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SEASONALITY OF PRESCRIBED FIRE IN THE SOUTHERN APPALACHIANS

A Thesis Presented to the Graduate School of Clemson University

In Partial Fulfillment of the Requirements for the Degree Master of Science Forest Resources

by Matthew Christopher Vaughan December 2020

Accepted by: Dr. Donald Hagan, Committee Chair Dr. William Bridges Jr. Dr. Kyle Barrett Dr. Adam Coates Dr. Steve Norman

ABSTRACT

There has been growing interest in recent decades in using prescribed fire for hazardous fuels reduction and ecological restoration in the southern Appalachian Mountains. The application of prescribed fire in forests of this region has typically occurred in the dormant season, but with managers often looking for more opportunities to burn. In this study, we compared the effects of dormant season and early growing season burn treatments on fire behavior, fuel consumption, and the structure and composition of plant communities in relation to topographic and meteorological influences on fire behavior. Replicated treatments were analyzed using univariate, bivariate, and multivariate methods to quantify and evaluate effects on response variables. Our results indicated that fuel moisture was lower and temperatures were higher in early growing season burns than in dormant season burns. This pattern likely contributed to the greater proportion of plot area burned in the early growing season, reflecting fire spread into parts of the landscape that would remain unburned in the dormant season. Season of burn had few significant effects on understory plant abundance and diversity. In the midstory, early growing season burns were most effective among treatments in reducing shrub density, with the greatest differences concentrated in the smallest size classes. Early growing season burns reduced midstory red maple (Acer rubrum L.) density to a greater extent than dormant season burns, though other mesophytic hardwood species may have responded differently. The combination of environmental gradients of elevation, burn severity, and change in canopy cover best explained changes in midstory community composition. In conclusion, early growing season prescribed burns may result in more variable fire behavior yet can still be expected to achieve a similar level of fuel consumption in comparison to dormant season burns. Burning in the early growing season can expand opportunities for meeting management objectives with prescribed fire and be at least as effective as burning in the dormant season in reducing the abundance of mesophytic hardwoods. Season of burn has implications for fuel consumption and response of vegetation that managers can incorporate in using prescribed fire for restoration of fire-excluded forest communities in the southern Appalachians.

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TABLE OF CONTENTS

Pag	e
TITLE PAGEi	
ABSTRACTii	
ACKNOWLEDGMENTSiv	
LIST OF TABLES	
LIST OF FIGURES	
1 CHAPTER ONE11.0 Abstract11.1 Introduction31.1.1 Background31.1.2 Research questions61.2 Methods81.2.1 Study area81.2.2 Study design91.2.3 Field sampling and data preparation101.2.4 Meteorological variables141.2.5 Topographic variables151.2.6 Statistical analyses171.3 Results181.3.1 Meteorology, fuel moisture, and burn coverage181.3.2 Time-integrated heating and fuel consumption201.3.3 Topographic effects on fire behavior21	
1.4 Discussion221.4.1 Conclusions28Tables and Figures30References41	
2 CHAPTER TWO 49 2.0 Abstract 49 2.1 Introduction 51 2.1.1 Background 51 2.1.2 Research questions 56 2.2 Methods 59 2.2.1 Study area 59	
2.2.2 Study design	

Table of Contents (Continued)

Page

2.2.3 Field sampling and data preparation	61
2.2.4 Landscape variables	
2.2.5 Statistical analyses	
2.3 Results	
2.3.1 Cover and density	
2.3.2 Species richness and diversity	
2.3.3 Canopy cover	
2.3.4 Ordination with environmental factors	
2.4 Discussion	
2.4.1 Conclusions and management implications	
Tables and Figures	
References	

LIST OF TABLES

Table

Page

List of Tables (Continued)

Table 2.4. Summary of treatment effects on midstory vegetation cover analyzed using aone-way ANOVA. Response variables are averaged by plot (sample unit; 500 m²) acrossindividual subplots.98

Table 2.9. Multivariate summary of diversity measures by replicate and treatment, preand post-treatment. α = alpha diversity (non-proportionate; mean species richness, *S*); γ = gamma diversity (total species richness, S); β_W = beta diversity (Whittaker's beta); β_D = beta diversity (half changes corresponding to average community dissimilarity, *D*)..... 111

LIST OF FIGURES

Figure

Page

Figure 1.2. Representative diagram indicating the layout, orientation, and dimensions of each plot with interior grid point intersections. The (x, y) Cartesian coordinate pairs for each grid point represent the longitudinal (x) and latitudinal (y) distance from the origin.

List of Figures (Continued)

Figure Page
Figure 1.8. Scatterplots with linear regressions of mean bole scorch height (y-axis; m) vs. topographic variables Topographic Position Index (TPI) and Heat Load Index (HLI) (x-axis; rows) aggregated by plot for all plots in each unit (series) by burn treatment (columns).
Figure 2.1. Map depicting the replicates comprised of treatment units with plots established in this study. "AP" refers to replicates in the Andrew Pickens Ranger District whereas "CR" refers to replicates in the Chattooga River Ranger District. See Table 2.1 for further information on treatment units
Figure 2.2. Representative diagram indicating the layout, orientation, and dimensions of each plot with interior grid point intersections, subplots, and understory quadrats. The (x, y) Cartesian coordinate pairs for each grid point represent the longitudinal (x) and latitudinal (y) distance from the origin
Figure 2.3. Summary of treatment effects on understory vegetation density analyzed using a one-way ANOVA. Error bars represent standard error associated with each treatment and letters represent significant differences between treatments. 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
Figure 2.4. Summary of treatment effects on midstory vegetation density analyzed using a one-way ANOVA. Error bars represent standard error associated with each treatment and letters represent significant differences between treatments. 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
Figure 2.5. Comparison of change in canopy cover (%) by treatment
Figure 2.6. Plot of non-metric multidimensional scaling (NMDS) ordination results based on understory species importance values (IVs). Circles represent sites (plots) and arrows represent change vectors indicating plot movement from pre- to post-treatment by treatment
Figure 2.7. Plot of non-metric multidimensional scaling (NMDS) ordination results based on midstory species importance values (IVs). Circles represent sites (plots) and arrows represent change vectors indicating plot movement from pre- to post-treatment by treatment

1 CHAPTER ONE

SEASONALITY OF PRESCRIBED FIRE IN THE SOUTHERN APPALACHIANS: HOW DO BEHAVIOR AND FIRST-ORDER EFFECTS VARY BETWEEN SEASONS OF BURN?

1.0 Abstract

Despite the common use and traditional cultural acceptance of fire throughout much of the southeastern United States, substantial uncertainty remains regarding its practical implementation throughout the year. Opportunities to burn within prescriptive meteorological windows vary seasonally and along biogeographical gradients, particularly in mountainous terrain where topography can have heightened effects on fire behavior. Managers are often looking for options to expand the number of burn days that can be used to mitigate hazardous fuels and promote desirable habitat. For this study, we compared prescribed burns conducted in the dormant and early growing seasons in the southern Appalachian Mountains to evaluate the effects of season of burn in relation to the environmental factors influencing ignition on the day of burn. Response to burn treatments were quantified by proportion of plot area burned, surface fuel consumption, and timeintegrated thermocouple heating, with fuel moisture, meteorological, and topographic variables analyzed as predictors that may explain differences in fire behavior and effects. Our results suggested that both time-integrated thermocouple heating and its variability were greater in early growing season burns than in dormant season burns, though surface fuel consumption did not vary by season of burn. Lower fuel moisture and warmer temperatures, interacting with topography, likely contributed to these seasonal differences and resulted in greater burn coverage in the early growing season than in the dormant season. Early growing season burns in the southern Appalachians will likely have more variable fire behavior yet may still be expected to accomplish a similar level of fuel consumption to dormant season burns. The variability in fire behavior observed more commonly in growing season burns may further result in greater heterogeneity of fire effects across the landscape.

1.1 Introduction

1.1.1 Background

Fire is firmly embedded in the natural history and human experience of the American Southeast (Southeast). Evidence suggests that fire has been prevalent in the Southeast for at least the last several centuries, if not millennia, from the written accounts of explorers who described pervasive smoke and open woodlands (Fowler and Konopik 2007), to reconstructions of past fire occurrence using physical measurements synthesized by researchers today (Delcourt and Delcourt 1998; Lafon et al. 2017). Humans before and after Euro-American settlement in the 1700s and 1800s used fire to shape habitat for their livelihood (Owsley 1949; Stewart 2002; Abrams and Nowacki 2008), fostering a culture of burning that may inform our present treatment of fire. Recognizing that decades of fire suppression in the 1900s often led to hazardous fuel accumulation and forest "mesophication" (Nowacki and Abrams 2008), policymakers and land managers have increasingly endorsed and implemented prescribed fire in recent decades to reduce wildfire risk and promote ecosystem health and resiliency (Pyne 1982; Rothman 2007; Waldrop and Goodrick 2012). Today, more area is treated with prescribed fire on an annual basis in the Southeast than in any other region of North America (Wade et al. 2000; Kobziar et al. 2015; Melvin 2018).

Temporal considerations influence practitioners' ability to leverage fire for achievable outcomes, often in attempts to restore the use of fire across previously firesuppressed landscapes. Chronological reconstructions of historical fire regimes suggest patterns of past fire occurrence and are often used as a reference point for the frequency and timing of modern prescribed fire to elicit potential fire effects (Freeman et al. 2017). At the finest scale, the relative position of fire scars within tree growth rings may indicate intra-annual variability of past fire occurrence. Some fire scar studies throughout the Southeast suggest that the majority of fire events were recorded between annual rings: after cessation of tree ring growth in the fall and before resumption of new growth in the spring (Guyette et al. 2006b, 2009; Flatley et al. 2013). Other studies, however, suggest a greater frequency of scars in earlywood and latewood rings during the growing season (Huffman et al. 2004; Henderson 2006; Stambaugh et al. 2011). Inferences of seasonality from tree rings, however, may be based on ambiguous or limited information (Guyette et al. 2006a; Knapp et al. 2009; Lafon et al. 2017). Fire scars formed during tree dormancy, for example, may indicate fire occurrence during the fall, winter, or early spring. Formation of growth rings may vary in response to physiological factors independent of phenological timing, even amongst the same taxa (Barbaroux and Bréda 2002). Further, documented fires may not be representative of fire behavior at broader scales due to inherent limitations in sampling intensity (Hart and Buchanan 2012). The seasonality of historical fire regimes as interpreted in fire chronologies remains poorly understood, particularly regarding its connection with fire behavior across the landscape.

Evidence of the seasonal occurrence of historical fire regimes, coupled with our knowledge of fire seasonality today, is often conflicting and confounded by a lack of precision. Wildland fire is suggested to have occurred more often in different seasons prior to fire suppression than it does today, particularly in the Southeast's most fire-prone environments (Komarek 1965, 1974; Lafon 2010). Habitats favorable to forage and harvest

could be maintained by humans burning in a variety of seasons (Eldredge 1911; Jurgelski 2008), and the continued presence of endemic species dependent on fire to regenerate [e.g. Table Mountain pine (*Pinus pungens* Lamb.)] suggests that historical fires may have differed in pattern from what is often observed today (Williams 1998; Wade et al. 2000). Lightning ignitions may have ignited drier fuels under historically more open canopies, allowing further fire spread following spring and summer thunderstorms (Barden and Woods 1974; Cohen et al. 2007). Overriding meteorological patterns suggest, however, that growing season fires would be expected to be limited in extent in perpetuating pyrogenic habitat, particularly on parts of the landscape where fire behavior would be constrained by humid conditions created by a closed canopy. Area burned by wildland fire in the southern Appalachians today is strongly inversely proportional to the degree of overstory canopy closure (Norman et al. 2019), with most fires occurring before leaf expansion in the spring and after leaf abscission in the fall (Schroeder and Buck 1970). The seasonality of fire regimes is further confounded in mountainous topography, where less predictable fire behavior would be expected with a more heterogeneous temperature and moisture environment in a given area (Stambaugh and Guyette 2008; Lesser and Fridley 2016). Considering the drivers of the seasonality of fire behavior offers clues to understanding the effects of burning in different seasons.

The use of prescribed fire has expanded substantially in the southern Appalachians in recent decades amidst widespread efforts to reduce hazardous fuel loads, restore more open wildlife habitat, and stimulate regeneration of native oak (*Quercus* L.) and yellow pine (*Pinus* L.) (Van Lear and Waldrop 1989; Waldrop and Brose 1999; Brose et al. 2001). Using fire for these objectives has largely occurred in the dormant season before substantial spring green-up, mirroring traditional patterns of fire prescription in the Southeast more broadly (Van Lear and Waldrop 1989; Wade and Lunsford 1989). The dormant season may be considered to involve less operational risk of fire escape than burning in the growing season, particularly in late winter with still relatively low temperatures and predictable wind patterns (Mobley and Balmer 1981; Wade and Lunsford 1989; Robbins and Myers 1992). Further, spring burning has been perceived to have detrimental effects on wildlife species more vulnerable to fire at that stage of their life history (Landers 1981; Cox and Widener 2008). Despite the common practice and understanding of dormant season burning today, the behavior and effects of growing season burns remain less clear (Knapp et al. 2009; Reilly et al. 2012). For managers in the southern Appalachians who want to expand their program of prescribed burning, growing season burning could offer an added alternative to dormant season burning, allowing for increased opportunities to burn. It remains to be seen, however, whether growing season burns can accomplish the same fuels and restoration objectives as effectively as traditional dormant season burns, particularly for managers unfamiliar with this practice.

1.1.2 Research questions

Improved knowledge of how and why fire effects vary seasonally can improve how forested landscapes of the southern Appalachians are managed throughout the year. Changes in factors influencing flammability across varied topography may suggest the extent to which prescribed fire would be effective in achieving desired fire intensity and fuel consumption in different seasons and on different parts of the landscape. For this study, we compared seven prescribed burns conducted in the dormant and early growing seasons in the southern Appalachians to evaluate the effects of season of burn on surface fuel consumption and fire behavior. *In situ*, representative *ex situ*, and digital elevation model (DEM)-derived data were used to address the following questions:

- 1. How do meteorological conditions influencing surface fuel moisture and the coverage of area burned vary by season of burn?
- 2. How do time-integrated heating, surface fuel consumption, and the relationship between these variables differ by season of burn?
- 3. How are slope position and solar heat load related to fire behavior in dormant and early growing season burns?

For Question #1, we hypothesize that diurnal solar radiation and resulting average ambient temperatures will be higher in the early growing season, resulting in lower surface fuel moisture and greater proportions of treatment area burned than in the dormant season. For Question #2, we hypothesize that the degree and variability of time-integrated heating will be greater in early growing season burns than in dormant season burns. We also hypothesize that the degree and variability of litter and fine woody fuel consumption will be greater in early growing season burns, driven by variations in moisture of these fuel types. Further, we expect litter and duff consumption to rise at a greater rate with increases in time-integrated heating in dormant season burns than in early growing season burns. For Question #3, we hypothesize that the relationships between both slope position and solar heat load on metrics related to fire intensity will be more pronounced in dormant season burns than in early growing season burns.

1.2 Methods

1.2.1 Study area

This study was conducted in the Blue Ridge physiographic province of the southern Appalachian Mountains and adjacent Southern Inner Piedmont ecoregion in the southeastern United States, on public land administered by the U.S. Forest Service. Treatment replicates were located in both the Chattooga River (CR) Ranger District of Chattahoochee National Forest in Rabun and Stephens Counties, Georgia as well as the Andrew Pickens (AP) Ranger District of Sumter National Forest, in Oconee County, South Carolina (Figure 1.1). Unit elevations ranged from 222 m to 1430 m, 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 159 cm distributed relatively evenly throughout the year (NCEI 2020). Soil orders of Ultisols, Inceptisols, and Entisols were common, mostly underlain by metamorphic bedrock (e.g. granitic gneiss and schist) (Griffith et al. 2001, 2002).

Pre-treatment fuel loads were similar between treatments, averaging 6,684.4 kg ha⁻¹ for litter, 37,705.5 kg ha⁻¹ for duff, 14.1 cm for fuelbed height, 604.4 kg ha⁻¹ for 1-hr fuels, 1,881.7 kg ha⁻¹ for 10-hr fuels, 4,941.0 kg ha⁻¹ for 100-hr fuels, and 5,457.6 kg ha⁻¹ for 1,000-hr fuels across all study plots. Forest cover consisted primarily of oaks (*Quercus* L.), hickories (*Carya* L.), and pines (*Pinus* L.) across predominant ecological zones Dry-Mesic Oak-Hickory Forest, Shortleaf Pine-Oak Forest and Woodland, Mixed Oak / Rhododendron Forest, and Montane Oak-Hickory Forest (Simon et al. 2005; Simon 2015).

Substantial encroachment was present from mesophytic hardwoods [e.g. red maple (*Acer rubrum* L.)], mountain laurel (*Kalmia latifolia* L.), and rhododendron (*Rhododendron maximum* L.).

1.2.2 Study design

The study was laid out as a randomized complete block design, with treatments dormant season burn (d), growing season burn (g), and an unburned control (c) replicated three times. A fourth standalone dormant season burn in a planned additional replicate was also included for a total of 10 treatment units. Units ranged in area from 43 ha to 567 ha, with a mean area of 293 ha (Table 1.1). Twenty plots dispersed across a variety of slope positions were established within each treatment unit (except for 5 plots in the standalone unit), with data from a total of 180 plots entirely within unit perimeters used for analyses. Each plot was 30 x 30 m (900 m²), subdivided into (9) 10 m square (100 m²) subplots delineated by 16 grid point intersections and oriented with its outer boundaries running magnetic north (0°) and east (90°) from its point of origin (Figure 1.2). Transects (15.24 m in length) for measuring surface fuels were superimposed on each plot, separated by 20° magnetic azimuth emanating from the plot origin.

Prescribed burns were implemented by U.S. Forest Service fire practitioners as a part of official burn plans and coordinated with Clemson University for purposes of this study. Dormant season burns were defined as those occurring after autumn leaf-fall and before spring green-up (typically before last frost), whereas growing season burns were considered as those occurring in the early spring green-up period (typically after last frost) but before complete overstory canopy closure. Burn treatments occurred between January 31 - April 5 (dormant season) and April 18 - 24 (growing season) in 2018 and 2019 (Table 1.1). Firing methods included hand ignition using drip torches as well as remote aerial ignition using delayed aerial ignition devices dropped from a helicopter on some burns. A spot fire technique was used for hand ignitions, where possible.

1.2.3 Field sampling and data preparation

Fuels were measured before and after each burn to determine changes in surface fuel load across all plots. Complementary measurements of litter and duff consumption were taken at a greater sampling density in a subset of plots immediately following the burn. Fuel moisture was sampled the morning of and levels of heating were recorded throughout each burn day *in situ* in the same subset of "fire behavior plots". Measurements of bole scorch height were taken in all plots following each burn. Visual evidence of the presence or absence of fire (y/n) was noted at grid point intersections, with a 50% threshold of grid points indicating the presence of fire used to qualify plot-level burn treatment effects. Burn coverage was calculated as a proportion of plot area burned by dividing the number of grid points with visual evidence of fire presence at that intersection by the total number of grid points within a plot.

Fuel load

Fuel measurements of litter depth, woody fuelbed height, and fine woody debris counts (1-hr, 10-hr, and 100-hr) were taken in the growing season pre- and post-burn using a modified version of Brown's fuel transect sampling protocol (Brown 1974). This protocol was utilized in all plots within treatment units (3 transects per plot; n = 60 measurement units per treatment unit), with measurements taken at designated intervals along transects

emanating from the plot origin (3.66 m, 7.62 m, and 12.19 m). Slopes were derived from a digital elevation model along lines representing the length and orientation of each transect in a geographic information system (2019a). Further measurements of litter and duff consumption were taken at grid point intersections within a subset of 5 fire behavior plots per burn treatment (16 litter and 16 duff nails per plot; n = 80 measurement units for each fuel type per treatment unit) using depth reduction measurements along 30 cm nails. Nails for this purpose were driven into the ground prior to ignition so that the heads were at the same pre-burn height as the fuel type being measured. Post-burn fuel height was marked on the nail within 24 hr after burn completion to determine changes in litter and duff depth. All fuel depth and height measurements were recorded to the nearest 0.64 cm.

Raw fuel measurements were used to calculate fuel weight per area (load) for each fuel type, aggregated by plot (Brown's protocol) or grid point (nail method). The absolute value of post-burn load minus pre-burn load was used as the metric of response (consumption). The average change in fuel load for each fuel type (Brown's protocol) in unburned control units was subtracted from the corresponding burn treatment changes in fuel load in the same replicate to account for expected change in fuel load in the absence of fire. Bulk density (weight per volume), quadratic mean diameter, specific gravity, and non-horizontal correction coefficients were chosen from representative values for the region and forest type (Ottmar and Andreu 2007; Buchanan 2009). The degree and variability of surface fuel consumption as quantified by changes in litter load (kg ha⁻¹); woody fuelbed height (cm); and 1-hr, 10-hr, and 100-hr woody fuel load (kg ha⁻¹) measured using Brown's fuel transect sampling protocol as well as changes in litter and duff load (kg

ha⁻¹) measured using the nail method were compared between dormant and growing season burn treatments.

Fuel moisture

Fuel moisture was measured *in situ* for litter and 1-hr woody (pooled) as well as 10-hr woody fuels in fire behavior plots on the day of burn prior to ignition. Grab samples for this purpose (approx. 20 g) were collected by each plot corner and center (origin/SW, NW, NE, SE, and center), with disturbance of the surface fuel bed minimized at sampling locations (5 litter/1-hr woody and 5 10-hr woody fuel samples per plot; n = 25 measurement units for each fuel type per treatment unit). All samples were sealed in 946 mL bags and weighed in the lab upon unsealing (wet weight), dried in an oven at 75 °C for 48 hr, and re-weighed after drying (dry weight). Fuel weight measurements for this purpose were recorded to the nearest 0.01 g. Relative moisture content for these fuels was calculated using the formula $\frac{wet weight - dry weight}{dry weight}$ (Cannon and Parkinson 2019) and averaged by plot.

Fire behavior

Temperature was recorded continuously *in situ* before, during, and after passage of flaming fronts on each day of burn using thermocouple probes. HOBO data loggers were programmed to log temperature at a 1 s interval throughout the burn day (recording period 09:01:58), which were then attached to Type K thermocouple probes, packaged, and buried in the ground (approx. 15 cm deep) prior to ignition. Probes (sheath diameter = 0.1016 cm) protruded aboveground and were oriented such that the tip faced downward at a uniform height above the litter surface (2.54-5.08 cm) (Figure 1.3). Thermocouples were positioned to record temperatures at each grid point intersection within the subset of 5 fire behavior

plots per unit coincident with nail measurements of litter and duff consumption (16 probes per plot; n = 80 measurement units per treatment unit). Data logger and probe packages were retrieved within 48 hr after deployment with temperature measurements subsequently downloaded from each device. Data from loggers showing abnormal temperature profiles uncharacteristic of passage of a flaming front (i.e. suggesting recording failure) were excluded from analyses. Deployment of thermocouple arrays allowed for gathering an intensive suite of temperature measurements in plots across different landscape positions within treatments.

Fundamental measurements of fire behavior are needed to establish meaningful mechanistic links between fire behavior and its effects (O'Brien et al. 2018a; Yedinak et al. 2018). Thermocouple probes are inherently limited in their ability to capture the complete transference of thermal energy in a wildland fire; therefore, probe temperatures do not represent the true level of fire intensity experienced at a given point. Temperatures recorded by thermocouple probes, however, are related to fireline intensity and were used in this study as an index of heating for comparison (Kennard et al. 2005; Bova and Dickinson 2008). Metrics of fire behavior were derived from thermocouple temperature profiles, calculated via different approaches and thresholds using the MATLAB software program. Following initial comparisons of these metrics, the time integral of absolute temperature above 60 °C (ABS60 approach) was chosen as the representative thermocouple heating metric relative to fire intensity for subsequent analysis. The time integral of temperature is the Riemann sum approximation of the product of time step and temperature, representing both the relative degree and residence time (i.e. "dose") of fire-

induced heating experienced at a thermocouple probe tip. 60 °C was chosen as a conservative lower threshold of heating that may damage the vascular cambium of woody plants and is predictive of surface fuel consumption during and after passage of a flaming front (Dickinson and Johnson 2004; Bova and Dickinson 2008). The degree and variability of time-integrated thermocouple heating (ABS60 approach: $\int ABS60$; °C s) as well as the relationship between pooled litter and duff consumption (nail method; kg ha⁻¹) vs. $\int ABS60$ at plot grid point intersections (aggregated as plot averages) were compared between dormant and growing season burn treatments.

Bole scorch height was measured at all plot grid point intersections within burn units as an estimate of flame length complementary to thermocouple temperature recordings (Pomp et al. 2008). Measurements of scorch height were taken on the nearest charred bole (2.54 cm precision) within 3.05 m of each grid point (16 points per plot; n =320 measurement units per treatment unit) and averaged by plot. Scorch heights likely underestimate true flame length (Cain 1984) and were not measured on yellow pines [e.g. pitch pine (*Pinus rigida* Mill.) or shortleaf pine (*Pinus echinata* Mill.)] due to the increased likelihood of fire spread on the bark of these trees irrespective of representative surface flame heights.

1.2.4 Meteorological variables

Meteorological conditions represented by solar radiation, wind velocity, air temperature, fuel temperature, and relative humidity (RH) were gathered *ex situ* from the nearest Remote Automatic Weather Station (RAWS) at similar elevation to each treatment unit (MesoWest 2019). RAWS that provided the source of this data included the Andrew

Pickens (Station ID: WLHS1), Tallulah (Station ID: TULG1), and Chattooga (Station ID: CHGG1) stations in northeastern Georgia and northwestern South Carolina, all within 21 km of corresponding burn locations. Solar radiation was summed and remaining variables were averaged between 08:00 and 19:59 local time, adjusted relative to daylight savings time clock forward dates on March 11, 2018 and March 10, 2019 (12 measurements of each variable at 1-hr increments on the hour). Additionally, the reported Keetch-Byram Drought Index (KBDI) was gathered for each corresponding burn day, accessed through the Weather Information Management System (WIMS) (2019b). The degree and variability of both meteorological conditions (RAWS/WIMS) and fuel moisture (grab samples) on burn days as quantified by total solar radiation (KW-hr/m²), air temperature (°C), fuel temperature (°C), wind speed (m/s), RH (%), KBDI, pooled litter and 1-hr woody fuel moisture (%) were compared between dormant and growing season burn treatments.

1.2.5 Topographic variables

Topography may be expected to influence fire behavior as a function of how it amplifies or constrains environmental characteristics enabling fire spread across a heterogeneous landscape (Fridley 2009). Slope position on a gradient from valley to peak may influence the amount and duration of heating experienced over the course of a prescribed fire across different parts of a mountainous landscape. Cumulative diurnal solar radiation as a function of aspect influences the magnitude and extent of the drying of fuels available for combustion and therefore may also influence fire behavior. Topographic variables were derived from a digital elevation model (DEM) in a geographic information system (GIS) to evaluate topographic effects on metrics of fire behavior utilized in this study. A DEM covering the study area was downloaded as part of the National Elevation Dataset from the U.S. Geological Survey's The National Map Viewer at a spatial resolution of 1/9 arc-second and transformed to a Universal Transverse Mercator (UTM) Zone 17 projected coordinate system (3.18 m cell size) (2019a). The DEM had pits removed using TauDEM and was clipped to the necessary extent for analysis in ArcGIS for Desktop (Tarboton 2015; 2019a). Each index variable was normalized to a scale of 0-1 using the Raster Calculator tool and extracted using the Extract Multi Values to Points tool (2019a).

Topographic Position Index (TPI) was used to quantify slope position, based on the relative difference between a given point's elevation and the average elevation of its surrounding terrain within a defined window (Guisan et al. 1999; De Reu et al. 2013a). Lower values represent more sheltered parts of the landscape whereas higher values represent greater exposure. A rectangular window of 1000 x 1000 m was chosen to define the focal area, with its average elevation subtracted from each cell in the DEM using the ArcGIS Geomorphometry and Gradient Metrics Toolbox to derive TPI (Evans et al. 2014a, b; Evans 2017; Naito 2017; 2019a). Heat Load Index (HLI) was used to quantify solar radiation as a function of aspect, further incorporating the effects of slope and latitude to linearize compass azimuth such that it ranges from the lowest values on northeast-facing slopes to the highest values on southwest-facing slopes (Beers et al. 1966; McCune and Keon 2002). HLI was derived from the DEM using the ArcGIS Geomorphometry and Gradient Metrics Toolbox (Evans et al. 2014b; 2019a). TPI and HLI were averaged by plot area and related to bole scorch height (m) as topographic predictors of fire behavior,

compared between dormant and growing season burns by individual burns and treatment means.

1.2.6 Statistical analyses

A statistical model was developed that related continuous dependent variables of interest to treatments and replicates using analysis of variance (ANOVA) techniques to evaluate the effect of season of burn on the means of responses and their variability. Model effects on responses included treatment (fixed), replicate (random), replicate crossed with treatment (random), and/or plot nested within treatment and replicate (random). For some variables the model residuals did not follow a normal distribution with stable variance across treatments, and therefore either a Kruskal-Wallis rank-based ANOVA (Boos and Brownie 1992) or a generalized linear model with an exponential distribution was used to test the treatment effect on responses. Degree of response variability was quantified as the coefficient of variation (CV), calculated as the ratio of the standard deviation to the mean or absolute value of the mean of the response. Model effects on response variability included treatment (fixed) and/or replicate (random). Either a Wilcoxon rank sum test (Mann-Whitney U test) or a generalized linear model with an exponential distribution was used to test the treatment effect on the CV of responses.

Relationships among continuous variables were also related to the burn treatments and replicates with a statistical model using ANOVA techniques. Descriptive statistics of ordinary least squares regression modeling the linear fit between variables by unit was used in bivariate analysis of treatment effect, with the slope of the linear line of best fit used as the response and associated root mean square error (RMSE) as the variability of response. Bivariate model effects on response included treatment (fixed), replicate (random), and replicate crossed with treatment (random) whereas bivariate model effects on response variability included treatment (fixed) and replicate (random) only.

Across all models of treatment effects, response variable observations were aggregated at different levels but were considered independent at the unit level. For rank-based models, an ordinary least squares approach was used with restricted maximum likelihood or expected mean squares methods. Generalized linear models with an exponential distribution used a reciprocal link function with a maximum likelihood estimation method. A log transformation was used on heavily skewed distributions in bivariate relationships. Statistical significance was evaluated either at the $\alpha = 0.05$ level (non-ranked values) or $\alpha = 0.10$ level (ranked values). JMP and R software programs were used for making all statistical calculations and figures.

1.3 Results

1.3.1 Meteorology, fuel moisture, and burn coverage

Total solar radiation was significantly greater in growing season burns (6.7 KW-hr/m² with 0.5 KW-hr/m² SE) than in dormant season burns (5.4 KW-hr/m² with 0.8 KW-hr/m² SE) (ranked; p = 0.09). Air temperature was significantly greater in growing season burns (21.7 °C with 2.3 °C SE) than in dormant season burns (10.6 °C with 1.8 °C SE) (ranked; p = 0.07). Fuel temperature was significantly greater in growing season burns (26.0 °C with 2.2 °C SE) than in dormant season burns (14.1 °C with 2.8 °C SE) (ranked; p = 0.03). Other meteorological variables measured by RAWS or reported in WIMS of wind speed, RH, and KBDI were not significantly different between burn treatments

(ranked; p = 0.53, 0.58, and 0.22 respectively). The CV of air temperature was significantly greater in dormant season burns (48.4%) than in growing season burns (21.3%) (ranked; p = 0.05). The CV of other meteorological variables measured by RAWS of fuel temperature, wind speed, and RH were not significantly different between burn treatments (ranked; p = 0.12, 0.41, and 0.81 respectively).

Pooled litter and 1-hr woody fuel moisture was significantly greater in dormant season burns (39.2% with 6.3% SE) than in growing season burns (17.9% with 2.7% SE) (ranked; p = 0.01). 10-hr woody fuel moisture was also significantly greater in dormant season burns (38.9% with 8.0% SE) than in growing season burns (14.6% with 1.0% SE) (ranked; p = 0.06). The CV of both pooled litter and 1-hr woody fuel moisture as well as 10-hr woody fuel moisture were not significantly different between burn treatments (ranked; p = 0.17 and 0.26 respectively). A summary of results of statistical comparisons of treatment effects on fuel moisture (grab samples) and meteorological conditions (RAWS/WIMS) can be found in Table 1.2.

The proportion of plot area burned was significantly greater in growing season burns (92.7% with 3.0% SE) than in dormant season burns (65.0% with 5.0% SE) (ranked; p = 0.03) (Figure 1.4). The CV of the proportion of area burned was also significantly greater in dormant season burns (65.6%) than in growing season burns (24.3%) (ranked; p = 0.03). The linear relationship of the proportion of plot area burned vs. pooled litter and 1-hr woody fuel moisture by treatment illustrating these patterns is shown in Figure 1.5.

1.3.2 Time-integrated heating and fuel consumption

Time-integrated thermocouple heating ($\int ABS60$) was significantly greater in growing season burns (173,203.0 °C s with 78,306.3 °C s SE) than in dormant season burns (36,820.9 °C s with 3,309.3 °C s SE) (L-R χ^2 135.72; p < 0.01) (Figure 1.6). The CV of $\int ABS60$ was also significantly greater in growing season burns (337.9%) than in dormant season burns (67.3%) (L-R χ^2 4.34; p = 0.04). The degree and variability of time-integrated thermocouple heating ($\int ABS60$) were further compared between dormant and growing season burns by individual burns and treatment means throughout burn days (Figure 1.7).

Litter consumption; woody fuelbed height; and 1-hr, 10-hr, and 100-hr woody fuel consumption as measured using Brown's fuel transect sampling protocol were not significantly different between burn treatments (ranked; p = 0.77, 1.00, 0.40, 0.99, and 0.79 respectively). Litter consumption as measured using the nail method was also not significantly different between burn treatments (ranked; p = 0.77, 1.00, 0.40, 0.99, and 0.79 respectively). Litter consumption as measured using the nail method was also not significantly different between burn treatments (ranked; p = 0.77). Duff consumption was significantly greater in growing season burns (135.6 kg ha⁻¹ with 54.8 kg ha⁻¹ SE) than in dormant season burns (0.0 kg ha⁻¹ with 0.0 kg ha⁻¹ SE) (ranked; p < 0.01). The CV of litter consumption as measured using Brown's fuel transect sampling protocol was significantly greater in growing season burns (78.4%) than in dormant season burns (50.5%) (ranked; p = 0.04). The CV of woody fuelbed height was significantly greater in dormant season burns (629.2%) than in growing season burns (256.9%) (ranked; p = 0.04). The CV of litter treatments (ranked; p = 0.90, 0.13, and 0.63 respectively). The CV of litter consumption as measured using the nail method was significantly greater in dormant

season burns (94.4%) than in growing season burns (41.1%) (ranked; p = 0.02). The CV of duff consumption was unable to be compared between burn treatments due to limitations of ranking values of zero. A summary of results of statistical comparisons of treatment effects on fuel consumption for all methods used can be found in Table 1.3.

Slope of the linear line of best fit between pooled litter and duff consumption vs. log-transformed $\int ABS60$ was not significantly different between dormant season burns (slope = 457.3, $r^2 = 0.09$) and growing season burns (slope = 584.4, $r^2 = 0.11$) (p = 0.29). Root mean square error (RMSE) associated with this regression was also not significantly different between dormant season burns (RMSE = 1,000.6) and growing season burns (RMSE = 2,018.8) (p = 0.69). Data from treatment unit AP1D was excluded from these regression comparisons as its quantity was insufficient to perform the analysis.

1.3.3 Topographic effects on fire behavior

Slope of the linear line of best fit between bole scorch height vs. TPI was not significantly different between dormant season burns (slope < 0.1, r^2 < 0.01) and growing season burns (slope < 0.1, r^2 < 0.01) (p = 0.91). Root mean square error (RMSE) associated with this regression was also not significantly different between dormant season burns (RMSE = 0.4) and growing season burns (RMSE = 0.6) (p = 0.21). The proportion of variance in bole scorch height predictable from TPI (r^2) ranged from 0.00 – 0.43 among individual dormant season burns vs. from 0.00 – 0.17 among growing season burns.

Slope of the linear line of best fit between bole scorch height vs. HLI was not significantly different between dormant season burns (slope = 2.2, $r^2 = 0.16$) and growing season burns (slope = 1.4, $r^2 = 0.04$) (p = 0.80). Root mean square error (RMSE) associated

with this regression was also not significantly different between dormant season burns (RMSE = 0.4) and growing season burns (RMSE = 0.5) (p = 0.14). The proportion of variance in bole scorch height predictable from HLI (r^2) ranged from 0.02 – 0.34 among individual dormant season burns vs. from 0.00 – 0.18 among growing season burns.

1.4 Discussion

Characterizing differences in prescribed fire based solely upon season of burn may be limited in explanatory power as these differences may simultaneously reflect the influence of meteorological conditions prevalent in a given season as well as influences of topography, vegetation, and other components of the fire environment (Prebyl 2012; Norman et al. 2017). Relating variability in fire behavior and its effects to causal environmental mechanisms both constrained by and independent of a given season allows for meaningful interpretations of prescribed fire seasonality for both scientists and managers (O'Brien et al. 2018a; Hiers et al. 2020). This study examined factors of the fire environment related to season of burn to gain a better understanding of how these parameters influence prescribed fire and to contextualize observations of prescribed fire behavior and its first-order effects. Knowledge of how patterns of prescribed fire may be related to season and the uncertainty associated with seasonal drivers of given fire effects at varying spatiotemporal scales may be applied to further restoration goals.

Following the winter solstice in the Northern Hemisphere, average ambient temperatures begin to rise throughout the winter and spring as a result of increasing photoperiod from a more direct sun angle. Reflecting this trend and supporting our hypothesis, diurnal solar radiation and mean ambient temperatures (both of air and fuel) were greater in early growing season burns than in dormant season burns, all occurring in phenological sequence between the winter and summer solstices. Significant differences in litter and fine woody fuel moisture sampled on burn days prior to ignition were consistent with higher levels of drying expected with increasing solar radiation (and thereby temperatures) under open canopies. Warmer, precipitation-free periods typically increase in frequency by late winter in the Southeast, with favorable atmospheric conditions for prescriptive fire spread following passage of cold fronts (Robbins and Myers 1992; Chiodi et al. 2018). Higher temperatures and drier fuels alone with burning in the early growing season would be expected to contribute to increased ignition probability and combustion of greater intensity and rate of spread than burning in the dormant season (Brose and Van Lear 1998). Other key prescription window parameters influencing fire behavior of wind speed, RH, and KBDI did not vary by season of burn, however. Consistently low KBDI values reflect long term trends in the southern Appalachians for the period of January-April in which burns were conducted for this study (Keetch and Byram 1968). These results suggest that seasonal variability of prescribed fire behavior before overstory canopy closure may be influenced by solar radiation and fuel moisture more than other environmental conditions that remained similar between seasons.

Burn coverage in plots dispersed throughout treatment units showed significant differences that may provide evidence for seasonal patterns of fire spread. Operational methods and spatiotemporal patterns of ignition have large influences on fire spread within a prescribed burn but were beyond experimental control in this study. Additionally, the area and topographic heterogeneity of dormant season burn units (mean area = 363.5 ha)

was greater than that of growing season burn units (mean area = 190.6 ha). Notwithstanding these considerations, proportions of plot area burned were significantly greater in the growing season than in the dormant season, likely driven in part by warmer and drier environmental conditions in the early growing season before overstory canopy closure. The representative variability of plot area burned was significantly greater in dormant season burns than in early growing season burns. Yet the range of plot area burned was equivalent for both treatments and the variability of meteorological conditions and surface fuel moisture did not consistently differ by season of burn. These patterns indicate that ignition probability is greater when burning in the early growing season, but do not necessarily suggest that fire spread or other characteristics of fire behavior will be more uniform when prescribed burns are implemented in this season.

Both the degree and variability of time-integrated thermocouple heating were greater in early growing season burns than in dormant season burns. Similar to a nearby study with burns conducted at the same time of year, warmer air temperatures in the early growing season likely influenced fire intensity as less additional heat was required for combustion to occur under such conditions (Keyser et al. 2019). Temporal variation in the relative amount and duration of heating experienced throughout the burn day also differed by season of burn. Observed differences between burn treatments in both the degree and variability of time-integrated thermocouple heating were most pronounced in the mid-afternoon (approx. 14:30-15:30), whereas seasonal patterns in this regard were more similar between approx. 13:00-14:30 and 15:30-17:30. Dormant season burns were more limited in their distribution of periods of high temperature pulses (\geq 60 °C s), with early

growing season burns having such periods starting before and continuing after those of dormant season burns. These patterns suggest that surface temperatures from combustion in a prescribed fire respond more positively to the warmest and driest part of the day in the mid-late afternoon in the early growing season than those in dormant season burns. Even if recent precipitation saturates surface fuels to a similar degree as in the dormant season, greater solar radiation in the early growing season may lower the moisture of forest fuels more rapidly, which may have implications for fire effects (Byram and Jemison 1943).

There was little indication based on the results of our study that surface fuel consumption per given area varied by season of burn. Greater proportions of plot area were burned in the early growing season, but for plots with at least 50% of grid points indicating fire presence, plot-level fuel load reduction largely did not differ between burn treatments. Among fuel types measured, only duff consumption was significantly greater in early growing season burns, which may reflect greater duff fuel availability from drier conditions at the fuelbed surface (Ferguson et al. 2002; Waldrop et al. 2010). Such a relationship between fuel moisture and consumption would not explain the lack of seasonal differences observed for litter and woody fuel consumption, however. We further hypothesized that the variability of surface fuel consumption would be greater in early growing season burns than in dormant season burns, but our results also largely do not support this. Some greater variability in litter load reduction in early growing season burns and change in woody fuelbed height in dormant season burns was observed, but seasonal differences did not consistently vary in the same direction. Further, there were no treatment differences in the variability of woody fuel load reduction.

Our findings of surface fuel consumption ran contrary to our hypothesis as we expected warmer and drier conditions in the early growing season to result in greater surface fuel consumption than in the dormant season. In contrast, another study in the southern Appalachians found higher KBDI as a strong predictor of increased fuel consumption (Jenkins et al. 2011). The range of dates of burn and KBDI in different seasons was much greater in that study than ours, however, which may limit its comparability. Nevertheless, similar meteorological conditions of wind speed, RH, and KBDI on days of burn may have contributed to more predictable surface fuel consumption than would be expected otherwise by seasonal differences in temperature and fuel moisture. Further, fuel consumption (largely driven by fire residence time) may be less correlated with fuel moisture in comparison to ignition probability and rate of spread affecting the coverage of area burned. In longleaf pine savannas of the Coastal Plain, a study of fire regime dynamics over several years found that fuel consumption did not correlate with eight intra-annual periods dispersed throughout the year but that fire intensity varied considerably as a function of rate of spread (Glitzenstein et al. 1995). Greater pulses of heating not necessarily resulting in increased surface fuel consumption in a prescribed fire may suggest that environmental variations of different scales are influencing the relationship between fire behavior and its effects.

Fire would be expected to behave differently under the same meteorological conditions across topography of the southern Appalachians due to its multi-faceted heterogeneity (Schwartz et al. 2016; Jiménez et al. 2018). Seasonal variations in weather patterns may amplify or confound topographic effects and suggest how the seasonality of

fire is represented on different parts of a landscape within a given burn unit. For example, low moisture retention on exposed slopes and ridges receiving high levels of solar radiation may be further pronounced with drying winds under an open canopy following autumn leaf fall, thereby creating a fuel bed conducive to greater fire intensity and rates of spread (Dickinson et al. 2016; Norman et al. 2017). Further, increased plant transpiration in the process of budburst and leaf expansion in the spring green-up period may lead to greater variability in live fuel moisture. Such phenological changes influencing moisture distribution could affect fire behavior and inhibit fuel consumption to a greater degree in early growing season burns than would be expected otherwise. Regardless of plant activity, however, seasonal variations in live fuel moisture in a given environment may help explain fine-scale differences in fire effects (Sparks et al. 2002; Slocum et al. 2003).

Lower fuel moisture driven by greater intensity of solar radiation and reflected by warmer temperatures likely allowed fire to spread to parts of the landscape and burn at greater intensity in many cases than dormant season conditions would permit. This seasonal pattern is reflected in the bivariate relationships between bole scorch height (measured in all plots) and topographic indices of slope position and solar heat load. The results of our study suggest that the linear relationship and its variability between bole scorch height vs. TPI and HLI largely did not differ by season of burn. However, the proportion of bole scorch height predictable by these indices is moderately strong in some individual burns and was likely influenced by variable ignition patterns within the same season of burn. Further, it appears from the slopes of the linear lines of best fit that bole scorch height was less constrained by HLI in the early growing season than in the dormant season. This is evidenced by the relative seasonal differences in the range in bole scorch height relative to the corresponding range of HLI: bole scorch height increased with increasing heat load over a greater range of heat load in the early growing season than in the dormant season. Therefore, solar heat load experienced at a given point on the landscape as a function of aspect, slope, and latitude may be more influential to fire behavior in the dormant season than in the early growing season.

1.4.1 Conclusions

Early growing season burns had a greater degree and variability of time-integrated heating induced by fire than did dormant season burns, influenced by warmer and drier burn day conditions from increased levels of solar radiation. Differences in surface temperatures by season of burn were most pronounced during the mid-late afternoon on burn days. These patterns of fire behavior correlated with greater ignition probabilities within early growing season burns with fuel moisture being less of a limiting factor to fire spread. Per given area that fire spread in treatment units, however, surface fuel consumption largely did not differ by season of burn, suggesting that increased fire intensity does not necessarily result in increased fuel consumption. Nevertheless, burning a given unit in the early growing season is likely to reduce fuel loads as or more effectively than in the dormant season.

If burning in the early growing season results in higher fire intensity and variability of fire behavior across a greater area than in the dormant season, then early growing season burns may also lead to greater landscape heterogeneity. Topography as primarily related to solar radiation may be more influential to fire behavior in the dormant season in which ignition probability due to overall solar radiation is lower to begin with than in the early growing season. Ultimately, greater variability in fire behavior can be expected in early growing season burns that can be used to promote functional diversity for restoration objectives. Managers in the southern Appalachians may consider growing season burns as a viable alternative to traditional dormant season burns to expand their ability to enhance ecosystem resiliency across fire-suppressed landscapes.

TABLES AND FIGURES

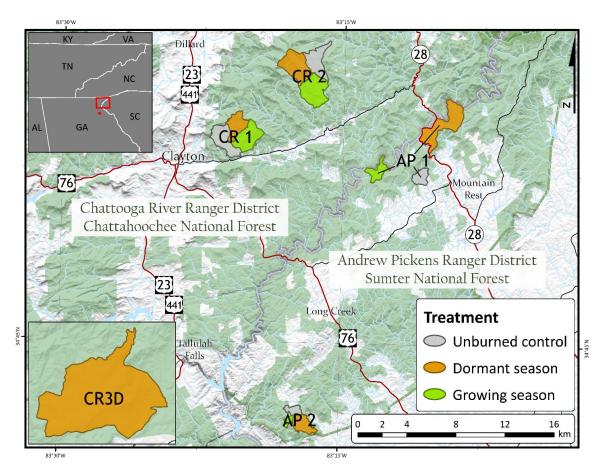


Figure 1.1. Map depicting the replicates comprised of treatment units with plots established in this study. "AP" refers to replicates in the Andrew Pickens Ranger District whereas "CR" refers to replicates in the Chattooga River Ranger District. CR 1 had pre-burn data collected but burns in this replicate did not occur and therefore no data was used from it for this study. Additional potential replicates and treatment units were identified but plots were never established in them for this study based on the likelihood of such burn operations occurring within the study time frame. See Table 1.1 for further information on treatment units.

Replicate	Treatment	Unit	Area (ha)	Date of burn	Elevation range (m)
AP 1	Unburned control (C)	AP1C	133.8	n/a	498 - 625
	Dormant season burn (DS)	AP1D	538.1	01/31/18	480 - 772
	Growing season burn (GS)	AP1G	160.5	04/18/18	454 - 560
AP 2	Unburned control (C)	AP2C	80.8	n/a	360 - 470
	Dormant season burn (DS)	AP2D	205.3	03/18/19	275 - 468
	Growing season burn (GS)	AP2G	43.3	04/21/18	312 - 462
CR 2	Unburned control (C)	CR2C	323.2	n/a	704 – 1,157
	Dormant season burn (DS)	CR2D	441.5	04/05/18	724 – 1,430
	Growing season burn (GS)	CR2G	435.3	04/24/19	622 - 963
CR 3	Dormant season burn (DS)	CR3D	566.5	03/03/18	222 - 386

Table 1.1. Listing of treatment units used in this study by replicate and corresponding treatment, with area, date of burn (if applicable), and elevation range. These units represent those with data that was used in analysis for this study, i.e. does not include replicates and/or treatment units where burns did not occur or in which plots were never established.

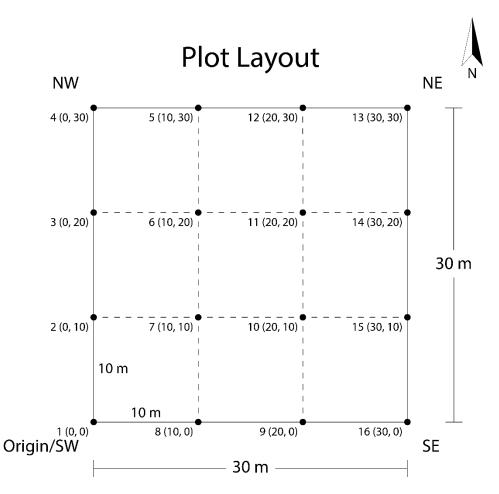


Figure 1.2. Representative diagram indicating the layout, orientation, and dimensions of each plot with interior grid point intersections. The (x, y) Cartesian coordinate pairs for each grid point represent the longitudinal (x) and latitudinal (y) distance from the origin.

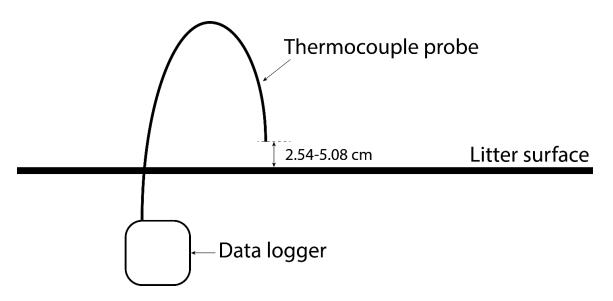


Figure 1.3. Diagram of thermocouple setup deployed at each plot grid point intersection. Data loggers were buried belowground in order to be shielded from the extreme temperatures of the fire aboveground. Probes attached to and extending from the data loggers were arranged with the tip at a uniform height and orientation above the litter surface.

Table 1.2. Summary of statistical comparisons of meteorological conditions from Remote Automatic Weather Stations (RAWS) or as reported in the Weather Information Management System (WIMS) and fuel moisture collected in the field (grab samples) on burn days by variable and burn treatment. Statistical analyses were performed using a non-parametric Kruskal-Wallis rank-based standard least squares ANOVA aggregated by plot (grab samples) or unit (RAWS/WIMS) with fixed effect of treatment and random effects of replicate and/or replicate crossed with treatment (response) or fixed effect of treatment and random effect of replicate (variability of response). Treatment values with statistical significance ($\alpha = 0.10$) are reported in boldface.

Response variable (* $\alpha = 0.10$)	Burn treatment	Mean (with SE)	Coefficient of variation (%)					
Meteorological conditions (RAWS/WIMS)								
Total solar radiation [KW-hr/m ²]	DS	5.4 (0.8)	n/a					
Response: F ratio = 7.24, <i>p</i> = *0.09	GS	6.7 (0.5)	n/a					
Air temperature [°C]	DS	10.6 (1.8)	48.4					
Response: F ratio = 12.00, <i>p</i> = *0.07 Variability: F ratio = 10.07, <i>p</i> = *0.05	GS	21.7 (2.3)	21.3					
Fuel temperature [°C]	DS	14.1 (2.8)	59.9					
Response: F ratio = 36.07, <i>p</i> = *0.03 Variability: F ratio = 9.96, <i>p</i> = 0.12	GS	26.0 (2.2)	32.2					
Wind speed [m/s]	DS	1.5 (0.3)	50.6					
Response: F ratio = 0.54 , $p = 0.53$ Variability: F ratio = 0.88 , $p = 0.41$	GS	1.6 (0.4)	34.1					
Relative humidity (RH) [%]	DS	27.2 (1.4)	49.4					
Response: F ratio = 0.38, $p = 0.58$ Variability: F ratio = 0.07, $p = 0.81$	GS	31.4 (3.1)	40.7					
Keetch-Byram Drought Index (KBDI)	DS	23.8 (12.6)	n/a					
Response: F ratio = 2.51, $p = 0.22$	GS	61.7 (13.4)	n/a					
Fuel moisture (grab samples)								
Litter and 1-hr woody [%]	DS	39.2 (6.3)	36.0					
Response: F ratio = 71.08, <i>p</i> = *0.01 Variability: F ratio = 3.75, <i>p</i> = 0.17	GS	17.9 (2.7)	27.1					
10-hr woody [%]	DS	38.9 (8.0)	39.6					
Response: F ratio = 9.79, p = *0.06 Variability: F ratio = 1.83, p = 0.26	GS	14.6 (1.0)	20.9					

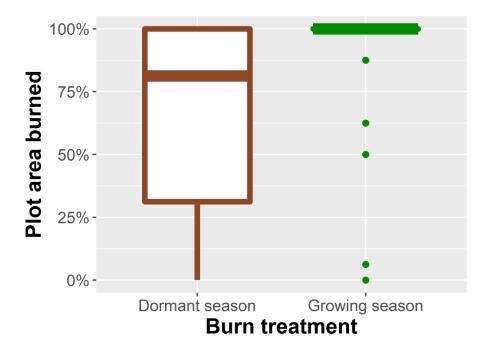


Figure 1.4. Boxplot of proportion of plot area burned (y-axis; %) by burn treatment (x-axis). Proportions were calculated based on the number of grid points indicating evidence of fire presence per plot.

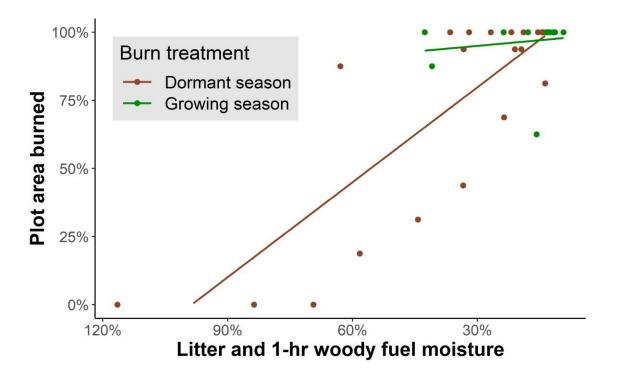


Figure 1.5. Scatterplot with linear regression of proportion of plot area burned (y-axis; %) vs. pooled litter and 1-hr woody fuel moisture (x-axis, reversed; %), aggregated by plot in subset of fire behavior plots by burn treatment (series). Proportions were calculated based on the number of grid points indicating evidence of fire presence per plot.

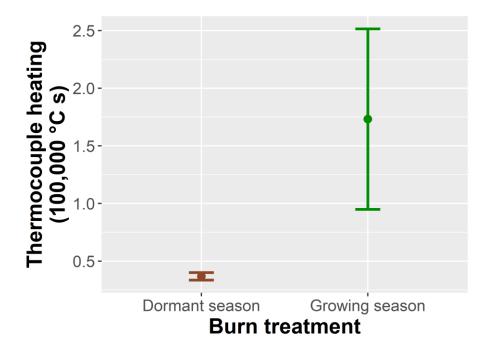


Figure 1.6. Plot of means of the time integral of thermocouple probe temperature (ABS60 approach) with error bars representing associated standard error (y-axis; $^{\circ}C$ s) by burn treatment (x-axis).

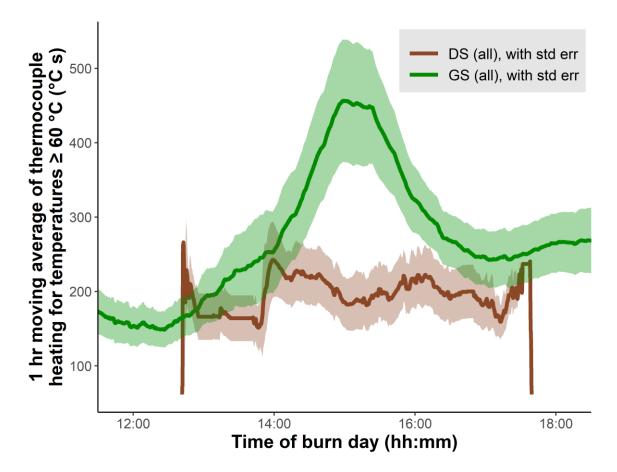


Figure 1.7. Plot of 1 hr, centered rolling mean (moving average) of the time integral of thermocouple probe temperature (ABS60 approach) (y-axis; °C s) vs. time of day (x-axis; hh:mm), by burn treatment from 11:30 am - 6:30 pm on burn days. Time of day was adjusted to account for daylight savings time clock forward dates in March 2018 and March 2019. Series include error bars (shaded area) representing associated standard error around the mean.

Table 1.3. Summary of statistical comparisons of fuel consumption by sampling protocol, fuel type, and burn treatment. Statistical analyses were performed using a non-parametric Kruskal-Wallis rank-based standard least squares ANOVA aggregated by plot with fixed effect of treatment and random effects of replicate, replicate crossed with treatment, and plot nested within treatment and replicate (response) or fixed effect of treatment and random effect of replicate (variability of response). Treatment values with statistical significance ($\alpha = 0.10$) are reported in boldface.

Response variable (* $\alpha = 0.10$)	Burn treatment	Mean (with SE)	Coefficient of variation (%)					
Fuel consumption (Brown 1974) [$ \Delta $]								
Litter [kg ha ⁻¹]	DS	5,344.1 (518.6)	50.5					
Response: F ratio = 0.14, $p = 0.77$ Variability: F ratio = 25.45, $p = *0.04$	GS	4,195.2 (430.0)	78.4					
Woody fuelbed height [cm]	DS	5.7 (2.2)	629.2					
Response: F ratio = 0.00, $p = 1.00$ Variability: F ratio = 23.88, $p = *0.04$	GS	4.0 (1.3)	256.9					
1-hr woody [kg ha ⁻¹]	DS	220.9 (59.8)	83.7					
Response: F ratio = 1.10, $p = 0.40$ Variability: F ratio = 0.02, $p = 0.90$	GS	221.5 (41.6)	400.9					
10-hr woody [kg ha ⁻¹]	DS	786.0 (326.8)	141.3					
Response: F ratio = 0.00, $p = 0.99$ Variability: F ratio = 4.19, $p = 0.13$	GS	299.0 (188.9)	627.4					
100-hr woody [kg ha ⁻¹]	DS	5,483.1 (1,653.5)	128.0					
Response: F ratio = 0.09 , $p = 0.79$ Variability: F ratio = 0.29 , $p = 0.63$	GS	2,737.9 (539.2)	271.3					
Litter and duff consumption (nail method) $[\Delta]$								
Litter [kg ha ⁻¹]	DS	2,664.6 (124.0)	94.4					
Response: F ratio = 3.52, $p = 0.17$ Variability: F ratio = 27.17, $p = *0.02$	GS	4,365.0 (141.4)	41.1					
Duff [kg ha ⁻¹]	DS	0.0 (0.0)	n/a					
Response: F ratio = 204.82, <i>p</i> *< 0.01	GS	135.6 (54.8)	n/a					

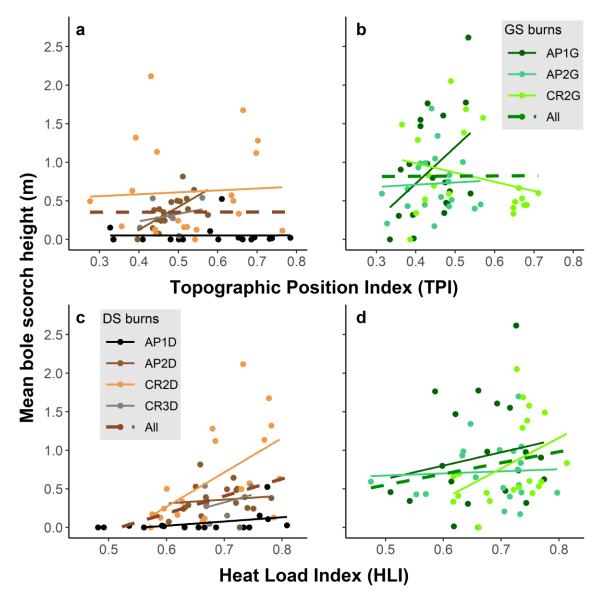


Figure 1.8. Scatterplots with linear regressions of mean bole scorch height (y-axis; m) vs. topographic variables Topographic Position Index (TPI) and Heat Load Index (HLI) (x-axis; rows) aggregated by plot for all plots in each unit (series) by burn treatment (columns).

REFERENCES

- Abrams MD, Nowacki GJ (2008) Native Americans as active and passive promoters of mast and fruit trees in the eastern USA. Holocene 18:1123–1137
- Barbaroux C, Bréda N (2002) Contrasting distribution and seasonal dynamics of carbohydrate reserves in stem wood of adult ring-porous sessile oak and diffuseporous beech trees. Tree Physiol 22:1201–1210. https://doi.org/10.1093/treephys/22.17.1201
- Barden LS, Woods FW (1974) Characteristics of lightning fires in southern Appalachian forests. In: Proceedings, 13th Tall Timbers fire ecology conference, 1973 October 14-15, Tallahassee, FL. Tall Timbers Research Station, Tallahassee, FL, pp 345– 361
- Beers TW, Dress PE, Wensel LC (1966) Notes and observations: aspect transformation in site productivity research. J For 64:691–692
- Boos DD, Brownie C (1992) A rank-based mixed model approach to multisite clinical trials. Biometrics 48:61–72. https://doi.org/10.2307/2532739
- Bova AS, Dickinson MB (2008) Beyond "fire temperatures": calibrating thermocouple probes and modeling their response to surface fires in hardwood fuels. Can J For Res 38:1008–1020. https://doi.org/10.1139/X07-204
- Brose PH, Schuler TM, Van Lear DH, Berst J (2001) Bringing fire back: the changing regimes of the Appalachian mixed-oak forests. J For 99:30–35
- Brose PH, Van Lear DH (1998) Responses of hardwood advance regeneration to seasonal prescribed fires in oak-dominated shelterwood stands. Can J For Res 28:331–339. https://doi.org/10.1139/cjfr-28-3-331
- Brown JK (1974) Handbook for inventorying downed woody material. Ogden, UT
- Buchanan B (2009) Fuel constants comparisons
- Byram GM, Jemison GM (1943) Solar radiation and forest fuel moisture. J Agric Res 67:149–176
- Cain MD (1984) Height of stem-bark char underestimates flame length in prescribed burns. Fire Manag Notes 45:17–21

- Cannon K, Parkinson T (2019) Fuel moisture sampling. In: Fire Behav. F. Ref. Guid. PMS 437. https://www.nwcg.gov/publications/pms437/fuel-moisture/fuelmoisture-sampling. Accessed 18 Dec 2019
- Chiodi AM, Larkin NS, Varner JM (2018) An analysis of southeastern US prescribed burn weather windows: seasonal variability and El Niño associations. Int J Wildl Fire 27:176–189. https://doi.org/10.1071/WF17132
- Cohen D, Dellinger B, Klein RN, Buchanan B (2007) Patterns in lightning-caused fires at Great Smoky Mountains National Park. Fire Ecol 3:68–82
- Cox J, Widener B (2008) Lightning-season burning: friend or foe of breeding birds? Misc. Publ. No. 17 16
- De Reu J, Bourgeois J, Bats M, et al (2013) Application of the topographic position index to heterogeneous landscapes. Geomorphology 186:39–49. https://doi.org/10.1016/j.geomorph.2012.12.015
- Delcourt PA, Delcourt HR (1998) The influence of prehistoric human-set fires on oakchestnut forests in the southern Appalachians. Castanea 63:337–345
- Dickinson MB, Hutchinson TF, Dietenberger M, et al (2016) Litter species composition and topographic effects on fuels and modeled fire behavior in an oak-hickory forest in the eastern USA. PLoS One 11:1–30. https://doi.org/10.1371/journal.pone.0159997
- Dickinson MB, Johnson EA (2004) Temperature-dependent rate models of vascular cambium cell mortality. Can J For Res 34:546–559. https://doi.org/10.1139/x03-223
- Eldredge IF (1911) Fire problems on the Florida National Forest. In: Proceedings, Society of American Foresters Annual Meeting. Society of American Foresters, Washington, DC, pp 166–170

Esri (2019) ArcGIS for Desktop

Evans A (2017) TPI window size and shape

Evans A, Odom R, Resler L, et al (2014a) Developing a topographic model to predict the northern hardwood forest type within Carolina Northern Flying Squirrel (Glaucomys sabrinus coloratus) recovery areas of the southern Appalachians. Int J For Res 2014:1–11

Evans JS, Oakleaf J, Cushman SA, Theobald D (2014b) An ArcGIS toolbox for surface

gradient and geomorphometric modeling

- Ferguson SA, Ruthford JE, McKay SJ, et al (2002) Measuring moisture dynamics to predict fire severity in longleaf pine forests. Int J Wildl Fire 11:267–279. https://doi.org/10.1071/wf02010
- Flatley WT, Lafon CW, Grissino-Mayer HD, LaForest LB (2013) Fire history, related to climate and land use in three southern Appalachian landscapes in the eastern United States. Ecol Appl 23:1250–1266. https://doi.org/10.1890/12-1752.1
- Fowler C, Konopik E (2007) The history of fire in the southern United States. Hum Ecol Rev 14:165–176
- Freeman J, Kobziar LN, Rose EW, Cropper WP (2017) A critique of the historical-fireregime concept in conservation. Conserv Biol 31:976–985. https://doi.org/10.1111/cobi.12942
- Fridley JD (2009) Downscaling climate over complex terrain: High finescale (<1000 m) spatial variation of near-ground temperatures in a montane forested landscape (Great Smoky Mountains). J Appl Meteorol Climatol 48:1033–1049. https://doi.org/10.1175/2008JAMC2084.1
- Glitzenstein JS, Platt WJ, Streng DR (1995) Effects of fire regime and habitat on tree dynamics in north Florida longleaf pine savannas. Ecol Monogr 65:441–476. https://doi.org/10.2307/2963498
- Griffith GE, Omernik JM, Comstock JA, et al (2001) Ecoregions of Alabama and Georgia
- Griffith GE, Omernik JM, Comstock JA, et al (2002) Ecoregions of North Carolina and South Carolina
- Guisan A, Weiss SB, Weiss AD (1999) GLM versus CCA spatial modeling of plant species distribution. Plant Ecol 143:107–122
- Guyette RP, Dey DC, Stambaugh MC, Muzika R-M (2006a) Fire scars reveal variability and dynamics of eastern fire regimes. In: Dickinson MB (ed) Proceedings, fire in eastern oak forests: delivering science to land managers, 2005 November 15-17, Columbus, OH. General Technical Report NRS-P-1. U.S. Department of Agriculture Forest Service, Northern Research Station, Newtown Square, PA, pp 20–39
- Guyette RP, Spetich MA, Stambaugh MC (2006b) Historic fire regime dynamics and forcing factors in the Boston Mountains, Arkansas, USA. For Ecol Manage 234:293–304

- Guyette RP, Stambaugh MC, Dey DC (2009) Developing and using fire scar histories in the southern and eastern United States
- Hart JL, Buchanan ML (2012) History of fire in eastern oak forests and implications for restoration. In: Dey DC, Stambaugh MC, Clark SL, Schweitzer CJ (eds)
 Proceedings, 4th fire in eastern oak forests conference, 2011 May 17-19,
 Springfield, MO. General Technical Report NRS-P-102. U.S. Department of Agriculture Forest Service, Northern Research Station, Newtown Square, PA, pp 34–51
- Henderson JP (2006) Dendroclimatological analysis and fire history of Longleaf pine (Pinus palustris Mill.) in the Atlantic and Gulf Coastal Plain. University of Tennessee, Knoxville
- Hiers JK, O'Brien JJ, Varner JM, et al (2020) Prescribed fire science: the case for a refined research agenda. Fire Ecol 16:11. https://doi.org/10.1186/s42408-020-0070-8
- Huffman JM, Platt WJ, Grissino-Mayer HD, Boyce CJ (2004) Fire history of a barrier island slash pine (Pinus elliottii) savanna. Nat Areas J 24:258–268
- Jenkins MA, Klein RN, McDaniel VL (2011) Yellow pine regeneration as a function of fire severity and post-burn stand structure in the southern Appalachian Mountains. For Ecol Manage 262:681–691. https://doi.org/10.1016/J.FORECO.2011.05.001
- Jiménez PA, Muñoz-Esparza D, Kosović B (2018) A high resolution coupled fireatmosphere forecasting system to minimize the impacts of wildland fires: applications to the Chimney Tops II wildland event. Atmosphere (Basel) 9:. https://doi.org/10.3390/atmos9050197
- Jurgelski WM (2008) Burning seasons, burning bans: fire in the southern Appalachian mountains, 1750-2000. Appalach J 35:170–217
- Keetch JJ, Byram GM (1968) A drought index for forest fire control. Asheville, NC
- Kennard DK, Outcalt KW, Jones D, O'Brien JJ (2005) Comparing techniques for estimating flame temperature of prescribed fires. Fire Ecol 1:75–84. https://doi.org/10.4996/fireecology.0101075
- Keyser TL, Greenberg CH, McNab WH (2019) Season of burn effects on vegetation structure and composition in oak-dominated Appalachian hardwood forests. For Ecol Manage 433:441–452. https://doi.org/10.1016/J.FORECO.2018.11.027

- Knapp EE, Estes BL, Skinner CN (2009) Ecological effects of prescribed fire season: a literature review and synthesis for managers. Albany, CA
- Kobziar LN, Godwin D, Taylor L, Watts AC (2015) Perspectives on trends, effectiveness, and impediments to prescribed burning in the southern U.S. Forests 6:561–580. https://doi.org/10.3390/f6030561
- Komarek E V. (1974) Effects of fire on temperate forests and related ecosystems: southeastern United States. In: Kozlowski TT, Ahlgren CE (eds) Fire and ecosystems. Academic Press, New York, pp 251–277
- Komarek E V. (1965) Fire ecology: grasslands and man. In: Proceedings, 4th Tall Timbers fire ecology conference, 1965 March 18-19, Tallahassee, FL. Tall Timbers Research Station, Tallahassee, FL, pp 169–220
- Lafon CW (2010) Fire in the American South: vegetation impacts, history, and climatic relations. Geogr Compass 4:919–944. https://doi.org/10.1111/j.1749-8198.2010.00363.x
- Lafon CW, Naito AT, Grissino-Mayer HD, et al (2017) Fire history of the Appalachian region: a review and synthesis. U.S. Department of Agriculture Forest Service, Southern Research Station, Asheville, NC
- Landers JL (1981) The role of fire in bobwhite quail management. In: Wood GW (ed)
 Proceedings, Prescribed fire and wildlife in Southern forests, 1981 April 6-8,
 Myrtle Beach, SC. The Belle W. Baruch Forest Science Institute of Clemson
 University, Georgetown, SC, pp 73–80
- Lesser MR, Fridley JD (2016) Global change at the landscape level: relating regional and landscape-scale drivers of historical climate trends in the southern Appalachians. Int J Climatol 36:1197–1209. https://doi.org/10.1002/joc.4413
- McCune B, Keon D (2002) Equations for potential annual direct incident radiation and heat load. J Veg Sci 13:603–606
- Melvin MA (2018) Prescribed fire use survey report
- MesoWest (2019) MesoWest surface weather maps. https://mesowest.utah.edu/cgibin/droman/mesomap.cgi? Accessed 27 Dec 2019
- Mobley HE, Balmer WE (1981) Current purposes, extent, and environmental effects of prescribed fire in the South. In: Wood GW (ed) Proceedings, Prescribed fire and wildlife in Southern forests, 1981 April 6-8, Myrtle Beach, SC. The Belle W. Baruch Forest Science Institute of Clemson University, Georgetown, SC, pp 15–21

Naito AT (2017) Basic TPI steps

- NCEI (2020) Mean temperature and precipitation data for CLAYTON 1 SSW, GA US [GHCND:USC00091982]; CORNELIA, GA US [GHCND:USC00092283]; and LONG CREEK, SC US [GHCND:USC00385278]. Asheville, NC
- Norman SP, Hargrove WW, Christie WM (2017) Spring and autumn phenological variability across environmental gradients of Great Smoky Mountains National Park, USA. Remote Sens 9:. https://doi.org/10.3390/rs9050407
- Norman SP, Vaughan MC, Hargrove WW (2019) Contextualizing Appalachian fire with sentinels of seasonal phenology. In: Proceedings, United States-International Association for Landscape Ecology, 2019 April 7-11, Fort Collins, CO. p 21
- Nowacki GJ, Abrams MD (2008) The demise of fire and "mesophication" of forests in the eastern United States. Bioscience 58:123–138
- O'Brien JJ, Hiers JK, Varner JM, et al (2018) Advances in mechanistic approaches to quantifying biophysical fire effects. Curr For Reports 4:161–177. https://doi.org/10.1007/s40725-018-0082-7
- Ottmar RD, Andreu A (2007) Litter and duff bulk densities in the southern United States
- Owsley FL (1949) Plain folk of the old South. Louisiana State University Press, Baton Rouge, LA
- Pomp JA, McGill DW, Schuler TM (2008) Investigating the relationship between bole scorch height and fire intensity variables in the Ridge and Valley physiographic province, West Virginia. In: Jacobs DF, Michler CH (eds) Proceedings, 16th central hardwoods forest conference, 2008 April 8-9, West Lafayette, IN. General Technical Report NRS-P-24. U.S. Department of Agriculture Forest Service, Northern Research Station, Newtown Square, PA, pp 506–515
- Prebyl TJ (2012) An analysis of the patterns and processes associated with spring forest phenology in a southern Appalachian landscape using remote sensing. University of Georgia
- Pyne SJ (1982) Fire in America: a cultural history of wildland and rural fire. Princeton University Press, Princeton, NJ
- Reilly MJ, Waldrop TA, O'Brien JJ (2012) Fuels management in the southern Appalachian mountains, hot continental division [Chapter 6]. U.S. Department of Agriculture Forest Service, Southern Research Station, Asheville, NC

Robbins LE, Myers RL (1992) Seasonal effects of prescribed burning in Florida: a

review. Misc. Publ. No. 8 96

- Rothman HK (2007) Blazing heritage: a history of wildland fire in the national parks. Oxford University Press, New York
- Schroeder MJ, Buck CC (1970) Fire weather: a guide for application of meteorological information to forest fire control operations. U.S. Government Printing Office, Washington, DC
- Schwartz NB, Urban DL, White PS, et al (2016) Vegetation dynamics vary across topographic and fire severity gradients following prescribed burning in Great Smoky Mountains National Park. For Ecol Manage 365:1–11. https://doi.org/10.1016/j.foreco.2016.01.027
- Simon SA (2015) Ecological zones in the Southern Blue Ridge Escarpment: 4th approximation. Asheville, NC
- Simon SA, Collins TK, Kauffman GL, et al (2005) Ecological zones in the Southern Appalachians: first approximation. U.S. Department of Agriculture Forest Service, Southern Research Station, Asheville, NC
- Slocum MG, Platt WJ, Cooley HC (2003) Effects of differences in prescribed fire regimes on patchiness and intensity of fires in subtropical savannas of Everglades National Park, Florida. Restor Ecol 11:91–102. https://doi.org/10.1046/j.1526-100X.2003.00115.x
- Sparks JC, Masters RE, Engle DM, Bukenhofer GA (2002) Season of burn influences fire behavior and fuel consumption in restored shortleaf pine-grassland communities. Restor Ecol 10:714–722. https://doi.org/10.1046/j.1526-100X.2002.01052.x
- Stambaugh MC, Guyette RP (2008) Predicting spatio-temporal variability in fire return intervals using a topographic roughness index. For Ecol Manage 254:463–473. https://doi.org/10.1016/j.foreco.2007.08.029
- Stambaugh MC, Guyette RP, Marschall JM (2011) Longleaf pine (Pinus palustris Mill.) fire scars reveal new details of a frequent fire regime. J Veg Sci 22:1094–1104. https://doi.org/10.1111/j.1654-1103.2011.01322.x
- Stewart OC (2002) Forgotten fires: Native Americans and the transient wilderness. University of Oklahoma Press, Norman, OK
- Tarboton DG (2015) Terrain analysis using digital elevation models (TauDEM)
- Van Lear DH, Waldrop TA (1989) History, uses, and effects of fire in the Appalachians. Asheville, NC

- Wade DD, Brock BL, Brose PH, et al (2000) Fire in eastern ecosystems [Chapter 4]. U.S. Department of Agriculture Forest Service, Rocky Mountain Research Station, Ogden, UT
- Wade DD, Lunsford JD (1989) A guide for prescribed fire in southern forests. Atlanta, GA
- Waldrop TA, Brose PH (1999) A comparison of fire intensity levels for stand replacement of Table mountain pine (Pinus pungens Lamb.). For Ecol Manage 113:155–166. https://doi.org/10.1016/S0378-1127(98)00422-8
- Waldrop TA, Goodrick SL (2012) Introduction to prescribed fire in Southern ecosystems. Asheville, NC
- Waldrop TA, Phillips RJ, Simon DM (2010) Fuels and predicted fire behavior in the southern Appalachian Mountains after fire and fire surrogate treatments. For Sci 56:32–45
- Williams CE (1998) History and status of Table Mountain pine–pitch pine forests of the southern Appalachian Mountains (USA). Nat Areas J 18:81–90
- WIMS (2019) Weather Information Management System. https://nap.nwcg.gov/NAP/. Accessed 27 Dec 2019
- Yedinak KM, Strand EK, Hiers JK, Varner JM (2018) Embracing complexity to advance the science of wildland fire behavior. Fire 1:8. https://doi.org/10.3390/fire1020020

2 CHAPTER TWO

EFFECTS OF SEASON OF BURN ON FIRE-EXCLUDED PLANT COMMUNITIES IN THE SOUTHERN APPALACHIANS, USA

2.0 Abstract

Since the 1990s, there has been growing interest in the use of prescribed fire for ecological restoration of predominantly closed-canopy forests in the southern Appalachians. The use of prescribed fire here has often been focused on reducing hazardous fuel loads and has typically occurred in the dormant season prior to spring greenup. Burning at this time of year may limit outcomes for altering species composition, however, with the links between season of burn and effects on vegetation remaining poorly understood. In this study, we compared the effects of dormant and early growing season burning in the southern Appalachians on the abundance and diversity of plant communities in relation to topography and fire behavior. Treatment effects on plant groups were distinguished by growth habit, tree group, life history, and management species of interest. Explanatory variables included elevation, slope position, heat load, burn severity, bole scorch height, litter consumption, and canopy cover. Season of burn had few significant effects on understory plant cover, density, and diversity. In the midstory, however, early growing season burns were more effective than other treatments in reducing shrub density and generally more effective in reducing woody stem density than unburned controls, with the greatest differences concentrated in the smallest size classes. Early growing season burns reduced midstory red maple density to a greater extent than dormant season burns,

though other mesophytic hardwoods may respond differently. Changes in woody stem density suggest that the seasonal timing of fire had a substantial effect on species composition as a result of fire behavior, driven in part by higher ambient air temperatures and lower fuel moisture later in the calendar year in the Northern Hemisphere before canopy closure. The combination of environmental gradients of elevation, burn severity, and change in canopy cover best explained changes in midstory community composition, in which ordinated sites shifted in opposite directions as a result of season of burn. Greater extent of area burned in the early growing season can extend opportunities for treatment with prescribed fire and be as effective, if not more so, when combined with burning in the dormant season to suppress the prevalence of mesophytic hardwoods in the advance regeneration layer. Season of burn influences vegetative response in ways that managers can leverage to refine and expand the use of prescribed fire for restoration of forest communities in the southern Appalachians.

2.1 Introduction

2.1.1 Background

Fire, both natural and anthropogenic in origin, shapes forest ecosystems of the southern Appalachian Mountains. Charcoal evidence, fire scar records, and the presence of endemic populations of fire-adapted flora attest to the regular occurrence of fire in the region for at least the last several thousand years before present (Delcourt and Delcourt 1998; Noss 2012; Lafon et al. 2017). Practices of woods burning transcended Euro-American settlement, particularly in remote areas where it was often essential to human subsistence (Owsley 1949; Pyne 1982; Stewart 2002). Mean fire return intervals of 5-7 years were common across many parts of the landscape since at least the 1700s (Lafon et al. 2017). By the early-mid 1900s, however, concerns regarding destructive fires often resulting from rapid deforestation prompted management policies at all levels of government to actively suppress fire wherever it occurred (Williams 1989; Dombeck et al. 2004). Nationwide fire suppression efforts in the twentieth century were largely effective in reducing fire frequency in the Southeast (Pyne 1982), with widespread implications for the form and function of plant communities in the southern Appalachians and beyond (Harrod et al. 1998; Nowacki and Abrams 2008).

Light is often constrained from reaching the forest floor with fewer gaps created and maintained in the canopy as a result of fire exclusion. Compounding this effect, ericaceous shrubs such as great rhododendron (*Rhododendron maximum* L.) and mountain laurel (*Kalmia latifolia* L.) are more competitive in the absence of fire, and have become more dominant (Elliott et al. 1999). Under such dense layers of the overstory and midstory, light-dependent forbs and graminoids in the understory are unlikely to persist (Harrod et al. 2000). Regeneration of overstory species adapted to periodic disturbance is often more challenging in this environment without intensive treatments (Lorimer 1993; Baker and Van Lear 1998; Abrams 2005; Schwartz et al. 2016). Forest communities have shifted in composition towards a greater prevalence of mesophytic hardwoods [e.g. red maple (*Acer rubrum* L.)] that are often competitive across a variety of site conditions and may come to dominate, particularly in high-quality mesic sites (Abrams 1998; Nowacki and Abrams 2008). Historical communities of oak (*Quercus* spp.) and pine (*Pinus* spp.) are often degraded and relegated to the most xeric landscape positions (Williams 1998; Abrams 2003). In response to forests changing in undesirable directions, managers have increasingly embraced prescribed fire in recent decades as a tool for ecological restoration in the southern Appalachians (Vose et al. 1997; Brose et al. 2001). Reintroduction of fire to fire-excluded plant communities presents management challenges, however, as the prescriptive methods to best achieve given restoration objectives often remain less clear.

Opportunities for fire managers to burn are often limited by meteorological and vegetation conditions that would allow robust fire spread and adequate smoke dispersion (Waldrop and Goodrick 2012; Chiodi et al. 2018). When such prescriptive preconditions are met, managers often burn in the late dormant season in order to reduce fuel loads and prepare for vegetative regeneration (Van Lear and Waldrop 1989; Reilly et al. 2012). Increased photoperiod in the late winter and early spring allows for surface fuels to dry more rapidly following precipitation events, facilitating more even ignition and continuous fire spread (Robbins and Myers 1992). Canopy closure and developing convective weather

patterns, however, increase and maintain understory humidity to levels such that by summer, fire ceases to be a viable management tool (Norman et al. 2017, 2019). The late winter and early spring period accounts for most of the annual prescribed burning in the southern Appalachians; however, less precedent exists for burning in the early growing season portion at its end shoulder (Wade and Lunsford 1989; Wade et al. 2000; Knapp et al. 2009). A more refined understanding of the seasonal dynamics of prescribed fire may allow for an expansion of opportunities for the advancement of restoration outcomes.

Season of burn may influence patterns of forest succession through variable fire behavior and by altering the resource environment of plants in different periods of phenological progression. Underlying physiological characteristics—manifested as fire adaptations—determine the vulnerability of plants to disturbance via fire through inherent structural defenses and life history strategies to capture and utilize resources for survival, growth, and propagation (Grime 1977; Clarke et al. 2013; Bär et al. 2019). Species that have the capacity to rapidly regenerate could be expected to displace more fire-sensitive competitors, particularly in seasons corresponding to a favorable environment for new growth (Platt et al. 1988; Hiers et al. 2000). Alternatively, fire behavior in given seasons may prevent the utilization of resources for regeneration. Plants may need to replace a greater amount of lost biomass during periods of high resource abundance in the growing season, for example, siphoning vital energy that more protected plants would not have to expend before entering dormancy in the fall (Regier et al. 2010). Both immediate (first order) and delayed (second order) injuries may be caused by variable exposure of constituent plant structures to lethal levels of heating and ultimately cause mortality (Michaletz and Johnson 2007, 2008).

Fire occurrence in different seasons may further influence competition and alter patterns of succession by stimulating or suppressing the development of latent vegetation. Reductions in surface fuel load as a result of fire can provide new opportunities for the establishment of plants that were previously suppressed (Hutchinson 2006; Phillips and Waldrop 2008). Dormant seeds in the soil and those to be imminently dispersed from established plants may be more likely to germinate and establish as a result of increased access to light and warmer temperatures (Silvertown 1980; Baskin and Baskin 1988). Alternatively, heat transference to the soil seed bank as influenced by surface fuel moisture and fire residence time may destroy extant seeds given sufficient intensity (Dayamba et al. 2010). Seeds recently dispersed may be consumed by fire on the fuelbed surface, thereby reducing the pool of seeds of a given species that could establish in that season. For example, red maple seeds are typically dispersed in the spring and early summer (April-July) (Walters and Yawney 1990), eastern white pine (Pinus strobus L.) seeds disperse following cone maturation in the late summer and fall (September-October) (Krugman and Jenkinson 1974; Wendel and Smith 1990), whereas yellow-poplar (Liriodendron tulipifera L.) seeds may be dispersed throughout the fall and winter (October-March) (Beck 1990). Consideration of how prescribed fire influences seed regeneration potential may suggest which seasons of burn would be most effective for altering relative plant abundance for desired community composition.

Seasonality of fire regimes interacts with topography as a function of how fire behavior is amplified or constrained by environmental characteristics enabling fire spread. Slope position along elevational gradients may influence the amount and duration of heating experienced over the course of a burn across different parts of a heterogeneous landscape (Fridley 2009; Schwartz et al. 2016). Cumulative diurnal solar radiation as a function of aspect influences the magnitude and extent of the drying of fuels available for combustion (Kreye et al. 2020). Patterns of litter and duff consumption, as driven by fuel moisture and available fuel, may induce tree mortality as a result of aerial exposure of roots and fire spread around the base of the stem (Ferguson et al. 2002). Degrees of heating more likely to be caused by fire behavior in different seasons may predict the level of damage sustained by plants with variable ability to withstand heat energy and suggest the relative importance of topography in carrying fire across the landscape.

With modern prescribed fire infrequently occurring in the growing season, studies have attempted to elucidate the treatment effects of burning in different seasons on vegetation in the Southeast. Foundational studies in the Coastal Plain provide insights into how frequency and season of prescribed fire influences plant mortality, regeneration, and diversity over multiple decades (Waldrop et al. 1992; Glitzenstein et al. 2008). In the Santee Fire Plot Study (1946-89), herbaceous cover was greatest with dormant season burning, whereas growing season burning was more effective in reducing hardwood stem densities (Waldrop et al. 1987; White et al. 1991). Results from the study of fire regimes at St. Marks National Wildlife Refuge, Florida (1980-2004) indicated that species diversity was least with late growing-season burning and greatest with dormant-season burning (Platt et al. 1988). Unlike in the Coastal Plain, however, fewer studies compare fire effects in different seasons in the southern Appalachians. Previous season of burn studies in the region have primarily measured the response of woody species at smaller scales, with limited evidence of treatment effects by season (Vander Yacht et al. 2017; Clabo and Clatterbuck 2019; Keyser et al. 2019). At the landscape scale, the causes and effects of season of burn on plant communities remain poorly understood and are often confounded with environmental variability irrespective of defined seasons (O'Brien et al. 2018b).

2.1.2 Research questions

For this study, we sampled vegetation pre- and post-treatment to evaluate the effects of season of burn on plant abundance and diversity. Data were collected from replicated burn (dormant season, early growing season) and unburned control treatments across management units to address the following questions:

- How does season of burn affect absolute plant cover and density in understory, midstory, and/or overstory vegetation strata?
 - a. By growth habit (forb, graminoid, shrub, tree, vine)?
 - b. By tree group (hickory, mesophytic hardwood, red oak, white oak, white pine, yellow pine, other)?
 - c. By life history of woody plants (germinant, established, sprout)?
 - d. By management species of interest (red maple, mountain laurel)?
- 2. How does season of burn affect species richness and diversity (α , β , and γ) in understory and midstory strata?
- 3. How does season of burn affect canopy cover?

4. Which environmental factors best explain relative shifts in community composition as related to season of burn in understory and midstory strata?

For Question #1, we hypothesized that forb and graminoid cover and density would increase the greatest following early growing season burns in comparison to dormant season burns. We also hypothesize that effects on woody vegetation in the understory by season of burn would be limited to red maple and other mesophytic hardwoods, with a greater decrease in density in the early growing season. We further expected increases in germinant and sprout density of woody stems relative to those established of the same vegetation following a single burn treatment. Herbaceous species, often dominant in earlier stages of succession, may respond more positively following growing season burns due to (a) more favorable photoperiod and temperature for regrowth and flowering (Platt et al. 1988; Streng et al. 1993) and (b) decreased abundance of competing woody species post-fire than in dormant season burns (Knapp et al. 2009). Slower growing woody species may be less sensitive to seasonal differences in growing conditions prior to canopy closure unless burn treatments can significantly increase canopy openness (Keyser et al. 2019).

We hypothesized that there will be greater decreases in midstory stem density (including red maple and mountain laurel) with early growing season burns than in dormant season burns. In contrast to the understory, woody stems of midstory shrubs and trees consumed by surface fire are less likely to be represented within the same stratum by the completion of sampling for this study. Therefore, drier fuels and greater temperatures observed in the early growing season (Chapter 1) led us to think that higher intensity fires (more likely later in the year before canopy closure) will result in greater net midstory mortality, particularly of stems of the smallest size classes. We further expected that early growing season burns will result in greater decreases in midstory (including mountain laurel) cover and mountain laurel height than with dormant season burns.

For Question #2, we hypothesized that species richness and diversity will be significantly greater following early growing season burns than in dormant season burns as a result of changes in the proportionate (relative) abundance of plants of different growth habits. We expected this difference to be primarily driven by both (a) greater increases in the relative abundance of forbs and graminoids and (b) greater decreases in the relative abundance (reduction in dominance) of certain woody species, including mesophytic hardwood trees, in the early growing season than in the dormant season.

For Question #3, we hypothesized that change in canopy cover will not significantly differ by season of burn. However, we do expect a positive understory response from decreases in canopy cover as a result of disturbance from fire. Differences between burn treatments in the abundance and diversity of understory vegetation would, therefore, be expected to be explained by factors other than decreases in canopy cover that may occur.

Significantly lower fuel moisture and higher air and fire temperatures were observed in the early growing season than in the dormant season (Chapter 1). For Question #4, we expected that environmental gradients related to fire behavior will explain seasonal variability in community response between burn treatments. We hypothesized that topographic measures of slope position and heat load will explain a greater degree of variability in plant community composition in the dormant season than in the early growing season. Fire behavior measures of burn severity, bole scorch height, and litter consumption are expected to explain a minimal degree of community composition between treatments as differences in these variables were expected to align with burn treatments.

2.2 Methods

2.2.1 Study area

This study was conducted in the Blue Ridge physiographic province of the southern Appalachian Mountains in the southeastern United States. Treatment replicates were located in both the Chattooga River (CR) Ranger District of Chattahoochee National Forest in Rabun County, Georgia as well as the Andrew Pickens (AP) Ranger District of Sumter National Forest, in Oconee County, South Carolina (Figure 2.1). Area contained within treatment units ranged in elevation from 275 m to 1,427 m, 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 166 cm distributed relatively evenly throughout the year (NCEI 2020). Soil orders of Ultisols, Inceptisols, and Entisols were common, mostly underlain by metamorphic bedrock (e.g. granitic gneiss and schist) (Griffith et al. 2001, 2002).

Pre-treatment fuel loads were similar between treatments, averaging 6,579.7 kg ha⁻¹ for litter, 14.2 cm for fuelbed height, 606.6 kg ha⁻¹ for 1-hr fuels, 1,880.0 kg ha⁻¹ for 10-hr fuels, 4,906.6 kg ha⁻¹ for 100-hr fuels, and 5,341.3 kg ha⁻¹ for 1,000-hr fuels across all study plots. Across predominant ecological zones of Dry-Mesic Oak-Hickory Forest, Shortleaf Pine-Oak Forest and Woodland, Mixed Oak / Rhododendron Forest, and Montane Oak-Hickory Forest, forest cover consisted largely of oaks (*Quercus* L.),

hickories (*Carya* L.), and pines (*Pinus* L.) (Simon et al. 2005; Simon 2015). Substantial woody encroachment was present from mesophytic hardwoods (e.g. red maple) and ericaceous shrubs (e.g. mountain laurel and great rhododendron).

2.2.2 Study design

The study was laid out as a randomized complete block design, with treatments dormant season burn (d), growing season burn (g), and an unburned control (c) 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 2.1). Twenty plots dispersed across a variety of slope positions were established within each treatment unit, with data from a total of 180 plots used for analyses. Each plot was 30 x 30 m (900 m²), subdivided into (9) 10 m square (100 m²) subplots delineated by 16 grid point intersections and oriented with its outer boundaries running magnetic north (0°) and east (90°) from its point of origin (Figure 2.2).

Prescribed burns were implemented by U.S. Forest Service fire practitioners as a part of official burn plans and coordinated with Clemson University for purposes of this study. Dormant season burns were defined as those occurring after autumn leaf-fall and before spring green-up (typically before last frost), whereas growing season burns were considered as those occurring in the early spring green-up period (typically after last frost) but before complete overstory canopy closure. Burn treatments occurred between January 31 -April 5 (dormant season) and April 18 - 24 (growing season) in 2018 and 2019 (Table 2.1). Firing methods included hand ignition using drip torches as well as remote aerial ignition using delayed aerial ignition devices dropped from a helicopter on some burns. A spot fire technique was used for hand ignitions, where possible.

2.2.3 Field sampling and data preparation

Vegetation was sampled in each forest layer (understory, midstory, and overstory) using repeated measures before and after each burn to determine changes in response to treatment. Pre-burn vegetation measurements were taken within 1-2 growing seasons (2016-17) preceding each burn (2018-19). Post-burn vegetation measurements were taken in the second growing season (2019-20) following each burn. Visual evidence of the presence or absence of fire (y/n) was noted at grid point intersections, with a 50% threshold indicating the presence of fire used to qualify plot-level burn treatment effects.

Vegetation

Understory vegetation was defined as living plants < 1.37 m in height and was recorded based on a modified form of the standard 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 (n = 1,620 measurement units). Plants within each quadrat were identified to species when possible. Individual woody plants were tallied at or above the root collar within life history (germinant, established, sprout) and height (< 10 cm, 10-50 cm, \geq 50 cm) classes. Germinants, often visibly succulent, were those that appeared to have sprouted within the same growing season at the time of sampling. Established plants were those that appeared to have sprouted sample and the stress that were attached to a parent stem above the root collar. Unique plants were assigned cover classes that represented the proportion of the quadrat covered by the projection of that plant: (1) 0-1%, (2) 1-2%, (3) 2-5%, (4) 5-10%, (5) 10-25%, (6) 25-50%, (7) 50-75%, (8)

75-100%. Cover classes were converted to the midpoint of the proportion range and transformed using an arcsine-square root transformation according to the following formula: $\frac{2}{\pi} * \arcsin \sqrt{cover \ proportion}$ (Sokal and Rohlf 1995; McCune and Grace 2002).

Midstory vegetation was defined as woody stems ≥ 1.37 m in height and < 10 cm diameter at 1.37 m (breast) height above ground level. Overstory vegetation was defined as woody stems ≥ 1.37 m in height and ≥ 10 cm diameter at breast height (DBH). Midstory vegetation was sampled within 5 of 9 subplots (odd-numbered subplots #1, 3, 5, 7, 9) per plot (n = 900 measurement units), whereas overstory vegetation was sampled within the same geometry of 2 of the 3 treatment replicates (n = 600 measurement units). Live stems were identified to species when possible. Dead stems were identified as either unknown hardwoods or unknown softwoods, unless they could be readily distinguished at the species or genus level following recent mortality. Individual midstory plants (shrubs and trees) were tallied within the following DBH classes: (1) < 3 cm, (2) 3-6 cm, and (3) 6-10 cm. DBH of overstory plants (shrubs and trees) was measured for each individual. Proportion of midstory cover, both for mountain laurel and total overall, and maximum height of mountain laurel, alive and dead, was visually estimated for each subplot. Midstory cover proportion was transformed using an arcsine-square root transformation as also used with understory cover classes.

Unique plants recorded were identified with taxonomic correspondence to the U.S. Department of Agriculture (USDA) Natural Resources Conservation Service (NRCS) PLANTS Database. Individual plants (typically species) were assigned to a functional group based on growth habit according to the PLANTS Database. If multiple growth habits were listed for a given plant, a representative habit was chosen from among them. The subshrub classification was not used, and additional groups were defined using combinations of growth habits: herb (form, graminoid) and woody (shrub, tree, vine). Among trees, hickory included *Carya* spp., mesophytic hardwood was assigned according to genera and species listed by Nowacki and Abrams (2008), red oak (*Quercus* spp.) included *Q. coccinea*, *Q. falcata*, *Q. marilandica*, *Q. rubra*, and *Q. velutina*, white oak (*Quercus* spp.) included *Q. alba*, *Q. montana*, and *Q. stellata*, white pine included *Pinus* strobus, yellow pine (*Pinus* spp.) included *P. echinata*, *P. pungens*, *P. rigida*, *P. taeda*, and *P. virginiana*, and other included all other trees.

Plant functional group response variables were aggregated (summed or averaged) across subplots by plot (sample unit), with paired absences excluded for calculating Δ response values from pre- to post-treatment. Count data were transformed for parametric analysis of treatment effect using a logarithmic transformation according to the following formula (x = count): $\log_2(x + 1)$. Similarly, for multivariate analysis, abundance values were transformed according to the following formula: $\log_2(x) + 1$ for x > 0 (Anderson et al. 2006). A logarithm of base 2 was used to balance quantitative dispersion of untransformed counts vs. compression towards presence-absence scaling at higher logarithm bases (McCune and Grace 2002). For comparison of treatment effect, count data were expressed as absolute density per unit area. Importance values (IVs) were obtained by averaging (1) relative density, (2) relative cover, and (3) relative frequency (understory) or (1) relative density and (2) relative frequency (midstory) of each species for multivariate

analysis. Relative density and relative cover were calculated according to the Wisconsin double standardization method, by relativizing species abundance first by species maximum and second by plot total (Bray and Curtis 1957). Relative frequency was calculated by standardizing log-transformed count by frequency length (Oksanen 1983).

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 to express the compositional variation within understory plant communities sampled. Species richness was calculated by plot as mean plant richness. α -diversity (proportionate) was calculated by plot as the H' Shannon-Wiener index of diversity. Both species richness and H' were quantified overall and by plant functional group. γ -diversity was calculated as the total plant species richness by treatment unit and overall. β -diversity, representing the degree of compositional separation between plots, was calculated both as β_W (Whittaker's beta) as well as β_D (half changes). 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). Changes in diversity values from pre- to post-treatment (Δ) were analyzed as treatment effects.

Canopy cover

Proportion of forest canopy cover was estimated to quantify the relative degree of understory light availability. Canopy cover values were derived using pictures taken of a spherical densiometer held at breast height over each subplot quadrat reflecting the view overhead. Open sky dot count values ranged from 0-96 and were converted to proportion of canopy cover according to the following formula: $1 - (dot \ count \ * \ 0.0104)$. The difference between post- and pre-treatment canopy cover proportion (Δ) was used as the metric of response.

Litter consumption

Litter depth was measured in the growing season prior to and following burn treatments at all plots, with measurements taken at designated intervals (3.66 m, 7.62 m, and 12.19 m) along transects emanating from the plot origin (3 transects per plot; n = 540measurement units). Raw litter depth measurements were used to calculate fuel weight per area (load), aggregated by plot. The absolute value of post- minus pre-treatment load was used as the metric of response (net consumption). The average change in litter load in unburned control units was subtracted from the corresponding burn treatment changes in fuel load in the same replicate to account for expected change in fuel load in the absence of fire. Bulk density (weight per volume) were chosen from representative values for the region and forest type (Ottmar and Andreu 2007; Buchanan 2009).

Bole scorch height

Bole scorch height was measured at all plot grid point intersections within burn units as an estimate of flame length. Measurements of scorch height were taken on the nearest charred bole within 3.05 m of each grid point and averaged by plot (16 points per plot; n = 2,880 measurement units). Scorch heights likely underestimate true flame length (Cain 1984) and were not measured on yellow pines [e.g. pitch pine (*Pinus rigida* Mill.) or shortleaf pine (*Pinus echinata* Mill.)] due to the increased likelihood of fire spread on the bark of these trees irrespective of representative surface flame heights.

2.2.4 Landscape variables

Topographic variables

Topographic variables were derived from a digital elevation model (DEM) in a geographic information system (GIS) to evaluate topographic effects on metrics of fire behavior utilized in this study. A DEM covering the study area was downloaded as part of the National Elevation Dataset from the U.S. Geological Survey's The National Map Viewer at a spatial resolution of 1/9 arc-second and transformed to a Universal Transverse Mercator (UTM) Zone 17 projected coordinate system (3.18 m cell size) (2019a). The DEM had pits removed using TauDEM and was clipped to the necessary extent for analysis in ArcGIS for Desktop (Tarboton 2015; 2019a). Each index variable was normalized to a scale of 0-1 using the Raster Calculator tool and extracted using the Extract Multi Values to Points tool (2019a).

Topographic Position Index (TPI) was used to quantify slope position, based on the relative difference between a given point's elevation and the average elevation of its surrounding terrain within a defined window (Guisan et al. 1999; De Reu et al. 2013b). Lower values represent more sheltered parts of the landscape whereas higher values represent greater exposure. A rectangular window of 1000 x 1000 m was chosen to define

the focal area, with its average elevation subtracted from each cell in the DEM using the ArcGIS Geomorphometry and Gradient Metrics Toolbox to derive TPI (Evans et al. 2014a, b; Evans 2017; Naito 2017; 2019a). Heat Load Index (HLI) was used to quantify solar radiation as a function of aspect, further incorporating the effects of slope and latitude to linearize compass azimuth such that it ranges from the lowest values on northeast-facing slopes to the highest values on southwest-facing slopes (Beers et al. 1966; McCune and Keon 2002). HLI was derived from the DEM using the ArcGIS Geomorphometry and Gradient Metrics Toolbox (Evans et al. 2014b; 2019a). TPI and HLI were averaged by plot area as topographic predictors of fire behavior.

dNBR burn severity

Severity of the burn treatments used in this study was quantified as a continuous gradient using remote sensing to detect changes in vegetation across the landscape. Temporal difference in the Normalized Burn Ratio (dNBR = NBR_{pre-burn} - NBR_{post-burn}) was calculated in a geographic information system (GIS) using reflectance values in spectral bands sensitive to changes resulting from burning (Key and Benson 2006). Pre- and post-burn imagery for this purpose was gathered from the European Space Agency (ESA) Sentinel-2 satellite Multispectral Instrument at a spatial resolution of 20 m [bands: 8A (Near Infrared) and 12 (Shortwave/Mid Infrared)]. Positive dNBR values represent decreased greenness in comparison between growing seasons before vs. after the burn whereas negative dNBR values represent increased greenness.

2.2.5 Statistical analyses

Parametric

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 season of burn on vegetation response. Model effects included treatment (fixed), replicate (random), replicate crossed with treatment (random), and/or plot nested within treatment and replicate (random). Model 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. Parametric analyses of treatment effect were performed using JMP Pro 14.3.0 (SAS 2018).

Multivariate

Relative changes in understory and midstory community composition in relation to treatments and environmental variables were assessed using nonmetric multidimensional scaling (NMDS). NMDS, a non-parametric and unconstrained ordination method, uses ranked distances to find the configuration of a specified number of dimensions (axes) relating site and species dissimilarities with minimum departure from monotonicity in its solution (Clarke 1993). Standardized species IVs representing relative abundance were used to calculate distance measures for the NMDS using the Bray-Curtis coefficient, a proportion coefficient equivalent to Sørensen similarity for quantitative data (Bray and Curtis 1957; Faith et al. 1987; McCune and Grace 2002). Euclidean distance was used for calculating environmental gradient distances for correlation with ordination axes. Procrustes analysis was used in comparing iterative solutions to determine convergence, with the final configuration rotated such that the first axis explained the greatest variance (Oksanen et al. 2019). To depict the results of the NMDS, sites (plots) were plotted in ordination space with change vectors overlaid indicating the average movement of plots by the centroid of plot points of each treatment by sampling period from pre- to post-treatment.

NMDS ordination configurations were related to environmental variables according to sampling period relative to application of treatment: elevation, TPI, HLI, and canopy cover (pre-treatment) or elevation, TPI, HLI, dNBR, bole scorch height, Δ litter load, and Δ canopy cover (post-treatment). Environmental variable correlations with ordination axes were quantified as direction cosines of vectors, with the strength of the correlation expressed as a squared coefficient (r²). Explanation of changes in community assemblages were assessed according to combinations of environmental variables with the strongest correlation with species dissimilarities using Spearman's rank correlation coefficient (ρ). All multivariate community analyses were performed using RStudio in the R programming language and software environment (2020; R Core Team 2020). Functions included within the *vegan* package were used to produce the NMDS ordination and relate environmental variables to community configurations (Oksanen et al. 2019).

2.3 Results

2.3.1 Cover and density

Understory

For change in understory cover, there were no significant treatment effects for plants of any growth habit, tree group, or management species of interest (all *p*-values > 0.05 or n/a). A summary of results of comparison of treatment effects on change in

understory cover by growth habit, tree group, and management species of interest can be found in Table 2.2. For change in understory density, there were no significant treatment effects for plants of any growth habit (all *p*-values > 0.05). A summary of results of comparison of treatment effects on change in understory density by growth habit can be found in Figure 2.3.

Change in density of understory sprout stems of trees was significantly greater in growing season burns (17,191 ha⁻¹) and dormant season burns (16,869 ha⁻¹) vs. unburned controls $(1,833 \text{ ha}^{-1})$ (p-value = 0.01). There were no other significant treatment effects for change in understory density of woody stems by growth habit and life history (all *p*-values > 0.05 or n/a). Change in density of sprout stems of mesophytic hardwoods was significantly greater in growing season burns (13,026 ha⁻¹) and dormant season burns $(13,065 \text{ ha}^{-1})$ vs. unburned controls $(1,176 \text{ ha}^{-1})$ (*p*-value = 0.02). Change in density of all other trees was significantly greater in growing season burns (6,914 ha⁻¹) vs. dormant season burns (2,049 ha⁻¹) and unburned controls (1,206 ha⁻¹) (*p*-value = 0.01). There were no other significant treatment effects for change in understory density of trees by group and life history (all *p*-values > 0.05 or n/a). Change in density of established stems of Acer rubrum was significantly different in growing season burns (-9,581 ha⁻¹) vs. unburned controls (25,256 ha⁻¹) but was not significantly different between treatments in pairwise comparisons with dormant season burns $(3,000 \text{ ha}^{-1})$ (*p*-value = 0.01). There were no other significant treatment effects for change in understory density by management species of interest (Acer rubrum and Kalmia latifolia) by life history (all p-values > 0.05 or n/a). A summary of results of comparison of treatment effects on change in understory density of woody plants by growth habit and life history, trees by group and life history, and management species of interest by life history can be found in Table 2.3.

Midstory

There were no significant treatment effects for change in *Kalmia latifolia* or all midstory cover (all *p*-values > 0.05). A summary of results of comparison of treatment effects on change in midstory cover can be found in Table 2.4.

Change in density of all midstory vegetation was significantly different in growing season burns (-1,585 ha⁻¹) vs. unburned controls (517 ha⁻¹) but was not significantly different between treatments in pairwise comparisons with dormant season burns (-813 ha-¹) (*p*-value = 0.01). For shrubs, change in density was significantly different between each treatment both overall, growing season burns (-814 ha⁻¹) vs. dormant season burns (-305 ha⁻¹) vs. unburned controls (645 ha⁻¹) (*p*-value < 0.01), and for DBH class < 3 cm, growing season burns (-609 ha⁻¹) and dormant season burns (-356 ha⁻¹) vs. unburned controls (439 ha⁻¹) (*p*-value < 0.01). Change in density of trees was significantly different in growing season burns (-889 ha⁻¹) vs. unburned controls (-74 ha⁻¹) but was not significantly different between treatments in pairwise comparisons with dormant season burns (-526 ha⁻¹) (pvalue = 0.02). For trees of DBH class 3-6 cm, change in density was significantly different in growing season burns (-249 ha⁻¹) and dormant season burns (-388 ha⁻¹) vs. unburned controls (-12 ha⁻¹) (*p*-value = 0.01). Among all midstory vegetation, change in density of stems of DBH class < 3 cm was significantly different in growing season burns (-1,058 ha⁻ ¹) vs. unburned controls (329 ha⁻¹) but was not significantly different between treatments in pairwise comparisons with dormant season burns (-399 ha⁻¹) (p-value = 0.04). Change in density of all midstory vegetation of stems of DBH class 3-6 cm was significantly different in growing season burns (-385 ha⁻¹) and dormant season burns (-361 ha⁻¹) vs. unburned controls (159 ha⁻¹) (*p*-value < 0.01). There were no other significant treatment effects for change in midstory density by growth habit and DBH class (all *p*-values > 0.05). A summary of results of comparison of treatment effects on change in midstory density by growth habit and DBH class (all *p*-values > 0.05).

Change in density of all mesophytic hardwoods was significantly different in growing season burns (-561 ha⁻¹) vs. unburned controls (-17 ha⁻¹) but was not significantly different between treatments in pairwise comparisons with dormant season burns (-376 ha-¹) (*p*-value = 0.01). For mesophytic hardwoods of DBH class 3-6 cm, change in density was significantly different between each treatment: dormant season burns (-236 ha⁻¹) vs. growing season burns (-176 ha⁻¹) vs. unburned controls (4 ha⁻¹) (*p*-value < 0.01). Change in density of all red oaks was significantly different in growing season burns (-74 ha⁻¹) vs. unburned controls (-5 ha⁻¹) but was not significantly different between treatments in pairwise comparisons with dormant season burns (-59 ha⁻¹) (*p*-value = 0.04). For red oaks of DBH class 3-6 cm, change in density of was significantly different in dormant season burns (-67 ha⁻¹) vs. unburned controls (0 ha⁻¹) but was not significantly different between treatments in pairwise comparisons with growing season burns (-38 ha⁻¹) (p-value = 0.03). Change in density of other trees of DBH class 3-6 cm was significantly different in growing season burns (-55 ha⁻¹) vs. unburned controls (3 ha⁻¹) but was not significantly different between treatments in pairwise comparisons with dormant season burns (-73 ha⁻¹) (*p*-value = 0.03).

Change in density of all Acer rubrum was significantly different in growing season burns (-356 ha⁻¹) vs. dormant season burns (-219 ha⁻¹) and unburned controls (15 ha⁻¹) (pvalue < 0.01). For *Acer rubrum* of DBH class < 3 cm, change in density of was significantly different in growing season burns (-216 ha⁻¹) vs. unburned controls (6 ha⁻¹) but was not significantly different between treatments in pairwise comparisons with dormant season burns (-73 ha⁻¹) (*p*-value = 0.04). For Acer rubrum of DBH class 3-6 cm, change in density was significantly different in growing season burns (-128 ha⁻¹) and dormant season burns (-130 ha^{-1}) vs. unburned controls (3 ha⁻¹) (*p*-value < 0.01). Change in density of Kalmia *latifolia* of DBH class < 3 cm was significantly different in growing season burns (-494 ha⁻ ¹) vs. unburned controls (497 ha⁻¹) but was not significantly different between treatments in pairwise comparisons with dormant season burns (-323 ha⁻¹) (*p*-value = 0.03). Change in the maximum height of Kalmia latifolia was not significantly different between burn treatments (p-value = 0.49). There were no other significant treatment effects for change in midstory density of trees by group and DBH class or management species of interest by DBH class (all *p*-values > 0.05 or n/a). A summary of results of comparison of treatment effects on change in midstory density of trees by group and DBH class and management species of interest by DBH class can be found in Table 2.5.

Overstory

For change in overstory density, there were no significant treatment effects for plants of any growth habit (shrubs or trees), trees of any group, or management species of interest (*Acer rubrum*) (all *p*-values > 0.05 or n/a). A summary of results of comparison of treatment effects on change in overstory density can be found in Table 2.6.

2.3.2 Species richness and diversity

Understory

For change in understory species richness and *H*', there were no significant treatment effects for plants of any growth habit (all *p*-values > 0.05 or n/a). A summary of results of comparison of treatment effects on change in understory species richness and *H*' can be found in Table 2.7. Change in γ , β_W (Whittaker's beta), and β_D (half changes) were not significantly different between burn treatments (*p*-values = 0.85, 0.21, and 0.11, respectively).

Midstory

Change in species richness of shrubs of DBH class < 3 cm was significantly different in growing season burns (-0.91) vs. unburned controls (-0.07) but was not significantly different between treatments in pairwise comparisons with dormant season burns (-0.69) (*p*-value = 0.03). Change in species richness of trees of DBH class 3-6 cm was significantly different in growing season burns (-2.56) vs. unburned controls (-0.29) but was not significantly different between treatments in pairwise comparisons with dormant season burns (-1.94) (*p*-value = 0.02). Change in species richness of all midstory vegetation of DBH class 3-6 cm was significantly different in growing season burns (-2.25) (*p*-value = 0.02). Change in *H*' (Shannon-Wiener index) of all midstory vegetation of DBH class 3-6 cm was significantly different in growing season burns (-0.60) vs. unburned controls (-0.11) but was not significantly different in growing season burns (-0.60) vs. unburned controls (-0.11) but was not significantly different in growing season burns (-0.60) vs. unburned controls (-0.11) but was not significantly different between treatments in pairwise comparisons with dormant season burns (-0.60) vs. unburned controls (-0.11) but was not significantly different between treatments in pairwise comparisons with dormant season burns (-0.60) vs.

burns (-0.27) (*p*-value = 0.02). There were no other significant treatment effects for change in midstory species richness and *H*' by growth habit and DBH class (all *p*-values > 0.05 or n/a). A summary of results of comparison of treatment effects on change in midstory species richness and *H*' can be found in Table 2.8. Change in γ was not significantly different between burn treatments (*p*-value = 0.44). Change in β_W (Whittaker's beta) was significantly greater in growing season burns (1.12) vs. unburned controls (0.11) but was not significantly different between treatments in pairwise comparisons with dormant season burns (0.28) (*p*-value = 0.04). Change in β_D (half changes) was significantly greater in growing season burns (0.28) and dormant season burns (0.20) vs. unburned controls (-0.06) (*p*-value < 0.01).

2.3.3 Canopy cover

Change in canopy cover was significantly different in growing season burns (-5.5%) and dormant season burns (-4.0%) vs. unburned controls (2.9%) (*p*-value < 0.01). A summary of results of comparison of treatment effects on canopy cover can be found in Figure 2.5.

2.3.4 Ordination with environmental factors

Multivariate community ordination using NMDS of understory species IVs resulted in pre- and post-treatment final stress values of 0.25 and 0.26, respectively, with resolution on 2 axes after 755 and 20 iterations, respectively (Figure 2.6). For the pre-treatment NMDS ordination, elevation alone was the environmental variable with the strongest correlation with understory community configuration ($\rho = 0.40$). With elevation excluded, TPI and HLI together had the strongest correlation ($\rho = 0.23$). For the post-treatment NMDS ordination, elevation alone was the environmental variable with the strongest correlation with understory community configuration ($\rho = 0.31$). With elevation excluded, TPI, HLI, bole scorch height, and Δ litter load together had the strongest correlation ($\rho = 0.21$).

Using the same NMDS procedure, ordination of midstory species IVs resulted in pre- and post-treatment final stress values of 0.28, with resolution on 2 axes after 35 and 37 iterations, respectively (Figure 2.7). For the pre-treatment NMDS ordination, elevation alone was the environmental variable with the strongest correlation with understory community configuration ($\rho = 0.43$). With elevation excluded, TPI alone had the strongest correlation ($\rho = 0.19$). For the post-treatment NMDS ordination, elevation, dNBR, and Δ canopy cover together was the subset of environmental variables with the strongest correlation with understory community configuration ($\rho = 0.34$). With elevation excluded, TPI, dNBR, bole scorch height, and Δ canopy cover together had the strongest correlation ($\rho = 0.25$). A summary of results of environmental variable correlations with NMDS ordination axes can be found in Table 2.10.

2.4 Discussion

Seasonal differences in fire effects should be understood relative to meteorological and topographic controls of fire behavior (Chapter 1) and the causal mechanisms that alter patterns of succession (Kreye et al. 2018; O'Brien et al. 2018b). Patterns of photoperiod, temperature, and fuel moisture on different parts of the landscape may predict the behavior of prescribed fire in different seasons. Fire effects on vegetation reflect plants' life history strategies and adaptations to environments modified by fire in different seasons. Plants may be variably affected by fire prescribed in a given season based on the ability to withstand heat damage and exploit resource availability relative to their competitors. Further, seasonal timing of fire may select for plants according to their fluctuating ability to retain existing nutrient reserves, capture and assimilate light and nutrients, and distribute resources to replace lost tissues (Kozlowski 1992; Bond and van Wilgen 1996; Furze et al. 2019). Consideration of the seasonal timing of prescribed fire relative to the interaction between both fire behavior and variable fire effects on vegetation allows for an understanding of which factors associated with season of burn may be driving changes in plant communities.

Past studies of the effects of fire seasonality in the southern Appalachians have demonstrated similar effects of burning in different seasons. For a single species [shortleaf pine (*Pinus echinata* Mill.)], season of burn did not affect seedling survival, though sprout height became greater with burning earlier (April) rather than later (July, November) in the year (Clabo and Clatterbuck 2019). At the stand scale (≤ 20 ha), fire applied in parts of the dormant (March) and growing (April, October) seasons indicated few significant differences of season of burn on changes in woody stem density (Vander Yacht et al. 2017; Keyser et al. 2019). Multiple prescribed fires, even when combined with mechanical treatments, are often not sufficient to change community structure and composition (Oakman et al. 2019). Response of understory vegetation in closed-canopy forests may be only marginally affected by surface fires in different seasons if fire behavior is insufficient in creating sizable canopy gaps to increase light availability (Alexander et al. 2008; Hutchinson et al. 2012a). Further, changes in the relative abundance of different plant populations within a community may be more sensitive to variability in fire behavior on a given burn day than burning in different periods of phenological progression (Keyser et al. 2019).

The results of our study suggest that understory cover and density were largely unaffected by season of burn at the functional group level. Few significant treatment effects were detected that would indicate that understory plants of particular growth habits or in different stages of life history responded differently to single-entry burns applied in different seasons. Contrary to our hypothesis, we did not find evidence to suggest that early growing season burns were more effective in increasing forb and graminoid abundance, even with greater photoperiod and warmer ambient temperatures. While reductions in litter load may enhance understory germination, litter consumption did not significantly differ between season of burn treatments used in this study (Chapter 1). Some of the few significant differences in understory abundance between treatments were between the burn treatments and unburned controls, including absolute density of both all tree sprouts and mesophytic hardwood tree sprouts. These results reflect the common observation of natural regeneration (e.g. basal sprouting from parent midstory/overstory trees) as a vegetative response to fire that does not cause immediate mortality to the entire plant (Elliott et al. 1999; Brose and Van Lear 2004). Growing season burns, were, however, more effective than the other treatments in increasing the absolute density of other trees often present but not dominant in the forest midstory, such as sourwood (Oxydendrum arboreum (L.) DC.), black locust (Robinia pseudoacacia L.), and American holly (Ilex opaca Aiton). Trees in the "other" group were the most difficult to classify among tree groups with often divergent characteristics and therefore treatment differences observed may not reflect a functional response shared by most species within that group.

Growing season burns were also more effective than unburned controls in decreasing the absolute density of established red maple (Acer rubrum L.) in the understory, though not in comparison to dormant season burns. Changes in the abundance of established red maples as a result of burn treatments likely reflects both the mortality of stems present prior to the burn as well as the consumption of seeds by fire that would have become established within the second completed growing season following burning. Red maple is a dominant mesophytic competitor to the advance regeneration of oaks and hickories and is capable of prolific germination rates, even under high shade (Walters and Yawney 1990; Abrams 1998; Hutchinson et al. 2008). In comparison to most other tree species in eastern deciduous forests, red maple is among the earliest and most vigorous in initiating stem growth in the spring (Jacobs 1965). If red maples are preferentially allocating resources to growth during this period, then this species may be more sensitive to disturbance in the early growing season (Trickett 2018). Nevertheless, while burning in the growing season was the most effective treatment in reducing established understory red maples, growing season burns did not reduce the density of germinant and sprout stems of this species nor were more effective in doing so than the other treatments. Therefore, changes in the abundance of understory red maple should continue to be monitored after a single burn, particularly if reproductive red maples remain present in the overstory.

In contrast to the understory, the results of our study suggest that season of burn had many significant effects on the structure and composition of the midstory, with implications for the pool of advance regeneration. Growing season burns were more effective than the other treatments in reducing the absolute density of midstory shrubs. Dormant season burns, in comparison, reduced shrub density to a lesser extent than growing season burns, whereas unburned controls saw an increase in shrub density. Supporting our hypothesis, results of treatment effects on midstory shrubs and trees generally indicated that growing season burns were more effective than unburned controls in reducing stem density overall, but with the greatest differences concentrated in smaller diameter classes. Dormant season burns were inconsistently either significantly different or not different from unburned controls in comparisons of midstory response by defined plant groups. Burning in the dormant and/or growing season significantly reduced the density of red oaks in comparison to the unburned controls. Treatment response in the midstory may reveal which shrubs and trees are most susceptible to fire-induced mortality as a result of fire behavior more likely to occur in that season.

Growing season burns conducted in this study had higher levels of solar radiation, air temperature, and fuel temperature as well as lower fine fuel moisture than in dormant season burns (Chapter 1). Whereas wind speed, relative humidity (RH), and the Keetch-Byram Drought Index (KBDI) did not significantly differ by season of burn, timeintegrated temperatures recorded by thermocouple probes during and after passage of flaming fronts were significantly higher in growing season burns than in dormant season burns. Accordingly, greater area was burned within growing season burn units than in units burned in the dormant season. Such variability in fire behavior on burn days suggests that mortality of woody stems may differ based on the extent, intensity, and severity of fire throughout each unit. Early growing season burns, for example, reduced the midstory density of red maple (a mesophytic hardwood) more effectively but of mesophytic hardwoods overall of 3-6 cm DBH class less effectively than dormant season burns. This pattern may suggest that mesophytic hardwood species other than red maple [e.g. yellow-poplar, blackgum (*Nyssa sylvatica* Marshall), flowering dogwood (*Cornus florida* L.)] responded differently to burn treatments (Phillips and Waldrop 2008), which would have implications for targeting season of burn for desired species composition among tree groups.

Differentiating seasonal fire effects on mesophytic hardwood regeneration is critical if the management objective is to use prescribed fire to reverse the effects of mesophication in mixed oak-hickory and pine forests. More severe fire that does not completely consume a given mesophytic hardwood individual could induce equivalent or greater resprouting vigor than less severe fire, particularly after a single burn (Lawes and Clarke 2011). Sprouting stems with the capacity to rapidly recruit into the midstory would offset the effect of higher fire severity unless the disturbance caused by burning reached a cumulative threshold of severity and frequency to deplete the reserves necessary to regenerate (Hutchinson et al. 2012b; Clarke et al. 2013; Arthur et al. 2015). Lack of nutrient uptake may help contribute to this threshold as fire occurrence when trees are less able to replace lost nutrients may curtail resprouting ability of a species that would otherwise resprout more vigorously in response to higher levels of disturbance (Schwemlein and Williams 2007). Though higher fire temperatures have been shown to maintain or increase red maple sprout abundance (Clark and Schweitzer 2013; Arthur et al. 2015), early growing

season burns in our study were still of sufficient severity to reduce midstory red maple density to a greater extent than dormant season burns with a single treatment. Lower severity fire in dormant season burns, in contrast, may be more effective in reducing the density of other mesophytic hardwoods that managers may be attempting to suppress, at least in the short term. It is less clear, however, how the correlation between five severity and sprout abundance persists over time and in relation to season of burn (Brose et al. 2013). Forest midstories with substantial mesophytic hardwood encroachment may see a reduction in the abundance of red maple and mesophytic hardwoods overall with repeated applications of both dormant and growing season fire (Arthur et al. 2015; Vander Yacht et al. 2019).

Differences in species richness and diversity as a result of season of burn may reflect altered patterns of relative abundance of competing plants comprising heterogeneous communities. No significant effects of treatments on changes in understory species richness or diversity were detected in this study, a finding which did not support our hypothesis. Changes in the density of understory plant populations that did occur in response to treatments, therefore, were not sufficient to alter community-level patterns of composition. Timing of fire occurrence as it would affect non-woody vegetation (herbaceous, i.e. forbs and graminoids) in the early growing season should be considered relative to the physiological breaking of dormancy, even when aboveground biomass is absent (Baskin and Baskin 1988). In contrast to season of burn studies on herbaceous response in the Coastal Plain, growing season burns for this study were restricted to a narrow range of the calendar year (April 18-24) at the very earliest stages of the respective growing seasons, particularly at higher elevations. Herbaceous plants may not benefit from a favorable growth environment in the early growing season if resource advantages do not compensate for disruption of phenological progression in the spring green-up period. Fire applied during different periods of understory plant growth and dormancy—with effects monitored thereafter—may reveal how season of burn might facilitate community-level shifts in species diversity impacting ecosystem resiliency.

Burning later vs. earlier in the calendar year in the Northern Hemisphere before canopy closure occurs under a longer photoperiod and likely warmer ambient temperatures following the same amount of time since the last precipitation (Schroeder and Buck 1970). This pattern alone likely explains a large degree of seasonal variability in fire behavior between dormant and early growing season burns. While phenological development may visually appear similar between the late dormant season (e.g. mid-March) and the early growing season (e.g. mid-April), greater coverage of plot area burned and release of thermal energy in the early growing season likely influenced midstory structure and composition in our study. Absolute changes in midstory stem density documented also may reflect changes in the relative dominance of midstory plants (Baker and Van Lear 1998; Albrecht and McCarthy 2006). While significant treatment effects on midstory species richness and diversity were sparse, effects that did differ by treatment generally suggested that early growing season burns reduced species richness and diversity to a greater extent that unburned controls but did not differ in effect from dormant season burns. Midstory stems consumed by fire may not necessarily regenerate and re-recruit into the midstory by the completion of the second growing season following treatment (post-burn sampling period used in this study). Reductions in midstory species richness and diversity, therefore, may at least partially reflect the slower recovery of vegetation that has resprouted but not yet reached the midstory. For example, many dead midstory stems of mountain laurel had vigorous basal resprouting accounted for in post-burn measurements of the understory. Though changes in understory sprout density were not significantly different by season of burn (for mountain laurel or otherwise), understory sprouting of many woody species documented in the early growing season may result in changes in species richness and diversity of the advance regeneration layer in later periods post-fire not captured by this study.

Burn treatments used in this study—largely surface fires as prescribed by management—were unlikely to be of sufficient intensity to cause significant immediate overstory tree mortality, except for at the most xeric and exposed parts of the landscape. Accordingly, we did not expect substantial differences in changes in (growing season) canopy cover as a result of any treatment over the course of this study. Nevertheless, canopy cover was reduced to a greater extent with burn treatments in comparison to the unburned control, though such changes were modest. Regardless of the extent of first-order effects on the overstory, prescribed surface fire may have delayed, second-order effects on the overstory and cause non-lethal injuries to midstory shrubs and trees that would inhibit the development of foliage shading the understory (Yaussy and Waldrop 2010). Such changes in light availability may also influence the moisture environment of the understory and thereby levels of surface water retention and soil moisture (North et al. 2005; Rodríguez-Calcerrada et al. 2008).

84

Lower fuel moisture driven by greater intensity of solar radiation and reflected by warmer temperatures likely allowed fire to spread to parts of the landscape and burn at greater intensity in many cases than dormant season conditions would permit (Chapter 1). Nevertheless, changes in understory community composition at the species level were modest and did not clearly correlate with environmental gradients of topography and measures of fire behavior. In the midstory, however, plots in dormant season burns and early growing season burns shifted in species composition in opposite directions according to gradients of elevation, burn severity, and change in canopy cover. Sites were positioned along a substantial elevational gradient (> 600 m) that likely influenced the biogeographical ordering of plant communities sampled in our study irrespective of variables more directly linked to fire behavior in burn treatments (Whittaker 1956). Therefore, with elevation excluded from analysis, the combination of slope position, burn severity, bole scorch height, and change in canopy cover explained the greatest degree of variability in midstory community response. Each of these factors contributed to altered relative abundance of species comprising the midstory community as reflected in changes in the absolute abundance of species and groups thereof documented. Whereas measures of fire behavior may have been consistently higher in early growing season burns, such variables still explained variability in community response between treatments.

2.4.1 Conclusions and management implications

Season of burn may be expressed as the relationship between fire behavior and the structure, composition, and function of plant communities in a given phenological period and environmental context. The magnitude and duration of the transference of thermal

energy may variably influence the competitive ability of plants in different periods of phenological progression (Dickinson and Johnson 2001; Regier et al. 2010). Accordingly, patterns of population response, as influenced by season of burn, have implications for the structure, composition, and function of plant communities throughout succession. Treatment effects were largely concentrated in the midstory, where growing season burns were most effective in reducing shrub density and were comparable in effect to dormant seasons burns in reducing stem density overall. Changes in stem density following a single prescribed burn will likely attenuate over time, but prescribed burns applied when seeds have recently been dispersed in the early growing season may be effective in reducing the abundance of red maple and other mesophytic hardwoods. Season of burn did not significantly alter canopy cover, but growing season fire behavior in closed-canopy forests may be more effective in reducing midstory shrub density as a result of greater levels of stem consumption. Despite concerns of negative effects on wildlife, early growing season burns may improve wildlife habitat with repeated application over longer periods. Many wildlife species may be just as capable of survival in an early growing season burn as compared to burning at other times of the year (Kilburg et al. 2014). Early growing season burns were at least as effective as dormant season burns in altering species composition for restoration objectives. Evaluating the effects of fire applied in different seasons on the distribution of vegetation may better inform fire management centered around the environmental variability that those seasons represent.

TABLES AND FIGURES

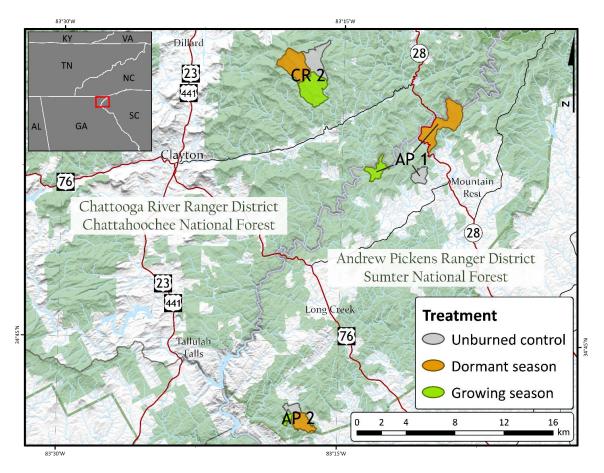


Figure 2.1. Map depicting the replicates comprised of treatment units with plots established in this study. "AP" refers to replicates in the Andrew Pickens Ranger District whereas "CR" refers to replicates in the Chattooga River Ranger District. See Table 2.1 for further information on treatment units.

Replicate	Treatment	Unit	Area (ha)	Date of burn	Elevation range (m)
	Unburned control (C)	AP1C	134	n/a	498 - 625
AP 1	Dormant season burn (DS)	AP1D	538	01/31/18	480 - 772
	Growing season burn (GS)	AP1G	160	04/18/18	454 - 560
	Unburned control (C)	AP2C	81	n/a	360 - 470
AP 2	Dormant season burn (DS)	AP2D	205	03/18/19	275 - 468
	Growing season burn (GS)	AP2G	43	04/21/18	312 - 462
	Unburned control (C)	CR2C	323	n/a	704 - 1,157
CR 2	Dormant season burn (DS)	CR2D	436	04/05/18	734 - 1,427
	Growing season burn (GS)	CR2G	446	04/24/19	622 - 966

Table 2.1. Listing of treatment units used in analysis in this study by replicate and corresponding treatment, with area (ha), date of burn (if applicable), and elevation range (m).

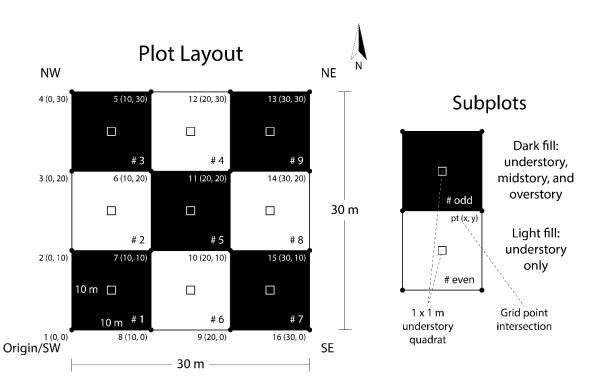


Figure 2.2. Representative diagram indicating the layout, orientation, and dimensions of each plot with interior grid point intersections, subplots, and understory quadrats. The (x, y) Cartesian coordinate pairs for each grid point represent the longitudinal (x) and latitudinal (y) distance from the origin.

exclusion of paired absences. Response variable (* α = 0.05)	Treatment	Mean (± SE)	Tukey HSD
Cover $[\Delta \Sigma \text{ (proportion m}^{-2})]$			
By growth habit			
A 11	С	$+1.04 (\pm 0.13)$	
All F ratio = 0.36 , $p = 0.72$	DS	$+1.46 (\pm 0.19)$	
1^{-1} 1 1 1 1 0 - 0.50, $p = 0.72$	GS	$+1.82 (\pm 0.23)$	
Earth	С	+0.11 (± 0.04)	
Forb F ratio = $0.67, p = 0.56$	DS	$+0.10 (\pm 0.08)$	
F 1000 = 0.07, p = 0.000	GS	$+0.32 (\pm 0.09)$	
Commingial	С	$+0.07~(\pm 0.03)$	
Graminoid F ratio = 2.08 , $p = 0.24$	DS	$+0.24 (\pm 0.03)$	
F 1000 = 2.08, p = 0.24	GS	$+0.30 (\pm 0.04)$	
	С	$+0.14 (\pm 0.05)$	
Herb (forb, graminoid)	DS	$+0.32 (\pm 0.09)$	
F ratio = $1.23, p = 0.38$	GS	+0.58 (± 0.11)	
	С	$+0.09 (\pm 0.02)$	
Vine Exercise $= 1.24$, $n = 0.26$	DS	$+0.07 (\pm 0.03)$	
F ratio = $1.34, p = 0.36$	GS	$+0.26 (\pm 0.04)$	
Sharah	С	+0.31 (± 0.07)	
Shrub F ratio = $0.04, p = 0.96$	DS	$+0.24 (\pm 0.10)$	
1° 1auo = 0.04, $p = 0.90$	DS GS	$+0.27 (\pm 0.08)$	
Tree	С	$+0.51 (\pm 0.08)$	
Tree F ratio = $0.38, p = 0.70$	DS	$+0.84 (\pm 0.11)$	
1^{1} 1auo = 0.38, $p = 0.70$	GS	$+0.72 (\pm 0.10)$	
	С	+0.91 (± 0.12)	
Woody (vine, shrub, tree) E ratio = 0.12 , $n = 0.80$	DS	$+1.14 (\pm 0.15)$	
F ratio = $0.12, p = 0.89$	GS	$+1.24 (\pm 0.16)$	
Tree by group			
History	С	$+0.04 (\pm 0.02)$	
Hickory Exercise $= 2.58$, $n = 0.24$	DS	-0.03 (± 0.01)	
F ratio = $2.58, p = 0.24$	GS	$+0.02 (\pm 0.02)$	
Mesophytic hardwood	С	+0.29 (± 0.04)	

Table 2.2. Summary of treatment effects on understory vegetation cover analyzed using a one-way ANOVA. Response variables represent absolute changes and are summed by plot (sample unit; 9 m²) across individual subplot quadrats. Group means may not equal the sum of subgroup means due to the exclusion of paired absences.

F ratio = $1.10, p = 0.41$	DS	$+0.46~(\pm 0.06)$	
	GS	$+0.59 (\pm 0.09)$	
	С	+0.10 (± 0.03)	
Red oak	DS	$+0.09 (\pm 0.03)$	
F ratio = $1.45, p = 0.33$	GS	$+0.00 (\pm 0.02)$	
	С	+0.09 (± 0.03)	
White oak	DS	$+0.07 (\pm 0.05)$	
F ratio = 1.35 , $p = 0.36$	GS	$-0.03 (\pm 0.02)$	
	С	-0.01 (± 0.02)	
White pine F ratio = 24.36	DS	-0.11 (± 0.05)	
F ratio = 24.36	GS	$-0.20 (\pm 0.03)$	
	С	+0.01 (± 0.02)	
Yellow pine	DS	$+0.15 (\pm 0.02)$	
F ratio = $0.41, p = 0.69$	DS GS C	$+0.06~(\pm 0.02)$	
	С	+0.08 (± 0.03)	
Other	DS	$+0.20 (\pm 0.06)$	
F ratio = 2.23 , $p = 0.21$	GS	+0.23 (± 0.04)	
Species of interest: Acer rubrum	ļ		
	С	+0.18 (± 0.03)	
All	DS	+0.17 (± 0.03)	
F ratio = $0.70, p = 0.56$	GS	$+0.10 (\pm 0.05)$	
Species of interest: Kalmia latifolia			
	С	-0.02 (± 0.02)	
All	DS	+0.13 (± 0.07)	
F ratio = $0.40, p = 0.70$	GS	$+0.08 (\pm 0.06)$	

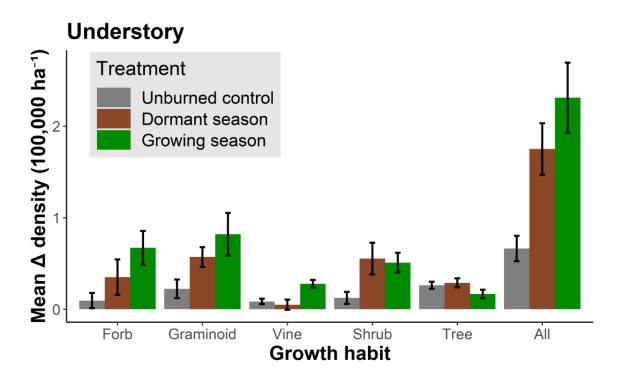


Figure 2.3. Summary of treatment effects on understory vegetation density analyzed using a one-way ANOVA. Error bars represent standard error associated with each treatment and letters represent significant differences between treatments. Response variables represent absolute changes and are summed by plot (sample unit; 9 m²) across individual subplot quadrats. Group means may not equal the sum of subgroup means due to the exclusion of paired absences.

Table 2.3. Summary of treatment effects on understory vegetation density analyzed using a one-way ANOVA. 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.

Response variable $(* \alpha = 0.05)$	Treatment	Mean (± SE)	Tukey HSD
Density $[\Delta \Sigma (\text{count ha}^{-1})]$			
Woody by growth habit and l	ife history		
All			
Germinant	С	-4762 (± 1444)	
F ratio = $0.17, p = 0.85$	DS	+11533 (± 2806)	
1^{1} 1 and -0.17 , $p = 0.85$	GS	+347 (± 2245)	
Established	С	+50584 (± 8112)	
Established F ratio = 0.12 , $p = 0.89$	DS	+67716 (± 24014)	
1^{1} 1 and -0.12 , $p = 0.89$	GS	+62579 (± 11745)	
Sprout	С	-263 (± 1517)	
Sprout F ratio = $2.83, p = 0.17$	DS	$+10586 (\pm 10057)$	
17100 - 2.03; p = 0.17	GS	+30774 (± 7029)	
Vine			
	С	-3761 (± 1223)	
Germinant	DS	+1296 (± 682)	
F ratio = 0.90, $p = 0.60$	GS	-2857 (± 1504)	
	С	+9435 (± 3062)	
Established Exercise $= 0.20$, $n = 0.82$	DS	+4568 (± 5472)	
F ratio = $0.20, p = 0.83$	GS	+28433 (± 4130)	
	С	-1111 (± 786)	
Sprout F ratio = 0.28 , $p = 0.87$	DS	-370 (± 980)	
F fatto = 0.28; $p = 0.87$	GS	$+889 (\pm 2288)$	
Shrub			
	С	-489 (± 767)	
Germinant	DS	-648 (± 571)	
F ratio = 0.75 , $p = 0.52$	GS	-2222 (± 782)	
	С	+14061 (± 5994)	
Established	DS	+60540 (± 24318)	
F ratio = 0.07 , $p = 0.94$	GS	+36790 (± 10147)	
Sprout	С	-1773 (± 1766)	

F ratio = 0.39	DS	-5778 (± 12119)	
	GS	+18786 (± 8686)	
Tree			
	С	-4789 (± 1291)	
Germinant	DS	+12564 (± 2868)	
F ratio = 0.14 , $p = 0.88$	GS	+2407 (± 1981)	
	С	+27326 (± 3528)	
Established	DS	+4290 (± 2860)	
F ratio = 2.82, $p = 0.17$	GS	-1329 (± 4471)	
	С	+1833 (± 607)	b
Sprout	DS	+16869 (± 2530)	а
F ratio = 16.82, <i>p</i> = *0.01	GS	+17191 (± 2207)	a
Tree by group and life history			
	С	+185 (± 301)	
Hickory F ratio = 1.23, <i>p</i> = 0.41	DS	-635 (± 344)	
	GS	+133 (± 275)	
	С	-1111	
Germinant	DS	n/a	
	GS	n/a	
	С	-196 (± 319)	
Established	DS	-1111 (± 356)	
F ratio = 3.53 , $p = 0.35$	GS	-48 (± 284)	
G	С	+2593 (± 980)	
Sprout	DS	+1852 (± 370)	
F ratio = $0.22, p = 0.81$	GS	+1481 (± 370)	
	С	+24840 (± 3763)	
Mesophytic hardwood F ratio = 0.68 , $p = 0.57$	DS	+24660 (± 3531)	
1° 1400 – 0.08, p – 0.57	GS	$+19385 (\pm 4003)$	
Commingent	С	-4831 (± 1052)	
Germinant F ratio = 0.42 , $p = 0.68$	DS	+8254 (± 2172)	
1^{1} 1410 = 0.42, p = 0.08	GS	+3684 (± 1901)	
Established	С	+26045 (± 3600)	
F ratio = 4.68 , $p = 0.09$	DS	+9321 (± 1966)	
1 1000 - 7.00, p = 0.09	GS	+5952 (± 3608)	
Sprout	С	+1176 (± 551)	b
Sprout F ratio = 14.82, <i>p</i> = *0.02	DS	+13065 (± 2173)	а
1 1 a = 17.02, p = 0.02	GS	+13026 (± 2107)	а

Dadaal	С	+566 (± 324)
Red oak F ratio = $2.83, p = 0.20$	DS	$+660 (\pm 686)$
$1^{-1}auo = 2.83, p = 0.20$	GS	-933 (± 500)
	С	-1111
Germinant	DS	+1111
	GS	-1111
Established	С	+392 (± 283)
Established F ratio = 2.06	DS	-1148 (± 604)
1° 1au0 – 2.00	GS	-2111 (± 488)
C	С	+1667 (± 1174)
Sprout F ratio = 2.22	DS	+4188 (± 1290)
Γ ratio = 2.22	GS	+2857 (± 545)
X 71-141-	С	+169 (± 961)
White oak Exactly $r = 1.26$ $n = 0.27$	DS	-1926 (± 2732)
F ratio = $1.26, p = 0.37$	GS	-3262 (± 1452)
Commission	С	$+556 (\pm 1667)$
Germinant F ratio = $1.00, p = 0.64$	DS	n/a
r 1auo = 1.00, p = 0.04	GS	-1111 (± 0)
	С	-222 (± 945)
Established Example 22	DS	-4713 (± 2714)
F ratio = 1.47, $p = 0.33$	GS	-5725 (± 1401)
C	С	+1852 (± 786)
Sprout E ratio = 0.00 , n = 0.02	DS	+4931 (± 1196)
F ratio = $0.09, p = 0.92$	GS	+5906 (± 1930)
W/hite nine	С	-152 (± 544)
White pine F ratio = 10.43	DS	-3778 (± 2399)
1° 10.43	GS	-12912 (± 2760)
Comminant	С	-1111
Germinant F ratio = 1.15	DS	-1111
1° 1au0 – 1.15	GS	-4321 (± 1692)
Fatablishad	С	-101 (± 551)
Established F ratio = 16.95	DS	-3556 (± 2177)
1° 1atio = 10.95		
	GS	-11667 (± 2476)
Vallow nine	GS C	-11667 (± 2476) +171 (± 516)
Yellow pine E ratio = 0.29, $n = 0.77$		
Yellow pine F ratio = 0.29 , $p = 0.77$	С	+171 (± 516)
_	C DS	+171 (± 516) +6768 (± 1431)

	GS	+556 (± 743)	
	С	+1389 (± 458)	
Established	DS	+417 (± 725)	
F ratio = 0.03 , $p = 0.97$	GS	+2281 (± 661)	
	С	n/a	
Sprout	DS	n/a	
-	GS	n/a	
	С	+1206 (± 1432)	b
Other	DS	+2049 (± 1156)	b
F ratio = 19.51, <i>p</i> = *0.01	GS	+6914 (± 1351)	а
	С	-1190 (± 1637)	
Germinant	DS	+778 (± 760)	
F ratio = $0.19, p = 0.83$	GS	-278 (± 658)	
	С	+1818 (± 1105)	
Established	DS	$+609 (\pm 880)$	
F ratio = $4.52, p = 0.09$	GS	+4547 (± 1206)	
	С	-101 (± 694)	
Sprout F ratio = 0.00	DS	+2778 (± 2527)	
F = 1000	GS	+5244 (± 1204)	
Species of interest: Acer rubri	ит		
	С	+23504 (± 4143)	
All	DS	+13519 (± 2849)	
F ratio = $6.42, p = 0.12$	GS	+1006 (± 2746)	
	С	-6111 (± 1213)	
Germinant	DS	+6144 (± 1344)	
F ratio = $0.47, p = 0.66$	GS	+4521 (± 2399)	
	С	+25256 (± 3953)	а
Established Exercise $= 20.05$ $= = *0.01$	DS	$+3000 (\pm 1788)$	ab
F ratio = 30.05, <i>p</i> = *0.01	GS	-9581 (± 1881)	b
C	С	+787 (± 674)	
Sprout F ratio =7.35, <i>p</i> = 0.06	DS	+10053 (± 1979)	
1 Tatlo = 7.55; p = 0.00	GS	+11026 (± 2057)	
Species of interest: Kalmia lat	tifolia		
A 11	С	-850 (± 1142)	
All	DS	+16875 (±4787)	
F ratio = $3.99, p = 0.11$	GS	+28089 (± 9032)	
Germinant	С	-1605 (± 494)	

F ratio = 0.51	DS GS	-1111 (± 0) -1111 (± 0)
T (11' 1 1	С	-317 (± 760)
Established	DS	+185 (± 926)
F ratio = 10.02	GS	-8444 (± 3588)
G , ,	С	-231 (± 1374)
Sprout	DS	+19286 (± 5571)
F ratio = $4.76, p = 0.11$	GS	+34630 (± 10451)

Response variable (* α = 0.05)	Treatment	Mean (± SE)	Tukey HSD
Cover [$\Delta \Sigma$ (proportion 0.01 m	n ⁻²)]		
	С	$-0.06 (\pm 0.09)$	
<i>Kalmia latifolia</i> F ratio = 0.12 , $p = 0.89$	DS	-0.24 (± 0.13)	
1^{1} 1410 = 0.12, p = 0.89	GS	$-0.22 (\pm 0.09)$	
Tatal	С	-0.27 (± 0.11)	
Total E rotia = 0.02 , n = 0.47	DS	-0.95 (± 0.20)	
F ratio = 0.93 , $p = 0.47$	GS	-0.70 (± 0.14)	

Table 2.4. Summary of treatment effects on midstory vegetation cover analyzed using a one-way ANOVA. Response variables are averaged by plot (sample unit; 500 m^2) across individual subplots.

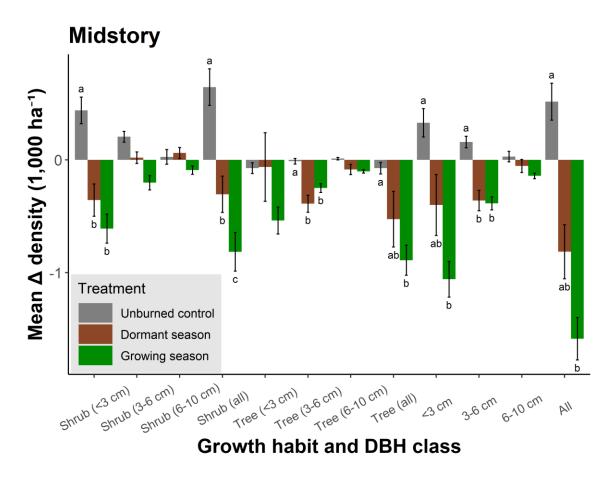


Figure 2.4. Summary of treatment effects on midstory vegetation density analyzed using a one-way ANOVA. Error bars represent standard error associated with each treatment and letters represent significant differences between treatments. Response variables represent absolute changes and are summed by plot (sample unit; 500 m²) across individual subplots. Group means may not equal the sum of subgroup means due to the exclusion of paired absences.

paired absences. Response variable (* $\alpha = 0.05$)	Treatment	Mean (± SE)	Tukey HSD
Density $[\Delta \Sigma (\text{count ha}^{-1})]$			
Tree by group and DBH class			
III' - 1	С	-45 (± 18)	
Hickory F ratio = 0.01 , $p = 0.99$	DS	-45 (± 19)	
1^{-1} 1	GS	-6 (± 10)	
< 2 am	С	-38 (± 15)	
< 3 cm	DS	-68 (± 29)	
F ratio = $1.75, p = 0.58$	GS	-19 (± 9)	
2.6	С	-26 (± 17)	
3 - 6 cm	DS	-23 (±16)	
F ratio = 0.05 , $p = 0.95$	GS	+9 (± 19)	
< 10	С	-4 (± 6)	
6 - 10 cm	DS	+77 (± 58)	
F ratio = $1.25, p = 0.39$	GS	+6 (± 12)	
	С	-17 (± 38)	а
Mesophytic hardwood	DS	-376 (± 165)	ab
F ratio = 24.69, <i>p</i> = *0.01	GS	-561 (± 80)	b
	С	-25 (± 38)	
< 3 cm	DS	-104 (± 167)	
F ratio = $6.40, p = 0.07$	GS	-333 (± 64)	
2 6 2 2	С	+4 (± 16)	а
3 - 6 cm F ratio = 95.23, <i>p</i> < *0.01	DS	-236 (± 51)	b
1^{1} 1410 – $33.23, p < 10.01$	GS	-176 (± 35)	с
<u>(10</u>	С	+5 (± 7)	
6 - 10 cm	DS	-43 (± 22)	
F ratio = $9.21, p = 0.05$	GS	-63 (± 10)	
Dad cal	С	-5 (± 11)	а
Red oak F ratio = 7.82, <i>p</i> = *0.04	DS	-59 (± 37)	ab
$1^{-1}au0 = 1.02, p = 10.04$	GS	-74 (± 22)	b
< 3 cm	С	-3 (± 10)	
F ratio = 5.36, $p = 0.08$	DS	+3 (± 47)	

Table 2.5. Summary of treatment effects on midstory vegetation density analyzed using a one-way ANOVA. Response variables represent absolute changes and are summed by plot (sample unit; 500 m²) across individual subplots. Group means may not equal the sum of subgroup means due to the exclusion of paired absences.

	GS	-66 (± 19)	
2. 6	С	0 (± 8)	а
3 - 6 cm F ratio = 12.97, <i>p</i> = *0.03	DS	-67 (± 21)	b
r 1auo - 12.97, p - 90.03	GS	-38 (± 26)	ab
(10 and	С	-4 (± 7)	
6 - 10 cm	DS	-37 (± 23)	
F ratio = 8.76	GS	-26 (± 18)	
	С	+5 (± 10)	
White oak $E_{ratio} = 7.00$, $n = 0.07$	DS	-59 (± 33)	
F ratio = 7.00, $p = 0.07$	GS	-58 (± 31)	
	С	+1 (± 9)	
< 3 cm	DS	-23 (± 33)	
F ratio = $5.02, p = 0.08$	GS	-80 (± 51)	
2.6	С	-2 (± 13)	а
3 - 6 cm	DS	-44 (± 21)	b
F ratio = 12.97, <i>p</i> = *0.03	GS	-16 (± 6)	ab
< 10	С	+7 (± 5)	
6 - 10 cm	DS	-7 (± 21)	
F ratio = 8.76	GS	-4 (± 10)	
XX71 ''	С	-9 (± 24)	
White pine	DS	-108 (± 53)	
F ratio = 1.63 , $p = 0.31$	GS	-323 (± 155)	
	С	+1 (± 20)	
< 3 cm	DS	-94 (± 53)	
F ratio = $2.57, p = 0.19$	GS	-345 (± 173)	
2.6	С	-17 (± 12)	
3 - 6 cm	DS	-60 (± 40)	
F ratio = $0.21, p = 0.82$	GS	-68 (± 39)	
	С	+4 (± 9)	
6 - 10 cm F ratio = 2.08	DS	$+40 (\pm 55)$	
F 1400 – 2.08	GS	-36 (± 10)	
V -11	С	-11 (± 9)	
Yellow pine	DS	-78 (± 32)	
F ratio = 0.43 , $p = 0.69$	GS	-78 (± 55)	
	С	+5 (± 15)	
< 3 cm	DS	-58 (± 17)	
F ratio = 3.85	GS	-75 (± 38)	
3 - 6 cm	С	-8 (± 8)	

F ratio = 0.45	DS	-35 (± 16)	
	GS	-53 (± 64)	
	С	-13 (± 11)	
6 - 10 cm	DS	-20 (± 25)	
F ratio = $0.04, p = 0.96$	GS	-32 (± 24)	
	С	-30 (± 20)	
Other	DS	+33 (± 110)	
F ratio = $2.42, p = 0.20$	GS	-102 (± 50)	
	С	-42 (± 20)	
< 3 cm	DS	+135 (± 140)	
F ratio = $1.18, p = 0.39$	GS	-37 (± 51)	
2 (С	+3 (± 9)	a
3 - 6 cm	DS	-73 (± 29)	ab
F ratio = 8.60, <i>p</i> = *0.03	GS	-55 (±12)	b
	С	+7 (± 7)	
6 - 10 cm	DS	-41 (± 17)	
F ratio = $2.17, p = 0.23$	GS	-27 (± 8)	
Species of interest: Acer rubrur	n		
	С	+15 (± 31)	а
All	DS	-219 (± 69)	а
F ratio = 47.91, <i>p</i> < *0.01	GS	-356 (± 57)	b
	С	+6 (± 32)	a
< 3 cm	DS	-73 (± 57)	ab
F ratio = 9.72, <i>p</i> = *0.04	GS	-216 (± 49)	b
2.6	С	+3 (± 13)	a
3 - 6 cm	DS	-130 (± 31)	b
F ratio = 37.92, <i>p</i> < *0.01	GS	-128 (± 28)	b
	С	+8 (± 6)	
6 - 10 cm	DS	-37 (±16)	
F ratio = 5.58 , $p = 0.07$	GS	-37 (± 10)	
Species of interest: Kalmia latij	folia		
	С	+703 (± 173)	
All	DS	-225 (± 161)	
F ratio = $6.55, p = 0.05$	GS	-642 (± 130)	
	С	+497 (± 127)	a
< 3 cm	DS	-323 (± 146)	ab
F ratio = 9.53, <i>p</i> = *0.03	GS	-494 (± 83)	b

	С	+203 (± 51)	
3 - 6 cm	DS	+64 (± 53)	
F ratio = $9.56, p = 0.07$	GS	-158 (± 67)	
6 10	С	+27 (± 68)	
6 - 10 cm	DS	+99 (± 62)	
F ratio = $1.37, p = 0.37$	GS	-94 (± 40)	

$\frac{\text{Response variable}}{(* \alpha = 0.05)}$	Treatment	Mean (± SE)	Tukey HSD
Density $[\Delta \Sigma (\text{count ha}^{-1})]$			
	С	+50 (± 15)	
All	DS	+25 (±27)	
F ratio = $2.83, p = 1.00$	GS	-32 (± 24)	
Tree by group			
	С	0 (± 6)	
Hickory	DS	+9 (± 10)	
F ratio = 2.44	GS	+5 (± 8)	
	С	+1 (± 7)	
Mesophytic hardwood F ratio = 1.94	DS	-1 (± 14)	
F ratio = 1.94	GS	-18 (± 9)	
	С	-1 (± 5)	
Red oak	DS	-14 (± 8)	
F ratio = 5.31	GS	-10 (± 5)	
	С	+9 (± 6)	
White oak	DS	+17 (± 8)	
F ratio = 3.08	GS	-1 (± 7)	
XX71 ''	С	+6 (± 9)	
White pine F ratio = 4.33	DS	+120	
F 100 = 4.35	GS	-16 (± 13)	
 X7_11	С	+4 (± 8)	
Yellow pine F ratio = 0.50	DS	+6 (± 16)	
F fatto = 0.30	GS	-13 (± 15)	
	С	+21 (± 9)	
Other Example $= 17.20$	DS	$+8(\pm 6)$	
F ratio = 17.39	GS	$+8 (\pm 9)$	
Species of interest: Acer rubrun	n		
A 11	С	+4 (± 5)	
All F ratio = 5.73	DS	-5 (± 8)	
$1^{-1}auo = 3.75$	GS	-7 (± 7)	

Table 2.6. Summary of treatment effects on overstory vegetation density analyzed using a one-way ANOVA. Response variables represent absolute changes and are summed by plot (sample unit; 500 m²) across individual subplots. Group means may not equal the sum of subgroup means due to the exclusion of paired absences.

Response variable $(* \alpha = 0.05)$	Treatment	Mean (± SE)	Tukey HSD
Species richness $[\Delta]$			
By growth habit			
Forb	C	+1.07 (± 0.19)	
F ratio = $0.40, p = 0.70$	DS CS	$+1.36 (\pm 0.33)$	
	GS	$+1.89 (\pm 0.31)$	
Graminoid	C	$+0.17 (\pm 0.08)$	
F ratio = 2.57, $p = 0.20$	DS GS	$+0.64 (\pm 0.17)$	
	<u>C</u>	$+0.84 (\pm 0.12)$	
Herb (forb, graminoid)	-	$+1.24 (\pm 0.23)$	
F ratio = $0.70, p = 0.55$	DS GS	$+2.00 (\pm 0.39)$	
	<u>C</u>	$+2.73 (\pm 0.35)$	
Vine	DS	$+0.22 (\pm 0.10)$	
F ratio = $0.88, p = 0.48$		$+0.14 (\pm 0.19)$	
	GS C	$+0.52 (\pm 0.10)$	
Shrub		$-0.14 (\pm 0.11)$	
F ratio = 1.39	DS GS	$+0.81 (\pm 0.21)$	
		$+0.91 (\pm 0.19)$	
Tree	C	$+0.61 (\pm 0.27)$	
F ratio = 0.03 , $p = 0.97$	DS GS	$+0.78 (\pm 0.30)$	
		$+0.61 (\pm 0.31)$	
Woody (vine, shrub, tree)	C	$+0.69 (\pm 0.34)$	
F ratio = $0.49, p = 0.64$	DS CS	$+1.72 (\pm 0.49)$	
H' (Shannon-Wiener index) [Δ	GS 1	+2.04 (± 0.43)	
11 (Shannon- whener muck) [Δ	1		
By growth habit			
Forb	С	$+0.29 (\pm 0.06)$	
FOID F ratio = 1.36	DS	$+0.26~(\pm 0.08)$	
- Tutto - 1.50	GS	$+0.13 (\pm 0.07)$	
Graminoid	С	$+0.10 (\pm 0.08)$	_
F ratio = 0.37 , $p = 0.71$	DS	$+0.16~(\pm 0.08)$	

Table 2.7. Summary of treatment effects on understory species richness and α -diversity (*H*') analyzed using a one-way ANOVA. Response variables are aggregated by plot (sample unit; 9 m²) across individual subplot quadrats. Group means may not equal the sum of subgroup means due to the exclusion of paired absences.

	GS	$+0.30 (\pm 0.07)$
	С	+0.25 (±0.06)
Herb (forb, graminoid)	DS	$+0.25 (\pm 0.07)$
F ratio = 0.01 , $p = 0.99$	GS	$+0.26~(\pm 0.06)$
¥7:	С	$+0.09 (\pm 0.04)$
Vine	DS	$+0.04 (\pm 0.05)$
F ratio = $0.21, p = 0.83$	GS	+0.11 (± 0.03)
	С	-0.02 (± 0.04)
Shrub E ratio $= 2.00$, $n = 0.24$	DS	+0.11 (± 0.06)
F ratio = $2.09, p = 0.24$	GS	$+0.26~(\pm 0.05)$
	С	-0.06 (± 0.05)
Tree E ratio $= 0.12$ r $= 0.98$	DS	$+0.03 (\pm 0.05)$
F ratio = $0.13, p = 0.88$	GS	$+0.04 (\pm 0.06)$
Weeder (wine showh tree)	С	$+0.08 (\pm 0.04)$
Woody (vine, shrub, tree)	DS	$+0.20 (\pm 0.05)$
F ratio = 0.63 , $p = 0.57$	GS	$+0.12 (\pm 0.04)$

Response variable (* $\alpha = 0.05$)	Treatment	Mean (± SE)	Tukey HSD
Species richness $[\Delta]$			
By growth habit and DBH c	lass		
Charab	С	0.00 (± 0.10)	
Shrub F ratio = $2.15, p = 0.23$	DS	-0.19 (± 0.16)	
$r_{1allo} = 2.13, p = 0.23$	GS	-0.45 (± 0.15)	
< 2 am	С	-0.07 (± 0.10)	А
< 3 cm F ratio = 8.67, <i>p</i> = *0.03	DS	-0.69 (± 0.14)	ab
$r_{100} = 0.07, p = 0.03$	GS	-0.91 (± 0.15)	В
2 6	С	$+0.14 (\pm 0.07)$	
3 - 6 cm F ratio = 6.29, $p = 0.05$	DS	-0.31 (± 0.14)	
r 100 = 0.29, p = 0.03	GS	$-0.44 (\pm 0.09)$	
(10 ····	С	$0.00 (\pm 0.05)$	
6 - 10 cm	DS	-0.11 (± 0.08)	
F ratio = 0.31 , $p = 0.75$	GS	$0.00 \ (\pm \ 0.07)$	
E.	С	-0.92 (± 0.26)	
Tree	DS	-1.50 (± 0.42)	
F ratio = 1.29, $p = 0.40$	GS	-1.91 (± 0.30)	
2	С	-1.19 (± 0.29)	
< 3 cm	DS	-3.78 (± 0.47)	
F ratio = $4.60, p = 0.09$	GS	-3.25 (± 0.40)	
• •	С	-0.29 (± 0.18)	А
3 - 6 cm	DS	-1.94 (± 0.51)	ab
F ratio = 15.99, <i>p</i> = *0.02	GS	-2.56 (± 0.28)	В
	С	-0.07 (± 0.17)	
6 - 10 cm	DS	-0.75 (± 0.35)	
F ratio = $2.59, p = 0.20$	GS	$-1.60 (\pm 0.25)$	
By DBH class			
	С	-1.25 (± 0.32)	
< 3 cm	DS	-4.47 (± 0.53)	
F ratio = 5.72, $p = 0.06$	GS	-4.16 (± 0.45)	
3 - 6 cm	С	-0.15 (± 0.19)	А
F ratio = 16.07, $p = *0.02$	DS	-2.25 (± 0.56)	ab
· L		()	

Table 2.8. Summary of treatment effects on midstory species richness and α -diversity (*H*') analyzed using a one-way ANOVA. Response variables are aggregated by plot (sample unit; 500 m²) across individual subplots. Group means may not equal the sum of subgroup means due to the exclusion of paired absences.

	GS	-3.00 (± 0.31)	В
6 10 am	С	-0.07 (± 0.19)	
6 - 10 cm F ratio = 1.71, $p = 0.30$	DS	-0.86 (± 0.37)	
171400 - 1.71, p - 0.50	GS	$-1.60 (\pm 0.27)$	
H' (Shannon-Wiener index) [Δ]			
By growth habit and DBH class			
<u>Charach</u>	С	-0.01 (± 0.03)	
Shrub	DS	-0.16 (± 0.06)	
F ratio = $1.63, p = 0.31$	GS	-0.14 (± 0.06)	
	С	$-0.05 (\pm 0.04)$	
< 3 cm F ratio = 0.07	DS	-0.14 (± 0.07)	
F rano = 0.07	GS	$-0.08~(\pm 0.08)$	
2	С	+0.01 (± 0.03)	
3 - 6 cm	DS	+0.01 (± 0.09)	
F ratio = $0.79, p = 0.50$	GS	-0.06 (± 0.04)	
	С	$-0.02 (\pm 0.02)$	
6 - 10 cm	DS	$-0.05 (\pm 0.04)$	
F ratio = 8.58	GS	$+0.07 (\pm 0.05)$	
	С	-0.11 (± 0.03)	
Tree	DS	-0.19 (± 0.06)	
F ratio = $6.30, p = 0.08$	GS	-0.31 (± 0.06)	
	С	-0.18 (± 0.04)	
< 3 cm	DS	$-0.49 (\pm 0.09)$	
F ratio = $1.20, p = 0.39$	GS	$-0.39 (\pm 0.08)$	
	С	-0.08 (± 0.05)	
3 - 6 cm	DS	-0.19 (± 0.10)	
F ratio = $45.95, p = 0.23$	GS	-0.55 (± 0.10)	
	С	-0.02 (± 0.04)	
6 - 10 cm	DS	$-0.14 (\pm 0.08)$	
F ratio = $2.04, p = 0.25$	GS	$-0.37 (\pm 0.07)$	
By DBH class			
	С	-0.26 (± 0.04)	<u> </u>
< 3 cm	DS	$-0.53 (\pm 0.09)$	
F ratio = $1.26, p = 0.37$	GS	$-0.38 (\pm 0.07)$	
3 - 6 cm	С	-0.11 (± 0.04)	А
F ratio = 16.16, <i>p</i> = *0.02	DS	-0.27 (± 0.11)	ab

	GS	-0.60 (± 0.09)	В
6 - 10 cm F ratio = 1.93, $p = 0.26$	С	-0.03 (± 0.04)	
	DS	-0.14 (± 0.07)	
	GS	-0.35 (± 0.07)	

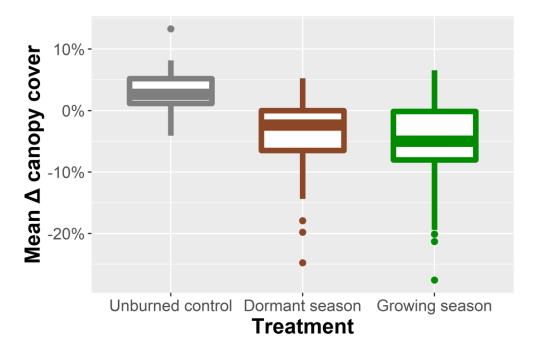


Figure 2.5. Comparison of change in canopy cover (%) by treatment.

Replicate	Treatment	n	Pre-treatment				Post-treatment			
			α (\overline{S})	γ (S)	$\beta_{\rm W}$	β _D	α (\overline{S})	γ (S)	β_{W}	β _D
Understory	-	_	-			-	_			
(all)	С	59	12.54	86	5.86	1.66	14.47	91	5.29	1.58
	DS	36	16.67	99	4.94	1.98	20.39	106	4.20	1.67
	GS	56	16.75	116	5.93	1.73	21.52	124	4.76	1.60
Midstory										
(all)	С	59	9.63	44	3.57	1.38	8.64	41	3.74	1.29
	DS	36	13.56	51	2.76	1.55	10.14	48	3.73	1.66
	GS	55	10.09	47	3.66	1.46	5.80	43	6.41	1.66

Table 2.9. Multivariate summary of diversity measures by replicate and treatment, pre- and post-treatment. α = alpha diversity (non-proportionate; mean species richness, \overline{S}); γ = gamma diversity (total species richness, S); β_W = beta diversity (Whittaker's beta); β_D = beta diversity (half changes corresponding to average community dissimilarity, \overline{D}).

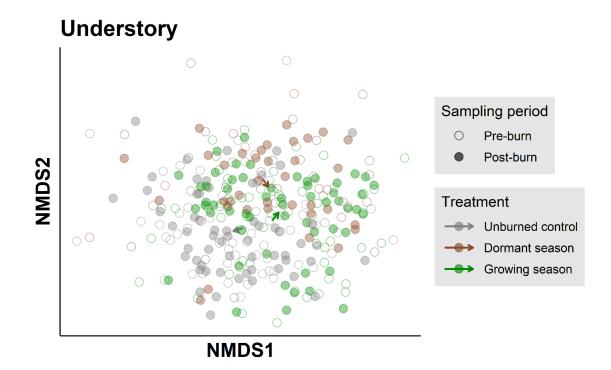


Figure 2.6. Plot of non-metric multidimensional scaling (NMDS) ordination results based on understory species importance values (IVs). Circles represent sites (plots) and arrows represent change vectors indicating plot movement from pre- to post-treatment by treatment.

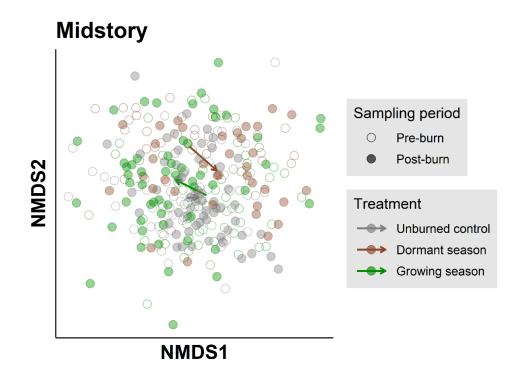


Figure 2.7. Plot of non-metric multidimensional scaling (NMDS) ordination results based on midstory species importance values (IVs). Circles represent sites (plots) and arrows represent change vectors indicating plot movement from pre- to post-treatment by treatment.

Environmental variable	Pre-treat	ment		Post-treatment			
	NMDS1	NMDS2	\mathbf{r}^2	NMDS1	NMDS2	\mathbf{r}^2	
Understory	-	-	-	-	-		
Elevation	-0.81	0.58	0.60	-0.57	0.82	0.57	
TPI	-0.81	0.59	0.30	-0.65	0.76	0.30	
HLI			0.04	0.05	1.00	0.04	
dNBR	n/a	n/a	n/a	0.18	0.98	0.06	
Bole scorch height	n/a	n/a	n/a	0.59	0.81	0.10	
Δ litter load	n/a	n/a	n/a	-0.02	-1.00	0.30	
Pre-burn canopy cover	-0.42	0.91	0.06	n/a	n/a	n/a	
Δ canopy cover	n/a	n/a	n/a	0.01	-1.00	0.13	
Midstory							
Elevation	-1.00	-0.10	0.39	0.92	-0.38	0.26	
TPI	-0.92	0.38	0.13	1.00	0.10	0.21	
HLI			0.01			0.01	
dNBR	n/a	n/a	n/a	0.38	0.93	0.09	
Bole scorch height	n/a	n/a	n/a	-0.35	0.94	0.12	
Δ litter load	n/a	n/a	n/a	-0.91	-0.41	0.05	
Pre-burn canopy cover			0.01	n/a	n/a	n/a	
Δ canopy cover	n/a	n/a	n/a	-0.39	-0.92	0.14	

Table 2.10. Summary of environmental variable correlations with NMDS ordination axes after 999 permutations. Only vector direction cosines of significant correlations ($\alpha = 0.05$) are displayed for each axis (NMDS1 and NMDS2). "n/a" values refer to correlations of variables that would not apply for that sampling period.

REFERENCES

- Abrams MD (2005) Prescribing fire in eastern oak forests: is time running out? North J Appl For 22:190–196. https://doi.org/10.1093/njaf/22.3.190
- Abrams MD (1998) The red maple paradox. Bioscience 48:355–364. https://doi.org/10.2307/1313374
- Abrams MD (2003) Where has all the white oak gone? Bioscience 53:927–939. https://doi.org/10.1641/0006-3568(2003)053[0927:WHATWO]2.0.CO;2
- Albrecht MA, McCarthy BC (2006) Effects of prescribed fire and thinning on tree recruitment patterns in central hardwood forests. For Ecol Manage 226:88–103. https://doi.org/10.1016/j.foreco.2005.12.061
- Alexander HD, Arthur MA, Loftis DL, Green SR (2008) Survival and growth of upland oak and co-occurring competitor seedlings following single and repeated prescribed fires. For Ecol Manage 256:1021–1030. https://doi.org/10.1016/j.foreco.2008.06.004
- Anderson MJ, Ellingsen KE, McArdle BH (2006) Multivariate dispersion as a measure of beta diversity. Ecol Lett 9:683–693. https://doi.org/10.1111/j.1461-0248.2006.00926.x
- Arthur MA, Blankenship BA, Schörgendorfer A, et al (2015) Changes in stand structure and tree vigor with repeated prescribed fire in an Appalachian hardwood forest. For Ecol Manage 340:46–61. https://doi.org/10.1016/j.foreco.2014.12.025
- Baker TT, Van Lear DH (1998) Relations between density of rhododendron thickets and diversity of riparian forests. For Ecol Manage 109:21–32. https://doi.org/10.1016/S0378-1127(98)00259-X
- Bär A, Michaletz ST, Mayr S (2019) Fire effects on tree physiology. New Phytol 223:1728–1741. https://doi.org/10.1111/nph.15871
- Baskin CC, Baskin JM (1988) Germination Ecophysiology of Herbaceous Plant Species in a Temperate Region. Am J Bot 75:286–305. https://doi.org/10.1002/j.1537-2197.1988.tb13441.x
- Beck DE (1990) Liriodendron tulipifera L. yellow-poplar
- Beers TW, Dress PE, Wensel LC (1966) Notes and observations: aspect transformation in site productivity research. J For 64:691–692

Bond WJ, van Wilgen BW (1996) Fire and Plants. Chapman and Hall, London

- Bray JR, Curtis JT (1957) An ordination of the upland forest communities of southern Wisconsin. Ecol Monogr 27:325–349. https://doi.org/10.2307/1942268
- Brose PH, Dey DC, Phillips RJ, Waldrop TA (2013) A meta-analysis of the fire-oak hypothesis: does prescribed burning promote oak reproduction in eastern North America? For Sci 59:322–334. https://doi.org/10.5849/forsci.12-039
- Brose PH, Schuler TM, Van Lear DH, Berst J (2001) Bringing fire back: the changing regimes of the Appalachian mixed-oak forests. J For 99:30–35. https://doi.org/10.1093/jof/99.11.30
- Brose PH, Van Lear DH (2004) Survival of hardwood regeneration during prescribed fires: the importance of root development and root collar location. In:
 Proceedings, upland oak ecology symposium. General Technical Report SRS-73. U.S. Department of Agriculture Forest Service, Southern Research Station, Asheville, NC, pp 123–127
- Buchanan B (2009) Fuel constants comparisons
- Cain MD (1984) Height of stem-bark char underestimates flame length in prescribed burns. Fire Manag Notes 45:17–21
- Chiodi AM, Larkin NS, Varner JM (2018) An analysis of southeastern US prescribed burn weather windows: seasonal variability and El Niño associations. Int J Wildl Fire 27:176–189. https://doi.org/10.1071/WF17132
- Clabo DC, Clatterbuck WK (2019) Shortleaf pine (Pinus echinata, Pinaceae) seedling sprouting responses: clipping and burning effects at various seedling ages and seasons. J Torrey Bot Soc 146:96–110. https://doi.org/10.3159/TORREY-D-18-00004.1
- Clark SL, Schweitzer CJ (2013) Red Maple (Acer Rubrum) Response To Prescribed Burning on the William B . Bankhead National Forest , Alabama. 271–276
- Clarke KR (1993) Non-parametric multivariate analyses of changes in community structure. Aust J Ecol 18:117–143. https://doi.org/10.1111/j.1442-9993.1993.tb00438.x
- Clarke PJ, Lawes MJ, Midgley JJ, et al (2013) Resprouting as a key functional trait: how buds, protection and resources drive persistence after fire. New Phytol 197:19–35. https://doi.org/10.1111/nph.12001

- Dayamba SD, Savadogo P, Zida D, et al (2010) Fire temperature and residence time during dry season burning in a Sudanian savanna-woodland of West Africa with implication for seed germination. J For Res 21:445–450. https://doi.org/10.1007/s11676-010-0095-y
- De Reu J, Bourgeois J, Bats M, et al (2013) Application of the topographic position index to heterogeneous landscapes. Geomorphology 186:39–49. https://doi.org/10.1016/j.geomorph.2012.12.015
- Delcourt PA, Delcourt HR (1998) The influence of prehistoric human-set fires on oakchestnut forests in the southern Appalachians. Castanea 63:337–345
- Dickinson MB, Johnson EA (2001) Fire effects on trees. In: Johnson EA, Miyanishi K (eds) Forest Fires: Behavior and Ecological Effects. Academic Press, New York, pp 477–525
- Dombeck MP, Williams JE, Wood CA (2004) Wildfire policy and public lands: integrating scientific understanding with social concerns across landscapes. Conserv Biol 18:883–889. https://doi.org/10.1111/j.1523-1739.2004.00491.x
- Elliott KJ, Hendrick RL, Major AE, et al (1999) Vegetation dynamics after a prescribed fire in the southern Appalachians. For Ecol Manage 114:199–213. https://doi.org/10.1016/S0378-1127(98)00351-X
- Evans AM (2017) Considerations for the size and shape of TPI windows
- Evans AM, Odom R, Resler L, et al (2014a) Developing a topographic model to predict the northern hardwood forest type within Carolina Northern Flying Squirrel (Glaucomys sabrinus coloratus) recovery areas of the southern Appalachians. Int J For Res 2014:11
- Evans JS, Oakleaf J, Cushman SA, Theobald D (2014b) An ArcGIS toolbox for surface gradient and geomorphometric modeling
- Faith DP, Minchin PR, Belbin L (1987) Compositional dissimilarity as a robust measure of ecological distance. Vegetatio 69:57–68
- Ferguson SA, Ruthford JE, McKay SJ, et al (2002) Measuring moisture dynamics to predict fire severity in longleaf pine forests. Int J Wildl Fire 11:267–279. https://doi.org/10.1071/wf02010
- Fridley JD (2009) Downscaling climate over complex terrain: high finescale (<1000 m) spatial variation of near-ground temperatures in a montane forested landscape (Great Smoky Mountains). J Appl Meteorol Climatol 48:1033–1049. https://doi.org/10.1175/2008JAMC2084.1

- Furze ME, Huggett BA, Aubrecht DM, et al (2019) Whole-tree nonstructural carbohydrate storage and seasonal dynamics in five temperate species. New Phytol 221:1466–1477. https://doi.org/10.1111/nph.15462
- Glitzenstein JS, Streng DR, Masters RE, Platt WJ (2008) Clarifying long-term impacts of fire frequency and fire season in southeastern Coastal Plain pine savannas. In: Stringer WC, Andre J, Yarrow G (eds) Managing an Ecosystem on the Edge. Proceedings of the 6th Eastern Native Grass Symposium, 2008 October 7-10, Columbia, SC. Clemson University College of Agriculture, Forestry, and Life Sciences, Clemson, SC, pp 13–18
- Griffith GE, Omernik JM, Comstock JA, et al (2001) Ecoregions of Alabama and Georgia
- Griffith GE, Omernik JM, Comstock JA, et al (2002) Ecoregions of North Carolina and South Carolina
- Grime JP (1977) Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. Am Nat 111:1169–1194
- Guisan A, Weiss SB, Weiss AD (1999) GLM versus CCA spatial modeling of plant species distribution. Plant Ecol 143:107–122
- Harrod JC, Harmon ME, White PS (2000) Post-fire succession and 20th century reduction in fire frequency on xeric southern Appalachian sites. J Veg Sci 11:465–472. https://doi.org/10.2307/3246576
- Harrod JC, White PS, Harmon ME (1998) Changes in xeric forests in western Great Smoky Mountains National Park, 1936-1995. Castanea 63:346–360
- Hiers JK, Wyatt R, Mitchell RJ (2000) The effects of fire regime on legume reproduction in Longleaf pine savannas: is a season selective? Oecologia 125:521–530. https://doi.org/10.1007/s004420000469
- Hutchinson TF (2006) Fire and the herbaceous layer of eastern oak forests. Fire East oak For Deliv Sci to L Manag 136–149
- Hutchinson TF, Long RP, Ford RD, Sutherland EK (2008) Fire history and the establishment of oaks and maples in second-growth forests. Can J For Res 38:1184–1198. https://doi.org/10.1139/X07-216
- Hutchinson TF, Long RP, Rebbeck J, et al (2012a) Repeated prescribed fires alter gapphase regeneration in mixed-oak forests. Can J For Res 42:303–314. https://doi.org/10.1139/X11-184

- Hutchinson TF, Yaussy DA, Long RP, et al (2012b) Long-term (13-year) effects of repeated prescribed fires on stand structure and tree regeneration in mixed-oak forests. For Ecol Manage 286:87–100. https://doi.org/10.1016/j.foreco.2012.08.036
- Jacobs RD (1965) Seasonal height growth patterns of sugar maple, yellow birch, and red maple seedlings in upper Michigan. U.S. Department of Agriculture Forest Service, Lake States Forest Experiment Station, St. Paul, MN
- Key CH, Benson NC (2006) Landscape assessment (LA): sampling and analysis methods. U.S. Department of Agriculture Forest Service, Rocky Mountain Research Station, Fort Collins, CO
- Keyser TL, Greenberg CH, McNab WH (2019) Season of burn effects on vegetation structure and composition in oak-dominated Appalachian hardwood forests. For Ecol Manage 433:441–452. https://doi.org/10.1016/j.foreco.2018.11.027
- Kilburg EL, Moorman CE, Deperno CS, et al (2014) Wild turkey nest survival and nestsite selection in the presence of growing-season prescribed fire. J Wildl Manage 78:1033–1039. https://doi.org/10.1002/jwmg.751
- Knapp EE, Estes BL, Skinner CN (2009) Ecological effects of prescribed fire season: a literature review and synthesis for managers. U.S. Department of Agriculture Forest Service, Pacific Southwest Research Station, Albany, CA
- Koleff P, Gaston KJ, Lennon JJ (2003) Measuring beta diversity for presence-absence data. J Anim Ecol 72:367–382. https://doi.org/10.1046/j.1365-2656.2003.00710.x
- Kozlowski TT (1992) Carbohydrate sources and sinks in woody plants. Bot Rev 58:107– 222
- Kreye JK, Hiers JK, Varner JM, et al (2018) Effects of solar heating on the moisture dynamics of forest floor litter in humid environments: composition, structure, and position matter. Can J For Res 48:1331–1342. https://doi.org/10.1139/cjfr-2018-0147
- Kreye JK, Kane JM, Varner JM, Hiers JK (2020) Radiant heating rapidly increases litter flammability through impacts on fuel moisture. Fire Ecol 16:10. https://doi.org/10.1186/s42408-020-0067-3
- Krugman SL, Jenkinson JL (1974) Pinus L. pine. In: Schopmeyer CS (ed) Seeds of Woody Plants in the United States. Agriculture Handbook 450. U.S. Government Printing Office, Washington, DC, pp 598–638

- Lafon CW, Naito AT, Grissino-Mayer HD, et al (2017) Fire history of the Appalachian region: a review and synthesis. U.S. Department of Agriculture Forest Service, Southern Research Station, Asheville, NC
- Lawes MJ, Clarke PJ (2011) Ecology of plant resprouting: Populations to community responses in fire-prone ecosystems. Plant Ecol 212:1937–1943. https://doi.org/10.1007/s11258-011-9994-z
- Lorimer CG (1993) Causes of the oak regeneration problem. In: Loftis DL, McGee CE (eds) Oak Regeneration: Serious Problems, Practical Recommendations.
 Proceedings of a conference, 1992 September 8-10, Knoxville, TN. General Technical Report SE-84. U.S. Department of Agriculture Forest Service, Southeastern Forest Experiment Station, Asheville, NC, pp 14–39
- McCune B, Grace JB (2002) Analysis of Ecological Communities. MjM Software Design, Gleneden Beach, OR
- McCune B, Keon D (2002) Equations for potential annual direct incident radiation and heat load. J Veg Sci 13:603–606
- Michaletz ST, Johnson EA (2007) How forest fires kill trees: a review of the fundamental biophysical processes. Scand J For Res 22:500–515. https://doi.org/10.1080/02827580701803544
- Michaletz ST, Johnson EA (2008) A biophysical process model of tree mortality in surface fires. Can J For Res 38:2013–2029. https://doi.org/10.1139/X08-024

Naito AT (2017) Basic TPI steps

- NCEI (2020) Mean temperature and precipitation data for CLAYTON 1 SSW, GA US [GHCND:USC00091982]; CORNELIA, GA US [GHCND:USC00092283]; and LONG CREEK, SC US [GHCND:USC00385278]. National Centers for Environmental Information, Asheville, NC
- Norman SP, Hargrove WW, Christie WM (2017) Spring and autumn phenological variability across environmental gradients of Great Smoky Mountains National Park, USA. Remote Sens 9:. https://doi.org/10.3390/rs9050407
- Norman SP, Vaughan MC, Hargrove WW (2019) Contextualizing Appalachian fire with sentinels of seasonal phenology. In: Proceedings of a conference of the United States-International Association for Landscape Ecology, 2019 April 7-11, Fort Collins, CO. p 21

- North M, Oakley B, Fiegener R, et al (2005) Influence of light and soil moisture on Sierran mixed-conifer understory communities. Plant Ecol 177:13–24. https://doi.org/10.1007/s11258-005-2270-3
- Noss RF (2012) Forgotten grasslands of the South. Island Press, Washington, DC
- Nowacki GJ, Abrams MD (2008) The demise of fire and "mesophication" of forests in the eastern United States. Bioscience 58:123–138. https://doi.org/10.1641/B580207
- O'Brien JJ, Hiers JK, Varner JM, et al (2018) Advances in mechanistic approaches to quantifying biophysical fire effects. Curr For Reports 4:161–177. https://doi.org/10.1007/s40725-018-0082-7
- Oakman EC, Hagan DL, Waldrop TA, Barrett K (2019) Understory vegetation responses to 15 years of repeated fuel reduction treatments in the Southern Appalachian Mountains, USA. Forests 10:21. https://doi.org/10.3390/f10040350
- Oksanen J (1983) Ordination of boreal heath-like vegetation with principal component analysis, correspondence analysis and multidimensional scaling. Vegetatio 52:181–189. https://doi.org/10.1007/BF00044995
- Oksanen J, Blanchet FG, Friendly M, et al (2019) vegan: Community Ecology Package
- Ottmar RD, Andreu A (2007) Litter and duff bulk densities in the southern United States
- Owsley FL (1949) Plain folk of the old South. Louisiana State University Press, Baton Rouge, LA
- Peet RK, Wentworth TR, White PS (1998) A flexible, multipurpose method for recording vegetation composition and structure. Castanea 63:262–274
- Phillips RJ, Waldrop TA (2008) Changes in vegetation structure and composition in response to fuel reduction treatments in the South Carolina Piedmont. For Ecol Manage 255:3107–3116. https://doi.org/10.1016/j.foreco.2007.09.037
- Platt WJ, Evans GW, Davis MM (1988) Effects of fire season on flowering of forbs and shrubs in longleaf pine forests. Oecologia 76:353–363. https://doi.org/10.1007/BF00377029
- Pyne SJ (1982) Fire in America: a cultural history of wildland and rural fire. Princeton University Press, Princeton, NJ
- R Core Team (2020) R: A Language and Environment for Statistical Computing

- Regier N, Streb S, Zeeman SC, Frey B (2010) Seasonal changes in starch and sugar content of poplar (Populus deltoides × nigra cv. Dorskamp) and the impact of stem girdling on carbohydrate allocation to roots. Tree Physiol 30:979–987. https://doi.org/10.1093/treephys/tpq047
- Reilly MJ, Waldrop TA, O'Brien JJ (2012) Fuels management in the southern Appalachian mountains, hot continental division [Chapter 6]. U.S. Department of Agriculture Forest Service, Southern Research Station, Asheville, NC
- Robbins LE, Myers RL (1992) Seasonal effects of prescribed burning in Florida: a review. Misc. Publ. No. 8 96
- Rodríguez-Calcerrada J, Mutke S, Alonso J, et al (2008) Influencia de la espesura de un pinar albar (Sistema Central, España) en la disponibilidad de luz y agua en el sotobosque, y la supervivencia de robles plantados en su interior. Investig Agrar Sist y Recur For 17:31–38. https://doi.org/10.5424/srf/2008171-01021

SAS (2018) JMP Pro

- Schroeder MJ, Buck CC (1970) Fire weather: a guide for application of meteorological information to forest fire control operations. U.S. Government Printing Office, Washington, DC
- Schwartz NB, Urban DL, White PS, et al (2016) Vegetation dynamics vary across topographic and fire severity gradients following prescribed burning in Great Smoky Mountains National Park. For Ecol Manage 365:1–11. https://doi.org/10.1016/j.foreco.2016.01.027
- Schwemlein DJ, Williams RA (2007) Effects of landscape position and season of burn on fire temperature in Southern Ohio's mixed oak forests. Gen Tech Rep South Res Station USDA For Serv 101:250–257
- Silvertown J (1980) Leaf-Canopy-Induced Seed Dormancy in a Grassland Flora. New Phytol 85:109–118. https://doi.org/10.1111/j.1469-8137.1980.tb04452.x
- Simon SA (2015) Ecological zones in the Southern Blue Ridge Escarpment: 4th approximation. Asheville, NC
- Simon SA, Collins TK, Kauffman GL, et al (2005) Ecological zones in the Southern Appalachians: first approximation. U.S. Department of Agriculture Forest Service, Southern Research Station, Asheville, NC

Sokal RR, Rohlf FJ (1995) Biometry, 3rd edn. W. H. Freeman & Co., New York

- Stewart OC (2002) Forgotten fires: Native Americans and the transient wilderness. University of Oklahoma Press, Norman, OK
- Streng DR, Glitzenstein JS, Platt WJ (1993) Evaluating effects of season of burn in Longleaf pine forests: a critical literature review and some results from an ongoing long-term study. In: Hermann SM (ed) The Longleaf Pine Ecosystem: Ecology, Restoration and Management. Proceedings of the 18th Tall Timbers fire ecology conference, 1991 May 30-June 2, Tallahassee, FL. Tall Timbers Research Station, Tallahassee, FL, pp 227–263

Tarboton DG (2015) Terrain analysis using digital elevation models (TauDEM)

- Trickett TC (2018) Fire and vegetation dynamics in the southern Appalachian Mountains. Clemson University
- Van Lear DH, Waldrop TA (1989) History, uses, and effects of fire in the Appalachians. Asheville, NC
- Vander Yacht AL, Barrioz SA, Keyser PD, et al (2017) Vegetation response to canopy disturbance and season of burn during oak woodland and savanna restoration in Tennessee. For Ecol Manage 390:187–202. https://doi.org/10.1016/j.foreco.2017.01.029
- Vander Yacht AL, Keyser PD, Barrioz SA, et al (2019) Reversing mesophication effects on understory woody vegetation in mid-Southern oak forests. For Sci 65:289–303. https://doi.org/10.1093/forsci/fxy053
- Vose JM, Swank WT, Clinton BD, et al (1997) Using fire to restore pine/hardwood ecosystems in the southern Appalachians of North Carolina. In: Greenlee JM (ed) Fire Effects on Rare and Endangered Species and Habitats. Proceedings of a conference, 1995 November 13-16, Coeur d'Alene, ID. International Association of Wildland Fire, Fairfield, WA, pp 149–154
- Wade DD, Brock BL, Brose PH, et al (2000) Fire in eastern ecosystems [Chapter 4]. U.S. Department of Agriculture Forest Service, Rocky Mountain Research Station, Ogden, UT
- Wade DD, Lunsford JD (1989) A guide for prescribed fire in southern forests. U.S. Department of Agriculture Forest Service, Southern Region, Atlanta, GA
- Waldrop TA, Goodrick SL (2012) Introduction to prescribed fire in Southern ecosystems. U.S. Department of Agriculture Forest Service, Southern Research Station, Asheville, NC

- Waldrop TA, Van Lear DH, Lloyd FT, Harms WR (1987) Long-term studies of prescribed burning in loblolly pine forests of the southeastern Coastal Plain. Asheville, NC
- Waldrop TA, White DL, Jones SM (1992) Fire regimes for pine-grassland communities in the southeastern United States. For Ecol Manage 47:195–210. https://doi.org/10.1016/0378-1127(92)90274-D
- Walters RS, Yawney HW (1990) Acer rubrum L. red maple
- Wendel GW, Smith HC (1990) Pinus strobus L. eastern white pine
- White DL, Waldrop TA, Jones SM (1991) Forty years of prescribed burning on the Santee fire plots: effects on understory vegetation. In: Nodvin SC, Waldrop TA (eds) Fire and the Environment: Ecological and Cultural Perspectives.
 Proceedings of an international symposium, 1990 March 20-24, Knoxville, TN. General Technical Report SE-69. U.S. Department of Agriculture Forest Service, Southeastern Forest Experiment Station, Asheville, NC, pp 51–59
- Whittaker RH (1960) Vegetation of the Siskiyou Mountains, Oregon and California. Ecol Monogr 30:279–338. https://doi.org/10.2307/1943563
- Whittaker RH (1956) Vegetation of the Great Smoky Mountains. Ecol Monogr 26:1–80. https://doi.org/10.2307/1943577
- Williams CE (1998) History and status of Table Mountain pine-pitch pine forests of the southern Appalachian Mountains (USA). Nat Areas J 18:81–90
- Williams M (1989) Americans and their forests: a historical geography. Cambridge University Press, Cambridge, UK
- Yaussy DA, Waldrop TA (2010) Delayed Mortality of Eastern Hardwoods After Prescribed Fire. 1–4
- (2019) ArcGIS for Desktop
- (2020) RStudio Desktop