Forest Ecology and Management 516 (2022) 120244

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Effects of burn season on fire-excluded plant communities in the southern Appalachian Mountains, USA

Matthew C. Vaughan [a], Donald L. Hagan [b,*], William C. Bridges Jr [c], Kyle Barrett [d], Steve Norman [e], T. Adam Coates [f], Rob Klein [g]

[a] Department of Forestry and Environmental Conservation, Clemson University, 261 Lehotsky Hall, 128 McGinty Court, Clemson, SC 29634, USA
[b] Department of Forestry and Environmental Conservation, Clemson University, 202 Lehotsky Hall, 128 McGinty Court, Clemson, SC 29634, USA
[c] School of Mathematical and Statistical Sciences, Clemson University, O-117 Martin Hall, 220 Parkway Drive, Clemson, SC 29634, USA
[d] Department of Forestry and Environmental Conservation, Clemson University, 244 Lehotsky Hall, 128 McGinty Court, Clemson, SC 29634, USA
[e] Southern Research Station, United States Department of Agriculture Forest Service, 200 W. T. Weaver Boulevard, Asheville, NC 28804, USA
[f] Department of Forest Resources and Environmental Conservation, Virginia Tech, 228F Cheatham Hall, 310 West Campus Drive, Blacksburg, VA 24061, USA
[g] Interior Region 2, United States Department of the Interior National Park Service, USA

ARTICLE INFO

Keywords:
Burn season
Vegetation
Abundance
Diversity
Red maple
Mountain laurel

ABSTRACT

Following decades of fire exclusion, managers are increasingly implementing prescribed fire in southern Appalachian forests. To date, the use of prescribed fire in the region has often been focused on reducing hazardous fuel loads and has typically occurred in the dormant season. Understanding the effects of burning in different periods of plant growth may reveal how burn season influences patterns of vegetative succession. In this study, we compared the effects of prescribed burn treatments conducted in the dormant season (January-early April) vs. the early growing season (mid-late April) on changes in plant abundance by understory, midstory, and overstory forest strata. Plant groups were distinguished by growth habit, stem origin, functional characteristics, and species of management interest (red maple (*Acer rubrum* L.) and mountain laurel (*Kalmia latifolia* L.)). Burn season had minimal effect on understory cover, density, richness, or diversity. In the midstory, early growing season burns were more effective in reducing shrub density than dormant season burns ($-1{,}585 \pm 188$ ha^{-1} vs. -813 ± 240 ha^{-1}, respectively), with greater differences among smaller stems. Early growing season burns also reduced midstory red maple density to a greater degree than dormant season burns (-356 ± 57 ha^{-1} vs. -219 ± 69 ha^{-1}), a response that was not observed among other mesophytic hardwood species. Burning slightly reduced canopy cover, but neither canopy cover nor overstory density response varied by burn season. Our results demonstrate that managers may find increased opportunities to promote forest restoration objectives in the southern Appalachians by extending the use of prescribed fire into the early growing season.

1. Introduction

Plant communities throughout much of the southern Appalachian Mountains are shifting in composition away from species adapted to frequent disturbance. Wildland fire suppression policies initiated in the twentieth century excluded fire from landscapes where it had occurred frequently for centuries (Dombeck et al., 2004; Lafon et al., 2017). In fire's absence, forest stand dynamics are being impacted by heightened plant competition from fire-sensitive, shade-tolerant species (Nowacki and Abrams, 2008). Historical oak (*Quercus* spp.) and yellow pine (*Pinus* spp. subgenus *Diploxylon*) communities are being encroached on by ericaceous shrubs such as mountain laurel (*Kalmia latifolia* L.) and mesophytic hardwood trees like red maple (*Acer rubrum* L.) (Lorimer, 1993; Abrams, 1998; Williams, 1998; Elliott et al., 1999). Increased stem density blocking light to the understory makes it more challenging for forbs and graminoids to persist and for dominant overstory species to successfully regenerate (Harrod et al., 2000). In response to such trends, prescribed fire treatments have increasingly been incorporated into active forest management in the southern Appalachians (Vose et al., 1997; Warwick, 2021).

Decisions surrounding how and when to implement prescribed fire are largely driven by meteorological conditions facilitating fire behavior that can be sustained to consume fuels and kill vegetation within management prescriptions (Waldrop and Goodrick, 2012; Chiodi et al.,

* Corresponding author.
E-mail address: dhagan@clemson.edu (D.L. Hagan).

https://doi.org/10.1016/j.foreco.2022.120244
Received 21 January 2022; Received in revised form 31 March 2022; Accepted 19 April 2022
Available online 30 April 2022

2018). Most of the annual prescribed burning in the southern Appalachians today takes place towards the end of winter in the Northern Hemisphere in the dormant season (Van Lear and Waldrop, 1989; Reilly et al., 2012). Extended daylight and a higher sun angle following the winter solstice allow for more rapid fuel drying after precipitation events (Byram and Jemison, 1943). As spring progresses, however, deciduous leaf expansion in the overstory keeps surface fuels wetter over longer periods by insulating the forest understory from wind and solar radiation (Knapp et al., 2009). Fire occurrence is significantly lower through the summer, with fires from lightning ignitions often soon extinguished by moist fuels under closed canopies (Cohen et al., 2007; Norman et al., 2017, 2019). Temperature and precipitation patterns in the late dormant season have been considered ideal for supporting low-moderate fire severity to reduce surface fuel loads while minimizing effects on the overstory (Mobley and Balmer, 1981; Wade and Lunsford, 1989). Less precedent exists, however, for burning in the spring green-up period in the growing season, particularly for altering forest composition.

Fire energy release can cause first- and second-order plant injuries that result in mortality but may also stimulate plant responses that promote survival. Underlying physiological and morphological traits drive fire adaptations within the resource environment of plants in different growth periods (Michaletz and Johnson, 2007; Clarke et al., 2013; Bär et al., 2019). Burn timing may influence plant regeneration due to seasonal variations in the allocation of existing nutrient reserves relative to the photosynthetic capacity to replenish lost nutrients. Surviving plants that are able to regenerate structures more quickly may be able to outcompete others, especially when in a post-fire environment favorable for new growth (Platt et al., 1988; Hiers et al., 2000). Alternatively, plants may need to replace a greater amount of biomass following fire in the same season, draining resources that unburned plants would not have to expend before entering dormancy (Regier et al., 2010). Processes of seed dispersal and seedling development suggest how burn season may impact plant reproduction in relation to patterns of fire severity. Dormant seeds in the seed bank and those that will soon be dispersed from mature plants post-fire may be more likely to germinate following sufficient litter and duff consumption due to increased air temperatures and light availability (Silvertown, 1980; Baskin and Baskin, 1988; Jenkins et al., 2011). Seeds recently dropped on the forest floor may be consumed by fire, however, curtailing the likelihood of successful plant reproduction (Dayamba et al., 2010). Consideration of the seasonality of fire effects on vegetation through processes driving mortality, regeneration, and reproduction within the resource environment allows for understanding how fire timing may influence plant community response.

Previous studies evaluating fire effects on vegetation in the southern Appalachians and adjacent Piedmont have primarily measured woody species responses and shown limited evidence of differential response by burn season. Prescribed fire implemented in parts of the dormant (March) vs. growing (April, October) seasons largely did not affect changes in woody stem density in oak-dominated hardwood/mixed pine-hardwood stands (Vander Yacht et al., 2017; Keyser et al., 2019). Increased fire severity with lower soil moisture later in the growing season (August, October) has been shown to benefit yellow pine reproduction in xeric pine forests (Jenkins et al., 2011). At the species level, shortleaf pine (*Pinus echinata* Mill.) has been shown to have fewer sprouts and shorter sprout height following burning later (June-July) vs. earlier (April) in the growing season (Trickett, 2018; Clabo and Clatterbuck, 2019). Red maple was demonstrated to have shorter sprout height following burning in the early growing season (April) compared to the late dormant season (March) and mid growing season (July) (Trickett, 2018). In comparison with another mesophytic hardwood tree species, Ruswick et al., 2021 found that burn season did not result in different starch concentrations affecting sweetgum (*Liquidambar styraciflua* L.) sapling resprouting.

In the Coastal Plain, a decades-long study in a loblolly pine (*Pinus taeda* L.) plantation in South Carolina found that repeated winter burns were more effective for increasing herbaceous ground cover, whereas repeated summer burns were more effective for decreasing hardwood stem density (Waldrop et al., 1987; White et al., 1991). Robertson and Hmielowski, 2014 similarly found that the resprout growth rate of woody plants was lower following early growing season burns (April-June) than late dormant season burns (February-March) in an upland longleaf pine (*Pinus palustris* Mill.) savanna in southern Georgia. Burn season effects among different studies should be interpreted in light of variable environmental conditions influencing fire behavior (Robbins and Myers, 1992; Knapp et al., 2009; O'Brien et al., 2018; Ruswick et al., 2021). Seasonal dynamics of fire regimes require further investigation that take into account fire weather and fuel characteristics on a given burn day to isolate mechanisms driving fire effects.

For this study, we compared changes in previously fire-excluded oak- and pine-dominated forests in the southern Appalachians following prescribed fire to better understand the seasonality of fire effects on plant communities. Vegetation data were collected across landscape-scale units to evaluate the effect of burn season on forest structure and composition as quantified by the following responses:

- Absolute abundance (cover and density) and height of plants in the understory, midstory, and overstory; including by growth habit, stem origin, diameter, tree group, and/or species
- Species richness and alpha, beta, and gamma diversity of plants in the understory and midstory, including by growth habit and diameter
- Canopy cover

Single-entry prescribed burns conducted in the dormant season and early growing season were used as treatments. We tested the following burn season hypotheses:

1. Often prevalent in earlier stages of succession, forb and graminoid cover and density will increase to a greater degree following early growing season burns than with dormant season burns due to a more favorable photoperiod and temperatures for regrowth and flowering as well as less woody competition.
2. Woody stem cover, density, and height will decrease to a greater degree following early growing season burns than with dormant season burns, with this effect the most pronounced for red maple and other fire-sensitive mesophytic hardwood species, due to drier fuels and higher fire temperatures observed in early growing season burns.
3. Species richness and alpha, beta, and gamma diversity will increase to a greater degree following early growing season burns than with dormant season burns, driven by forb and graminoid recruitment, decreased dominance of mesophytic hardwood species, and increased overall community heterogeneity.
4. In largely closed-canopy forests, change in canopy cover will not differ by burn season due to insufficient fire severity in either season to impact the overstory. Therefore, any differences in understory composition between burn seasons would be explained by factors other than light availability.

Burn day variability in meteorological conditions, fuel moisture, fire behavior, and fuel consumption is summarized in Vaughan et al., 2021 (also see *2.2. Study design* below).

2. Methods

2.1. Study area

This study was located in the southern Appalachian region of the southeastern United States, specifically in the Southern Crystalline Ridges and Mountains ecoregion of the Blue Ridge physiographic province of the Appalachian Mountains (Griffith et al., 2001, 2002).

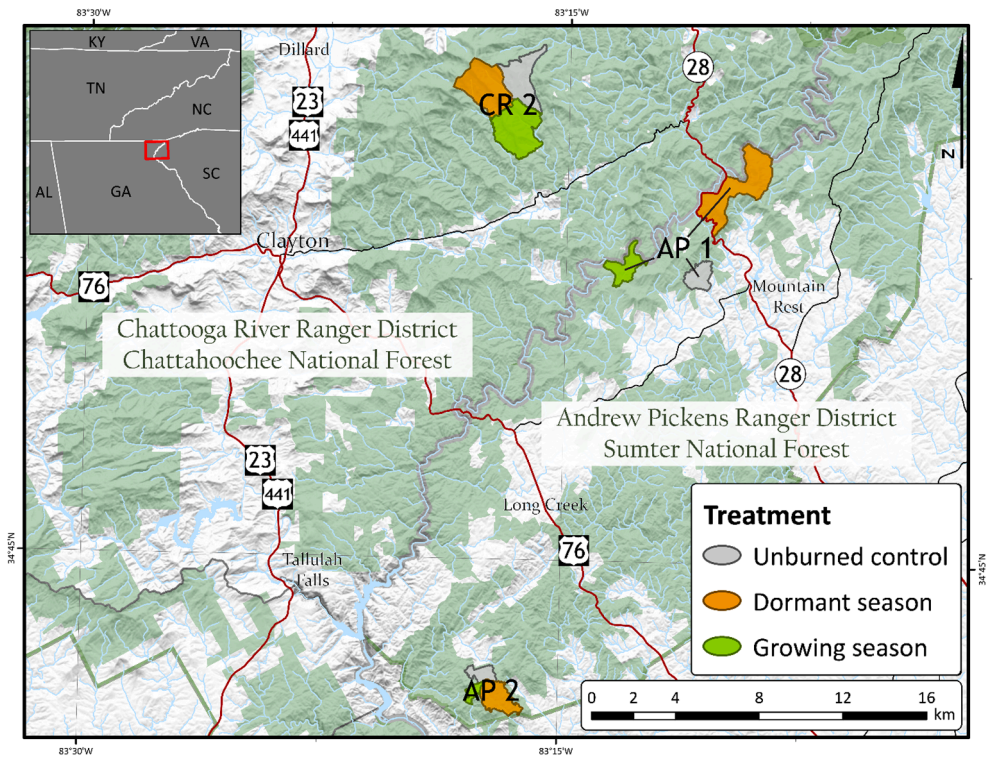

Fig. 1. Map depicting the replicated treatment units utilized for this study. "AP" refers to replicates in the Andrew Pickens Ranger District; "CR" refers to replicates in the Chattooga River Ranger District. See Table 1 for further information on treatment units.

Table 1
Summary of characteristics of treatment units by block and treatment including area, elevation range, and date of burn (if applicable). Additional environmental variables are summarized by burn season in Vaughan et al. (2021).

Block	Unit	Treatment	Area (ha)	Elevation range (m)	Date of burn
AP 1	Mongold Gap	C	134	498–625	
	Russell Mountain	DS	538	480–772	01/31/18
	Moss Mill	GS	160	454–560	04/18/18
AP 2	Little Brasstown	C	81	360–470	
	Joels Ridge	DS	205	275–468	03/18/19
	Drummond Creek	GS	43	312–462	04/21/18
CR 2	Rock Ridge	C	323	704–1,157	
	Big Ridge	DS	436	734–1,427	04/05/18
	Ducks Nest Gap	GS	446	622–966	04/24/19

Treatment units were located in the Andrew Pickens (AP) Ranger District, Sumter National Forest in Oconee County, South Carolina and the Chattooga River (CR) Ranger District, Chattahoochee National Forest in Rabun County, Georgia (Fig. 1).

Treatment unit elevations ranged from 275 m to 1,427 m (Table 1), encompassing a variety of landforms from lower slopes in sheltered coves to exposed ridges and upper slopes of high peaks. Mean monthly temperatures ranged from 4 °C in January to 24 °C in July, with mean annual precipitation of 1,664 mm distributed mostly evenly throughout the year (NCEI, 2020). Ultisols, Inceptisols, and Entisols were common soil orders found across the study area, mostly underlain by metamorphic bedrock (e.g., granitic gneiss and schist) (Griffith et al., 2001, 2002).

Forest overstory cover in treatment units consisted primarily of oaks (*Quercus* L. spp.), hickories (*Carya* Nutt. spp.), and pines (*Pinus* L. spp.) within Dry-Mesic Oak-Hickory Forest, Shortleaf Pine-Oak Forest and Woodland, Mixed Oak/Rhododendron Forest, and Montane Oak-Hickory Forest ecozones common in the region (Simon et al., 2005; Simon 2015). Substantial midstory encroachment was present from mesophytic hardwood trees (e.g., red maple (*Acer rubrum* L.)), mountain laurel (*Kalmia latifolia* L.), and great rhododendron (*Rhododendron maximum* L.). Understory ground cover was generally sparse, with red maple seedlings and greenbrier vines (*Smilax* L. spp.) frequently found under dense midstory shrub layers. Pre-treatment fuel characteristics were similar among treatments with thick layers of litter (mean 6.0 cm) and duff (mean 8.8 cm) typical of fire-excluded forests in the region (Vaughan et al., 2021).

2.2. Study design

The study was designed as a randomized complete block design, with unburned control (C), single dormant season burn (DS), and single growing season burn (GS) treatments replicated three times for a total of 9 treatment units. Treatment units ranged in area from 43 ha to 538 ha, with a mean area of 263 ha (Table 1). Growing season burns had greater solar radiation, air temperature, and fuel temperature along with lower fine fuel moisture than dormant season burns (Vaughan et al., 2021). Wind speed, relative humidity (RH), and the Keetch-Byram Drought Index (KBDI) did not significantly differ by burn season, but time-integrated fire temperatures recorded by thermocouple probes were higher in growing season burns than dormant season burns (Vaughan et al., 2021).

Twenty plots stratified across a variety of slope, aspect, and landscape positions were established within each treatment unit, with 177 total plots used as sample units in analyses. Each plot was 30 m × 30 m (900 m^2) and subdivided into nine 10 m × 10 m (100 m^2) subplots delineated by 16 grid point intersections, with outer boundaries running magnetic north (0°) and east (90°) from the point of origin (Fig. 2).

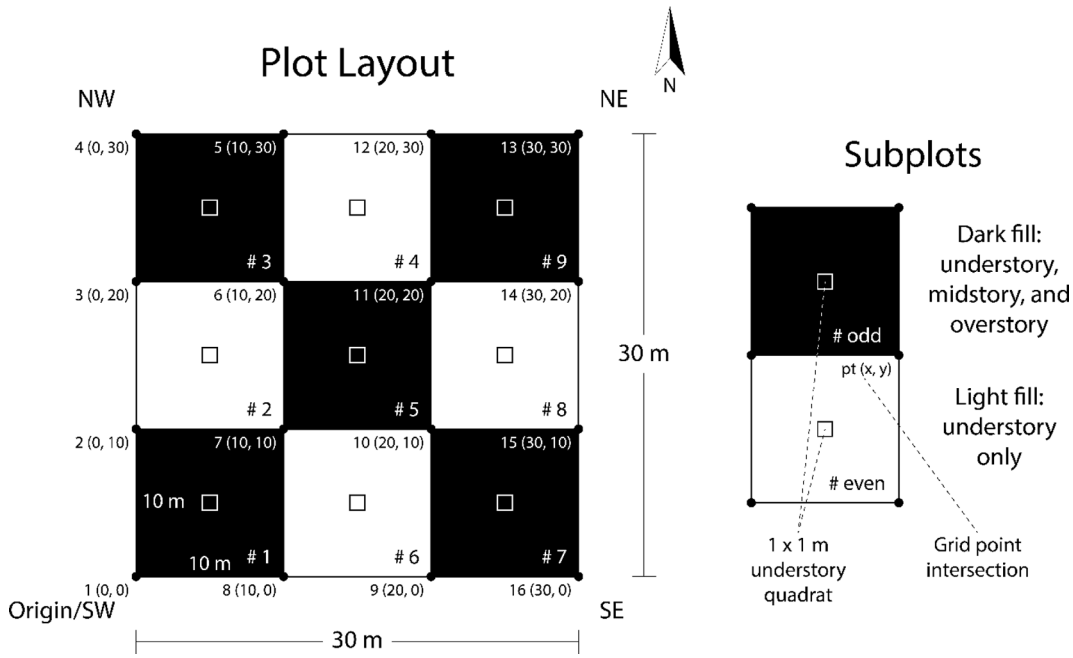

Fig. 2. Diagram showing plot layout, orientation, and dimensions with interior grid point intersections, subplots, and understory quadrats. Cartesian coordinate pairs for each grid point represent the longitudinal (x) and latitudinal (y) distance (m) from the plot origin.

Table 2
Summary of vegetation types represented in forest strata and stem origin classes by growth habit, tree group, and species. The presence of 'x' in a given row-column intersection denotes applicable classification in both categories.

Vegetation type	Understory stem origin			Midstory (by DBH)	Overstory
	Germinant	Established	Sprout		
Growth habit					
Forb					
Graminoid					
Vine	x	x	x		
Shrub	x	x	x	x	x
Tree	x	x	x	x	x
Tree group					
Hickory	x	x	x	x	x
Mesophytic hardwood	x	x	x	x	x
Red oak	x	x	x	x	x
White oak	x	x	x	x	x
White pine	x	x		x	x
Yellow pine	x	x	x	x	x
Other	x	x	x	x	x
Species					
Acer rubrum L.	x	x	x	x	x
Kalmia latifolia L.	x	x	x	x	

Prescribed burns were implemented in 2018 and 2019 by the U.S. Forest Service and coordinated with Clemson University for purposes of this study. Dormant season burn treatments occurred after autumn leaf-fall and before the start of spring green-up (between January 31–April 5), while growing season burn treatments were those occurring during the spring green-up period before complete overstory leaf-out (between April 18–24) (Table 1). Red maple trees had begun flowering by some later dormant season burns, but leaf flush had not begun until after dormant season burns. Firing methods included hand ignition with drip torches in addition to helicopter aerial ignition on some burns. When possible, a spot fire technique was used for hand ignitions to simulate aerial ignitions.

2.3. Field sampling and data preparation

Vegetation data were collected separately for the forest understory, midstory, and overstory in the same plots before and after each treatment to quantify changes following the presence or absence of fire (Δ response variables). Pre-burn vegetation data were collected in 2016 and 2017 within 1–2 growing seasons preceding each burn. Post-burn vegetation data were collected in 2019 and 2020 in the second growing season following each burn. Presence or absence of fire (y/n) was noted at grid point intersections based on observations of charred surface fuels within 24 h following burn completion. A threshold of 50% of grid points indicating fire presence was used to qualify burn treatments for variables quantified by plot.

2.3.1. Vegetation inventory

Understory vegetation was defined as living plants < 1.37 m in height and was recorded following a modified Carolina Vegetation Survey (CVS) protocol (Peet et al., 1998). Quadrats (1 m^2) were used to sample understory vegetation, centered at each of 9 subplots per plot (Fig. 2). Plants were identified to species when possible and tallied within each quadrat. Individual woody plants were classified at or above the root collar by germinant, established, or sprout stem origin reflecting life history stage. Unique plants were assigned cover classes that represented the proportion of the quadrat that it covered: (1) 0–1%, (2) 1–2%, (3) 2–5%, (4) 5–10%, (5) 10–25%, (6) 25–50%, (7) 50–75%, or (8) 75–100%. Understory cover classes were then converted to the midpoint of the class range for use in analyses.

Midstory vegetation was defined as woody stems ≥ 1.37 m in height and < 10 cm diameter at 1.37 m above ground level (DBH); overstory vegetation was defined as woody stems ≥ 10 cm DBH. Midstory vegetation was sampled within 5 of 9 subplots (odd-numbered subplots #1, 3, 5, 7, 9) per plot, whereas overstory vegetation was sampled in the same odd-numbered subplots in 2 of the 3 blocks (Fig. 2). Live midstory and overstory stems were identified to species when possible and tallied within sampled subplots. Individual midstory shrubs and trees were further assigned the following DBH classes: (1) < 3 cm, (2) 3–6 cm, or (3) 6–10 cm. Midstory cover, both for mountain laurel and total overall, and maximum height of live mountain laurel were visually estimated as

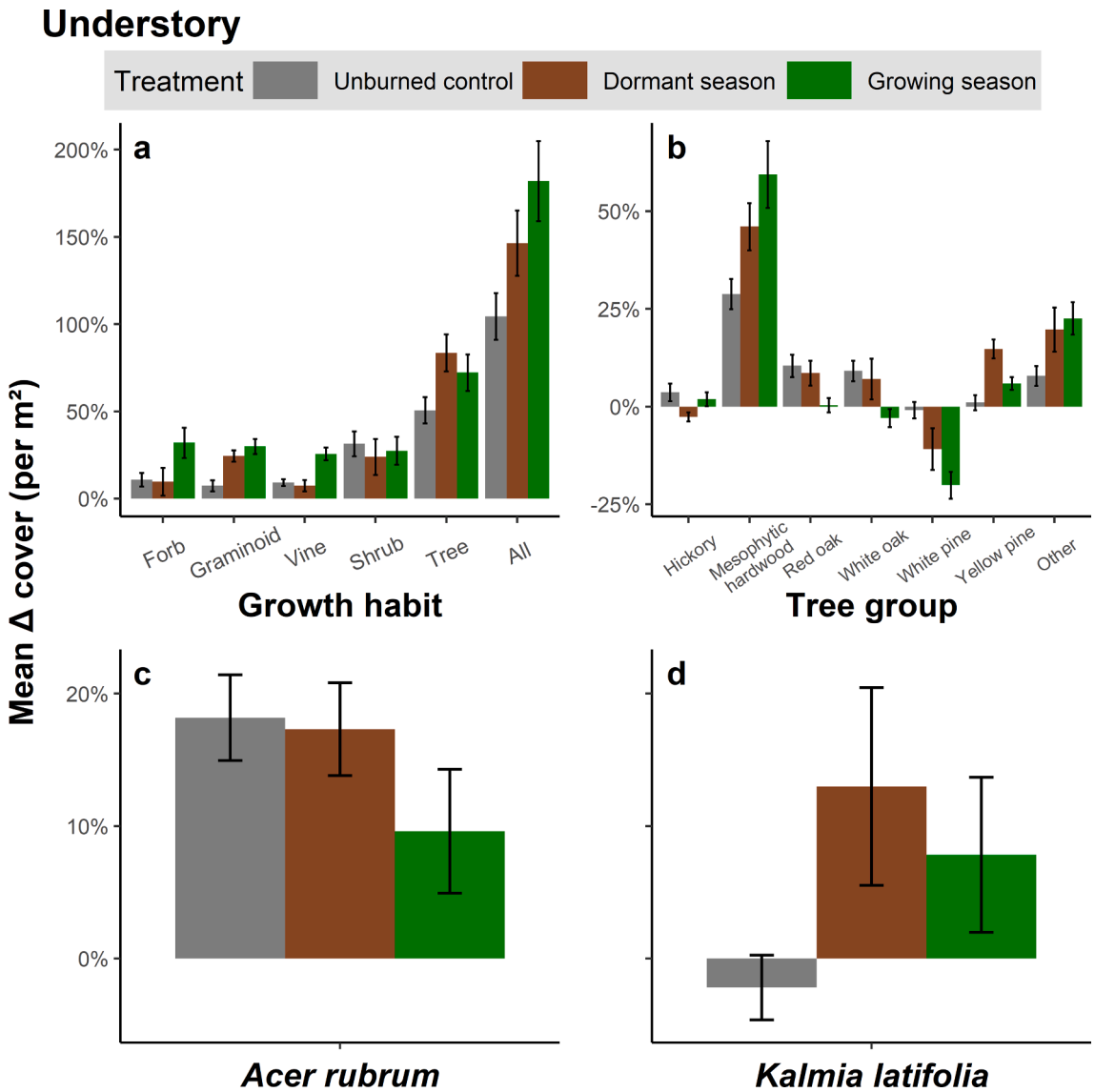

Fig. 3. Summary of treatment effects on understory vegetation cover analyzed using an analysis of variance (ANOVA) followed by Tukey's test if the ANOVA indicated a significant treatment effect: (a) all by growth habit, (b) trees by group, (c) red maple (*Acer rubrum*), and (d) mountain laurel (*Kalmia latifolia*). Error bars represent standard error associated with the mean of each treatment. Response variables represent absolute changes and are summed by plot (sample unit; 9 m^2) across individual subplot quadrats. Group means may not equal the sum of subgroup means due to the exclusion of paired absences. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

a proportion of the area of each subplot. Proportion of forest canopy cover was estimated as a measure of relative canopy closure using a concave spherical densiometer held at 1.37 m above the center of quadrats upon understory sampling.

Plants were uniquely identified and classified according to accepted taxa in the U.S. Department of Agriculture (USDA) Natural Resources Conservation Service (NRCS) PLANTS Database (USDA NRCS, 2022). Unique plants (primarily species) were assigned to a functional group based on growth habit as a forb, graminoid, vine, shrub, or tree. Additional functional groups were defined using combinations of these growth habits: herb (forb, graminoid) and woody (vine, shrub, tree). Trees were grouped by taxonomic and/or functional similarities: hickory included *Carya* Nutt. spp.; mesophytic hardwood included fire-sensitive, shade-tolerant species (such as *Acer* L. spp., *Betula* L. spp., *Liriodendron tulipifera* L., and *Nyssa sylvatica* Marsh.) (Nowacki and Abrams, 2008); red oak (*Quercus* L. spp.) included *Q. coccinea* Münchh., *Q. falcata* Michx., *Q. marilandica* Münchh., *Q. rubra* L., and *Q. velutina* Lam.; white oak (*Quercus* L. spp.) included *Q. alba* L., *Q. montana* Willd., and *Q. stellata* Wangenh.; white pine (*Pinus* L. spp.) included *P. strobus* L.; yellow pine (*Pinus* L. spp. subgenus *Diploxylon*) included *P. echinata* Mill., *P. pungens* Lamb., *P. rigida* Mill., *P. taeda* L., and *P. virginiana* Mill.; and other included remaining species not included in the above tree groups (such as *Hamamelis virginiana* L., *Ilex opaca* Aiton, and *Oxydendrum arboreum* (L.) DC.). Understory cover values by plant functional group may overestimate true cover in some cases when multiple plants in the same group shared the same area within quadrats. Plant functional group response values were aggregated by summing or averaging variables in applicable classes (Table 2) across subplots by plot, with paired absences excluded for calculating changes from pre- to post-treatment.

2.3.2. Species richness and diversity

Species richness and proportionate measures of alpha (α), gamma (γ), and beta (β) diversity were calculated for plots, treatment units, and overall. Species richness was calculated as mean species richness by plot. α-diversity (proportionate) was calculated as the *H'* Shannon-Wiener

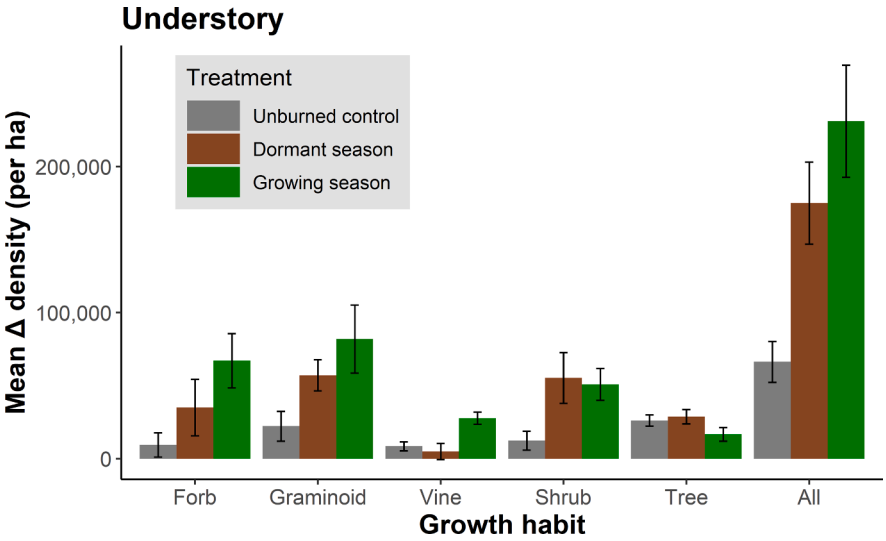

Fig. 4. Summary of treatment effects on all understory vegetation density by growth habit analyzed using an analysis of variance (ANOVA) followed by Tukey's test if the ANOVA indicated a significant treatment effect. Error bars represent standard error associated with the mean of each treatment. Response variables represent absolute changes and are summed by plot (sample unit; 9 m^2) across individual subplot quadrats. Group means may not equal the sum of subgroup means due to the exclusion of paired absences.

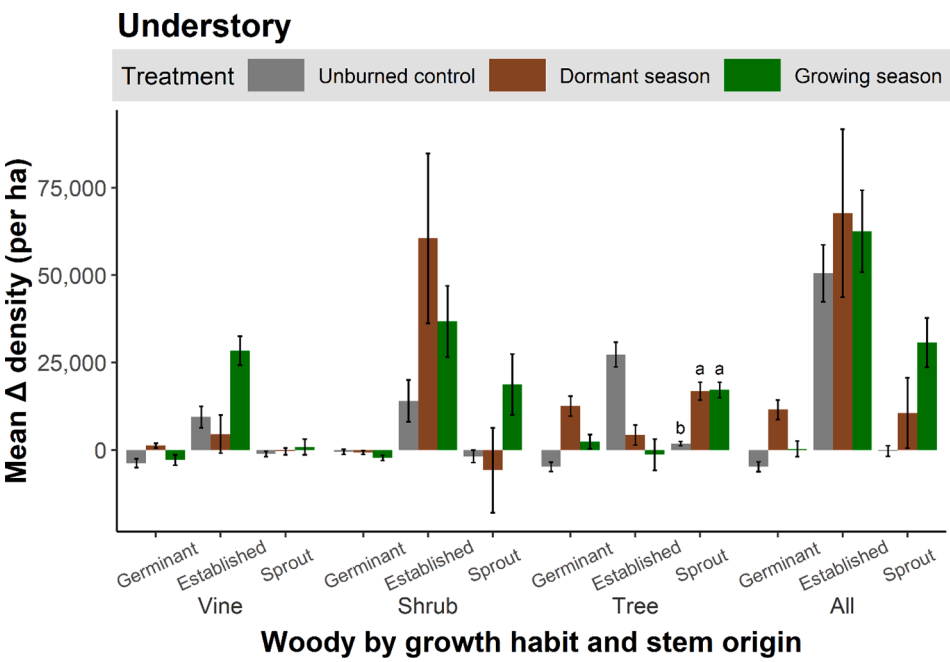

Fig. 5. Summary of treatment effects on woody understory vegetation density by growth habit and stem origin analyzed using an analysis of variance (ANOVA) followed by Tukey's test if the ANOVA indicated a significant treatment effect. Error bars represent standard error associated with the mean of each treatment. Response variables represent absolute changes and are summed by plot (sample unit; 9 m^2) across individual subplot quadrats. Group means may not equal the sum of subgroup means due to the exclusion of paired absences. Treatment means with different lower-case letters were statistically different at $\alpha = 0.05$.

index of diversity by plot. γ-diversity, representing landscape-level diversity, was calculated as the total plant species richness by treatment unit. β-diversity was represented as β_W (Whittaker's beta) and β_D (half changes) to quantify the degree of compositional separation between plots. Both measures β_W and β_D were applied to no specific underlying environmental gradient based on presence-absence and quantitative data, respectively (McCune and Grace, 2002). β_W represents overall community heterogeneity and was calculated according to the following formula: $(\gamma/\alpha) - 1$ (Whittaker, 1960; Koleff et al., 2003). β_D, measured as half changes, corresponds to the average dissimilarity (D, expressed as a proportion coefficient) among plots and was calculated according to the following formula: $\frac{\log(1-D)}{\log(0.5)}$ (McCune and Grace, 2002).

2.4. Statistical analyses

Understory and midstory cover were transformed using an arcsine-square root transformation, improving normality as proportional values (Sokal and Rohlf, 1995; McCune and Grace, 2002). Plant counts were transformed using a logarithmic transformation to be represented as density within sample units (Anderson et al., 2006). A statistical model was developed that related continuous dependent variables of interest to treatments and replicates using a one-way analysis of variance (ANOVA) to evaluate the effect of burn season on vegetation response. Model effects included treatment (fixed), block (random), block crossed with treatment (random), and/or plot nested within treatment and block (random). Residuals of transformed Δ response variables largely followed a normal distribution with stable variance across treatments. Statistical significance was evaluated at the $\alpha = 0.05$ level, with post-hoc tests (Tukey's HSD) used for pairwise comparisons when there was a significant treatment effect. All analyses were performed using JMP Pro 15.1.0 and RStudio Desktop (up to v. 1.4.1717) in the R programming language and software environment (up to 4.1.0) (SAS, 2019; R Core Team, 2021; RStudio, 2021).

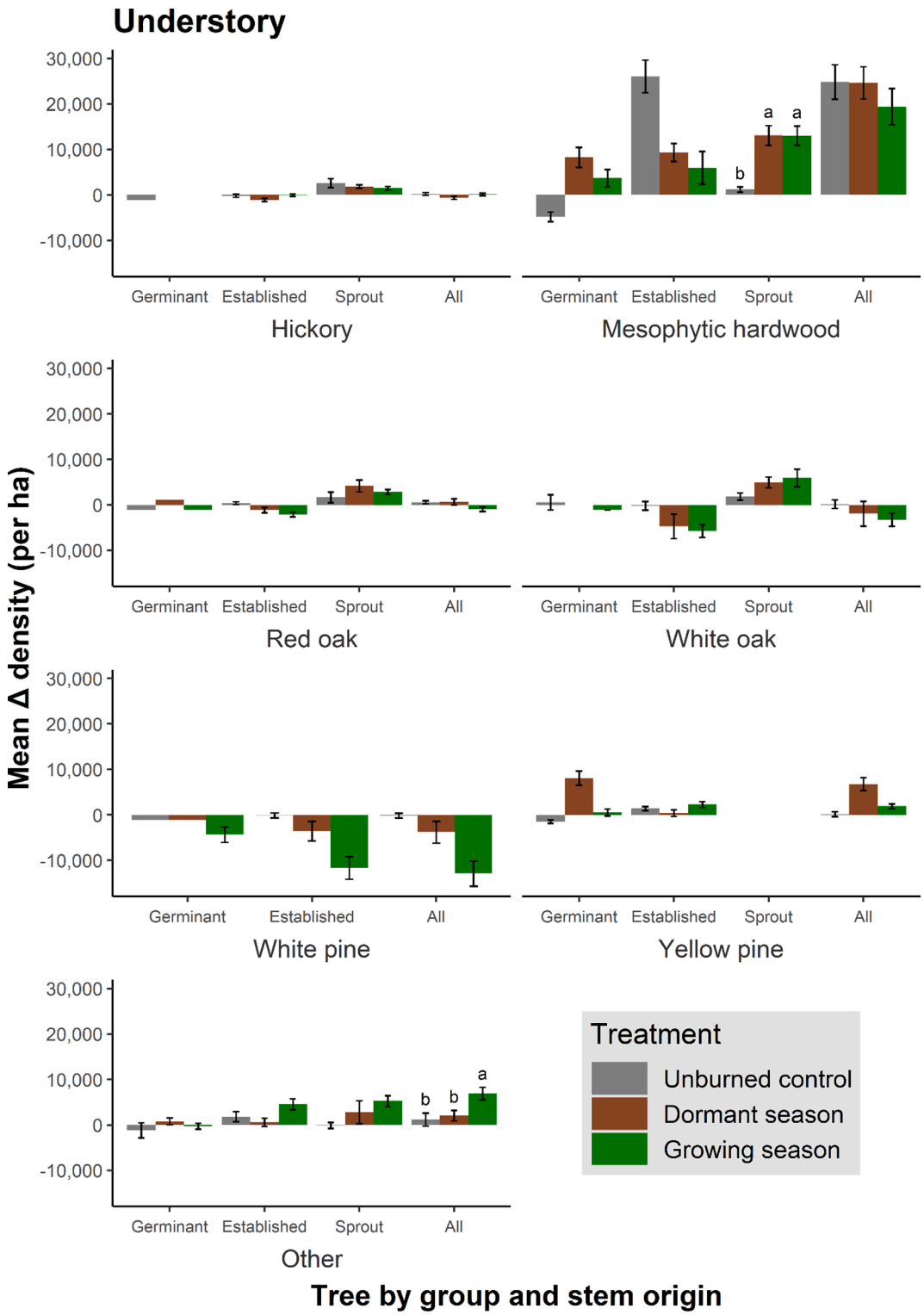

Fig. 6. Summary of treatment effects on understory tree vegetation density by group and stem origin analyzed using an analysis of variance (ANOVA), followed by Tukey's test if the ANOVA indicated a significant treatment effect. Error bars represent standard error associated with the mean of each treatment. Response variables represent absolute changes and are summed by plot (sample unit; 9 m^2) across individual subplot quadrats. Group means may not equal the sum of subgroup means due to the exclusion of paired absences. Treatment means with different lower-case letters were statistically different at $\alpha = 0.05$.

3. Results

3.1. Plant absolute abundance

3.1.1. Understory

Cover for nearly all understory growth habits, tree groups, and species increased during the study period regardless of treatment. There were no significant treatment effects ($P > 0.05$ or n/a) (Fig. 3).

Similar to understory cover, there were increases in understory density for all growth habits but no significant differences among treatments ($P > 0.05$) (Fig. 4). When analyzed by stem origin, there was a significantly greater increase in tree sprout density following dormant

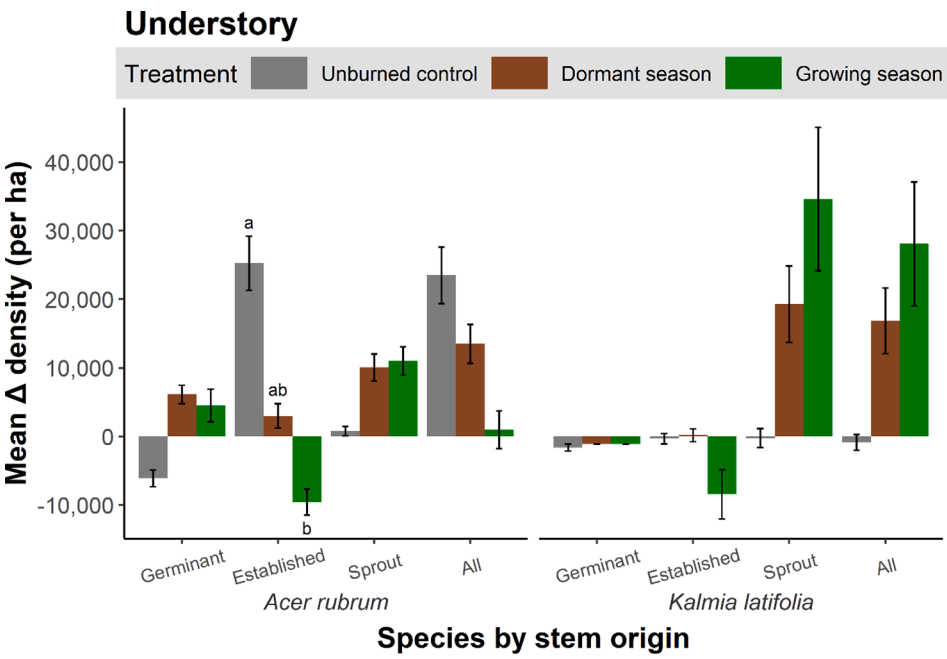

Fig. 7. Summary of treatment effects on understory vegetation density of red maple (*Acer rubrum*) and mountain laurel (*Kalmia latifolia*) by stem origin analyzed using an analysis of variance (ANOVA), followed by Tukey's test if the ANOVA indicated a significant treatment effect. Response variables represent absolute changes and are summed by plot (sample unit; 9 m^2) across individual subplot quadrats. Group means may not equal the sum of subgroup means due to the exclusion of paired absences. Treatment means with different lower-case letters were statistically different at $\alpha = 0.05$. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 3
Summary of treatment effects on midstory vegetation cover analyzed using an analysis of variance (ANOVA) followed by Tukey's test if the ANOVA indicated a significant treatment effect. Response variables are averaged by plot (sample units *n*; 500 m^2) across individual subplots.

Response variable (*α = 0.05)	Treatment	Mean (±SE)	Tukey HSD	Sample units *n*
Cover [Δ Σ (proportion 0.01 m^{-2})]				
Kalmia latifolia	C	-0.06 (±0.09)		59
$F_{2,\ 3.8} = 0.12$, $P = 0.89$	DS	-0.24 (±0.13)		36
	GS	-0.22 (±0.09)		55
Total	C	-0.27 (±0.11)		59
$F_{2,\ 4.0} = 0.93$, $P = 0.47$	DS	-0.95 (±0.20)		36
	GS	-0.70 (±0.14)		55

season burns (+16,869 ± 2,530 ha^{-1}) and growing season burns (+17,191 ± 2,207 ha^{-1}) than with unburned controls (+1,833 ± 607 ha^{-1}) ($P = 0.01$). There were no other significant treatment effects for change in understory density of woody stems by growth habit or stem origin ($P > 0.05$ or n/a) (Fig. 5).

When evaluated by understory tree groups and stem origin, there were no significant treatment effects on hickory, red oak, white oak, white pine, or yellow pine density ($P > 0.05$ or n/a). However, mesophytic hardwood tree sprout density increased to a significantly greater degree following dormant season burns (+13,065 ± 2,173 ha^{-1}) and growing season burns (+13,026 ± 2,107 ha^{-1}) than with unburned controls (+1,176 ± 551 ha^{-1}) ($P = 0.02$). Additionally, there was a significantly greater increase in total understory stem density in the "other" tree group following growing season burns (+6,914 ± 1,351 ha^{-1}) than with dormant season burns (+2,049 ± 1,156 ha^{-1}) and unburned controls (+1,206 ± 1,432 ha^{-1}) ($P = 0.01$) (Fig. 6).

Among individual species, both dormant season and growing season burn treatments resulted in significantly smaller changes in established understory *Acer rubrum* stem density (+3,000 ± 1,788 ha^{-1} and -9,581 ± 1,881 ha^{-1}, respectively) relative to unburned controls (+25,256 ± 3,953 ha^{-1}) ($P = 0.01$). The two burn treatments were not significantly different between each other, however. There were no other significant treatment effects by stem origin class or overall on understory density of *Acer rubrum*. Likewise, there were no significant treatment effects for understory *Kalmia latifolia* density ($P > 0.05$ or n/a) (Fig. 7).

3.1.2. Midstory

Midstory cover, both for *Kalmia latifolia* and total overall, decreased across all treatments over the study period. There were no significant differences among treatments ($P > 0.05$) (Table 3).

Midstory shrub stem density increased in the unburned control treatment and decreased in the two burn treatments. The largest decrease was observed following growing season burns (-1,585 ± 188 ha^{-1}), which was significantly different from the changes with both dormant season burns (-813 ± 240 ha^{-1}) and unburned controls (+517 ± 164 ha^{-1}) ($P = 0.01$). This treatment effect was primarily driven by reductions in the smallest DBH class (< 3 cm). A similar, though less pronounced, effect was observed for midstory trees, where growing season burns had the greatest reduction in density (-889 ± 133 ha^{-1}), followed by dormant season burns (-526 ± 246 ha^{-1}) and unburned controls (-74 ± 51 ha^{-1}). For midstory trees, the two burn treatments were not significantly different between each other, but growing season burns were significantly different from unburned controls ($P = 0.02$). These differences were also primarily driven by reductions in smaller stems (< 3 cm and 3–6 cm DBH) (Fig. 8).

When evaluated by midstory tree groups and stem origin, there were no significant treatment effects on hickory, white pine, or yellow pine density ($P > 0.05$ or n/a). For mesophytic hardwood trees, unburned controls remained relatively unchanged (-17 ± 38 ha^{-1}), whereas reductions were observed following both growing season and dormant season burns (-561 ± 80 ha^{-1} and -376 ± 165 ha^{-1}, respectively). While the two burn treatments were not significantly different between each other, growing season burns significantly differed from unburned controls ($P = 0.01$). These differences were largely driven by mortality patterns in the < 3 cm and 3–6 cm DBH classes. Likewise, for midstory red oak density, there was a modest reduction in unburned controls (-5 ± 11 ha^{-1}) and a significantly larger reduction following growing season burns (-74 ± 22 ha^{-1}) ($P = 0.04$). Changes for the dormant season treatment (-59 ± 37 ha^{-1}) were not significantly different from either unburned controls or dormant season burns. Modest changes in stem

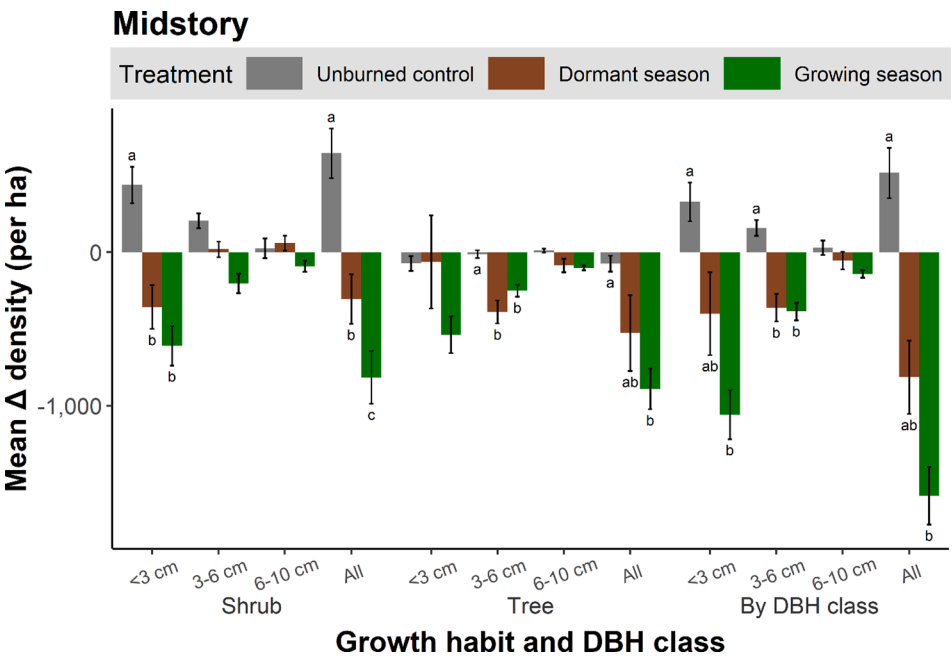

Fig. 8. Summary of treatment effects on all midstory vegetation stem density by growth habit and DBH class analyzed using an analysis of variance (ANOVA) followed by Tukey's test if the ANOVA indicated a significant treatment effect. Error bars represent standard error associated with each treatment mean. Response variables represent absolute changes and are summed by plot (sample unit; 500 m^2) across individual subplots. Group means may not equal the sum of subgroup means due to the exclusion of paired absences. Treatment means with different lowercase letters were statistically different at $\alpha = 0.05$.

density were also observed for "other" midstory trees, with significant reductions in the 3–6 cm DBH class following growing season burns (-55 ± 12 ha^{-1}) relative to unburned controls (+3 ± 9 ha^{-1}) ($P = 0.03$). Neither of these treatments were significantly different from dormant season burns (-73 ± 29 ha^{-1}) (Fig. 9).

In the absence of fire, midstory *Acer rubrum* stem density stayed relatively unchanged across diameter classes. However, there were significant reductions in total midstory *Acer rubrum* density following growing season burns, relative to all other treatments (-356 ± 57 ha^{-1} vs. -219 ± 69 ha^{-1} and + 15 ha^{-1} ± 31 ha^{-1} with dormant season burns and unburned controls, respectively) ($P < 0.01$). In contrast with changes in *Acer rubrum*, midstory *Kalmia latifolia* stem density increased in the absence of fire. Midstory *Kalmia latifolia* density decreased following growing season burns across all diameter classes but was not significantly different from dormant season burns. In the < 3 cm DBH class, both growing season and dormant season burns were significantly different from unburned controls (-494 ± 83 ha^{-1} and -323 ± 146 ha^{-1} vs. + 497 ± 127 ha^{-1}, respectively) (Fig. 10). Change in the maximum height of *Kalmia latifolia* was not significantly different between treatments ($P = 0.49$).

3.1.3. Overstory

In the absence of fire, overstory tree density remained constant or increased, depending on functional group. Reductions following growing season and dormant season burns were not significantly different between treatments ($P > 0.05$ or n/a) (Fig. 11).

Forest canopy cover increased in the absence of fire (+2.9% ± 3.2%) and decreased significantly following burn treatments (-5.5% ± 7.2% and -4.0% ± 7.0% with growing season and dormant season burns, respectively) ($P < 0.01$). However, changes with growing season burns were not significantly different in comparison to dormant season burns (Fig. 12).

3.2. Species richness and diversity

3.2.1. Understory

With the exception of shrubs in unburned controls, understory species richness generally increased across all treatments over the study period. However, there were no significant differences among treatments for any growth habit. Likewise for *H'*, there were increases across all treatments – except for shrubs and trees in unburned controls – with no significant differences among treatments ($P > 0.05$ or n/a) (Table 4). Changes in γ, β_W (Whittaker's beta), and β_D (half changes) were not significantly different among treatments ($P = 0.85$, 0.21, and 0.11, respectively).

3.2.2. Midstory

In contrast with the understory, midstory species richness generally decreased across treatments, but there were no significant treatment effects for either shrubs or trees ($P > 0.05$). Likewise, *H'* also decreased across treatments, with no significant treatment effects ($P > 0.05$) (Table 5).

Change in γ was not significantly different between burn treatments ($P = 0.44$). However, change in β_W (Whittaker's beta) was significantly greater following growing season burns (+1.12 ± 0.13) than with unburned controls (+0.11 ± 0.20) but was not significantly different from dormant season burns (+0.28 ± 0.18) ($P = 0.04$). Change in β_D (half changes) was significantly greater with growing season and dormant season burn treatments (+0.28 ± 0.08 and +0.20 ± 0.04, respectively) vs. unburned controls (-0.06 ± 0.03) ($P < 0.01$).

4. Discussion

4.1. Understory

Understory vegetation composition was largely unaffected by burn season in our study. Few significant effects were detected that would suggest understory plants, regardless of growth habit or life history stage, respond differently to dormant season vs. early growing season burn treatments. The greater increase in understory stem density in the dissimilar "other" tree group following early growing season burns was disproportionately driven by sourwood (*Oxydendrum arboreum* (L.) DC.) and black locust (*Robinia pseudoacacia* L.), likely reflecting vigorous sprouting by those species. Understory response to disturbance, particularly of shade-intolerant species, is likely to be limited in closed-canopy forests without lasting increases in light availability (Hutchinson et al., 2012; Barefoot et al., 2019; Oakman et al., 2019). Burn treatments decreased canopy cover to a greater degree compared to unburned controls, but change in canopy cover did not differ by burn season. Further, small declines in canopy cover from a single fire may be quickly

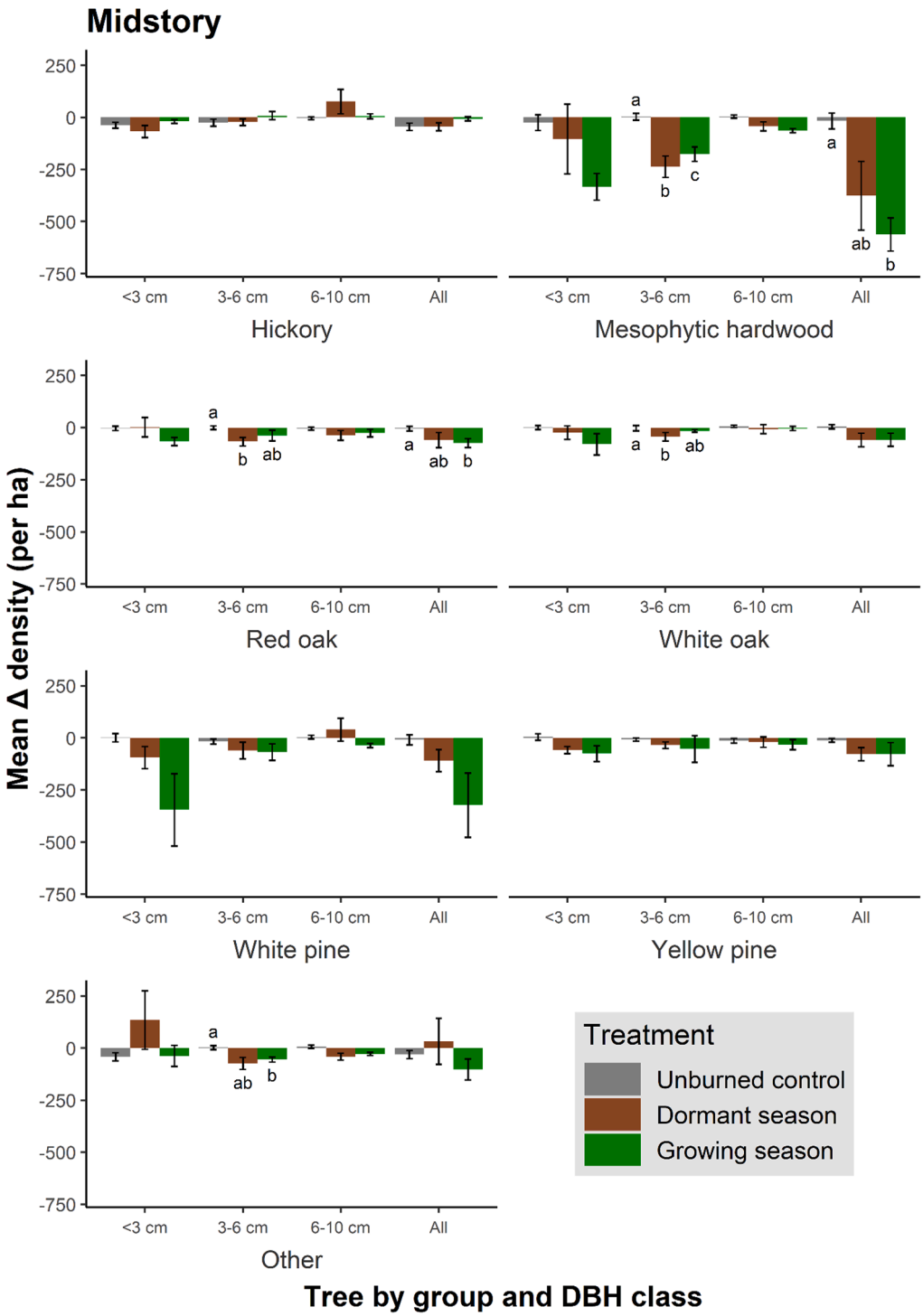

Fig. 9. Summary of treatment effects on midstory tree vegetation density by group and DBH class analyzed using an analysis of variance (ANOVA) followed by Tukey's test if the ANOVA indicated a significant treatment effect. Error bars represent standard error associated with each treatment mean. Response variables represent absolute changes and are summed by plot (sample unit; 500 m^2) across individual subplots. Group means may not equal the sum of subgroup means due to the exclusion of paired absences. Treatment means with different lower-case letters were statistically different at $\alpha = 0.05$.

reversed in following growing seasons (Alexander et al., 2008). Understory plants, while particularly susceptible to top-kill, reflect the beginning of vegetative re-growth with patterns that may require successive disturbances to alter.

Changes in species abundance as a result of seasonal burning potentially reflect not only damage to plant structures present pre-burn but also patterns of plant regeneration and reproduction post-burn. Observed treatment differences in understory tree sprout density reflect the common process of stem regeneration via basal sprouting by trees in response to fire (cf. Elliott et al., 1999; Brose and Van Lear, 2004). Trees may be less able to sustain resprouting ability following burning at times when carbohydrates stored belowground in dormancy are being utilized aboveground to produce new foliage during annual periods of active growth (Waldrop et al., 1987). However, our results

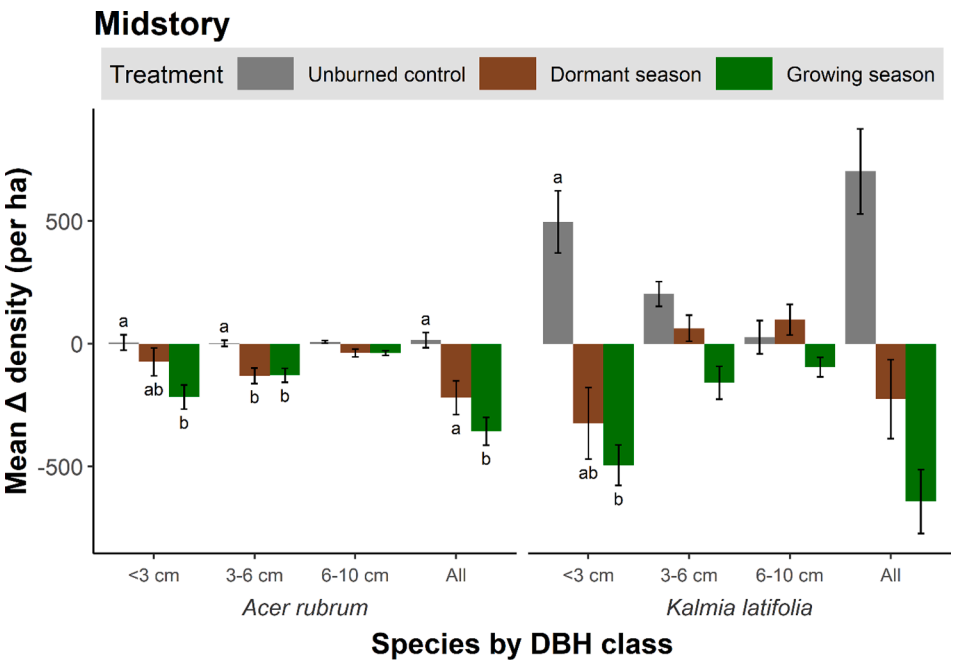

Fig. 10. Summary of treatment effects on midstory vegetation density of red maple (*Acer rubrum*) and mountain laurel (*Kalmia latifolia*) by DBH class analyzed using an analysis of variance (ANOVA) followed by Tukey's test if the ANOVA indicated a significant treatment effect. Error bars represent standard error associated with each treatment mean. Response variables represent absolute changes and are summed by plot (sample unit; 500 m^2) across individual subplots. Group means may not equal the sum of subgroup means due to the exclusion of paired absences. Treatment means with different lower-case letters were statistically different at $\alpha = 0.05$. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

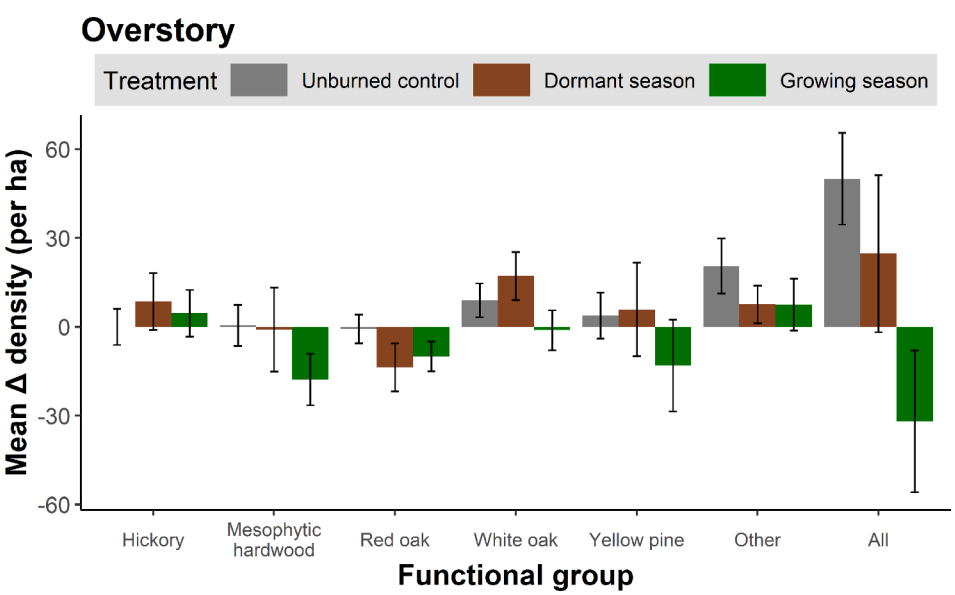

Fig. 11. Summary of treatment effects on overstory vegetation density by functional group analyzed using an analysis of variance (ANOVA) followed by Tukey's test if the ANOVA indicated a significant treatment effect. Error bars represent standard error associated with each treatment mean. Response variables represent absolute changes and are summed by plot (sample unit; 500 m^2) across individual subplots. Group means may not equal the sum of subgroup means due to the exclusion of paired absences.

demonstrated little evidence for such a pattern, with no differential effects of burn season on understory sprouts or stems otherwise for red maple or mesophytic hardwoods overall. Germination of mesophytic hardwood species like red maple may have had a similar response to surface fuel load reduction as litter consumption did not significantly differ by burn season (Vaughan et al., 2021). Red maple requires little light to germinate and is among the earliest and most vigorous trees in initiating and maintaining stem growth in the spring, making it a strong understory competitor with oaks and hickories for acquiring light and nutrients (Jacobs, 1965; Walters and Yawney, 1990; Abrams, 1998; Hutchinson et al., 2008). Typically dispersed by early spring in the southern Appalachians, red maple seeds may have been partially consumed by later dormant season burns and/or had losses offset by intact seeds with prolific germination rates (cf. Keyser et al., 2012). Burn timing relative to single species phenology may be used to interpret fire effects on that species but should further be considered relative to the response of functional groups over longer seasonal periods within larger plant communities.

Contrary to our hypothesis, we did not find evidence to suggest that early growing season burns were more effective than dormant season burns in increasing forb and graminoid abundance. Differences in species richness and diversity as a result of burn season would reflect compositional shifts in the relative abundance of competing plants in response to disturbance. The lack of treatment effects for such variables suggests that understory plant community heterogeneity remained largely unchanged by burning in different seasons. Burn timing as it would affect herbaceous species composition should be considered relative to the breaking of dormancy, even when aboveground biomass is absent (Baskin and Baskin, 1988). In the Coastal Plain, for example, Platt et al., 1988 found that forb and shrub species diversity was least following late growing season burns and greatest following dormant season burns in longleaf pine (*Pinus palustris* Mill.) forests in northern

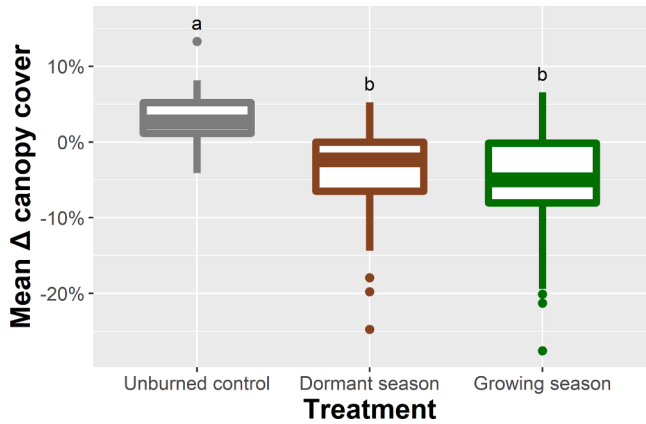

Fig. 12. Comparison of change in canopy cover (%) by treatment. Treatment means with different lower-case letters were statistically different at α = 0.05.

Florida. In contrast to most burn season studies on herbaceous response in the Coastal Plain, however, growing season burn treatments used for this study only occurred in its earliest stages. Herbaceous plants may not benefit from a favorable growth environment if resource advantages do not compensate for disruption of phenological progression in the spring green-up period. Fire applied in different parts of the growing season and across gradients of light availability may better reveal how burn season could facilitate shifts in southern Appalachian herbaceous communities.

4.2. Midstory and overstory

In contrast to the understory, we found several significant effects of burn season in the midstory. Early growing season burns were most effective in reducing overall midstory shrub stem density, often comprised of shrubs such as great rhododendron and mountain laurel. Elevated fire temperatures and greater area burned within units may be responsible for the greater midstory top-kill observed with early growing season burns vs. dormant season burns (Vaughan et al., 2021). Such variability in fire severity on burn days suggests that midstory woody species density is likely influenced by patterns of fire behavior characteristic of different seasons. Early growing season burns reduced red maple, overall mesophytic hardwood, and red oak density in the midstory, but had the same negative effect as dormant season burns on mesophytic hardwoods overall and red oaks. Mesophytic hardwood species other than red maple (e.g., yellow-poplar, blackgum (*Nyssa sylvatica* Marsh.), flowering dogwood (*Cornus florida* L.)) may respond differently to burn treatments (Phillips and Waldrop, 2008), revealing implications for using fire seasonality to reduce mesophytic hardwood competition and promote oak regeneration. Negative impacts on desirable species (e.g., red oaks) should continue to be monitored to ensure that prescribed burns promote desired forest composition.

Distinguishing seasonal fire effects on species regeneration is important for management objectives intended to reverse the process of mesophication. More variable yet higher fire temperatures in early growing season burns (Vaughan et al., 2021) were associated with reduced midstory red maple density in comparison to dormant season burns. Decreases in midstory density will likely be offset to some degree, however, by increases in understory sprouting of the same species. Higher levels of proxies of fire intensity (temperature and bole char height) have been shown in other studies to maintain or increase red maple sprout abundance (Clark and Schweitzer, 2013; Arthur et al., 2015). Fire temperatures in dormant season burns, in comparison, may be more effective in reducing the stem density of other mesophytic hardwoods, at least in the short term. It remains unclear, however, whether burn season effects on the regeneration of mesophytic hardwoods or other species will persist over time (Brose et al., 2013; Keyser

Table 4
Summary of treatment effects on understory species richness and α-diversity (*H'*) analyzed using an analysis of variance (ANOVA) followed by Tukey's test if the ANOVA indicated a significant treatment effect. Response variables are aggregated by plot (sample units *n*; 9 m^2) across individual subplot quadrats. Group means may not equal the sum of subgroup means due to the exclusion of paired absences.

Response variable (*α = 0.05)	Treatment	Mean (±SE)	Tukey HSD	Sample units *n*
Species richness [Δ]				
By growth habit				
Forb	C	+1.07 (±0.19)		59
$F_{2,\ 4.0} = 0.40$, $P = 0.70$	DS	+1.36 (±0.33)		36
	GS	+1.89 (±0.31)		56
Graminoid	C	+0.17 (±0.08)		59
$F_{2,\ 3.6} = 2.57$, $P = 0.20$	DS	+0.64 (±0.17)		36
	GS	+0.84 (±0.12)		56
Herb (forb, graminoid)	C	+1.24 (±0.23)		59
$F_{2,\ 4.0} = 0.70$, $P = 0.55$	DS	+2.00 (±0.39)		36
	GS	+2.73 (±0.35)		56
Vine	C	+0.22 (±0.10)		59
$F_{2,\ 4.2} = 0.88$, $P = 0.48$	DS	+0.14 (±0.19)		36
	GS	+0.52 (±0.10)		56
Shrub	C	-0.14 (±0.11)		59
$F_{2,\ n/a} = 1.39$	DS	+0.81 (±0.21)		36
	GS	+0.91 (±0.19)		56
Tree	C	+0.61 (±0.27)		59
$F_{2,\ 4.4} = 0.03$, $P = 0.97$	DS	+0.78 (±0.30)		36
	GS	+0.61 (±0.31)		56
Woody (vine, shrub, tree)	C	+0.69 (±0.34)		59
$F_{2,\ 4.1} = 0.49$, $P = 0.64$	DS	+1.72 (±0.49)		36
	GS	+2.04 (±0.43)		56
H' (Shannon-Wiener index) [Δ]				
By growth habit				
Forb	C	+0.29 (±0.06)		59
$F_{2,\ n/a} = 1.36$	DS	+0.26 (±0.08)		36
	GS	+0.13 (±0.07)		56
Graminoid	C	+0.10 (±0.08)		59
$F_{2,\ 3.9} = 0.37$, $P = 0.71$	DS	+0.16 (±0.08)		36
	GS	+0.30 (±0.07)		56
Herb (forb, graminoid)	C	+0.25 (±0.06)		59
$F_{2,\ 3.1} = 0.01$, $P = 0.99$	DS	+0.25 (±0.07)		36
	GS	+0.26 (±0.06)		56
Vine	C	+0.09 (±0.04)		59
$F_{2,\ 2.3} = 0.21$, $P = 0.83$	DS	+0.04 (±0.05)		36

(*continued on next page*)

Table 4 (*continued*)

Response variable (*α = 0.05)	Treatment	Mean (±SE)	Tukey HSD	Sample units *n*
	GS	+0.11 (±0.03)		56
Shrub $F_{2,\ 4.0} = 2.09$, $P = 0.24$	C	-0.02 (±0.04)		59
	DS	+0.11 (±0.06)		36
	GS	+0.26 (±0.05)		56
Tree $F_{2,\ 4.0} = 0.13$, $P = 0.88$	C	-0.06 (±0.05)		59
	DS	+0.03 (±0.05)		36
	GS	+0.04 (±0.06)		56
Woody (vine, shrub, tree) $F_{2,\ 4.3} = 0.63$, $P = 0.57$	C	+0.08 (±0.04)		59
	DS	+0.20 (±0.05)		36
	GS	+0.12 (±0.04)		56

Table 5
Summary of treatment effects on midstory species richness and α-diversity (*H'*) analyzed using an analysis of variance (ANOVA) followed by Tukey's test if the ANOVA indicated a significant treatment effect. Response variables are aggregated by plot (sample units *n*; 500 m^2) across individual subplots.

Response variable (*α = 0.05)	Treatment	Mean (±SE)	Tukey HSD	Sample units *n*
Species richness [Δ]				
By growth habit				
Shrub $F_{2,\ 3.9} = 2.15$, $P = 0.23$	C	0.00 (±0.10)		59
	DS	-0.19 (±0.16)		36
	GS	-0.45 (±0.15)		55
Tree $F_{2,\ 2.9} = 1.29$, $P = 0.40$	C	-0.92 (±0.26)		59
	DS	-1.50 (±0.42)		36
	GS	-1.91 (±0.30)		55
H' (Shannon-Wiener index) [Δ]				
By growth habit				
Shrub $F_{2,\ 3.6} = 1.63$, $P = 0.31$	C	-0.01 (±0.03)		59
	DS	-0.16 (±0.06)		36
	GS	-0.14 (±0.06)		55
Tree $F_{2,\ 3.0} = 6.30$, $P = 0.08$	C	-0.11 (±0.03)		59
	DS	-0.19 (±0.06)		36
	GS	-0.31 (±0.06)		55

et al., 2017). Forest midstories with substantial mesophytic hardwood encroachment will likely see a reduction in mesophytic hardwood abundance overall (including red maple) with repeated applications of both dormant season and growing season burns (Arthur et al., 2015; Vander Yacht et al., 2019).

Changes in midstory stem density may further suggest patterns of recruitment through influences on relative plant dominance (Baker and Van Lear, 1998; Albrecht and McCarthy, 2006). The lack of treatment effects on species richness and diversity may indicate, in part, midstory plants top-killed by fire not being re-recruited into the same layer by the completion of the second growing season post-burn. Midstory mountain laurel, for example, commonly had vigorous basal resprouting, shifting growing space to the understory (Elliott et al., 1999). Though changes in understory sprout density were not significantly different by burn season (for mountain laurel or otherwise), understory sprouting of woody species may result in delayed decreases in species richness and diversity of the advance reproduction layer in later periods post-fire. Future studies of burn season effects on vegetation should assess changes in diversity of forest strata over longer time periods.

Prescribed fire treatments used in this study were not expected to be of sufficient intensity to cause significant overstory mortality (Arthur et al., 1998; Elliott et al., 1999). While observed reductions in canopy cover were modest, fire may lead to further second-order effects on the overstory. Patterns of litter and duff consumption, as driven by fuel moisture and fuel loads, may induce delayed tree mortality as a result of fire spread around the base of the bole (Ferguson et al., 2002). Fire may also cause non-lethal injuries to and stress responses in larger shrubs and trees, reducing shading to the understory (Yaussy and Waldrop, 2010). Changes in understory light availability are likely to alter the moisture environment and thereby levels of surface water retention and fuel moisture (North et al., 2005; Rodríguez-Calcerrada et al., 2008). Intensive, repeated treatments will likely be necessary to alter overstory function and have the greatest effect on understory composition.

5. Conclusion

This study was designed to test overall treatment effects of representative dormant season vs. early growing season prescribed burns on the composition of forest strata. Burn season effects were largely concentrated in the midstory, where early growing season burns were most effective for reducing shrub and red maple density. Marginal decreases in canopy cover did not differ by burn season and are unlikely to result in greater light availability to the understory in later growing seasons without more intensive treatments. Changes in species composition following a single burn will likely attenuate over time and future research should incorporate seasonal effects of repeated burns and/or burns conducted during later portions of the growing season. Our results provide evidence that early growing season burns are a viable option for southern Appalachian fire managers seeking to expand their burn programs for restoring fire-excluded forests.

CRediT authorship contribution statement

Matthew C. Vaughan: Conceptualization, Methodology, Software, Formal analysis, Investigation, Data curation, Writing – original draft, Writing – review & editing, Visualization. **Donald L. Hagan:** Conceptualization, Methodology, Investigation, Resources, Data curation, Writing – review & editing, Visualization, Supervision, Project administration, Funding acquisition. **William C. Bridges Jr.:** Methodology, Software, Writing – review & editing. **Kyle Barrett:** Methodology, Software, Writing – review & editing. **Steve Norman:** Conceptualization, Methodology, Writing – review & editing. **T. Adam Coates:** Conceptualization, Methodology, Writing – review & editing. **Rob Klein:** Conceptualization, Methodology, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

This work was supported by the Joint Fire Science Program (Project #16-1-0612) and by USDA National Institute of Food and Agriculture under project number SC-1700586. Technical Contribution No. 7054 of the Clemson University Experiment Station. The authors would like to

thank the USDA Forest Service (Andrew Pickens Ranger District, Francis Marion and Sumter National Forests; and Chattooga River Ranger District, Chattahoochee-Oconee National Forests) for permission to collect field data and for conducting the prescribed burns. The authors would further like to acknowledge Trey Trickett, Emily Oakman, Tom Waldrop, Gregg Chapman and the many undergraduate and graduate students who assisted with data collection.

Data statement

The datasets used and/or analyzed during the current study are archived at Clemson University, Clemson, SC, USA, and available from the corresponding author on reasonable request. Programming code for all analyses performed in R is archived and available online in a GitHub repository [https://github.com/gishokie95/ms2-veg].

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