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Vegetation response varies by season of burning in pine woodlands across the southeastern US

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Abstract

Background 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 loblolly and shortleaf pine woodlands have been summarized widely, the effects of fire during all seasons of the year are not well understood. We implemented 72 burns at 9 sites throughout the southeastern US, 2020–2023, to evaluate how fire treatment during the dormant, early growing-, mid-growing-, and late growing-season on a 2-year fire-return interval may affect understory composition, structure, and species diversity indices.

Results 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 was less in all treatments compared to control. However, after two fire events, coverage of semi-woody and woody understory plants increased in the dormant-season treatment and woody understory plants increased in the mid-growing-season treatment, whereas neither increased in the early- and late growing-season treatments. These results indicate growing-season fire sets-back semi-woody and woody vegetation better than dormant-season fire if intensity is adequate to top-kill the plants. Forb coverage increased following all seasons of burning, but the increase was greatest in the late growing-season treatment. Coverage of graminoids decreased in control and in the mid- and late growing-season treatments, partially because of fire timing and because understory sunlight was reduced from an average of 54% to 39% over 4 years as overstory tree crowns expanded following thinning. Percent visual obstruction was least following early growing-season fire. Understory species richness increased in all treatments as well as control.

Conclusion 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, and each produced different effects that could allow managers to better meet objectives in 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.

Keywords Fire season, Fire effects, Forb response, Pine ecosystems, Fire-return interval, Understory vegetation, Prescribed fire

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Resumen

Antecedentes Los bosques abiertos de pinos se encuentran a través de todo el sudeste de los EEUU. Los raleos y las quemas prescriptas son usados comúnmente para establecer y manejar bosques de estos pinos con objetivos múltiples, entre los que frecuentemente se incluyen la producción maderera y el hábitat para la fauna. Aunque los efectos del fuego tanto en bosques de Pinus taeda como en de Pinus echinata han sido resumidos de manera amplia, los efectos del fuego durante todas las estaciones del año no son todavía bien comprendidos. Implementamos 72 quemas en 9 sitios a través del sudeste de los EEUU entre 2020-2023, para evaluar cómo tratamientos de fuegos aplicados durante las estaciones de dormición, crecimiento temprano, crecimiento intermedio y crecimiento tardío en un intervalo de 2 años de retorno del fuego, puede afectar la composición del sotobosque, la estructura, y los índices de diversidad de las especies.

Resultados La intensidad del fuego y la cobertura del área quemada fueron mayores en el tratamiento realizado durante la dormición, y menores en el realizado durante la etapa de crecimiento intermedio. La cobertura de semi-leñosas y leñosas en el sotobosque fue menor en todos los tratamientos en relación al control. Desde luego, y después de dos eventos de fuego, la cobertura de las semi-leñosas y leñosas se incrementó en la estación de dormición y las plantas leñosas del sotobosque se incrementaron en la etapa de crecimiento intermedio, mientras que ninguna se incrementó en los tratamientos de fuegos tempranos o tardíos. Estos resultados indican que la estación de crecimiento condiciona mejor la vegetación semi-leñosa y leñosa que la estación de dormición, si la intensidad de las quemas es la adecuada para matar los meristemas apicales de las plantas. Las malezas de hoja ancha se incrementaron luego del fuego en todas las estaciones, aunque su incremento fue mayor en el tratamiento llevado a cabo en la estación de crecimiento tardía. La cobertura de graminoides decreció en el control y en los tratamientos de quema realizados durante las estaciones de crecimiento intermedia y tardía, parcialmente dado por el momento de aplicación del fuego y porque la luz que llegaba a la superficie se redujo en promedio de un 54% a un 39% en los 4 años, dada por la expansión en las coberturas de copas de los árboles en los rodales raleados. El porcentaje de obstrucción visual fue menor luego del tratamiento de quema realizado en la estación de crecimiento temprana. La riqueza de especies en el sotobosque se incrementó en todos los tratamientos y también en el control.

Conclusiones Documentamos cambios en la composición de plantas y estructura relacionadas con la estacionalidad e intensidad en la aplicación de quemas luego de 2 eventos de fuegos y en 2 años de intervalo de retorno del fuego. Todos los tratamientos cambiaron la composición del sotobosque, y cada uno de estos tratamientos produjo diferentes efectos que pueden permitir a los gestores de los recursos cumplir con la obtención de sus objetivos en sistemas dominados generalmente por pinos amarillos del sudeste. Las quemas realizadas en distintas estaciones de crecimiento ofrecen una mayor flexibilidad a través del año para cumplir con distintos objetivos, incluyendo el manejo del hábitat para la fauna, más allá de la tradicional ventana de prescripción realizada normalmente durante la estación de dormición.

Background

Fire plays a critical role in maintaining pine ecosystems in the southeastern US (Pyne 1982, Ryan et al. 2013). Fire sets-back ecological succession, enables shade-intolerant plant species to compete against encroaching hardwood species, and influences food and cover availability for many wildlife species (Masters et al. 1996; Drewa et al. 2002; Steen et al. 2013; Harper et al. 2016; McGranaham and Wonkka 2021). Several pine species have physical adaptations that allow them to persist with frequent fire, such as shortleaf pine (*Pinus echinata*), which develops thick bark and a basal crook that allows it to resprout following topkill (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., 2009). Species such as shortleaf pine, 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; Pile et al. 2017; Stambaugh et al. 2020). Frequent fire intense enough to suppress hardwood encroachment and competition can be used to promote these pine ecosystems.

Fire frequency and intensity regulate plant composition and structure (Glitzenstein et al. 1995; Beckage and Stout 2000, Meunier et al. 2021). Frequent fire-return intervals are requisite to maintain Southern yellow pine ecosystems (Masters 2006, Stambaugh et al. 2011; Stewart et al. 2015, Robertson et al. 2021). In the third and fourth years following a fire, understory 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*]; Waldrop et al. 1992, Glitzenstein et al. 2003, Gonzalez-Benecke et al. 2015). 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 would ultimately compete with overstory pines (Brockway and Lewis 1997; Kirkman et al. 2004, Glitzenstein et al. 2008). Fire intensity also is important because low-intensity fire may not top-kill relatively small-diameter hardwood stems which may advance into the overstory (Hoffmann and Solbrig 2003). The effect of fire intensity and frequency on plant structure strongly influences wildlife use, as some species select open understory conditions whereas others select more dense cover (Engstrom et al. 1984; Barton et al. 2014; McCord et al. 2014, Rosche et al. 2019; Turner et al. 2024). Relatively low-intensity fire may mimic historical fire regimes (Huffman 2006) and prevent overstory mortality while still accomplishing management objectives (Wade and Johansen 1988).

Season of burning may change vegetation composition in pine systems. Managers traditionally 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 other times of year, which facilitates burning (Sparks et al. 2002, Waldrop and Goodrick 2012; Weir 2009). However, chronic dormant-season burning may promote continual resprouting of top-killed trees (Waldrop et al., 1992, Streng et al. 1993; Knapp et al. 2009; Ryan et al. 2013; Weir and Scasta 2017) and, if fire-return intervals are 1–2 years, extensive grass coverage with relatively low species diversity (Sparks et al. 2009). 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). For example, several studies have reported growing-season burns are more effective at reducing midstory stem density and resprouting than dormant-season burns (Drewa et al. 2006; Knapp et al. 2009; Resop et al. 2023; Zeitler et al. 2025), which may be caused by greater above-ground carbohydrate storage during the growing season (Robertson and Hmielowski 2014). Recent research evaluating the differential effects of burning during the dormant and growing season largely has involved fire during the first half (April–July) of the growing season (Hiers et al. 2000, Cronan et al. 2015, Baruzzi et al. 2022, Resop et al. 2023). Varying the timing of growing-season fire may help diversify plant communities and reduce prevalence of woody species in the understory (Robertson and Hmielowski 2014; Lashley et al. 2015). Furthermore, burning during all seasons of the year increases the number of potential burn days (Chiodi et al. 2018) and provides managers more opportunities to reach objectives.

Although previous research has investigated the effects of early growing-season fire (e.g., Hiers et al. 2000; Melcher et al. 2023), few have studied 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; Turner et al. 2025a). Fire intensity during the mid- (June–July) to latter (September–October) portions of the growing season can be limiting because of increased fuel moisture (Brose and Van Lear 1998, 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 latter portion of the 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). Generally, previous studies have assessed only 2–3 seasons of fire. To our knowledge, only two other studies have investigated four burn seasons in southeastern pine ecosystems: Streng et al. (1993) and Zeitler et al. (2025), the latter of which only had one year of seasonal burn treatments and reported only woody resprouting rates. Streng et al. (1993) reported long-term impacts of four burn seasons over ten years. However, they collected understory plant composition only once, which limited their ability to track changes over time. Further, their study was at only one location, which limited extrapolation over a broader area. More work comparing the effects of burning during all seasons of the year is needed to better guide decision making and meet management objectives (Knapp et al. 2009; Harper et al. 2016).

To assess differential effects of burning throughout the year on plant communities in Southern pine systems, we implemented a field experiment across nine sites in four states that included dormant, early growing-, mid-growing-, and late growing-season fire treatments and 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 decreased woody plant coverage in the understory, whereas dormant-season fire would lead to increased grass and woody plant coverage in the understory. We

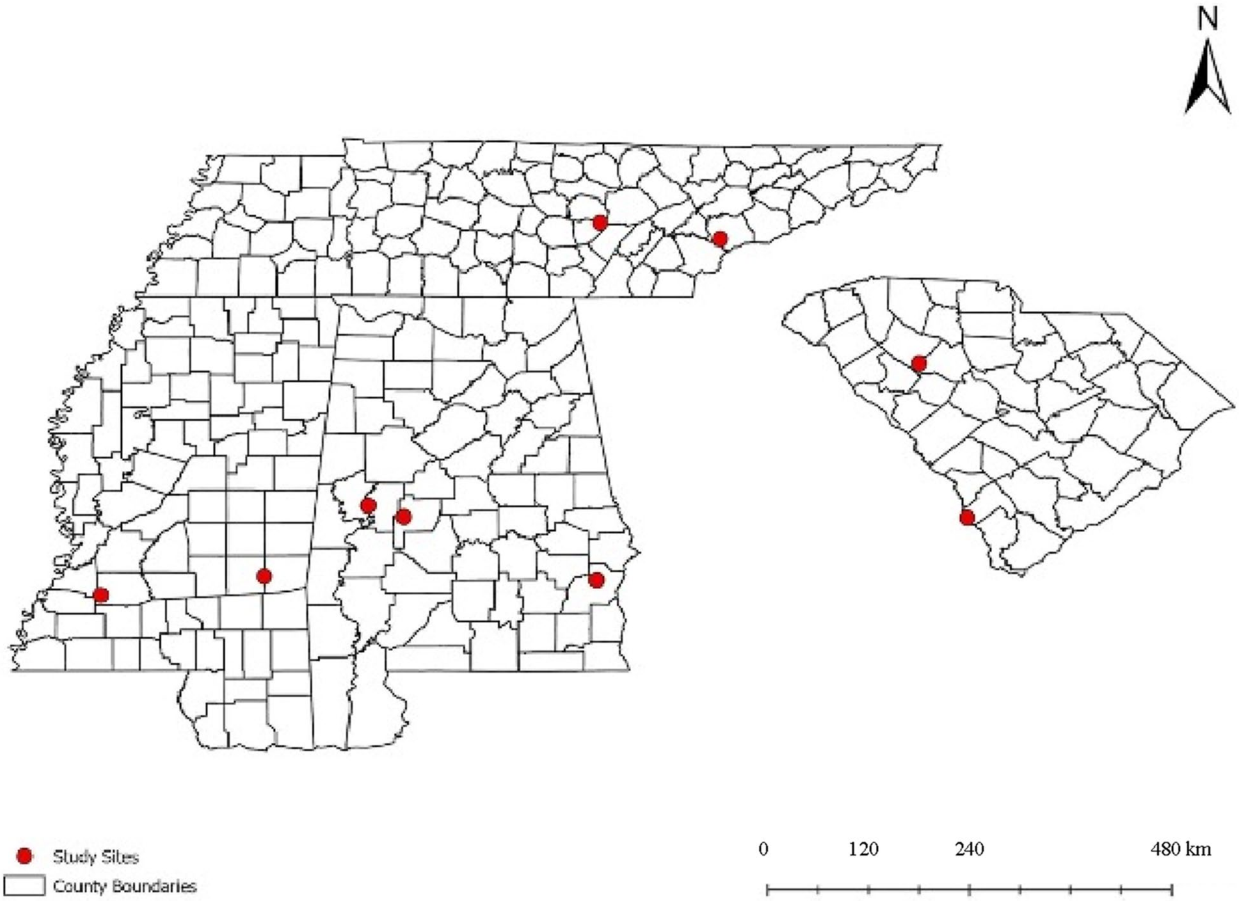

Fig. 1 Study site locations in Tennessee, Mississippi, Alabama, and South Carolina, USA where we studied fire effects on vegetation during all seasons of the year, 2020–2023

predicted dormant- and late growing-season fire would lead to increased forb coverage because fire during those periods would allow warm-season forbs to complete flowering and seed maturity. 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 S1, Fig. 1, Turner and Harper 2024). The 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 when we initiated the study. The Bridgestone site was a shortleaf pine planting that was established 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 to 148 cm and 13 ℃ to 19 ℃ (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 (CON) 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. Each burn was completed on a single day and was completed within 1–3 h. Burns were conducted with 30–65% RH, 1–15 m/s surface winds, and 11–35 ℃ ambient temperature (Table S2).

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 (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 (Waldrop et al 1992; Robertson et al. 2021). 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 recorded 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 s and converted the average rate of spread 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 ℃ to 427 ℃. 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 30.5 cm Type K thermocouples that were 5 mm in diameter (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 ℃ at one-second intervals. Although neither fire tiles nor dataloggers provide perfect measures of fire intensity, they provide a useful index for comparison of relative intensity. After each fire treatment, we mapped unburned areas using a smartphone application (OnX Maps, Missoula, MT, USA) or a handheld GPS.

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 or genus 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-m 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-m radius plots.

We measured understory vegetation structure 10-m from plot center in both directions 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 four, 0.5-m tall 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 at 1.37 m from the ground looking from plot center to the board, which was held by another person at the 15- and 35-m 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 (Turner et al. 2024).

Analysis

We used our burn coverage maps to create a buffer with a 25-m radius around each sampling point to determine which points burned completely during each treatment. We excluded 4 transects in total from points that were not burned in the most recent burn treatments from 2020–2023. We created understory vegetation classes of forbs, graminoids (including sedges and rushes), semi-woody (vines and brambles), and woody (shrubs and understory trees). We calculated percent coverage of each vegetation class by dividing the number of points containing at least one observation of the vegetation class by the total 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. We calculated species richness as 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 $E = \frac{H}{H_{MAX}}$, where E is species evenness, H is the Shannon–Wiener diversity index, and H_{MAX} is the natural log of the species richness. We converted visual obstruction to percentages and for each treatment, and we calculated the average visual obstruction for each stratum. We summarized values into categories of visual obstruction at different heights (< 0.5 m, < 1 m, < 1.5 m, and < 2 m).

We conducted all linear model and ANOVA analyses using Program R (R Foundation, Vienna, Austria, R Core Team 2022). We analyzed differences between fire treatments for the percent cover of each vegetation class, midstory and overstory stem count, basal area, diversity indices, PAR, and visual obstruction with mixed-effects ANOVAs in the nlme package (Pinheiro et al. 2022). We averaged transect values of the response variables to provide a stand-level average for each site. We used site as a random effect, treatment as a fixed effect, and year as a numerical covariate to account for the observations taken over time to create a repeated measures analysis. We performed a Tukey's post-hoc test to compare the marginal means of the burn treatments using the emmeans (Lenth 2023) and multcomp packages (Hothorn et al. 2008). For each burn treatment, we also tested for changes in percent coverage of each vegetation class over the course of the study. We used year as a numerical predictor and site as a random effect. Finally, we performed ANOVAs to compare differences in fire temperature, rate-of-spread, flame length, and burn coverage between seasons. We did not consider fire intensity or weather variables within our vegetation models as we were primarily interested in quantifying typical conditions and fire intensity during various seasons rather than determining the influence of weather on fire effects.

Results

We burned each treatment unit twice from 2020 to 2023 for a total of 72 individual burns. Average burn coverage for both iterations of fire treatments was greater in the DOS and EGS treatments than in the LGS and MGS treatments ($P \leq 0.05$; Table 1). Fire temperatures (℃) recorded by fire tiles in both iterations of treatment implementation were greater in the EGS (176.4 ± 31.2[SE]) 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 iteration of treatments, fire temperatures recorded by dataloggers were greater in the DOS treatment compared to the MGS treatment ($P < 0.05$), but fire temperatures in the EGS and LGS treatments were similar ($P > 0.05$; Table 1). Average flame lengths in the DOS treatment were longer than in all other treatments ($P \leq 0.001$). Rate-of-spread in the DOS and EGS treatments was greater than in MGS and LGS treatments ($P \leq 0.02$ Table 1). Ambient weather conditions during the various treatments were consistent with fire behavior results in that air temperature and RH were greatest and in-stand wind speed was least during MGS treatment (Table S2). Litter depth (cm) was reduced in all fire treatments compared to CON ($P \leq 0.02$). DOS (1.08 ± 0.20) and EGS (1.01 ± 0.20) had less litter than LGS (1.72 ± 0.20) and MGS (2.18 ± 0.20) ($P < 0.04$; Table 1).

Forb coverage increased following all burn treatments ($p < 0.04$), but not the control ($P = 0.944$). Forb coverage increased 5.6 ± 1.3% ($P = 0.0001$) each year in the LGS treatment, 5.6 ± 1.4% ($P = 0.0005$) each year in the DOS treatment, 4.4 ± 1.4% ($P = 0.0054$) each year in the EGS treatment, and 4.1 ± 1.8% ($P = 0.0304$) each year in the MGS treatment. Over the course of the study, forb coverage was greater in DOS and LGS treatments compared to CON ($P \leq 0.05$) with the greatest effect in the LGS treatment ($P < 0.001$; Table 2 and Fig. 2a). Coverage of graminoids did not differ between treatment (Table 2 and Fig. 2b), but graminoid coverage decreased over time in control (6.5 ± 1.7% decrease per year, $P < 0.0001$), MGS (4.8 ± 2.1% decrease per year, $P = 0.027$), and LGS (4.6 ± 2.3% decrease per year, $P = 0.050$) treatments. All treatments had less semi-woody ($P \leq 0.003$) and woody ($P \leq 0.005$) understory plant coverage than the control, and the EGS treatment had less semi-woody coverage than the DOS and MGS treatments ($P < 0.001$; Table 2 and Figs. 2c and 2 d). Semi-woody plant coverage in the control increased 4.0 ± 1.7% ($P = 0.0249$) each year, and DOS treatments increased by 3.8 ± 1.8% ($P = 0.0483$) each year. Woody plant coverage increased 5.1 ± 1.1% ($P < 0.0001$) each year in control units, 3.8 ± 1.1% ($P = 0.0023$) each year in the DOS treatment, and 3.1 ± 1.3% ($P = 0.0301$) each year in the MGS treatment. Midstory stem density was less ($P \leq 0.002$) in all treatments compared to control but did not differ among treatments (Table 3 and Fig. 3).

Table 1 Mean (SE) rate of spread (m/hr), flame length (cm), burn coverage (%), fire temperature recorded by dataloggers (℃), and litter depth (cm) for fire treatments over four years (2020–2023) and after two iterations of fire treatments during the dormant (DOS), early growing- (EGS), mid-growing- (MGS), and late (LGS) growing-seasons at nine sites dominated by shortleaf or loblolly pine in Tennessee, South Carolina, Alabama, and Mississippi. Group refers to letters of significance from a pairwise comparison analysis

Treatment	*Rate-of-spread*	*Group*	*Flame length*	*Group*	*Burn coverage*	*Group*	*Fire temperature*	*Group*	*Litter depth*	*Group*
DOS	78.9 ± 21.9	a	82 ± 8	a	99 ± 0.4	a	171.1 ± 13.1	a	1.08 ± 0.20	a
EGS	73.1 ± 21.1	a	69 ± 4	b	98 ± 0.6	a	135.6 ± 17.5	ab	1.01 ± 0.20	a
MGS	36.5 ± 9.1	b	30 ± 4	b	75 ± 8	b	108.4 ± 11.6	b	2.18 ± 0.20	b
LGS	48.4 ± 15.3	b	43 ± 2	b	89 ± 3	b	129.6 ± 29.1	ab	1.72 ± 0.20	b

Table 2 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 at nine sites dominated by shortleaf or loblolly pine in Tennessee, South Carolina, Alabama, and Mississippi. Column means with the same letter are not different (α = 0.05), and group refers to letters of significance from a pairwise comparison analysis

Treatment	*Mean forb coverage*	*Group*	*Mean graminoid coverage*	*Group*	*Mean semi-woody coverage*	*Group*	*Mean woody coverage*	*Group*
Control	13.5 ± 3.9	a	39.2 ± 7.6	a	50.5 ± 6.6	c	34.7 ± 6.3	b
DOS	26.0 ± 3.9	bc	45.6 ± 7.6	a	41.8 ± 6.6	b	25.3 ± 6.3	a
EGS	19.0 ± 3.9	ab	39.2 ± 7.6	a	30.0 ± 6.6	a	20.9 ± 6.3	a
MGS	19.3 ± 3.9	abc	41.1 ± 7.6	a	41.4 ± 6.6	b	25.3 ± 6.3	a
LGS	26.6 ± 3.9	c	38.7 ± 7.6	a	37.4 ± 6.6	ab	25.4 ± 6.3	a

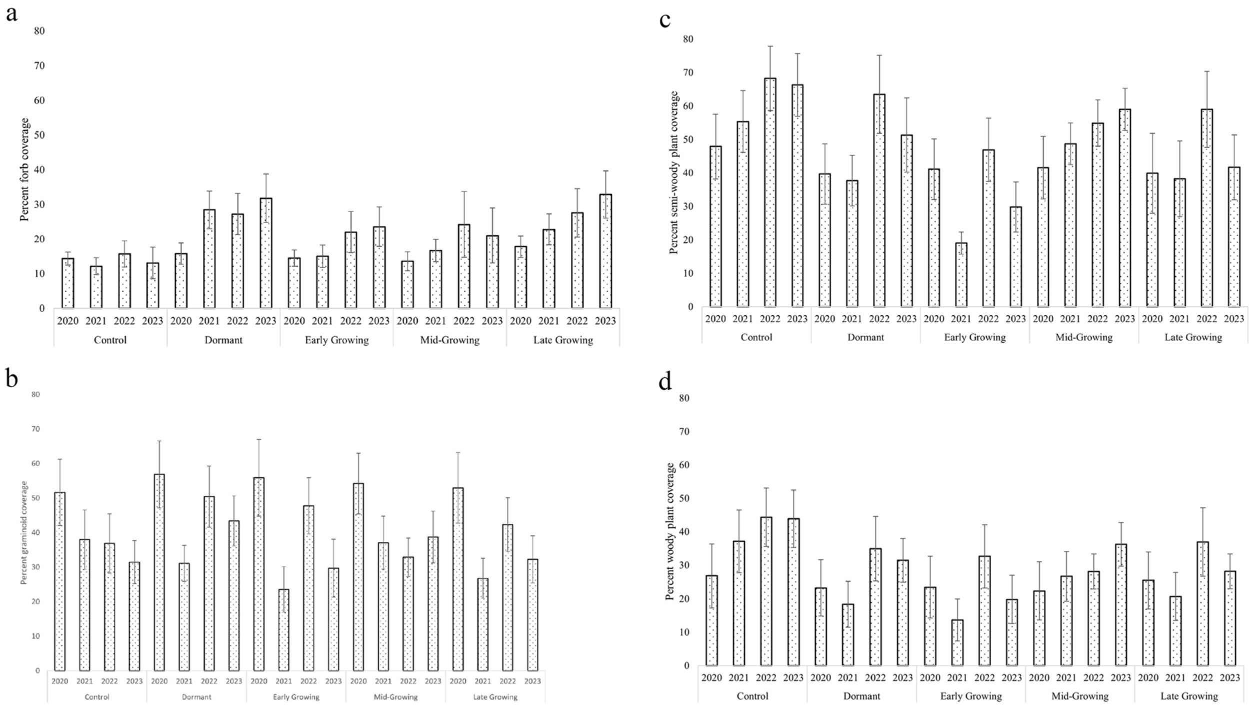

Fig. 2 **a** Percent coverage values for forbs over four years (2020–2023) and after two iterations of dormant (DOS), early growing- (EGS), mid-growing- (MGS), and late (LGS) growing-season fire at nine sites dominated by shortleaf or loblolly pine in Tennessee, South Carolina, Alabama, and Mississippi. 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. **b** Percent coverage values for graminoids 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. **c** 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. **d** 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

Table 3 Mean overstory stem area expressed in basal area (m^2) 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 treatments during the dormant (DOS), early growing- (EGS), mid-growing- (MGS), and late (LGS) growing-seasons at nine sites dominated by shortleaf or loblolly pine in Tennessee, South Carolina, Alabama, and Mississippi. Column means with the same letter are not different ($\alpha = 0.05$), and group refers to letters of significance from a pairwise comparison analysis

Treatment	*Overstory TPH*	*Group*	*Overstory BA/ha*	*Group*	*Mean midstory stem count*	*Group*	*Mean PAR*	*Group*
Control	131 ± 32.6	a	7.8 ± 1.4	a	2253 ± 323	b	50.0 ± 6.0	ab
DOS	162 ± 32.6	b	9.6 ± 1.4	bc	950 ± 323	a	53.4 ± 6.0	b
EGS	150 ± 32.6	a	8.8 ± 1.4	b	879 ± 323	a	50.6 ± 6.0	ab
MGS	176 ± 32.6	b	10.3 ± 1.4	bc	1184 ± 323	a	51.3 ± 6.0	ab
LGS	162 ± 32.6	b	10.5 ± 1.4	c	929 ± 323	a	44.9 ± 6.0	a

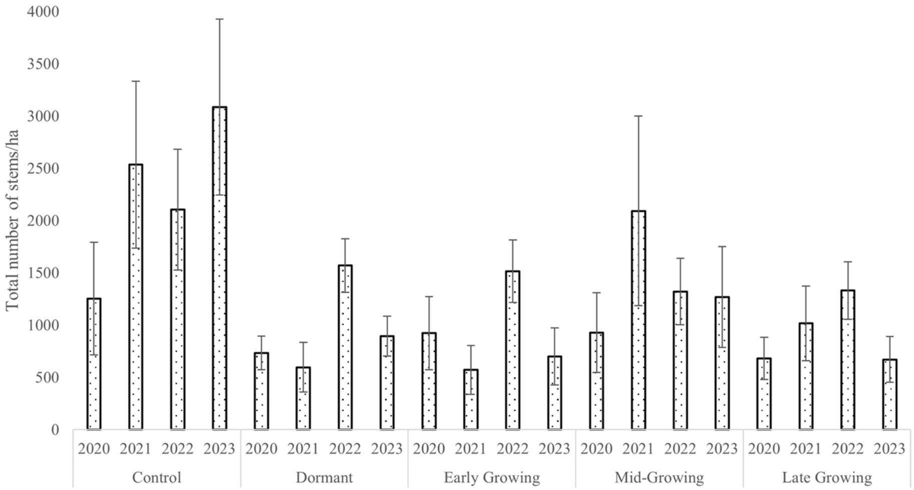

Fig. 3 Average number of midstory stems per hectare over four years (2020–2023) and after two iterations of dormant (DOS), early growing- (EGS), mid-growing- (MGS), and late (LGS) growing-season fire at nine sites dominated by shortleaf or loblolly pine in Tennessee, South Carolina, Alabama, and Mississippi. 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

The number of overstory trees per hectare was less than pre-treatment levels by an average of 6.2 ± 2.8 trees/ha in all treatments and control from 2020 to 2023 ($P = 0.030$). Overstory basal area was greater by 1.8 ± 0.6 m^2/ha in the DOS treatment ($P = 0.002$), 2.5 ± 0.6 m^2/ha in the MGS treatment ($P < 0.001$), and 2.7 ± 0.6 m^2/ha in the LGS treatment ($P < 0.001$; Table 3) than the unburned control. PAR values declined ($P < 0.001$) by an average of 15% in all treatments and control over the duration of the study, and PAR was less in the LGS treatment than in the DOS treatment ($P = 0.037$; Table 3 and Fig. 4).

Visual obstruction below 0.5 m was less ($P < 0.001$) in the EGS treatment compared to control and the DOS 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 ± 3.1, $P < 0.001$). Visual obstruction below 1.5 m and 2 m was less ($P < 0.001$) in all treatments compared to control, but there was no difference among treatments (Table 4).

Plant species richness increased over time in all treatments and control such that, on average, there were 4.1 (± 0.3) more species in the treatments in 2023 compared

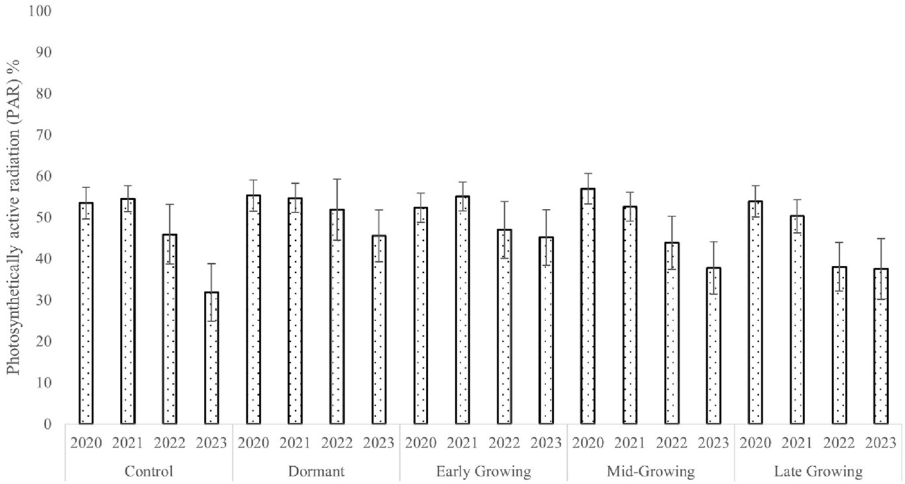

Fig. 4 Average photosynthetically active radiation (PAR) over four years (2020–2023) and after two iterations of dormant (DOS), early growing- (EGS), mid-growing- (MGS), and late (LGS) growing-season fire at nine sites dominated by shortleaf or loblolly pine in Tennessee, South Carolina, Alabama, and 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

Table 4 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 during the dormant (DOS), early growing- (EGS), mid-growing- (MGS), and late (LGS) growing-seasons at nine sites dominated by shortleaf or loblolly pine in Tennessee, South Carolina, Alabama, and Mississippi. Column means with the same letter are not different (α = 0.05), and group refers to letters of significance from a pairwise comparison analysis

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

to 2020 ($P \leq 0.001$). The DOS treatment had greater species richness by an average of 4.6 (± 2.2) species compared to the EGS treatment ($P = 0.002$; Table S3). There was no difference in the Shannon-Weiner diversity index and species evenness between treatments and control.

Discussion

We documented changes in plant community composition, structure, and species richness following two iterations of prescribed fire during different seasons of the year, which supported our hypothesis that burning during different seasons would alter these metrics. 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 stem density. Coverage of brambles, vines, shrubs, and understory tree seedlings or sprouts was less in all treatments compared to control. Contrary to our prediction, forb coverage increased in all treatments, but the increase was greatest in the LGS treatment, despite less-intense fire temperatures. Graminoid coverage was not different among treatments, though coverage decreased in unburned control, MGS, and LGS treatments over time, which is consistent with previous work that indicates burning during the EGS and DOS may maintain or promote coverage of graminoids (Howe 1994, Steuter 1987). Understory woody plant coverage increased from pretreatment levels in control, DOS, and MGS treatments but not in the EGS and LGS treatments, suggesting both seasonal and intensity effects. We did not detect any difference in plant diversity, but plant species richness was increased in all treatments and the control, which did not support our prediction.

Prescribed fire primarily is implemented to set-back succession (Albrecht and McCarthy 2006; Harper 2007, 2017; Block et al. 2016; Greene et al. 2016). All of our treatments set-back succession compared to control, but we documented differential effects among treatments that were representative of season and intensity. Both EGS and LGS treatments maintained semi-woody plant coverage similar to pre-treatment levels, contrary to Turner et al. (2024), who reported greater bramble and tree coverage following LGS fire than EGS fire. Although coverage of semi-woody and woody plants was less following DOS and MGS fire compared to control, coverage of woody plants increased in both treatments and cover of semi-woody plants increased in DOS treatments when compared to pretreatment levels. Resop et al. (2023) reported a similar increase in bramble coverage following dormant-season fire when compared to growing-season fire despite greater fire intensity, rate of spread, and flame lengths. Fire intensity, rate of spread, flame lengths, and burn coverage all were least in MGS, which indicates the MGS treatment lacked the intensity and coverage to top-kill as many woody stems. Our results are consistent with (Drewa et al. 2006; Knapp et al. 2009; Resop et al. 2023; Zeitler et al. (2025), which reported growing-season fire sets-back woody composition better than dormant-season fire, but fire intensity obviously has to be sufficient to top-kill the woody stems to realize an effect. Although not statistically different, midstory stem density in MGS in 2023 was nearly double that in EGS and LGS.

Control of semi-woody and woody plants influences vegetation structure and resources for various wildlife species. 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 set-back the vegetation relatively early in its growth cycle and provided more open structure through mid-summer that may be desirable for some wildlife species. For example, wild turkeys (*Meleagris gallopavo*) often select open structure for brooding because of decreased visual obstruction and increased openness at ground level (Peoples et al. 1995, Wood et al. 2018, 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), and white-tailed deer (*Odocoileus* virginianus) select greater visual obstruction during fawning (Uresk et al. 1999; Chitwood et al. 2017), which was provided in treatments two growing seasons after fire. Various understory songbirds, such as Bachman's sparrow (*Peucaea aestivalis*), select an open understory for reproduction (Engstrom et al. 2005; Fish et al. 2018). 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 (Wilson et al. 1995; Brawn 2006; King et al. 2007; White and Seginak 2000; Kendrick et al. 2013). Thus, burning throughout the year can maintain open conditions to meet life-history requirements of various wildlife species, with EGS burning being especially effective at reducing visual obstruction during the summer immediately after fire.

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 2001; McGranaham and Wonkka 2021; Robertson et al. 2021; Wieczorkowski and Lehmann 2022). Forb diversity is the largest contributor to understory plant diversity in fire-maintained grasslands and savannas (Pokorny et al. 2004; Bond and Parr 2010) and forb coverage is important to achieve many wildlife objectives (Greene et al. 2019; Harper et al. 2025; Turner et al. 2025b). Increased forb coverage has been linked to increased nutritional carrying capacity for white-tailed deer (Edwards et al. 2019; Nanney et al. 2018; Harper et al. 2021), enhanced brooding cover for wild turkeys (Peoples et al. 1995, Yeldell et al. 2017; Johnson 2019; 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 (Steffan-Dewenter and Tscharntke 2002, Gefellers et al. 2020). After two iterations of fire treatments on a 2-year interval, forb coverage in the LGS treatment was nearly twice that of the control. Forb coverage in the LGS and DOS treatments was approximately 1.4 times greater than forb coverage in the EGS and MGS treatments. Increased forb coverage following the LGS and DOS treatments likely is related to plant phenology, whereby most of the warm-season forbs had matured and produced seed prior to DOS and LGS treatments but were set-back or killed during their growth or reproductive cycle by the EGS and MGS treatments (Howe 1994; Pavlovic et al. 2011). 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, Resop et al. 2023, Weir and Scasta 2017). Consideration of fire seasonality effects on forb coverage has implications for several management objectives, and our results suggest LGS and DOS fire best promote forbs.

Understory sunlight availability can alter plant composition, especially herbaceous plants that require near 50% sunlight (Peterson et al. 2007, Charles-Dominique et al. 2018, McKinney et al. 2023). Percent PAR transmittance averaged 54% across all units in 2020 prior to treatment implementation but had declined to 39% by 2023. The decrease in PAR was a result of crown expansion of retained overstory trees, not midstory development, as all fire treatments reduced midstory density and structure. Several of the stands in our study had been thinned to an average BA of 9.5 m^2/ha approximately three years prior to our study (Turner and Harper 2024). By 2023, BA had increased to 10.9 m^2/ha and the reduced PAR 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 common 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 virginiana*), and low panicgrasses (*Dichanthelium* spp.) were less abundant. Thinning to achieve a BA less than 9.5 m^2/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 did not differ from control, but plant species richness in DOS was greater than in EGS. 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 (Naeem et al. 1994; Siemenn et al. 1998, Fontaine et al. 2005). Our plant species evenness and diversity scores were similar to Kirkman et al. (2004), who reported similar species evenness (0.80) but a lower diversity index score (2.0) in a longleaf pine ecosystem. More even distribution and abundance of more plant species can provide increased food and cover for wildlife, which may influence species occupancy and space use (MacArthur and Pianka 1966;

Murdoch et al. 1972; Cardinale et al. 2002). Species composition and distribution also can have implications on fire spread and behavior (Wragg et al. 2018). Overall, our study demonstrated that fire during any season after two iterations of treatment generally maintained metrics of plant diversity.

Conclusions

Our study confirms that fire seasonality can 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. Fire intensity and burn coverage in the MGS and LGS treatments were less than in the DOS and EGS treatments, and the lower intensity and coverage in the MGS treatment was evident in plant community responses compared to treatments applied during other portions of the growing season. 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 management is an objective and indicates no single season of burning is best for all species or objectives. Plant composition was influenced by season of burning and by the amount of sunlight entering the canopy. Canopy reduction should allow a minimum of 50% sunlight to support early successional plant species in the understory. Managers also should consider plant phenology when understory plant composition is an objective, especially when increased forb coverage is desirable. Forb coverage increased most in the LGS and DOS treatments likely because the plants were not flowering when the fires occurred, so considering fire season relative to plant phenology is important. Varying the season of burning has implications for many wildlife species. Our results indicate prescribed fire can be implemented successfully in the early, mid-, and late portions of the growing season with meaningful impact to plant communities. Managers can use our results to better 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.

Abbreviations

DOS	Dormant season
EGS	Early growing season
MGS	Mid-growing season
LGS	Late growing season
DBH	Diameter-at-breast height
PAR	Photosynthetically active radiation

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s42408-025-00439-3.

Supplementary Material 1; Table S1 Dominant tree species, age of stand, tree density, basal area, percent sunlight, soil type (NRCS 2022), elevation, slope, aspect, and coordinates of nine sites included in study to investigate the effects of season of burning on the plant community in Alabama, Mississippi, South Carolina, and Tennessee at the onset of the study in 2020. Table S2 Mean air temperature (℃), in-stand wind speed (m/s), and relative humidity (%) for fire treatments over four years (2020–2023) and after two iterations of fire treatments during the dormant (DOS), early growing- (EGS), mid-growing- (MGS), and late (LGS) growing-seasons at nine sites dominated by shortleaf or loblolly pine in Tennessee, South Carolina, Alabama, and Mississippi. Table S3 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 at nine sites dominated by shortleaf or loblolly pine in Tennessee, South Carolina, Alabama, and Mississippi. Column means with the same letter are not different ($\alpha = 0.05$). Table S4. Output of the linear mixed effects model examining the effects of treatment and year on forb percent cover over four years (2020–2023) 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. Table S5. Output of the linear mixed effects model examining the effects of treatment and year on grass percent cover over four years (2020–2023) 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. Table S6. Output of the linear mixed effects model examining the effects of treatment and year on semi-woody percent cover over four years (2020–2023) 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. Table S7. Output of the linear mixed effects model examining the effects of treatment and year on woody understory percent cover over four years (2020–2023) 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 (National Resource Conservation Service (NRCS), 2022).

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Authors' contributions
JTB coordinated fire treatments, conducted data collection, analysis, and wrote the first draft of the manuscript. SGM coordinated fire treatments, conducted data collection, and aided with analysis. MAT coordinated the first round of fire treatments, the first year of data collection, and aided with analysis. MML helped with analysis and editing the manuscript. WDG aided with fire treatments and assisted in editing the manuscript. EVW assisted with editing the manuscript. CAH conceived of the study, secured funding, coordinated fire treatments, and assisted writing the manuscript. All authors read and approved the final manuscript.

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Data availability
Contact the corresponding author for data requests.

Declarations

Ethics approval and consent to participate
Not applicable.

Consent for publication
Not applicable.

Competing interests
The authors declare no competing interests.

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