (BSCA) in Trinity and Houston Counties, Texas, USA. Due to recent management, there were several stands in various stages of the restoration prescription and some stands that had received variations of the standard prescription. These stands presented an opportunity to isolate the effects of the various elements of the prescription in altering the trajectory of the stands. To accomplish this, a chronosequence was created. The chronosequence study design is advantageous because it substitutes space (in this study, the several stands previously mentioned) for the time that would have been required for a longitudinal study on an individual stand divided into several treatment combinations. Through the chronosequence, the two-year study addressed initial trends in regeneration demographics and dynamics over four years and three trajectories (“standard herbicide prescription”, “no herbicide prescription”, “delayed herbicide prescription”; described below). This approach assumed that all stands had physical attributes and management histories sufficiently similar that their structure and composition would have been similar if not for the effects of the treatments applied. Given the information, time, and other resources available, the chronosequence structure was a viable choice to produce information regarding initial regeneration demographics and dynamics for forest managers.

The first treatment in the restoration prescription was a winter harvest to reduce overstory basal area within the range of approximately 9 m²/ha to 14 m²/ha. During the following winter, approximately one year later, the stands were treated with a dormant

season prescribed burn for slash reduction and to promote regeneration of fire-adapted species. Near the end of the growing season following the dormant season prescribed burn, an herbicide application was used with the objective of reducing abundance or vigor of yaupon and sweetgum sprouts and thickets. The herbicide was applied by skidder-sprayer and on a per-hectare basis included 0.50 kilograms acid equivalent of glyphosate, 0.21 kilograms acid equivalent of triclopyr, and 0.008 kg acid equivalent of saflufenacil with 0.38 liters per hectare of Elite Supreme Surfactant (Red River Specialties, Inc., Shreveport, LA, USA). At the beginning of the growing season following the herbicide application, just as sweetgum began to leaf out, the stands were treated with a growing season prescribed burn. Growing season prescribed burns were expected to provide better control of woody plants than dormant season prescribed burns. This series of treatments represents the “standard herbicide prescription”. The “no herbicide prescription” was the same in timing and treatments but did not involve any herbicide application. The “delayed herbicide prescription” was the same in treatments as the standard herbicide prescription, but the herbicide application and dormant season prescribed burn were delayed by one year.

Starting Condition: Naturally regenerated stand	Year 1		Year 2		Year 3		Year 4	
	Dormant	Growing season	Dormant	Growing season	Dormant	Growing season	Dormant	Growing season
Standard Prescription				Herbicide appl. 5* SA2a		Growing season burn SA2a 8* SA2a		
Delayed Herbicide Prescription						Herbicide appl. 7* SA3		Growing season burn SA3 10* SA3
No Herbicide Prescription		2* SA1b ↔	Dormant D o r m a n t			Growing season burn SA2b 9* SA2b		
No Action	1* SA1a	↔ SA1a	4* SA1b	↓ SA1b				
			3* SA1a	↓ SA1a				

Figure 1: Shows the standard restoration prescription and variants being studied at BSCA. Shared coloration shows times during which the alternate prescriptions share treatment histories and thus should share structures and compositions. Time since harvest is displayed across the top of table, and periods sampled in the chronosequence are denoted by the red symbols. Numbers and letters indicate in which Study Area data for that chronosequence stage were collected.

- 1* Understory and midstory species abundance and size distributions sampled and the chronosequence timestep with which they are associated.
- ↔ Denotes growing seasons for which growth and survival rates across species of interest are sampled by tracking individual saplings.
- ↓ Denotes point at which only seedling measurements were taken, no growth data collected.

Figure 1: Diagram indicating which stands represented each stage in the prescription for the three chronosequences, along with which seedlings were tracked to represent topkill, mortality, and growth effects of each treatment.

Study Sites

All study areas were located on “South Boggy Slough” in Trinity County, which had a larger proportion of stands originating from natural regeneration, whereas “North Boggy Slough” contained more forests of plantation origin (Figure 1, Figure 2). Nearly all Boggy Slough had experienced prescribed burning, but the exact history of burning varied across stands. Recent burning and other management history is described for each Study Area in the section that follows (Table 1).

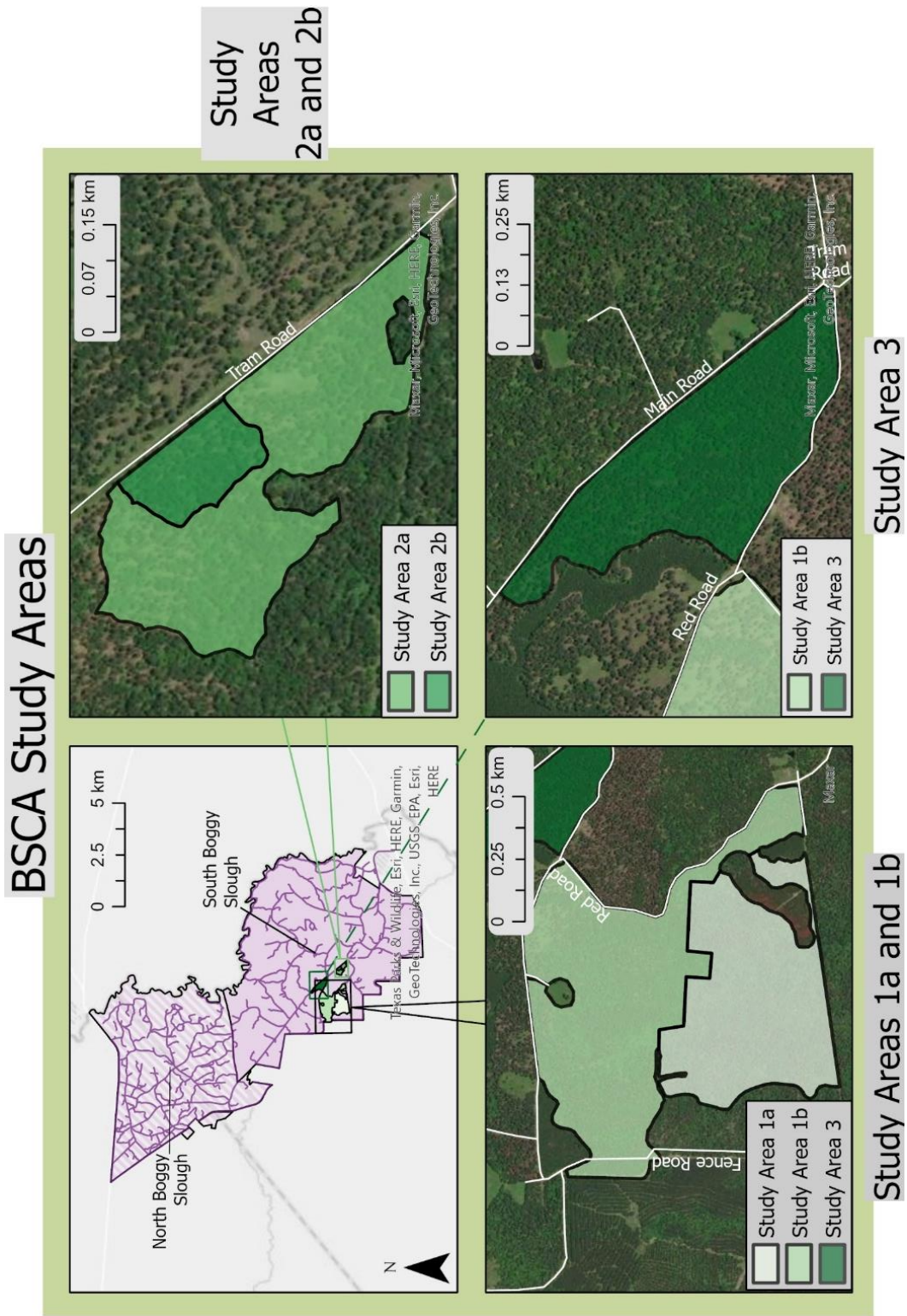


Figure 2: Maps depicting the locations of each study area in the context of all Boggy Slough, demonstrating the paired nature of Study Areas 1a and 1b as well as 2a and 2b.

Table 1. The area in hectares of each Study Area, their composition as described by the Soil Survey Staff, all historical management available in BSCA's provided GIS data, and management performed during the study. Superscripts indicate NRCS ESDs: 1 Loamy upland ecological site type; 2 Loamy claypan upland; 3 Terrace; 4 Southern sandy loam upland; 5 Clayey bottomland and Loamy bottomland.

Study Area	Area (ha)	Soil Series (% slope) (% of area) (Soil Survey Staff)	Previous Management	Contemporary Management
SA1a	46.8	Kellison loam (5-15%) ² (40.8%) Herty loam (1-3%) ² (44.1%) Fuller sandy loam (0-3%) ¹ (11%) Other ³ (3.9%)	Burns: April 2015; March 2017;	Dormant season prescribed burn (2023)
SA1b	64.4	Kellison loam (5-15%) ² (49.3%) Fuller sandy loam (0-3%) ¹ (25.8%) Penning v. fine sandy loam (0-2%) ¹ (11.3%) Other ^{2,3} (13.1%)	March 2018; April 2019	Harvest (2022); Dormant season prescribed burn (2023)
SA2a	9.6	Fuller sandy loam (0-1%) ¹ (44.5%) Herty loam (1-3%) ² (27%) Ozias-Pophers complex (0-1%) ⁵ (20.2%) Other ^{4,2} (8.1%)	Burns: May 2013 Feb. 2021 March 2021 Harvest: 2020 Dormant burn: 2021	Herbicide application (2021) Growing season prescribed burn (2022)
SA2b	1.8	Herty loam (1-3%) ² (39.4%) Fuller sandy loam (0-1%) ¹ (31.3%) Ozias-Pophers complex (0-1%) ⁵ (29.1%)	Burns: May 2013 Feb. 2021 March 2021 Harvest: 2020 Dormant burn: 2021	Growing season prescribed burn (2022)
SA3	16.5	Penning v. fine sandy loam (0-2%) ¹ (77.4%) Fuller fine sandy loam (1-3%) ¹ (14.5%) Other ² (7.9%)	Burns: April 2015; April 2019; Feb. 2021 Harvest: 2019	Herbicide application (2021)

Study Area One (SA1) was a 111.2 ha stand that received its first treatment in the restoration prescription in Winter 2022. The first treatment, a harvest, took place during the early months of 2022. Study Area One was divided into Study Area 1a (SA1a) and Study Area 1b (SA1b) due to roughly half of the stand having been marked for harvest (generally the north half) and half having had no planned harvest (the south half). SA1 was composed of two stands delineated by Boggy Slough's former parent corporation, stands 5019 and 5020, and was classified as "Natural Pine". The stand's upland overstory was a heterogeneous mix ranging from areas dominated by loblolly pine and shortleaf pine to those with a more significant component of upland oak species, especially southern red oak, post oak, and blackjack oak. More moisture-demanding species grew near drainages that occurred throughout the area. The regeneration layer varied widely from areas of heavy cover by competitors of interest, especially yaupon, to those where yaupon and sweetgum were scarce.

SA1a served to address both pre-harvest conditions and regeneration demographics as well as the survival, topkill, and growth rates of species of interest in an unharvested condition. SA1a also furnished some information on dormant season prescribed fire behavior in an unharvested stand. Meanwhile, SA1b provided data representing demographic changes and survival, topkill, and growth rates following harvest as well as survival following dormant season prescribed burning, but before herbicide application. SA1b provided the same type of fire behavior data as SA1a but in relation to a harvested stand.

Study Area Two (SA2) was an 11.4 ha portion of Stand 5019 that was classified as "Natural Pine" and was harvested in 2020. The Study Area was divided in two: Study

Area 2a (SA2a), which received an herbicide application on the standard schedule, and Study Area 2b (SA2b), which had the same management history, but received no herbicide application. This Study Area was further along in the restoration prescription than SA1, since the harvest and prescribed burn were carried out in the spring of 2021 and foliar herbicide application was done during late summer 2021. The overstory was a heterogeneous mix of pines, oaks, and other hardwoods, while the understory and midstory contained both desirable species and varying densities of yaupon and sweetgum competition.

SA2a provided data regarding regeneration demographics at the time of herbicide application, growth rates, topkill rates, mortality rates, and demographic information following herbicide application and growing season prescribed burning. Growing season prescribed burn fire behavior data was also collected in SA2a. SA2b provided data regarding growth dynamics and regeneration demographics as well as fire intensity at the same points in time as SA2a but without any herbicide application.

Study Area 3 (SA3) was a 16.5 ha portion of Stand 5019 that was classified as “Natural Pine” and was harvested in early 2019. This Study Area was not subdivided. As with Study Areas One and Two, it was a heterogeneous mix of overstory pine and oak with an understory and midstory that included areas of varying seedling and sapling abundance. This stand received a foliar herbicide application at the same time as SA2a, however it was distinguished by the fact that harvesting took place one year earlier than on SA2. The result was that SA3 represented the standard prescription with its herbicide application delayed by one year.

SA3 provided data regarding regeneration demographics two years following harvest and dormant season burning as well as growth rate, topkill rate, mortality rate, and demographic information following herbicide application and growing season prescribed burning. SA3 also provided growing season prescribed burn behavior data.

Plot Generation and Selection

Intensive sampling plots were randomly located in Study Areas 2a, 2b, and 3 using ArcGIS Pro by ESRI. First, a smaller version of each Study Area was created using the “Buffer” tool to create a buffer of twenty meters within the boundaries. This buffered polygon served as the constraining feature for the “Create Random Points” tool, thereby keeping all random points at least twenty meters from any edges to minimize edge effects. The “Create Random Points” tool was used to generate thirty random points within the buffered SA2a and SA3 as well as fifteen random points in the buffered SA2b. All random points were required to be generated at least twenty meters from any others to avoid overlapping overstory plots. These plots were ranked by using a Texas Instruments TI-83 Plus graphing calculator with a random seed to generate random numbers between one and thirty for SA2a and SA3 or between one and fifteen for SA2b. Plots were installed in the order generated by the random number generator. Six plots were installed in SA2a, five plots in SA2b, and seven plots in SA3.

Since SA1 had not yet been homogenized by the effects of harvesting, and due to the larger and more heterogeneous management history of the stand relative to SA2 and SA3, the plot selection process differed in this stand. Pre-harvest data on overstory, understory, and midstory data were collected to constrain the selection of plots to those in areas with similar composition and structure to SA2 and SA3.

To collect the data used to characterize the plots in SA1, a grid and sampling locations were generated using ArcGIS Pro by ESRI. The grid was created using the “Create Fishnet” tool and had cells that were one hectare in size. Points were regularly spaced 100 meters apart in the North/South and East/West directions, producing a grid of one sampling point per hectare. Due to the irregular shape of the Study Area, some sampling points fell near edge features (roads, fields, etc.). To reduce the impact of edge effects, sampling points which fell within 25 meters of an edge feature (Figure 3) were moved back perpendicular to the edge for a distance equal to one half the distance between the edge and the next grid cell (Figure 4). A web map was created for navigation in the field and a form was created for recording data in the field.

Pilot data collection was completed in January of 2022. At each sampling point overstory and understory data were recorded. Overstory data were collected using a variable-radius prism plot (10 BAF prism). The species and diameter at breast height (DBH; 1.37 m above the ground) of each “in” tree was recorded to aid in characterizing the species composition, basal area, and trees per acre by species across the Study Area. Understory sampling was carried out using a 1x5 meter belt transect, offset from the prism plot center by two meters to the east. The transect ran north to south. Within the transect, the species and height of each woody plant under 1.37 meters tall were recorded and the DBH and species of all individuals greater than 1.37 meters tall and less than 11.43 cm DBH were recorded.

The plots used for more intensive sampling as a part of the chronosequence in SA1 were selected by using the pilot data to stratify the plots into eight categories. These categories were defined by whether they fell into the area marked for harvest or not,

whether they had relatively high ($BA > 20.7 \text{ m}^2/\text{ha}$) or low ($BA \leq 20.7 \text{ m}^2/\text{ha}$) overstory basal area, and whether they had high or low levels of competition from yaupon and/or sweetgum. A high level of competition was defined by greater than one midstory yaupon or sweetgum and a low level of competition was defined by one or fewer midstory yaupon or sweetgum in the 1x5 meter belt transects surveyed during the collection of pilot data. After stratification the plots were ranked using Microsoft Excel's "RAND" function to generate random numbers associated with each plot within a category, followed by the "INDEX" and "RANK" functions together to list the plots in each category in random order. Plots were installed in the order ranked and if the plot was deemed unsuitable in the field (ex. plot falls within a log landing), sampling was moved down the list in sequential order. Eight plots were installed in each SA1a and SA1b.

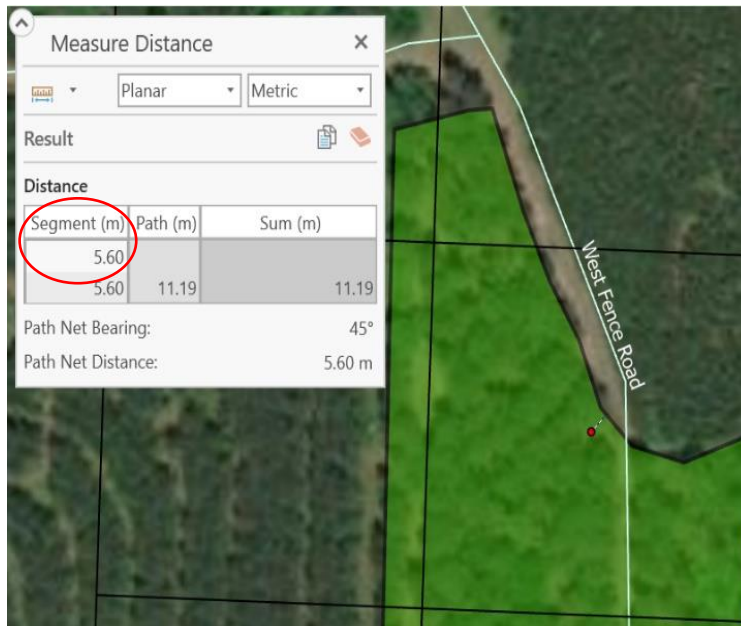


Figure 3: Map showing plot location less than 25 meters from an edge feature, in this case a road. Sources: Basemap: Esri, Maxar, EarthStar Geographics, and the GIS User Community. Polygons: Acorn Outdoors.

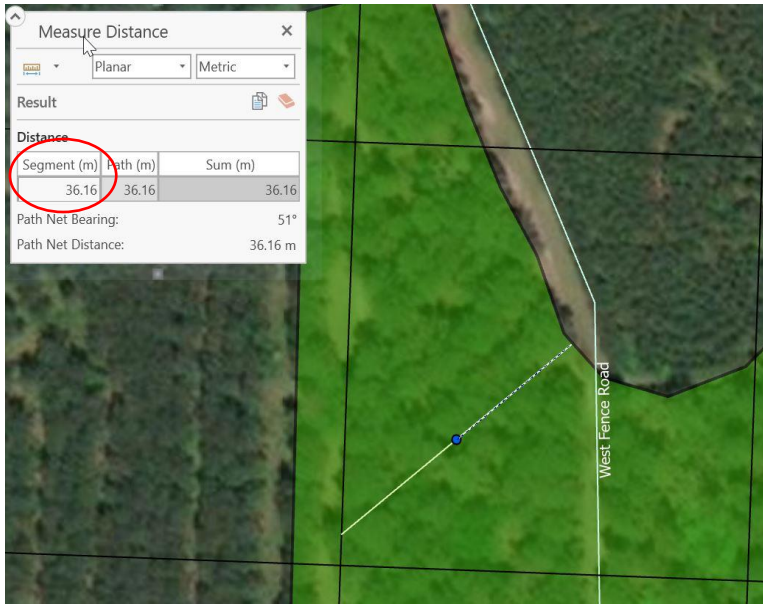


Figure 4: Map showing new plot placed at the midpoint between the edge feature and grid cell boundary, at least 25 meters from any edge features. Sources: Basemap: Esri, Maxar, EarthStar Geographics, and the GIS User Community. Polygons: Acorn Outdoors.

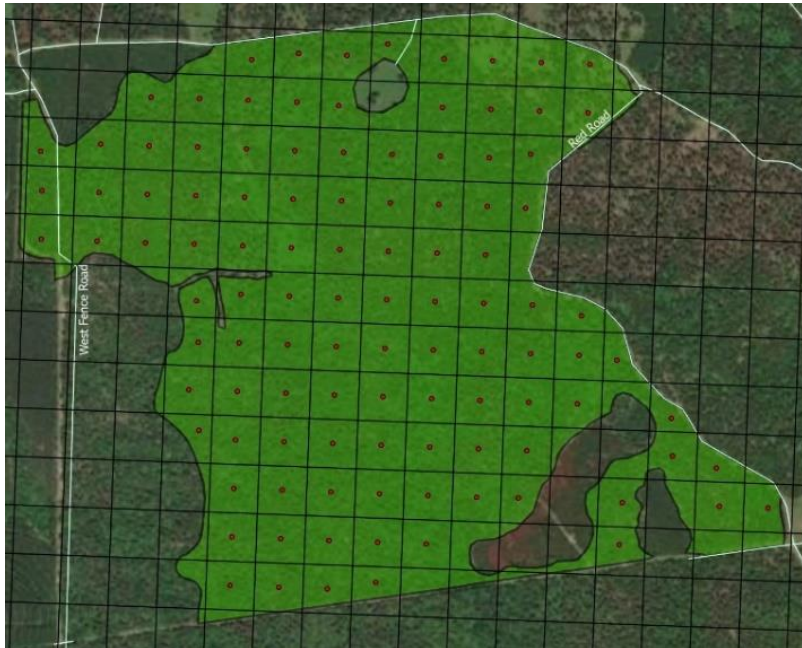


Figure 5: Map showing the corrected plot locations for all of Study Area 1. Sources: Basemap: Esri, Maxar, EarthStar Geographics, and the GIS User Community. Polygons: Acorn Outdoors.

Data Collection

Overstory Sampling

The overstory at each plot was sampled in a 1/20th hectare (radius= 12.62m) fixed-area circle plot. The species and DBH of each tree greater than 11.43 cm DBH were recorded to the nearest one tenth of a centimeter. Overstory trees were sampled only once, in April and May of 2022.

Midstory and Understory Demographics Sampling

Midstory and understory sampling was done in two 1/200th hectare (radius= 3.99m) subplots at each sampling location, offset from the plot center by six meters to the east and six meters to the west. Within each subplot, the DBH and species of all midstory (DBH≤11.43) stems were recorded. Additionally, a tally of all seedlings and saplings by species or genus in three height classes (1: 0-50 cm; 2: 50-100 cm; 3: 100-137 cm) was recorded. Midstory and understory sampling was performed in the spring of 2022 and resampled following the 2022 growing season.

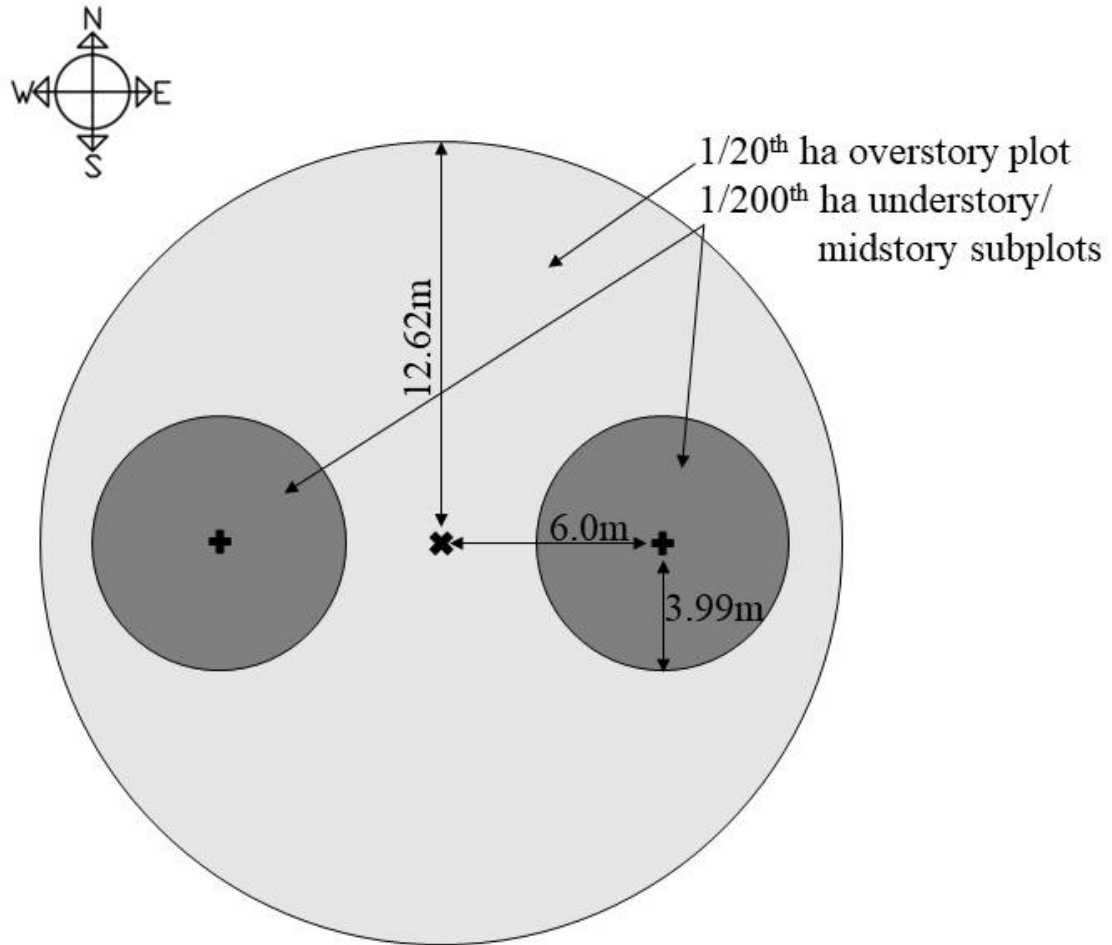


Figure 6: Plot layout for overstory, midstory, and understory sampling in all Study Areas.

Tracked Seedlings Sampling

The same plots as in the demographics data collection were used as the starting point for locating and tagging seedlings to be tracked in each Study Area. Within each plot, up to 24 seedlings were tagged and tracked to compare the outcomes of treatments based on 1) species groups (four levels), 2) initial height class (three levels), and 3) local density (two levels). The four species groups of interest were oaks, shortleaf pine, yaupon holly, and sweetgum, with up to six individuals of each species selected, depending on availability by initial height class and local density. Height classes included 0-50 cm, 50-

100 cm, and 100-150 cm. Local density could be either 'lone' or 'clumped', indicating the local crowding of other stems around the target individual. Lone seedlings were those growing without other significant woody vegetation surrounding them or significant impediments to the movement of a fire front. Clumped seedlings were growing in an area of greater woody plant density such that the environment appeared to have the potential to modify fire behavior. Lone and clumped conditions were determined according to the best judgement of the researcher. The seedling closest to plot center that met the criteria was systematically selected for sampling in all cases, provided that all selected seedlings were at least one meter away from each other. Table 2 provides a summary of the criteria used to avoid arbitrary or biased seedling selection. Aluminum tree tags were attached to pin flags and placed as close to the seedling as possible without being in contact with the stem.

All seedlings were measured in the spring of 2022 and resampled following the 2022 growing season. During the first sampling, the following information was collected: tag number, height class, distance from plot center (m), azimuth from plot center, species, groundline diameter (GLD, mm), height (cm), status (alive and undamaged, alive with logging damage, partial herbicide top-kill, top-killed), number of woody stems in a fifty centimeter radius, distance to nearest yaupon or sweetgum (cm; within two meters), height class of nearest yaupon or sweetgum, and GLD of nearest yaupon or sweetgum. Following the 2022 growing season, all seedlings were relocated and measured for status (alive, dead, top-killed and resprouted, partially top-killed), total height, GLD, distance to the nearest competitor, height class of the nearest competitor, and GLD of the nearest competitor.

Table 2. Selection criteria for tagged and tracked seedlings.

Tagged Seedling Selection Criteria	
1.	Choose the closest appropriate seedling to the plot center.
2.	Seedlings must be within 20 meters of plot center.
3.	Height class designation was determined based upon the height of the seedling as it stood naturally.
4.	Tagged seedlings were a minimum one meter of any other tagged seedlings.
5.	Clumped/lone designations were subjective and were determined by the same individual for all seedlings. These designations were meant to speak to the overall potential for surrounding vegetation to interfere with prescribed fire or herbicide treatments.
6.	Seedlings with abnormal growth form or damage (under fallen tree, deer browse or rub damage, etc.) were not tagged.
7.	The nearest competitor must be a yaupon or sweetgum and must be within two meters of the selected seedling. If none occur in this radius, none were recorded.
8.	Nearest competitor must be of a different individual or sprout clump, but the number of woody stems may include other individuals and stems of the same sprout clump.

Prescribed burn sampling

Prior to each prescribed burn, a subset of tagged seedlings were paired with a 1.8 meter type-K thermocouple (bead diameter approximately 1.5 mm) and 4-Channel HOBO Thermocouple Datalogger (Onset Computer Corporation, Bourne, MA, USA) to collect data on convective air temperature near the seedling's base during the burn. The dataloggers recorded thermocouple temperature once per second. Preference was given to seedlings in close enough proximity to each other to allow one centrally buried datalogger to record thermocouple readings from multiple seedlings. Thermocouples were balanced across "lone" and "clumped" seedlings to the extent possible.

Post-burn Sampling for Fire Intensity

Following the growing season prescribed burns in SA2a, SA2b, and SA3 as well as the dormant season prescribed burn in SA1a and SA1b, all tagged seedlings were relocated and sampled for fire effects. First, pin flags and/or tags that melted were replaced. Second, a 0.5 m² (70.71 cm per side) PVC quadrat was placed centered on the seedling. The percentage of fuels consumed during the prescribed burn (as defined by the percentage of black) as well as any fire damage to the seedling itself was recorded. Seedling damage classes were no char, char, and top-gone. No char seedlings had no blackened areas on the stem, charred seedlings had some blackened area on the stem, and top-gone seedlings had been entirely consumed by the burn or had only a small stub remaining in the ground.

Analysis

Software

Throughout the analyses the “glmer” and “lmer” functions from the “lme4” package in R were used for the analysis of mixed models (R Core Team, 2022), and values were visualized using the “ggplot” function in the “tidyverse” package and “ggarrange” function from the “ggpubr” package for RStudio (Bates *et al.* 2015; Wickham *et al.* 2019; Kassambara, 2023). Mixed models including plot as the random term were preferred in all analyses, but due to lack of replication in the case of demographics analyses and small sample sizes, mixed model convergence was often an issue. In the cases where mixed models would not converge, the “glm” function from the base R stats package was used with the same model structure, less the random term (R Core Team, 2022). The “Anova” function from the “car” package was used to detect

significant effects of the independent variables and their interactions, and the “emmeans” function from the “emmeans” package was used to perform post-hoc comparisons of estimated marginal means among predictor levels with a Bonferroni adjustment (Fox and Weisberg, 2019; Lenth, 2023).

Changes in Demographics

To address Objective 1, changes in stem counts across time in the three treatment variants at Boggy Slough, data were separated into three datasets representing the 1: standard restoration prescription, 2: no-herbicide prescription, and 3: delayed-herbicide prescription. The three treatment series representing the respective prescriptions were **1**: timestep levels 1, 2, 4, 5, 8; **2**: levels 1, 2, 4, 6, 9; and **3**: levels 1, 2, 4, 7, 10 (Figure 1; Table 3). Understory count data were analyzed by height class, and midstory data were converted to stem counts per hectare to be analyzed as a fourth height class alongside the understory data. Due to the abundance of zero-counts, a negative binomial distribution was used with a generalized linear model to analyze stem counts per hectare as the dependent variable and independent variables of species group (“sppgrp”, levels: *ilevom*, *quercus*, *pinus*), chronosequence timestep (levels: 1 – 10, dependent upon the prescription), and the interaction of species group and chronosequence timestep as fixed effects. In some cases, low sample sizes prevented reliable estimates from models using a negative binomial distribution, and a Gaussian distribution was used instead. Chi-squared tests were used to detect significant effects of the independent variables with the threshold of significance being $\alpha=.05$, and contrasts with a Bonferroni adjustment were used to compare levels within variables.

Topkill and Mortality

To address Objective 2, the mechanisms behind stem count changes within size classes, seedling-level topkill and mortality were examined. Topkilled seedlings were alive at initial sampling, but by the time of resampling, the aboveground portion of the plant had died, and it had resprouted from the base. Mortality was defined by seedlings that were alive at initial sampling and were either entirely gone or had no living tissue above ground level at resampling and no visible sprouts/buds at the base.

To analyze rates of topkill, generalized linear models with a binomial distribution were used. In these models, topkill and mortality were included as the dependent variables. Independent variables included the fixed-effects of treatment (levels: 1 – 7) (Table 1), species group (“sppgrp”, levels: *ilevom*, *liqsty*, *quercus*, *pinus*), and either initial height (“height1”, continuous) or initial groundline diameter (“gld1”, continuous), and the interaction of these variables. Separate models were run to include initial height and initial groundline diameter, since the two variables would be correlated if included in the same model. Sweetgum was excluded from analyses due to a small sample size, with no observations occurring in some treatments. Chi-squared tests were used to detect significant effects of the independent variables with the threshold of significance being $\alpha=.05$, and contrasts with a Bonferroni adjustment were used to compare levels within categorical variables.

Table 3. Treatment codes used in modeling, the management activities associated with each, and the restoration prescriptions in which each are included.

Treatment #	Treatment Action	Prescription(s)
1	No action	Standard Herbicide, No Herbicide Delayed Herbicide
2	Harvest	Herbicide, No Herbicide Delayed Herbicide
3	Dormant burn, no harvest	None - Control
4	Dormant burn, harvest	Herbicide, No Herbicide Delayed Herbicide
5	Herbicide + growing season burn	Standard Herbicide
6	Growing season burn	No Herbicide
7	Delayed Herbicide + Growing Season Burn	Delayed Herbicide

Height Growth

To further explore Objective 2, the mechanisms behind stem count changes within size classes, seedling-level height growth over one growing season following each treatment was investigated. Seedling-level data were split into two groups: 1) the height growth of seedlings that were topkilled by the previous treatment and 2) those seedlings that had not been topkilled. Treatments for which no height growth data over the subsequent growing season was collected were excluded from the analyses (treatments three and four – dormant season prescribed burn treatments).

To analyze rates of height growth in each group, linear mixed-effects models were used. For modeling height growth when seedlings were not topkilled, the height difference between the initial sampling and post-growing season sampling was used as

the response variable. To model height growth among seedlings that were topkilled, the height at resampling was used as the response variable, as these seedlings started the growing season at zero centimeters tall. Independent variables included the fixed-effects of treatment (levels: 1 – 7) (Table 3), species group (“sppgrp”, levels: *ilevom*, *liqsty*, *quercus*, *pinus*), and either initial height (“height1”, continuous) or initial groundline diameter (“gld1”, continuous), and the interaction of these variables. Separate models were run to include initial height and initial groundline diameter, since the two variables would be correlated if included in the same model. In both models, plot was included as a random factor. Due to convergence issues with the mixed model for height growth following topkill, a generalized linear model without plot as a random variable was used. Treatments for which there were fewer than five seedlings that resisted topkill were excluded from the analyses of height growth (treatments five and seven). Similarly, treatments in which fewer than five seedlings were topkilled were excluded from the analyses of height growth following topkill (treatments one and two). Results were presented from either the model using height or groundline diameter as the initial size variable, depending on which model had a lower AIC, indicating a better fit to the data. Chi-squared tests were used to detect significant effects of the independent variables with the threshold of significance being $\alpha=.05$.

Fuel Consumption

To address Objective 3, first broad drivers of fuel consumption, first, average fuel consumption was calculated at a plot level. Generalized linear models were used to examine the relationship between broad, plot level characteristics and the average fuel consumption in that plot. Independent variables each modeled against average fuel

consumption as the dependent variable in individual models included treatment, basal area, midstory yaupon stem count, and understory yaupon stem count. When multiple independent variables were significant, their relationship was evaluated using a generalized linear model.

To investigate the factors influencing variability of percent fuel consumption across and within treatments, seedling-level independent variable data were used to predict the dependent variable of measured percent fuel consumption around each seedling. Potential independent variables evaluated included treatment, seedling species group, environment (lone vs. clumped) distance class to the nearest competitor (1: 0-49 cm; 2: 50-99 cm; 3: 100-149 cm; 4: 150-200 cm, and 5: >200 cm), height class of the nearest competitor (same levels as previously listed), groundline diameter of the nearest competitor (continuous), and the count of woody stems within 50 centimeters of the seedling (continuous).

After individual independent variables were tested against percent fuel consumption, logical combinations of independent variables were tested together in plots to detect any interacting variables. To look for evidence of facilitation effects in the form of variable relationships across species groups, species group was included in all these models. Interactions tested to determine the effect of clumped/lone environment with species group included treatment, environment, and woody stem count within a 50-centimeter radius of the seedling. To determine the effect of the nearest competitor, species group and treatment were tested for their interaction with distance to nearest competitor, height class of the nearest competitor, and groundline diameter of the nearest competitor, as well as the interaction of each size variable with the distance class

variable. All analyses of fuel consumption around target seedlings used generalized linear models with a binomial distribution.

The relationship between the two significant predictors of fuel consumption (treatment and stem count within a 50-centimeter radius) was evaluated to aid in the interpretation of results for Objective 3 by indicating whether the variables were strongly correlated. Treatment was used to predict stem count in a generalized linear model with a negative binomial distribution. Further, the relationship between clumped and lone environmental designations and stem count was modeled to determine if these variables were correlated. Again, a generalized linear model with a negative binomial distribution was used with environment as the independent variable and count of stems around the seedling as the dependent variable.

Fire Effects

To evaluate the influence of a seedling's local environment on fire effects in terms of likelihood of char, topkill, and mortality, generalized linear models with a binomial distribution were used. To predict the likelihood of stem char the independent variables fuel consumption, species group, and two local environmental measures were used: local density (lone/clumped) or count of stems within 50 centimeters of the target seedling.

To investigate the impact on a seedling's local environment on the likelihood of topkill and mortality, individual models were run for each species. Treatments included in the treatment variable were limited to those for which there were at least five observations of species in each level of the dependent variable (topkilled/resisted topkill or mortality/survival). Sweetgum was excluded from the topkill analyses due to the lack

of sufficient variation in the observations. Multiple models for each species were then run to test the effects of multiple local environmental variables on topkill and mortality. Independent variables included treatment level, target seedling groundline diameter, local density (clumped/lone), count of stems within 50 centimeters of the seedling (continuous), the distance class to the nearest competitor (1: 0-49 cm; 2: 50-99 cm; 3: 100-149 cm; 4: 150-200 cm; 5: >200cm) , the height class of the nearest competitor (1: 0-49 cm; 2: 50-99 cm; 3: 100-150 cm; >150cm), and the groundline diameter of the nearest competitor (continuous). The categorical independent variables were only tested when there were at least five observations in each level of the variable tested.

Chapter IV – Results

Changes in Demographics

Standard Herbicide Prescription

Overall stem counts in the height class one (0-49 cm) were nominally higher at the end of the treatment series than at the beginning. The opposite pattern was seen for the midstory (<136 cm), with lower counts at the end of the sequence than the beginning (Figure 7E). Overall stem counts did not change for height class two (50-99 cm) and did not vary across timestep for height class three (100-136 cm) (Figure 7B & Figure 7D). There was a significant interaction of the effects of chronosequence timestep and species group in only height class one (Table 4). In both height classes two and four timestep and species group were significant, but their interaction was not. In timestep three only species group was significant.

In height class one, pine, oak, and yaupon counts were not significantly different at the beginning than at the end of the treatment series (Figure 7A). Pine counts were significantly lower than yaupon counts immediately following harvest, one growing season after harvest, and one growing season after prescribed burning (Figure 7A). Oak counts were less than those of yaupon at only one growing season following harvest (Figure 7A).

Table 4. Summarized output from models for the effect of timestep, species group, and their interaction on stem counts across height classes in the standard herbicide prescription. * denote statistically significant effects according to a p-value < 0.05.

Prescription	Height Class	Distribution	Independent Variable	Chi-sq.	Df	P-value
Standard Herbicide	1 (0-49 cm)	Negative Binomial	timestep	7.598	4	0.107
			species group	94.456	2	<0.001*
			timestep*sppgrp	18.562	8	0.017*
	2 (50-99 cm)	Negative Binomial	timestep	14.966	4	0.005*
			species group	48.917	2	<0.001*
			timestep*sppgrp	10.679	8	0.221
	3 (100-137 cm)	Gaussian	timestep	3.655	4	0.4547
			species group	32.103	2	<0.001*
			timestep*sppgrp	11.096	8	0.196
4 (>137cm)	Gaussian	timestep	10.973	4	0.027*	
		species group	23.813	2	<0.001*	
		timestep*sppgrp	9.309	8	0.317	

In height class two there was no interaction between timestep and species group (Table 4). Yaupon was most abundant, followed by oak and pine throughout the treatment series (Figure 7C). Overall counts were not significantly different at the end of the treatment series than at the beginning, but there was a significantly higher stem count one growing season following the dormant season prescribed burn than directly following the timber harvest (Figure 7B).

In height class three only species group was a significant predictor of abundance. There was no interaction between timestep and species, and counts did not vary significantly across the timesteps. Yaupon counts were higher than oak and pine counts at all points in the chronosequence (Figure 7D).

Both species and timestep were significant predictors of midstory stem counts, but their interaction was not significant. Overall midstory stem counts were significantly lower at the end of the chronosequence than at the beginning, but intermediate timesteps did not significantly differ from initial or final stem counts (Figure 7E). Although the abundance of yaupon in the midstory declined through the prescription, it was higher than oak and pine at all timesteps (Figure 7E & Figure 7F).

Standard Herbicide Prescription

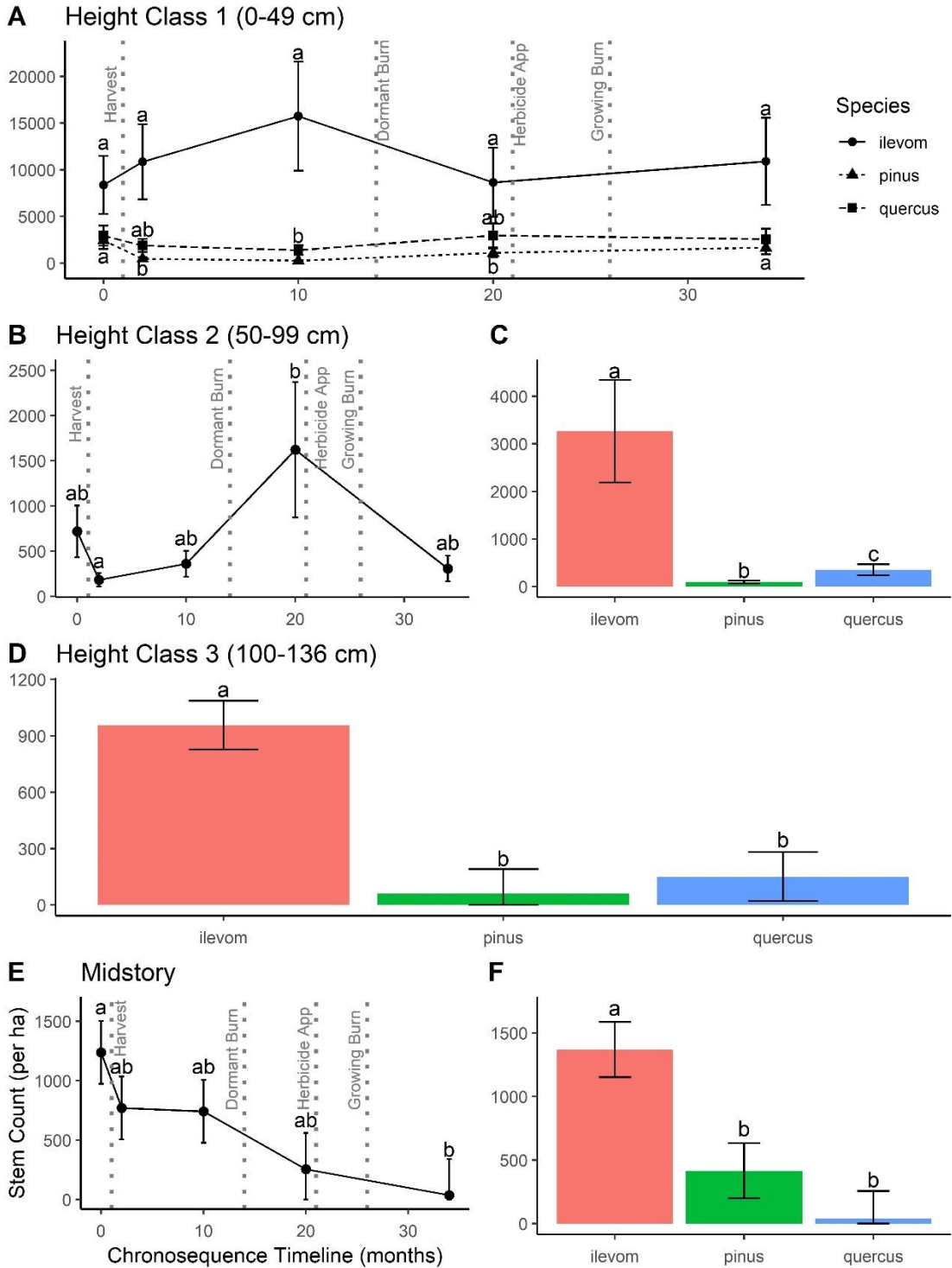


Figure 7: Standard herbicide prescription stem counts per hectare by species and timestep. Interactions of species and timestep are graphed together, otherwise significant independent variables are visualized separately. Error bars represent one standard error. Different letters indicate significant differences between species within that timestep. When pine and oak counts do not differ, they share a letter. Vertical lines indicate the timing of management actions. Note different y-axis scales.

No Herbicide Prescription

There was a significant interaction of the effects of chronosequence timestep and species group in all height classes except for the midstory (Table 5). Timestep and species group both had a significant effect on stem counts in the midstory height class, but their interaction was not significant (Table 5).

In height class one, none of pine, oak, or yaupon counts were significantly different at the beginning than at the end of the treatment series (Figure 8A). Pine counts were significantly lower than yaupon counts immediately following harvest, and lower than both yaupon and oak one growing season after harvest (Figure 8A). However, yaupon, pine, and oak counts did not significantly differ one growing season after dormant season prescribed burning or growing season prescribed burning (Figure 8A).

Table 5. Summarized output from models for the effect of timestep, species group, and their interaction on stem counts across height classes in the no herbicide prescription. * denote statistically significant effects according to a p-value < 0.05.

Prescription	Height Class	Distribution	Independent Variable	Chi-sq.	Df	P-value
No Herbicide	1 (0-49 cm)	Negative Binomial	timestep	21.218	4	<.001*
			species group	80.261	2	<.001*
			timestep*sppgrp	39.999	8	<.001*
	2 (50-99 cm)	Gaussian	timestep	10.82	4	0.029*
			species group	117.458	2	<.001*
			timestep*sppgrp	18.003	8	0.021*
	3 (100-137 cm)	Gaussian	timestep	12.089	4	0.017*
			species group	42.624	2	<.001*
			timestep*sppgrp	22.421	8	0.004*
	4 (>137cm)	Gaussian	timestep	10.54	4	0.032*
			species group	21.684	2	<.001*
			timestep*sppgrp	9.251	8	0.322

In height class two, none of the species had significantly lower counts at the end of the treatment series than at the beginning. Yaupon was most abundant prior to treatment and one growing season following harvest, while oak and pine counts were not significantly different at these timesteps (Figure 8B). At all other timesteps, yaupon, pine, and oak counts do not differ significantly (Figure 8B).

In height class three only yaupon was lower at the end of the sequence than at the beginning, while pine and oak counts did not differ significantly from the beginning at the end. Yaupon was more abundant than pine or oak prior to treatment, but it was not different from pine or oak at any other timesteps (Figure 8C).

Both species and timestep were significant predictors of midstory stem counts, but their interaction was not significant. Overall midstory stem counts were not significantly lower at the end of the chronosequence than at the beginning (Figure 8D). Although the nominal abundance of yaupon in the midstory declined through the prescription, it was higher than oak and pine at all timesteps (Figure 8D & Figure 8E).

No Herbicide Prescription

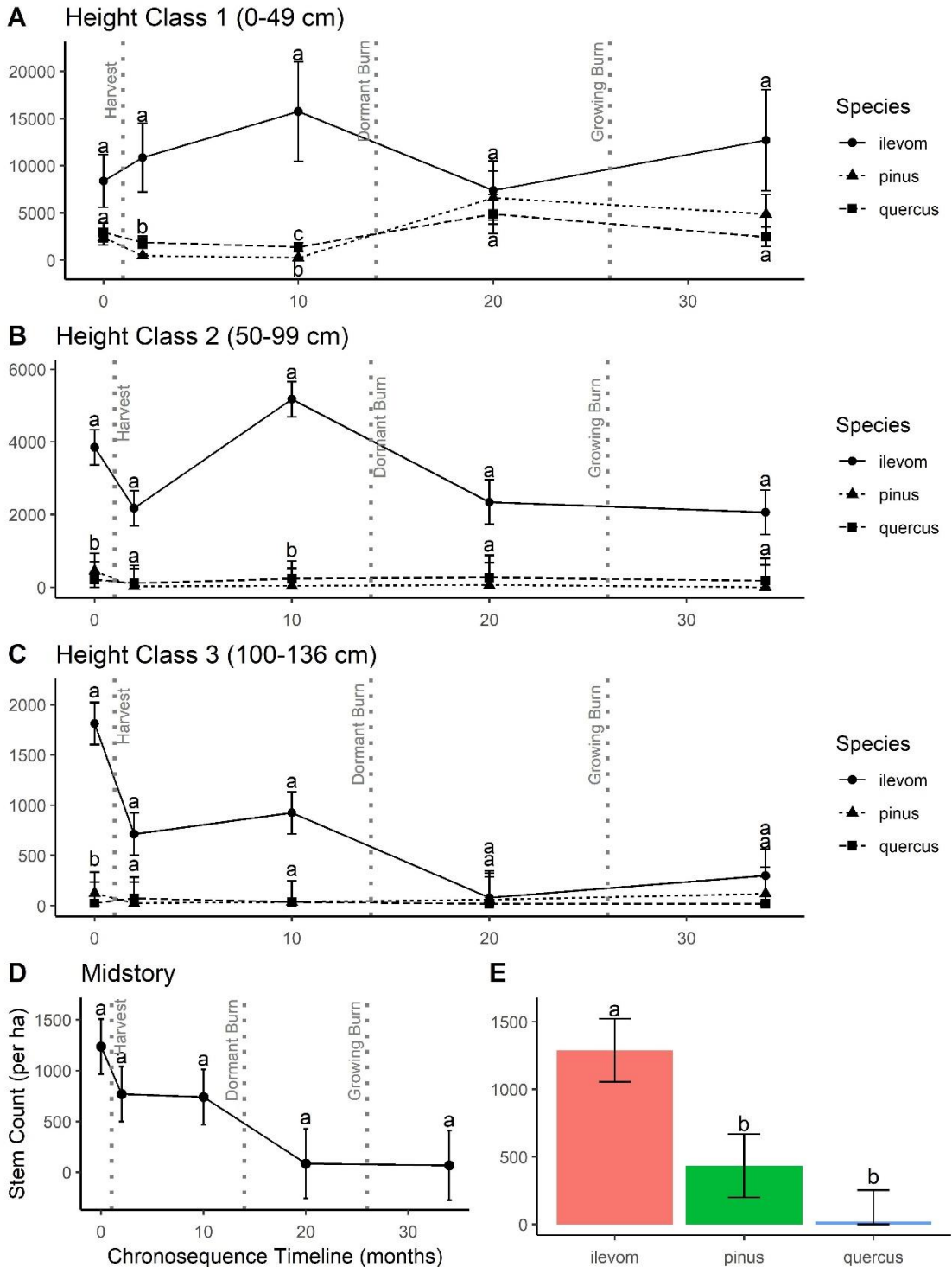


Figure 8: No herbicide prescription stem counts per hectare by species and timestep. Interactions of species and timestep are graphed together, otherwise significant independent variables are visualized separately. Line type and point shape indicate species, and error bars represent one standard error. Different letters indicate significant differences between species within that timestep. When pine and oak counts do not differ, they share a letter. Vertical lines indicate the timing of management actions. Note different y-axis scales.

Delayed Herbicide Prescription

Overall, stem counts did not change significantly from the beginning of the treatment series to the end in height class one (0-49 cm) or height class two (50-99 cm) (Figure 9A & Figure 9B). However, overall stem counts did decrease by the end of the sequence compared to pre-treatment counts in height class three (100-136 cm), and midstory (<136 cm) (Figures 9C & 9D).

There was a significant interaction of the effects of chronosequence timestep and species group in only height classes one and three (Table 6). Timestep and species group both had a significant effect on stem counts in the midstory height class, but their interaction was not significant (Table 6). In height class two, only species group was a significant predictor of stem counts (Table 6).

In height class one, only pine was significantly lower at the end of the treatment series than at the beginning. Yaupon and oak counts were not significantly different at the end of the treatment series than they were at the beginning. Yaupon, pine, and oak counts did not differ prior to harvest, but yaupon exceeded both pine and oak one growing season after harvest and at the end of the treatment series (Figure 9A). Yaupon counts also exceeded those of pine immediately following harvest and two growing seasons following dormant season burning, but oak counts were not significantly different from yaupon or pine at those points. (Figure 9A).

Table 6. Summarized output from models for the effect of timestep, species group, and their interaction on stem counts across height classes in the delayed herbicide prescription. * denote statistically significant effects according to a p-value < .05.

Prescription	Height Class	Distribution	Independent Variable	Chi-sq.	Df	P-value
Delayed Herbicide	1 (0-49 cm)	Negative Binomial	timestep	13.329	4	0.01*
			species group	123.639	2	<.001*
			timestep*sppgrp	19.849	8	0.011*
	2 (50-99 cm)	Gaussian	timestep	4.103	4	0.392
			species group	85.146	2	<.001*
			timestep*sppgrp	6.97	8	0.54
	3 (100-137 cm)	Gaussian	timestep	14.162	4	0.007*
			species group	46.311	2	<.001*
			timestep*sppgrp	22.206	8	0.005*
	4 (>137cm)	Gaussian	timestep	14.5	4	0.006*
			species group	23.42	2	<.001*
			timestep*sppgrp	11.906	8	0.155

In height class two, timestep did not have a significant effect on counts. Yaupon was most abundant throughout the sequence of treatments (Figure 9B).

In height class three only yaupon was lower at the end of the sequence than at the beginning, while pine and oak counts did not differ significantly at the end from the beginning. Yaupon was more abundant than pine or oak prior to treatment, but it was not different from pine or oak at any other timesteps (Figure 9C).

Both species and timestep were significant predictors of midstory stem counts, but their interaction was not significant (Table 6). Overall midstory stem counts were significantly lower at the end of the chronosequence than at the beginning (Figure 9D). Although the nominal abundance of yaupon in the midstory declined through the prescription, it was higher than oak and pine at all timesteps (Figure 9D & Figure 9E).

Delayed Herbicide Prescription

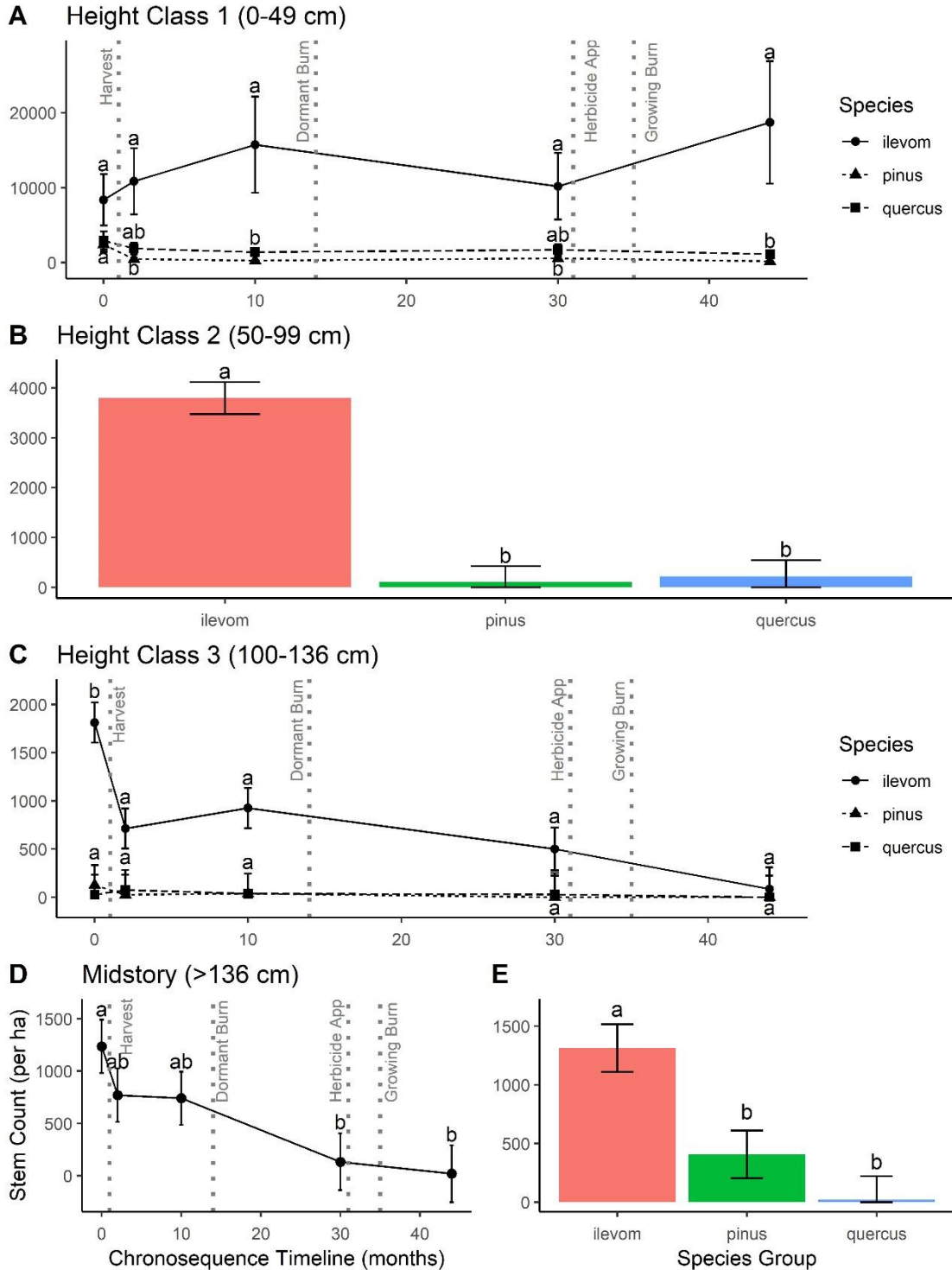


Figure 9: Delayed herbicide prescription stem counts per hectare by species and timestep. Interactions of species and timestep are graphed together, otherwise significant independent variables are visualized separately. Line type and point shape indicate species, and error bars represent one standard error. Different letters indicate significant differences between species within that timestep. When pine and oak counts do not differ, they share a letter. Vertical lines indicate the timing of management actions. Note different y-axis scales.

Topkill and Mortality

Probability of Topkill

The model using groundline diameter as the size variable was a marginally better fit to the data with an AIC of 343.11, compared to the AIC of 353.82 for the height model, and was used to visualize and report the results of the interaction of height and species group (Table 7).

Table 7. Summary of output from two models with differing size variables predicting the probability of topkill. Significant p-values are indicated in bold font and by an asterisk.

Response	Independent Variables	Chi-sq.	Df	P-value
Probability of Topkill	initial height	0.07	1	0.788
	treatment	481.55	6	<.001*
	species group	1.47	2	0.48
	height*treatment	4.57	6	0.600
	height*sppgrp	14.07	2	<.001*
	treatment*sppgrp	11.46	12	0.490
	height*treatment*sppgrp	11.43	12	0.493
	Probability of Topkill	initial GLD	0.07	1
treatment		472.17	6	<.001*
species group		1.08	2	0.583
GLD*treatment		12.07	6	0.060
GLD*sppgrp		19.62	2	<.001*
treatment*sppgrp		15.2	12	0.231
GLD*treatment*sppgrp		6.86	12	0.867

There was a significant effect of treatment on the probability of topkill (Figure 10). Harvest alone did not lead to a high likelihood of topkill, but the probability of topkill by dormant season burning was significantly higher if the stand had been harvested than if it had not (Figure 10). When the probability of topkill was modeled using height as the initial size variable, growing season burning in a harvested stand also resulted in a significantly higher probability of topkill than in an unharvested area that

was burned in the dormant season. This difference was not significant in the model using groundline diameter as the initial size variable.

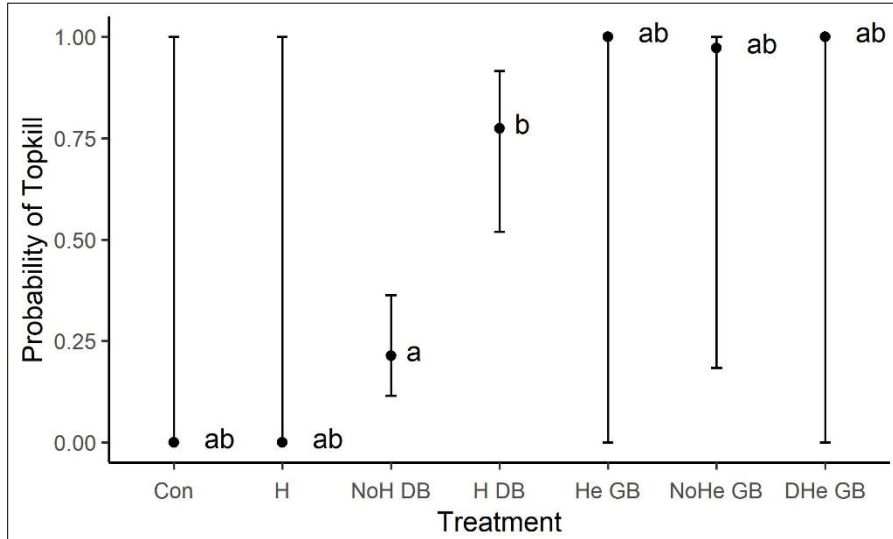


Figure 10: Probability of topkill by treatment from groundline diameter model. Different letters indicate significant differences between treatments. Numbers on the x-axis indicate treatments (Con: no action; H: harvest; NoH DB: dormant season burn in an unharvested stand; H DB: dormant season burn in a harvested stand; He GB: late summer herbicide followed by a spring growing season burn; NoHe GB: spring growing season burn (no herbicide); DHe GB: delayed (one year) late summer herbicide followed by a spring growing season burn).

The interaction of species group and initial groundline diameter also had a significant effect on the likelihood of topkill (Table 7). There was a positive relationship between diameter and the likelihood of topkill for yaupon and oak (Figure 11), but the relationship for pine was negative. At approximately twelve millimeters or greater in groundline diameter, yaupon appeared more likely than pine to be topkilled in all treatments (Figure 11).

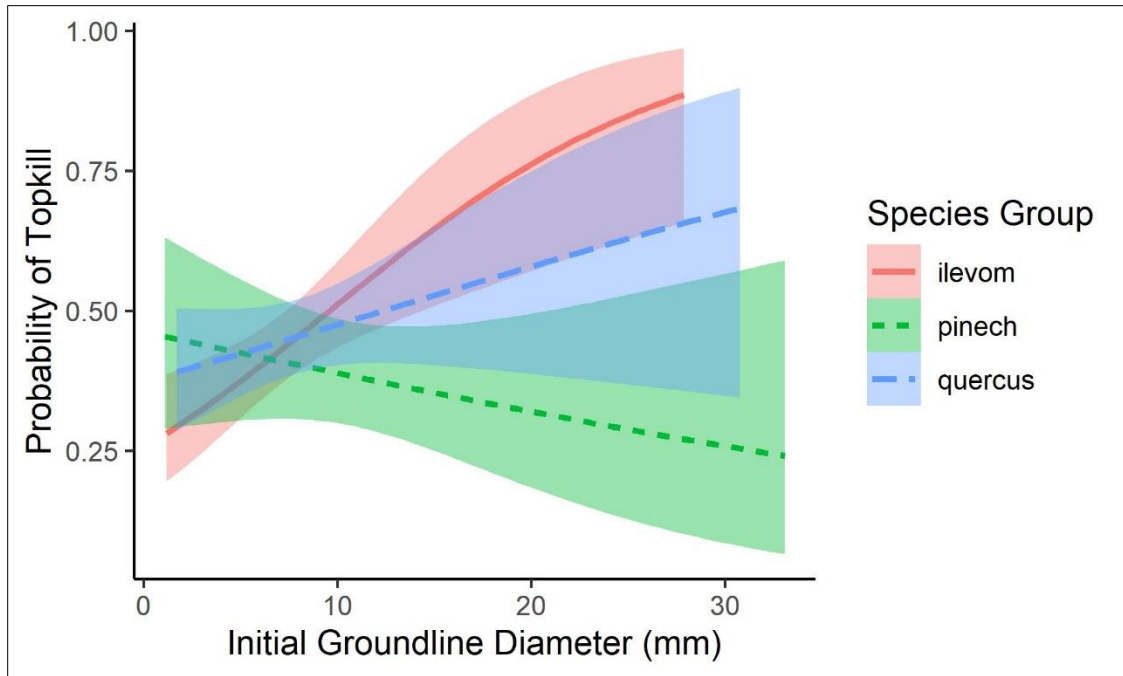


Figure 11: The probability of topkill by initial groundline diameter and species group. Shaded areas represent standard errors.

Probability of Mortality

The model using groundline diameter as the size variable fit the data slightly better with an AIC of 430.1 as opposed to the AIC of 441.08 for the model including height. Due to its better fit of the data, the model using groundline diameter was used to visualize and present the results for likelihood of mortality.

Table 8. Summary of output from two models with differing size variables predicting the probability of mortality. Significant p-values are indicated in bold font and by an asterisk.

Response	Independent Variables	Chi-sq.	Df	P-value
Probability of Mortality	initial height	1.004	6	0.316
	treatment	136.707	3	<.001*
	species group	90.21	3	<.001*
	height*treatment	12.064	6	0.061
	height*sppgrp	2.34	3	0.505
	treatment*sppgrp	27.179	17	0.055
	height*treatment*sppgrp	5.997	17	0.993
	Probability of Mortality	initial GLD	1.694	1
treatment		133.697	6	<.001*
species group		92.613	3	<.001*
GLD*treatment		19.756	6	0.003*
GLD*sppgrp		2.276	3	0.517
treatment*sppgrp		28.429	17	0.040*
GLD*treatment*sppgrp		6.621	17	0.988

There was a significant interaction of species group and treatment (Table 8). The likelihood of mortality was greater for sweetgum having been treated with herbicide followed by a spring growing season prescribed burn than for oak and yaupon experiencing the same treatment (Figure 12). The probability of mortality for all other species and treatment combinations was not significantly different than any others.

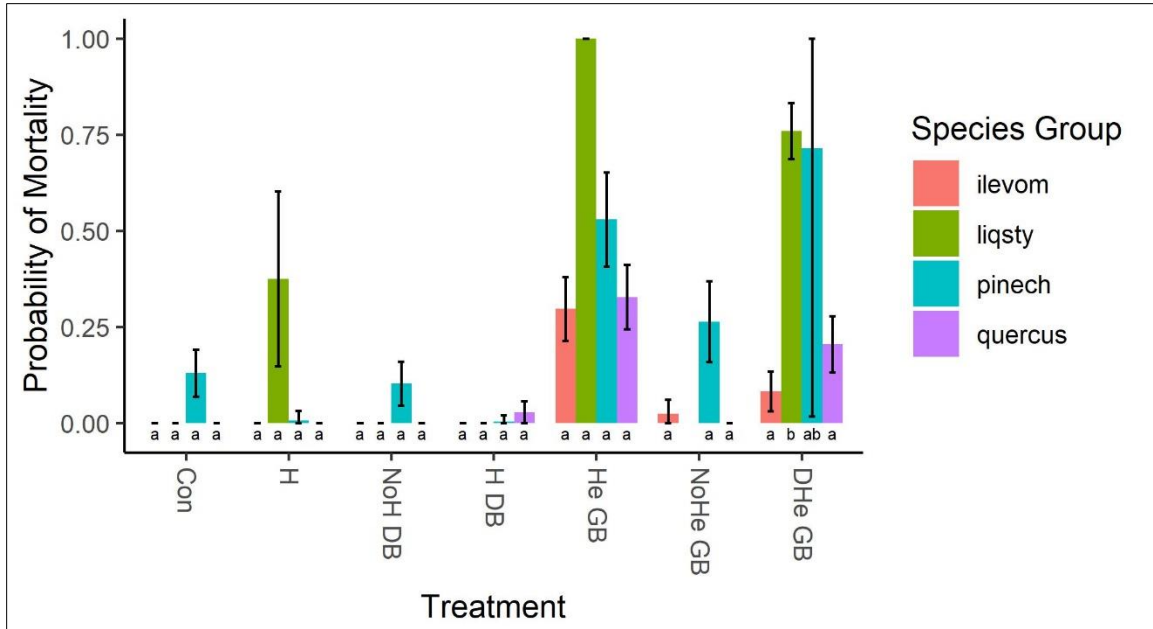


Figure 12: The probability of mortality for each species within each treatment. Missing bars indicate no mortality or a lack of data for that species*treatment combination. Letters indicate significant differences between species within a treatment. Error bars represent one standard error. Con: no action; H: harvest; NoH DB: dormant season burn in an unharvested stand; H DB: dormant season burn in a harvested stand; He GB: late summer herbicide followed by a spring growing season burn; NoHe GB: spring growing season burn (no herbicide); DHe GB: delayed (one year) late summer herbicide followed by a spring growing season burn.

There was also a significant interaction between initial groundline diameter and treatment. Plotting the probability of mortality by groundline diameter and treatment demonstrated that in the case of most treatments, the likelihood of mortality decreased with increasing groundline diameter (Figure 13). However, the likelihood of mortality increased with increasing groundline diameter in the case of treatments that involved herbicide application (treatments 5 and 7) (Figure 13). Above approximately three millimeters in initial groundline diameter, the probability of mortality was greater in treatments involving herbicide than no action, harvest, dormant season burning, or growing season burning (Figure 13). At larger groundline diameters (twenty-five millimeters or greater), the probability of topkill from growing season burning alone may not have been significantly less than growing season burning following an herbicide application (Figure 13).

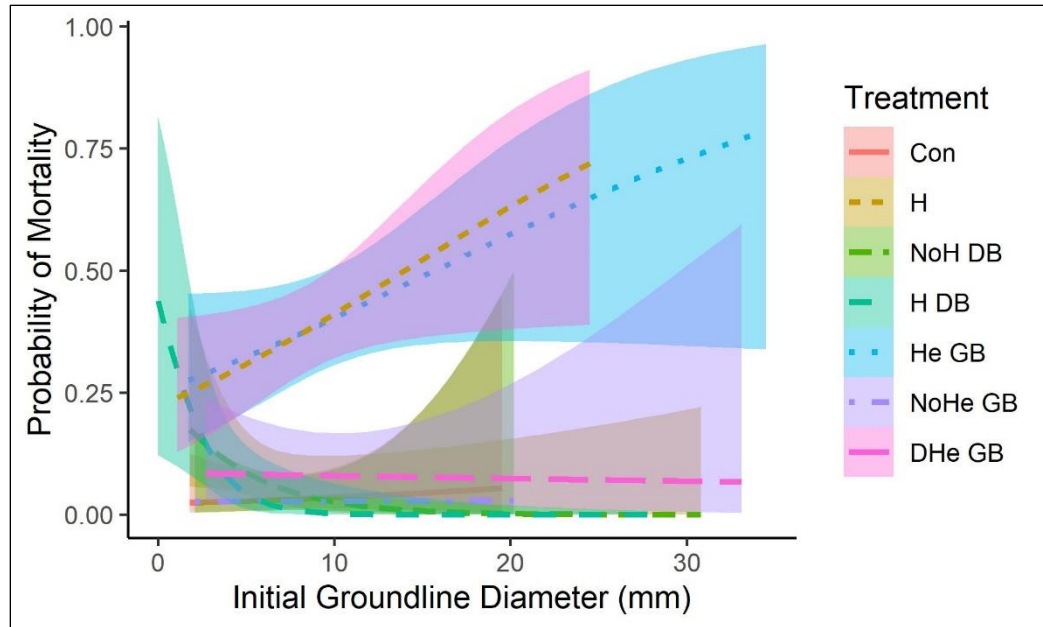


Figure 13: The probability of mortality across all species within each treatment. Shaded areas represent standard errors. Treatment numbers correspond to management actions (Con: no action; H: harvest; NoH DB: dormant season burn in an unharvested stand; H DB: dormant season burn in a harvested stand; He GB: late summer herbicide followed by a spring growing season burn; NoHe GB: spring growing season burn (no herbicide); DHe GB: delayed (one year) late summer herbicide followed by a spring growing season burn).

Height Growth

Seedlings Not Topkilled

The linear mixed model for the height growth of a seedling during the growing season following a given treatment showed a significant effect of treatment, the interaction of treatment and species group, and the interaction of initial height, treatment, and species group (Table 9). The linear mixed effects model did not converge when initial groundline diameter was used as the size variable.

Table 9. Summary of output the linear mixed model predicting height growth following a treatment, using initial height as the size variable. Significant p-values are indicated in bold font and by an asterisk.

Model	Independent Variables	Chi-sq.	Df	P-value
Height Growth	initial height	1.4182	1	0.234
No topkill	treatment	6.1374	2	0.046*
	species group	3.6797	3	0.298
	height*treatment	3.2895	2	0.193
	height*sppgrp	2.6582	3	0.447
	treatment*sppgrp	9.2835	3	0.026*
	height*treatment*sppgrp	9.0118	3	0.029*

In a no action scenario (treatment one), the larger the initial size of oak, yaupon, and sweetgum, the more they grew in height over the course of the growing season (Figure 14). This relationship was strongest with oak, and oaks that were greater than approximately 50 cm in height at the beginning of the growing season grew more than all other species (Figure 14). The growth rate of pine did not change or was slightly lower with increasing height in a no action scenario (Figure 14).

Following harvest, the relationship between initial size and height growth was reversed for oak, pine, and sweetgum. Larger oaks grew less in the growing season following harvest, and larger pines grew much more than smaller pines following harvest (Figure 8). Smaller sweetgum grew more following harvest than larger sweetgum (Figure

14). The relationship between initial size and height growth remained positive for yaupon, but the magnitude of this relationship was less than that for pine (Figure 14).

After a growing season prescribed burn, sufficient individuals that resisted topkill were only available in the yaupon species group to estimate the relationship between initial size and height growth over the following season. The relationship between initial height and growth following growing season prescribed burning was strongly negative for yaupon (Figure 14).

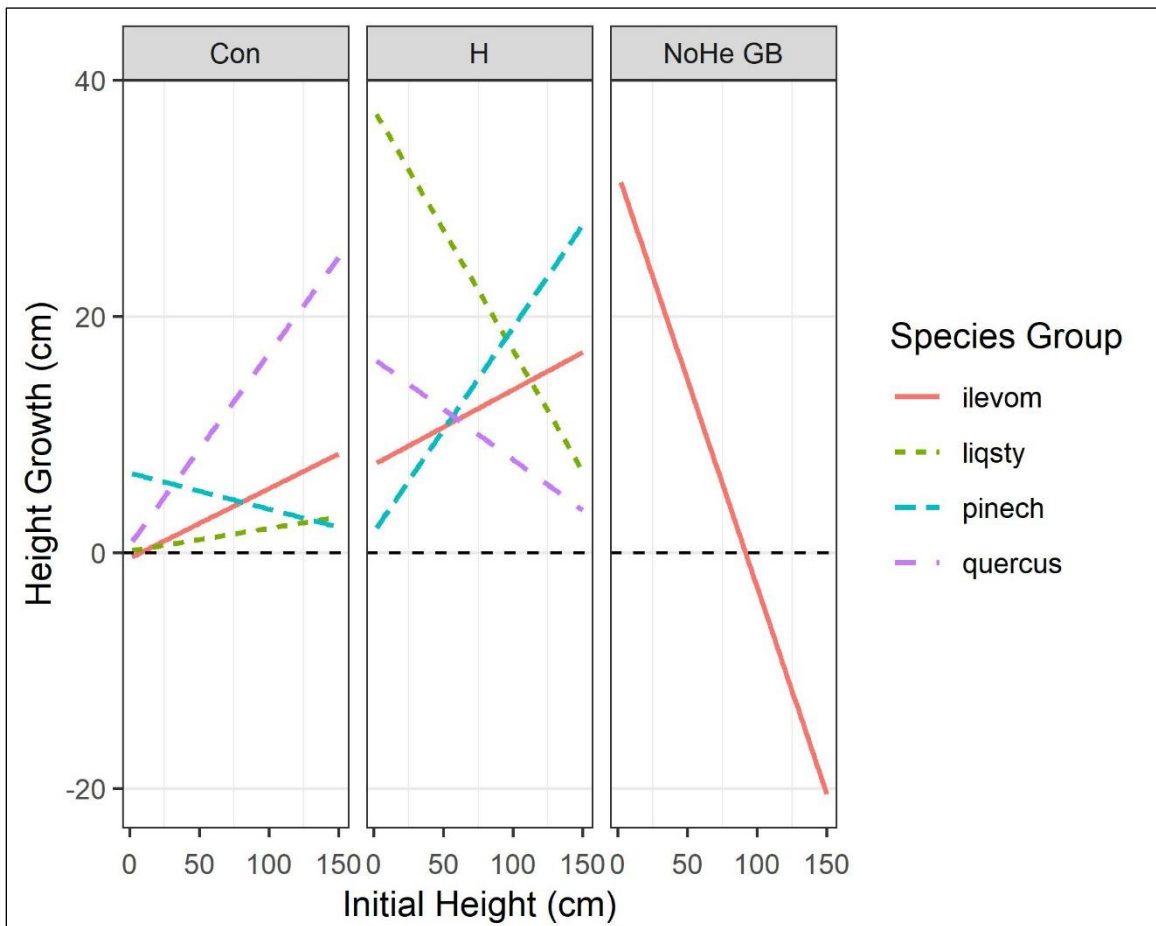


Figure 14: Height growth of individuals that resisted topkill over one growing season following three different treatments: Con: no action; H: harvest; NoHe GB: growing season prescribed burning.

Seedlings Topkilled

The linear model for the height growth of a seedling during the growing season following a given treatment was a better fit when initial height was included as the size variable, an AIC of 1520.1, than when initial groundline diameter was included as the size variable, an AIC of 1531.3. The model including initial height showed a significant effect of initial height, treatment, and species group, as well as their interactions (Table 10).

Table 10. Summary of output the linear models predicting height growth following a treatment, using initial height and initial groundline diameter as the size variables. Significant p-values are indicated in bold font and by an asterisk.

Model	Independent Variables	Chi-sq.	Df	P-value
Height Growth	initial height	53.25	1	<.001*
Topkill	treatment	6.849	2	0.033*
	species group	16.379	3	0.001*
	height*treatment	7.116	2	0.028*
	height*sppgrp	9.136	3	0.028*
	treatment*sppgrp	13.286	4	0.01*
	height*treatment*spprp	14.863	3	0.002*
	initial GLD	45.994	1	<.001*
	treatment	5.767	2	0.056
	species group	28.782	3	<.001*
	GLD*treatment	0.408	2	0.816
	GLD*sppgrp	17.654	3	0.001*
	treatment*sppgrp	9.89	4	0.042*
	GLD*treatment*sppgrp	5.297	3	0.151

After a late summer herbicide application and spring growing season prescribed burn, oaks that were larger initially grew more in height (Figure 15). Above approximately 100 cm in initial height, oak grew more in height than yaupon or pine (Figure 15). The height growth of shortleaf pine and yaupon were independent of initial height, but yaupon grew more than shortleaf pine at all initial heights (Figure 15).

Over one growing season following a spring growing season prescribed burn, oak and shortleaf pine maintained the relationship between initial height and growth that they had following an herbicide application and growing season burn. However, the relationship between the initial height of yaupon and its height growth was strongly positive, and above approximately 50 cm in initial height yaupon grow more than pine or oak.

During the growing season after an herbicide application delayed by one year relative to the standard herbicide prescription, and a spring growing season burn, oak and yaupon maintained a strong positive relationship between initial height and height growth. The magnitude of this relationship remained stronger for yaupon, and above approximately 50 cm in initial height, yaupon grew more than sweetgum or pine. Sweetgum had a very similar relationship as oak between initial height and height growth following the delayed herbicide and growing season burn.

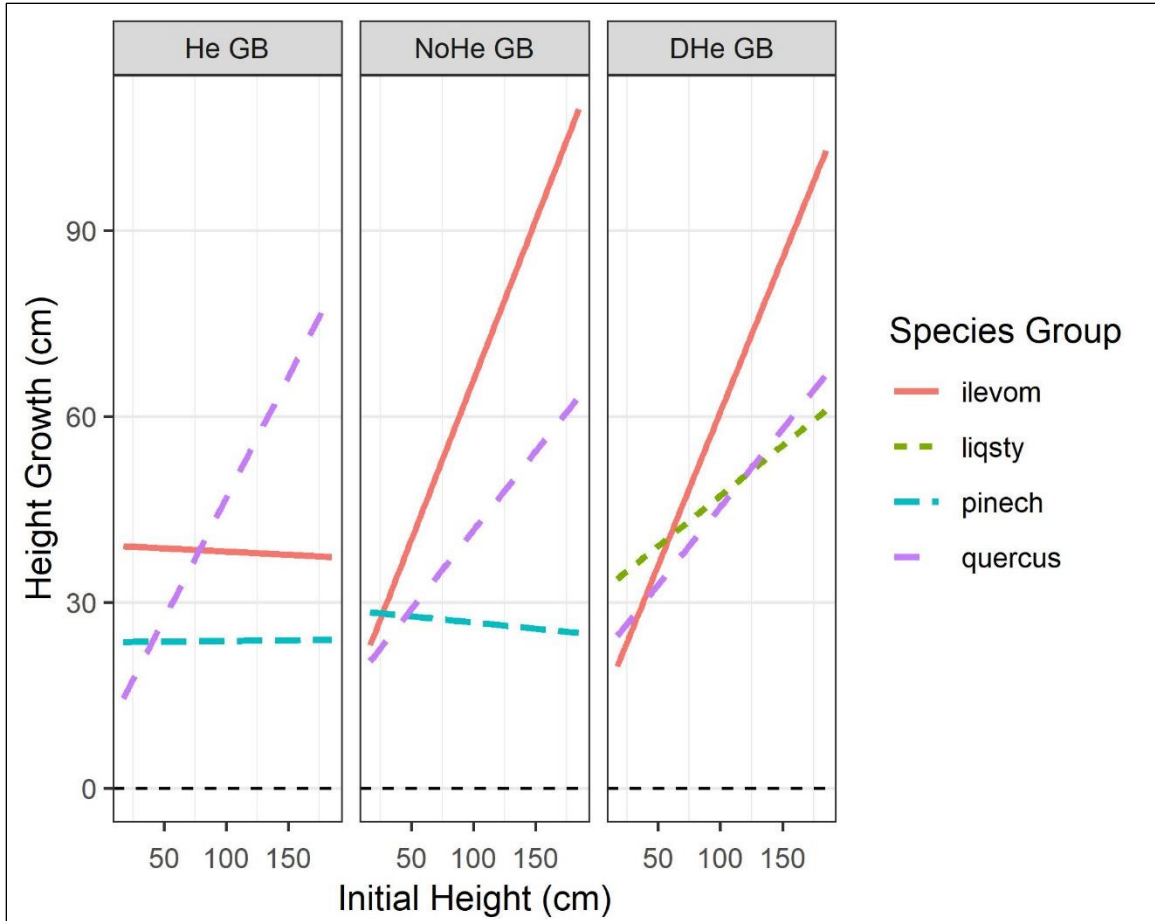


Figure 15: Height growth of individuals that were topkilled following three different treatments: He GB: late summer herbicide application followed by a spring growing season prescribed burn; NoHe GB: spring growing season prescribed burn only; DHe GB: delayed herbicide and growing season prescribed burn.

Fuel Consumption

Both treatment and the stem count of midstory yaupon were found to be significant predictors of average fuel consumption at the plot level (Table 11). Modeling average fuel consumption by treatment resulted in a better fit with an AIC of 287.57 as compared to modeling average fuel consumption by the count of midstory yaupon stems with an AIC of 308.51.

Table 11. Summary of the output of several models for average fuel consumption at the stand level. Black bars separate each model. Each model only has one independent variable. Significant p-values are indicated by bold font and an asterisk.

Model	Independent Variables	Chi-sq.	Df	P-value
Average Fuel Cons.	treatment	75.336	4	<.001*
(stand level)				
	basal area	3.5171	1	0.061
	midstory yaupon count	19.576	1	<.001*
	understory yaupon count	0.00004	1	0.995

The dormant season prescribed burn in an unharvested stand resulted in the lowest average fuel consumption, and the growing season prescribed burn in the stand that received a delayed herbicide application was the highest (Figure 16). Average fuel consumption was lower than all other treatments in the stand that was burned without harvesting (Figure 16). Average fuel consumption was lower in the stand burned during the dormant season following a harvest than the stand with a delayed herbicide application but was not different from the stand that had an herbicide application on the normal schedule or the stand that received no herbicide application (Figure 16). The average fuel consumption on the stands that received an herbicide application on the standard schedule and received no herbicide application were not different from that of the stand that received a delayed herbicide application (Figure 16). Midstory yaupon stem counts were also a significant predictor of average fuel consumption, and higher midstory yaupon counts led to lower average fuel consumption (Figure 17).

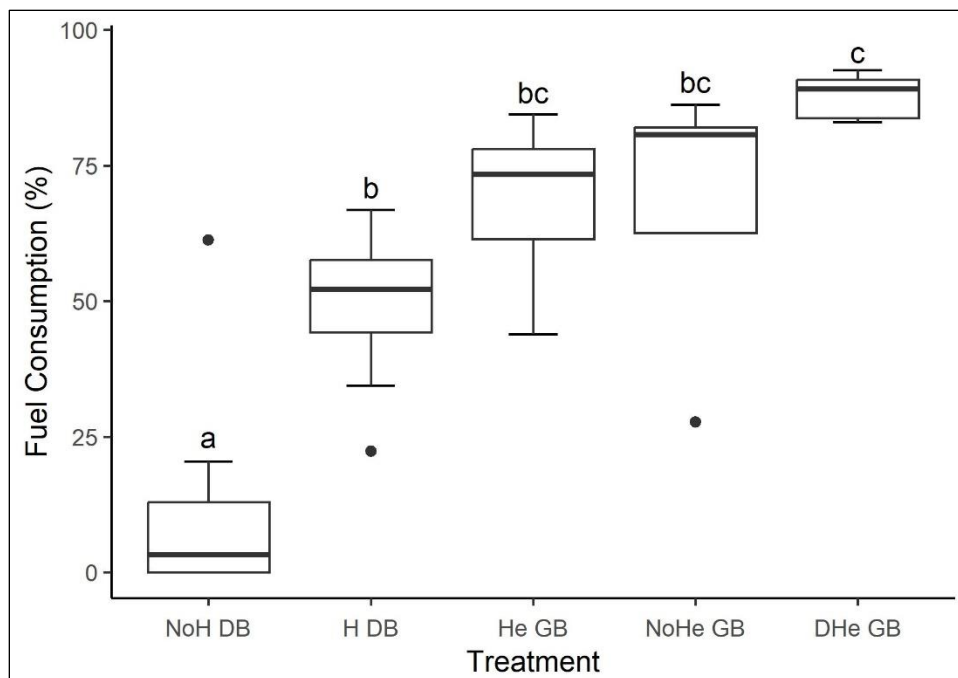


Figure 16: Mean fuel consumption at the stand level across all treatments involving fire. Treatments are NoH DB: dormant season prescribed burn without a harvest; H DB: dormant season prescribed burn following a harvest; He GB: spring growing season burn following an herbicide application; NoHe GB: spring growing season burn; DHe GB: spring growing season burn following an herbicide application delayed by one year relative to treatment He GB.

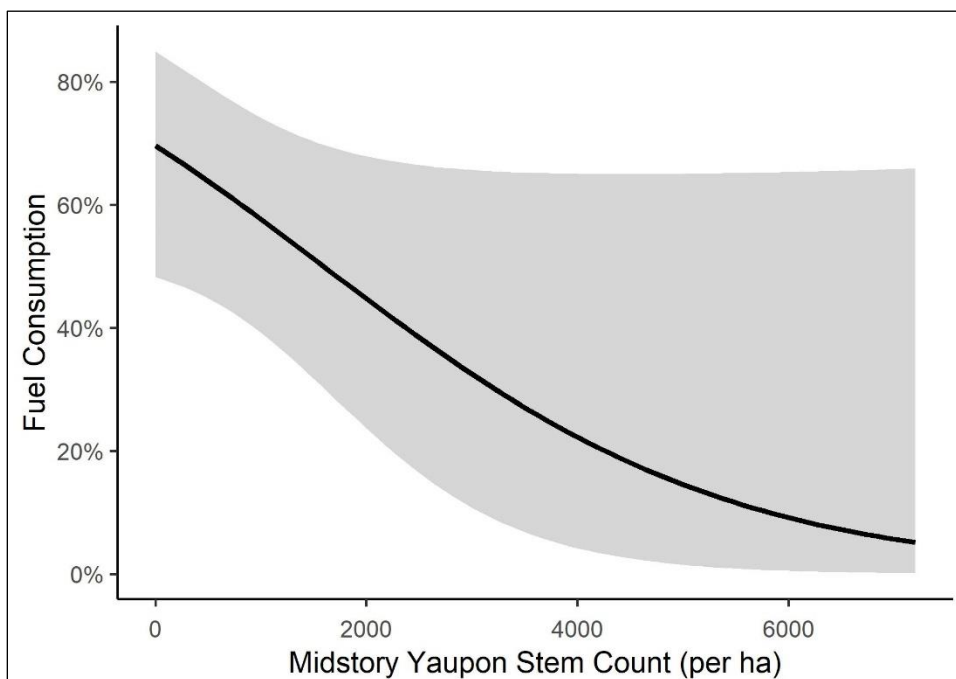


Figure 17: Estimated stand level mean fuel consumption across a range of midstory yaupon counts.

Treatment and the count of stems in a 50-centimeter radius around the seedling were significant predictors of the percentage of fuel consumed at the seedling level (Table 12). While the count of stems and seedling environment are strongly correlated (Table 13; Figure 18), local density (clumped/lone) itself was not a significant predictor of the percent of fuel consumed around the seedling (Table 12).

Table 12. Summary of the output of two models of percent fuel consumption at the individual seedling level. The black bar separates the models. Significant p-values are indicated by bold font and an asterisk.

Model	Independent Variables	Chi-sq.	Df	P-value
Fuel Consumption	treatment	153.06	4	<.001*
	species group	0.327	3	0.955
	local density	0.23	1	0.632
	treatment*sppgrp	7.365	11	0.769
	treatment*local density	2.087	4	0.719
	sppgrp*local density	0.396	3	0.941
	trt*sppgrp*local density	2.047	10	0.996
	treatment	138.073	4	<.001*
species group	0.814	3	0.846	
ct_stems (50-cm radius)	4.944	1	0.026*	
treatment*sppgrp	9.135	11	0.609	
treatment*ct_stems	1.616	4	0.806	
sppgrp*ct_stems	1.25	3	0.741	
trt*sppgrp*ct_stems	6.566	11	0.833	

Table 13. Summary of the model output exploring the relationship between treatment and count of stems within a 50-centimeter radius of the seedling. Significant p-values are indicated by bold font and an asterisk.

Model	Independent Variables	Chi-sq.	Df	P-value
Local Density (clumped/lone)	treatment	39.303	4	<.001*
	count of stems	148.116	1	<.001*
	treatment*ct_stems	16.57	4	0.002*

Pairwise comparisons showed that dormant season prescribed burning in the absence of harvesting resulted in less fuel consumption than any other treatment (Figure 19). Growing season prescribed burning following a delayed herbicide application resulted in greater fuel consumption than either dormant season prescribed burn, but not significantly greater fuel consumption than either of the other growing season prescribed burn treatments (Figure 19). Fuel consumption due to growing season prescribed burning in the standard and no herbicide prescriptions was not significantly different than due to dormant season prescribed burning following a harvest (Figure 19). There was a greater proportion of fuel consumed as the count of woody stems within 50 centimeters of the target seedling increased (Figure 20).

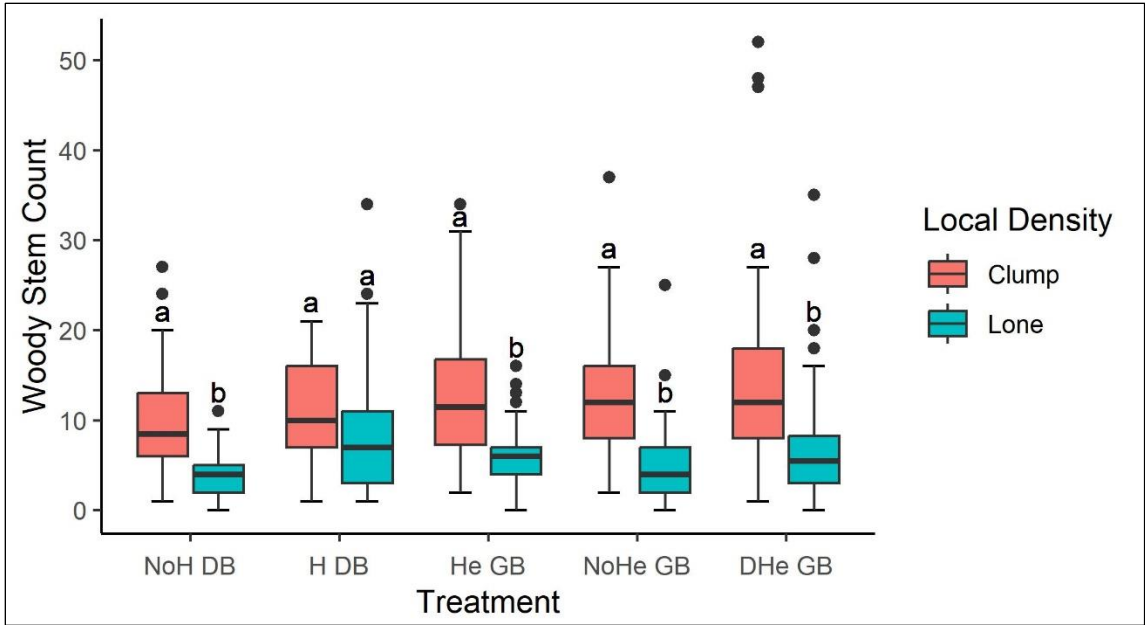


Figure 18: Woody stem count within a 50-centimeter radius of each seedling. Different letters indicate significant differences between clumped and lone local densities within a treatment.

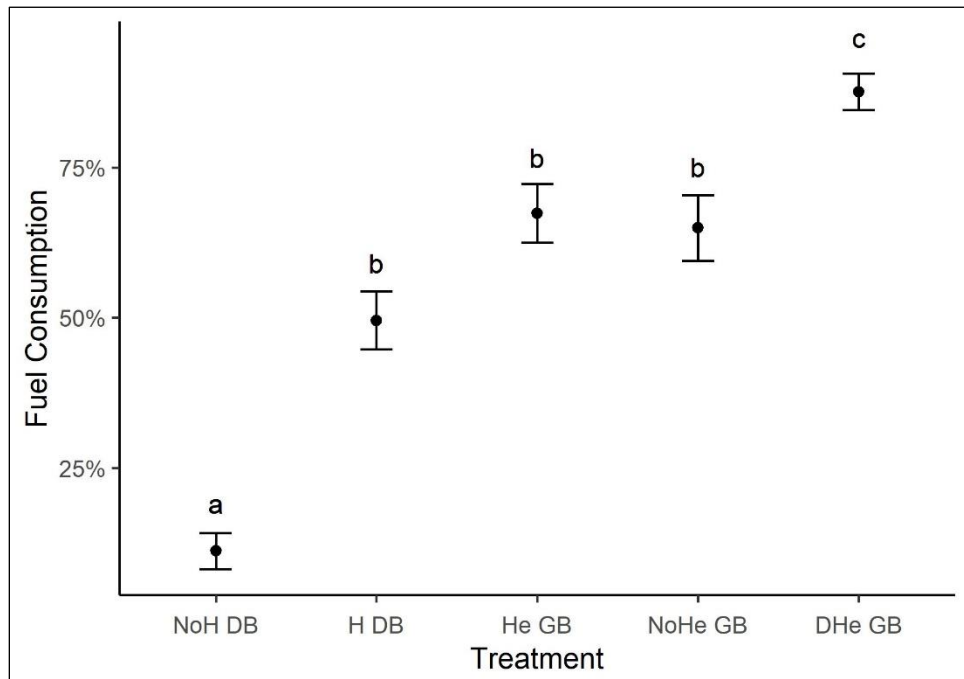


Figure 19: Percent of fuel consumed around each seedling across treatments. Different letters indicate significant differences between treatments. Treatments are NoH DB: dormant season prescribed burn without a harvest; H DB: dormant season prescribed burn following a harvest; He GB: spring growing season burn following an herbicide application; NoHe GB: spring growing season burn; DHe GB: spring growing season burn following an herbicide application delayed by one year relative to treatment He GB.

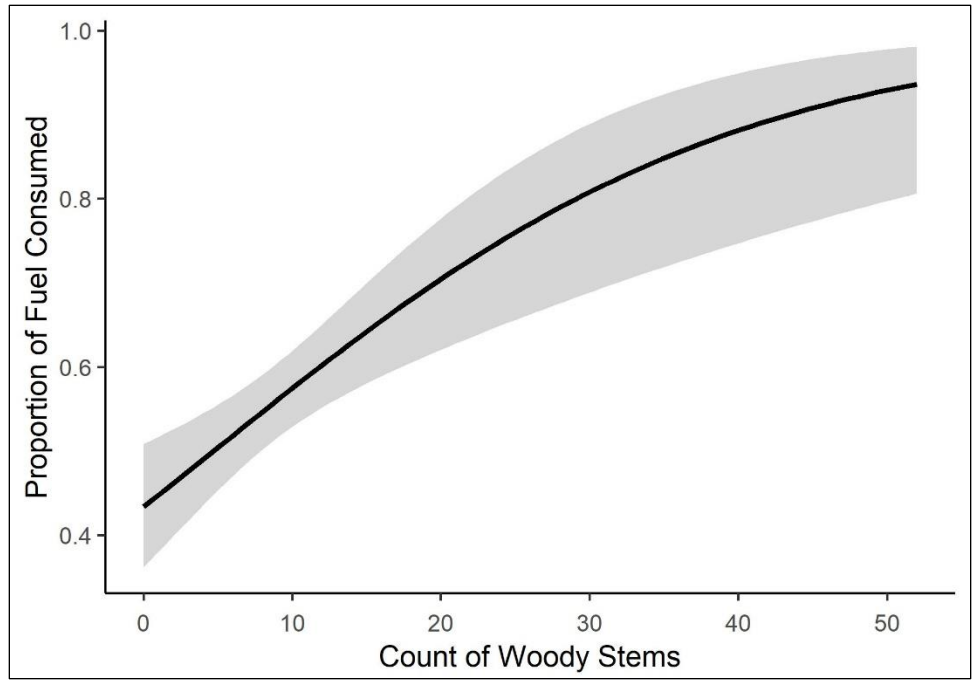


Figure 20: Proportion of fuel consumed around each seedling by the count of woody stems within 50 centimeters of the seedling.

Across all models intended to detect variation of local environmental effects on fuel consumption between species to indicate facilitation effects, treatment remained the only significant independent variable (Table 14). Similarly, in models intended to describe the effects of the seedling's local environment on fuel consumption, only treatment was a significant predictor of fuel consumption (Table 15).

Table 14. Summary of the output of several models for percent fuel consumption at the individual seedling level to test facilitation effects. Black bars separate each model. Abbreviations include NC: nearest competitor within 200 centimeters; dc: distance class from the target seedling; hc: height class; sppgrp: species group; trt: treatment; gld: groundline diameter. Significant p-values are indicated by bold font and an asterisk.

Model	Independent Variables	Chi-sq.	Df	P-value
Fuel Consumption	treatment	138.435	4	<.001*
Facilitation Effects	species group	0.149	3	0.985
	NC_distance class (dc)	3.254	4	0.516
	treatment*sppgrp	7.133	11	0.788
	treatment*NC_dc	11.485	16	0.779
	sppgrp*NC_dc	5.089	11	0.927
	trt*sppgrp*NC_dc	6.02	26	1
	treatment	136.008	4	<.001*
	species group	0.28	3	0.964
	NC_height class (hc)	2.719	4	0.606
	treatment*sppgrp	7.63	11	0.746
	treatment*NC_hc	4.978	14	0.986
	sppgrp*NC_hc	4.771	11	0.942
	trt*sppgrp*NC_hc	7.967	24	0.999
	treatment	149.928	4	<.001*
	species group	0.364	3	0.948
	NC_gld	0.439	1	0.508
	treatment*sppgrp	7.902	11	0.722
	treatment*NC_gld	0.274	4	0.992
	sppgrp*NC_gld	2.565	3	0.464
	trt*sppgrp*NC_gld	11.552	11	0.398

Table 15. Summary of the output of several models for percent fuel consumption at the individual seedling level to test the effects of the local area/environment. Black bars separate each model. Abbreviations include NC: nearest competitor within 200 centimeters; dc: distance class from the target seedling; hc: height class; sppgrp: species group; trt: treatment; gld: groundline diameter. Significant p-values are indicated by bold font and an asterisk.

Model	Independent Variables	Chi-sq.	Df	P-value
Fuel Consumption	treatment	161.724	4	<.001*
Area Effects	NC_groundline diameter	0.53	1	0.466
	treatment*NC_gld	0.551	4	0.968
	treatment	151.698	4	<.001*
	NC_height class	3.285	4	0.511
	treatment*NC_hc	4.807	14	0.988
	treatment	160.542	4	<.001*
	NC_distance class	3.602	4	0.463
	treatment*NC_dc	11.07	16	0.805
	treatment	154.262	4	<.001*
	NC_distance class	2.88	4	0.578
	NC_groundline diameter	0.008	1	0.927
	treatment*NC_dc	11.745	16	0.761
	treatment*NC_gld	1.167	4	0.884
	NC_dc*NC_gld	3.16	3	0.368
	trt*NC_dc*NC_gld	4.7	12	0.967
	treatment	147.481	4	<.001*
	NC_distance class	1.422	3	0.701
	NC_height class	0.778	3	0.855
	treatment*NC_dc	7.887	12	0.794
	treatment*NC_hc	1.993	10	0.996
	NC_dc*NC_hc	4.05	9	0.908
	trt*NC_dc*NC_hc	8.473	20	0.988

Fire Effects – Char, Topkill, and Mortality

Treatment was the only significant predictor of whether a seedling’s stem would be charred following a fire (Table 16). Neither of the local environmental variables were significant at the $\alpha=.05$ level (Table 16). Although treatment was a significant predictor of the likelihood of stem char, there were no significant differences between treatments when post-hoc comparisons were carried out (Figure 21).

Table 16. Summary of model output regarding the effects of treatment, species group, and each of two local environmental variables on the likelihood of stem char. The solid black bar separates individual models. Local density refers to whether the seedling was designated as “clumped” or “lone” and local density refers to the number of woody stems within a 50-centimeter radius of the seedling.

Model	Independent Variables	Chi-sq.	Df	P-value
Probability of Stem Char				
	treatment	187.092	4	<.001*
	species group	3.349	2	0.187
	local density	0	1	0.995
	treatment*sppgrp	5.585	8	0.694
	treatment*local density	8.014	4	0.091
	sppgrp*local density	0.996	2	0.608
	trt*sppgrp*local density	11.703	8	0.165
Probability of Topkill				
	treatment	171.566	4	<.001*
	species group	3.006	2	0.223
	count of stems	1.395	1	0.238
	treatment*sppgrp	6.741	8	0.565
	treatment*count of stems	6.829	4	0.145
	sppgrp*count of stems	1.554	2	0.460
	trt*sppgrp*count of stems	7.978	8	0.436

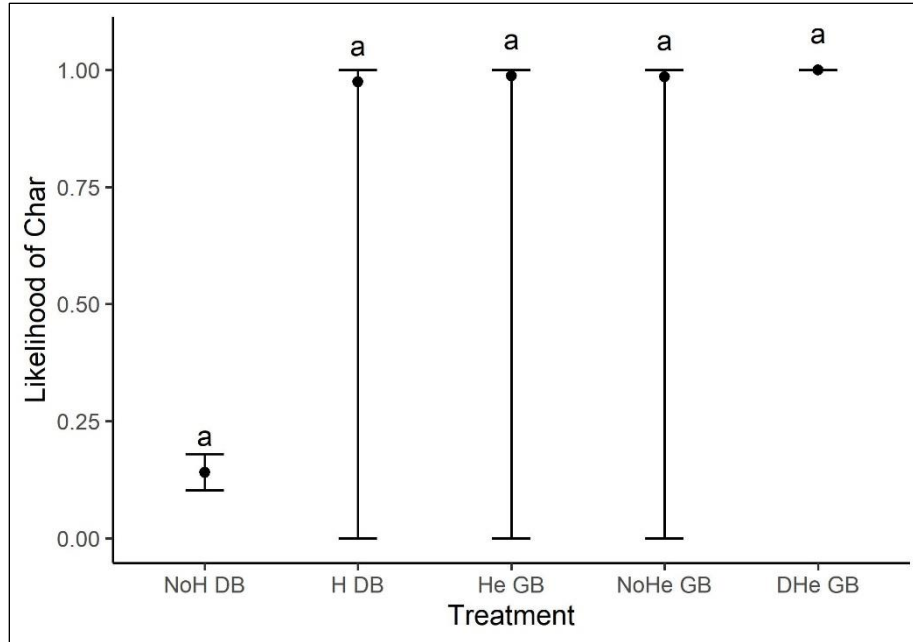


Figure 21: Likelihood of stem char for all species as modeled by treatment. Different letters would indicate significant differences between treatments. Treatments are NoH DB: dormant season prescribed burn without a harvest; H DB: dormant season prescribed burn following a harvest; He GB: spring growing season burn following an herbicide application; NoHe GB: spring growing season burn; DHe GB: spring growing season burn following an herbicide application delayed by one year relative to treatment He GB.

As in previous analyses, treatment and groundline diameter remained significant predictors of the likelihood of topkill for yaupon and oak species (Table 4; Table 17; Table 18). Treatment was significant in the model including stem count as the local environmental variable, along with the interaction of groundline diameter and count of stems within 50 cm of the target seedling (Table 17). For oak and pine, no local environmental variables were significant predictors of the likelihood of topkill, nor did any approach the threshold of significance (Table 18; Table 19).

Table 17. Effects of treatment, species group, and two local environmental variables on the likelihood of topkill for yaupon due to dormant season burning in a harvested stand, growing season burning, and herbicide application plus growing season burning. Black bars separate individual models. NC is the abbreviation for “nearest competitor”.

Model	Independent Variables	Chi-sq.	Df	P-value
Yaupon Topkill – Treatments 4, 5, & 6				
Local Density	groundline diameter (gld)	10.3276	1	0.001*
(Trt 4 & 6 only)	treatment	0.0737	1	0.786
	local density	0.0596	1	0.807
	gld*treatment	0.041	1	0.84
	gld*density	0.0217	1	0.883
	treatment*density	1.2965	1	0.255
	gld*treatment*density	0.0014	1	0.970
Local Stem Count				
	gld	9.5635	1	0.002*
	treatment	6.183	2	0.045*
	count of stems	0.05	1	0.823
	gld*treatment	0.2542	2	0.881
	gld*ct_stems	4.7423	1	0.029*
	treatment*ct_stems	0.8057	2	0.668
	gld*treatment*ct_stems	5.7621	2	0.056
NC Groundline Dia.				
	gld	11.2625	1	.001*
	treatment	4.624	2	0.099
	NC groundline diameter	0.1526	1	0.696
	gld*treatment	0.9788	2	0.613
	gld*NC gld	0.0991	1	0.753
	treatment*NC gld	5.1547	2	0.076
	gld*treatment*NC gld	0.4445	2	0.801

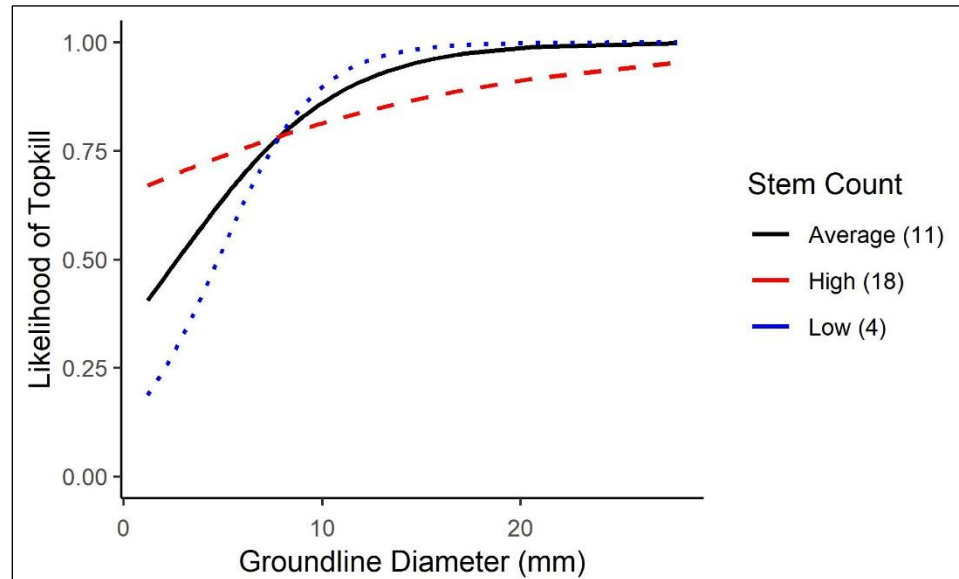


Figure 22: Likelihood of topkill for yaupon in treatments five, six, and seven as modeled by the interaction of the seedling's groundline diameter and the count of woody stems within a 50-centimeter radius. Line type corresponds to the count of stems, the solid line being the median count, dashed line being a high count and the dotted line being low count.

The groundline diameter of yaupon was demonstrated to be positively correlated with the likelihood of topkill in previous analyses (Table 7). When modeled alongside the local count of woody stems, the two predictors interacted (Table 16). Higher local stem counts (Median + one standard deviation = 18 mm) were associated with a lower rate of increasing likelihood of topkill as groundline diameter increases than median and low local stem counts (Figure 22). Low local stem counts (median – one standard deviation = 4) were associated with a faster initial increase in likelihood of topkill with increasing groundline diameter (Figure 22). The rate of increasing likelihood of topkill with increasing groundline diameter with a median local stem count (median = 11) was intermediate between the higher and lower counts, but more similar overall to lower counts (Figure 16).

Table 18. Summary of model output regarding the effects of treatment, species group, and each of two local environmental variables on the likelihood of topkill for oak species due to dormant season prescribed burning in unharvested and harvested stands. The solid black bars separate individual models. Local density refers to whether the seedling was designated as “clumped” or “lone” and local density refers to the number of woody stems within a 50-centimeter radius of the seedling. NC is the abbreviation for “nearest competitor”.

Model	Independent Variables	Chi-sq.	Df	P-value
Oak Topkill – Treatments 3 & 4				
Local Density	groundline diameter (gld)	0.4026	1	0.526
	treatment	18.8262	1	<.001*
	local density	1.6874	1	0.194
	gld*treatment	0.1133	1	0.736
	gld*density	1.3138	1	0.252
	treatment*density	1.292	1	0.256
	gld*treatment*density	1.2738	1	0.259
Local Stem Count				
Local Stem Count	gld	0.0595	1	0.807
	treatment	19.1839	1	<.001*
	count of stems	0.214	1	0.644
	gld*treatment	0.125	1	0.724
	gld*ct_stems	0.4827	1	0.487
	treatment*ct_stems	1.4986	1	0.221
	gld*treatment*ct_stems	0.3539	1	0.552
NC Groundline Dia.				
NC Groundline Dia.	gld	0.0014	1	0.97
	treatment	15.5586	1	<.001*
	NC groundline diameter	0.0499	1	0.823
	gld*treatment	0.0418	1	0.838
	gld*NC gld	0.4782	1	0.489
	treatment*NC gld	0.0749	1	0.784
	gld*treatment*NC gld	0.9954	1	0.318

Table 19. Summary of model output regarding the effects of treatment, species group, and each of two local environmental variables on the likelihood of topkill for pine due to a dormant season prescribed burn in an unharvested stand. The solid black bars separate individual models. Local density refers to whether the seedling was designated as “clumped” or “lone” and local density refers to the number of woody stems within a 50-centimeter radius of the seedling. NC is the abbreviation for “nearest

Model	Independent Variables	Chi-sq.	Df	P-value
Pine Topkill – Treatment 3				
Local Density	groundline diameter (gld)	0.10272	1	0.749
	local density	0.91563	1	0.339
	gld*density	0.35953	1	0.549
Local Stem Count				
Local Stem Count	gld	0.08286	1	0.7735
	count of stems	0.51372	1	0.4735
	gld*ct_stems	0.02401	1	0.8769
NC Groundline Dia.				
NC Groundline Dia.	gld	0.000485	1	0.9824
	NC groundline diameter	0.200161	1	0.6542
	gld*NC gld	0.29118	1	0.5889

The interaction of the target seedling’s groundline diameter and its nearest competitor’s groundline diameter was significant in the model predicting yaupon mortality (Table 20). Groundline diameter alone was significant in the model including the count of woody stems within 50 centimeters of the target seedling as the local environmental variable (Table 20). No models showed any effect of any local environmental variables on the likelihood of mortality for oak, pine, or sweetgum (Table 21; Table 22; Table 23).

Table 20. Summary of model output regarding the effects of treatment, species group, and each of two local environmental variables on the likelihood of mortality for yaupon due to an herbicide application and a growing season prescribed burn. The solid black bars separate individual models. Local density refers to whether the seedling was designated as “clumped” or “lone” and local density refers to the number of woody stems within a 50-centimeter radius of the seedling. NC is the abbreviation for

Model	Independent Variables	Chi-sq.	Df	P-value
Yaupon Mortality – Treatment 5				
Local Density	groundline diameter (gld)	2.8314	1	0.092
	local density	3.179	1	0.075
	gld*density	0.5919	1	0.442
Local Stem Count				
Local Stem Count	gld	4.099	1	0.043*
	count of stems	3.1125	1	0.078
	gld*ct_stems	0.0349	1	0.852
NC Groundline Dia.				
NC Groundline Dia.	gld	1.4635	1	0.226
	NC groundline diameter	1.0323	1	0.310
	gld*NC gld	11.5661	1	0.001*

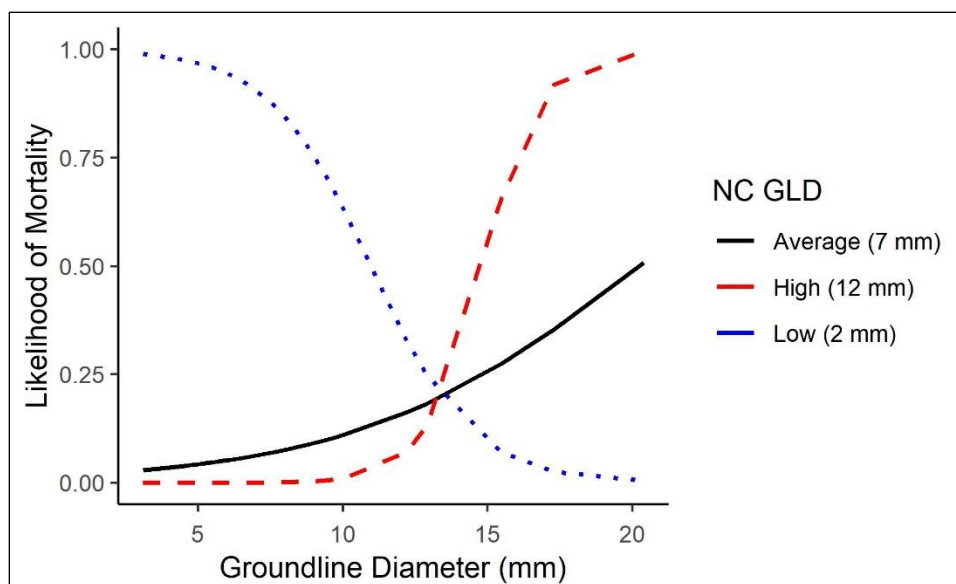


Figure 23: Likelihood of mortality for yaupon in treatment five as modeled by the interaction of the seedling's groundline diameter and the nearest competitor's (NC) groundline diameter (GLD). Line type corresponds to the nearest competitor's groundline diameter, the solid line being the median GLD, dashed line being a high GLD, and the dotted line being a low GLD.

Previous analyses demonstrated mortality in treatment five had a positive relationship with groundline diameter regardless of the species (Table 8; Figure 13). For yaupon, the effects of groundline diameter and the groundline diameter of the nearest competitor interacted when predicting the likelihood of mortality from treatment five (Table 20). Given a larger nearby competitor (GLD = 12 mm), the relationship between the target yaupon's groundline diameter and likelihood of mortality was strongly positive (Figure 23). Given nearby competitor with a GLD smaller than the median (GLD = 2mm), the relationship between the target seedling's groundline diameter and mortality was strongly negative (Figure 23). The relationship when the nearby competitor's size was the median (GLD = 7mm) was positive but not as strongly positive as for larger nearby competitors (Figure 23).

Table 21. Summary of model output regarding the effects of treatment, species group, and each of two local environmental variables on the likelihood of mortality for oak due to an herbicide application and growing season prescribed burn. The solid black bars separate individual models. Local density refers to whether the seedling was designated as “clumped” or “lone” and local density refers to the number of woody stems within a 50-centimeter radius of the seedling. NC is the abbreviation for “nearest

Model	Independent Variables	Chi-sq.	Df	P-value
Oak Mortality – Treatment 5				
Local Density	treatment	1.3637	1	0.243
	groundline diameter (gld)	0.02348	1	0.878
	local density	1.80452	1	0.179
	treatment*gld	0.12392	1	0.725
	treatment*local density	0.25215	1	0.616
	gld*local density	0.57392	1	0.449
	treatment*gld*local den.	1.94569	1	0.163
Local Stem Count				
	treatment	0.96995	1	0.325
	gld	0.25349	1	0.615
	stem count	0.10283	1	0.749
	treatment*gld	0.16934	1	0.681
	treatment*count of stems	0.36906	1	0.544
	gld*count of stems	0.08452	1	0.771
	treatment*gld*ct_stems	2.10339	1	0.147
NC Distance Class				
	gld	0.0019	1	0.965
Treatment 5 only	NC distance class (dc)	3.8462	4	0.427
	gld*NC dc	4.2866	4	0.369
NC Groundline Dia.				
	treatment	0.552	1	0.458
	gld	0.0924	1	0.761
	NC gld	3.5721	1	0.059
	treatment*gld	0.0915	1	0.762
	treatment*NC gld	0.0458	1	0.83
	gld*NC gld	0.1807	1	0.671
	treatment*gld*NC gld	1.2684	1	0.26

Table 22. Summary of model output regarding the effects of treatment, species group, and each of two local environmental variables on the likelihood of mortality for pine due to an herbicide application and growing season prescribed burn. The solid black bars separate individual models. Local density refers to whether the seedling was designated as “clumped” or “lone” and local density refers to the number of woody stems within a 50-centimeter radius of the seedling. NC is the abbreviation for “nearest competitor”.

Model	Independent Variables	Chi-sq.	Df	P-value
Pine Mortality – Treatment 5				
Local Density	groundline diameter (gld)	0.29812	1	0.585
	local density	1.0293	1	0.31
	gld*density	1.34114	1	0.247
Local Stem Count				
Local Stem Count	gld	0.11176	1	0.738
	count of stems	2.58074	1	0.108
	gld*ct_stems	0.52356	1	0.469
NC Height Class				
NC Height Class	gld	0.4571	1	0.499
	NC height class (hc)	8.2572	4	0.083
	gld*NC hc	6.119	3	0.106
NC Groundline Dia.				
NC Groundline Dia.	gld	1.37961	1	0.24
	NC groundline diameter	0.32065	1	0.571
	gld*NC gld	0.70696	1	0.401

Table 23. Summary of model output regarding the effects of treatment, species group, and each of two local environmental variables on the likelihood of mortality for sweetgum due to a delayed herbicide application and growing season prescribed burn. The solid black bars separate individual models. Local density refers to whether the seedling was designated as “clumped” or “lone” and local density refers to the number of woody stems within a 50-centimeter radius of the seedling. NC is the abbreviation for

Model	Independent Variables	Chi-sq.	Df	P-value
Sweetgum Mortality				
–				
Treatment 7				
Local Density	groundline diameter (gld)	0.80874	1	0.369
	local density	1.64652	1	0.199
	gld*density	0.03739	1	0.847
–				
Local Stem Count	gld	0.39188	1	0.531
	count of stems	0.677	1	0.411
	gld*ct_stems	0.21419	1	0.644
–				
NC Groundline Dia.	gld	0.28981	1	0.5903
	NC groundline diameter	0.58812	1	0.443
	gld*NC gld	0.30434	1	0.581

Chapter V – Discussion

Most contemporary upland stands in the East Texas Pineywoods have developed under a policy of fire suppression that has led to the development of forests with dense midstories and an increasing abundance of historically excluded fire-sensitive species, a pattern observed across the eastern United States (Nowacki and Abrams, 2008). Yaupon holly and sweetgum are species historically excluded by fire that pose significant challenges to managers who wish to restore these upland stands to their historical fire-maintained woodland structure and composition. Considerable existing research has been devoted to understanding the efficacy of various treatments in restoring stands subject to “mesophication” throughout the eastern United States (e.g., Alexander *et al.* 2021; Radeloff *et al.* 2000; Vander Yacht *et al.* 2019). However, knowledge of best practices regarding this restoration process in the East Texas Pineywoods is scarce. This study evaluated the effects of Boggy Slough Conservation Area’s restoration treatments on regeneration demographics with the end goal of restoring upland mixed pine-oak woodlands in the East Texas Pineywoods. Additionally, this study explored rates of growth, topkill, and mortality associated with treatments, species, and local-seedling environmental variables that caused changes in demographics.

All treatment sequences resulted in lower midstory densities, representing a shift toward the historical two-storied woodland stand structure described by Bragg (2002). Reintroducing fire to the system resulted in high levels of topkill across all species, a consistent decreasing trend in the abundance of large yaupon, and higher rates of topkill among larger yaupon than similarly sized pines. Analyses of the effects of seedlings’ local environmental conditions reinforced findings that the likelihood of topkill for

yaupon was positively correlated with increasing size. Herbicide applications led to higher mortality rates across all species, as expected. However, while we expected greater abundances of woody seedlings, especially larger and closer nearby yaupon and sweetgum, to moderate fire behavior and thereby enhance seedling survival and resistance to topkill, we were not able to demonstrate this effect. In fact, fuel consumption was greater with an increasing number of woody stems near the target seedling.

Demographics Changes and Driving Mechanisms

Treatments dramatically reduced the abundance of midstory and large understory stems in these stands, but the resprouting and growth following topkill augmented counts in the lower height classes. All the species of interest have adaptations that allow them to survive disturbance by resprouting. Vines (1960) stated that yaupon was able to produce root sprouts, the ability of oaks to sprout at the stump and root collar is well documented (Larsen and Johnson, 1998), Mattoon (1915) reported on shortleaf pine's ability to sprout from its basal crook, and Kormanik and Brown (1967) described the tendency of sweetgum to sprout from the roots following disturbance. Each prescription showed the potential to reduce midstory density, an important component of restoring woodland structure, but abundant advanced regeneration less than one meter tall remained.

While the change in stem counts in the larger size classes seemingly conflicts with the general expectation that larger individuals are less likely to be topkilled, the bulk of the stems sampled were yaupon and oaks, and the range of groundline diameters represented in this study (up to approximately 3 centimeters in diameter) are smaller than those necessary to confer resistance to fire topkill in fire-adapted species such as oaks, let alone yaupon (Arthur *et al.* 2012). Further, larger oaks and yaupon often were freely

growing individuals in areas with less woody competition. This finding is supported by the research of Loftis (2004), which discussed the necessity of improving the understory light environment and reducing competition to develop large oak advance regeneration. Practices which improve the understory light environment for the development of large advanced reproduction may also improve the fire environment, as the research of Vander Yacht *et al.* (2020) demonstrated by showing the importance of canopy disturbance and increased light levels to growth of grasses and forbs, fine fuels. This meant that large advanced reproduction were likely in areas where more fine fuels could accumulate and fuel moisture was lower, allowing the fire to reach them more readily than smaller individuals growing in higher-competition environments (Maynard and Brewer, 2013; Whitehead *et al.* 2006). The theory that more open growing conditions allowed the development of larger advanced reproduction and simultaneously contributed to their greater likelihood of topkill seemingly contrasts with findings from the analysis of fuel consumption, in which higher fuel consumption was observed around seedlings with a higher number of woody stems within 50 cm. These high stem counts could erroneously suggest a high-competition environment, however, if they were overtopped by the tracked seedling and did not affect local conditions to a great degree.

Shortleaf pine showed the opposite pattern in likelihood of topkill—a decreasing probability of topkill with increasing groundline diameter. It appears that shortleaf pine is able to develop some resistance to topkill within the range of groundline diameters studied, as found by Walker and Wiant (1966). This finding emphasizes the key element in an individual's ability to resist topkill—its bark thickness (Lawes *et al.* 2011; Nolan *et al.* 2020). Shortleaf pine develops sufficiently thicker bark at the same diameters as oak

and yaupon to resist topkill when they cannot (Walker and Wiant, 1966). As a result, it is more likely to resist topkill with increasing size in the range studied, even if that greater size is associated with a lower-competition environment that promotes fire. Shortleaf pine counts were low in all size classes and treatments, so population trends are not obvious when compared to oak and yaupon. However, shortleaf pine's ability to resist topkill at higher rates than similar diameter oak and yaupon may represent an important management implication in the restoration of these stands. Dense regeneration may not be required to maintain the overstory structure of a woodland system. Cannon *et al.* (2022) found that annual mortality of mature overstory trees was less than two stems per hectare, per year in a longleaf pine woodland. Understanding the annual rate of shortleaf pine mortality and quantifying the ability of low-intensity fires to selectively release shortleaf pine from competition may help managers maintain the shortleaf overstory component through time if burning is introduced when shortleaf is resistant and its competitors are not. Targeting periods when shortleaf pine is more likely to resist topkill than its competitors may be critical, as Fillingim (2023) demonstrated that while shortleaf pine can sprout following topkill, it will likely be overtopped and suppressed if there are faster-growing resprouting competitors nearby.

Sweetgum was not abundant in many of our sample plots, so varied treatment effects could not be definitively identified. Anecdotally, the ability of sweetgum (outside of our plots) to resist topkill from fire is more similar to that of pine and greater than that of oak or yaupon, but fire is reported to be a highly damaging agent to young sweetgum and led to decay and insect infestation over time (Kormanik, 1990). All species of interest except sweetgum were relatively well represented across all stands. This indicates that

sweetgum may be a more local management concern which requires targeted control efforts, as compared to the widespread and consistently abundant yaupon holly. As the restoration of these stands progresses, the increased light conditions in the understory will be more appropriate for the regeneration of sweetgum than they were previously, and root suckering in response to the disturbance is likely (Kormanik, 1967). If mature trees were not harvested or if root suckers escape damage from herbicide and prescribed fire, future seed production and establishment of seedlings may be an issue, especially during fire-free periods designed to recruit oaks and pines. However, sweetgum seeds are not widely dispersed by wind (Cuttenberg, 1952), so with the continued use of prescribed fire sweetgum will likely remain a more locally important species than yaupon following these restoration treatments. Monitoring and active management of the sweetgum populations across these stands remains an important objective, but intensive treatments may only be necessary in a localized, targeted manner.

While the overall effects of the three treatments series differed little, the relative counts of oak and pine as compared to yaupon increased across all three understory height classes in only the no-herbicide prescription. This disparity in the performance of small pines may be explained by the severe effects of herbicide on pine regeneration in the other stands, as the herbicide Detail (BASF Corporation, Research Triangle Park, NC, USA) in the spray mix applied in other treatments, in conjunction with glyphosate, is particularly damaging to pine species (Self and Ezell, 2022). However, the data do not offer a clear explanation of why small oaks in the stand not treated with herbicide seemed to be increasing in abundance relative to yaupon. Oak's consistent growth rate following topkill regardless of herbicide application indicates that oaks are relatively resistant to the

effects of the herbicide mix used in Boggy Slough's restoration treatments. However, previous research has demonstrated the negative effects on oaks by herbicides included in Boggy Slough's spray mix (Peairs and Clatterbuck, 2020). However, the mix rates used in this restoration treatment were lower than those typically used in southern plantation site preparation, as they were intended to reduce the vigor of competition rather than eliminate all understory vegetation. Since the data do not otherwise indicate particularly negative effects of the herbicide application on small oaks, the difference could be related to differences inherent to the sites, or to unknown historical treatments. While the mechanism behind the improved performance of oak is unclear, the performance of small oak and pine relative to that of small yaupon was noticeably better in the stand which received no herbicide treatment. Yet, all treatments effectively reduced competition from midstory and large understory yaupon.

Our analyses made clear that including herbicide in the prescription increased the rate of mortality, regardless of the species, supporting our expectations that herbicide would negatively impact all species. Mortality rates were low for all seedlings in areas not treated with herbicide, but the probability of mortality increased with increasing groundline diameter in treatments five and seven, both herbicide applications on the standard schedule and delayed by one year. Observationally, however, herbicide had a greater effect on pines and sweetgum than oak and yaupon. This effect was likely statistically undetectable due to the relatively small sample sizes for pine and sweetgum relative to oak and yaupon.

Our results supported our hypothesis that larger yaupon may shield smaller oak and pine advance regeneration from the herbicide application, thereby allowing release of

those smaller individuals following herbicide mortality of the larger, overtopping plants. Nix (2004) studied this effect in the release of overtopped cherrybark (*Q. pagoda*) and Shumard (*Q. shumardii*) oaks in the coastal plain of South Carolina and saw promising results. Our finding that larger individuals were more likely to suffer mortality from the combined effects of herbicide application and growing season prescribed burning than smaller individuals may also provide evidence of this effect. However, all herbicides used in Boggy Slough's treatment require thorough coverage of foliage for effective vegetation control (BASF, 2017; Dow AgroSciences, 2020; Monsanto, 2018), but sprouts may have a lower amount of leaf area exposed to the herbicide than larger stems while having similarly sized root systems. It is unclear whether increased mortality of larger individuals reflects shielding of the smaller individuals or if this may reflect insufficient leaf area for effective assimilation of herbicides and thereby control, which was not available on the smaller individuals. Other research has indicated that, much as better growing conditions lead to the larger individuals that are more likely to be topkilled by fire, better growing conditions also can increase the efficacy of herbicides (Hammerton, 1967; Riethmuller-Haage *et al.* 2007), although these studies are often done on herbaceous plants. While herbicide may enhance the control of large yaupon and sweetgum, it may have a counterproductive effect where advanced regeneration is dominated by oak and pine.

Height growth was analyzed separately for individuals that had resisted topkill and those that had been topkilled, with the understanding that sprout-origin stems often grow at different rates than seed-origin stems (Bond and Midgley, 2001). As seen in previous analyses, rates of topkill were very high in all stands treated with a burn, and

very low in those without a burn. For that reason, the analysis of growth for individuals that resisted topkill and those that were topkilled aligned with unburned and burned stands, respectively. The exception is the height growth of yaupon in the no-herbicide, growing season prescribed treatment combination. Sufficient yaupon resisted topkill and were topkilled in this stand to present the height growth of each.

Growth rates of individuals not topkilled differed among species prior to harvest with pine, yaupon, and sweetgum growing relatively slowly, and oak's growth rate was positively correlated with increasing initial height. This aligns with existing knowledge of pine and sweetgum preferring full light environments for optimum growth, and of yaupon being a moderately slow growing, understory plant (Walker and Wiant, 1966; Kormanik, 1990; Coladonato, 1992). It is widely understood that oaks can establish and grow to a competitive size as advanced regeneration with an intact overstory, particularly a relatively low-density overstory like that at Boggy Slough (Loftis, 2004). Larger oaks growing at greater rates than smaller oaks may represent a consistent relative growth rate. Alternatively, oaks sampled across the range of sizes may be similar in age or time of establishment while larger individuals occupy spaces of better growing conditions. In this case, the positive relationship between the initial height of an individual and its growth rate would reflect the microsite quality. Other research has indicated that size and age are not always positively correlated, and that overstory stems may be the same age as midstory stems that were suppressed during even-aged stand development (Guldin, 1994; Loewenstein, 2005). The dynamic seen between overstory and midstory stem ages may extend to larger and smaller understory stem ages as well.

Harvest benefitted the growth of pine and to a lesser degree yaupon, but it had mixed effects on oak and sweetgum. Following harvest, pine had a strong positive relationship between its initial size and its growth rate, reflecting the successful response of advanced reproduction to release through harvesting. This is unsurprising given the common historical use of shelterwood methods to regenerate pine throughout the Pineywoods (Rosson, 2000). Yaupon did not respond as rapidly but did demonstrate somewhat increased growth rates following harvest along with a positive correlation between initial size and growth. The negative correlation between initial size and height growth for oak was an unexpected result, given that shelterwood practices are often recommended for oak management, particularly when large advance regeneration is present (Loftis, 2004). The negative correlation between the growth of sweetgum and initial size is also difficult to explain. It is possible that larger oak and sweetgum were more likely to be damaged during logging, particularly given that pine tends to establish as an even-aged cohort in canopy gaps (Shelton and Cain, 2000; Brockway and Outcalt, 1998). If pines were clustered in gaps caused by mature tree death, there would not be reason for harvesters to enter those clusters. This is contrary to oak and sweetgum, which grow best in full sunlight, but could more easily establish under mature trees that were more likely to be cut during the harvesting operation, thereby exposing them to mechanical injury and subsequently resulting in reduced growth following logging events. Stanturf and Meadows (1994) elaborated on the importance of protecting advanced oak regeneration from logging damage on high productivity sites, where competition is likely to be intense. Smaller advanced reproduction of these species may

have been less likely to be damaged and therefore better able to take advantage of the release from overstory competition.

Growth of yaupon that resisted topkill from a spring growing season burn was strongly negatively related to the initial size of the individual. This aligns with observations in which large yaupon that were not topkilled by the fire often still sustained damage to foliage from high air temperatures during the fire, causing dieback over the course of the growing season. Delayed fire effects are not uncommon, and Yaussy and Waldrop (2010), found that mortality due to prescribed burning continued for four years following the treatment due to various damages and stresses. In contrast, smaller individuals may have experienced some foliar damage but had less height to recover and achieved positive height growth over the course of the season. Height growth was unrelated to initial height when topkilled by herbicide applied on the standard schedule and a subsequent spring growing season burn. However, it demonstrated a strong positive correlation between initial height and height growth following topkill during the growing season following a spring growing season burn only and an herbicide application delayed by a year followed by a spring burn.

Our results may indicate that herbicide applications one growing season following prescribed burning are more effective than herbicide applications two growing seasons following prescribed burning for reducing the growth of yaupon. It is not clear what may be driving this dynamic. Perhaps yaupon is still recovering from the loss of both its stems and evergreen foliage due to the dormant season burn when herbicide is applied at the end of the growing season. Moreira *et al.* (2012) showed that with great losses of aboveground biomass, root carbohydrates must be used to regrow shoots and leaves,

stressing the plant. Additionally, Pausas *et al.* (2015) reported that stomatal conductance is increased in the leaves on new sprouts, and Varanasi *et al.* (2016) demonstrated stomatal conductance is positively correlated with foliar herbicide efficacy. Delayed herbicide application would give yaupon more time to recover from the dormant season prescribed burn, but it would also give yaupon leaves more time to age. Chachalis *et al.* (2001) found that the leaves of some species developed a more hydrophobic cuticle with age, reducing the efficacy of glyphosate, one of the herbicides used at Boggy Slough. As such, decreased root carbohydrate reserves, increased stomatal conductance, and more hydrophilic leaf cuticles may have combined effects that improve the efficacy of herbicides in the control of yaupon one growing season following dormant season prescribed burning rather than two.

Oak's relationship between initial height and growth following topkill was consistently positive, similar to the pattern seen in oaks in an unharvested condition, but growth was consistently much greater following topkill than in the unharvested condition. Good growth following topkill among oaks is not surprising, given their well-known root-focused growth strategy and sprouting ability following topkill (Larsen and Johnson, 1998). Sander (1971) also demonstrated that the growth of oak sprouts was positively correlated with the size of the original advanced reproduction stem. These results indicate that providing the opportunity for large oak advanced regeneration to develop is important even if those individuals are subsequently topkilled by the reintroduction of fire, as their more rapid growth following topkill increases the likelihood of recruitment to the midstory without being overtopped by competitors.

Shortleaf pine did not demonstrate a positive relationship between initial size and height growth following topkill, in keeping with recent research by Fillingim (2023) in the Missouri Ozarks. The height growth of shortleaf pine following topkill was consistently less than that of oaks and yaupon. Fillingim (2023) hypothesized that this may represent divergent growth strategies between oaks and shortleaf pine, wherein shortleaf pine produces many short sprouts to maximize photosynthetic leaf area and replenish root carbohydrate stores, while oaks produce fewer, taller shoots to quickly overtop competitors. This finding reinforces the importance of capitalizing on the ability of shortleaf pine to develop resistance to topkill during a fire-free period at smaller diameters than some of its competitors.

Sweetgum showed growth patterns very similar to that of oak following a delayed herbicide application and spring growing season prescribed burn, but sample sizes were insufficient to estimate growth rates in the standard herbicide and no herbicide treatments. In general, it is expected that sweetgum would demonstrate greater growth rates than associated oaks (Dey, 2002), so this result may indicate the efficacy of this treatment combination in making oak more competitive with sweetgum. Additionally, research has found that fire improves oak's competitive position relative to fire sensitive competitors including sweetgum, but this effect is likely transitory without repeated prescribed burning (Brose *et al.* 1998). However, interpretability is limited by the lack of comparison between treatments and the single growing season worth of data.

Fuel Consumption, Facilitation, and Local Environmental Effects

By evaluating fire behavior at the stand level and seedling-level, we determined that stand-level variables had a greater influence on fire behavior and found no support for our hypotheses that high local counts of stems or “clumped” conditions would inhibit fire. Unsurprisingly, as most individuals in all burned stands beside the unharvested stand were topkilled, fuel consumption was strongly aligned with treatment. More interestingly, however, fuel consumption was not well predicted by understory yaupon counts, which heavily influenced the classification of seedlings as “clumped” or “lone”. We expected that “clumped” seedlings would see a lower degree of fuel consumption and concomitant reduction in topkill and mortality rates due to increased surface fuel moisture in the clumped microenvironment and the high moisture of live plant tissues (Agee, 1996), but our results did not support this hypothesis. This is potentially explained by the findings of Tiller (2020), who demonstrated that yaupon foliage is highly combustible. Understory yaupon with foliage at a low heights may be easily ignited during low intensity burns and does not constrain the spread of fire. Additionally, herbicide application could have led to the desiccation of these stems, making them more flammable. Engle and Stritzke (1990) observed increased damage from prescribed fire to juniper (*Juniperus* spp.) due to an herbicide application’s drying effect on the foliage.

Contrary to our findings regarding understory yaupon counts, the count of midstory yaupon stems was the best quantitative predictor of average fuel consumption. This aligned with our expectation that midstory yaupon thickets would create microenvironmental conditions poorly suited to the spread of fire due to their ability to suppress the growth and accumulation of fine fuels like grasses and promote higher litter moisture through dense evergreen shade and small, flat-lying, and compacted leaf litter.

Agee (1996) demonstrated the importance of fuel moisture in these microenvironments, and Nowacki and Abrams (2008) discussed this tendency of historically excluded fire-sensitive species to create fire-suppressing understory conditions across the eastern United States. Additionally, herbicides provided little control of yaupon thickets observationally, as only the edges could be treated with the boom sprayer. By means of these effects, dense thickets of yaupon could act as natural firebreaks, resulting in fire shadows with low average fuel consumption. This makes clear the importance of controlling yaupon thickets when restoring these upland stands and reintroducing regular prescribed fire, as opposed to targeting individual or small pockets of large yaupon that were shown to be relatively vulnerable in our other analyses.

There was no evidence for the facilitation of oak and pine by yaupon and sweetgum, but yaupon does seem to have some conspecific facilitative effects in dense clusters while remaining vulnerable as widely spaced, freely growing individuals. Research on prescribed fire and red maple (*Acer rubrum* L.) has revealed a similar phenomenon in which larger individuals at the middle of a sprout clump are protected by smaller individuals around the periphery of the clump from fire effects (Schweitzer *et al.* 2023). The greater stem counts directly around a given yaupon stem reduced the strength of the positive relationship between increasing groundline diameter and the likelihood of topkill. Similarly, large individuals with small nearby competitors have a very low probability of mortality – large individuals at the center of yaupon sprout clusters are unlikely to be topkilled or die. Other research has demonstrated that mortality rates from fire tend to be higher for smaller individuals of many species (Knapp *et al.* 2015; Waldrop *et al.* 1992). However, we found that small yaupon near large yaupon are less

likely to suffer mortality than large yaupon near other large yaupon. Perhaps yaupon stems become decadent and less vigorous with increasing size and age, and these small yaupon represent sprouts from the larger stem's root system which respond following the death of the main stem, while the main stem does not resprout.

Additionally, small yaupon associated with small neighbors have lower levels of survival. These stems are likely all sprouts and may reflect the death of single shoots while the clonal plant continues to grow via undamaged stems, such as those larger stems at the center of sprout clumps. This dynamic is reflected in other, better documented species such as quaking aspen (*Populus tremuloides*), in which the vigor and abundance of sprouts is related to the degree of shoot damage and death (Shier and Smith, 1979). In quaking aspen, this response is triggered due to an imbalance between crown produced auxins and root produced cytokinins (Perala, *et al.* 1990). With sufficient remaining live stems, living crowns produce enough auxin to suppress sprouting, and living shoots prevent cytokinins from accumulating in the root system and promoting sprouting (Perala *et al.* 1990). As such, disturbances must be sufficiently severe to lead to meaningful sprouting, and if a similar mechanism applies to yaupon, the death of a small number of sprouts would not be sufficient to promote the development of replacement sprouts. Also in quaking aspen, decadent, undisturbed clones, are less able to regenerate by sprouting than younger, more vigorous clones due to root die-off over time (Schier, 1975). Increasing rates of mortality in larger yaupon may have an analogous cause. None of these theories can be sufficiently substantiated by the evidence with a great level of confidence, however, these multiple lines of evidence indicate that larger, freely growing, yaupon are most likely to suffer topkill or mortality.

Limitations

Broadly speaking, the opportunistic quality of this study – taking advantage of several stands at multiple stages of restoration but not treated with a study design in mind – is one of its major limitations. The primary consequence is the lack of replication for findings of stand-level demographics changes. Due to the lack of replication, it is not possible to definitively state to what degree changes were caused by treatments as opposed to differences in site or the vagaries of implementation across a stand. That said, the managers at Boggy Slough felt that these stands were representative of most stands being restored there, and that the chronosequence structure was appropriate.

Sample size was a constraint in analyzing the effects of some treatments on sweetgum and pine. Sweetgum in particular was only locally abundant, which resulted in poor representation in the plots of all stands except Study Area 3. In contrast, shortleaf pine was well distributed throughout the stands, but was again locally abundant, so only small numbers were available in most plots. Revised methods to vary the sampling radius of different species based upon their relative abundance in the different species could have alleviated this issue.

Given the timeline of this study, we were unable to collect growth data following the dormant season burning in the harvested and unharvested stands. This information would have helped distinguish the effects of growing season burns from those of dormant season burns, but to some degree this information can be inferred from population demographics data.

Lastly, our ability to detect the effects of local environmental variables on fire behavior and effects was restricted due to our relatively sample size and the inherent

variability of fire behavior. Given number of levels within our independent variables, including seven treatment, four species, and two local density levels, and our sample size of 740 seedlings, there was little statistical power to draw conclusions about the effects of these different levels individually and in combination. We were able to generate some general findings regarding local environmental effects on the fire effects for yaupon, the species best represented, but no independent variables were significant for other species. These measures may have implications in terms of fire effects, but our sample sizes were too small and independent variables too numerous to demonstrate them statistically. Kabrick *et al.* (2015) selected the largest competitor within two meters to examine the effects of competition on shortleaf pine growth, and this sort of measure may have been more relevant to the modification of fire behavior than the nearest competitor within two meters, which was our measure.

Research and Management Recommendations

There is considerable potential for further research to help guide the restoration of Pineywoods uplands, varying from questions of theory to those more focused on practice. On the theoretical end, similar studies more focus on seedling-level dynamics could better elucidate any potential facilitation or other local-area effects on seedling survival and growth. Particularly useful would be greater sample sizes to increase statistical power in addition to a wider range of sizes tested, to help detect differences in size to achieve resistance to fire effects for lone individuals and those growing in denser environments. Additionally, more highly controlled burning conditions may help reduce the noise in fire behavior data and allow stronger conclusions to be drawn. In this study, there were no oak or yaupon large enough to have considerable resistance to fire effects without a high

level of moderation of fire behavior by the environment. This made it difficult or impossible to detect potential subtle effects of the seedling's local environment on outcomes.

It would be helpful to better understand the role that the herbaceous component of this system is playing, and the effects that the treatments have on it. Observationally, the areas treated with herbicide had much sparser herbaceous cover immediately following the treatment than the stand not treated with herbicide. It would be useful to know to what degree herbicide application affects the diversity of herbaceous flora and if this affects fire behavior. Investigation into the timeline from herbicide treatment to the recovery of equivalent herbaceous cover and diversity of a stand treated similarly, less herbicide, would also be valuable if the restoration of diverse pyrophytic ground flora is an objective.

Long-term prescribed burning studies are scarce. Additional knowledge about the effects of long-term burning with varying return intervals and seasonality would provide useful information to managers regarding the time it takes to exhaust root carbohydrate reserves for different species and how this varies by seasonality of burning. Existing studies like those of Waldrop (1987) and Knapp *et al.* (2015) have demonstrated the potential for annual burning to exhaust well-established oak and sweetgum and lead to eventual mortality, but similar evidence does not yet exist for yaupon. Of particular interest would be whether dormant season burning could select against yaupon, as it is evergreen and does not withdraw nutrients to its root system during the dormant season to the same degree as deciduous trees like oaks.

Finally, research into the rate of overstory mortality and whether it is balanced by recruitment from the understory and midstory following restoration treatments would be of great practical use. This would influence a better understanding of the degree to which overstory basal area should be reduced to promote herbaceous flora in conjunction with the reintroduction of fire. The overstory must not be thinned to the degree that there are insufficient midstory stems to keep pace with mortality and maintain the desired overstory structure thereafter. Leaving greater residual basal area would also provide additional large downed-woody-debris over time that could create fire shadows and facilitate pockets of regeneration in the future.

Based on the results of this study and observations in the field, several management actions may be recommended. Current management activities are successful in reducing midstory density and increasing fuel consumption. Removing midstory yaupon mechanically or chemically should be prioritized, as dense midstory yaupon appears to be the most significant impediment to the effective use of prescribed fire in these stands. In general, in areas where yaupon are more widely spaced, especially as individual or small groups of stems, prescribed fire without the use of herbicides may provide sufficient control to maintain these yaupon at small sizes through repeated topkilling and preventing the establishment of new individuals. Knowing that even large yaupon, when not in dense, continuous thickets, have very little resistance to topkill, fire-free periods to allow the release of accumulated advance regeneration of desired species until they develop resistance to topkill may be possible while yaupon remains sensitive. After this point, if fire is reintroduced, yaupon will likely be topkilled back to a ground-cover size and the larger desirable species can recruit to the overstory. A key question is

the density at which yaupon suppresses fine fuels and thus the effective reintroduction of prescribed burning, which should guide managers in making decisions regarding when yaupon densities are at a state that can support a fire-free interval.

Where there are large populations of sweetgum, prescribed fire alone appears unlikely to provide sufficient control unless implemented at very frequent return intervals (preferably annually), especially during the growing season (Waldrop *et al.* 1992). As such, the targeted application of herbicide to areas with large populations of sweetgum, along with the reintroduction of fire, is likely the best course of action for control in the short term. The use of herbicide spray mixes containing Detail (saflufenacil) where pine regeneration is desired should be avoided. The efficacy of the mix for control of sweetgum without Detail will have to be re-evaluated. To promote greatest herbicide efficacy for the control of yaupon, it should not be delayed more than one growing season following prescribed burning.

Chapter VI – Conclusion

This study took place in the Pineywoods of East Texas at the Boggy Slough Conservation Area and sought to further the knowledge of restoration treatment effects on regeneration dynamics in largely fire-excluded mixed pine-oak uplands. Fire suppressed stands often have significant competition from species historically restricted to fire-protected areas like bottomlands and drainages. Competition from yaupon and sweetgum in stands historically dominated by shortleaf pine and upland oaks has been especially challenging to managers attempting to restore these sites to their former structure and composition. Due to the ability of these well-established competitors to sprout vigorously following harvest or fire damage, a series of intensive treatments has been used at Boggy Slough to give oaks and pines a competitive advantage. The treatment series included harvesting, dormant season prescribed burning, herbicide application, and growing season prescribed burning. Several stands having been treated with various components of this sequence allowed the researchers to use a chronosequence to investigate the individual and combined effects of the treatments on pines, oaks, sweetgum, and yaupon.

We collected population-level data to examine trends in abundance within the species groups of interest in the midstory and across three height classes in the understory. In addition, we tagged 519 seedlings and collected data on their local environments, nearby competitors, and initial dimensions, and resampled these individuals after treatments to investigate growth, topkill, and survival across species, sizes, and local conditions. We analyzed these data to understand population-level trends,

seedling-level drivers of those trends, and local conditions that drove seedling level responses.

Results showed that the prescription used at Boggy Slough successfully restored the desired two-layered woodland structure by eliminating much of the dense midstory. Harvesting significantly improved the growth rate of advanced shortleaf pine regeneration, and larger advanced shortleaf pine regeneration was unlikely to be topkilled by fires that topkilled yaupon and oak. In addition, herbicide applications appeared to effectively control sweetgum and reduce the growth rate of yaupon, while not severely affecting oak advanced regeneration. Overall, treatments appeared to successfully reduce the abundance of large yaupon across these stands, and the tendency of larger yaupon to be readily topkilled by prescribed fires is promising for ongoing management using prescribed fire in these stands.

However, the abundance of small yaupon was not significantly affected by these treatments, including herbicide application, and consistent management in the future will be critical to avoid yaupon reasserting its domination of these stands. Additionally, the herbicide mix was effective at controlling desired advance regeneration of pine in addition to sweetgum, so revisiting the herbicide mix and removing the saflufenacil component may be necessary to allow shortleaf pine regeneration to establish.

Future research to illuminate the effects of repeated prescribed fire on the survival of yaupon and sweetgum would be valuable in guiding these restoration efforts in the future. Additionally, better understanding of the longer-term effects of these treatments, especially herbicide application, on species composition would be useful. Managers working to restore or otherwise manage upland mixed pine-oak sites like those at Boggy

Slough should take from this research that harvesting and the reduction of midstory density is key to the successful reintroduction of prescribed fire. Additionally, the herbicide spray mix used at Boggy Slough may not be necessary unless sweetgum is present or there are very high densities of yaupon that will not be controlled by fire. Lastly, protecting large advance shortleaf pine reproduction prior to the reintroduction of prescribed fire will likely result in some recruitment to the midstory as its competitors are more readily topkilled by fire at similar sizes.

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