Turner *et al. Fire Ecology* (2025) 21:6
https://doi.org/10.1186/s42408-025-00350-x

Fire Ecology

Association for Fire Ecology

ORIGINAL RESEARCH

Open Access

Effect of growing season fire timing on oak regeneration

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Abstract

Background Oaks (*Quercus* spp.) are an important component of eastern hardwood forests, and compositional shifts away from oak are well-documented. Shelterwood harvests often are paired with prescribed fire to promote oak regeneration, as oaks may gain a competitive advantage following fire. However, we are unaware of any studies comparing the effects of multiple fires during the early-growing season (EGS) and late-growing season (LGS) following a shelterwood harvest with reserves on oak regeneration. Additionally, relatively little is known about the response of the red oak group (*Erythrobalanus*) versus the white oak group (*Leucobalanus*) regeneration to fire during different seasons.

Results We initiated a study in east Tennessee, USA in 2010 by implementing a shelterwood with reserves in four upland oak-hickory stands. Each stand contained an EGS treatment, a LGS treatment, a shelterwood treatment with no fire (SW), and an unharvested, unburned control (CON). From 2012 to 2023, we burned the EGS and LGS treatment units six times each. By 2023, the unburned SW treatment was dominated by mesophytes with almost no oaks present in the midstory. Red oak and total understory oak regeneration was promoted by LGS relative to EGS, SW, and CON. White oak regeneration was promoted by EGS compared to CON but did not differ between fire seasonality treatments. Both burn seasons decreased the number and proportion of mesophytes, but the response of other species varied by treatment. The proportion of sassafras was increased by EGS and LGS relative to SW, but did not differ from CON. The proportion of sumac was greatest in EGS, followed by LGS, and was similarly low in CON and SW. Thus, fire increased oak abundance, but also promoted other fire-tolerant upland species.

Conclusions Our results indicate timing of fire during the growing season can positively influence oak regeneration but does not eliminate competition. Additional management practices may be necessary as the stand develops to release oaks after burning is stopped or the fire-return interval is lengthened.

Keywords Early-growing season fire, Fire effects, Late-growing season fire, Mesophication, Oak-hickory forest, Prescribed fire, Red oak, Regeneration, Upland hardwood forest, White oak

Resumen

Antecedentes Los robles (*Quercus* spp.) son componentes importantes de los bosques de madera dura del Este de los EEUU, y los cambios composicionales que se registran hacia otro tipo de comunidades alejadas de los robledales están bien documentadas. Las talas de protección se empalman frecuentemente con quemas prescriptas para promover la regeneración de los robles, dado que éstos pueden tener ventajas competitivas contra otras especies luego de fuegos. Sin embargo, no tenemos conocimiento de estudios que comparen los efectos de fuegos múltiples

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durante la estación de crecimiento temprana (EGS) con la estación tardía (LGS) luego de una corta de selección con reservas en la regeneración de los robles. Adicionalmente, muy poco se conoce sobre la respuesta en la regeneración del grupo de los robles rojos (Erythrobalanus) versus el grupo de los robles blancos (Leucobalanus) después de incendios y durante diferentes estaciones.

Resultados Iniciamos un estudio en el este de Tennessee, EEUU, en 2010 mediante la implementación de cortas de selección con reservas en cuatro rodales de roble y nogal pecán. Cada rodal contenía un tratamiento EGS, uno LGS, un tratamiento de corta de selección sin quemas (SW), y otro sin talar y sin quemar, control (CON). Desde 2012 a 2023, quemamos las unidades de los tratamientos EGS y EGS seis veces cada uno. Para 2023, el tratamiento sin quemas (SW), estaba dominado por mesófitas con casi ningún roble presente en su estrato medio. Los robles rojos y la regeneración total de robles en el estrato superficial fue promovido por el tratamiento LGS en relación con los tratamientos EGS, SW, y CON. La regeneración de roble blanco fue promovida por el tratamiento EGS en comparación con el tratamiento CON, aunque no difirieron en relación a la estacionalidad de los tratamientos con quemas. En ambas estaciones de crecimiento decrecieron el número y proporción de mesófitas, aunque la respuesta de otras especies varió con cada tratamiento. La proporción de sassafras (Sassafras albidum) se incrementó por el tratamiento EGS y LGS en relación con SW, aunque no difirieron con el CON. La proporción de sumac (Rhus typhina) fue mayor en EGS, seguido por LGS, y fue similarmente baja en CON y SW. El fuego, entonces, incrementó la abundancia de robles, pero también promovió a otras especies de altura tolerantes al fuego.

Conclusiones Nuestros resultados indican que la temporada de quema durante la estación de crecimiento puede influenciar positivamente la regeneración de los robles, aunque no elimina la competencia. Prácticas de manejo adicionales pueden ser necesarias mientras el rodal se está desarrollando, para liberar los robles luego que el fuego es detenido o se extiende el tiempo de retorno del fuego.

Background

Oak (*Quercus* spp. L.) regeneration failure in eastern US forests poses a significant ecological and economic risk. Oak-hickory (*Carya* spp. Nutt.) forests account for more than 30% of eastern U.S. forests and provide important forest products and resources for numerous wildlife species (McShea et al. 2007; Oswalt et al. 2017). Overstory oak abundance may influence populations and nutrition of several wildlife species that consume acorns, including white-tailed deer (*Odocoileus virginianus* Zimmermann), eastern gray squirrel (*Sciurus carolinensis* Gmelin), black bear (*Ursus americanus* Pallas), and ruffed grouse (*Bonasa umbellus* Linnaeus; Feldhamer et al. 1989, McShea and Schwede 1993, McShea 2000, Devers et al. 2007, Azad et al. 2017). Additionally, oaks provide important forest products that offer economic value to the region (Luppold 2019). Compositional shifts away from oak to mesophytic species are common, with species such as red maple (*Acer rubrum* L.), yellow-poplar (*Liriodendron tulipifera* L.), and American beech (*Fagus grandifolia* Ehrh.) often outcompeting oak seedlings following canopy reduction (Cook et al. 1998; Nowacki and Abrams 2008; Dey 2014; Alexander et al. 2021; Ryan et al. 2024). Understanding the response of understory oaks to treatments designed to decrease oak competitors is important to reverse mesophication through management.

Important differences exist in the regeneration strategies of upland species in the red oak group (*Erythrobalanus*) and white oak group (*Leucobalanus*). White oak acorns germinate relatively soon after they fall, whereas red oak acorns overwinter and germinate the following spring (Fox 1982; Smallwood et al. 2001). Seedling growth rates differ by species within each group with white oak (*Quercus alba* L.) exhibiting a slower growth rate than northern red oak (*Quercus rubra* L.; Rebbeck et al. 2011, Brose and Rebbeck 2016). Variation also is present in fire tolerance of advanced oak regeneration, with some studies reporting white oak species as more fire-tolerant than red oaks (Fan et al. 2012; Izbicki et al. 2020), and some reporting greater mortality of white oaks than red oaks (Alexander et al. 2008, Green et al. 2010). These collective differences between groups may influence their response to forest management practices implemented to improve oak regeneration.

Several silvicultural techniques have been developed to regenerate oaks, including the shelterwood and burn system (Brose et al. 1999a; Brose 2010). Oaks do not effectively regenerate under full shade, but they commonly are outcompeted following a clearcut harvest, especially on high-quality sites (Gammon et al. 1960; Stringer 2016; Swaim et al. 2016). A two-step shelterwood harvest or shelterwood with reserves may provide better light conditions to accumulate seedlings and saplings, but fast-growing mesophytes often outcompete oak seedlings before they can be recruited into the midstory or overstory (Hill and Dickmann 1988; Schlesinger et al. 1993; Atwood et al. 2011). Upland oaks are fire-adapted, and prescribed fire may provide regenerating oaks a competitive advantage over mesophytes (Signell et al. 2005; Iverson et al. 2008; Beasley et al. 2022). However, overstory reduction and prescribed fire also may promote favorable conditions for species such as sassafrass (*Sassafras albidum* (Nutt.) Nees) and sumac (*Rhus* spp. L.), which are more fire-tolerant than mesophytes (DeSelm et al. 1991; Arthur et al. 2012). Although fire generally is accepted as a tool to promote upland oak regeneration, the role of frequency, intensity, and seasonality of fire on regeneration are not well understood.

Fire influences multiple aspects of oak regeneration, including acorn germination, seedling/sapling survival, and competition with other species (Dey and Fan 2009). Although fire may provide oaks an advantage in regeneration, fire generally decreases acorn survival (Greenberg et al. 2012; Nation et al. 2021). Acorn survival and seedling emergence may vary based on the season of fire and oak species (Wang et al. 2005; Greenler et al. 2020). Season of burning also influences competition, with fire during the growing season typically being more effective at reducing competition than dormant season fire (Brose et al. 1999a, 2013; Brose 2010). There also may be differences in competition control and seedling growth based on the timing of fire within the growing season (Harper et al. 2016; Izbicki et al. 2020; Zeitler et al. 2025). Several studies have investigated the influence of early-growing season (EGS) and late-growing season (LGS) fire on oak regeneration, but most have involved the effects of relatively few fires and/or only evaluated a single season (Brose 2010; Keyser et al. 2019; Xin and Williams 2019; Vaughan et al. 2022). Timing of fire also may influence understory response based on fire intensity and coverage related to prevalent conditions during a season, with EGS and dormant season fire typically being more intense and having greater coverage than LGS (Vander Yacht et al. 2017; Turner et al. 2024).

Given the importance of oaks and the problems associated with regeneration to maintain oak forests, we designed a field experiment to test the effects of prescribed fire during the EGS and LGS paired with a shelterwood with reserves on oak regeneration. Specifically, we compared red and white oak regeneration 13 years after shelterwood harvest with reserves (with no fire), shelterwood with reserves and six EGS fires, shelterwood with reserves and six LGS fires, and an unharvested and unburned control. We hypothesized shelterwood cuts without fire would have limited midstory oaks because of competition from mesophytic species. We also hypothesized understory regeneration composition would change with the inclusion of fire treatments, and we predicted burned treatments would have a lesser proportion and number of mesophytic species and a greater proportion and number of regenerating oaks relative to the unburned treatment or control. We hypothesized differences in oak regeneration based on the timing of burning, and we predicted greater oak understory stem counts following LGS compared to EGS based on seasonal effects and reduced intensity and coverage of LGS burns. Finally, we predicted fire-tolerant oak competition would vary based on fire timing and species, with greater competition in LGS because of reduced fire intensity and coverage.

Methods

Study area

We conducted our study in four upland hardwood stands on Chuck Swan State Forest and Wildlife Management Area (hereafter, CSF) in Union and Campbell Counties, Tennessee, USA. CSF was an 8,216-ha area located in the southern Appalachian Ridge and Valley physiographic province. All stands were classified as white oak-red oak-hickory (USDA Forest Service Forest Type 503). The four stands were called Big Springs Picnic, Big Springs Y, Crumley Loop, and Long Hollow, based on their location, and all stands were located on predominantly south- to west-facing slopes. Overstory species composition included white oak, black oak (*Quercus velutina* Lam.), northern red oak, southern red oak (*Quercus falcata* Michx.), pignut hickory (*Carya glabra* (Mill.) Sweet), mockernut hickory (*Carya tomentosa* (Lam. Ex Poir.) Nutt), yellow-poplar, red maple, American beech, blackgum (*Nyssa sylvatica* Marshall), and black cherry (*Prunus serotina* Ehrh.). Mean annual temperature at CSF was 13.1℃ and mean annual precipitation was 128.5 cm (NOAA 2023). Soils in the Long Hollow and Big Springs Y stands were predominately Clarksville cherty silt loam. The Big Springs Picnic stand had predominantly Fullerton gravelly silt loam soils, and the Crumley Loop stand had predominately Fullerton and Bodine gravelly silt loam soils (NRCS 2023). Stands were 70–140 years old based on previous harvest records, and the average upland oak site index was 21 m at base age 50.

Treatments

We divided each stand into four equal-sized treatment units that were roughly square-shaped as part of a randomized block design. Each treatment unit was approximately 1.6 ha, and we randomly assigned them into the following treatments: control (CON), shelterwood without fire (SW), shelterwood + late growing-season fire (LGS), and shelterwood + early growing-season fire (EGS). The CON treatment units received no timber harvest or fire during the course of the study and were primarily surrounded by closed-canopy forest (i.e., adjacent treatments involving a timber harvest were located only on one or two sides) to minimize edge effects. The SW, LGS, and EGS treatments were harvested using the shelterwood with reserves method in fall 2010. No preparation cut was implemented in these stands prior to the 2010 harvest. These treatment units were being managed as an irregular shelterwood, with the remaining overstory trees being retained indefinitely. Our objective for the shelterwood harvest was to reduce basal area (BA) to approximately 13 m^2/ha and allow approximately 30% sunlight to the understory, which is desirable for oak regeneration (Johnson et al. 2009) and to promote understory conditions favorable for white-tailed deer and wild turkey (*Meleagris gallopavo* Linnaeus). We retained primarily oaks and hickories, but also retained some select black cherry and blackgum for soft mast production for several wildlife species. The SW treatment units were not burned after the 2010 harvest and were allowed to develop into a two-aged stand at the time of the study.

Two years after the initial harvest, we began applying prescribed fire in the LGS and EGS treatment units. Our objective was to burn the LGS and EGS treatments on a 2-year fire-return interval. We burned LGS treatments in 2012, 2014, 2016, 2017, 2019, and 2022, and we burned EGS treatments in 2013, 2015, 2017, 2018, 2020, and 2023. This burning regime resulted in six burns for each treatment with an average fire-return interval of 2.2 years, and we burned all replicates with a given treatment on the same day to ensure consistency of fire weather and timing. We primarily burned LGS units during September–October prior to leaf drop, but 2017 LGS fires were applied in November because of limited burn conditions earlier in the fall. We burned EGS treatments in mid-April–early May after leaf emergence of deciduous trees.

For both LGS and EGS fires, we used a combination of low-intensity backing, strip-heading, and flanking fires to maintain a desired average flame length of < 0.5 m. All burns were conducted with air temperatures between 16 and 27℃, relative humidity between 20 and 50%, in-stand wind speed between 1.6 and 6.4 km/h, and mixing height between 1000 and 2100 m. We removed slash from the base of overstory trees to minimize cambium damage from burning debris (Brose and Van Lear 1999). On average, our EGS burns were more intense with more complete coverage compared to LGS burns (Turner et al. 2024).

Data collection

We randomly placed four sampling points within each treatment unit to collect overstory and regeneration data in July 2023. Each random point was located > 30 m from the plot edges to minimize edge effects. We established a 0.04-ha fixed-radius plot at each sampling point and documented species and diameter at breast height (DBH) for all overstory trees (≥ 11.4 cm DBH) within the plot. We also established a 0.004-ha midstory plot at each sampling point where we counted midstory stems of each species ≥ 1.4 m tall and < 11.4 cm DBH. Finally, we established a 30-m long, 0.3-m wide belt transect at the center of each sampling plot to count seedlings and sprouts of all species < 1.4-m tall. We recorded seedlings and sprouts by species together and included stems arising from both seed germination and resprouting (hereafter referred to as understory stems to include both seedlings and sprouts). For resprouting stems, we counted only a single stem arising from each root system (Hutchinson et al. 2012; Izbicki et al. 2020).

We also collected understory sunlight data along each transect. We took fifteen readings along each transect at 1-m intervals at a height of 1.4 m using an AccuPAR ® LP-80 PAR/LAI ceptometer (Decagon Devices, INC., Pullman, WA) to quantify photosynthetically active radiation (PAR) available to understory stems in each stand. Simultaneous readings were taken in full sunlight, and the percent PAR was calculated by dividing in-stand by full sunlight readings (Turner et al. 2020, 2024).

Analysis

We used Program R (R Core Team 2023) for all analyses. We used mixed-effects analysis of variance (ANOVA) in package lme4 in Program R to test for differences in PAR, red oak overstory BA, red oak overstory trees per hectare, white oak overstory BA, white oak overstory trees per hectare, and mesophyte overstory BA (Bates et al. 2015). We included stand as a random effect in all analyses to account for differences between stands.

To test for differences in understory and midstory regeneration by treatment, we grouped stems into the following categories: red oak group, white oak group, mesophyte (including red maple, yellow-poplar, and American beech), sassafras, and sumac. Although we present figures with the actual stem density for comparison to other studies, analyses related to understory and midstory stems were conducted using count data, which allowed us to analyze right-skewed regeneration data that best fit a Poisson distribution. We used generalized mixed-effect models with a Poisson distribution to analyze differences in counts of red oak, white oak, total oak, mesophyte, sumac, and sassafras stems by treatment, with stand as a random effect. We also calculated the relative proportion of understory stems by dividing the count within each category by the total seedling count at a transect. We then analyzed the proportional data using linear mixed-effect ANOVAs with treatment as a fixed effect and stand as a random effect. We analyzed the total count of midstory stems and mesophyte midstory stems using generalized mixed-effect models with a Poisson distribution and treatment as a random effect. We did not test for differences in other midstory categories because of limited detections. We back-transformed all Poisson estimates by exponentiating model beta values to aid in result interpretation. We used the emeans package (Lenth 2024) to conduct a Tukey post hoc test and set $\alpha = 0.05$ for all statistical analyses.

Results

Overstory and sunlight

Average overstory basal area in harvested treatments was 13.6 (± 2.3 SE) m^2/ha, whereas the average overstory basal area in control units was 25.5 (± 6.2) m^2/ha. Red oak overstory basal area across all treatments and control averaged 6.3 (± 3.0) m^2/ha and did not differ between treatments ($p = 0.221$). White oak group overstory basal area across all treatments and control, which included only *Quercus alba*, averaged 4.1 (± 1.3) m^2/ha. There was a difference in white oak basal area between EGS and SW ($p = 0.012$), with EGS averaging 7.3 (± 1.4) m^2/ha and SW averaging 1.2 (± 0.8) m^2/ha. Mesophyte overstory basal area averaged 1.1 (± 0.8) m^2/ha among EGS, LGS, and SW, whereas CON averaged 7.2 (± 2.2) m^2/ha. There was a greater mesophyte basal area in CON compared to EGS ($p < 0.001$), LGS ($p < 0.001$), and SW ($p < 0.001$).

There was some variation in red oak overstory trees per hectare, but it did not reach statistical significance ($p = 0.064$). Red oak overstory trees per hectare was 38.6 (± 11.9) in CON, 17.0 (± 8.9) in EGS, 23.2 (± 8.1) in LGS and 12.4 (± 5.6) in SW. However, there was a marginally significant difference between red oak trees per hectare between CON and SW ($p = 0.063$). White oak overstory trees per hectare also did not vary by treatment ($P = 0.094$). White oak overstory trees per hectare averaged 24.7 (± 6.7) in CON, 27.8 (± 7.4) in EGS, 10.8 (± 5.3) in LGS, and 10.8 (± 6.8) in SW.

Understory PAR was greater in burned units than CON or SW. EGS and LGS had 27.3 (± 6.8) and 38.1 (± 12.4) percent PAR, respectively, and did not differ ($p = 0.150$). CON had 3.2 (± 1.2) percent PAR, which was less than EGS ($p < 0.001$) and LGS ($p < 0.001$). SW had 2.6 (± 0.7) percent PAR, which was less than EGS ($p < 0.001$) and LGS ($p < 0.001$) but not different from CON ($p = 0.999$).

Understory regeneration

We detected a total of 327 red oak and 272 white oak understory stems on our transects. Black oak was the most abundant red oak species with 156 stems, followed by northern red oak with 127 stems, southern red oak with 42 stems, and scarlet oak with 2 stems. White oak (*Quercus alba*) represented 267 of the white oak group stems, and 5 were chestnut oak (*Quercus montana* Willd.). Understory stem counts of red oak were 7152.8 (± 3122.9) stems/ha in CON, 2361.1 (± 896.5) stems/ha in EGS, 10,416.7 (± 5258.9) stems/ha in LGS, and 2777.8 (± 439.2) stems/ha in SW (Fig. 1). Understory stem counts of white oak were 3611.1 (± 2081.8) stems/ha in CON, 5763.9 (± 1790.8) stems/ha in EGS, 4652.8 (± 2767.1) stems/ha in LGS, and 4861.1 (± 2572.3) stems/ha in SW. Understory stem counts of mesophytes were 35,208.3 (± 5884.2) stems/ha in CON, 5902.8 (± 3139.4) stems/ha in EGS, 7361/1 (± 2899.0) stems/ha in LGS, and 12,083.3 (± 1939.5) stems/ha in SW (Fig. 2). Understory stem counts of sumac were 69.4 (± 69.4) stems/ha in CON, 36,597.2 (± 12,230.3) stems/ha in EGS, 22,222.2

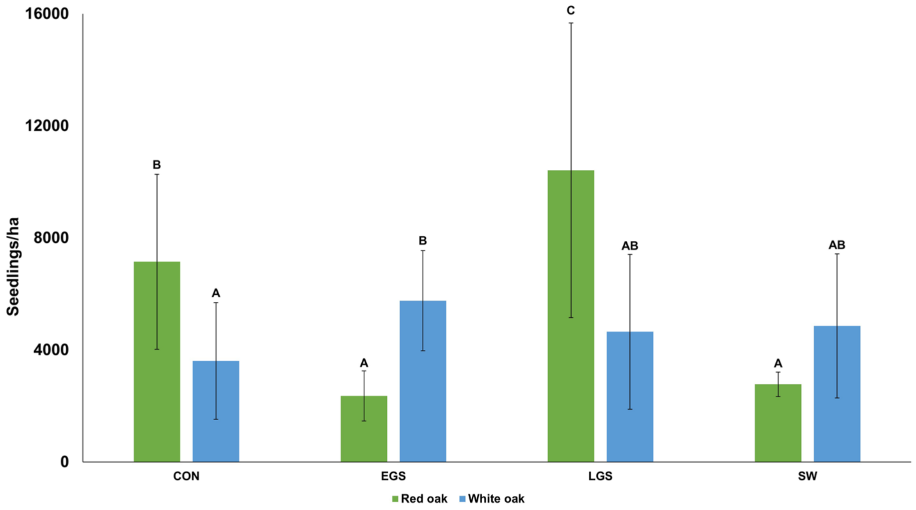

Fig. 1 Red oak (*Erythrobalanus*) and white oak (*Leucobalanus*) group understory stems per hectare in oak-hickory forest stands following early-growing season fire + shelterwood (EGS), late-growing season fire + shelterwood (LGS), and shelterwood (SW) treatments compared to control (CON) during July 2023 in Tennessee, USA. Different letters within an oak group represent significant differences between treatments

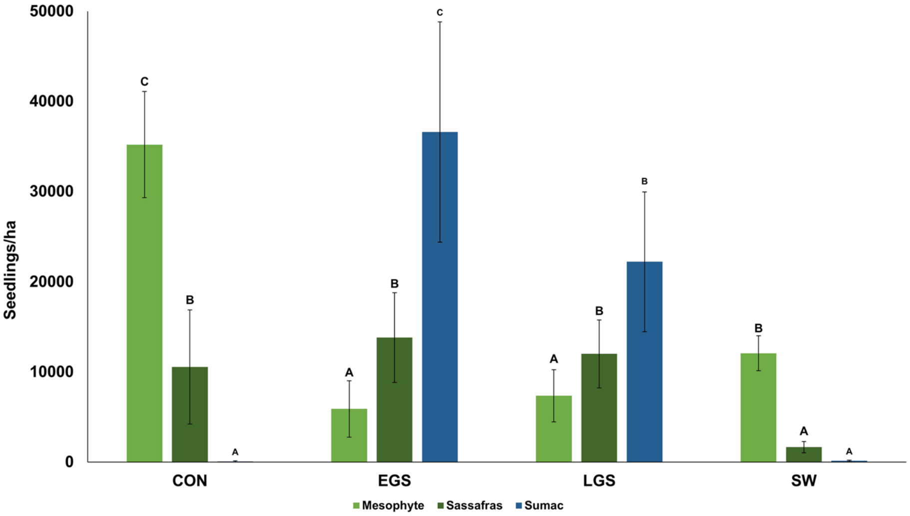

Fig. 2 Mesophyte, sassafras (*Sassafras albidum*), and sumac (*Rhus* spp.) understory stems per hectare in oak-hickory forest stands following early-growing season fire + shelterwood (EGS), late-growing season fire + shelterwood (LGS), and shelterwood (SW) treatments compared to control (CON) during July 2023 in Tennessee, USA. Mesophyte species include red maple (*Acer rubrum*), yellow-poplar (*Liriodendron tulipifera*), and American beech (*Fagus grandifolia*). Different letters within a group/species/genus represent significant differences between treatments

(± 7742.1) stems/ha in LGS, and 138.9 (± 80.2) stems/ha in SW. Understory stem counts of sassafras were 10,555.6 (± 6337.4) stems/ha in CON, 13,819.2 (± 4981.2) stems/ha in EGS, 12,013.9 (± 3772.0) stems/ha in LGS, and 1666.7 (± 631.4) stems/ha in SW.

LGS had 1.5 (± 1.1) times as many red oak understory stems as CON ($p = 0.017$), 3.6 (± 1.2) times as many as SW ($p < 0.001$), and 4.4 (± 1.2) times as many as EGS ($p < 0.001$; Table 1). CON had 3.0 (± 1.2) times as many red oak stems as EGS ($p < 0.001$) and 2.6 (± 1.2) times as many as SW ($p < 0.001$). EGS and SW had similar red oak stem counts ($p = 0.792$). EGS had 1.6 (± 1.2) times as many white oak understory stems as CON ($p = 0.040$) but did not differ from SW ($p = 0.826$) or LGS ($p = 0.558$). SW white oak stem counts did not differ from LGS ($p = 0.972$) or CON ($p = 0.274$), and LGS white oak stem counts also did not differ from CON ($p = 0.515$. LGS had 1.4 (± 1.1) times as many total understory oak stems as CON ($p = 0.007$), 1.9 (± 1.1) times as many as EGS ($p < 0.001$), and 1.9 (± 1.1) times as many as SW ($p < 0.001$). CON did not differ from SW ($p = 0.075$) or EGS ($p = 0.099$). EGS and SW had similar numbers of total understory oak stems ($p = 0.999$).

CON had 2.7 (± 1.1) times as many mesophyte understory stems as SW ($p < 0.001$), 4.8 (± 1.1) times as many as LGS ($p < 0.001$), and 6.0 (± 1.1) times as many as EGS ($p < 0.001$). SW had 1.7 (± 1.1) times as many mesophyte stems as LGS ($p < 0.001$) and 2.2 (± 1.1) times as many as EGS ($p < 0.001$). Mesophyte counts were similar between EGS and LGS ($p = 0.427$). EGS had 1.6 (± 1.1) times as many sumac understory stems as LGS ($p < 0.001$), 263.2 (± 2.0) times as many as SW ($p < 0.001$), and 526.9 (± 2.7) times as many as CON ($p < 0.001$). LGS had 159.8 (± 2.0) times as many sumac stems as SW ($p < 0.001$) and 319.9 (± 2.7) times as many as CON ($p < 0.001$). Sumac stem counts did not differ between SW and CON ($p = 0.942$). EGS had 8.0 (± 1.2) times as many sassafras understory stems as SW ($p < 0.001$) but did not differ from LGS ($p = 0.531$). Sassafras stems were marginally different between EGS and CON ($p = 0.059$), with 1.3 (± 1.1) times

Table 1 Back-transformed parameter estimates (*β*) and 95% confidence intervals (CI) of red oak group (*Erythrobalanus*; RO), white oak (*Leucobalanus*; WO) group, and total understory oak (TO) seedlings in oak-hickory forest stands following early-growing season fire + shelterwood (EGS), late-growing season fire + shelterwood (LGS), and shelterwood (SW) treatments compared to control during July 2023 in Tennessee, USA. The intercept represents the control treatment and random effects for the site are included

	RO *β*	**RO CI**	**WO *β***	**WO CI**	**TO *β***	**TO CI**
Intercept	5.42	2.27–12.60	2.68	1.20–5.85	8.39	4.13–16.90
EGS	0.33	0.22–0.48	1.60	1.13–2.27	0.75	0.59–0.96
LGS	1.46	1.14–1.88	1.29	0.90–1.86	1.40	1.14–1.72
SW	0.41	0.28–0.58	1.39	0.97–2.00	0.74	0.58–0.94

as many stems in EGS. LGS had 7.0 (± 1.2) times as many sassafras stems as SW ($p < 0.001$), but was similar to CON ($p = 0.648$). Finally, CON had 6.1 (± 1.2) times as many sassafras stems as SW ($p < 0.001$; Table 2, Fig. 2).

Models evaluating the relative proportion of red oak ($p = 0.109$) and white oak ($p = 0.158$) understory stems by treatment were not significant, but we detected differences among treatments in the proportion of sassafras ($p = 0.002$), mesophyte ($p < 0.001$), and sumac ($p < 0.001$).

CON had 47.0 (± 5.7) percent greater mesophyte relative abundance than EGS ($p < 0.001$) and 41.5 (± 5.7) percent more than LGS ($p < 0.001$). SW had 34.2 (± 5.8) percent greater proportion of mesophytes than EGS ($p < 0.001$) and was similar to CON ($p = 0.134$). SW had 28.6 (± 5.8) percent more mesophytes than LGS ($p < 0.001$). The proportion of mesophytes did not differ between LGS and EGS ($p = 0.767$). EGS had 15.0 (± 4.1) percent greater sassafras relative abundance compared to SW ($p = 0.003$) and LGS had 13.8 (± 4.1) percent greater sassafras relative abundance compared to SW ($p = 0.008$). The proportion of sassafras did not differ between EGS and CON ($p = 0.249$), LGS and CON ($p = 0.400$), SW and CON ($p = 0.284$), or EGS and LGS ($p = 0.990$). EGS had 41.6 (± 4.9) percent greater sumac relative abundance compared to SW ($p < 0.001$), 41.2 (± 4.8) percent more than CON ($p < 0.001$), and 13.2 (± 4.8) percent more than LGS ($p = 0.036$). LGS had 28.3 (± 4.9) percent greater relative sumac abundance than SW ($p < 0.001$) and 28.0 (± 4.8) percent more than CON ($p < 0.001$). Sumac relative abundance did not differ between CON and SW ($p = 0.999$; Fig. 3).

Midstory stems

No oak midstory stems were present in EGS or LGS. Only 1.9% (2/101; 12.4 stems/ha) of the stems in the CON midstory plots were white oak, and no red oak midstory

Table 2 Back-transformed parameter estimates (β) and 95% confidence intervals (CI) of mesophyte (MESO), sassafras (*Sassafras albidum*; SAS), and sumac (*Rhus* spp.; SMC) seedlings in oak-hickory forest stands following early-growing season fire + shelterwood (EGS), late-growing season fire + shelterwood (LGS), and shelterwood (SW) treatments compared to control during July 2023 in Tennessee, USA. Mesophyte species include red maple (*Acer rubrum*), yellow-poplar (*Liriodendron tulipifera*), and American beech (*Fagus grandifolia*). The intercept represents the control treatment and random effects for site are included

	MESO β	MESO CI	SAS β	SAS CI	SMC β	SMC CI
Intercept	32.5	26.65–37.05	8.01	3.85–16.50	0.03	0.001–0.52
EGS	0.17	0.13–0.21	1.31	1.06–1.62	527.00	119.31–9244.32
LGS	0.21	0.17–0.26	1.14	0.92–1.42	320.00	72.29–5616.49
SW	0.36	0.31–0.43	0.16	0.10–0.25	2.00	0.19–43.04

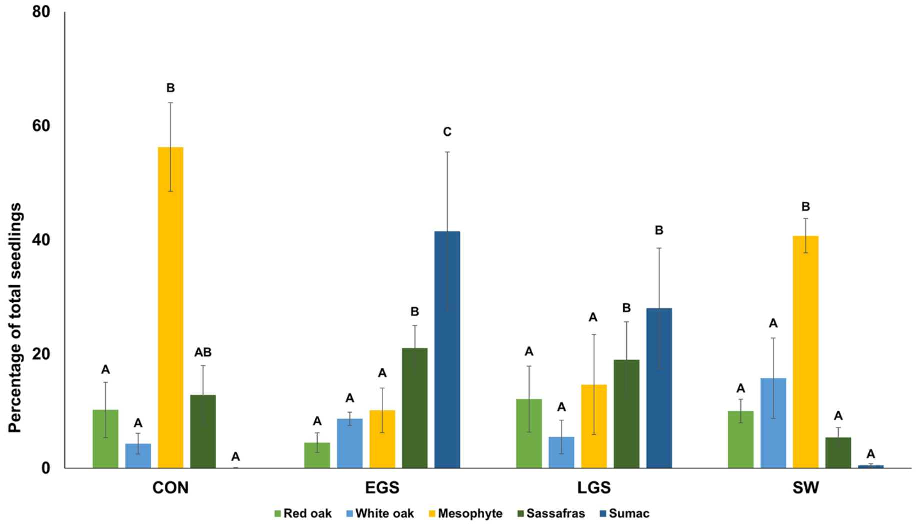

Fig. 3 The proportion of red oak group (*Erythrobalanus*), white oak group (*Leucobalanus*), mesophyte, sassafras (*Sassafras albidum*), and sumac (*Rhus* spp.) understory stems in oak-hickory forest stands following early-growing season fire + shelterwood (EGS), late-growing season fire + shelterwood (LGS), and shelterwood (SW) treatments compared to control (CON) during July 2023 in Tennessee, USA. Mesophyte species include red maple (*Acer rubrum*), yellow-poplar (*Liriodendron tulipifera*), and American beech (*Fagus grandifolia*). Different letters within a group/species/genus represent significant differences between treatments

stems were present in CON. There was an average of 222.4 mesophyte midstory stems/ha in CON. In the SW plots, 0.3% (2/785; 13.2 stems/ha) midstory stems were white oak, 0.9% (7/785; 46.1 stems/ha) midstory stems were red oak, and 66.1% (559/785; 3683.4 stems/ha) were mesophytes. There were an average of 92.7 sassafras and 74.1 sumac midstory stems/ha in LGS, but only 6.2 sumac stems/ha in EGS with no sassafras or mesophytes. Total midstory stems were greatest in SW, with 6.6 (± 1.1) times as many as LGS ($p < 0.001$), 8.3 (± 1.1) times as many as CON ($p < 0.001$), and 84.0 (± 1.4) times as many as EGS ($p < 0.001$). LGS had 12.7 (± 1.4) times as many midstory stems as EGS ($p < 0.001$) but was similar to CON ($p = 0.313$). CON had 10.1 (± 1.4) times as many stems as EGS ($p < 0.001$).

Discussion

Frequent prescribed fire paired with shelterwood harvests that decreased BA by 47%, allowing approximately 30% sunlight into the understory, accumulated understory oak regeneration, but there were differences in response to seasonality. Consistent with our hypothesis, red oak and total oak regeneration were promoted by LGS over all other treatments. White oak regeneration was promoted by EGS relative to CON but was similar in SW and LGS treatments. Both LGS and EGS reduced the total and relative abundance of mesophytic species compared to SW and CON, supporting our hypothesis. However, fire failed to increase the proportion of understory oak to competitor stems because of increased density of sumac and sassafras. We did not detect midstory oaks in burned units because of our fire frequency, but SW also had limited oak recruitment into the midstory. Sassafras seedling density was similar among fire treatments, whereas sumac seedling density was less in LGS compared to EGS, which contradicted our hypothesis of greater competition following less-intense LGS fire.

Several factors may have resulted in improved oak regeneration following LGS relative to EGS fire. Fire intensity and burn coverage were less on average with our LGS fire treatments than EGS fire treatments (Turner et al. 2024), which is similar to what others have reported (Brose et al. 1999a; Vander Yacht et al. 2017). It is reasonable to expect that relatively patchy burn coverage would allow increased survival and recruitment of total oak understory stems (Bigelow and Whelan 2019). Additionally, fire season may influence oak understory stems independent of intensity, as LGS fires may give a competitive advantage to fire-tolerant species more than EGS fires (Zeitler et al. 2025). It is interesting to note that with a 50% reduction in overstory trees and only 23.2 overstory red oak trees/ha, we recorded > 10,000 red oak stems/ha in the understory. Additionally, there was an average of > 2 times the number of overstory white oak trees in the EGS treatment than in the LGS treatment, yet understory white oak regeneration did not differ between fire treatments. Thus, we may have detected an influence of fire seasonality on white oak regeneration had overstory composition been more similar between treatments. Regardless of season, fire intensity and burn coverage with a ~ 2-year fire-return interval were sufficient to prevent white or red oak understory stems from regenerating into the midstory after 11 years. If the fire-return interval is lengthened substantially or suspended after achieving adequate understory oak regeneration with sufficient sunlight following the removal of undesirable overstory trees and suppressing oak competition with multiple fires (Cuprewich and Sanders 2024), we would expect rapid recruitment of understory oak stems into the midstory.

Timing of acorn drop should be an obvious consideration when implementing LGS fire. If fire occurs prior to acorn drop, germination, and oak seedling survival should be increased (Greenberg et al. 2012; Nation et al. 2021). Fire generally has a negative impact on acorn survival unless the acorns have been cached (Greenberg et al. 2012). LGS fire can be implemented prior to acorn drop if fire weather conditions allow, but conditions may delay the ability to implement LGS after acorn drop (especially into October). We did not measure acorn drop by collecting acorns, but our observations while implementing the LGS treatment indicated red oak acorns had dropped prior to implementing LGS fire in some but not all years. White oak (*Q. alba*) acorns had either already dropped or were in the process of dropping each year when we implemented the LGS treatments. In 2022, white oak acorns had dropped when we implemented the LGS treatment, but the red oak acorns had not. Greenberg et al. (2012) cautioned against burning in the fall because reduced acorn survival may reduce oak regeneration, but our results indicate such concern may not be warranted. Regardless, our objective was to investigate the cumulative effect of relatively frequent fire on oak regeneration, which included years with no fire between treatment events, which allowed oak seedlings to accumulate in the understory. Thus, our understory stem counts represent both seedlings and sprouts, and our results represent conditions typically encountered when burning hardwood stands whereby it is impossible to predictably burn at a specific time related to acorn drop in any given year. We also did not identify good acorn producers prior to the shelterwood harvest, but if oak regeneration is an objective, identifying those trees prior to harvest may be an important consideration to maximize acorn abundance regardless of the season fire is implemented (Brooke et al. 2019).

Fire applied during either season reduced mesophyte abundance compared to CON or SW, but mesophytes still comprised a significant proportion of understory stems. Remaining mesophytes in the understory or overstory may continue to reduce litter flammability, which is problematic given that frequent fire promotes the regeneration of many oak species (Kreye et al. 2018; Varner et al. 2021; Babl-Plauche et al. 2022). Additionally, the reduction in mesophyte density failed to increase the proportion of oak regeneration, which matches the results of a meta-analysis by Brose et al. (2013). Thus, six fires during EGS or LGS provided an advantage to understory oaks, but significant competition persisted. Our shelterwood harvest removed all mesophytes in the overstory of each stand, but the relatively small size of our treatment units (1.6 ha) likely allowed seed from mature trees outside the treatment units to blow into our treatment units each year. If mesophytic overstory trees were removed from a larger area, it is less likely we would have seen such persistence of mesophytes in the understory.

Consideration should be given to the response of more fire-tolerant species when managing upland hardwoods with fire. Sassafras and sumac both responded positively to canopy reduction and fire, and they were persistent in resprouting, which enabled them to comprise a notable proportion of understory stems in our stands. Other studies in upland oak systems have reported similar results (Alexander et al. 2008; Vander Yacht et al. 2019; Resop et al. 2023). EGS fire generally promotes or fails to control sumac (Evans 1983; Nippert et al. 2021), and our results indicate LGS fire may be more effective at maintaining lower sumac coverage. Hajny et al. (2011) reported LGS fire reduced smooth sumac (*Rhus glabra* L.) density, which they related to a negative influence on seed production. Thus, LGS fire may serve as a useful tool when sumac density reduction is desirable for tree regeneration or other management objectives. Sassafras also responded positively to EGS and LGS compared to SW, but there was no density or proportional response related to fire seasonality, which mirrors the results Vander Yacht et al. (2017) reported after a single fire during each season. Given the relative abundance of sumac and sassafras in our stands, noncommercial forest stand improvement using an herbicide application may be used in the future (Turner et al. 2020, 2021). It is important to note sassafras and sumac likely are not as important of oak competitors as mesophytes, as oaks may stratify above them in the future. Nonetheless, understory and midstory trees can reduce oak seedling survival and growth (Loftis et al. 1990, Lorimer et al. 1994), and the response of these species to fire season should be considered.

Our study adds to the growing body of literature indicating shelterwood harvests rarely result in improved oak recruitment without the addition of fire. Understory sunlight suitable for oak regeneration was maintained for more than a decade following canopy reduction with frequent fire during either season (Johnson et al. 2009), whereas sunlight levels in SW were similar to CON. A relatively dense midstory in SW had regenerated, but approximately 2/3 of the stems were mesophytes. Conversely, only 1% of stems in SW were oaks, despite our shelterwood harvests retaining primarily overstory oak and hickory. Although SW had similar white oak understory stem counts compared to EGS and LGS, these seedlings were unable to recruit into the midstory without release from competition (Royse et al. 2010; Izbicki et al. 2020). Using repeated fire following a shelterwood with reserves allows managers to either stop burning and develop a two-age stand or continue burning to stockpile understory oak regeneration depending on their objectives (Brose et al. 1999b). Although our study focused on a shelterwood with reserves, our results have applications for those implementing a two-step shelterwood, as removing the overwood is unlikely to further promote oaks if strong competition persists. Future studies should investigate whether there are changes in the cumulative effects of multiple fires on regeneration after burning is stopped, as SW, EGS, and LGS all promoted the recruitment of different species.

Conclusions

Relatively frequent EGS and LGS fire paired with shelterwood with reserves increased understory oaks, and seasonality of fire influenced species composition. Red oak and total understory oak regeneration was promoted by LGS, whereas white oak regeneration responded similarly to EGS and LGS. Relatively frequent fire during either season reduced the density and proportion of mesophytic species, but also tended to promote sumac and sassafras. LGS had lower sumac density relative to EGS, whereas sassafras density was not influenced by fire season. Thus, managers may need to consider additional follow-up treatments to reduce competition of species that readily resprout following fire. SW alone failed to successfully regenerate oaks into the midstory, with mesophytes comprising the majority of midstory saplings. We recommend managers apply fire to promote oak regeneration following shelterwood harvests that retain oaks and remove mesophytic species from the overstory, allowing approximately 30% sunlight into the stand. Frequent fire may be needed initially until there are sufficient oak understory stems present, after which burning may be ceased or implemented less frequently.

Abbreviations

ANOVA	Analysis of variance
BA	Basal area

CON	Control
CSF	Chuck Swan State Forest and Wildlife Management Area
DBH	Diameter at breast height
EGS	Early-growing season
LGS	Late-growing season
PAR	Photosynthetically active radiation
SW	Shelterwood

Acknowledgements
We thank S. Hendrickson, the Chuck Swan State Forest staff, and the Tennessee Division of Forestry for assistance with treatment implementation and logistical support. We thank the University of Tennessee School of Natural Resources and Tennessee Valley Authority for financial support.

Authors' contributions
CH conceived the original research idea, implemented treatments, acquired funding, and served as project supervisor. MT, JB, and SM implemented treatments, designed data collection protocol, and collected the data. MT led analysis and writing. All authors contributed to the final article review and editing.

Funding
School of Natural Resources, The University of Tennessee.
Tennessee Valley Authority.

Data availability
The datasets used and/or analyzed during the current study are available from the authors on reasonable request.

Declarations

Ethics approval and consent to participate
Not applicable.

Consent for publication
Not applicable.

Competing interests
The authors declare that they have no competing interests.

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Received: 17 September 2024 Accepted: 14 January 2025

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