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Fire versus herbivory for oak woodland restoration: burning achieves short-term structural and compositional objectives whereas browsing alone fails to reduce stem densities and promote ground flora

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Abstract

Background Declines in ecologically beneficial fire, coincident with alterations to native herbivory and intensive land use, have led to dynamic changes in woodland structure and composition, leading to midstory densification and reductions in ground flora abundance and diversity. Frequent, low intensity fire is key to achieving woodland restoration objectives and prescribed burns are often used to meet management goals. For a variety of reasons, the use of prescribed fire is often limited. Further, growing season prescribed burning is often suggested to have a greater impact on woody stems than dormant season applications, but its implementation is difficult. Targeted herbivory may emulate many aspects of prescribed fire holding the potential to diversify management strategies for restoration. We designed a replicated, experimental study to evaluate targeted browsing and prescribed burning for achieving restoration objectives, specifically, a two layered oak woodland with a diverse and abundant native ground flora. The six treatments included: (1) spring browsing, (2) fall browsing, (3) dormant-season and fall browsing, (4) dormant-season prescribed fire, (5) spring browsing plus dormant-season prescribed fire, and (6) an untreated control.

Results Results suggest that fire had an overriding effect on the reduction of midstory stems that was not comparable to the browsing treatments. Burning reduced leaf litter, increased bare soil exposure and forb coverage. Browsing may reduce the accumulation of woody stems when compared to the control, but this effect was not statistically meaningful. Differences in browsing seasonality and frequent browsing were also not statistically important but trends suggest a greater influence of spring browsing for meeting woodland objectives. Browsing may also exert compositional changes to woodlands because of forage preferences by goats.

Conclusions To achieve woodland objectives in the short-term, fire is necessary to quickly reduce midstory densities, increase light availability, consume leaf litter, and thereby promote native ground flora abundance and diversity which may not be achieved with targeted browsing alone. Further, the interaction of fire and herbivory suggest that browsing preferences may influence structural and compositional outcomes associated with pyric herbivory regimes in woodlands that require further investigation.

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Keywords Goats, Ground flora, Regeneration, Mastication, Forbs, Leaf litter, Hickory, Quercus, Carya, Central hardwoods

Resumen

Antecedentes La declinación de los fuegos ecológicamente beneficiosos, coincidente con alteraciones causadas a los herbívoros nativos y el uso intensivo de la tierra, ha llevado a cambios dinámicos en la composición y estructura de algunos bosques, lo que lleva a una densificación de los estratos intermedios del bosque y a una reducción en la abundancia y diversidad de la flora cercana a la superficie del suelo. Los fuegos frecuentes, de baja intensidad, son claves para alcanzar los objetivos de restauración de bosques, y las quemas prescriptas son frecuentemente usadas para alcanzar los objetivos de manejo. Por una variedad de razones, el uso de las quemas prescriptas es frecuentemente limitado. Además, las quemas durante la estación de crecimiento son muchas veces sugeridas ya que tienen un mayor impacto en los tallos de plantas arbóreas que las aplicadas durante la estación de dormición, aunque su implementación es dificultosa. Algunos herbívoros específicos pueden emular muchos aspectos de las quemas prescriptas, teniendo el potencial de diversificar las estrategias de manejo para la restauración. Diseñamos un estudio experimental con réplicas, para evaluar los efectos específicos del ramoneo y de las quemas prescriptas para alcanzar objetivos de restauración, específicamente a dos estratos de rodales de roble con abundante y diversa flora superficial. Los seis tratamientos incluyeron: (1) ramoneo en primavera; (2) ramoneo en otoño; (3) estación de dormición y ramoneo en otoño; (4) estación de dormición y quema prescripta, (5) ramoneo en primavera más una quema en la estación de dormición; y (6) tratamiento de control.

Resultados Los resultados sugieren que el fuego tiene un efecto predominante en la reducción de tallos leñosos de especies del estrato medio que no fue comparable con los tratamientos de ramoneo. La quema redujo la broza de hojas (hojarasca superficial) e incrementó la exposición del suelo desnudo y la cobertura de malezas de hoja ancha. El ramoneo, por otro lado, pudo reducir la acumulación de tallos leñosos cuando se lo comparó con el control, aunque su efecto no fue estadísticamente significativo. Las diferencias en la estacionalidad del ramoneo y el ramoneo frecuente tampoco fueron estadísticamente importantes, aunque las tendencias sugieren una mayor influencia del ramoneo de primavera para alcanzar los objetivos de restauración del bosque. El ramoneo puede asimismo causar cambios composicionales en esos bosques, dadas las preferencias de diferentes forrajes por las cabras.

Conclusiones Para alcanzar objetivos de restauración del bosque en el corto plazo, el fuego es necesario para reducir rápidamente la densidad de la vegetación en el dosel medio, incrementar la disponibilidad de luz, consumir la hojarasca, y por lo tanto promover la abundancia y diversidad de la flora nativa superficial (sotobosque), que no podría alcanzarse con sólo el ramoneo. Asimismo, la interacción del fuego y la herbivoría sugiere que la preferencia por el ramoneo puede influenciar los resultados estructurales y composicionales asociados con regímenes de fuego asociados a herbívoros en bosques que requieren de más investigaciones.

Background

Similarities between herbivory and fire effects on vegetation are numerous and widespread across a range of ecosystems and vegetation types (Bond 2005). Both may be considered above-ground, plant-consuming disturbances that play critical roles in forming the structure and function of plant community composition (Noy-Meir 1995; Churski et al. 2017). Historically, herbivory interacted with fire regimes, dramatically shaping vegetation patterns over time and landscapes (Archibald et al. 2019). However, with the extinction of mega-herbivores, contemporary alterations to fire regimes, impacts from diverse land uses, and fragmentation, the structure and composition of woodlands in North America have been greatly altered (Gill et al. 2009; Smith et al. 2019; Mueller et al. 2021; Thomas-Van Gundy et al. 2021; Perrotti et al.

2022). Although no analog woodland communities may exist today, the effects of prescribed burning and domesticated herbivory may promote desired outcomes for the structure, composition, and function of woodland plant communities.

Woodlands in the Midwest US are defined by over-story canopy conditions that range from 30 to 90% cover with a minimal midstory and are characterized by dense, species-rich ground flora (Nelson 2010; Dey et al. 2016). Many of these woodland communities reflect modern alterations to their disturbance regimes including increases in fire at the time of Euro-American settlement followed by fire suppression, intensive and unregulated grazing practices by domesticated livestock, past subsistence farming, and subsequent land abandonment (Guyette et al. 2012). As a result, many remnant woodlands

today are overstocked with a dense midstory (Brewer 2001; Hanberry et al. 2014; Hanberry and Abrams 2018) and a sparse and depauperate ground flora, often dominated by ruderal and/or invasive plants (Bowles and McBride 1998; Peterson and Reich 2008; Brewer et al. 2015; Vander Yacht et al. 2020). Maintaining or restoring woodland conditions requires specific disturbance regimes that reduce woody stems, leaf litter, and canopy cover, while promoting the density and diversity of herbaceous ground flora (Anderson 1983; Brose et al. 2013; Knapp et al. 2015, 2017; Maginel et al. 2019). Typically, prescribed fire is the management choice utilized to achieve woodland objectives, but its use can be limited, and fire alone, without herbivory, may be ineffective at controlling sprouting woody species (Ascoli et al. 2013).

In contrast to uncontrolled or continuous grazing, targeted herbivory (browsing or grazing, depending on livestock) can be defined as a controlled disturbance regime which uses livestock to achieve land management objectives, primarily related to vegetation or fuels. Targeted herbivory integrates the seasonality, frequency, duration, and intensity with elements of livestock management and plant ecology to achieve desired plant community composition and structure (Bailey et al. 2019). For example, goats (*Capra hircus*) may consume a wide variety of plant species but prefer lignified, woody plants (i.e., intermediate browsers). Goats can also stand on their hind legs, increasing browse heights up to 2 m and can effectively defoliate midstory trees and shrubs. Targeted herbivory can be used to instigate or supplement a frequent low-intensity growing- or dormant-season disturbance regime.

As the application of targeted herbivory is not limited by weather conditions (in comparison to prescribed fire), browsing pressure can be applied year-round. Targeted herbivory can reduce fuels (limit fire risk) adjacent to infrastructure and negate smoke concerns, constraints often associated with prescribed burning (Ryan et al. 2013). However, few studies have examined the effect of browsing on woodland structure and composition including the effect of browsing seasonality and impacts to forest shrubs and herbaceous plants (Sabo 2019). The interaction between the seasonality of herbivory and plant phenology may affect individual plant fitness and overall plant species composition over time. For example, plants that are dependent on seed for reproduction may be at a competitive disadvantage if herbivory occurs prior to seed maturation when compared to those that have already produced seed or those that reproduce through vegetative sprouting or belowground reproductive organs (Hadar et al. 1999). Furthermore, browsing preference for a specific plant species may vary throughout the year. Studies have documented that the preference for

herbaceous species by browsing species including deer, sheep, and goats will be greatest during spring and summer months when nutritional value and digestibility are at their highest (Miranda et al. 2011; Glasser et al. 2012; Manousidis et al. 2016).

Both prescribed fire and targeted herbivory may reduce the density of woody stems (Harrington and Kathol 2009) and thereby increase the abundance of herbaceous species (Augustine and McNaughton 1998; Raffaele et al. 2011; Maginel et al. 2019). Though studies on the interactive effect of herbivory and fire (pyric-herbivory) regimes in woodland ecosystems in the US is sparse, literature from other countries suggest that a combination of the two may result in an increase in the abundance of ground flora and a reduction in woody stem densities greater than either disturbance alone (Staver et al. 2009; Raffaele et al. 2011). For example, browsers can reduce fuel loads and alter the vertical structure of vegetation (Smit and Coetsee 2019). Furthermore, the current fire regime can influence herbivory by altering forage quantity, quality, composition, and availability (Griffin and Friedel 1984; Ferwerda et al. 2006).

To evaluate the utility of targeted browsing to meet oak woodland objectives and to compare its affect to prescribed burning, we developed an experimental approach to investigate changes to woodland structure and composition as it related to evaluating (1) browsing as a prescribed fire surrogate, (2) browsing seasonality to target plant phenology, and (3) the compounding effects of targeted herbivory and prescribed fire. To test the potential of targeted herbivory, alone or in conjunction with prescribed burning for achieving structural and compositional goals for oak woodlands, we compared treatment outcomes for the overstory, midstory, and understory including the effects on tree regeneration and ground flora.

We hypothesized that:

- 1) Prescribed burning would reduce woody species and increase ground flora coverage more than browsing or the control due to woody plant top-kill and associated reductions in leaf litter
- 2) Browsing would decrease the density of midstory and understory woody stems as goats are indeterminate feeders, preferring woody plants
- 3) Two browsing events within the same year would result in greater reductions in woody stems than either spring or fall browsing alone due to repeated stress associated with browsing and regrowth
- 4) Spring browsing would have greatest negative effect on woody species when compared to fall browsing due to the upward translocation of non-structural carbohydrate stores in the spring that is commonly

cited in the literature (Conway et al. 1999; Richburg 2005)

- 5) The combination of browsing and burning would result in the greatest reduction of woody stems with subsequent increases in the coverage of ground flora when compared to other treatments due to the increased frequency and variability of disturbance events

This research has important implications for evaluating the use of targeted browsing and prescribed fire and browsing combined for vegetation management but also improves our understanding of fire-herbivory interactions in forested ecosystems.

Methods

Study area

This research occurred on the Houston/Rolla/Cedar Creek District of the United States Department of Agriculture (USDA) Forest Service, Mark Twain National Forest (MTNF) in south-central Missouri, USA (lat 37° 53' 34" N; long 92° 01' 06" W) on a site referred to as the Onyx Project area. The Onyx Project area is located in the Ozark Highlands ecological section of the Ozark Broadleaf Forest ecoregion, Humid Temperate Domain (Bailey 1995). Karst topography and its features are a defining characteristic of the region (McNab & Avers 1994). Elevation is 300 m above sea level with slopes ranging from 1 to 25%. Sandstone and dolomite underlie primarily Ultisol and Alfisol soils formed from hillslope sediment, residuum, and loess (McNab and Avers 1994; Soil Survey Staff 2019). Due to high local variability, most of the soil map units are complexes that included the series Bendavis (Typic Hapludults) and Poynor (Typic Paleudults) on shoulder slopes and Tonti (Typic Fragiudults), Viburnum (Acquic Paleudults), and Viraton (Oxyaquic Fragiudults) on summits (Soil Survey Staff 2019). Mean annual temperature is 13.1 °C. The average daily temperature in January is −2.2 °C, and the average daily temperature in July is 23.3 °C. The climate record period from 1888 to 2021 shows the mean annual precipitation is 1226 mm with May the wettest month (NOAA 2021).

Onyx Cave, a hibernacula for multiple bat species and a National Register of Historic Places, is located approximately 1 km from the project area. To improve foraging habitat for bats, woodland structure was created in 2012 by thinning trees smaller than 23 cm DBH, excluding dogwood (*Cornus florida* L.) with target residual basal area ranging from 16.1 to 18.4 m²/ha. However, due to smoke and lack of visibility concerns with the proximity of the project area to an interstate highway (approximately 0.5 km to the east), the project area

was masticated in 2017 to reduce midstory ingrowth and to encourage ground flora. Furthermore, the Onyx Project management plan does not allow for the use of herbicides.

Following overstory thinning and mastication, the stand conditions in 2019 upon project initiation would be described as a woodland overstory structure with a dense multi-stemmed woody dominated midstory and ground cover of abundant oak and hickory sprouts resulting from top-kill by mastication with minimal herbaceous ground flora. Common overstory tree species included white oak (*Quercus alba* L.), post oak (*Q. stellata* Wangenh.), and black oak (*Q. velutina* Lam.). Many overstory trees had large, spreading crowns and low, persistent primary branches indicative of past open woodland conditions. Common midstory tree and shrub species included black hickory (*Carya texana* Buckley), blackgum (*Nyssa sylvatica* Marshall), American plum (*Prunus americana* Marshall), fragrant sumac (*Rhus aromatica* Aiton), and blackberries (*Rubus* spp.). Common lianas species include Virginia creeper (*Parthenocissus quinquefolia* L.), poison ivy (*Toxicodendron radicans* L.), and grape vine (*Vitis* spp.). Common understory plants include American burnweed (*Erechtites hieraciifolius* L.), hairy sunflower (*Helianthus hirsutus* Raf.), elmleaf goldenrod (*Solidago ulmifolia* Muhl. Ex Willd), poverty oatgrass (*Danthonia spicata* L.), panic grasses (*Dichanthelium* spp.), broomsedge bluestem (*Andropogon virginicus* L.), American hogpeanut (*Amphicarpaea bracteata* L.), and smooth small-leaf ticktrefoil (*Desmodium marilandicum* L.). Invasive plants included Japanese honeysuckle (*Lonicera japonica* Thunb.), Amur honeysuckle (*Lonicera maackii* [Rupr.] Herder), and multiflora rose (*Rosa multiflora* Thunb.).

Experimental design

The study was conducted as randomized complete block design including six treatments and three replications (Fig. 1). Each experimental unit was between 1 and 3.2 ha in size and contained 4, 0.08-ha circular plots. Three treatments were designed to test the effects of browsing seasonality, they included (1) spring browse (SB; May), (2) fall browse (FB; September), and (3) early spring browse (bud break, referred to as “dormant browse” hereafter, DB; April) + fall browse (September; DB + FB). The SB treatment was selected for evaluation to maximize the effect of top-kill on woody species when the upward movement of carbohydrates to support leaf and flower development would make them most susceptible to mortality, thereby reducing midstory density. The FB treatment was selected for evaluation to reduce impact to resident ground flora by not adversely affecting their growth or fitness potential. The DB + FB treatment was

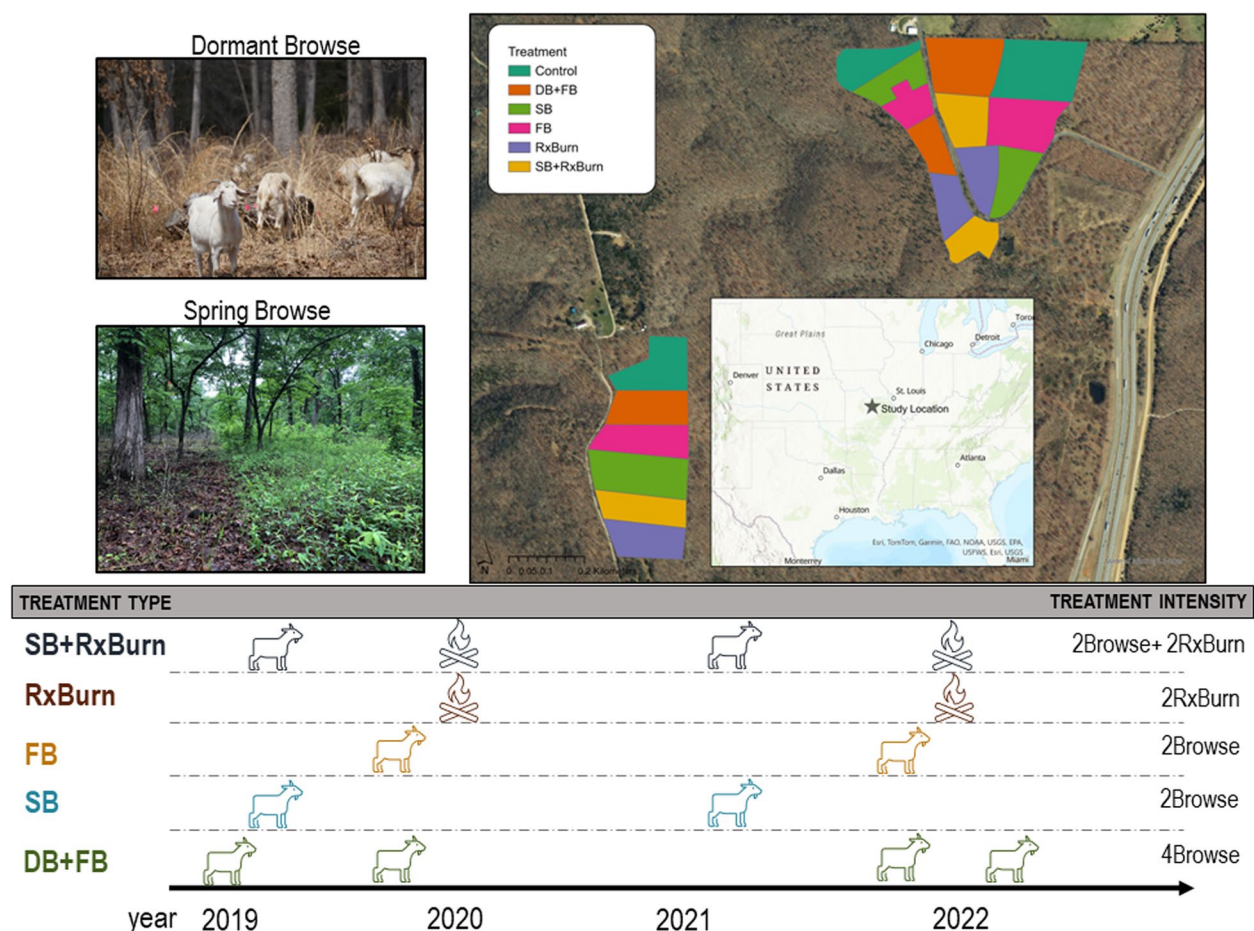


Fig. 1 Experimental layout and treatment timeline, including the total number of browsing and burning events by treatment and year at the Onyx Project area in the Ozark Highlands of south-central Missouri on the Mark Twain National Forest. Browse events are indicated by a goat symbol. Browsing occurred during the late dormant to early growing season (DB; pictured upper left), and during spring (SB; pictured center left) and fall (FB). Burning events are indicated by a fire symbol. Burning occurred during the late dormant season. Browsing and burning were evaluated for their potential to reduce woody mid- and understory stem densities to promote open oak woodland conditions

selected to evaluate the potential of repeated browsing in a single year to expedite restoration objectives. For comparison to the browsing treatments, two treatments evaluated the effect of prescribed burning including (4) prescribed fire (Rx; February) and (5) spring browse+prescribed fire 10 months later (SB+Rx). The compounding browse-fire treatment was designed to test supplementing prescribed fire with target herbivory and increasing the frequency of low-intensity disturbances. All treatments were compared to (6) an untreated control.

Browsing treatments occurred in 2019 and 2021 with a mixture of different meat goat breeds. All adult goats were nannies (adult females), many with kids (juveniles). Due to variability in treatment unit and herd size, a browsing threshold was established to maintain a consistent browsing level across all replications and treatment units. When approximately 85% of all vegetation

was browsed across an experimental unit, goats were removed. Temporary electric fencing was used to contain goats within each unit until the threshold was met.

Prescribed fires occurred prior to leaf-out in February 2020 and February 2022. Burns were conducted as hand-ignited strip head fires burning into backing fires. Fuels mainly consisted of leaf litter, 1-h fuels, 10-h fuels, and dried warm-season grasses. For the prescribed burns in 2020, flame lengths averaged between 0.3 and 0.6 m, with ambient air temperatures ranging between 12 and 20 °C and relative humidity ranging between 25 and 30%. The burn coverage in 2020 was patchy and primarily consumed litter and grasses with overall woody fuel consumption declining with time-lag class. Fire behavior produced better results in 2022 with greater and more contiguous fuel consumption, including consumption numerous 1000-h fuels (personal communication, Chad Randolph, Mark Twain National Forest supervisory fire

engine operator). Flame lengths averaged 0.6–1.2 m, with ambient air temperatures between 21 and 27 °C and relative humidity ranging from 15 to 22%.

Field measurements

Permanent vegetation plots were established prior to treatment in February 2019. Within each 0.08-ha plot, trees greater than or equal to 3.8 cm DBH were recorded by species, DBH, and status (dead or alive) (referred to as the “overstory,” although not all stems in this category are overstory trees). Four 3.6-m radius subplots, radiating from plot center in each cardinal direction, recorded midstory trees, and shrubs greater than or equal to 1 m tall and less than 3.8 cm DBH were inventoried by species and basal diameter. Within each subplot, four 1-m² understory quadrats were established at each cardinal direction from subplot center (0°, 90°, 180°, and 270°) for a total of 16 quadrats per plot. In each understory quadrat, trees less than 1 m tall were inventoried by species and height class (<10 cm and by 10 cm height classes thereafter). Additionally, ground cover percentage for bare soil and litter, as well as ground flora by functional group (forbs, grasses, “sedges” combined with rushes, legumes, shrubs, trees, and vines), was recorded. Each functional group was estimated independently, and total estimations could exceed 100%.

Pre-treatment data collection for woody stems (mid-story and reproduction) in the DB+FB, SB, and SB+Rx occurred prior to leaf out in March and April 2019. However, due to the sequence of browsing events and sampling, true pre-treatment data for ground cover was not collected prior to the dormant browse (DB+FB) or spring browse (SB, SB+Rx) events in 2019 because plants were still dormant. Sampling for these treatments occurred in the summer of 2019. Pre-treatment data for the C, FB, and Rx treatments were collected in summer 2019. Post-treatment sampling across all treatments occurred in the summers of 2020 and 2022. However, since the effect of our treatments to overstory trees was anticipated to be minimal, overstory trees were only sampled in 2019 and 2022.

Data analysis

We averaged treatment means for dependent variables to the experimental unit level. We compared outcomes across treatments using repeated measures, generalized mixed linear models with the block as a random effect. When required, distributions were adjusted within the model to meet model assumptions.

For overstory stems, we compared overstory density (trees per hectare), basal area (BA, m²/ha), and the change in density and BA from 2019 to 2022 by treatment for all species and for species groups separately. For

mid- and understory stems, and ground cover, we compared abundance (trees per hectare or percent coverage) from 2019, 2020, and 2022 by treatment. For midstory stems, we compared treatment effects for all species combined and separately by species groups. For understory reproduction, we binned heights into three height classes (small=0–40 cm tall, medium=41–70 cm tall, and large=71–100 cm tall).

For mid- and understory stems, and ground cover, we adjusted for differences in sampling crews and seasonal variations by assessing the relativized change from pre-treatment in 2019 to post-treatment in 2022 using the following equation:

$$change = \left(\frac{t2_i}{\sum t2} \right) - \left(\frac{t1_i}{\sum t1} \right)$$

where $t2_i$ is the index of interest for the i th species in 2022, and the sum of $t2$ is the total of that index value for that species across treatments in 2022 subtracted by the values in 2019. These values were then modeled by treatment with block included as a random effect.

To assess our specific hypotheses, within our models, we used specific linear contrasts to compare treatment effects across our outcomes for mid- and understory stem densities and ground cover, including the change in these metrics over the study period. For hypothesis 1, we compared burning treatments to all unburned treatments (C, DBFB, FB, and SB versus Rx and SB+Rx). For hypothesis 2, we compared browsing treatments to the control (DBFB, SB, and FB versus C). For hypothesis 3, we compared the highly frequent browsing treatment to the singular browsing treatments (DBFB versus SB and FB). For hypothesis 4, we compared browsing seasonality by contrasting spring and fall browsing treatments (SB versus FB). For hypothesis 5, we compared fire alone to the combination of browsing and burning (Rx versus SB+Rx).

Results

Overstory

As anticipated, there was no significant change in overstory tree (>3.8 cm DBH) density or basal area associated with treatment effects from 2019 to 2022 for any species group. Overstory density across the treatments and measurement periods was on average 180–182 trees per hectare with basal areas averaging 14.2–15.2 m²/ha (Supplementary Table 1). The study site was dominated by white oaks, red oaks, and hickories with few other species occupying the overstory. Large dogwoods were also abundant across the study site. Increases in the average density and basal area of all trees occurred in the control, SB, and FB treatments, whereas reductions in tree densities occurred in the DB+FB, Rx Burn, and

SB+Rx treatments. Severe drought in 2021–2022 may have resulted in the mortality of red oaks across all treatments when compared to other species groups. Treatments including fall browsing and burning led to mean decreases in dogwood stems (Supplementary Table 1).

Treatment effects on the midstory

For midstory stems (>1 m tall; <3.8 cm DBH), year and the interaction of treatment by year was significant across all species and species groups, except for eastern redcedar where treatment was a significant factor in its density (Table 1), that is, the control had more eastern redcedar stems than either SB or SB+Rx (Supplementary Table 2). Treatment was also significant for the change in density for all stems and white oaks (Table 1, Fig. 2). Generally, the control accumulated the most stems across the study period, but was similar to the browsing treatments, whereas the treatments that included fire had a reduction in stems (Fig. 2).

Treatment effects on seedlings

For small seedlings, the interaction of treatment by year ($F=3.6$; $p=0.005$) and year ($F=153.5$; $p<0.001$) were significant. Treatment was not significant ($F=1.9$; $p=0.188$). Densities of small seedlings generally increased in 2020 from pretreatment in 2019 and decreased in 2022 (Fig. 3). The density of medium seedlings was only influenced by year ($F=48.9$; $p<0.001$), whereas treatment ($F=1.6$; $p=0.0254$) and the interaction of treatment by year ($F=1.8$; $p=0.107$) were not significant (Fig. 3). For large seedlings, the interaction of treatment by year ($F=2.8$; $p=0.02$) and year ($F=13.5$; $p<0.001$) were significant (Fig. 3). Treatment was not significant ($F=0.2$; $p=0.972$). Densities of large reproduction were greatest in 2019 (2685 ± 1637) and 2020 (2280 ± 1151) and declined in 2022 (1229 ± 837) (Fig. 3).

For the density of seedlings, the interactive effect of treatment by year and year alone were significant for total density and the density of stems by species group (Table 2). Generally, densities were highest post-treatment in 2020 and lowest in 2022 following two rounds of treatments (Supplementary Table 3). Eastern redcedar was significantly different by treatment (Table 2), where the control had the most eastern redcedar stems and the SB treatment having the least (Supplementary Table 3).

Treatment effects on ground cover

Litter and bare soil coverage were significant for the effects of treatment, year, and treatment by year (Supplementary Table 4). The coverage of litter was highest in 2019 across all treatments, but the greatest reductions in litter occurred in the SB+Rx and Rx treatments which also facilitated increases in bare soil exposure (Fig. 4).

The coverage of forbs, grasses, legumes, and sedges were all influenced by the effect of year with increases generally associated with the 2020 sample year (Supplementary Table 4, Fig. 4). Forbs were also influenced by the interaction of treatment by year. Forb coverage was highest in the SB+Rx and Rx treatments in both 2020 and 2022 (Fig. 4), likely in response the prescribed fire treatments occurring several months prior to each sample period. The browsing treatments and the control all had declines in forb coverage from 2019 to 2022. Treatment was a significant factor in the coverage of grasses, with the SB having the most grass coverage (Supplementary Table 4, Fig. 4). Treatment differences and treatment by year differences were not detected for raw coverage of legumes and sedges.

The coverage of trees, shrubs, and vines were all influenced by the effect of time (Supplementary Table 4), with reductions in tree and vine coverage in 2022, compared to 2019 and 2020, and increases in shrub coverage in 2020 and 2022 (Fig. 4). Tree coverage had a significant interaction of treatment by year, with increases in coverage in 2020 in the control and browsing treatments but decreases in the burning treatments (Supplementary Table 4, Fig. 4). Treatment was significant for shrub coverage (Supplementary Table 4). The control had the greatest shrub coverage and the DB+FB treatment had the lowest coverage (Fig. 4).

The interaction of treatment by year was also significant for vine coverage (Supplementary Table 4), likely driven by declines in vine coverage for the Rx treatment in 2020 when all other treatments experienced increases (Fig. 4).

Hypothesis 1: The burning effect

As expected, burning generally decreased woody stem densities. Regarding midstory saplings, burning decreased total density and the density of stems across all species (Table 1, Supplementary Table 2; Fig. 2). Statistically, small seedlings increased with burning, but this result was due to large increases in seedlings in the Rx treatment (Fig. 3). Burning did not have a statistical effect on medium seedlings, but this might be attributed to declines also occurring in the DB+FB treatment. Burning resulted in declines in large seedlings. Generally, regardless of species, burning decreased seedling density but this effect was species dependent (Fig. 5). Burning decreased the number of ash seedlings but increased the density of hickory seedlings.

Ground cover was also significantly influenced by burning. As anticipated, litter coverage was greatly reduced, and bare soil exposure increased with burning (Fig. 6). Forbs and legumes also increased in coverage with burning. Although grass and sedge

Table 1 Model effects (*F* statistic and *p*-value) for midstory density (upper table) and the change in midstory density (lower table) by species group and model parameters. Linear contrasts test the effects of burning, browsing, frequent browsing, browsing seasonality, and burning and browsing; *p*-value significant at an alpha of 0.05

Model effects	All species		Ashes		Eastern redcedar		Hickories		Red oaks		White oaks	
Midstory stem density	F	p-value	F	p-value	F	p-value	F	p-value	F	p-value	F	p-value
	1.5	0.279	0.2	0.961	3.4	0.047	2.8	0.076	1.1	0.436	0.8	0.575
	477.5	<0.001	46.1	<0.001	5.4	0.011	274.1	<0.001	140.8	<0.001	74.9	<0.001
	1235.6	<0.001	149.8	<0.001	1.4	0.245	347.5	<0.001	84.8	<0.001	107.3	<0.001
	Contrasts											
	6.4	0.029	0.1	0.728	0.0	0.942	13.2	0.005	3.2	0.103	3.1	0.106
	0.1	0.829	0.5	0.512	14.3	0.004	0.1	0.813	0.5	0.499	0.0	0.982
	0.1	0.778	0.0	0.991	0.1	0.710	0.0	0.994	0.6	0.455	0.1	0.781
	0.9	0.376	0.2	0.645	1.1	0.317	0.8	0.395	0.9	0.376	0.7	0.409
	0.0	0.935	0.1	0.735	1.4	0.269	0.2	0.693	0.2	0.702	0.0	0.924
Model effects	All Species		Ashes		Eastern redcedar		Hickories		Red oaks		White oaks	
Change in midstory abundance												
F	p-value	F	p-value	F	p-value	F	p-value	F	p-value	F	p-value	
4.5	0.021	1.9	0.167	2.2	0.134	3.4	0.047	2.3	0.119	4.1	0.028	
Contrasts												
Not burned vs. burned	20.8	0.001	6.1	0.033	6.8	0.026	16.1	0.003	9.3	0.012	17.4	0.002
Control vs. browsed	0.5	0.499	3.1	0.109	2.6	0.139	0.2	0.641	1.9	0.199	0.2	0.669
DB+ FB vs. SB and FB	0.1	0.808	0.0	0.885	0.1	0.826	0.3	0.609	0.0	0.897	0.3	0.622
SB vs. FB	0.8	0.396	0.0	0.941	0.1	0.798	0.3	0.583	0.4	0.529	0.6	0.459
Rx vs. SB+ Rx	0.5	0.492	0.7	0.436	1.5	0.243	0.1	0.810	0.0	0.965	2.0	0.193

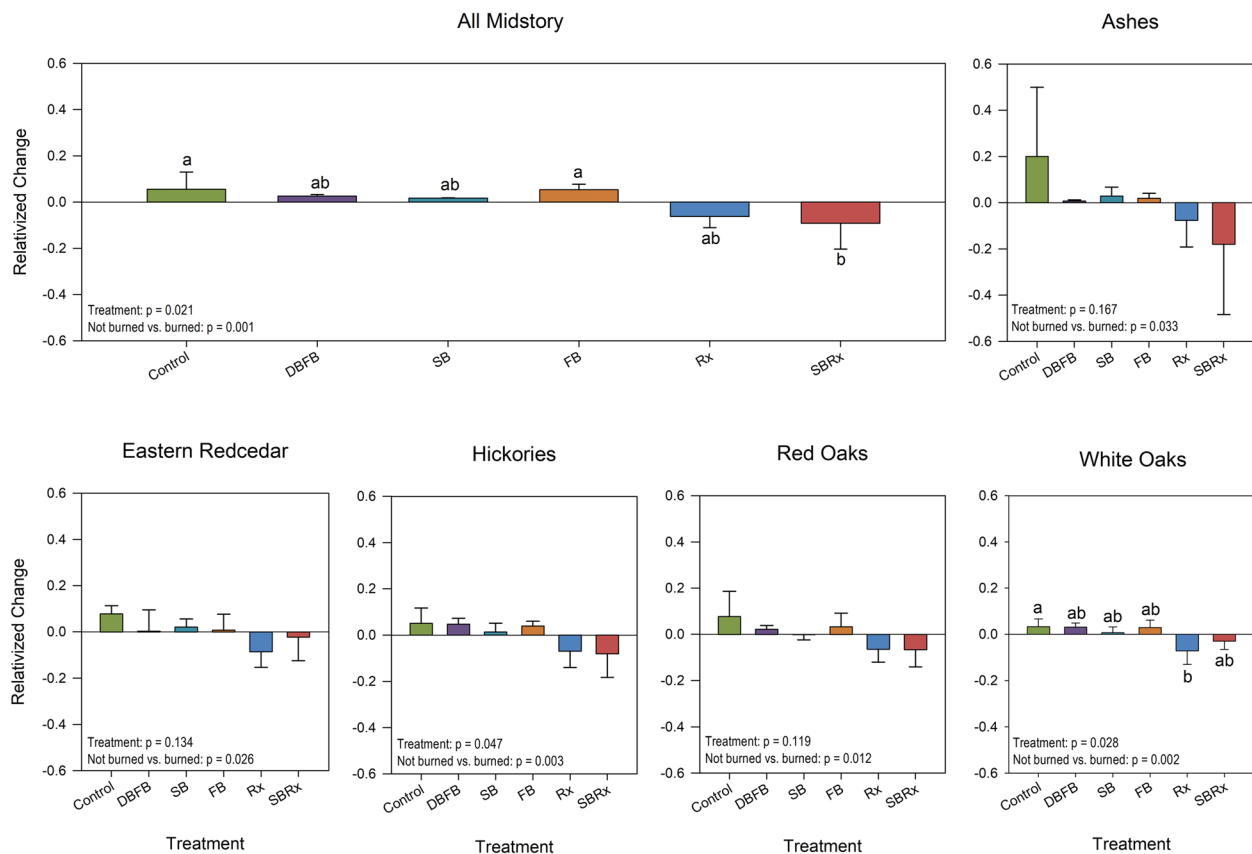


Fig. 2 Relativized change in midstory saplings (> 1 m tall, < 3.8 cm DBH) stem density from pre-treatment in 2019 to post-treatment in 2022. Control is represented by a green bar, dormant bud browse + fall browse (DBFB) is purple, spring browse (SB) is teal, fall browse (FB) is orange, prescribed burning (Rx) is blue, and spring browse + prescribed burning (SB + Rx) is red. Lower case letter indicate a significant difference between treatments. Significance determined at an alpha of 0.05

coverage showed positive associations with burning, their responses were not significant. Vine coverage was also reduced with burning, but this was driven by large reductions in the Rx treatment.

Hypothesis 2: The browsing effect

Compared to the control, few significant effects from browsing were detected. However, browsing was associated with declines in the density of midstory eastern redcedar, but this effect was not significant when assessed by the change in density (Table 1, Fig. 2). Although non-significant, browsing appeared to accumulate fewer midstory stems than the control, especially for ashes (Fig. 2). Although browsing had a negligible impact on seedlings, white oak seedlings generally declined with browsing, driven by the large effect of the SB and FB treatments. Shrub coverage also declined or accumulated less than the control with browsing (Fig. 6).

Hypothesis 3: The effect of frequent browsing

Frequent browsing (DB+FB) had negligible effects on midstory stems when compared to the other browsing treatments (Table 1; Fig. 2). For seedlings, although medium-sized seedlings declined in comparison to the SB and FB treatments, which increased, the effect was non-significant (Fig. 3). Furthermore, white oaks seedlings increased with DB+FB but declined with SB and FB (Fig. 5). The DB+FB treatment also had a greater negative effect on sedges than the SB and FB treatments (Fig. 6). Although non-significant, the ground coverage of sedges increased, and trees decreased with the DB+FB treatment.

Hypothesis 4: The effect of browsing seasonality

Differences in browsing season did not influence midstory saplings (Table 2). Although non-significant, SB did result in declines in small seedlings whereas FB had marginal increases (Fig. 3). Eastern redcedar had increased seedling abundance associated with SB whereas FB saw declines in seedling abundance (Table 2, Fig. 5). Although

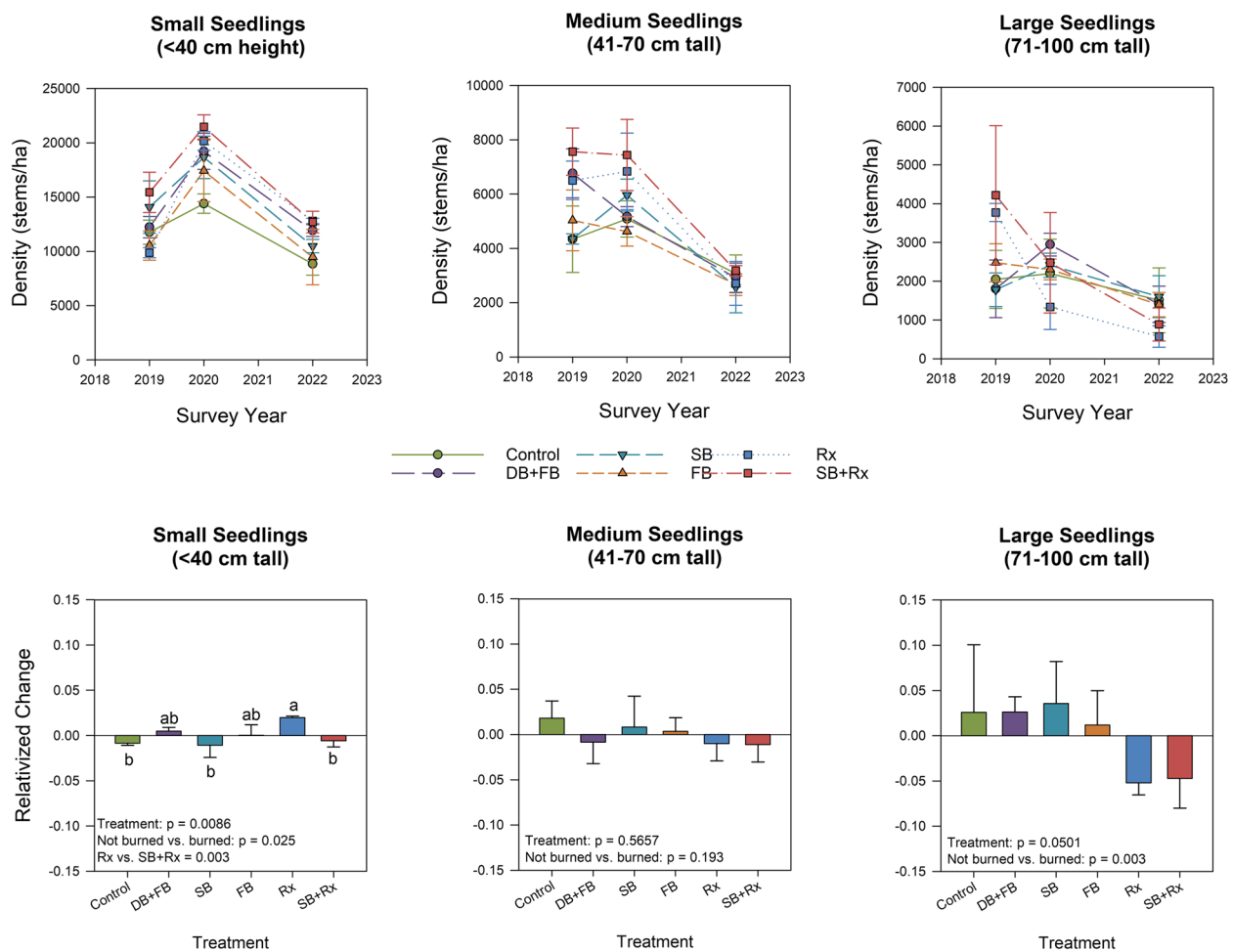


Fig. 3 Seedlings (< 1 m tall) by height class including the density by survey year and the relativized change in density from 2019 to 2022. Control is represented as green, dormant bud browse + fall browse (DBFB) is purple, spring browse (SB) is teal, fall browse (FB) is orange, prescribed burning (Rx) is blue, and spring browse + prescribed burning (SB + Rx) is red. Lower case letters indicate a significant difference between treatments. Significance determined at an alpha of 0.05

non-significant, ground coverage of grasses, legumes, shrubs, and vines increased in association with SB where they decreased with FB (Fig. 6).

Hypothesis 5: The effect of browsing and burning combined

Differences in the effect of Rx versus the combination of SB + Rx did not occur for midstory stems (Table 1), although greater reductions in total midstory stems did occur with SB + Rx (Fig. 2). Small seedlings increased with Rx, whereas they decreased with SB + Rx (Fig. 3). Although non-significant, red oak seedlings increased with Rx but decreased with SB + Rx (Fig. 5). The ground coverage of trees decreased with Rx, whereas their coverage increased with SB + Rx (Fig. 6). Furthermore,

although non-significant, vine coverage decreased with Rx but had marginal increases with SB + Rx.

Discussion

Fire and browsing shape the structure and composition of plant communities through the consumption of plant biomass. The utilization of prescribed fire and targeted browsing for woodland objectives is intended to reduce small woody stem densities and increase the abundance of ground flora. Although both can be considered a low-intensity disturbance, the influence they exert on the resulting structure and composition correspond to how biomass is consumed. For example, fire results in complete top-kill of woody plants by damaging the cambium (Bond and Midgley 2001), whereas browsing typically causes damage to only to the terminal and lateral buds affecting tree growth form and the resulting

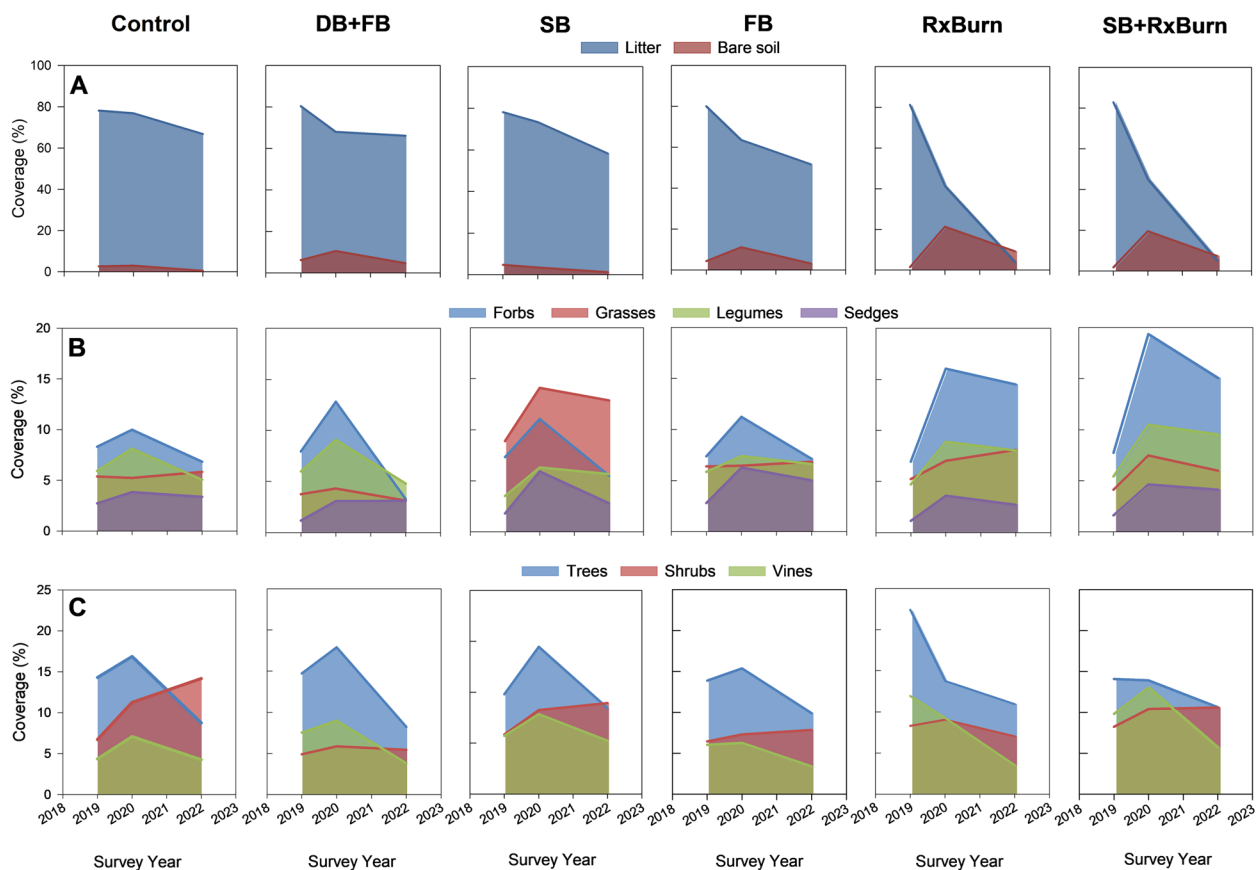


Fig. 4 Changes in ground cover from pre-treatment (2019) to post-treatment (2022) including the coverage of litter and bare soil (A: top panels), the coverage of forbs, grasses, legumes, and sedges (B: middle panels), and the coverage of trees, shrubs, and vines (C: bottom panels) by treatment

stem quality but rarely results in stem mortality after the seedling stage (Putman and Moore 1998; Côté et al. 2004; Midgley et al. 2010). Furthermore, although goats may consume leaf litter when higher quality forage is unavailable (Pfister and Malechek 1986), flammable leaf litter is the most important fuel component to the spread of surface fires in oak ecosystems (Varner et al. 2016), and fire's consumption of litter is not well mimicked by targeted browsing. Results from our study suggest that (1) prescribed burning has an overriding influence on the reduction of woody stems through top-kill resulting in increased forb coverage following the consumption of leaf litter and likely increases light availability, (2) the compounding disturbance of browsing with burning enhances reductions in woody stems but browsing preferences exert additional species filters that are not apparent with burning alone, (3) although not statistically meaningful, results and field observations suggest that targeted browsing regimes may suppress the accumulation of woody stems, and (4) spring browsing may have a greater impact on woody stems and may increase the coverage of grasses than when browsing occurs later in

the growing season. Importantly, browsing results also indicate that repeated, short duration browsing events, even 2 to 4 times within a 4-year period, may not result in achieving structural and compositional goals for oak woodlands.

The use of goat browsing is gaining attention from scientists and managers. Goats' capacity to serve as a vegetation management tool has been increasing as fuels reduction treatments and invasive plant control has continued to challenge management efforts at small and large scales (Lovreglio et al. 2014; Pile Knapp et al. 2023). Furthermore, silvopasture, an agroforestry technique combining livestock with wooded systems, is increasing in popularity (Smith et al. 2022; Poudel et al. 2024). With this increased interest and use, it is critical to understand how to utilize goats most effectively as a vegetation management tool and their impact on woodland ecosystems. Our results suggest that goat browsing can serve as a vegetation management tool, but browsing is not a direct surrogate for low-intensity, surface fire.

Herbivory and fire are both plant consuming disturbances that exert selective pressures on plant community

Table 2 Model effects (*F* statistic and *p*-value) for seedling density (upper table) and the change in midstory density (lower table) by species group and model parameters. Linear contrasts test the effects of burning, browsing, frequent browsing, browsing seasonality, and burning and browsing; *p*-value significant at an alpha of 0.05

Model effects	All species		Ashes		Eastern redcedar		Hickories		Red oaks		White oaks	
Regeneration density												
Treatment	F	p-value	F	p-value	F	p-value	F	p-value	F	p-value	F	p-value
Year	2.5	0.100	1.7	0.217	3.8	0.035	2.7	0.0856	0.7	0.648	1.6	0.251
Treatment x year	3459.8	<0.001	132.6	<0.001	7196.8	<0.001	2828.9	<0.001	771.3	<0.001	2384.9	<0.001
Contrasts	116.5	<0.001	196.8	<0.001	351.4	<0.001	254.1	<0.001	221.3	<0.001	229.1	<0.001
Not burned vs. burned	8.4	0.016	1.9	0.202	1.5	0.245	9.4	0.012	0.8	0.390	3.9	0.074
Control vs. browsed	0	0.883	2.8	0.125	0.6	0.468	0.01	0.915	2.2	0.169	1.1	0.319
DB+ FB vs. SB and FB	3.5	0.092	2.3	0.165	0.7	0.429	0.3	0.596	0.1	0.792	0.0	0.877
SB vs. FB	0.1	0.780	2.1	0.178	12.1	0.006	1.5	0.244	0.1	0.779	0.5	0.511
Rx vs. SB+ Rx	0.7	0.429	0.8	0.387	4.0	0.074	2.3	0.165	0.3	0.631	2.3	0.158
Model effects	All Species		Ashes		Eastern redcedar		Hickories		Red oaks		White oaks	
Change in regeneration abundance												
Treatment	F	p-value	F	p-value	F	p-value	F	p-value	F	p-value	F	p-value
Contrasts	2.2	0.138	2.0	0.167	0.6	0.718	2.7	0.085	0.8	0.588	3.7	0.075
Not burned vs. burned	5.4	0.042	6.1	0.033	0.2	0.708	11.2	0.007	0.1	0.749	4.0	0.075
Control vs. browsed	0.9	0.365	3.1	0.110	0.2	0.637	0.8	0.381	0.1	0.795	5.0	0.049
DB+ FB vs. SB and FB	0.0	0.986	0.0	0.885	0.7	0.431	0.1	0.763	1.3	0.278	8.1	0.017
SB vs. FB	1.1	0.324	0.0	0.941	1.8	0.208	1.3	0.283	0.1	0.820	0.1	0.819
Rx vs. SB+ Rx	3.5	0.091	0.7	0.436	0.0	0.9110	0.0	0.793	2.3	0.165	1.1	0.316

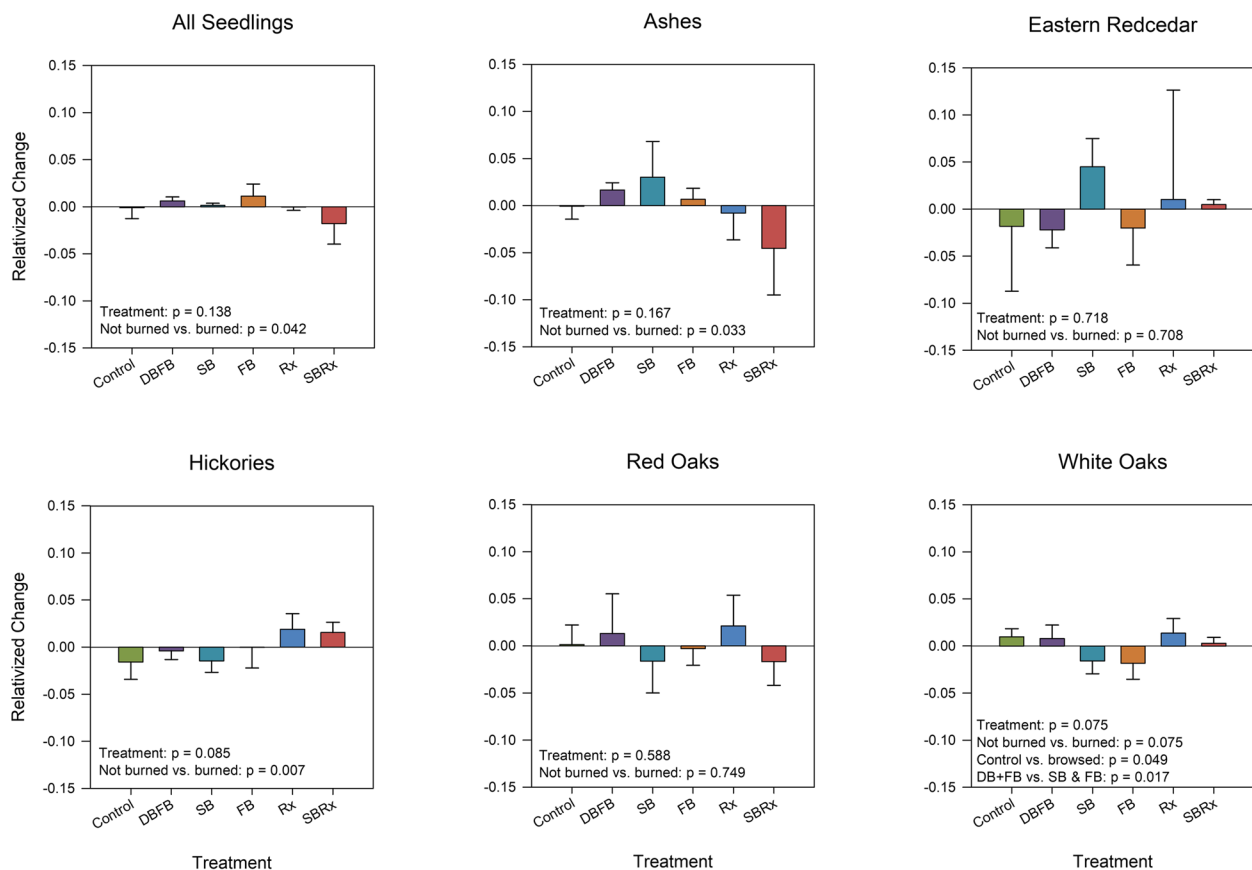


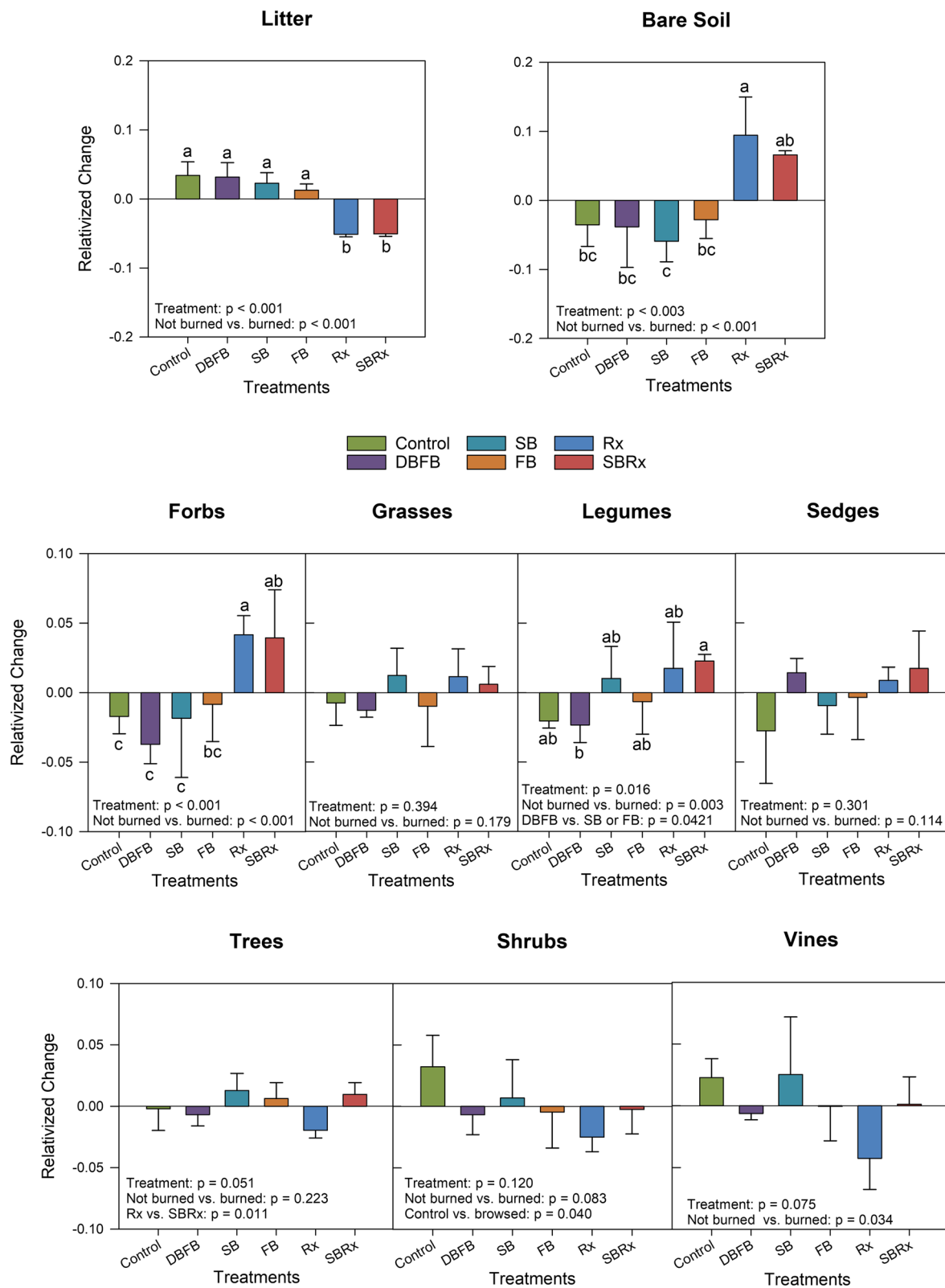
Fig. 5 Relativized change in seedling (< 1 m tall) stem density from pre-treatment in 2019 to post-treatment in 2022. Control is represented by a green bar, dormant bud browse + fall browse (DBFB) is purple, spring browse (SB) is teal, fall browse (FB) is orange, prescribed burning (Rx) is blue, and spring browse + prescribed burning (SB + Rx) is red. Lower case letters indicate a significant difference between treatments. Significance determined at an alpha of 0.05

structure and composition. The advantage of goats, when compared to other domesticated livestock, for woodland restoration is their preference for woody stems over herbaceous ones (Pfister and Malechek 1986; Dumont et al. 1995; Papachristou 1997), making them a good candidate for emulating the effects of low-intensity, surface fire. Goats prefer to browse plants that are easily reachable (Novais et al. 2023). As a consequence of browsing pressure, fewer stems may have recruited to the midstory between measurement periods (Beebe et al. 2022). This suggests that frequent browsing regimes may suspend or reduce the recruitment and densification of large

midstory stems and shrubs. However, large seedlings increased with browsing, which is likely attributed to the browsing down of larger apical and lateral stems from the midstory rather than through increases in new seedlings. Browsing preferences are typically dependent on species identity and biomass composition, which can vary seasonally (Bartolomé et al. 2020; Chebli et al. 2020; Novais et al. 2023). Although midstory ash and eastern redcedar stems had negligible increases, hickories and white oaks accumulated similarly to the control. Hickories were one of the least preferred species on our sites, and they were often one of the last species targeted by goats. Localized

(See figure on next page.)

Fig. 6 Relativized change in understory ground cover (< 1 m tall) including litter and bare soil, forbs, grasses, legumes and sedges, and the change in coverage for trees, shrubs, and vines from pre-treatment in 2019 to post-treatment in 2022. Control is represented by a green bar, dormant bud browse + fall browse (DBFB) is purple, spring browse (SB) is teal, fall browse (FB) is orange, prescribed burning (Rx) is blue, and spring browse + prescribed burning (SB + Rx) is red. Lower case letters indicate a significant difference between treatments. Significance determined at an alpha of 0.05

**Fig. 6** (See legend on previous page.)

dominance of hickory in the Central Hardwoods Region, USA, is suspected to be partially attributed to where unrestricted, high-impact, browsing occurred historically (Pile Knapp et al. 2021). It is important to note that the browsing approach we prescribed had little effect on the coverage of litter or bare ground, suggesting minimal soil disturbance which is often a concern with domesticated livestock.

Goats can have large seasonal variation in their diets, potentially affecting species-level outcomes associated with our seasonal browsing treatments (Pfister and Malechek 1986; Manousidis et al. 2016). Spring browsing appeared to have a greater effect on midstory hickories, red oaks, and white oaks where stems accumulated less than in the DB+FB or FB treatments. Increased browse pressure on oaks and hickories in the spring is likely attributed to increased tannin accumulation as the growing season progresses resulting in increased browse avoidance and the abundance of palatable expanding oak and hickory foliage when ground flora was minimal. Spring browsing, even with burning, resulted in declines in the smallest seedlings, especially of hickories and oaks. Spring browsing also saw increases in the coverage of trees, shrubs, and vines which was likely the result of browsing reducing stem heights and increasing compensatory lateral growth of woody species. In contrast, shrubs and vines decreased in both the DB+FB and FB treatments, and trees increased in the FB treatment.

The selection of plants by goats is highly dependent on foliage availability and phenological state of the plant which can depend on the season and weather (Manousidis et al. 2016). Additionally, forbs with showy flowers and large fruits can have increased browse pressure, and due to the apical growth of forb species, growing season browsing can be highly detrimental to some forbs (Shipley 1999; Hülber et al. 2005). The FB treatment was included in the experiment with the intention of browsing after the seed set and dispersal of spring ephemerals and other ground flora but while green forage was still available for the goats. While forbs declined in all browsing treatments and the control, the FB treatment declined less so than the other browse treatments. This also follows findings of other studies that report higher rates of browsing on herbaceous vegetation in the summer than in the fall likely due to increased structural carbohydrates and decreased nutritive value (Manousidis et al. 2016). Spring browsing was associated with increases in the coverage of grasses and legumes, whereas they declined in the DB+FB and FB treatments. The spring browsing experimental units had initially higher grass coverage prior to the start of the study likely allowing them to quickly respond to reductions in woody stem densities with browsing. Sedge coverage increased in the DB+FB

treatment when they declined with SB and FB. Leaf litter browsing is known to occur when minimal green forage is available (Pfister and Malechek 1986), but we did not see reductions in leaf litter in either the DB+FB or FB treatments when living forage availability was at its lowest.

The effects of burning, especially when combined with overstory thinning, are well-described in the literature, with decreases in tree density associated with increases in the coverage of ground flora (Hutchinson et al. 2005b; Maynard and Brewer 2013; Knapp et al. 2015, 2017; Vander Yacht et al. 2020). In our study, the effect of burning alone was as expected. Burning decreased overstory and midstory stems and reduced large seedlings when compared to browsing treatments. The reduction in midstory stems was indiscriminate across species with declines in ashes, eastern redcedar, hickories, and oaks. However, the effect of fire on seedlings densities was consistent with the fire tolerance of the species groups, where the density of ash decreased while hickory and white oak increased (Brose and Van Lear 1999; Brose et al. 1999, 2013, 2014). The accumulation of leaf litter can strongly influence the composition and diversity of ground flora (Facelli and Pickett 1991), with increasing litter decreasing plant abundance and diversity (Brewer 1999, 2023; Hiers et al. 2007; Loydi et al. 2013). However, responses to litter reductions may be species dependent. Some species require increased light availability along with reductions in leaf litter (Maynard and Brewer 2013) where others, especially those with persistent seedbanks, may not (Hutchinson et al. 2005a; Brewer 2016). In our study, burning decreased leaf litter cover and likely increased solar exposure to the soil surface due to the reduction in midstory stems, thus facilitating an increase in forb and legume coverage from fire.

Research on the response of plant communities to fire and browsing are often examined independently, but when approached interactively, the two processes are often different than the sum of their individual effects (Fuhlendorf and Engle 2004). The compounding disturbance of browsing and burning resulted in the greatest reductions in overstory and midstory stems when compared to all treatment types, including burning alone. In addition to direct mortality by fire to trees, small amounts of bark removal by eating or rubbing from browsing can increase stem susceptibility to fire damage (Midgley et al. 2010). Small seedlings and the seedlings of ashes and red oaks were the most impacted by the combination of browsing and burning. Slightly less bare soil exposure was recorded for browsing and burning than burning alone, as were fewer forbs. However, legumes increased more with the combined treatment. The coverage of tree seedlings responded positively to the

combined treatment, whereas in the burning only treatment, tree and vine coverage declined.

Management recommendations

Targeted browsing in conjunction with prescribed burning can help to achieve woodland objectives for open midstories and spring browsing may increase the coverage of grasses and legumes. However, the effect of prescribed burning on reducing woody stems and increasing ground flora abundance was unrivaled. Where the use of prescribed burning is restricted and ground flora is a desired objective, other silvicultural actions may be necessary to reduce leaf litter along with browsing, such as further reducing overstory canopy cover or mechanical scarification and mowing. Short-term browsing regimes may be helpful for suppressing woody midstories and for reducing the continuity of live surface fuels by increasing space between individual stems, which may be an important consideration for fuel reduction treatments when burning is not an option. Furthermore, forage availability and quality may be greatly reduced without fire, especially in the dormant and late growing seasons. If the desire is to maintain herbivory regimes, efforts to increase forage, such as enrichment seeding or planting, may be necessary. Additionally, it may be beneficial to select against species that are unfavorable to goats during the initial overstory thinning, such as hickories, to reduce future regeneration potential.

The results of the study treatments were influenced by thinning and mastication done before study establishment, which created more open stand conditions and higher light levels in the understory. Results may vary if these treatments were applied to previously untreated fully stocked, closed canopy forests or those with different management histories. If reduction of woody density in the mid- and understory is an initial restoration objective, applying prescribed fire and browsing treatments to forests before overstory thinning may be beneficial because the increased shade of the overstory can limit the recovery of woody sprouts, increasing their mortality with repeated browsing and prescribed fire (Dey and Hartman 2005; Fan and Dey 2014; Pile Knapp et al. 2024). In any case, repeated disturbances in a year can be achieved using combinations of treatments such as prescribed fire and browsing to improve conditions in woodland understories that promote herbaceous flora development in the early stages of restoration.

Conclusions

Forest fragmentation, cultural acceptance of fire and smoke, and logistical constraints associated with prescribed burning will continue to hamper management efforts to restore and sustain fire-dependent open ecosystems. Furthermore,

neglecting the role of large herbivores in structuring plant communities may exacerbate woodland management objectives that are based on historical conditions and intend to modify current vegetation conditions that are far removed from the natural range of variation in natural communities after decades of fire suppression. Domesticated livestock herbivory in the woods is often viewed negatively as destroyers of natural communities; however, with thoughtful consideration and management, browsers such as goats may help reach conservation goals for woodland management (Papachristou et al. 2005). Although this project investigated aspects of woodland browsing and burning, there is still much to learn regarding seasonality, frequency, and long-term effects on community structure and dynamics as ecosystems respond to both treatments individually and combined.

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s42408-024-00336-1>.

Supplementary Material: Table 1. Mean ($\pm$ standard error) density (trees per hectare) and basal area (m^2/ha) and the change in density and basal area of overstory trees (> 3.8 cm DBH) by species group and treatment in 2019 (pre-treatment) and 2022 (post-treatment). No significant differences for density or basal area among treatments were detected for any species group. Values highlighted in bold indicate a mean reduction in density or basal area between measurement periods. Significance determined at an alpha of 0.05. Supplementary Table 2. Mean ($\pm$ standard error) density (trees per hectare) of midstory trees (< 3.8 cm DBH) by species group and treatment in 2019 (pre-treatment), 2020, and 2022. Upper case letters represent a significant difference between treatments. Lower case letters represent a significant difference between years. Significance determined at an alpha of 0.05. Supplementary Table 3. Mean ($\pm$ standard error) density (trees per hectare) of understory reproduction (< 1 m tall) by species group and treatment in 2019 (pre-treatment), 2020, and 2022. Upper case letters represent a significant difference between treatments. Lower case letters represent a significant difference between years. Significance determined at an alpha of 0.05. Supplemental Table 4. Model effects for ground cover by type including treatment, year, the interaction of treatment by year, and the linear contrast comparing browsing to burning. *P*-value significant at an alpha of 0.05.

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Authors' contributions

GB contributed to data collection and was a major contributor to the writing of the manuscript. LPK made substantial contributions to the conception, design, analysis, data collection and interpretation, manuscript writing, and acquisition of resources. MS made substantial contributions to the conception, design, and manuscript writing. DD made substantial contributions to the conception, design, manuscript writing, and acquisition of resources. BD made substantial contributions to the conception, design, data collection, and acquisition of resources. DM made substantial contributions to data collection. JK made significant contributions to the design, data collection, and manuscript writing. All authors have read and approved the manuscript.

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Data availability

The datasets used and/or analyzed during the current study are available from the corresponding author 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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