RESTORATION ECOLOGY
The Journal of the Society for Ecological Restoration

RESEARCH ARTICLE

Season of burn has minimal effect on groundlayer community structure and composition in an Appalachian mixed-oak forest

Tara L. Keyser[1,2], Cathryn H. Greenberg[3]

The groundlayer flora has a disproportionate influence on ecosystem function and contributes to the biodiversity in temperate *Quercus* forests of eastern North America. Historically open understory conditions perpetuated, in part by fire, have become closed and homogenized by long-term fire exclusion, likely impacting the groundlayer community. We explored the effects of burn season (unburned = CON, dormant season = DSB, growing season = GSB) on groundlayer (<1 m) vegetation attributes pre- and post-burn. The difference (post-burn – pre-burn) in tree cover was greater in GSB (+8.22%) than DSB (+1.24%) and CON (+0.15%), while the change in forb cover was greater in GSB (+1.17%) than CON (−0.15%). Minor effects of burning were observed in diversity metrics, with the change in forb richness greater in GSB (+0.11 species/m^2) than CON (−0.78 species/m^2), while the change in tree richness was greater in GSB (+1.11 species/m^2) than DSB (−1.11 species/m^2) and CON (−1.67 species/m^2). Nonmetric multi-dimensional scaling provided evidence that between pre- and post-burn, modest composition shifts in DSB and GSB were associated with more open conditions and lower litter depth. Understory composition did not vary among burn treatments pre-burn, while post-burn, composition differed significantly between CON and DSB and DSB and GSB. However, overall, a growing season burn had relatively minor effects on the groundlayer community compared to a dormant season burn. A better understanding of multiple factors affecting groundlayer response to burning is critical to the effective use of prescribed burning in attaining restoration goals.

Key words: diversity, fire effects, herbaceous vegetation, mixed-oak forests, *Quercus*, restoration

Implications for Practice

- A single low-intensity growing versus dormant season burn had negligible and similar effects on the lifeform abundance and diversity of the groundlayer flora of a mixed-oak forest.
- Between pre- and post-burn time periods, species composition shifts were associated with slightly more open understory conditions and reduced litter depth. However, a shade-intolerant, highly competitive woody species, yellow-poplar (*Liriodendron tulipifera*), became an indicator of the growing season burn.
- A single growing season burn did not alter the groundlayer flora in a more efficient and meaningful manner relative to dormant season burns.
- Repeated burning, regardless of seasonality, and a greater degree of canopy reduction are likely necessary to modify the understory environment and facilitate the development of a more diverse and abundant groundlayer community.

Introduction

Temperate oak (*Quercus*) forests, including those common to eastern North America and central Europe, are undergoing a transition, whereby the relatively shade-intolerant to mid-tolerant oak and hickory (*Carya*) species prevalent in the forest overstory are being replaced by more shade-tolerant and primarily mesophytic species (Hédl et al. 2010; Fei et al. 2011). This species replacement is particularly evident in the forest understory and lower canopy layers (Fei & Steiner 2007; Spînu et al. 2020), where ubiquitous and heavily shaded conditions limit the establishment, growth, and recruitment of oak and hickory seedlings and saplings (and other shade-intolerant and mid-tolerant species) in the absence of disturbance (Aldrich et al. 2005; Annighöfer et al. 2015). The process of transitioning away from more xeric, disturbance-adapted oak species to more mesic and shade-tolerant species is termed mesophication (Nowacki & Abrams 2008). Mesophication threatens the long-term sustainability of oak-dominated forests and the ecosystem services they provide, such as water yield (Caldwell et al. 2016), wildlife

Author contributions: TLK, CHG conceived and designed the research; TLK assisted with data collection; TLK analyzed the data; TLK, CHG wrote and edited the manuscript.

[1]USDA Forest Service, Southern Research Station, 200 W.T. Weaver Boulevard, Asheville, NC 28804, U.S.A.
[2]Address correspondence to T. L. Keyser, email tara.keyser@usda.gov
[3]USDA Forest Service, Southern Research Station, 1577 Brevard Road, Asheville, NC 28806, U.S.A.

doi: 10.1111/rec.14131
Supporting information at:
http://onlinelibrary.wiley.com/doi/10.1111/rec.14131/suppinfo

habitat, food resources (McShea et al. 2007), and biodiversity (Hiers et al. 2014) along with economic values that include high-quality sawtimber (Dhungel et al. 2023) and livestock forage, among others (Stavi et al. 2022).

Prior to widespread fire suppression policies in the eastern United States in the early to mid-twentieth century, a relatively frequent anthropogenically driven fire regime was key in maintaining successional oak forests and abating mesophication across spatial and temporal scales (Delcourt et al. 1998; Lafon et al. 2017; Elliott et al. 2020). Altered disturbance regimes, including cessation of anthropogenic burning, have homogenized forest conditions and altered tree regeneration dynamics at stand (Grover et al. 2023), watershed (Elliott & Vose 2011), and landscape and regional scales (Woodbridge et al. 2022). Most temperate oak forests in both Europe and North America are closed-canopied, multi-layered, and mature (Keyser et al. 2014; Lanta et al. 2020) and represent conditions where mesophication is most severe or advanced (Woodbridge et al. 2022). Common activities used to slow or reverse mesophication, promote oak regeneration, and restore more open understory conditions include prescribed fire, thinning, and targeted application of herbicide (Vander Yacht et al. 2017*a*). These activities may concomitantly restore other key ecosystem attributes associated with more open conditions, including increased productivity and diversity of the groundlayer flora (Hanberry et al. 2020). Although the groundlayer flora constitutes less than 1% of aboveground forest biomass (Gilliam 2007), it has a disproportionate influence on nutrient cycling (Elliott et al. 2015), filters tree regeneration (De Lombaerde et al. 2021), provides wildlife food resources (Turner et al. 2020), and affects the abundance and diversity of arthropod and pollinator communities (Hanula et al. 2015).

Among the tools and treatments available, prescribed fire is most often used as a treatment that, over time, is presumed to restore open understory conditions and increase heterogeneity across large spatial scales in the diverse upland oak forests of eastern North America. Prescribed fire may elicit a change in the groundlayer flora by consuming forest floor material and increasing plant nutrient availability (Knoepp et al. 2009), creating spatially heterogenous understory light environments (Iverson et al. 2017), and stimulating germination from the buried seed bank (Keyser et al. 2012). Despite the increased use of prescribed fire to restore upland oak forests in the eastern United States, research on how it affects groundlayer vegetation is scarce, observational, or geographically limited. Low intensity dormant season burns rarely kill/topkill stems greater than 15 cm in diameter (Keyser et al. 2018), resulting in only minor and transient changes to forest structure and understory light availability (Arthur et al. 2015). Oakman et al. (2019) reported that even after conducting four dormant season burns over 15 years in a southeastern United States oak forest, forb, and graminoid cover remained similar to unburned conditions, suggesting that changes in groundlayer cover and abundance following fire are either short-lived (Hutchinson et al. 2005*a*) and/or depend on or interact with significant changes in forest structure (Vander Yacht et al. 2017*b*).

Differences in fire intensity and physiological activity of vegetation between growing and dormant season burns may interact to shape fire effects and resultant forest structure and composition (Knapp et al. 2009; Brose et al. 2013; Waldrop et al. 2016). For example, Barnes and Van Lear (1998) documented that a single growing season burn in a South Carolina upland oak forest was just as effective at creating open understory conditions as three dormant season burns due to increased fire intensity and resultant fire effects on woody vegetation. Although a single high-intensity growing season burn can increase oak seedling density and size by controlling competition from mesophytic seedlings (Brose 2010), a recent study in a southeastern United States oak forest found no benefit of a growing season versus dormant season burn on the diversity or abundance of groundlayer vegetation (<1.37 m) (Vaughan et al. 2022). Similarly, although Vander Yacht et al. (2017*b*) noted a significant increase in herbaceous diversity and richness after harvests that reduced basal area to less than 15 m^2/ha in an eastern Tennessee oak forest, a single follow-up burn conducted during the late growing or dormant season failed to further alter the characteristics of the groundlayer community.

Forest managers are increasingly burning during the growing season in efforts to extend limited burn windows (Chiodi et al. 2018) and accelerate restoration goals (Waldrop et al. 2016), highlighting the need for research addressing how season of burning affects forest vegetation structure and composition. A small but growing body of research on prescribed fire effects in upland oak forests suggests that burning during the growing season may be an important factor in controlling woody understory vegetation and creating the more open forest conditions (Brose et al. 2013; Melcher et al. 2023) conducive to development of a diverse and abundant groundlayer community (Hanberry et al. 2020). In this study, we examined the short-term effects of a single early growing versus dormant season burn on groundlayer flora. Our objectives were to determine: (1) How season of burn influences diversity of the groundlayer plant community, (2) the effects of season of burn on the abundance (cover) of groundlayer vegetation, including forbs, graminoids, vines, shrubs, and trees, and (3) the effects of season of burn on the groundlayer plant community composition.

Methods

Study Site and Treatments

This study was conducted on Bent Creek Experimental Forest (2500 ha) in the Pisgah National Forest in Asheville, North Carolina, United States. The study site falls within the Blue Ridge Mountains section of the Central Appalachian Broadleaf Forest—Coniferous Forest—Meadow Province (Cleland et al. 2007). Topography is characterized by low-elevation mountains with moderately steep slopes. Average temperatures range from 1.9°C in January to 28.9°C in July (https://www.ncei.noaa.gov/access/us-climate-normals/#dataset=normals-monthly&timeframe=30&location=NC&station=USC00310724).

In 2011, we established nine experimental units that ranged between 3.5 and 7.4 ha under a completely random design. Burn units were separated by fire lines and typically extended from the lower slope to the ridge crest. Average elevation of the units was 730 m (660–790 m), and the aspect was generally southwesterly. The nine units were mature (>100 years old), long-unburned upland oak forests with an overstory dominated by black oak (*Quercus velutina* Lam.), chestnut oak (*Q. montana* L.), scarlet oak (*Q. coccinea* Muenchh.), and white oak (*Q. alba* L.) and a lower canopy dominated by sourwood (*Oxydendrum arboretum* [L.] D.C.), red maple, and flowering dogwood (*Cornus florida* L.). Shortleaf (*Pinus echinata* Mill.) and eastern white pine (*P. strobus* L.) occurred sporadically throughout the units. Groundlayer cover was sparse, which was likely caused by low canopy openness (1.6–2.6% across all the nine units).

Three burn treatments were randomly assigned to the nine experimental units ($n = 3$). Treatments were: (1) growing season burn (GSB), (2) dormant season burn (DSB), and (3) control (CON). We used the phenology of woody vegetation to differentiate between dormant and growing season burn treatments. The GSB treatment was defined by the presence of new, small leaves on deciduous tree species (e.g. red maple and sourwood), and full flowering by dogwood and several oak species. In contrast, the absence of live leaves and flowering structures in deciduous tree species defined the DSB. Growing season burns were conducted on 26 April, 2013, and dormant season burns were conducted on 5 March, 2014. Ignition techniques utilized in both GSB and DSB were similar to those used throughout the region, with ignitions originating from established fire lines using backing and flanking fires. Interior ignition was completed using strip-head firing techniques. Using the closest, most representative remote automated weather station (RAWS) data, air temperature at the time of ignition, relative humidity, and 10-hour fuel moisture were 18.3°C, 26%, and 7%, respectively, in GSB and 8.3°C, 61%, and 8%, respectively, in DSB.

Sampling Methods

Prior to treatment, we installed three permanent, 0.05 ha circular sampling plots within each burn unit. Plots were randomly located within each burn unit and separated by at least 30 m. We measured groundlayer vegetation (vegetation <1 m tall) in eight, 1-m^2 quadrats located 6 m from each plot center in cardinal and off-cardinal directions. In each quadrat, we recorded cover by species rooted within the quadrats using six cover classes: 1 (<1%), 2 (1 to <5%), 3 (5 to <25%), 3 (25 to <50%), 4 (50 to <75%), 5 (75 to <95%), and 6 (95–100%). When identification to species was not possible, we identified to the genus level. In GSB and DSB, groundlayer cover was measured at the time of plot installation and four growing seasons following the burn; in CON, understory cover was recorded at the time of installation and five growing seasons following pre-treatment data collection. Nomenclature follows the USDA NRCS (2022).

Data Analysis

For all analyses, cover class data were converted to continuous values by using the midpoint of each cover class. Understory diversity of the groundlayer was quantified by species richness (S), evenness (J), and the Shannon Diversity Index (H'). In addition, we calculated S and H' of five lifeforms: forb, graminoid, shrub, tree, and vine. All diversity metrics and cover values were calculated at the plot-level (average of the eight, 1 m^2 quadrats) and then averaged to the unit-level (average of the three plots per unit). In addition, we calculated a unit-level value of S ($S\gamma$), which represents the total number of species observed across the 24, 1 m^2 quadrats in each experimental burn unit.

We evaluated the effects of burn season (GSB, DSB, and CON) on the difference (post-burn values – pre-burn values) in metrics that describe the groundlayer, including total cover, cover by lifeform, S, $S\gamma$, J, and H' using a mixed-effects general linear model. A similar analysis was conducted on diversity attributes (S and H') of each lifeform. For all models, treatment was the fixed effect and unit within treatment was a random effect. To improve normality and stabilize variance, some dependent variables were transformed using an arcsine-square root (cover data) or square root (richness) transformation. All post hoc multiple comparisons were performed using the adaptive false discovery rate (Benjamini & Hochberg 2000).

We used nonmetric multidimensional scales (NMS) to compare understory composition within and among burned and unburned units. Ordinations were performed using cover for each species averaged across the three plots (subsamples) at the experimental unit-level. Rare species, which were those species occurring on fewer than 5% of the stands, were removed from the species matrix. We used the slow-and-thorough autopilot (250 runs with real data and 250 runs with randomized data) in conjunction with the Sørensen's distance to obtain the final solution that minimized stress. Relationships between understory community composition and pre-burn and post-burn structural attributes (Table 1) were related to the NMS ordination results via joint plots. We used successional vectors to visualize changes in community composition for each stand between pre- and post-burn sampling periods.

We quantified differences in groundlayer community composition among treatments both pre- and post-burn using multi-response permutation procedures (MRPP). MRPP analyses were conducted using cover for each species averaged across the three plots (subsamples) per experimental unit. The chance-corrected within group agreement (A) and associated p value provided a quantitative measure of the differences in groundlayer community composition among the treatments. Within group distances for MRPP analyses were calculated using Sørensen's distance. MRPP results were further investigated with an indicator species analysis (ISA) to identify the affinity of any specific species for a particular treatment (Dufendre & Legendre 1997).

Due to the heterogeneity in groundlayer vegetation (Small & McCarthy 2002) coupled with variability in fire behavior and resultant fire effects arising from differences in fuelbed composition and environmental gradients (Franklin et al. 1997; Arthur et al. 2015) along with minimal replication ($n = 3$) of treatment units, we interpreted significance at an a priori $\alpha = 0.10$. We conducted univariate analyses with SAS v9.4 and multivariate analyses with PC-ORD v7.08 (McCune & Mefford 2018).

Table 1. Range of stand-level conditions (minimum and maximum), including overstory (stems ≥25 cm dbh) and midstory (stems ≥5 cm and <25 cm dbh) basal area (m^2/ha), canopy openness (%), and litter and duff depth (cm), prior to and after burning in an Appalachian hardwood forest (Keyser et al. 2019). Litter and duff depths were not remeasured in CON, so pre-burn depths were used to reflect post-burn depths.

	CON	*DSB*	*GSB*
Pre-burn			
Overstory	7.1, 25.1	19.6, 27.7	18.2. 21.8
Midstory	5.7, 20.5	6.8, 16.5	7.6, 13.2
Openness	2.4, 4.2	1.6, 2.6	1.6, 2.1
Litter	2.7, 4.3	6.3, 7.1	2.8, 4.6
Duff	2.5, 3.9	2.7, 5.2	2.8, 5.0
Post-burn			
Overstory	7.1, 25.1	19.2, 26.4	11.7, 21.0
Midstory	5.7, 18.6	4.9, 15.8	4.5, 11.2
Openness	5.0, 6.0	6.3, 8.5	5.2, 21.7
Litter	2.7, 4.3	1.1, 1.6	0.4, 1.2
Duff	2.5, 3.9	1.0, 2.4	2.3, 4.5

Results

Diversity

Across the study area, within the sample quadrats, we documented 73 species/morphospecies pre-burn (23 forbs, 9 graminoids, 13 shrubs, 5 vines, and 23 trees) and 80 species post-burn (23 forbs, 10 graminoids, 17 shrubs, 5 vines, and 25 trees) (Table S1). The difference between pre- and post-burn local S (species/m^2) was significantly greater in GSB (+4.78 species/m^2) than either CON (−2.11 species/m^2) or DSB (−1.11 species/m^2), while the difference in local H' was significantly greater in GSB (+0.51) than CON (−0.24) (Table 2). Burn treatment did not significantly affect the change in $S\gamma$ (species/24 m^2), with the difference between post-burn and pre-burn periods averaging +0.67 (2.22) species.

The difference between pre- and post-burn S and H' was not significantly affected by burn treatment for the graminoid, shrub, or vine lifeforms (Table 3). Between pre- and post-burn, forb S in GSB increased by 0.11 species/m^2, which was significantly different than the change in CON (−0.78 species/m^2). The change in tree S between pre- and post-burn in GSB (+1.11 species/m^2) was significantly different than the change in CON (−1.67 species/m^2) and DSB (−1.11 species/m^2). Between pre- and post-burn, tree H' changed significantly more in CON (−0.21) than in DSB (+0.07) and GSB (+0.04).

Cover

Prior to treatment, cover, across all units, averaged 0.63% for forbs, 0.13% (graminoids), 9.06% (shrubs), 10.73% (trees), and 0.86% (vines). Burn treatment had no significant effect on the difference in total, graminoid, vine, and shrub cover between pre- and post-burn time periods (Fig. 1). In comparison, forb cover in GSB increased by 1.17% between pre- and post-burn, which was significantly different than the change observed in CON (−0.15%). The change in tree cover was significantly affected by burn treatment, with the change in GSB (+8.22%) greater than the change in both CON (+0.15%) and DSB (+1.24%).

Community Composition

Species composition of the groundlayer community was best described by a three-dimensional solution in the NMS analysis (final stress = 10.20, $p = 0.0199$) (Fig. 2). The ordination explained 88.6% of the total variability in groundlayer vegetation composition, with the greatest proportion of variance explained by axis 1 (52.4%), followed by axis 2 (20.4%), and axis 3 (15.8%). Ecological attributes were significantly correlated with the axes that explained the greatest proportion of variability. The variables with the strongest correlation with axis 1 included overstory basal area (OSBA, $r = -0.576$) and duff depth (Duff, $r = 0.452$), while variables most strongly correlated with axis 2 included canopy openness (Open, $r = 0.528$), litter depth (Litter, $r = -0.612$), and duff depth ($r = -0.436$). Successional vectors provided evidence that the groundlayer composition of all units, but particularly those in DSB and GSB, shifted upwards in the ordination space toward more open conditions and lower litter depth post-burn.

The MRPP analysis conducted on pre-burn groundlayer composition provided no evidence ($A = 0.0864$, $p = 0.1160$) that composition varied among CON, DSB, or GSB units. The ISA identified two species that were indicative of CON and DSB prior to fire, with red maple an indicator of DSB ($p = 0.0324$) and eastern white pine an indicator of CON ($p = 0.0316$). Post-burn, however, the MRPP analysis suggested that groundlayer composition varied among treatments ($A = 0.1023$, $p = 0.0650$), with significant differences in post-fire composition between CON and DSB and DSB and GSB. Post-burn, we found that red maple ($p = 0.0322$) and eastern white pine ($p = 0.0324$) remained indicators of DSB and CON, respectively. In addition, we found yellow-poplar ($p = 0.0344$) was an indicator of GSB post-burn.

Table 2. Mean difference (SE) (post-burn – pre-burn) in alpha (i.e. species/m^2) diversity (S = species richness, J = evenness, and H' = Shannon diversity index) and stand-level diversity metrics ($S\gamma$ = species richness/24 m^2) of the total groundlayer community. CON, control/unburned; DSB, dormant season burn; GSB, growing season burn. Uppercase letters reflect significant differences among treatments.

Diversity metric	*CON*	*DSB*	*GSB*	p_{trt}
S	−2.11 (0.56)^{A}	−1.11 (1.35)^{A}	4.78 (1.95)^{B}	$F_{[2,6]} = 5.07$, $p = 0.0514$
J	−0.06 (0.04)	0.06 (0.01)	0.13 (0.13)	$F_{[2,6]} = 2.24$, $p = 0.1880$
H'	−0.24 (0.13)^{A}	0.10 (0.06)^{AB}	0.51 (0.27)^{B}	$F_{[2,6]} = 4.40$, $p = 0.0667$
$S\gamma$	−3.00 (0.58)	−2.00 (4.93)	7.00 (2.08)	$F_{[2,6]} = 3.14$, $p = 0.1168$

Table 3. Mean difference (SE) (post-burn – pre-burn) in diversity metrics (S = species richness and H' = Shannon diversity index) of individual lifeforms (species/m^2). CON, control/unburned; DSB, dormant season burn; GSB, growing season burn. Uppercase letters reflect significant differences among treatments.

Treatment	*CON*	*DSB*	*GSB*	p_{trt}
Forb S	−0.78 (0.11)^{A}	−0.33 (0.19)^{AB}	0.11 (0.22)^{B}	$F_{[2,6]} = 6.01, p = 0.0370$
Forb H'	−0.14 (0.15)	0.00 (0.17)	0.16 (0.10)	$F_{[2,6]} = 1.04, p = 0.4096$
Graminoid S	0.00 (0.19)	0.44 (0.80)	2.11 (0.99)	$F_{[2,6]} = 2.25, p = 0.1869$
Graminoid H'	0.00 (0.20)	0.19 (0.19)	0.32 (0.39)	$F_{[2,6]} = 0.36, p = 0.7144$
Shrub S	0.33 (0.84)	0.00 (0.39)	1.22 (0.62)	$F_{[2,6]} = 0.97, p = 0.4315$
Shrub H'	−0.07 (0.09)	0.09 (0.09)	0.22 (0.14)	$F_{[2,6]} = 1.81, p = 0.2426$
Vine S	0.00 (0.33)	−0.11 (0.11)	0.22 (0.22)	$F_{[2,6]} = 0.50, p = 0.6296$
Vine H'	−0.14 (0.11)	−0.08 (0.05)	0.10 (0.12)	$F_{[2,6]} = 1.69, p = 0.2611$
Tree S	−1.67 (0.38)^{A}	−1.11 (0.40)^{A}	1.11 (0.73)^{B}	$F_{[2,6]} = 7.72, p = 0.0219$
Tree H'	−0.21 (0.08)^{A}	0.07 (0.04)^{B}	0.00 (0.04)^{B}	$F_{[2,6]} = 6.67, p = 0.0299$

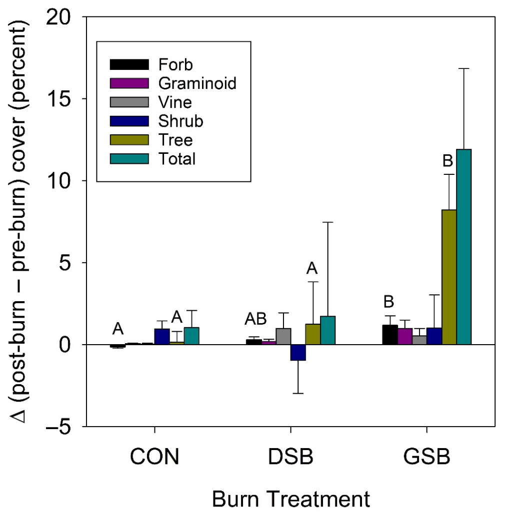

Figure 1. Difference between post-burn and pre-burn cover (percent), by lifeform, of the groundlayer vegetation (<1 m). Error bars indicate ± SE. Uppercase letters indicate significant differences among treatments.

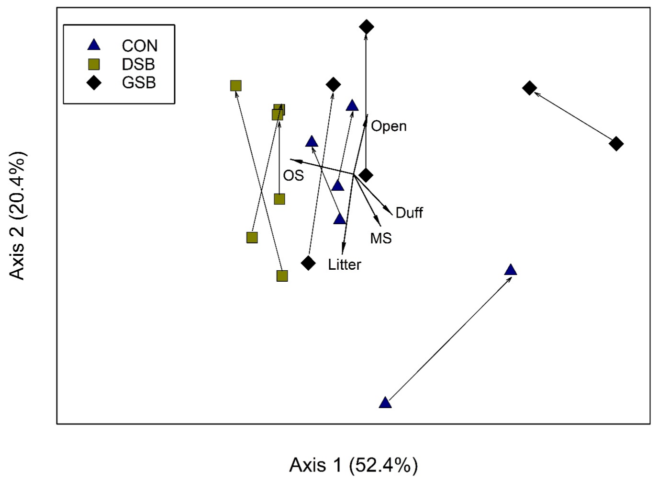

Figure 2. Nonmetric multi-dimensional scaling (NMS) ordination of the groundlayer community (vegetation <1 m tall) in species space comparing changes in species composition pre-burn and 4 years post-burn. Joint biplot vectors display the strength and correlation ($r^2 > 0.2$) between ordination axes and ecological conditions. Successional vectors display movement of units in ordination space over time (pre-fire vs. post-fire. Vector abbreviations: OS, overstory (stems ≥25 cm dbh) basal area (m^2/ha); MS, midstory (stems ≥5 and <25 cm dbh) basal area (m^2/ha); Open, canopy openness (%); Litter, litter depth (cm); Duff, duff depth (cm).

Discussion

We found that a single low-intensity burn, regardless of the season burned, had only minimal effects on groundlayer cover relative to unburned conditions. Although forb cover in GSB changed significantly more than in CON, groundlayer cover remained dominated by woody species across all treatments. Our results corroborate others showing that a single low-intensity burn generally has neutral to only slightly positive effects on herbaceous (forb plus graminoid) cover, likely due to the limited effect on forest structure, the understory light environment, and mineral soil exposure often required to stimulate germination (Elliott et al. 1999; Glasgow & Matlack 2007; Elliott & Vose 2010).

Burning during the growing season has been proposed to control woody competition more effectively than dormant season burns by more effectively depleting root carbohydrate reserves that have been translocated to stems and leaves during spring growth (Miller et al. 2019). We found no support for this hypothesis and, in fact, found the opposite; the change in tree cover in GSB (+8.22%) between pre- and post-burn was significantly greater than the change in CON and DSB. Results from fire-adapted southeastern pine forests have found greater mortality and topkill of understory broadleaved trees after growing season burns, with the qualification that this differential mortality between seasons was observed after multiple, repeated burns (Waldrop et al. 1992; Robertson & Hmielowski 2014). However, fire intensity can differ between dormant and growing season burns, with growing season burns often experiencing greater fire intensity due to warmer temperatures, lower relative humidity, and lower fuel moisture (Vander Yacht et al. 2020; Vaughan et al. 2021). Studies that control for differences in fire intensity between seasons generally show low mortality of hardwood seedlings even when topkilled during growing season burns (Ruswick et al. 2021). Prolific resprouting is common following topkill, leading to greater density and cover of woody species as resprouting individuals quickly capture any available growing space created by a burn (Chiang et al. 2005).

Studies that specifically address the effects of season of burn on groundlayer diversity in mixed-oak forests are sparse. Although there is some evidence that a single high-intensity growing season fire can alter the structure and composition of the understory woody vegetation more efficiently than a lower-intensity dormant season burn (Brose et al. 2013; Melcher et al. 2023), this does not appear to translate into meaningful changes in the composition and diversity of the groundlayer vegetation when the growing season burn is conducted early in the growing season and/or is of low intensity. For example, in the mountains of South Carolina, a single prescribed burn, regardless of whether it was conducted during the dormant (January–early April) or early growing (mid-April) season, had no effect on groundlayer diversity metrics in oak and oak-pine forests (Vaughan et al. 2022). Similarly, Vander Yacht et al. (2020) found no detectable differences in herbaceous species richness or diversity after an October versus March burn in an upland oak forest in the Appalachian Mountains. In our study, GSB caused a greater change in local richness of the total groundlayer (+4.78 species/m^2) than DSB (−1.11 species/m^2) or CON (−2.11 species/m^2). Although GSB elicited a greater change in forb richness (+0.11 species/m^2) than in CON (−0.78 species/m^2), it also caused a greater change in tree richness (+1.11 species/m^2) than either DSB (−1.11 species/m^2) or CON (−1.67 species/m^2). Static to decreasing diversity over time in undisturbed forests is associated with low understory light availability, which can lead to a depauperate herbaceous layer dominated by relatively few shade-tolerant species (Rogers et al. 2008; Plue et al. 2013; Borden et al. 2021). Although fire may have interacted with other natural and anthropogenic disturbances to have historically maintained a more rich and diverse groundlayer community (Hanberry et al. 2020), the efficacy and efficiency of a single low-intensity burn to increase groundlayer diversity and richness in contemporary mixed-oak forests have mixed results, with most studies—including ours—showing neutral to only negligible increases in richness and/or diversity (Elliott et al. 1999; Elliott & Vose 2010).

We found a significant but modest shift in species composition with burning, regardless of season; this was significantly associated with more open understory conditions and reduced litter depth. Results from the MRPP analysis post-burn, in part, confirmed the NMS ordination, with species composition differing between CON and DSB and DSB and GSB. Other studies indicate that post-burn canopy openness and litter depth influence groundlayer vegetation response and post-burn community composition (Harrod et al. 2000; Glasgow & Matlack 2007). Although canopy openness in our study remained largely similar among CON, DSB, and GSB, it increased slightly relative to pre-burn conditions in GSB (Keyser et al. 2019) and could be related to the modest shift in groundlayer species composition in GSB. Not surprisingly, red maple and eastern white pine were indicators of pre-burn conditions in the DSB and CON units. These two species are generalists and thrive in the forest understory in the absence of disturbance (Blankenship & Arthur 1999; Fei & Steiner 2007). Although eastern white pine and red maple remained indicators of CON and DSB post-burn, yellow-poplar was a new species indicative of post-burn conditions in GSB. This finding corroborates findings by Oakman et al. (2021) indicating that fire may promote the germination and subsequent establishment of yellow-poplar seedlings, which are often abundant in the buried seed bank (Keyser et al. 2012). Due to its shade intolerance, however, the yellow-polar cohort that established after GSB is unlikely to recruit into larger size classes without subsequent overstory disturbance or additional burns (Hutchinson et al. 2005*b*).

Meaningful changes to the groundlayer community, such as decreasing the abundance of woody trees and shrubs and increasing more shade-intolerant graminoids and forbs, require a greater reduction in overstory/midstory density than occurs during typical low-intensity prescribed burns. Although some studies (Willson et al. 2018; Maginel et al. 2019; Hutchinson et al. 2024) indicate that frequent burns repeated over the long term (e.g. decades) can promote the abundance and diversity of forbs and graminoids, others suggest burning must be coupled with mechanical thinning to effectively change the composition and make-up of the groundlayer (Bassett et al. 2020). In a southeastern Missouri oak forest, Knapp et al. (2015) found that annual burning conducted over 60 years reduced canopy cover via tree mortality of midstory saplings (stems ≥3 cm and <10 cm dbh), creating conditions that increased the herbaceous component of the groundlayer relative to unburned conditions. The authors report that periodic burning on a 4-year return interval, however, resulted in a similarly diverse groundlayer community, but cover was dominated by woody species, highlighting the rapid recovery of tree seedlings and shrubs during even a short fire-free interval. Vander Yacht et al. (2017*b*) report that fire following light thinnings, where basal areas exceeded 15 m^2/ha (>80% canopy closure), creates conditions that often maintain a woody-dominated groundlayer, whereas heavy overstory removal to levels below that threshold followed by fire may stimulate the seed bank, which coupled with a higher light environment, facilitates an increase in the richness, diversity, and total cover of herbaceous and graminoid components. Burning after thinning can further promote and/or maintain the herbaceous (forb plus graminoid) component over time (Willson et al. 2018; Barefoot et al. 2019; Bassett et al. 2020). In contrast, Oakman et al. (2019) reported a negligible change in herbaceous or graminoid cover and diversity after thinning and four dormant season burns that together reduced overstory basal area (stems >10 cm dbh) to approximately 15 m^2/ha in a mixed-oak forest similar to and within proximity (approximately 60 km) to our study site. The density of midstory stems (<10 cm dbh); however, in that thin/burn treatment exceeded control and burn only treatments by 8178 and 6869 stems/ha, respectively (Waldrop et al. 2016), likely restricting further herbaceous and graminoid development.

Limitations associated with this study are representative of those common in applied ecological research. Site availability, controlling environmental variability to the extent possible in a highly complex landscape, and a lack of similarity in design and forest conditions across disparate studies are all factors that limit the scope and applicability of results beyond any given study. In addition, the small burn units (maximum size of 7.4 ha) utilized in this study did not likely experience the variability in fire behavior and associated fire effects documented in other topographically complex landscape-level prescribed burning studies (e.g. Iverson et al. 2008; Vaughan et al. 2021). It is also possible that our experimental design characterized by low replication ($n = 3$) and sampling intensity (three sample plots randomly located per unit) did not capture the variability in fire effects on vegetation within any given experimental unit. Despite these limitations, our results tend to corroborate most other studies showing that a single early growing season burn does not substantially alter the groundlayer vegetation over a single dormant season burn, with the groundlayer dominated by woody species both pre- and post-burn in both burn treatments. Heterogeneous forest and fuels conditions, weather, and strong environmental gradients influence both fire severity and vegetation response (Arthur et al. 2015; Maginel et al. 2019), likely contributing to variation in results among studies addressing fire effects on groundlayer vegetation. In addition, despite relatively similar treatments, differences in the abundance and diversity of buried seed related to historic land use and previous management coupled with post-disturbance propagule availability further influence results (Schiffman & Johnson 1992; Reilly et al. 2006; Vander Yacht et al. 2017*b*). Comparisons among studies are further confounded by a lack of standardized definitions and metrics used to categorize growing versus dormant season; the timing of a burn within a "growing season" can greatly affect plant population responses based on changes in physiology across the annual cycle (Miller et al. 2019).

In addition to knowledge gaps regarding the effects of burn season on attaining restoration goals, the practicality of growing season burns is also a consideration. The timing of prescribed burning is limited by "burn windows" based on weather, fuels condition, smoke dispersal and air quality standards, and/or considerations for federally listed endangered species (Arthur et al. 2021). Due to limited burn windows in April–September (Chiodi et al. 2018), restricting prescribed burns to the growing season may be difficult to adhere to over the long term. Delays in implementing periodic burns while waiting for a growing season burn window that may or may not occur in any given year can slow or reverse gains made toward restoration goals by permitting recruitment of woody stems and reducing canopy openness (Chiang et al. 2005; Maginel et al. 2019). These practical issues and confounding variables affecting the outcomes of prescribed burning highlight the need for a systematic research approach to season of burn effects on groundlayer vegetation that incorporates factors such as repeated burning, vegetation physiology at the time of burn, environmental and edaphic factors contributing to fire behavior and effects, fire intensity, and canopy cover or light availability in the understory. A better understanding of multiple factors affecting groundlayer response to burning is critical to the efficient use of prescribed burning in attaining restoration goals.

Acknowledgments

This research was funded by the USDA Forest Service, Southern Research Station, Upland Ecology and Management Research Work Unit in partnership with the Pisgah Ranger District, USDA Forest Service, Pisgah National Forest. We thank K. Frick, J. Kerzwick, T. Roof, B. Benz, and J. Adams who provided logistical and field/data collection support. This paper was written and prepared by a U.S. Government employee on official time; and therefore, it is in the public domain and not subject to copyright. This research was supported the U.S. Department of Agriculture, Forest Service. The findings and conclusions in this publication are those of the author(s) and should not be construed to represent an official USDA, Forest Service, or U.S. Government determination or policy.

LITERATURE CITED

Aldrich PR, Parker GR, Romero-Severson J, Michler CH (2005) Confirmation of oak recruitment failure in Indiana old-growth forest: 75 years of data. Forest Science 51:406–416. https://doi.org/10.1093/forestscience/51.5.406

Annighöfer P, Beckschäfer P, Vor T, Ammer C (2015) Regeneration patterns of European oak species (*Quercus petraea* [Matt.] Liebl., *Quercus robur* L.) in dependence of environment and neighborhood. PLoS One 10: e0134935. https://doi.org/10.1371/journal.pone.0134935

Arthur MA, Blankenship BA, Schorgendorfer A, Loftis DL, Alexander HD (2015) Changes in stand structure and tree vigor with repeated prescribed fire in an Appalachian hardwood forest. Forest Ecology and Management 340:46–64. https://doi.org/10.1016/j.foreco.2014.12.025

Arthur MA, Varner JM, Lafon CW, Alexander HD, Dey DC, Harper CA, et al. (2021) Fire ecology and management in eastern broadleaf and Appalachian forests. Pages 105–147. In: Greenberg CH, Collins B (eds) Fire ecology and management: past, present, and future of US forested ecosystems. Springer International Publishing, New York. https://doi.org/10.1007/978-3-030-73267-7_4

Barefoot CR, Willson KG, Hart JL, Schweitzer CJ, Dey DC (2019) Effects of thinning and prescribed fire frequency on ground flora in mixed *Pinus*-hardwood stands. Forest Ecology and Management 432:729–740. https://doi.org/10.1016/j.foreco.2018.09.055

Barnes TA, Van Lear DH (1998) Prescribed fire effects on advanced regeneration in mixed hardwood stands. Southern Journal of Applied Forestry 22: 138–142. https://doi.org/10.1093/sjaf/22.3.138

Bassett TJ, Landis DA, Brudvig LA (2020) Effects of experimental prescribed fire and tree thinning on oak savanna understory plant communities and ecosystem structure. Forest Ecology and Management 464:118047. https://doi.org/10.1016/j.foreco.2020.118047

Benjamini Y, Hochberg Y (2000) On the adaptive control of the false discovery rate in multiple testing with independent statistics. Journal of Educational and Behavioral Statistics 25:60–83. https://doi.org/10.3102/10769986025001060

Blankenship BA, Arthur MA (1999) Prescribed fire affects eastern white pine recruitment and survival on eastern Kentucky ridgetops. Southern Journal of Applied Forestry 23:144–150. https://doi.org/10.1093/sjaf/23.3.144

Borden CG, Duguid MC, Ashton MS (2021) The legacy of fire: long-term changes to the forest understory from periodic burns in a New England oak-hickory forest. Fire Ecology 17:24. https://doi.org/10.1186/s42408-021-00115-2

Brose PH (2010) Long-term effects of single prescribed fires on hardwood regeneration in oak shelterwood stands. Forest Ecology and Management 20: 1516–1524. https://doi.org/10.1016/j.foreco.2010.07.050

Brose PH, Dey DC, Phillips RJ, Waldrop TA (2013) A meta-analysis of the fire-oak hypothesis: does prescribed burning promote oak regeneration in eastern North America. Forest Science 59:332–334. https://doi.org/10.5849/forsci.12-039

Caldwell PV, Miniat CF, Elliott KJ, Swank WT, Brantley ST, Laseter SH (2016) Declining water yiels from forested mountain watersheds in response to climate change and forest mesophication. Global Change Biology 22:2997–3012. https://doi.org/10.1111/gcb.13309

Chiang JM, Arthur MA, Blankenship BA (2005) The effect of prescribed fire on gap fraction in an oak forest understory on the Cumberland Plateau. Journal of the Torrey Botanical Society 132:432–441. https://doi.org/10.3159/1095-5674(2005)132[432:TEOPFO]2.0.CO;2

Chiodi AM, Larkin NS, Varner JM (2018) An analysis of southeastern US prescribed burn weather windows: season variability and El Niño associations. International Journal of Wildland Fire 27:176–189. https://doi.org/10.1071/WF17132

Cleland DT, Freeouf JA, Keys JE, Nowacki GJ, Carpenter CA, McNab WH (2007) Ecological subregions: sections and subsections for the conterminous United States. General Technical Report WO-76D. U.S. Department of Agriculture, Forest Service, Washington, D.C.

De Lombaerde E, Baeten L, Verheyen K, Perring MP, Ma S, Landuyt D (2021) Understory removal effects on tree regeneration in temperate forests: a meta-analysis. Journal of Applied Ecology 58:9–20. https://doi.org/10.1111/1365-2664.13792

Delcourt PA, Delcourt HR, Ison CR, Sharp WE, Gremillion KJ (1998) Prehistoric human use of fire, the eastern agricultural complex, and the Appalachian oak-chestnut forests: paleoecology of cliff palace pond, Kentukcy. American Antiquity 63:263–278. https://doi.org/10.2307/2694697

Dhungel G, Rossi D, Henderson JD, Abt RC, Sheffield R, Baker J (2023) Critical market tipping points for high-grade white oak inventory decline in the central hardwood region of the United Sates. Journal of Forestry 121:224–234. https://doi.org/10.1093/jofore/fvad005

Dufrene M, Legendre P (1997) Species assemblages and indicator species: the need for a flexible and asymmetrical approach. Ecological Monographs 67:345–366. https://doi.org/10.2307/2963459

Elliott KJ, Hendrick RL, Major AE, Vose JM, Swank WT (1999) Vegetation dynamics after a prescribed fire in the southern Appalachians. Forest Ecology and Management 114:199–213. https://doi.org/10.1016/S0378-1127(98)00351-X

Elliott KJ, Miniat CF, Medenblik AS (2020) The long-term case for partial-cutting over clear-cutting in the southern Appalachians U.S.A. New Forests 51:273–295. https://doi.org/10.1007/s11056-019-09731-y

Elliott KJ, Vose JM (2010) Short-term effects of prescribed fire on mixed oak forests in the southern Appalachians: vegetation response. The Journal of the Torrey Botanical Society 137:49–66. https://doi.org/10.3159/09-RA-014.1

Elliott KJ, Vose JM (2011) The contribution of the Coweeta hydrologic laboratory to developing an understand of long-term (1934–2008) changes in managed and unmanaged forests. Forest Ecology and Management 261:900–910. https://doi.org/10.1016/j.foreco.2010.03.010

Elliott KJ, Vose JM, Knoepp JD, Clinton BD, Kloeppel BD (2015) Function role of the herbaceous layer in eastern deciduous forest ecosystems. Ecosystems 18:221–236. https://doi.org/10.1007/s10021-014-9825-x

Fei SL, Kong NN, Steiner KC, Moser WK, Steiner EB (2011) Change in oak abundance in the eastern United States from 1980 to 2008. Forest Ecology and Management 262:1370–1377. https://doi.org/10.1016/j.foreco.2011.06.030

Fei SL, Steiner KC (2007) Evidence for increasing red maple abundance in the eastern United States. Forest Science 53:473–477. https://doi.org/10.1093/forestscience/53.4.473

Franklin SB, Robertson PA, Fralish JS (1997) Small-scale fire temperature patterns in upland *Quercus* communities. Journal of Applied Ecology 34:613–630. https://doi.org/10.2307/2404911

Gilliam FS (2007) The ecological significance of the herbaceous layer in temperate forest ecosystems. Bioscience 10:845–858. https://doi.org/10.1641/B571007

Glasgow LS, Matlack GR (2007) Prescribed burning and understory composition in a temperate deciduous forest, Ohio, U.S.A. Forest Ecology and Management 238:54–64. https://doi.org/10.1016/j.foreco.2006.08.344

Grover ZS, Forrester JA, Keyser TL, King JS, Altman J (2023) Growth response, climate sensitivity and carbon storage vary with wood porosity in a southern Appalachian mixed hardwood forest. Agricultural and Forest Meteorology 332:109358. https://doi.org/10.1016/j.agrformet.2023.109358

Hanberry BB, Bragg DC, Alexander HD (2020) Open forest ecosystems: an excluded state. Forest Ecology and Management 472:118256. https://doi.org/10.1016/j.foreco.2020.118256

Hanula JL, Horn S, O'Brien JJ (2015) Have changing forests conditions contributed to pollinator decline in the southeastern United States? Forest Ecology and Management 348:142–152. https://doi.org/10.1016/j.foreco.2015.03.044

Harrod JC, Harmon ME, White PS (2000) Post-fire succession and 20th century reduction in fire frequency on xeric southern Appalachian sites. Journal of Vegetation Science 11:465–472. https://doi.org/10.2307/3246576

Hédl R, Kopecký M, Komárek J (2010) Half a century of succession in a temperate oakwood: from species-rich community to mesic forest. Diversity and Distributions 16:267–276. https://doi.org/10.1111/j.1472-4642.2010.00637.x

Hiers JK, Walters JR, Mitchell RJ, Varner JM, Conner LM, Blanc LA, Stowe J (2014) Ecological value of retaining pyrophytic oaks in longleaf pine ecosystems. The Journal of Wildlife Management 78:383–393. https://doi.org/10.1002/jwmg.676

Hutchinson TF, Adams BT, Dickinson MB, Heckel M, Royo AA, Thomas-Van Gundy MA (2024) Sustaining eastern oak forests: synergistic effects of fire and topography on vegetation and fuels. Ecological Applications e2948. https://doi.org/10.1002/eap.2948

Hutchinson TF, Boerner REJ, Sutherland S, Sutherland EK, Ortt M, Iverson LR (2005*a*) Prescribed fire effects on the herbaceous layer of mixed-oak forests. Forest Ecology and Management 35:877–890. https://doi.org/10.1139/X04-189

Hutchinson TF, Sutherland EK, Yaussy DA (2005*b*) Effects of repeated prescribed fires on the structure, composition, and regeneration of mixed-oak forests in Ohio. Forest Ecology and Management 218:210–228. https://doi.org/10.1016/j.foreco.2005.07.011

Iverson LR, Hutchinson TF, Peters MP, Yaussy DA (2017) Long-term response of oak-hickory regeneration to partial harvest and repeated fires: influence of light and moisture. Ecosphere 8:e01642. https://doi.org/10.1002/ecs2.1642

Iverson LR, Hutchinson TF, Prasad AM, Peters MP (2008) Thinning, fire, and oak regeneration across a heterogenous landscape in the eastern U.S.: 7-year results. Forest Ecology and Management 255:3035–3050. https://doi.org/10.1016/j.foreco.2007.09.088

Keyser TL, Greenberg CH, McNab WH (2019) Season of burn effects on vegetation structure and composition in oak-dominated Appalachian hardwood forests. Forest Ecology and Management 433:441–452. https://doi.org/10.1016/j.foreco.2018.11.027

Keyser T, Malone J, Cotton C, Lewis J (2014) Outlook for the Appalachian-Cumberland forests: a subregional report from the southern Forest futures project. General Technical Report SRS-188. U.S. Department of Agriculture Forest Service, Southern Research Station, Asheville, North Carolina. https://doi.org/10.2737/SRS-GTR-188

Keyser TL, McDaniel VL, Klein RN, Drees DG, Burton JA, Forder MM (2018) Short-term stem mortality of 10 deciduous broadleaved species following prescribed burning in upland forests of the southern US. International Journal of Wildland Fire 27:42–51. https://doi.org/10.1071/WF17058

Keyser TL, Roof T, Adams JA, Simon D, Warburton G (2012) Effects of prescribed fire on the buried seed bank in mixed-hardwood forests of the southern Appalachian mountains. Southeastern Naturalist 11:669–688. https://doi.org/10.1656/058.011.0407

Knapp EE, Estes BL, Skinner CN (2009) Ecological effects of prescribed fire season: a literature review and synthesis for managers. USDA Forest Service General Technical Report PSWGTR-224. U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, Albany, California. https://doi.org/10.2737/PSW-GTR-224

Knapp BO, Stephan K, Hubbart JA (2015) Structure and composition of an oak-hickory forest after over 60 years of repeated burning in Missouri, U.S.A. Forest Ecology and Management 344:95–109. https://doi.org/10.1016/j.foreco.2015.02.009

Knoepp JD, Elliott KJ, Clinton BD, Vose JM (2009) Effects of prescribed fire in mixed oak forests of the southern Appalachians: forest floor, soil, and soil solution nitrogen responses. Journal of the Torrey Botanical Society 13:380–391. https://doi.org/10.3159/08-ra-052.1

Lafon CW, Nalto AT, Grissino-Mayer HD, Horn SP, Waldrop TA (2017) Fire history of the Appalachian region: a review and synthesis. General Technical Report SRS-219. U.S. Department of Agriculture Forest Service, Southern Research Station, Asheville, North Carolina. https://doi.org/10.2737/SRS-GTR-219

Lanta V, Mudrák O, Liancourt P, Dvorský M, Bartoš M, Chlumská Z, Šebek P, Čížek L, Doležal J (2020) Restoring diversity of thermophilous oak forests: connectivity and proximity to existing habitats matter. Biodiversity and Conservation 29:3411–3427. https://doi.org/10.1007/s10531-020-02030-5

Maginel CJ, Knapp BO, Kabrick JM, Muzika RM (2019) Landscape- and site-level responses of woody structure and ground flora to repeated prescribed fire in the Missouri Ozarks. Canadian Journal of Forest Research 49: 1004–1014. https://doi.org/10.1139/cjfr-2018-0492

McCune B, Mefford MJ (2018) *PC-ORD. Multivariate analysis of ecological data. Version 7.08*. Wild Blueberry Media, LLC, Corvallis, OR.

McShea WJ, Healy WM, Devers P, Fearer T, Koch FH, Stauffer D, Waldon J (2007) Forestry matters: decline of oaks will impact wildlife in hardwood forests. Journal of Wildlife Management 71:1717–1728. https://doi.org/10.2193/2006-169

Melcher AL, Hagan D, Barrett K, Ross B, Lorber J (2023) Changes in canopy cover and forest structure following dormant season and early growing season prescribed burns in the Southern Appalachians, U.S.A. Fire Ecology 19:27. https://doi.org/10.1186/s42408-023-00184-5

Miller RG, Tangney R, Enright NJ, Fontaine JB, Merritt DJ, Ooi MKJ, Ruthrof KX, Miller BP (2019) Mechanisms of fire seasonality effects on plant populations. Trends in Ecology & Evolution 34:1104–1117. https://doi.org/10.1016/j.tree.2019.07.009

Nowacki GJ, Abrams MD (2008) The demise of fire and "Mesophication" of forests in the eastern United States. Bioscience 58:123–138. https://doi.org/10.1641/B580207

Oakman EC, Hagan DL, Waldrop TA, Barrett K (2019) Understory vegetation responses to 15 years of repeated fuel reduction treatments in the southern Appalachian Mountains, U.S.A. Forests 10:350. https://doi.org/10.3390/f10040350

Oakman EC, Hagan DL, Waldrop TA, Barrett K (2021) Understory community shifts in response to repeated fire and fire surrogate treatments in the southern Appalachian Mountains, U.S.A. Fire Ecology 17:1–15. https://doi.org/10.1186/s42408-021-00097-1

Plue J, Van Gils B, De Schrijver A, Peppler-Lisbach C, Kerheyen K, Hermy M (2013) Forest herb layer response to long-term light deficit along a forest developmental series. Acta Oecologia 53:63–72. https://doi.org/10.1016/j.actao.2013.09.005

Reilly MJ, Wimberly MC, Newell CL (2006) Wildfire effects on plant species richness at multiple spatial scales in forest communities of the southern Appalachians. Journal of Ecology 94:118–130. https://doi.org/10.1111/j.1365-2745.2005.01055.x

Robertson KM, Hmielowski TL (2014) Effects of fire frequency and season on resprouting of woody plants in southeastern US pine-grassland communities. Oecologia 174:765–776. https://doi.org/10.1007/s00442-013-2823-4

Rogers DA, Rooney TP, Olson D, Waller DM (2008) Shifts in southern Wisconsin forest canopy and understory richness, composition, and heterogeneity. Ecology 89:2482–2492. https://doi.org/10.1890/07-1129.1

Ruswick SK, O'Brien JJ, Aubrey DP (2021) Carbon starvation is absent regardless of season of burn in *Liquidambar styracifula* L. Forest Ecology and Management 479:118588. https://doi.org/10.1016/j.foreco.2020.118588

Schiffman PM, Johnson WC (1992) Sparse buried seed bank in a southern Appalachian oak forest: implications for succession. American Midland Naturalist 127:258–267. https://doi.org/10.2307/2426532

Small CJ, McCarthy BC (2002) Spatial and temporal variability of herbaceous vegetation in an eastern deciduous forest. Plant Ecology 164:37–48. https://doi.org/10.1023/A:1021209528643

Spînu AP, Niklasson M, Zin E (2020) Mesophication in temperate Europe: a dendrochronological reconstruction of tree succession and fires in a mixed deciduous stand in Białowieża Forest. Ecology and Evolution 10:1029–1041. https://doi.org/10.1002/ece3.5966

Stavi I, Thevs N, Welp M, Zdruli P (2022) Provisioning ecosystem services related with oak (*Quercus*) systems: a review of challenges and opportunities. Agroforestry Systems 96:293–313. https://doi.org/10.1007/s10457-021-00718-3

Turner MA, Gulsby WD, Harper CA, Ditchkoff SS (2020) Improving coastal plain hardwoods for deer and turkeys with canopy reduction and fire. Wildlife Society Bulletin 44:705–712. https://doi.org/10.1002/wsb.1142

USDA NRCS (2022) The PLANTS database. National Plant Data Team. http://plants.usda.gov (accessed 6 Mar 2022)

Vander Yacht AL, Barrioz SA, Keyser PD, Harper CA, Buckley DS, Buehler DA, Applegate RD (2017*b*) Vegetation response to canopy disturbance and season of burn during oak woodland and savanna restoration in Tennessee. Forest Ecology and Management 390:187–202. https://doi.org/10.1016/j.foreco.2017.01.029

Vander Yacht A, Keyser PD, Barrioz SA, Kwit C, Stambaugh MC, Clatterbuck WK, Jacobs R (2020) Litter to glitter: promoting herbaceous groundcover and diversity in mid-southern U.S.A. oak forests using canopy disturbance and fire. Fire Ecology 16:17. https://doi.org/10.1186/s42408-020-00072-2

Vander Yacht AL, Keyser PD, Harper CA, Buckley DS, Saxton AM (2017*a*) Restoration of oak woodlands and savannas in Tennessee using canopy disturbance, fire-season, and herbicides. Forest Ecology and Management 406:351–360. https://doi.org/10.1016/j.foreco.2017.07.031

Vaughan MC, Hagan DL, Bridges WC Jr, Barrett K, Norman S, Coates TA, Klein R (2022) Effects of burn season on fire-excluded plant communities in the southern Appalachian Mountains, U.S.A. Forest Ecology and Management 516:120244. https://doi.org/10.1016/J.Foreco.2022.120244

Vaughan MC, Hagan DL, Bridges WC Jr, Dickinson MB, Coates TA (2021) How do fire behavior and fuel consumption vary between dormant and early growing season prescribed burns in the southern Appalachian Mountains. Fire Ecology 17:27. https://doi.org/10.1186/s42408-021-00108-1

Waldrop TA, Hagan DL, Simon DA (2016) Repeated application of fuel reduction treatments in the southern Appalachian Mountains, U.S.A.: implications for achieving management goals. Fire Ecology 12:1–20. https://doi.org/10.4996/fireecology.1202028

Waldrop TA, White DL, Jones SM (1992) Fire regimes for pine-grassland communities in the southeastern United States. Forest Ecology and Management 47:195–210. https://doi.org/10.1016/0378-1127(92)90274-D

Willson KG, Barefoot CR, Hart JL, Schweitzer CJ, Dey DC (2018) Temporal patterns of ground flora response to fire in thinned *Pinus-Quercus* stands. Canadian Journal of Forest Research 48:1171–1183. https://doi.org/10.1139/cjfr-2018-0132

Woodbridge M, Keyser T, Oswalt C (2022) Stand and environmental conditions drive functional shifts associated with mesophication in eastern US forests. Frontiers in Forests and Global Change 3:991934. https://doi.org/10.3389/ffgc.2022.991934

Supporting Information

The following information may be found in the online version of this article:

Table S1. Species frequency of occurrence (percent of total permanent plots [$n = 27$]) across treatments and sampling periods.

Coordinating Editor: Stephen Murphy

Received: 15 November, 2023; First decision: 9 February, 2024; Revised: 21 February, 2024; Accepted: 21 February, 2024