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An evaluation of vegetation response and forage availability for Odocoileus virginianus to fire seasonality in pine ecosystems in the southeastern United States

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To the Graduate Council:

I am submitting herewith a thesis written by Jacob Thomas Bones entitled "An evaluation of vegetation response and forage availability for Odocoileus virginianus to fire seasonality in pine ecosystems in the southeastern United States." I have examined the final electronic copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Wildlife and Fisheries Science.

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An evaluation of vegetation response and forage availability for *Odocoileus virginianus* to fire seasonality in pine ecosystems in the southeastern United States

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ABSTRACT

I evaluated the response of vegetation composition and structure, forage availability, and nutritional carrying capacity (NCC) for white-tailed deer (*Odocoileus virginianus*) in four seasons of burning nine pine stands in Tennessee, Mississippi, Alabama, and South Carolina, 2020–2023. I used data that we collected during the growing seasons of those four years to examine changes in composition, structure, and selected white-tailed deer (*Odocoileus virginianus*) forage to dormant season (January–March), early growing-season (April–May), mid-growing-season (June–July), and late growing-season (September–October) prescribed fire after two treatment iterations. I observed significant changes in the plant community and structure. Fire treatments moved the composition of the understory to more herbaceous species, which increased species diversity indices and resulted in a more open structure compared to the unburned Control stands. Quality of selected deer forages increased after two iterations of fire treatments, where all burned units had a greater nutritional carrying capacity compared to unburned Control units. My results highlight the importance of burning during all seasons of the year to enable more burn opportunities and grater flexibility in managing for white-tailed deer as well as other wildlife species.

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INTRODUCTION

Prescribed fire is a necessary management tool to maintain many plant communities that provide crucial resources for various wildlife species in the southeastern United States. Fire is a form of disturbance that can set-back or maintain ecological succession and enables shade-intolerant plant species to compete against encroaching hardwood species (McGranaham 2021). Pines such as shortleaf (*Pinus echinata*) and longleaf (*P. palustris*) depend on frequent fire disturbance to maintain a dominant position in the canopy (Brown and Smith 2000). These species declined in prevalence in the Southeast during the 19th and 20th centuries because of over-harvesting, fire suppression, and hardwood encroachment (South and Buckner 2004). Loblolly pines (*P. taeda)* were planted in the place of longleaf and shortleaf and became the dominant pine species on the landscape (Fox 2007).

Traditionally, managers have burned pine systems during the dormant season to set-back vegetation (Brockway 1997). The recurring use of fire consumes the litter layer, allows sunlight to reach the understory, and stimulates the seedbank (Keely 2009b). However, recent research and observation following management has indicated that diversifying timing of burning may lead to differential effects on the resulting plant composition (Towne 2008, Gruchy et al. 2009), which can have important implications for wildlife. Implementing prescribed fire during "non-traditional" times of the year also increases the number of potential burn days (Chiodi et al. 2018). Previous research has concentrated on investigating effects following fire during the dormant and early growing season (Streng 1993, Cronan et al. 2015, Decker et al. 2019). Scant data are available that compare fire effects during all seasons of the year. This study will examine the initial fire effects on vegetation composition and structure following burn treatment during all seasons of the year.

Yellow pines, including shortleaf and longleaf, have physical characteristics that contribute to their overall fire tolerance when compared to other tree species. Loblolly pines are considered as part of this group, but they do not share the same physical characteristics that make them as tolerant of fire (Stewart et al. 2015). Adaptations such as the basal crook of shortleaf pine allow seedlings and smaller trees to resprout following fire because of the underground bud that is shielded from the fire, just above the root collar. (Lilly et al. 2012). Other adaptations include thicker bark for insulation (Pausas 2015) and self-pruning that lessen the chance of fire reaching the canopy (Keeley 2012). These traits ensure that frequent, recurrent fires are less likely to harm mature trees and seedlings. If frequent fire is eliminated from the landscape, longleaf, shortleaf, and loblolly pine commonly are outcompeted by faster-growing hardwoods, such as sweetgum (*Liquidambar styraciflua*), elms (*Ulmus spp.*), maples (*Acer spp.*), or yellow-poplar (*Liriodendron tulipifera*), or the trees may persist with slower-growing hardwoods, such as hickories (*Carya spp.*) and oaks (*Quercus spp.*), but the shade of those species prevent future regeneration of pines and they are ultimately lost from the system (Robertson 2021). Fire provides a competitive advantage for these pine species when faced with hardwood encroachment because they are able to tolerate frequent fires. Pines are part of the mid-successional plant community and will be succeeded by other species without disturbance because hardwood tree species will eventually replace them in the overstory.

Historical accounts of explorers indicate coverage of longleaf and shortleaf pine was expansive throughout the southeastern US. Harvest records from the period indicate approximately 90 million acres of longleaf pine were cleared by 1900 (Rauscher et. al 2004). In the early part of the 20th century, the U.S. Forest Service led programs that discouraged the use of intentional fire with the belief that fire discourages or prevents forest regeneration and was a damaging agent to forests (Rother et. al 2020). Although burning continued in some parts of the Deep South, much of the historic range of shortleaf and longleaf pine experienced a period of fire suppression throughout the 20^{th} century. Much of the acreage previously covered in naturally regenerated yellow pine was converted to farmland. Once cash crops such as tobacco declined in the latter half of the century because of soil depletion and erosion, landowners began stocking loblolly pines in soil that had been depleted by agriculture, backed by funding provided by the Conservation Reserve Program (CRP) when that became available in 1985 to prevent further topsoil erosion (Londo et. al 2002). By 1999, loblolly pine plantations occupied 32 million acres on the landscape (Fox 2007), creating a need for management of the vegetation communities associated with them.

Since European settlement of the southeastern United States, as well as the pre-settlement era, fire has played a critical role in maintaining many pine ecosystems (Ryan et al 2013, Rother et al. 2020). Land-use change and silvicultural practices of yesteryear ensured these communities would not persist (Frost 1993). Loblolly pines were widely planted in the mid- to late twentieth century for increased fiber production (Fox 2007). Managers commonly burn loblolly pine plantations during the dormant season to reduce hardwood competition. The dormant season is a time that often has more stable weather patterns and less humidity, which facilitates burning. As fire research began to increase in the mid-20^{th} century, especially in longleaf pine systems, managers began to use fire in different seasons (Rother et. al 2020).

Fire can have direct and indirect effects on wildlife, many of which are dependent on burn coverage, intensity, and season of burning. Direct effects kill or injure wildlife. Indirect effects of fire influence food and cover resources and also can influence habitat use, daily movements, and home range size. Wildlife use of burned areas varies by species and time since the areas were last burned as the vegetation composition and structure changes over time. A diverse assemblage of understory vegetation can increase the number of insects present (Siemann 1998), which are a food source for many bird species including flycatchers (*Tyrannidae spp.*), wild turkey (*Meleagris gallopavo*), and some warblers (*Setophaga spp.*), as well as amphibians and reptiles. Lower vegetation height and a more open structure at ground level aids in brood rearing for northern bobwhite (*Colinus virginianus*) and wild turkeys (Martin 2012), as well as improved foraging conditions for white-tailed deer (*Odocoileus virginianus*), hereafter, "deer" (Lashley 2011). A host of wildlife species use areas that are maintained by frequent fire at various stages of their life history. Often, wildlife begin using areas immediately after burning. Direct effects, including mortality, depend on factors such as intensity, rate-of-spread, firing methods, and timing (Lyon et. al 1978). Herpetofauna are considered some of the most vulnerable species to fire, but many species exhibit traits that help them escape fire (Russell et. al 1999). Specifically, eastern box turtles (*Terrapene carolina carolina*) commonly burrow, flee, or withdraw into their shell (Harris et. al, 2020). Overall reptile captures were greatest in fire-maintained pine woodlands, particularly for Great Plains rat snake (*Elaphe emoryi*), fence lizard (*Sceloporus undulatus*), and ground skink (*Scincella lateralis*) (Perry et al. 2009). Once areas have been burned, many species take advantage of the responding plant community.

When most of the vegetation in the understory or midstory is consumed, the resulting structure is more open, providing a variety of subsequent benefits to wildlife that benefit from an understory dominated by herbaceous plants. Recently burned areas often are highly selected by deer because resprouting vegetation typically has greater nutritional value because of increased digestibility of the relatively young plant material (Westlake 2020). The open structure in the stand is beneficial for flycatchers and woodpeckers that require less "clutter" for foraging

(Knight 2005). Other bird species that forage and nest on the ground, such as northern bobwhite, use such areas extensively as there is typically open space at ground level under forb cover, which facilitates foraging for seed and insects (Hernandez 2007). Male wild turkeys also frequent areas soon after burning for foraging and mate attraction (Dickson 1992).

Nesting conditions for northern bobwhite are greatly improved when bunchgrass and forb species are abundant, and brood-rearing structure provided by annual forb species benefits both bobwhite and wild turkey (Devos et. al 1993, Kilburg et al. 2014, and Richardson et al. 2020). Additionally, the insects associated with these plants provide quail chicks and turkey poults with critical nutrition in the first few weeks after they hatch (Hernandez 2007). Nutritional carrying capacity can be influenced by an increase in forb coverage following growing-season burns, but is often avoided by lactating does because of decreased visual obstruction (Lashley 2015). Both annual and perennial forbs also yield higher-quality forage than woody species for white-tailed deer during the summer months, a period in which does are lactating and bucks are growing antlers (Hewitt 2011).

Fire return interval relates to time between fire events and can affect plant composition and structure. Several factors, such as latitude, annual precipitation, site productivity, and management objectives determine the most appropriate interval. In general, more shade-intolerant herbaceous species are promoted with a short interval, and more intermediate or shade-tolerant species, including semi-woody and woody species, are promoted with longer fire-return intervals. Typically, annual and perennial herbaceous plant species are replaced by semi-woody and woody species within 3 years after fire (Drewa et al. 2002). Although woody cover is necessary for many game and non-game species, it can dominate the understory and decrease herbaceous plant coverage without frequent disturbance. Fire intensity is another factor that must be considered when implementing prescribed fire in any environment. Intensity relates to the amount of energy of a fire when consuming fuels within a given amount of time (Heward 2013). Intensity is an important consideration because the amount of heat that a given fire creates, combined with residence time, influences top-kill of woody species (Keeley 2009a).

Burning in the growing season can change the composition of herbaceous plants to include more forb species, but little work has been conducted in the latter portion of the growing-season. (Knapp et al. 2009 and Robertson and Hmielowski 2014). Extensive work has demonstrated that dormant-season fire promotes resprouting of woody and semi-woody vegetation, including trees, shrubs, and brambles. Pine stands burned during the dormant season typically have greater coverage of grass species (Sparks et al. 2009).

Burning during different seasons of the year may influence plant composition. Late growing-season burning in the months of August and September in early successional communities may control woody stems that can dominate the understory (Gruchy et al. 2006). Late growing-season fire in hardwood systems may reduce density of woody stems and coverage of native warm season grasses while increasing forb coverage (Harper et al. 2016). Burning during the growing season not only increases the number of forbs present, but also may enhance availability of crude protein and phosphorus, which is strongly selected by deer (Rainer 2021). Varying the season of burn can diversify plant communities, increase available forage for deer, reduce the coverage of woody vegetation, and better meet the management objectives specific to each landowner or land manager (Greene 2016, Lashley 2015b, Meunier 2021).

Many state and federal agencies as well as private landholders in the southeastern United States manage yellow pine systems. There has been an increase in the restoration effort of both longleaf and shortleaf species as well as properties that still have naturally regenerated loblolly, shortleaf, or longleaf pine (Frost 2006, Hedrick 2007, Mitchell 2009). Land managers would benefit from increased knowledge of how burning at different times of the year can affect plant composition and structure and the resulting influence on wildlife. The purpose of this research is to investigate the effects of burning at different times of the year as related to the plant community and relate how burning at different times of the year may influence either food or cover for wildlife, particularly white-tailed deer.

The main objective of this study is to investigate the effects of burning during different seasons of the year on plant community composition and structure in mid-rotational stands of loblolly and shortleaf pine. The specific objectives are:

1. Compare the vegetation composition, structure, and diversity indices following dormant-, early growing-, mid-growing-, and late growing-season fire.
2. Compare forage availability estimates and nutritional carrying capacity (NCC) estimates for white-tailed deer following treatments to determine if burning during different seasons has a differential effect on NCC.

CHAPTER 1. AN EVALUATION OF VEGETATION RESPONSE TO PRESCRIBED FIRE SEASONALITY IN PINE ECOSYSTEMS OF THE SOUTHEASTERN UNITED STATES

ABSTRACT

Open pine woodlands occur throughout the southeastern United States. Thinning and prescribed fire commonly are used to establish and manage pine woodlands for multiple objectives, often including timber production and wildlife habitat. Although fire effects in pine woodlands have been summarized widely, information is lacking on the effects of fire during different seasons of the year, and no study to date has provided fire effects on the vegetation community following fire treatments during all seasons of the year. We implemented fire treatments in the dormant, early growing-, mid-growing-, and late growing-season on a 2-year fire-return interval to evaluate the effects of fire season on understory composition, structure, species richness, and evenness. Fire intensity and burn coverage were greatest in the dormant-season treatment and least in the mid-growing-season treatment. Coverage of semi-woody and woody plants in the understory decreased in all treatments compared to control. However, when compared to pretreatment levels after two fire events, coverage of semi-woody and woody plants increased following the dormant- and mid-growing-season treatments but remained consistent in the early- and late growing-season treatments, indicating growing-season fire sets-back semi-woody and woody vegetation better than dormant-season fire if intensity is adequate to top-kill the plants. Coverage of forbs increased following all seasons of burning, but the increase was greatest in the dormant- and late growing-season treatments, which did not set-back or kill warm-season forbs during their growth cycle. Coverage of grasses decreased in all treatments and control as sunlight entering the canopy was reduced from an average of 54% to 39% over 4 years as overstory tree crowns expanded following thinning. Visual obstruction was reduced most by early growing-season fire. Diversity index score was improved following dormant- and early growing-season fire, but species richness increased in all treatments as well as control.

We documented changes in plant composition and structure as related to fire seasonality and intensity after 2 fire events on a 2-year fire-return interval. All fire treatments changed understory composition significantly, and each produced different effects that could allow for better management of systems dominated by Southern yellow pines. Growing-season fire offers more flexibility throughout the year to accomplish objectives, including wildlife habitat management, beyond the traditional dormant-season burn window.

INTRODUCTION

Fire plays a critical role in maintaining pine ecosystems in the southeastern US (Pyne 1982, Mitchel and Duncan 2009, Ryan et al. 2013). Fire sets-back or maintains ecological succession, enables shade-intolerant plant species to compete against encroaching hardwood species, and influences food and cover availability for many wildlife species (Wilson et al. 1995, Drewa et al. 2002, Steen et al. 2013a, Harper et al. 2016, McGranaham and Wonkka 2021). Several pine species have physical adaptations that allow them to persist with frequent fire (Keeley 2012, Lilly et al. 2012, Pausas 2015). The recurring use of fire consumes the litter layer, allows sunlight to reach the understory, and stimulates pine seed and other shade-intolerant species to germinate (Keeley et al. 2009b). Species such as shortleaf pine (Pinus echinata), loblolly pine (P. taeda), and longleaf pine (P. palustris) depend on frequent disturbance to maintain a dominant position in the canopy (Mitchell et al. 2006, Stambaugh et al. 2020). Frequent fire that is intensive enough to suppress hardwood encroachment and competition ensures these pine ecosystems can persist.

Fire frequency and intensity regulate plant composition and structure (Glitzenstein et al. 1995, Beckage and Stout 2000). Frequent fire-return intervals are common where Southern yellow pine ecosystems are maintained (Sparks et al. 2002, Stambaugh et al. 2011, Robertson et al. 2021). In the third and fourth years following a fire, plant communities commonly shift to more semi-woody plants (such as Rubus spp.) and pioneering tree species (such as sweetgum [Liquidambar styraciflua], winged elm [Ulmus alata], and red maple [Acer rubrum]; Stewart et al. 2015, Gonzalez-Benecke et al. 2015, Meunier et al. 2021). Establishing a fire-return interval of 1–2 years (Arthur et al. 1998, Vander Yacht et al. 2020) that favors an herbaceous-dominated plant community may lead to a more diverse understory with reduced hardwood encroachment that ultimately would compete with overstory pines (Masters 2006, Darracq et al. 2016). Fire intensity also is important because low-intensity fire may not top-kill relatively small-diameter hardwood stems, and as these stems get larger, especially without frequent fire, they are able to grow into the overstory (Keeley 2009a). The effect of fire intensity and frequency on plant structure strongly influences wildlife use as some species prefer a more open environment whereas others select more dense cover (Steen et al. 2013b, Barton et al. 2014, Rosche et al. 2019, Turner et al. 2024). Relatively low-intensity fire may mimic historical fire regimes (Huffman 2006), can prevent overstory mortality, and still accomplish many management objectives (Wade and Johansen 1988).

Traditionally, managers have burned pine systems during the dormant season to reduce hardwood competition and set-back succession (Brockway and Lewis 1997, Rother et al. 2020). Weather patterns are relatively stable with less humidity during the dormant season than at other times of year, which facilitates burning (Waldrop and Goodrick 2012, Weir 2009). However, chronic dormant-season burning promotes the continual resprouting of top-killed trees and, if fire-return intervals are 1–2 years, understory communities often become dominated by grasses with relatively low species diversity (Sparks et al. 2009, Ryan et al. 2013, Resop et al. 2023). Increased species diversity, especially to include more forb species, benefits many wildlife species by providing enhanced food and cover resources (Carlson et al. 1993, Lashley et al. 2015, Block et al. 2016, Harper et al. 2021). Burning during the growing season may influence plant composition differently than burning during the dormant season (Waldrop et al. 1992, Howe 2011, Whelan et al. 2018). Recent research has begun to evaluate the differential effects of burning during the dormant and growing season, but most of this work has involved fire during the early portion of the growing season (April–June) and not later in the year (Streng et al. 1993, Hiers et al. 2000, Cronan et al. 2015, Decker and Harmon-Threatt 2019, Rother et al. 2020). Varying the season of burning may help diversify plant communities and reduce prevalence of woody species in the understory (Robertson and Hmielowski 2013, Lashley et al. 2015, Greene et al. 2016). Furthermore, burning during all seasons of the year increases the number of potential burn days (Chiodi et al. 2018) and may provide managers more opportunities to reach objectives.

Although previous research has investigated the effects of early growing-season fire (Harrington 1993, Melcher et al. 2023), few have looked at the effects of burning later in the growing season, whether in old-fields, hardwood systems, or pine systems (Lewis et al. 1964, Gruchy et al. 2006, Towne and Kemp 2008, Reilly et al. 2017, Ulyshen et al. 2021). Fire intensity during the mid- (June–July) to latter portions of the growing season (September–October) can be limiting in hardwood systems because of increased fuel moisture (Varner et al. 2015), and reduced fire intensity and burn coverage can promote an understory dominated by woody plants and brambles (Turner et al. 2024). Burning during the late growing season can influence plant composition by reducing coverage of woody species and native warm-season grasses and increasing coverage of forbs (Lewis et al. 1964, Gruchy et al. 2006). Additional work comparing the effects of burning during all seasons of the year in pine-dominated systems is needed to better guide decision making and meet management objectives (Knapp et al. 2009, Harper et al. 2016).

To gain a better understanding of the differential effects of burning throughout the year on plant communities in Southern pine ecosystems, we implemented a field experiment across nine sites in four states that included dormant, early growing-, mid-growing-, and late growing-season fire treatments with an unburned control. We hypothesized that burning during different seasons of the year would have a differential effect on plant composition and structure. We predicted growing-season fire would lead to increased forb coverage and decreased woody plant coverage in the understory, whereas dormant-season fire would lead to increased grass and woody plant coverage in the understory. We predicted early growing-season treatments would have a more open structure in the growing season following fire treatments, and midstory stems would be reduced by all treatments. We also predicted fire intensity and spread would be reduced with mid- and late growing-season fire compared to dormant- and early growing-season fire because of increased fuel moisture and greater relative humidity during the mid- to late growing season. Therefore, we also predicted there would be a greater reduction in midstory stems in the dormant- and early growing-season treatments. Lastly, we hypothesized all fire treatments would affect plant species richness, evenness, and diversity when compared to the unburned control. We predicted species richness would increase with all fire treatments, and we predicted species evenness and diversity would increase following mid- and late growing-season fire because of reduced fire intensity leading to a more even distribution of different plant species.

METHODS

Study area

We conducted our study at nine sites dominated either by loblolly or shortleaf pine in Tennessee, South Carolina, Alabama, and Mississippi, USA (**Table 1.1**, Turner and Harper 2024). Two sites in Tennessee included the Foothills Wildlife Management Area (WMA) in Blount County and the Bridgestone/Firestone Centennial Wilderness WMA in Van Buren County, both owned by the Tennessee Wildlife Resources Agency. The Foothills site had an overstory dominated by shortleaf pine and was 83 years old. The Bridgestone site was a shortleaf pine planting that was planted in 2014 and was dominated by shortleaf pine. Two sites in South Carolina included the Belfast WMA in Laurens County and the Hamilton Ridge WMA in Hampton County, both owned by the South Carolina Department of Natural Resources. The Belfast site had a loblolly pine overstory and was 27 years old. The Hamilton Ridge site also had a loblolly pine overstory and was 31 years old. Three sites in Alabama included the Barbour County WMA in Barbour County that was owned by the Alabama Wildlife and Freshwater Fisheries Division, and Mason Bend in Perry County, and Folsom in Hale County, both of which were privately owned. The Barbour site had an overstory dominated by loblolly pine and was 24 years old. Mason Bend had a loblolly pine overstory and was 21 years old. Folsom also had a loblolly pine overstory and was 18 years old. Two sites in Mississippi included the Copiah County WMA in Copiah County, owned by the Mississippi Department of Wildlife, Fisheries, and Parks, and Triple Creek in Clarke County, which was privately owned. Copiah had a shortleaf pine overstory and was 61 years old. Triple Creek had a loblolly pine overstory and was 25 years old. Annual average precipitation and temperature were similar among sites, ranging from 115 cm to 148 cm and 13 °C to 19 °C (U.S. Climate Data, 2024).

Study design

We used a randomized complete block design with each site serving as a treatment replicate (n = 9). We established five treatment units at each site, including dormant-season fire (DOS), early growing-season fire (EGS), mid-growing-season fire (MGS), late growing-season fire (LGS), and a control (CTL) that was not burned. We defined DOS as January through March, EGS as April through May, MGS as June through July, and LGS as August through October. The beginning of the EGS coincided with full leaf emergence of deciduous species, not just emergence of buds or when leaves of the earliest species appeared. Our treatment units were approximately two ha each and we delineated them with permanent firebreaks. We established four permanent plant sampling plots that were randomly located in each treatment unit, totaling 20 per site. We placed a metal post in the middle of each plot to define plot location.

We used relatively low-intensity fire to limit injury to overstory trees. Our firing technique depended on fuel moisture and consumption, wind speed, and relative humidity (RH). We initiated each burn with backing fire and, depending on intensity, we continued to use backing fire or applied flanking or strip-heading fire to achieve average flame lengths of about 40 cm. Our objective was to consume fine fuels and burn with sufficient intensity to top-kill semi-woody and woody species in the understory. All burns were conducted with 30–60% RH, 1–4 m/s surface winds, and 4–35 °C ambient temperature.

We implemented our fire treatments on a two-year fire-return interval beginning October 2020 after pre-treatment data collection in June–July (see Turner and Harper [2024] for evaluation of pre-burn conditions). A two-year return-interval commonly is used to maintain open pine woodlands and prevent woody species from dominating the understory and shading-out herbaceous plant species (McCord et al. 2014, Turner et al. 2024). We initiated treatments in

October 2020, beginning with the LGS fire treatment. We implemented the first iteration of the DOS fire treatment in January to March 2021, followed by the EGS fire treatment in April and May 2021. The MGS fire treatment was completed in June and July 2021 at all sites immediately following vegetation data collection. The second iteration of the LGS treatment was completed in September and October 2022. We completed the second DOS treatment in February and March 2023, and the second EGS treatments in April and May 2023. We completed the second MGS treatment in June and July 2023 immediately following vegetation data collection at each site.

We recorded fire behavior during and after each fire. We recorded firing methods as backing, flanking, or strip-heading fires. We logged air temperature, in-stand wind speed, and relative humidity using a Kestrel weather meter (Nielson-Kellerman, Boothwyn, PA, USA) at the time of first ignition. We then documented average flame length and rate of spread during the fire event. We defined flame length as the distance between the tip of the flame and the ground (or the surface of the remaining fuels) midway in the zone of active flaming (Rothermel and Deeming 1980). We estimated this height based on surrounding vegetation or other objects as a reference and repeated this measurement ten times along the active flame front to calculate an average. We also calculated the rate of spread from the same points along the flame front by recording the distance fire moved from each point in 60 seconds. We averaged these measurements and converted them to meters per hour. We recorded fire intensity using ceramic tiles (hereafter “fire tiles”) with Tempilaq temperature sensitive paint (LA-CO Industries, Inc, Elk Grove Village, IL, USA). We painted fire tiles with ten colors, each representing a temperature from 149 °C to 427 °C. We wrapped each tile in aluminum foil to protect the paint from ash and other debris, labeled them, and placed tiles upright within each of the four fixed sampling plots within each treatment unit prior to ignition. We collected the tiles after each burn and recorded the maximum temperature indicated by the highest temperature paint color that melted. Beginning with the LGS treatment in Fall 2022, we also monitored fire temperature using UX-100 HOBO dataloggers and 12” Type K thermocouples (Onset Computer Corporation, Bourne, MA, USA). We deployed dataloggers at each of the sampling plots alongside fire tiles prior to ignition. Dataloggers were capable of recording temperatures ranging from 0–900 °C at one-second intervals. After each fire treatment, we mapped unburned areas using a smartphone application (OnX Maps, Missoula, MT, USA) or a handheld GPS to compare burn coverage among seasons and between treatment years.

We sampled understory (<1.4 m tall) vegetation composition using line-point sampling (Godínez-Alvarez et al. 2009). We recorded vegetation along four, 50-m transects, each centered at one of the four sampling plots within each treatment and control unit. We identified vegetation to species at every meter mark, totaling 50 points per transect. We grouped understory plant species into vegetation class categories of brambles (Rubus spp. and Smilax spp.), forbs, ferns, grasses/sedges, shrubs, trees, vines, and “other” (bare ground, leaf litter, rock, moss, woody debris). We classified overstory trees as those >11.4 cm DBH. We recorded DBH of overstory species in a 11.3-meter-radius plot centered at each sampling point. We classified midstory trees as those <11.4 cm DBH and >1.4 m in height. We tallied all midstory trees in 5.0-meter radius plots.

We measured vegetation structure at the 15- and 35-meter marks along each transect using a modified vegetation profile board (Nudds 1977). The profile board was two meters tall, 0.25-m wide, and was divided into five strata. We estimated visual obstruction and recorded a visual obstruction value for each stratum, ranging from 0–5. A value of zero represented no visual obstruction, one represented 1–20% obstruction, two represented 21–40% obstruction, three represented 41–60% obstruction, four represented 61–80% obstruction, and five represented 81–100% obstruction. We estimated these values with one person kneeling at the center of the plot, looking toward the board, which was held by another person at the 15- and 35-meter marks. We measured photosynthetically active radiation (PAR) using two paired Accupar LP-80 ceptometer readings (Meter Environment, Pullman, WA, USA). One ceptometer was used outside of the stand with no canopy obstruction, and the other device was used to take 20 paired readings every 1 m, centered on the fixed points within each stand. The in-stand observer communicated with the out-of-stand observer with a radio or cell phone that ensured the paired readings were recorded at the same time. These measurements provided PAR within each treatment by dividing each reading taken in-stand with their associated reading outside the stand (Wall et. al 2010, Turner et al. 2024).

DATA ANALYSIS

We analyzed each vegetation class, midstory and overstory stem count, basal area, diversity index, PAR, and visual obstruction using Program R (R Foundation, Vienna, Austria) with mixed-effects ANOVAs in the nlme package (Pinheiro et al. 2022) to detect changes resulting from fire treatments from 2020–2023 in a repeated measures analysis. We used “Site” as a random effect, and averaged transect values to provide a stand level average for each site. We set our alpha level at 0.05, performed a Tukey’s post-hoc test, and assigned letters of significance for each category of interest using the emmeans (Lenth 2023) and multcomp packages (Hothorn et al. 2008). We performed ANOVAs to compare differences in fire temperature, rate-of-spread, flame length, and burn coverage between seasons. We used our burn coverage maps to create a buffer with a 25-m radius around each sampling point to ensure transect data did not include areas in a treatment unit that did not burn in the previous treatment. We calculated percent coverage of each vegetation class by dividing the number of observations of each vegetation class by the number of points for each transect. We also calculated plant species richness, the Shannon-Wiener diversity index, and species evenness for each treatment and year. Species richness was calculated by a count of the number of species we recorded in each treatment per year. We calculated the Shannon-Wiener diversity index with the formula $H= -\sum (p_i \times \ln p_i)$ where H is the diversity index and p_i is species abundance divided by the total abundance. We calculated species evenness with the formula $E=H/H\_MAX$, where E is species evenness, H is the Shannon-Wiener diversity index, and HMAX is the natural log of the species richness. We converted visual obstruction to percentages, averaged from readings on both transects for each stratum, then averaged by treatment. We summarized values into categories of <0.5 m, <1 m, <1.5 m, and <2 m.

RESULTS

Average burn coverage for both rounds of fire treatment was greater in the DOS and EGS treatments than in the LGS and MGS treatments ($P \leq 0.05$; **Table 1.2**). Fire temperatures (°C) recorded by fire tiles in both iterations of treatment implementation were greater in the EGS (176.4±31.2) and DOS (172.9±17.6) treatments than in the LGS (93.4±16.0) and MGS (44.4±15.4) treatments ($P \leq 0.007$). In the second round of treatments implemented in 2022–2023, fire temperatures recorded by dataloggers were greater in the DOS treatment compared to the MGS treatment ($P = 0.047$), but fire temperatures in the EGS and LGS treatments were similar ($P > 0.05$; **Table 1.2**). Average flame lengths in the DOS treatment were taller than in EGS, LGS, and MGS ($P \leq 0.001$). Rate-of-spread in DOS treatment was greater than in MGS and LGS treatments ($P \leq 0.02$), but not different from the EGS treatment ($P > 0.05$; **Table 1.2**).

Forb coverage increased in all treatments ($P \leq 0.039$), but the greatest effect occurred in the DOS and LGS treatments ($P < 0.001$; **Table 1.4** and **Figure 1.2**). Coverage of grasses did not differ by treatment (**Table 1.4** and **Figure 1.3**) but decreased in all treatments and control over the course of the study ($P \leq 0.001$). Semi-woody plant coverage decreased in the DOS, EGS, and LGS treatments ($P \leq 0.027$), but the effect size was greatest ($P \leq 0.004$) in the EGS and LGS treatments (**Table 1.4** and **Figure 1.4**). Understory woody plant coverage, which included tree seedlings and sprouts <1.37 m tall, decreased in all treatments ($P \leq 0.009$) when compared to control (**Table 1.4** and **Figure 1.5**). All treatments reduced ($P = 0.001$) the number of midstory stems per hectare (**Table 1.5** and **Figure 1.6**) when compared to control, but density of midstory stems did not differ among treatments.

The number of overstory trees per hectare decreased by an average of 10.9±4.7 in all treatments and control from 2020–2023 ($P = 0.022$). Overstory basal area increased by 1.7±0.6 m2/ha in the DOS treatment ($P = 0.005$), 2.4±0.6 m2/ha in the MGS treatment ($P < 0.001$), and 2.6±0.6 m2/ha in the LGS treatment ($P <0.001$; **Table 1.5**). PAR values declined ($P < 0.001$) by an average of 15% in all treatments and control over the duration of the study, but PAR in the DOS treatment was greater than control ($P = 0.037$; **Table 1.5** and **Figure 1.7**).

Visual obstruction below 0.5 m was reduced ($P < 0.001$) in the EGS treatment. Percent visual obstruction below 1 m was reduced in all treatments compared with control ($P \leq 0.031$), but visual obstruction below 1 m was least in the EGS treatment (72.1±3.07, $P < 0.001$). Visual obstruction below 1.5 m and 2 m were reduced ($P < 0.001$) in all treatments compared to control, but there was no difference among treatments (**Table 1.6**).

Plant species richness increased over time in all treatments and control from 131 species in 2020 to 224 in 2023 ($P = 0.013$; **Table 1.7** and **Figure 1.8**). Plant species richness was greater in MGS than in EGS ($P < 0.05$) but was similar among other treatments and control. The Shannon-Wiener plant diversity index was greater in the DOS and EGS treatments ($P \leq 0.008$), but the other treatments did not differ from control (**Table 1.7**). Plant species evenness was greater in the EGS treatment (0.78, $P = 0.002$) compared to control (**Table 1.7** and **Figure 1.9**), but was similar among fire treatments.

DISCUSSION

We documented major changes in plant community composition, structure, and diversity following two iterations of prescribed fire during different seasons of the year, which supported our hypothesis that burning during different seasons would alter plant composition and structure differently. Fire intensity and burn coverage varied by season and was least in the MGS treatment, which influenced effects on coverage of semi-woody and woody species in the understory as well as midstory density. Forb coverage increased in all treatments, whereas coverage of grasses, brambles, vines, shrubs, and tree seedlings or sprouts in the understory decreased in all treatments compared to control. Contrary to our prediction, forb coverage increased in all treatments, but the increase was greatest in LGS and DOS treatments, despite less-intense fire temperatures and less complete burn coverage in the LGS treatment. Grass coverage remained similar among treatments, which did not support our prediction, but likely was influenced by a reduction in PAR. Coverage of semi-woody and woody understory plants remained steady and similar in the EGS and LGS treatments when compared to pretreatment values, but increased from pretreatment levels in control, DOS, and MGS treatments, suggesting both seasonal and intensity effects. Plant diversity generally was improved by all treatments, but two fire events did not influence plant species richness, which did not support our prediction.

The primary reason for implementing prescribed fire is to maintain or set-back succession (Albrecht and McCarthy 2006, Block et al. 2016, Greene et al. 2016, Harper 2017). All of our treatments set-back succession compared to control, but we documented differential effects among treatments that were representative of season and intensity. The pattern of control of both semi-woody and woody understory plants was identical between ESG and LGS treatments, indicating two fire events on a 2-year return-interval during those seasons maintained coverage of those plants similar to pretreatment levels. Although coverage of semi-woody and woody understory plants was reduced following DOS and MGS fire compared to control, coverage of those plants trended upward in both treatments when compared to pretreatment levels. Gruchy et al. (2009) reported similar results in old-field communities, where burning treatments reduced woody plant coverage, but dormant-season fire was not as effective as late growing-season fire. Fire intensity, rate of spread, flame lengths, and burn coverage all were greatest in DOS and least in MGS, which indicates fire during the dormant season may control woody plants as well as fire during the mid-growing season, and that the MGS treatment lacked the intensity and coverage to top-kill as many woody stems. By 2023, midstory stem density in MGS was nearly double that in DOS, EGS, or LGS, which were nearly identical, further illustrating the lack of woody control with the less-intensive MGS fires. Drewa et al. (2002) and Robertson and Hmielowski (2016) also reported shrubs and small-diameter trees top-killed by fire were more likely to resprout following dormant-season fire than growing-season fire.

Control of semi-woody and woody plants strongly influences vegetation structure and may affect plant composition as well as wildlife habitat. Fire intensity was greater in the DOS treatment than the EGS treatment, yet visual obstruction in the DOS treatment was similar to control. Visual obstruction below 1 m was more open than control only in the EGS treatment, which indicates a seasonal effect as the vegetation was set-back relatively early in its growth cycle, providing a more open structure through mid-summer, which influences use by wildlife. Wild turkeys (Meleagris gallopavo) often select recently burned areas for brooding because of decreased visual obstruction and increased openness at ground level (Peoples et al. 1996, Wood et al. 2018, Wood et al. 2019, Nelson et al. 2022). Alternatively, wild turkeys typically select more dense vegetation for nesting (Badyaev 1995, Kilburg et al. 2014, Johnson et al. 2022), which was provided in treatments 2 growing seasons post-burning. Various understory songbirds, such as Bachman's sparrow (Peucaea aestivalis), select an open understory for nesting and brooding (Engstrom et al. 2005). All treatments reduced visual obstruction below 2 m, which created a more open midstory condition that various woodland obligate species, such as red-headed woodpecker (Melanerpes erythrocephalus), great crested flycatcher (Myiarchus crinitus), and eastern wood peewee (Contopus virens), select for foraging and nesting (White and Seginak 2000, King et al. 2007, Kendrick et al. 2013).

Control of woody species and promotion of herbaceous plants in the understory is requisite to maintain an open pine woodland, which requires an understory dominated by herbaceous plants (Faber-Langendoen et al. 2001, Rother et al. 2020, McGranaham and Wonkka 2021). Coverage of forbs is important to increase plant diversity metrics (Glitzenstein et al. 2008, Mitchell and Duncan 2009, Greene et al. 2016) and to achieve many wildlife objectives (Greene et al. 2019, Harper et al. 2025). After two iterations of fire treatments on a 2-year interval, forb coverage in the DOS and LGS treatments was >2 times that of the control. Forb coverage in the DOS and LGS treatments was, on average, 1.5 times greater than forb coverage averaged across the EGS and MGS treatments. Increased forb coverage following the DOS and LGS treatments likely is related to plant phenology, whereby most of the warm-season forbs have matured and produced seed prior to DOS and LGS fire, but are set-back or killed during their growth cycle by EGS and MGS fire (Howe 1994, Ripley et al. 2010). Previous research has indicated LGS fire may increase forb coverage and decrease coverage of other plants that can outcompete them (Lewis et al. 1964, Gruchy et al. 2006, Pavlovic et al. 2010, Reemts et al. 2019). Increased forb coverage has been linked to increased nutritional carrying capacity for white-tailed deer (Masters et al. 1996, Edwards et al. 2004, Lashley et al. 2011, Nanney et al. 2018, Harper et al. 2021), enhanced brooding cover for wild turkeys (Spears et al. 2010, Johnson 2019, Chamberlain et al. 2020, Nelson et al. 2022), increased insect availability for wild turkeys (Martin and McGinnes 1975, Healy 1984, Harper et al. 2001), and increased food and productivity for pollinators (Siemann 1998, Decker and Harmon-Threatt 2019, GeFellers et al. 2020). Thus, consideration of fire seasonality on forb coverage has many implications.

Understory plant composition can be altered by a reduction in sunlight caused by reduced control of woody species, especially herbaceous plants that require near >50% sunlight (Peterson et al. 2007, Charles-Dominque et al. 2018). Percent PAR averaged 54% across all units in 2020, but had declined to 39% by 2023. The decrease in PAR was related to relatively rapid crown expansion of retained overstory trees, not midstory development, as all fire treatments reduced midstory density and structure. The stands in our study had been thinned to an average BA of 9.5 m2/ha approximately 3 years prior to our study (Turner and Harper 2024). By 2023, BA had increased to 10.9 m2/ha and the reduced PAR likely limited shade-intolerant early successional plants in the understory. Stiff ticktrefoil (Desmodium obtusum), roundleaf thoroughwort (Eupatorium rotundifolium), trailing lespedeza (Lespedeza procumbens), mountain mint (Pycnanthemum incanum), wrinkle-leaf goldenrod (Solidago rugosa), fragrant goldenrod (S. odora), and slender woodoats (Chasmanthium laxum) were some of the more-dominant forbs and grasses present, which are able to persist with moderate shade (Carman 2001, Horn et al. 2005, Miller and Miller 2005). More shade-intolerant plants, such as common milkweed (Asclepias syriaca), horseweed (Conyza canadensis), pokeweed (Phytolacca americana), meadowbeauty (Rhexia virginica), prairie rosinweed (Silphium terebinthinaceum), goat's rue (Tephrosia virginica), and low panicgrasses (Dicanthelium spp.) were far less abundant. Thinning below 9.5 m2/ha will be necessary to maintain sunlight conditions required for these plants and better realize effects of burning during different seasons.

The influence of fire on plant diversity metrics was mixed. The plant species diversity index was improved following DOS and EGS fire, but plant species richness did not differ from control. Plant species richness increased over time in all treatments and control, likely because of the lingering effects of increased sunlight following overstory thinning, whereby all stands, except Bridgestone, were in a closed-canopy condition prior to thinning. However, PAR declined by approximately 1.4 times over the 4 years of the study to an average of 39% across all sites, which likely led to the decrease in grass coverage, especially among Dichanthelium spp., and limited forb coverage to no more than 26%. Plant species evenness, which is the proportion of the abundance each species relative to one another, is calculated using a combination of species richness and diversity (Pielou 1966). These metrics are important because they relate not only to the number of plant species present, but also to their abundance and distribution, which is important for plant community restoration and resilience as well as resource availability for wildlife (Kamba 2016, Westlake et al. 2020). Our plant species richness and diversity scores were similar to other studies examining restored pine woodland communities. Mitchell et al. (2015) reported species richness in longleaf pine stands had similar species richness (120) to our mean richness values (110). Kirkman et al. (2004) predicted similar species evenness (0.80), but a lower diversity index score (2.0). Better distribution and abundance of more plant species can provide increased food and cover for wildlife, which may influence species occupancy (Murdoch et al. 1972, Dickmann 1993) and space use (MacArthur and Pianka 1966, Wann et al. 2020). Species composition and distribution also can have implications on fire spread and behavior (Wragg et al. 2018).

MANAGEMENT IMPLICATIONS

Our study confirms that fire seasonality can strongly influence plant composition and structure in open pine woodlands after only two fire events using relatively low-intensity fire. Woody composition was influenced by season of burning, but the influence of seasonality was confounded by fire intensity. Our results likely would have been different if fire intensity had been the same across all treatments. Had we not measured and analyzed fire intensity, interpretation of our results likely would have been misleading. Fire intensity and burn coverage in the MGS and LGS treatments were less than in the DOS and EGS treatments, but the lower intensity and coverage in the MGS treatment was evident in plant community responses compared to other seasons. The effects of season and intensity also influenced vegetation structure, which is an important consideration for many wildlife species. That said, unburned patches of vegetation provide more structural heterogeneity and may retain food and cover resources important to some wildlife species, which makes fire seasonality an important consideration when wildlife is an objective and indicates no one season of burning is best for all species or objectives. Plant composition was influenced by season of burning and also by the amount of sunlight entering the canopy. Canopy reduction should allow a minimum of 40–50% sunlight to support early successional plant species in the understory (Naumburg and DeWald 1999, Valladares et al. 2016). Managers also should consider plant phenology when understory plant composition is an objective or of concern, especially when increased forb coverage is an objective. Varying the season of burning has implications for many wildlife species as well as aesthetics. Our results indicate prescribed fire can be implemented in early, mid-, and late summer with success and meaningful impact to plant communities. Managers can use our results to guide their fire-timing planning. Our results should provide them with confidence that they may not only promote a more diverse understory plant community, but also have many more burn days available beyond the traditional dormant season to reach objectives.

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APPENDIX

Table 1.1 Dominant tree species, age of stand, tree density, basal area, percent sunlight, soil type (NRCS 2022), elevation, slope, aspect, and coordinates of the nine sites.

Site	*Bridgestone*	*Barbour*	*Belfast*	*Copiah*	*Folsom*	*Foothills*	*Mason Bend*	*Triple Creek*	*Hamilton Ridge*
Dominant tree species	*Pinus echniata*	*Pinus taeda*	*P. taeda*	*P. echinata, P. taeda*	*P. taeda*	*P. echinata, Quercus alba*	*P. taeda*	*P. taeda*	*P. taeda*
Age (years)	8	24	27	61	18	83	21	25	31
Tree density (stems/ha)	N/A	175	175	141	450	89	299	116	121
Basal area (m^2/ha)	N/A	8	12	15	9	8	10	10	11
Sunlight (%)	100	58	50	45	53	66	16	52	56
Soils	Lonewood silt loam	Luverne-Springhill complex, sandy loam	Cecil sandy clay loam	Loring silt loam and Lorman-Smithdale association	Smithdale sandy loam	Ramsey stony fine sandy loam	Cahaba fine sandy loam	Savannah fine sandy loam	Eulonia fine sandy loam
Elevation (m)	557	113	169	101	95	377	30	93	15
Slope (%)	5 – 12	15 – 45	2 – 6	2 – 5	5 – 15	50 – 70	0 – 2	2 – 5	0 – 2
Aspect	NW/W	SW	W	S	S	SW/W	W/SW	S	SW
Coordinates	35°46'46.94"N, 85°18'55.24"W	31°58'5.50"N, 85°21'2.69"W	34°16'53.29"N, 81°53'13.77"W	31°48'25.63"N, 90°40'46.94"W	32°38'40.76"N, 87°25'33.42"W	35°36'25.70"N, 84° 1'36.80"W	32°45'46.22"N, 87°48'12.52"W	32°0'22.11"N, 88°55'9.70"W	32°38'8.59"N, 81°22'29.88"W

Table 1.2. Mean rate of spread (m/hr), flame length (cm), burn coverage (%), and fire temperature recorded by dataloggers (℃) for fire treatments.

Treatment	Rate-of-spread	Group	Flame length	Group	Burn coverage	Group	Fire Temperature	Group
DOS	78.9±21.9	a	82±8	a	99±0.4	a	171.1±13.1	a
EGS	73.1±21.1	a	69±4	b	98±0.6	a	135.6±17.5	ab
MGS	36.5±9.1	b	30±4	b	75±8	b	108.4±11.6	b
LGS	48.4±15.3	b	43±2	b	89±3	b	129.6±29.1	ab

Table 1.3 Mean air temperature (°C), in-stand wind speed (m/s), and relative humidity (%) for fire treatments.

Treatment	Air temperature	In-stand wind speed	Relative humidity
DOS	20.2±1.7	2.9±0.7	39.7±9.4
EGS	25.2±0.8	3.1±0.7	39.5±9.3
MGS	32.7±0.7	1.2±0.3	57.7±13.6
LGS	25.9±1.2	2.4±0.6	40.7±9.6

Table 1.4 Mean understory coverage of different plant groups after four years (2020–2023) and two iterations of dormant (DOS), early growing- (EGS), mid-growing- (MGS), and late (LGS) growing-season fire. Column means with the same letter are not different ($\alpha = 0.05$).

Treatment	Mean forb coverage	Group	Mean grass coverage	Group	Mean semi-woody coverage	Group	Mean woody coverage	Group
Control	13.5±3.9	a	39.7±6.1	a	59.9±7.3	b	38.5±6.4	b
DOS	26.0±3.9	b	46.3±6.1	a	48.2±7.3	ab	27.2±6.4	a
EGS	19.0±3.9	ab	40.2±6.1	a	35.2±7.3	a	24.0±6.4	a
MGS	19.3±3.9	ab	41.5±6.2	a	49.7±7.4	ab	27.5±6.5	a
LGS	25.6±3.9	b	39.0±6.1	a	44.4±7.3	a	27.8±6.4	a

Table 1.5 Mean overstory stem area expressed in basal area per hectare BA/ha, overstory (TPH) and midstory stem count, and percent photosynthetically active radiation (PAR) values over four years (2020–2023) and after two iterations of fire. Column means with the same letter are not different ($\alpha = 0.05$).

Treatment	Overstory TPH	Group	Overstory BA/ha	Group	Mean midstory stem count	Group	Mean PAR	Group
Control	134.5±26.9	a	7.8±1.4	b	902±135	b	50.0±6.0	ab
DOS	161.7±26.9	a	9.5±1.4	ab	376±135	a	53.4±6.0	b
EGS	144.9±26.9	a	8.5±1.4	b	382±135	a	50.6±6.0	ab
MGS	168.9±26.9	a	10.1±1.4	ab	510±136	a	51.3±6.0	ab
LGS	163.2±26.9	a	10.4±1.4	a	370±135	a	44.9±6.0	a

Table 1.6 Mean percent visual obstruction below 0.5 m, 1 m, and 1.5 m over four years (2020–2023) and after two iterations of fire treatments. Column means with the same letter are not different (α = 0.05).

Treatment	Mean visual obstruction <0.5 m	Group	Mean visual obstruction <1 m	Group	Mean visual obstruction <1.5 m	Group	Mean visual obstruction < 2 m	Group
Control	95.4±2.5	b	90.7±3.1	b	84.5±3.7	b	78.4±4.0	b
DOS	92.4±2.5	b	83.1±3.1	b	72.2±3.7	a	63.0±4.0	a
EGS	82.5±2.5	a	72.1±3.1	a	62.9±3.7	a	55.5±4.0	a
MGS	90.4±2.6	ab	81.9±3.1	b	72.2±3.7	a	64.1±4.1	a
LGS	90.1±2.5	ab	81.2±3.1	ab	72.3±3.7	a	64.6±4.0	a

Table 1.7 Mean values of the Shannon-Weiner plant diversity index, plant species richness, and plant species evenness over four years (2020–2023) after two iterations of dormant (DOS), early growing- (EGS), mid-growing- (MGS), and late (LGS) growing-season fire.Column means with the same letter are not different (α = 0.05).

Treatment	Mean diversity index	Group	Mean species richness	Group	Mean species evenness	Group
Control	3.38±0.12	a	102.8±10.5	ab	0.73±0.02	a
DOS	3.51±0.12	b	108.2±10.5	ab	0.75±0.02	ab
EGS	3.52±0.12	b	92.5±10.5	a	0.78±0.02	b
MGS	3.45±0.12	ab	109.5±10.5	b	0.74±0.02	a
LGS	3.49±0.12	ab	100.0±10.5	ab	0.76±0.02	ab

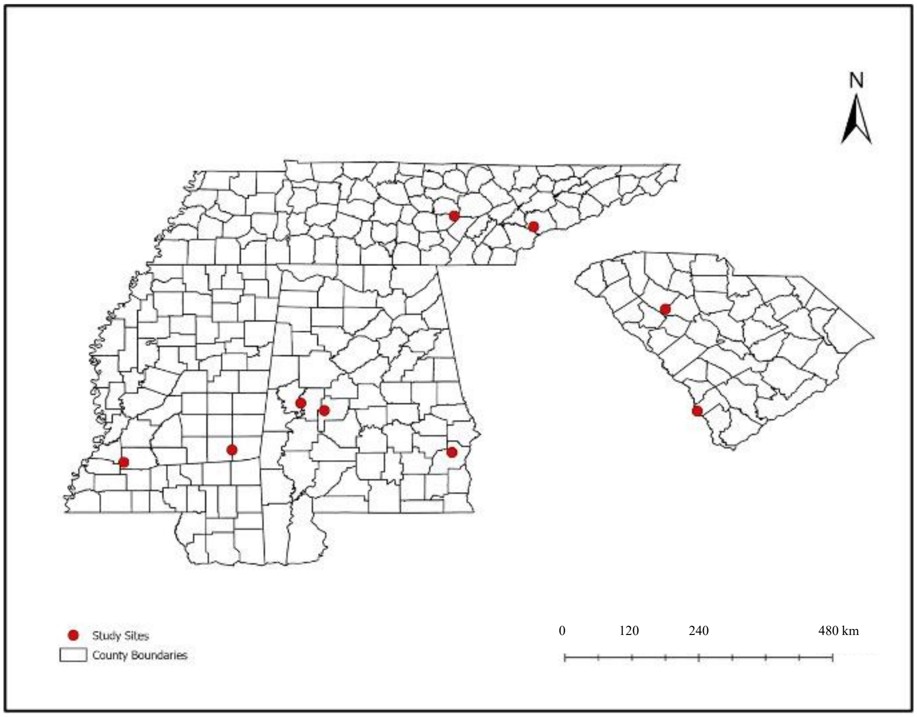

Figure 1.1. Study site locations in Tennessee, Mississippi, Alabama, and South Carolina, USA.

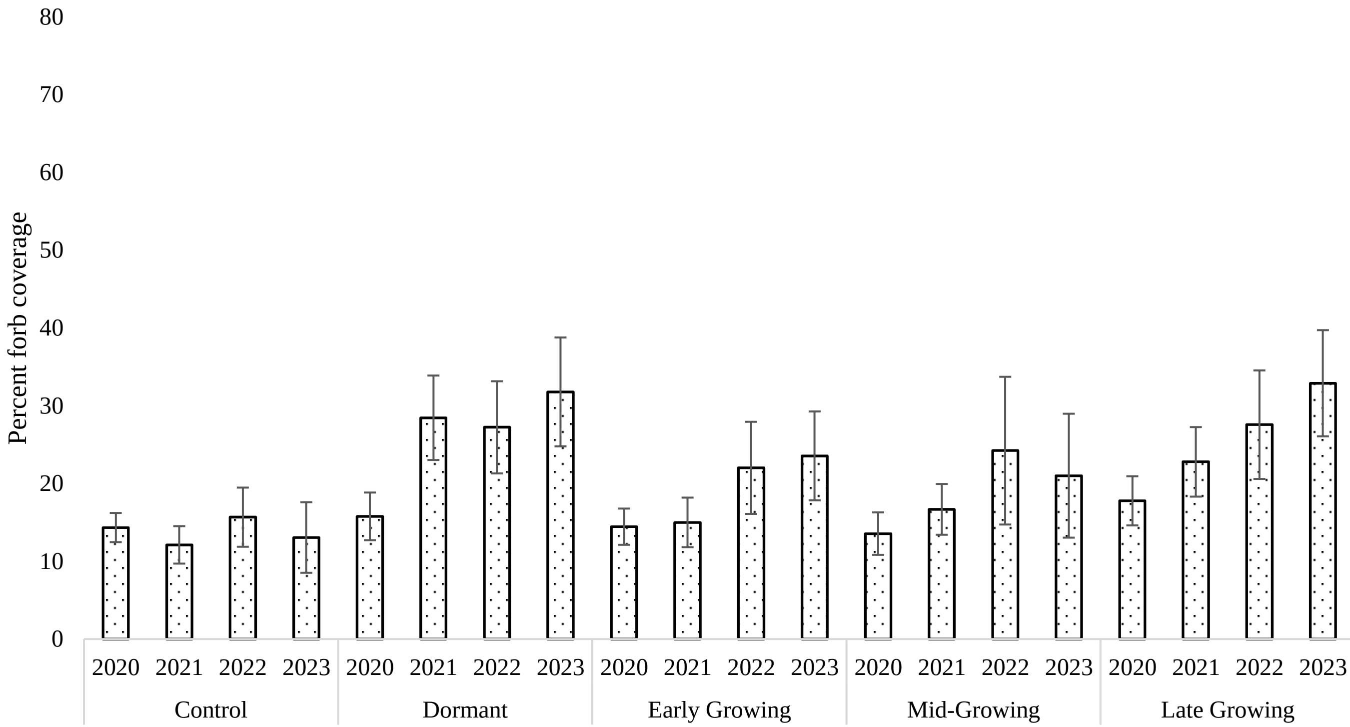

Figure 1.2 Percent coverage values for forbs over four years (2020–2023) and after two iterations of dormant (DOS), early growing- (EGS), mid-growing- (MGS), and late (LGS) growing-season fire at nine sites dominated by shortleaf or loblolly pine in Tennessee, South Carolina, Alabama, and Mississippi. Data for 2020 were collected prior to any treatment. The LGS treatment was implemented in the fall of 2020 and 2022. The DOS and EGS treatments were implemented prior to data collection in 2021 and 2023. The MGS treatment was implemented after data collection in 2021 and 2023. Error bars represent standard errors for each respective treatment and year.

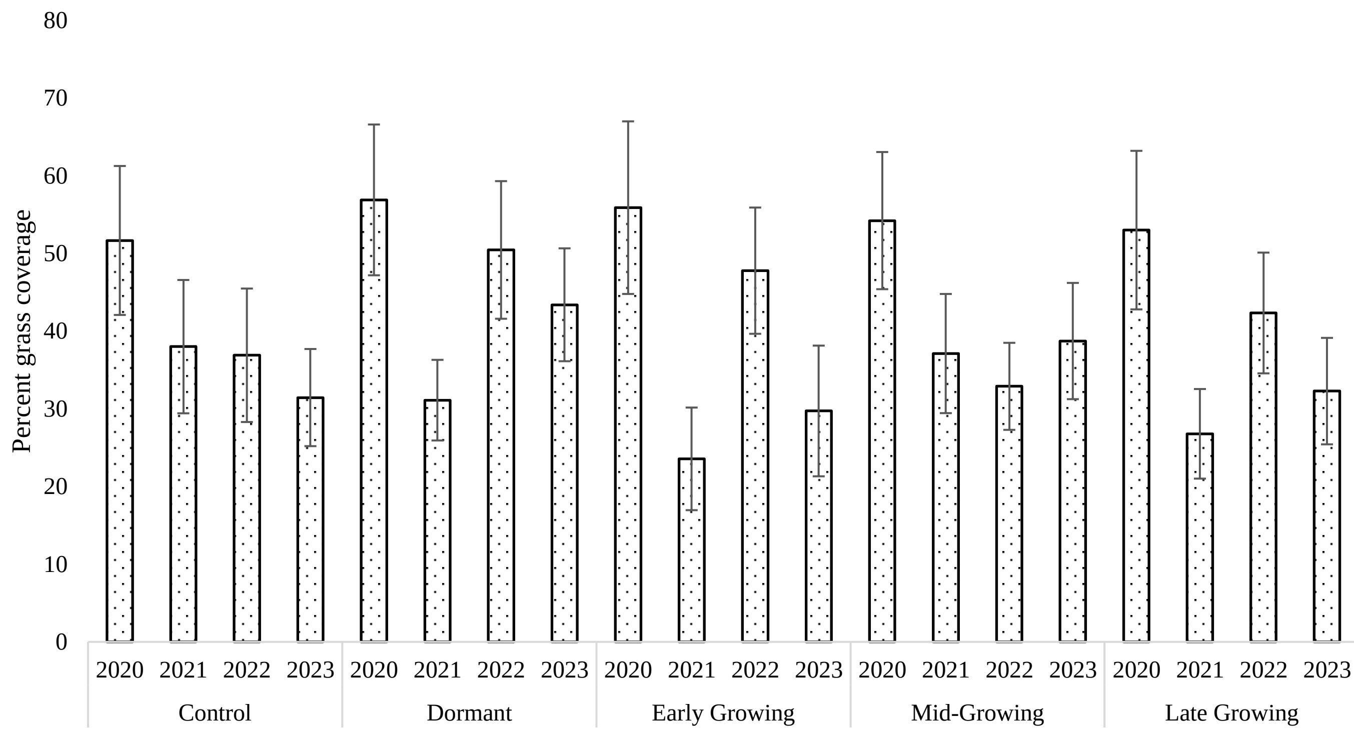

Figure 1.3 Percent coverage values for grasses over four years (2020–2023) and after two iterations of dormant (DOS), early growing- (EGS), mid-growing- (MGS), and late (LGS) growing-season fire at nine sites dominated by shortleaf or loblolly pine in Tennessee, South Carolina, Alabama, and Mississippi. Data for 2020 were collected prior to any treatment. The LGS treatment was implemented in the fall of 2020 and 2022. The DOS and EGS treatments were implemented prior to data collection in 2021 and 2023. The MGS treatment was implemented after data collection in 2021 and 2023. Error bars represent standard errors for each respective treatment and year.

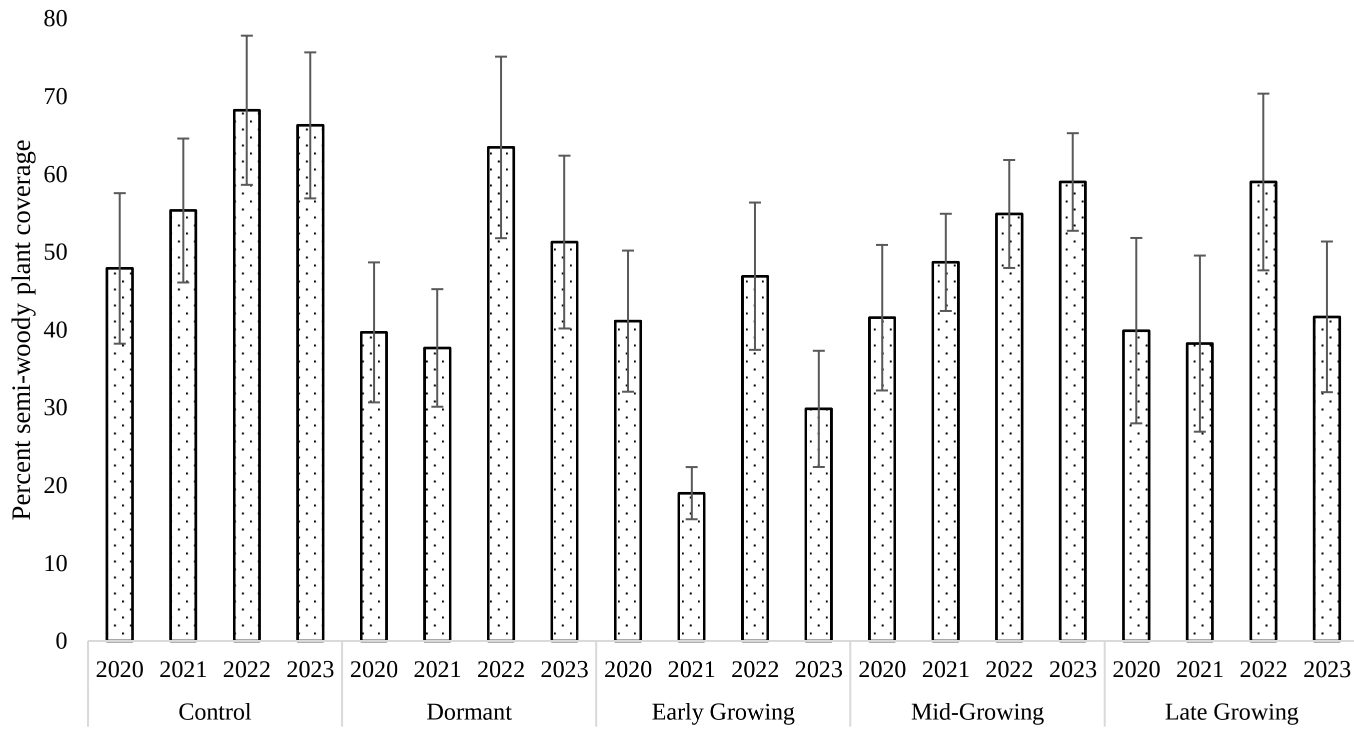

Figure 1.4 Percent coverage values for semi-woody plants over four years (2020–2023) and after two iterations of dormant (DOS), early growing- (EGS), mid-growing- (MGS), and late (LGS) growing-season fire at nine sites dominated by shortleaf or loblolly pine in Tennessee, South Carolina, Alabama, and Mississippi. Data for 2020 were collected prior to any treatment. The LGS treatment was implemented in the fall of 2020 and 2022. The DOS and EGS treatments were implemented prior to data collection in 2021 and 2023. The MGS treatment was implemented after data collection in 2021 and 2023. Error bars represent standard errors for each respective treatment and year.

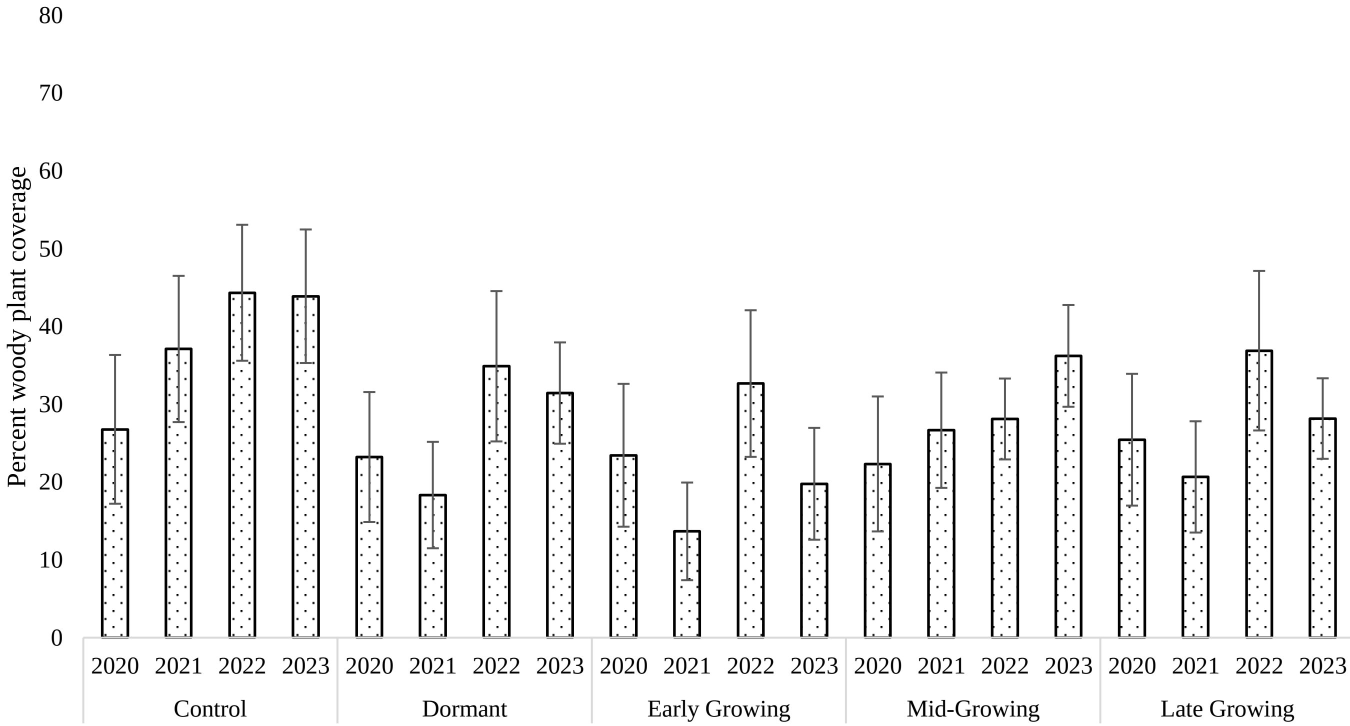

Figure 1.5 Percent coverage values for understory woody plants over four years (2020–2023) and after two iterations of dormant (DOS), early growing- (EGS), mid-growing- (MGS), and late (LGS) growing-season fire at nine sites dominated by shortleaf or loblolly pine in Tennessee, South Carolina, Alabama, and Mississippi. Data for 2020 were collected prior to any treatment. The LGS treatment was implemented in the fall of 2020 and 2022. The DOS and EGS treatments were implemented prior to data collection in 2021 and 2023. The MGS treatment was implemented after data collection in 2021 and 2023. Error bars represent standard errors for each respective treatment and year.

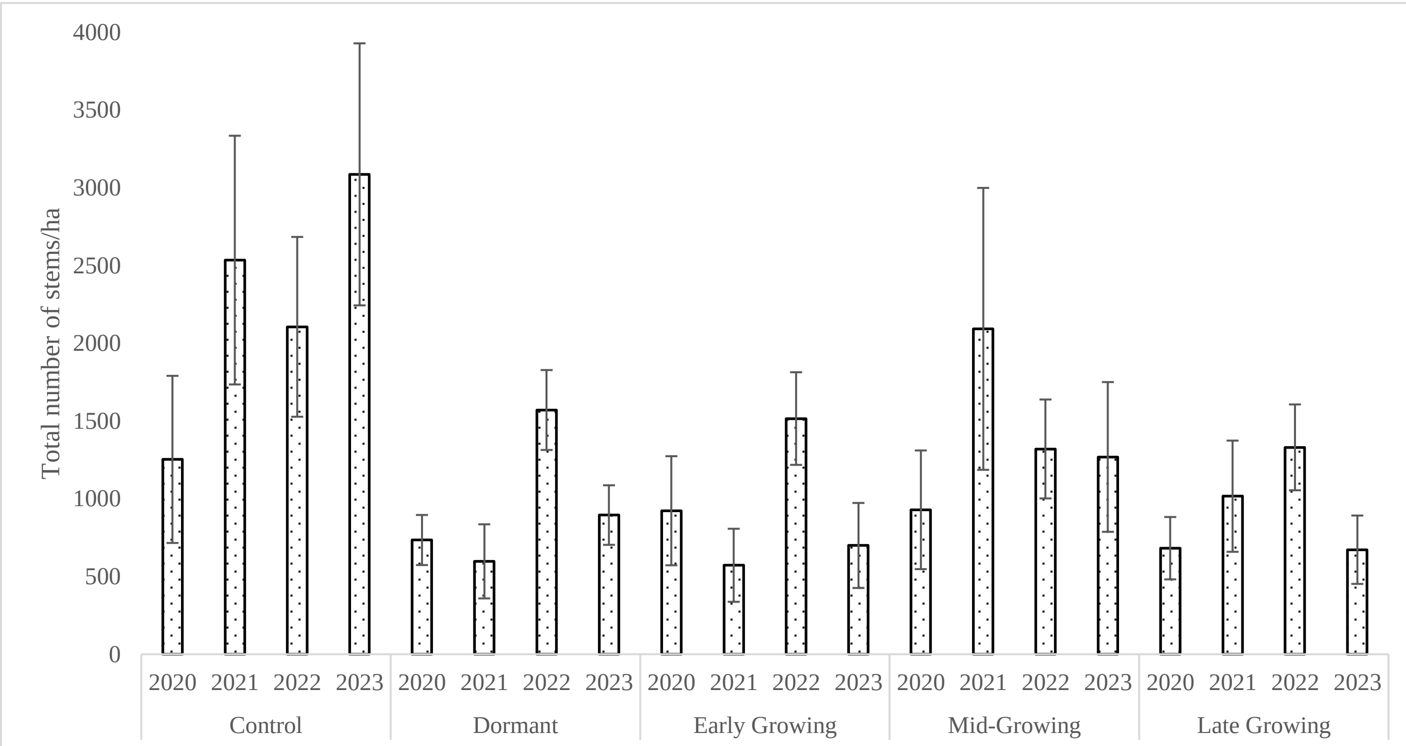

Figure 1.6 Average number of midstory stems per hectare over four years (2020–2023) and after two iterations of dormant (DOS), early growing- (EGS), mid-growing- (MGS), and late (LGS) growing-season fire at nine sites dominated by shortleaf or loblolly pine in Tennessee, South Carolina, Alabama, and Mississippi. Data for 2020 were collected prior to any treatment. The LGS treatment was implemented in the fall of 2020 and 2022. The DOS and EGS treatments were implemented prior to data collection in 2021 and 2023. The MGS treatment was implemented after data collection in 2021 and 2023. Error bars represent standard errors for each respective treatment and year.

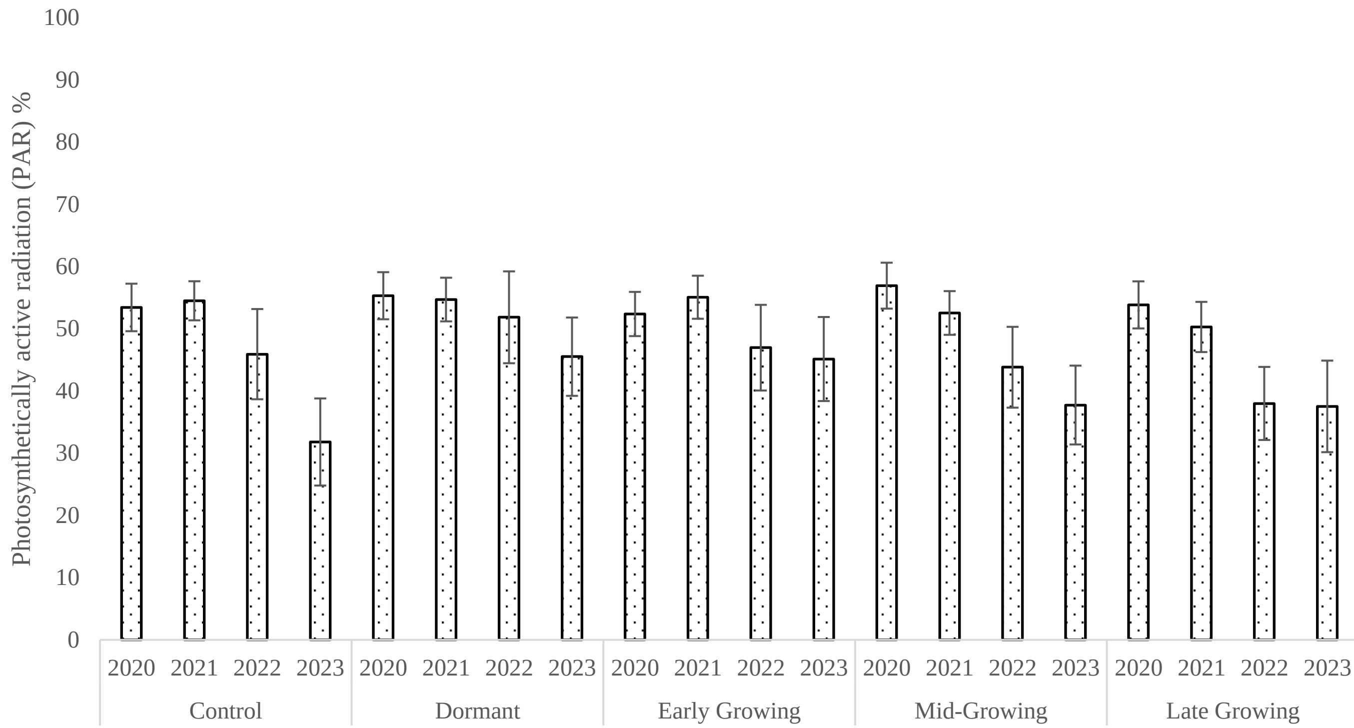

Figure 1.7 Average photosynthetically active radiation (PAR) over four years (2020–2023) and after two iterations of dormant (DOS), early growing- (EGS), mid-growing- (MGS), and late (LGS) growing-season fire at nine sites dominated by shortleaf or loblolly pine in Tennessee, South Carolina, Alabama, and Mississippi. Data for 2020 were collected prior to any treatment. The LGS treatment was implemented in the fall of 2020 and 2022. The DOS and EGS treatments were implemented prior to data collection in 2021 and 2023. The MGS treatment was implemented after data collection in 2021 and 2023. Error bars represent standard errors for each respective treatment and year.

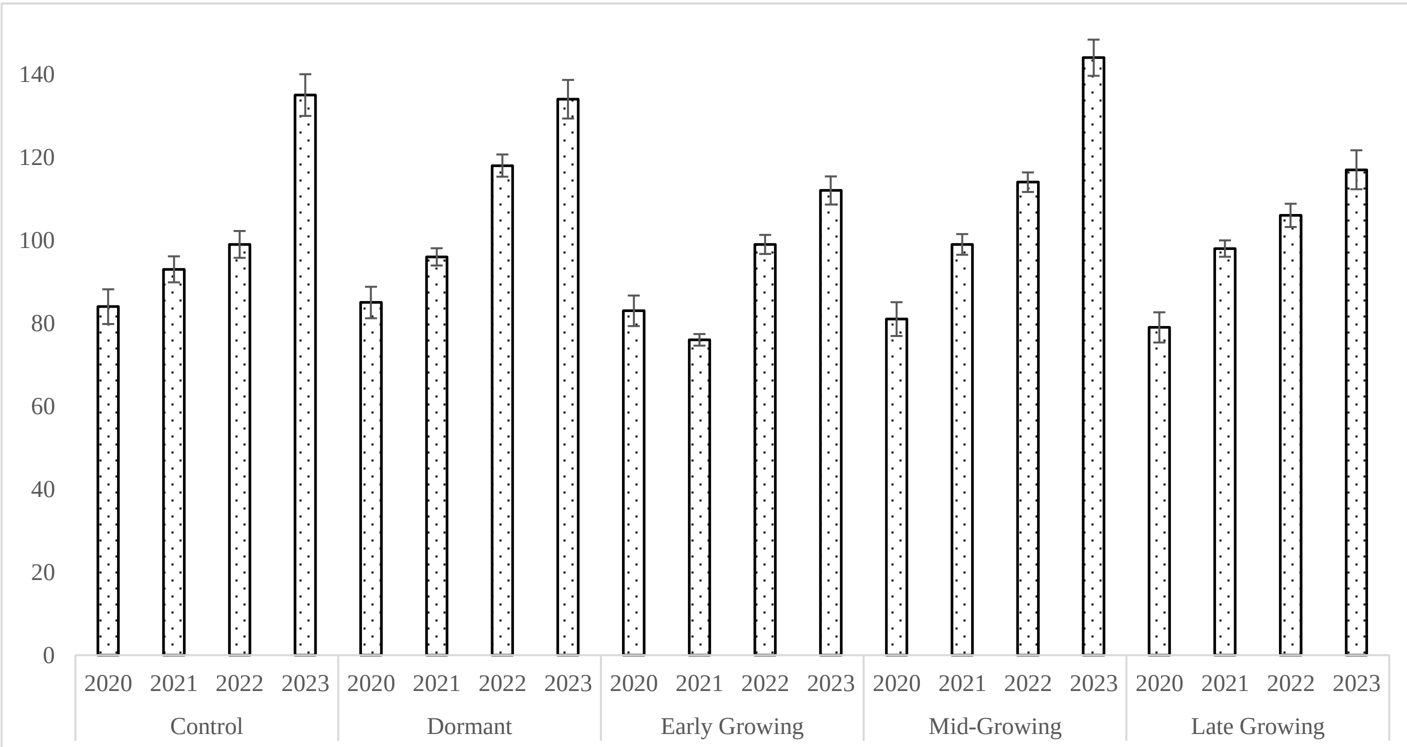

Figure 1.8 Plant species richness over four years (2020–2023) and after two iterations of dormant (DOS), early growing- (EGS), mid-growing- (MGS), and late (LGS) growing-season fire at nine sites dominated by shortleaf or loblolly pine in Tennessee, South Carolina, Alabama, and Mississippi. Data for 2020 were collected prior to any treatment. The LGS treatment was implemented in the fall of 2020 and 2022. The DOS and EGS treatments were implemented prior to data collection in 2021 and 2023. The MGS treatment was implemented after data collection in 2021 and 2023. Error bars represent standard errors for each respective treatment and year.

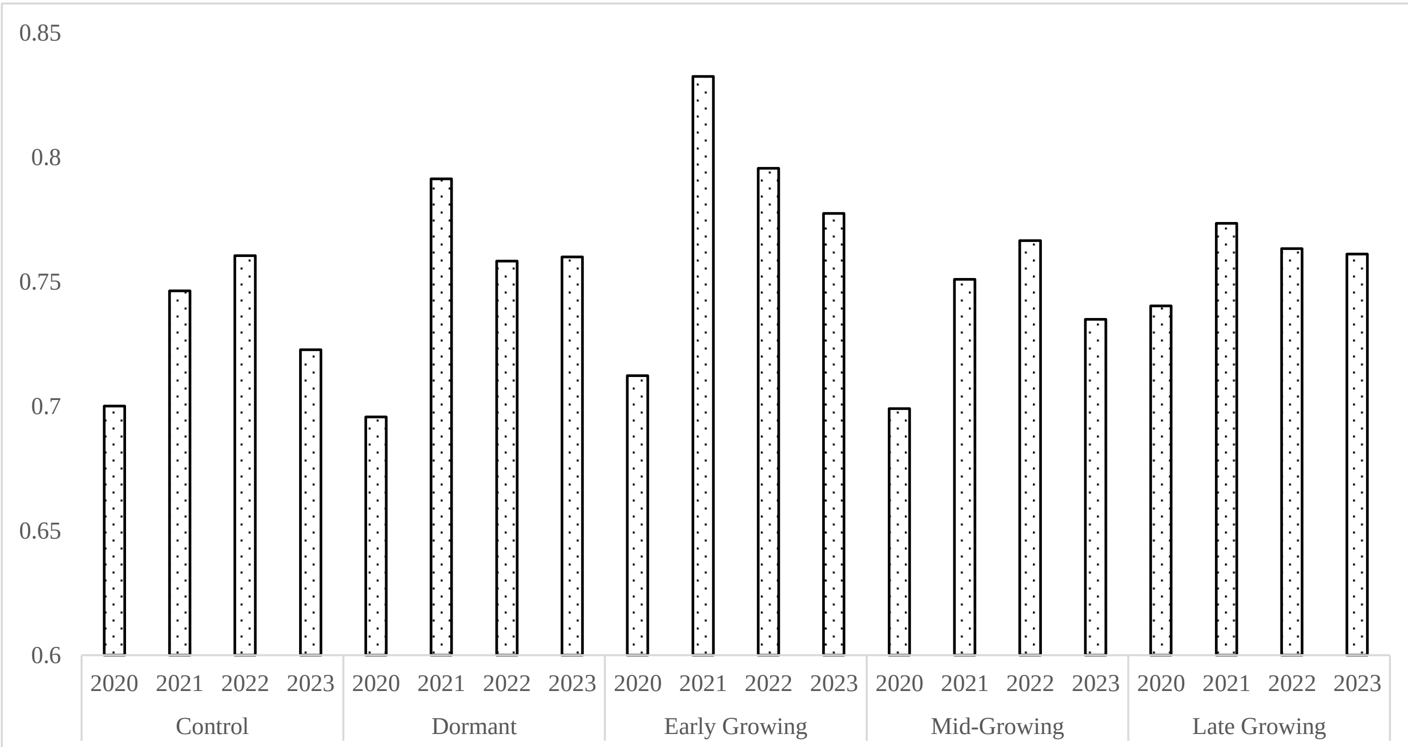

Figure 1.9 Plant species evenness over four years (2020–2023) and after two iterations of dormant (DOS), early growing- (EGS), mid-growing- (MGS), and late (LGS) growing-season fire at nine sites dominated by shortleaf or loblolly pine in Tennessee, South Carolina, Alabama, and Mississippi. Data for 2020 were collected prior to any treatment. The LGS treatment was implemented in the fall of 2020 and 2022. The DOS and EGS treatments were implemented prior to data collection in 2021 and 2023. The MGS treatment was implemented after data collection in 2021 and 2023. Error bars represent standard errors for each respective treatment and year.

CHAPTER 2. AN EVALUATION OF SELECTED DEER FORAGE BIOMASS AND NUTRITIONAL CARRYING CAPACITY TO PRESCRIBED FIRE SEASONALITY IN PINE ECOSYSTEMS OF THE SOUTHEASTERN UNITED STATES

ABSTRACT

Prescribed fire commonly is used to manage pine woodlands in the southeastern US. Wildlife management is a common objective for landowners and the white-tailed deer (*Odocoileus virginianus*) is the most common focal species. Landowners typically prescribe fire during the dormant season to set-back encroaching hardwood stems and stimulate germination of herbaceous plants and resprouting woody vegetation for enhanced deer forage. The effects of dormant-season fire on deer forage have been documented, but the effects of burning during other seasons are not well known and to date, no study has examined the effects of fire during all seasons on deer forage biomass and nutritional carrying capacity (NCC). We implemented a study to assess the effects of dormant- (DOS), early growing- (EGS), mid-growing- (MGS), and late growing-season (LGS) fire on deer forage biomass and NCC in previously thinned woodlands dominated by shortleaf (*Pinus echinata*) or loblolly (*P. taeda*) pine from 2020–2023. We collected forages three times throughout the 2023 growing season to determine how nutrient availability changed through the growing season. Selected deer forage biomass increased following all treatments. Availability of forbs was increased most by the DOS and LGS treatments. NCC was increased only by the DOS treatment, but nutritional quality increased in the weeks following both the EGS and MGS fires. This information can be used by managers to maximize the amount of high-quality forage for deer throughout the year and expand the burning window.

INTRODUCTION

Pine forests and woodlands are common across the southeastern United States. Loblolly (*Pinus taeda*), longleaf (*P. palustris*), and shortleaf pine (*P. echinata*) cover approximately 90 million acres across the region (Oswalt et al. 2019). Pine-dominated stands are managed primarily for timber, but wildlife often is a top objective for management (Blair et al. 1977, Iglay et al. 2006). The white-tailed deer (*Odocoileus virginianus*; hereafter deer) is the most popular game species in the eastern US (U.S. Fish and Wildlife Service 2023), and more landowners in the southeastern US manage their property for deer than any other species (Edwards et al. 2004). Closed-canopy pine stands typically allow only 2–5% sunlight to the forest floor, resulting in a poorly developed understory that provides little food or cover for deer and other species (Brennan et al. 1998, Eby et al. 2014, Turner and Harper 2024). As such, pine stands are thinned to promote tree growth (Masters et al. 2006, Mixon et al. 2010) and stimulate understory development for increased forage and cover for deer and other species (Shrauder and Miller 1969, Keeley et al. 2009b).

Prescribed fire commonly is used to manage pine woodlands following thinning (Cain et al. 1998, Mitchell et al. 2006, Darracq et al. 2016). Fire is used in pine woodlands to set-back or maintain ecological succession (McGranaham 2021), influence plant composition and structure (Greene et al. 2016), consume fine fuels and stimulate the seedbank (Ryan et al. 2013), and enhance habitat for various wildlife species (Brown and Smith 2000). Traditionally, managers have burned pine systems during the latter portion of dormant season (January–March), but chronic burning during this time of year often encourages resprouts of woody plants and increased coverage of grasses (Waldrop et al. 1992, Brockway and Lewis 1997, Gruchy et al. 2009, Knapp et al. 2009). Growing season fire has received increased interest in recent years, particularly during the early (April–May) and latter (August–October) portions of the growing seasons (Sparks et al. 2009, Cronan et al. 2015, Turner at al. 2024). Burning throughout the growing season promotes sprouting and germination of fresh vegetation that is more digestible to deer (Jeffrey et al. 1998, Iglay et al. 2010, Lashley et al. 2022).

Forage quantity and quality influence body condition, survival rates, and fawn recruitment, making the availability of high-quality forage a critical factor in deer management (Holter et al. 1979, Ramirez et al. 1996, Hanley 1997, Lashley and Harper 2012). Prescribed fire can influence vegetation composition and digestibility of plant material, potentially enhancing deer forage by increasing the abundance of palatable and nutritious plant species (Thill et al. 1987). Forbs are more palatable and higher in nutritional value compared to older, woody vegetation (Powell et al. 2022, Harper et al. in press), and recently burned areas often are highly selected by deer because forbs often germinate following fire if there is sufficient sunlight, and young resprouting woody vegetation is greater in nutritional quality than older plant material (Wood 1988, Lashley 2011, Westlake et al. 2020). Furthermore, prescribed fire can be used to influence the spatial distribution of forage by creating a mosaic of vegetation types that provide diverse foraging opportunities for deer and support dietary needs throughout the year (Knight 2005, Fulbright and Ortega-S 2014).

As concentrate selectors, deer typically select the most nutritious, digestible forage available to meet nutritional requirements for body maintenance, antler growth, and lactation (Short 1975, Hofmann 1989, Dykes et al. 2020). Nutrient demands differ for males and females, and demands change over time, but crude protein (CP) and phosphorus (P) often are limiting nutrients (Jacobson 1984, Turner 2024). Both CP and phosphorus needs vary widely based on age, sex, and time of year (Shin et al. 2000). A CP level of 6% is considered the minimum for basic bodily maintenance (Hewitt 2011). During antler growth in the spring and summer, males need approximately 12% CP, whereas females require approximately 14% CP to support lactation (French et al. 1956). Some plants that meet CP requirements do not always meet P requirements, but most plants that meet P requirements also meet CP requirements (Turner

2024). Phosphorus is most abundant in young forbs, which underlines the need for a variety of seasons of burn to provide access to more nutritious forage (Grasman and Hellgren 1993). Access to forages that provide the required CP and P levels is crucial for maximum antler growth and milk production, both of which occur during the growing season outside of the traditional burn window that typically offers less palatable forages such as woody stems and grasses (Carlson et al. 1993, Nichols et al. 2021).

Given the prevalence of pine stands being managed with prescribed fire throughout the Southeast and the interest among landowners to manage for deer, we developed a field study to better understand the effects of season of fire on deer forage. We compared forage biomass availability and nutritional carrying capacity (NCC) estimates for white-tailed deer following two iterations of fire treatments that included each season of the year from 2020–2023 to determine if burning during different seasons has a differential effect on deer forage biomass and NCC. We hypothesized that all fire treatments would positively influence deer forage biomass and quality when compared to control (i.e., no fire). We predicted that forage biomass and NCC during the growing season would be greatest following late growing-season and dormant-season treatments because vegetation would not be set-back during active growth. We predicted greater crude protein and phosphorus values during the growing season following early growing-season and mid-growing-season treatments because of greater availability of resprouting and recently germinated vegetation.

METHODS

Study area

We conducted our study at nine sites dominated either by loblolly or shortleaf pine in Tennessee, South Carolina, Alabama, and Mississippi, USA (Table 1, Turner and Harper 2024). Two sites in

Tennessee included the Foothills Wildlife Management Area (WMA) in Blount County and the Bridgestone/Firestone Centennial Wilderness WMA in Van Buren County, both owned by the Tennessee Wildlife Resources Agency. The Foothills site had an overstory dominated by shortleaf pine and was 83 years old. The Bridgestone site was a shortleaf pine planting that was planted in 2014 and was dominated by shortleaf pine. Two sites in South Carolina included the Belfast WMA in Laurens County and the Hamilton Ridge WMA in Hampton County, both owned by the South Carolina Department of Natural Resources. The Belfast site had a loblolly pine overstory and was 27 years old. The Hamilton Ridge site also had a loblolly pine overstory and was 31 years old. Three sites in Alabama included the Barbour County WMA in Barbour County that was owned by the Alabama Wildlife and Freshwater Fisheries Division, and Mason Bend in Perry County, and Folsom in Hale County, both of which were privately owned. The Barbour site had an overstory dominated by loblolly pine and was 24 years old. Mason Bend had a loblolly pine overstory and was 21 years old. Folsom also had a loblolly pine overstory and was 18 years old. Two sites in Mississippi included the Copiah County WMA in Copiah County, owned by the Mississippi Department of Wildlife, Fisheries, and Parks, and Triple Creek in Clarke County, which was privately owned. Copiah had a shortleaf pine overstory and was 61 years old. Triple Creek had a loblolly pine overstory and was 25 years old. Annual average precipitation and temperature were similar among sites, ranging from 115 cm to 148 cm and 13 °C to 19 °C (U.S. Climate Data, 2024).

Study design

We used a randomized complete-block design with each site serving as a treatment replicate. We created five treatment units at each site, including dormant-season fire (DOS), early growing-season fire (EGS), mid-growing-season fire (MGS), late growing-season fire (LGS), and a control (CTL) that was not burned. We defined DOS as January through March, EGS as April through May, MGS as June through July, and LGS as August through October. The beginning of the EGS coincided with leaf emergence of deciduous species, not just emergence of buds or when leaves of the earliest species appeared. Our treatment units were approximately two hectares each and we delineated them with permanent firebreaks. We established four standardized sampling plots in each treatment unit where we conducted all plant sampling, totaling 20 per site. Sampling points were placed >25 m from each treatment unit boundary to avoid edge effects. We collected deer forages during the growing seasons of 2020–2023.

We collected deer forages June–July 2020–2023 to coincide with peak milk production for lactating females (Diefenbach and Shea 2011). First, we established four, 50-m transects in each treatment unit. We then identified all understory plants to species at 1-m intervals along the transect and recorded evidence of deer herbivory as indicated by the damaged structure of the plant in accordance with the foraging habits of deer (Lashley et al. 2015c). We used this information, augmented by information from other deer forage studies (Shaw et al. 2010, Lashley et al. 2014, Nanney et al. 2018, Harper et al. 2021), to inform forage collection. We then placed three 0.5 m^2 PVC frames along each of the transects at the 12.5-, 25-, and 37.5-m marks. We collected portions of plants commonly browsed by deer ≤1.5 m in height. We collected young and older plant tissue of each species and sorted them separately because digestibility and nutrient content differ by age (Lashley et al. 2022, Turner et al. 2024, Harper et al. in press). We considered young tissue as the relatively smaller leaves closer to the tip of the stem, and the rest of the leaves as older (Lashley et al. 2014). We used burn coverage maps to create a buffer radius of 25 m, the distance the transect runs in either direction when centered on the sampling point, to exclude any forage data from plots that did not burn in the previous fire treatment.

In 2023, we collected forages during April–September to assess the effects of fire timing on plant digestibility and nutrient content over time. Pre-treatment forages were collected in April and May of 2023 at least four weeks after DOS treatments but prior to implementing the EGS treatment to coincide with the period in which males have the greatest nutritional requirements during antler growth (Brown et al. 1983). We collected forages again in June and July, at least four weeks after EGS treatments and immediately prior to implementing the MGS treatment during the same time that we collected samples in 2020–2022. We collected forages again in September at least four weeks after the MGS treatments to determine how resprouting plants differed from plants in unburned stands during a period in which forages are often nutritionally poor (Short 1975).

We placed forage samples into paper bags as they were collected and labeled them with the site name, date, treatment unit, species, and plant tissue age (young or older). We dried plant samples in an industrial forage drier at 50 ˚C for 72 hours (Nanney et al. 2018). We weighed samples with a Uline digital scale (Uline, Pleasant Prairie, Wisconsin, USA) to the nearest 0.1 g. After weighing, we combined all samples of a given species and age, by treatment, assigned them a unique numerical value, and sent a subsample to the Agricultural Service Laboratory at Clemson University in Clemson, South Carolina, USA and Custom Laboratory in Monett, Missouri, USA for wet chemistry nutrient analysis (Ondarza and Ward 2013). We extrapolated the dry weight of the samples from grams per 0.5 m^2 to kilograms per hectare (kg/ha) of available deer forage. We combined nutrient analysis results with forage biomass estimates to calculate the total number of deer days per hectare (dd/ha) for each treatment and site using an explicit nutritional constraints model (Hobbs and Swift 1985). We set a crude protein constraint (CP) at 14% to reflect the requirements of a female during lactation (Hewitt 2011). We sorted forages collected in each unit from highest to lowest CP and included all forages that maintained the average CP ≥14% nutritional threshold for our mixed-diet NCC model. We calculated forage values by averaging individual CP values that were above or below the minimum constraint until the average value was at the minimum value, at which point that became the threshold for the NCC.

DATA ANALYSIS

We used linear mixed effects models to test relationships of season of burning on forage biomass and NCC in Program R (R Foundation, Vienna, Austria) with mixed-effects ANOVAs in the nlme package (Pinheiro et al. 2022). We compared treatment units to control each year of the study, and then we performed a post-hoc, repeated measures analysis to asses treatment effects over the four years of the study. We grouped the collected species into the categories "forb," "semi-woody" (brambles and vines), and "woody" (shrubs and trees) to assess if fire season increased or decreased the overall availability of these functional groups. Young and old plant parts were analyzed separately when calculating nutritional carrying capacity (NCC) estimates. We analyzed NCC estimates for 2020–2023. When comparing among years, we only used the second (June–July) collection period in 2023 to maintain consistency with other years of the study. We analyzed forage biomass, NCC, crude protein, and phosphorus from each of the three collection periods in 2023 to track changes during that growing season while fire treatments were being implemented. For crude protein and phosphorus, we chose three genera and one species that were common across sites as a reference group to monitor nutrient changes related to fire timing. Browsed plant species eaten by deer and their level of preference were summarized by treatment and year, then tabulated to determine how often species were selected. We established a rate for browsing preference where $Preference\ rate = \left(\frac{number\ of\ browsing\ events}{total\ species\ occurance}\right) \bullet 100$, to standardize preference for each species by the number of times they were encountered on vegetation transects, reported as percentages.

RESULTS

2020–2023 forage collections

Selected forage biomass did not differ among treatment units in 2020 before the fire treatments were implemented (**Table 2.1**, **Figure 2.1**). In 2021 and 2022, forage biomass did not differ among treatments or control. After two iterations of fire treatments in 2023, forage biomass was greater in DOS ($P < 0.01$), MGS ($P = 0.02$) and LGS ($P = 0.03$) than control. Selected forb biomass was relatively low in 2020, and treatments did not differ from control prior to implementing the treatments (**Table 2.1**, **Figure 2.1**). Selected forb biomass in 2021 and 2022 did not differ between treatments and control, but in 2023, selected forb biomass was greater in DOS ($P < 0.01$) and LGS ($P = 0.02$) than control. The EGS treatment decreased semi-woody biomass by an average of 43.0±18.8 kg/ha compared to control ($P = 0.023$). There was no change in woody plant biomass in the four growing seasons sampled ($P = 0.33$; **Table 2.1**, **Figure 2.1**). NCC estimates did not differ from control in 2020–2023 (**Table 2.2**, **Figure 2.2**).

2023 Seasonal collections

Total selected deer forage biomass did not differ among treatments and control in the first collection in April/May 2023. By the second collection in June–July, forage biomass was greater in DOS ($P < 0.01$), MGS ($P = 0.02$) and LGS ($P = 0.03$) than control. In the third collection in September, forage biomass was greater in DOS, EGS, and LGS than control ($P \leq 0.02$). Selected forb biomass was greater in the first collection in the MGS treatment ($P \leq 0.05$) than in the other treatments and control. In the second collection, forb biomass was greater in DOS ($P < 0.01$) and LGS ($P = 0.02$) than control. In the third collection, forb biomass was greater in DOS, EGS, and

LGS treatments than control ($P \leq 0.01$). Selected semi-woody biomass in the first collection was less in DOS and LGS treatments than control ($P \leq 0.03$). Selected semi-woody biomass in the second collection was greater in the MGS and DOS treatments ($P \leq 0.05$), but treatments did not differ in the third collection ($P \geq 0.346$). Selected woody biomass did not differ ($P \geq 0.05$) among treatments or control in any of the three collection periods (**Table 2.3** and **Figure 2.3**).

In the first collection, percent CP and P did not differ among treatments and control (**Table 2.4** and **2.5**). In the second collection, percent CP was greater in the EGS treatment compared to the other treatments and control ($P < 0.001$), and percent P was greater in the EGS treatment compared to the other treatments and control ($P = 0.001$). In the third collection, percent CP and P were greater in the MGS treatment than in the other treatments and control. NCC estimates among treatments did not differ from control during the first or second collection. NCC was greatest in the DOS (13.8 dd/ha, $P < 0.01$) treatment in the September collection (**Table 2.6** and **Figure 2.4**).

Post-hoc repeated measures analysis

The treatment effect on total selected forage biomass did not differ between treatments, however, there was an increase in the average available biomass in all treatments over the course of the study ($P = 0.025$). Selected forb biomass increased in all treatments over four growing seasons ($P = 0.002$;) , but the increase was greatest in the LGS treatment compared to control ($P = 0.001$). NCC estimates increased in all treatments over the course of the study ($P \leq 0.001$) with the greatest effect in the DOS treatment ($P = 0.021$).

DISCUSSION

Selected deer forage biomass and NCC varied among fire-timing treatments and control over 4 years after two iterations of the treatments. Deer forage biomass did not differ among treatments and control until 2023, when both total forage biomass and forb biomass were greater in DOS and LGS treatments, supporting our hypothesis that these treatments would increase forb biomass. Contrary to our predictions, NCC estimates did not differ from 2020–2023, suggesting NCC was influenced most by the amount of semi-woody and woody forage present among treatments and that the increase in forb biomass in the LGS treatment was not enough to influence NCC. Our seasonal forage collections indicated that though there was no difference in forage biomass or NCC at the start of the growing season, by the end of the growing season, DOS, EGS, and LGS treatments contained greater forb biomass and NCC was increased in the DOS treatment because of increased amounts of semi-woody and woody forages. Contrary to our original hypothesis, the LGS treatment did not increase NCC compared to unburned control units.

Total forage was similar among treatment units and control in 2020 prior to implementing treatments and subsequently trended up in all treatments and control by 2022, which was the second growing season following the first iteration of the DOS, EGS, and LGS treatments. Other studies have reported increased forage biomass after implementing fire treatments (Edwards et al. 2004, Lashley et al. 2011, Nanney et al. 2018) and increases in other wildlife foods (Lashley et al. 2015). Deer forage in control consisted primarily of semi-woody and woody species, which often provide relatively lower levels of crude protein and phosphorus (Turner and Harper 2024). Total biomass remained relatively high before declining substantially in 2023, likely because of decreasing available sunlight because of increasing canopy closure and because many woody forage plants were growing beyond the reach of deer a few years following thinning. Deer forage biomass decreased in the EGS treatment in 2021 and 2023 because those units were burned only a few weeks prior to forage collection.

Forage quantity and quality influence NCC (Hobbs and Swift 1985). Considerable variance prevented us from realizing statistical differences in NCC in 2023 though treatments were approximately 3–4 times greater than control, which remained relatively constant over the four years of study. Nutritional carrying capacity estimates are influenced by different plant types, each of which offers different nutritional values over the course of the growing season and time since fire. Forbs on average provide greater nutrient density and are more digestible than semi-woody and woody forages (Lashley et al. 2014, Harper et al. 2025). However, when the nutritional quality of semi-woody and woody plants meets the minimum threshold used in the NCC calculation, those forages positively influence NCC. We used a constraint of 14% CP because that is representative of the nutritional needs of a lactating female with twin fawns (French et al. 1956, Hewitt 2011), and that threshold has been used in several other studies in the southeastern US (Meyer et al. 1984, Nanney et al. 2018, Harper et al. 2021, Turner et al. 2024). The DOS treatment encouraged resprouting of semi-woody and woody plants that contributed to a greater NCC, which supports previous literature that suggests woody plants play an important role in diet selection by deer in recently burned areas (Schindler et al. 2004, Nanney et al. 2018, Nichols et al. 2021). Forb biomass in the DOS and LGS treatments more than doubled from 2020 to 2023 but declined in control. The timing of the DOS and LGS treatments allowed warm-season forbs to mature, instead of setting them back during their growth cycle, which could lead to increased forb coverage in those treatment units over time.

We were able to discern differences in deer forage availability among fire-timing treatments after only two iterations of the treatments. Differences among treatments may become greater with additional implementation of treatments on a relatively short return-interval (e.g., 2 years; Ryan et al. 2013). McKinney (2023) recommended a fire return interval less than three years increased the production of understory plants. Shorter fire-return intervals ensure that semi-woody and woody plants, which were a significant portion of our collections, are continually top killed and better allow herbaceous species to germinate and persist (Brock and Brock 2004, Resop et al. 2024).

Multiple forage collections over the growing season of 2023 illustrated how forage availability and quality were similar among treatments and control soon after spring green-up, but how subsequent growing-season fire can influence both forage biomass and quality. The EGS treatment reduced forage biomass compared to the DOS and LGS treatments, but forage quality was increased because of the more-recently germinated and sprouting vegetation. Other studies have observed greater forage quality when more nutritious plants, such as forbs, are available (Lashley et al. 2011, Nanney et al. 2018). Newly germinating and recently resprouting plants are generally more nutritious and digestible than growth from previous growing seasons because they greater crude protein and phosphorus and have less non-digestible plant fibers (Carlson et al. 1993, Cherry et al. 2017). The same trend occurred following the MGS treatment with less forage biomass, but greater forage quality in the third forage collection. Although NCC was increased in the third collection period only in the DOS treatment, it is clear that burning different areas in relatively close proximity during different times of the growing season can be advantageous to deer because of the increased nutrition available from the more recently germinated and sprouting vegetation. Rainer et al. (2021) also reported that altering fire timing later in the growing season enhanced available nutrition during a time when nutrient availability is in steep decline.

Each of our fire-timing treatments proved advantageous for enhancing deer forage availability. Fire during each season of the year increased deer forage availability and quality.

Forage quality and quantity decline over time during the growing season, and our data illustrate how burning different areas through the growing season can provide pulses of high-quality forage through nutritionally demanding periods. Planning a burn regime that provides relatively recently germinated and sprouted vegetation over time and space would maximize availability of the most nutritious forage to deer. Burn units should be arranged such that lactating females have adequate access to cover juxtaposed or at least near highly nutritious food (Cherry et al. 2017, Chance et al. 2020). Burn unit sizes <15–20 ha would match core summer home range sizes (Beier and McCullough 1990), and altering the season of burning as well as the fire-return interval in various burn units would diversify forage and cover availability across a property to better meet nutritional requirements of a lactating doe as well as the cover requirements for fawning, which have increased visual obstruction (Rohm et al. 2010, Edge et al. 2023) and are set-back or disturbed less frequently than burn units dedicated to enhanced forage quality.

MANAGEMENT IMPLICATIONS

Prescribed fire can be used to increase and enhance deer forage in pine woodlands. Managers can expect to improve deer forage availability and quality by burning at any time of year. Burning during the latter portion of the growing season increased forb biomass most, but that did not lead to an increase in NCC compared to other fire-timing treatments. Our results indicate that where deer is an objective, managers should strive to burn different areas of a property during all seasons of the year to maintain pulses of highly digestible nutrition throughout the growing season when nutritional demands for deer are greatest. We recommend that where improved deer forage is an objective, having high-quality forage available spring through summer when nutritional requirements for deer are greatest by burning in all seasons is the most effective way to ensure high-quality nutrition is always available. Managers should be pleased to learn that burning during all times of the year has advantages for improving deer habitat because that allows more flexibility in meeting target burn-acreage objectives.

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APPENDIX

Table 2.1. Mean biomass (kg/ha ±SE) of forbs, semi-woody plants, woody plants, and all categories combined over four years (2020–2023) after two iterations of dormant (DOS), early growing- (EGS), mid-growing- (MGS) or late growing-season (LGS) fire treatment. We collected pretreatment data in 2020 before implementing fire treatments. We conducted LGS treatments in August–October, 2020 and 2022, DOS treatments in January–March, 2021 and 2023, EGS treatments in April–May, 2021 and 2023, and MGS treatments in June–July, 2021 and 2023 across nine study sites in Tennessee, South Carolina, Alabama, and Mississippi.

2020	Mean forb biomass	Group	Mean semi-woody biomass	Group	Mean woody biomass	Group	Mean biomass	Group
Control	56.2±22.9	a	113.7±24.4	a	112.8±48.4	a	263.1±42.6	a
DOS	52.3±18.5	a	124.0±29.2	a	132.3±57.8	a	308.7±46.1	a
EGS	49.0±11.7	a	87.9±19.7	a	129.7±60.2	a	266.6±52.7	a
MGS	47.6±19.7	a	129.1±32.0	a	185.5±82.2	a	368.0±73.2	a
LGS	61.6±35.4	a	117.6±14.2	a	145.0±35.0	a	331.6±42.8	a
2021								
Control	102.8±30.2	a	140.5±28.1	a	167.8±60.3	a	411.1±46.8	a
DOS	123.7±39.3	a	104.8±20.7	a	159.6±63.2	a	388.2±87.2	a
EGS	51.9±31.2	a	61.5±22.5	b	122.3±78.3	a	235.7±83.5	a
MGS	130.3±45.9	a	108.6±22.0	a	141.0±48.0	a	380.0±53.5	a
LGS	147.8±54.7	a	119.8±20.8	a	99.4±51.6	a	367.0±78.5	a
2022								
Control	42.3±26.5	a	208.3±49.1	a	365.8±234.7	a	616.4±80.3	a
DOS	105.0±51.3	a	186.1±42.5	a	195.8±63.2	a	487.0±101.9	a
EGS	121.2±55.2	a	187.5±96.4	a	174.5±73.3	a	483.1±95.6	a
MGS	157.7±117.5	a	163.4±36.2	a	158.0±58.1	a	479.1±106.6	a
LGS	119.5±75.1	a	194.3±41.5	a	305.1±56.8	a	618.9±107.6	a

Table 2.1 Continued

2023

Control	26.5±15.1	a	108.6±14.9	a	64.3±15.3	a	199.4±30.7	a
DOS	113.7±40.7	b	138.3±24.4	a	137.9±56.4	a	390.0±82.2	b
EGS	66.6±44.4	a	62.3±15.4	b	82.0±45.5	a	211.0±58.0	a
MGS	87.8±55.2	a	137.3±27.0	a	94.6±65.3	a	309.0±75.2	b
LGS	152.6±61.6	b	73.5±14.2	a	83.0±35.0	a	319.7±64.2	b

Table 2.2 Mean (±SE) nutritional carrying capacity estimates (NCC) in deer days per hectare (dd/ha) over four years (2020–2023) and after two fire treatments in dormant (DOS), early growing- (EGS), mid-growing- (MGS) and late growing-seasons (LGS). We collected pretreatment data in 2020 before implementing fire treatments. We conducted the LGS treatment in August–October 2020 and 2022, the DOS treatment in January–March 2021 and 2023, the EGS treatment in April–May 2021 and 2023, and the MGS treatment in June–July 2021 and 2023 across nine study sites in Tennessee, South Carolina, Alabama, and Mississippi.

	2020		2021		2022		2023	
	Mean NCC	Group	Mean NCC	Group	Mean NCC	Group	Mean NCC	Group
Control	6.8±3.0	a	3.0±1.8	a	4.4±3.0	a	6.6±2.5	a
DOS	4.7±2.6	a	12.4±6.3	a	9.2±6.3	a	26.0±11.5	a
EGS	4.3±2.1	a	1.9±0.8	a	9.6±4.7	a	23.4±6.7	a
MGS	7.4±3.6	a	3.4±0.9	a	7.8±2.5	a	21.8±8.0	a
LGS	5.5±0.8	a	10.1±5.6	a	6.0±4.6	a	18.8±6.3	a

Table 2.3 Mean biomass (kg/ha ±SE) of selected deer food plants over three collections in April/May (Collection 1), June/July (Collection 2), and September (Collection 3), 2023. We implemented the late growing-season treatment (LGS) in August–September 2022, the dormant-season treatment (DOS) in January–March 2023, the early growing-season treatment (EGS) in April–May 2023, and the mid-growing-season treatment (MGS) in June–July 2023 across nine study sites in Tennessee, South Carolina, Alabama, and Mississippi.

Collection 1	Mean forb biomass	Group	Mean semi-woody biomass	Group	Mean woody biomass	Group	Mean biomass	Group
Control	9.2±32.0	a	83.6±17.6	a	59.9±17.9	a	149.7±36.2	a
DOS	58.4±26.3	a	34.7±17.2	b	18.2±19.5	a	110.5±37.9	a
EGS	26.7±26.3	a	90.8±17.2	a	59.1±19.5	a	174.6±37.9	a
MGS	63.5±26.3	b	84.1±17.2	a	43.2±19.5	a	190.7±37.9	a
LGS	59.7±26.3	a	44.9±17.2	b	32.4±19.5	a	137.0±37.9	a
Collection 2								
Control	23.6±41.3	a	96.9±17.8	a	57.4±41.8	a	177.9±57.5	a
DOS	101.5±29.8	b	123.4±20.8	b	123.1±36.2	a	347.9±43.9	b
EGS	59.6±29.8	a	55.6±20.8	a	73.1±36.2	a	188.3±43.9	a
MGS	78.3±29.8	a	122.5±20.8	b	84.4±36.2	a	285.2±43.9	b
LGS	136.1±29.8	b	65.5±20.8	a	74.1±36.2	a	275.8±43.9	b
Collection 3								
Control	12.4±18.2	a	13.9±6.6	a	23.8±14.1	a	50.1±22.9	a
DOS	65.0±15.6	b	20.5±6.9	a	31.8±9.5	a	117.3±20.5	b
EGS	58.1±15.6	b	15.5±6.9	a	43.3±9.5	a	116.9±20.5	b
MGS	28.2±15.6	a	20.5±6.9	a	33.9±9.5	a	82.5±20.5	a
LGS	67.6±15.6	b	7.8±6.9	a	27.0±9.5	a	102.4±20.5	b

Table 2.4 Mean percent crude protein (CP, ±SE) of selected deer food plants over three collections in April/May (Collection 1), June/July (Collection 2), and September (Collection 3) in stands that were burned in dormant (DOS), early growing- (EGS), mid-growing- (MGS) and late growing-season (LGS) before and after their respective collections in 2023. We implemented the LGS treatment in August–September of 2022. We then implemented the DOS in January–March, 2023, EGS in April–May, 2023, and MGS in June–July, 2023 across nine study sites in Tennessee, South Carolina, Alabama, and Mississippi.

	Collection 1		Collection 2		Collection 3	
	Mean CP	Group	Mean CP	Group	Mean CP	Group
Control	14.8±1.4	a	11.1±0.6	a	11.4±1.0	a
DOS	17.1±1.2	a	11.3±0.6	a	9.9±0.9	a
EGS	15.1±1.2	a	14.6±0.6	b	10.9±0.9	a
MGS	15.2±1.3	a	11.5±0.6	a	13.8±0.9	b
LGS	16.0±1.2	a	11.5±0.6	a	11.5±0.9	a

Table 2.5 Mean percent phosphorus (P, ±SE), expressed as a percentage of the digestible plant matter of selected deer food plants over three collections in April/May (Collection 1), June/July (Collection 2), and September (Collection 3) in stands that were burned in dormant (DOS), early growing- (EGS), mid-growing- (MGS) and late growing-season (LGS) before and after their respective collections in 2023. We implemented the LGS treatment in August–September of 2022. We then implemented the DOS in January–March, 2023, EGS in April–May, 2023, and MGS in June–July, 2023 across nine study sites in Tennessee, South Carolina, Alabama, and Mississippi.

	Collection 1		Collection 2		Collection 3	
	Mean P	Group	Mean P	Group	Mean P	Group
Control	0.22±0.03	a	0.14±0.02	a	0.14±0.02	a
DOS	0.25±0.03	a	0.16±0.02	a	0.14±0.02	a
EGS	0.23±0.03	a	0.20±0.02	b	0.16±0.02	a
MGS	0.22±0.03	a	0.14±0.02	a	0.20±0.02	b
LGS	0.24±0.03	a	0.14±0.02	a	0.14±0.02	a

Table 2.6 Mean nutritional carrying capacity (NCC) in deer days per hectare (dd/ha ±SE) over three forage collection periods in April/May (Collection 1), June/July (Collection 2), and September (Collection 3) during the 2023 growing season following dormant (DOS), early growing- (EGS), mid-growing- (MGS), and late growing-season (LGS) fire treatments. We implemented the LGS treatment in August–September 2022, the DOS treatment in January–March 2023, the EGS treatment in April–May 2023, and the MGS treatment in June–July 2023 across nine study sites in Tennessee, South Carolina, Alabama, and Mississippi.

	Collection 1		Collection 2		Collection 3	
Treatment	Mean NCC	Group	Mean NCC	Group	Mean NCC	Group
Control	25.6±7.9	a	6.6±2.5	a	1.0±0.8	a
DOS	20.2±4.8	a	26.0±11.5	a	13.8±6.4	b
EGS	22.2±3.6	a	23.4±6.7	a	5.0±2.9	a
MGS	35.7±13.1	a	21.8±8.0	a	9.6±3.8	a
LGS	32.5±8.7	a	18.8±6.3	a	5.3±3.0	a

Table 2.7 Plant species collected as selected deer forages over four years (2020–2023) and two iterations of dormant (DOS), early growing- (EGS), mid-growing- (MGS) and late growing-season (LGS) fire treatments. We collected pretreatment data in 2020 before implementing fire treatments. We conducted the LGS treatment in August–October 2020 and 2022, the DOS treatment in January–March 2021 and 2023, the EGS treatment in April–May 2021 and 2023, and the MGS treatment in June–July 2021 and 2023 across nine study sites in Tennessee, South Carolina, Alabama, and Mississippi. We gave each plant a preference rate expressed as a percentage based on the ratio the plant was browsed to the total number of times it was encountered on vegetation transects. Species are listed in the order of the number of times they were encountered on the transect.

Species	Preference rate
Rubus spp.	1.35
Vitis spp.	0.22
Callicarpa americana	0.86
Campsis radicans	7.69
Vaccinium spp.	0.55
Hypericum hypericoides	5.56
Gelsemium sempervirens	2.22
Solidago canadensis	9.53
Helianthus spp.	2.63
Croton glandulosus	66.67
Euthamia graminifolia	1.46
Rhynchosia tomentosa	10.00
Solidago odora	1.28
Chamaecrista spp.	0.60
Symphyotrichum dumosum	1.59
Lespedeza virginica	1.22
Desmodium spp.	7.14

Table 2.7 Continued

Eupatorium spp.	5.52
Lespedeza hirta	1.44
Lobelia puberula	20.00
Eutrochium spp.	12.50
Acer rubrum	1.15
Diospyros virginiana	0.78
Nyssa sylvatica	1.92
Aralia spinosa	0.75
Rhus spp.	0.82
Erigeron canadensis	28.57
Ambrosia artemisiifolia	4.59
Smilax spp.	0.61
Verbesina helianthoides	12.50
Solidago rugosa	0.91
Pycnanthemum spp.	1.41
Doellingeria umbellata	13.33

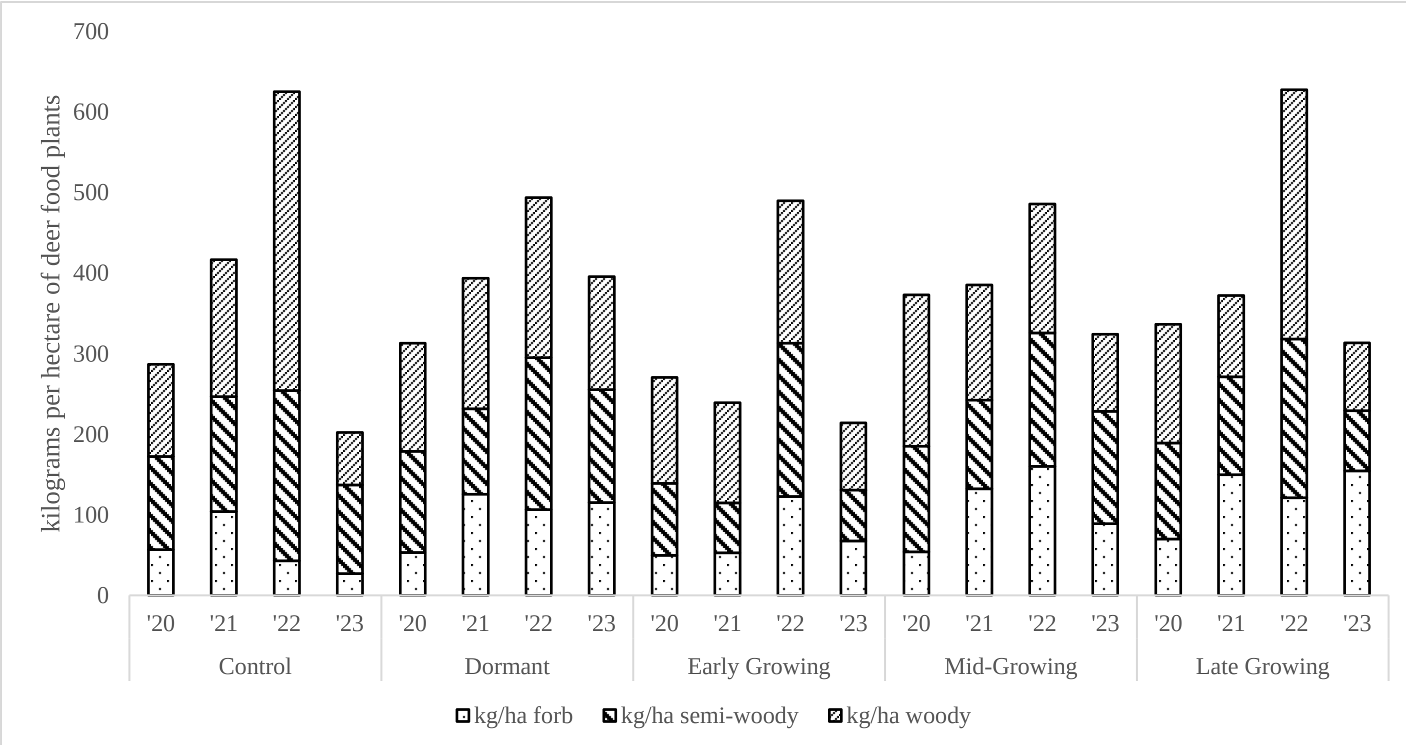

Figure 2.1. Total biomass (kg/ha ±SE) of deer forage of each forage-class (forbs, semi-woody, and woody) in each treatment, 2020–2023, across nine study sites in Tennessee, South Carolina, Alabama, and Mississippi. We collected forage data in 2020 prior to any treatment. We implemented the LGS treatment in the fall of 2020 and 2022. We implemented the DOS and EGS treatments prior to data collection in 2021 and 2023. We implemented the MGS treatment after data collection in 2021 and 2023.

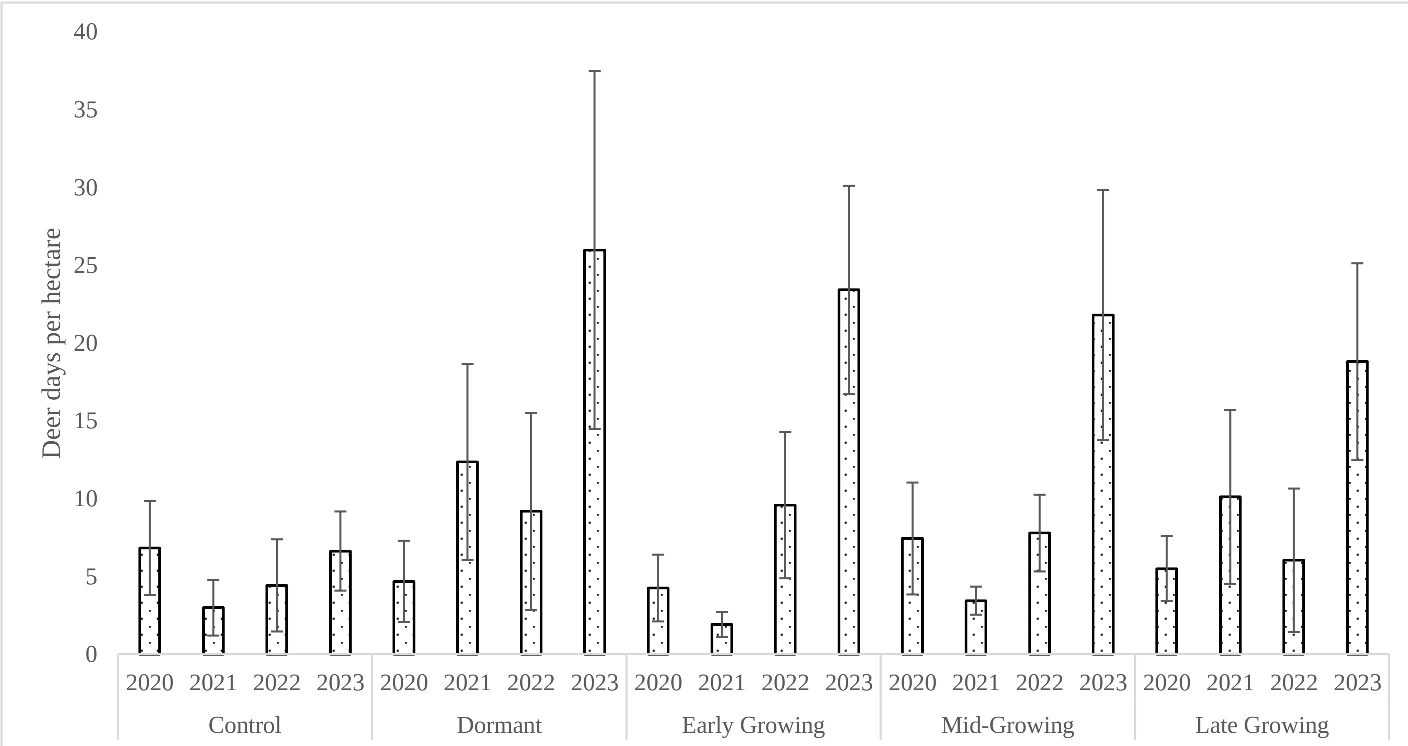

Figure 2.2. Nutritional carrying capacity estimates (deer days per hectare) in each treatment, 2020–2023, across nine study sites in Tennessee, South Carolina, Alabama, and Mississippi. We collected forage data in 2020 prior to any treatment. We implemented the LGS treatment in the fall of 2020 and 2022, We implemented the DOS and EGS treatments prior to data collection in 2021 and 2023. We implemented the MGS treatment after data collection in 2021 and 2023.

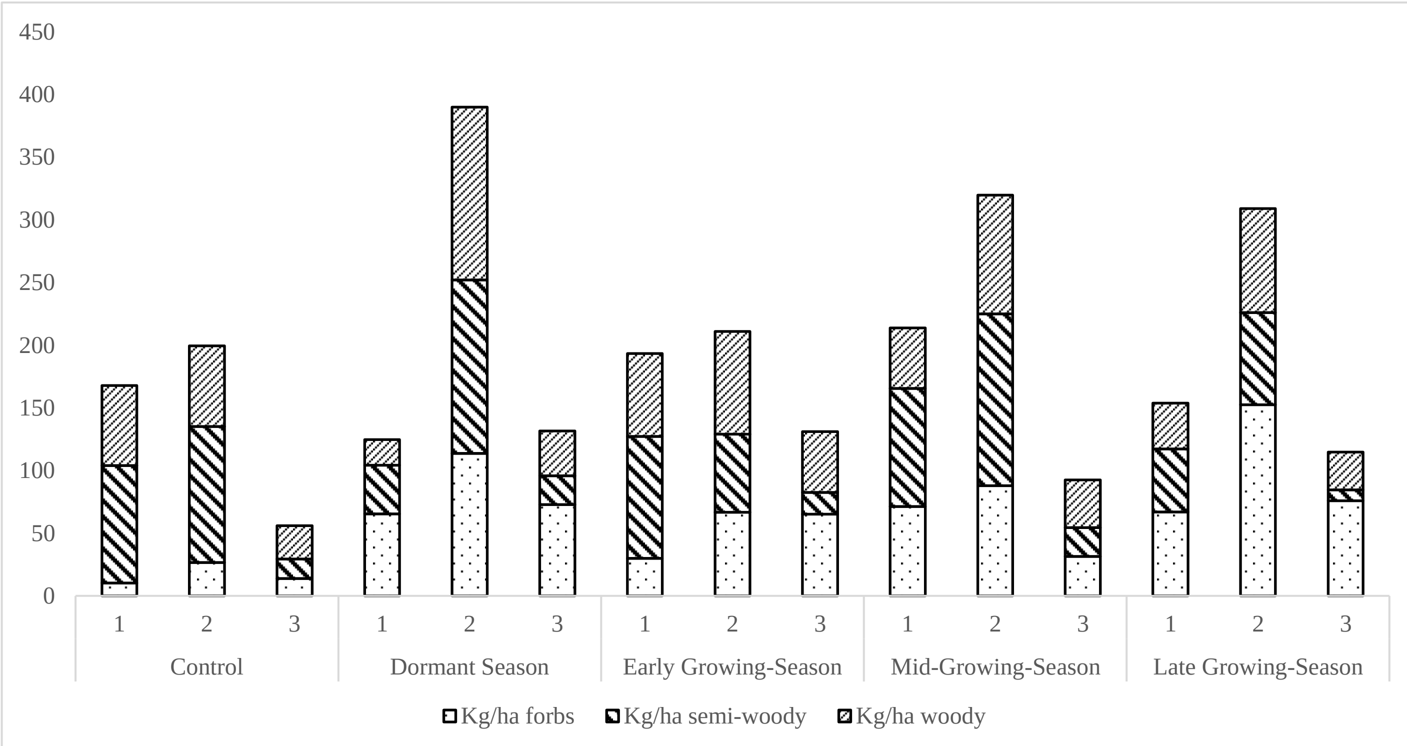

Figure 2.3. Total biomass (kilograms per hectare) of selected deer forages in each forage-class (forbs, semi-woody, and woody) for each treatment, over three collections in April/May (Collection 1), June/July (Collection 2), and September (Collection 3) in stands that were burned in dormant (DOS), early growing- (EGS), mid-growing- (MGS) and late growing-season (LGS) before and after their respective collections in 2023. We implemented the LGS treatment in August–September of 2022. We then implemented the DOS in January–March, 2023, EGS in April–May, 2023, and MGS in June–July, 2023 across nine study sites in Tennessee, South Carolina, Alabama, and Mississippi.

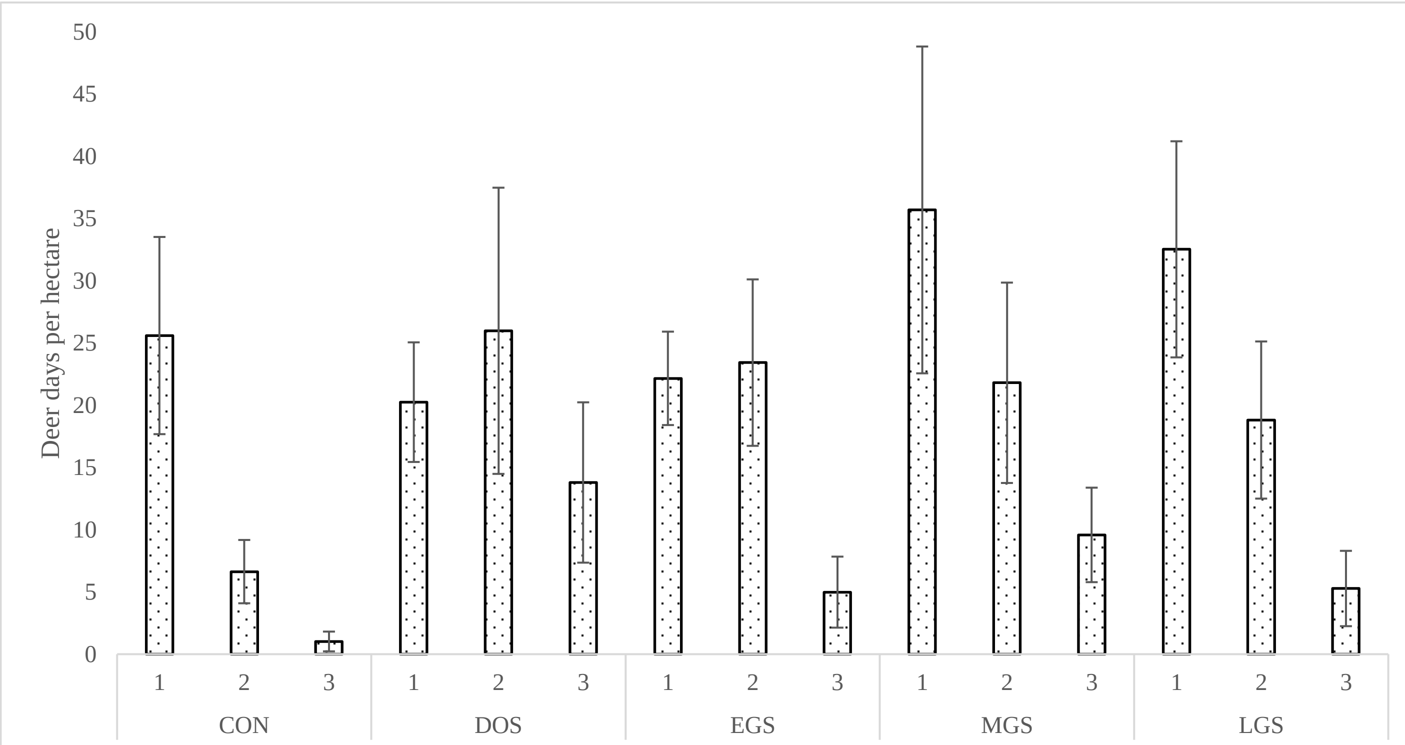

Figure 2.4. Nutritional carrying capacity (deer days per hectare) in each treatment, over three collections in April/May (Collection 1), June/July (Collection 2), and September (Collection 3) in stands that were burned in dormant (DOS), early growing- (EGS), mid-growing- (MGS) and late growing-season (LGS) before and after their respective collections in 2023. We implemented the LGS treatment in August–September of 2022. We then implemented the DOS in January–March, 2023, EGS in April–May, 2023, and MGS in June–July, 2023 across nine study sites in Tennessee, South Carolina, Alabama, and Mississippi.

CONCLUSION

Burning during different seasons of the year following canopy reduction that allowed >30% sunlight to the understory influenced plant composition and stand structure. There was considerable variation among the nine sites, which is expected when working across a broad geographical area. However, our data still indicated burning during the growing season reduced woody sprouting more than burning during the dormant season. Burning during the latter portion of the growing season (Sept/Oct) increased forb coverage more than burning during the other seasons, which was evident both in the understory plant coverage data as well as understory forage biomass data. Increased forb coverage and biomass, however, did not lead to an increased nutritional carrying capacity for deer because the increased biomass of leaves of resprouting woody species in the dormant-season treatment contributed to the nutritional carrying capacity when using a crude protein constraint of 14% and prevented differences among the growing-season treatments. Burning during the growing season influenced nutrient availability to deer. CP and P levels were greatest in the early growing-season treatment during the mid-summer forage collection, and greatest in the mid-growing-season treatment during the third forage collection in late summer. These results have important implications for managers who wish to increase deer forage availability and quality, indicating how burning at multiple times of the year can provide pulses of high-quality deer forage throughout the growing season if the scale of disturbance and its distribution across a property allows all deer on the property access to recently germinated and re-sprouting forage.

Burning during the early portion of the growing season provided a more open stand structure in mid-summer than burning during the other seasons because the vegetation was set-back a few weeks following green-up in spring. Fire intensity and spread, on average, were less in the mid-growing-season treatment than in the early growing-season treatment, which resulted in greater overall openness in the early growing-season treatment. Visual obstruction strongly influences occupancy for many wildlife species. Most notably for game species popular among landowners, wild turkey select a more open stand structure for loafing and foraging, whereas nesting may be more concentrated in areas with more visual obstruction. White-tailed deer select more open areas with >30% sunlight for increased forage availability but select areas with considerable visual obstruction for fawning and bedding. Thus, it is clear how burning in various seasons and at different fire-return intervals can be used to better manage for resources required by these and other wildlife species for various life-stage requirements. Considerations for burning during all seasons of the year also allow for more burn days and better enable managers to meet a diversity of objectives from wildlife habitat to aesthetics to ecosystem restoration.

VITA

Jake Bones was born in Austin, Texas, but grew up in Youngsville, North Carolina where he gained curiosity and passion for the outdoors through hunting and fishing with his peers. He moved to eastern Tennessee as a young adult to attend the University of Tennessee-Knoxville where he completed his Bachelor of Science degree in Wildlife and Fisheries Science in 2019. He worked for the Tennessee Wildlife Resources Agency prior to pursuing his Master of Science degree at the University of Tennessee-Knoxville.